THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT SOUTHERN HIGH LATITUDES

Edited by

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Foreword

The second IBMANT Symposium & Workshop was held in Ushuaia (Argentina) between October 19 and 24, 2003. It was organised jointly by the Alfred Wegener Institute for Polar and Marine Research (AWI, Bremerhaven, Germany) and the Centro Austral de Investigaciones Científicas y Técnicas (CADIC, Ushuaia, Argentina), and was combined with the ANDEEP Symposium dealing with recent deep-sea research in the Weddell and Scotia seas (see Deep-Sea Res. II Vol. 51, 2004). IBMANT II, following a first conference held in Punta Arenas, Chile in 1997 (see *Scientia Marina* Vol. 63, Suppl. 1, 1999) focussed on continental shelf and slope work over a wide latitudinal gradient between the northern Magellan region and the high Antarctic continental coasts. A total of 117 scientists from 13 countries participated in the combined meeting, and presentations were offered from 17 countries.

The idea of combining Antarctic deep-sea with shelf and slope studies, and including a wider geologic and oceanographic background, turned out to be very useful during this conference. The IBMANT/ANDEEP meeting was the first in which the two aspects were combined, leading to novel insights and innovative perspectives for research in the years to come.

The presentations and discussions during the meeting focussed on various central issues, most of which emerged repeatedly. In summary, major subjects discussed during the conference included the following items:

The final separation and isolation of the Antarctic continent, going along with the establishment of a vigorous circum-Antarctic current system and the origin of the Polar Front. These key events are supposed to have shaped the evolution, biogeography and biodiversity of the Southern Ocean. However, the various geological alternatives for these processes—in particular the opening of Drake Passage—have yet to be reconciled with molecular data on major extinction and radiation events. Perhaps the much greater similarity between the Antarctic and Magellan marine biota, as compared to the overlap between the Antarctic and Australia, could be a biological key in this context.

Advances and retreats of the Antarctic and Patagonian ice caps as further major driving forces on evolutionary time scales, and the impact of sea ice, glaciers and icebergs, i.e. present disturbance leading to ecological change. How much do we know about these processes?

The "barrier" effect of the Polar Front (Antarctic Convergence). To what extent is it reduced by eddies causing a certain amount of cross circulation? What role in these processes do the northern and southern branches of the Scotia Arc play? Do they act as stepping stones for biotic exchange between the Magellan region and the Antarctic?

The Circumpolar Current (West Wind Drift) and its role as an efficient transport vehicle towards the east. Is this function restricted to species with well-developed dispersal stages such as pelagic larvae? Are there other (including anthropogenic) means of dispersal? Is there any transport in E-W direction, e.g. by the East Wind Drift?

The degree of similarity between the marine biota of the Magellan region and their Antarctic relatives. How much overlap is there at species (genus, family) level in different taxa? What is the age of the present marine ecosystems on either side of the Drake Passage? Are there still effects resulting from the last glaciation?

The predominantly circum-Antarctic benthic distribution pattern on the Antarctic continental shelf has become a paradigm. However, what percentage of this "identical" fauna are cryptic species, as suggested by molecular methods? Is the high Antarctic an isolated ecosystem under present conditions, with speciation occurring rather by isolation than by exchange?

The ways of biotic exchange in the past, the role of the deep sea in these processes, emergence and submergence, radiation *in situ*. What was the respective role of these processes, particularly that of the deep-sea floor for Antarctic benthos?

The possibility of increased invasions due to global climate change. Present warming might enhance invasions into areas south of the Polar Front, because survival might be favoured due to reduced temperature differences. Are there any indications for such a development? In what way might it influence the existing communities, and what are the timescales we are dealing with?

Latitudinal clines in species richness. There does not seem to be a common pattern for all taxa, but is the paradigm of the "bell-shaped curve" with decreasing species numbers toward the pole true for some groups? To what extent do regional hotspots refer to sampling intensity rather than real differences in species diversity?

Characteristics of cold-water life histories, population dynamics and reproduction. Are there particular patterns in the Antarctic, and is there a latitudinal gradient from the Magellan region to the high Antarctic shelf? How strict are these rules?

Characteristics of cold-water physiology, especially stenothermy vs. eurythermy. What are the advantages and disadvantages of increasing stenothermy on the latitudinal gradient? Are there exceptions to such a cline, and how do species manage? Do things differ under the aspect of global warming? To what extent may temperature tolerance have influenced biogeography and biodiversity of the Southern Ocean in Earth history?

The impact of increased UV-B radiation on marine biota along the latitudinal gradient. Have increased UV values led to damage in shallow water organisms? What are the protective mechanisms? Are such mechanisms more frequent at higher latitudes?

Benthic assemblage structure along the latitudinal gradient. Are there consistent clines along this gradient, e.g. in abundance, biomass, productivity, distribution and diversity? Can data banks be helpful in managing the enormous amount of data assembled in the last few years?

Of course, not all of these questions were answered comprehensively during the Conference, but many of them received some clarification during the presentations and the discussions following them, and most were discussed in detail during the workshop that followed the oral and poster sessions (see Summary Review at the end of this volume). While it turned out advantageous to have colleagues from a wider frame of disciplines included in these discussions, it was felt that a future IBMANT meeting should be even more multidisciplinary, including an adequate share of physical oceanographers, geologists, palaeontologists and glaciologists.

The editors of this volume hope that the Ushuaia IBMANT Symposium and Workshop will have a strong impact on future activities in ecological and evolutionary research in the Southern Ocean. They would like to express their sincere thanks to all the organisations and institutions that contributed substantially to the success of the meeting and these proceedings.

The following international and national organisations and institutions provided support for travel and stay of keynote speakers and other participants:

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- Scientific Committee of Antarctic Research (SCAR)
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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
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Mesoscale eddies in the Subantarctic Front - Southwest Atlantic*

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SUMMARY: Satellite and ship observations in the southern southwest Atlantic (SSWA) reveal an intense eddy field and highlight the potential for using continuous real-time satellite altimetry to detect and monitor mesoscale phenomena with a view to understanding the regional circulation. The examples presented suggest that mesoscale eddies are a dominant feature of the circulation and play a fundamental role in the transport of properties along and across the Antarctic Circumpolar Current (ACC). The main ocean current in the SSWA, the Falkland-Malvinas Current (FMC), exhibits numerous embedded eddies south of 50°S which may contribute to the patchiness, transport and mixing of passive scalars by this strong, turbulent current. Large eddies associated with meanders are observed in the ACC fronts, some of them remaining stationary for long periods. Two particular cases are examined using a satellite altimeter in combination with in situ observations, suggesting that cross-frontal eddy transport and strong meandering occur where the ACC flow intensifies along the sub-Antarctic Front (SAF) and the Southern ACC Front (SACCF).

Keywords: southwest Atlantic, mesoscale, eddies, transport, Falkland-Malvinas Current.

RESUMEN: EDDIES DE MESOESCALA EN EL FRENTE SUBANTÁRTICO, ATLÁNTICO SUDOESTE. – Observaciones *in situ* y satelitales en el sudoeste del Océano Atlántico Sur revelan un intenso campo de eddies e indican la utilidad de la altimetría satelital para detectar, monitorear y mejorar la compresión de fenómenos de mesoescala en la región. Los ejemplos presentados sugieren que los eddies de mesoescala son una característica dominante de la circulación y juegan un papel fundamental en el transporte de propiedades a lo largo y a través de la Corriente Circumpolar Antártica (CCA). Al sur de 50°S la principal corriente en esta región, la Corriente de Malvinas exhibe numerosos eddies, los que pueden contribuir al patrón de manchas, y al transporte y la mezcla de trazadores pasivos de esta intensa y turbulenta corriente. En los frentes de la CCA se observan grandes eddies asociados con meandros, algunos de estos eddies permanecen estacionarios durante largos períodos de tiempo. Se analizan dos casos particulares empleando altimetría satelital en combinación con observaciones *in situ* que sugieren que donde la CCA se intensifica, a lo largo del Frente Subantártico y el Frente Sur de la CCA, se producen intensos transportes a través de la corriente y fuertes meandramientos.

Palabras clave: Atlántico suroccidental, mesoescala, eddies, transporte, Corriente de Falkland/Malvinas.

INTRODUCTION

The view of ocean currents as smooth, streamlined flows in geostrophic balance has been replaced by the modern view of the ocean as a turbulent fluid. Remote sensing and satellite-tracked drifting buoys have reinforced this view by resolving the broadband temporal and spatial variability associated with turbulent scales of motion (Stammer, 1997). Mesoscale turbulence arising from baroclinic and barotropic instability, wind forcing and topographic interactions influence the variability of ocean cur-

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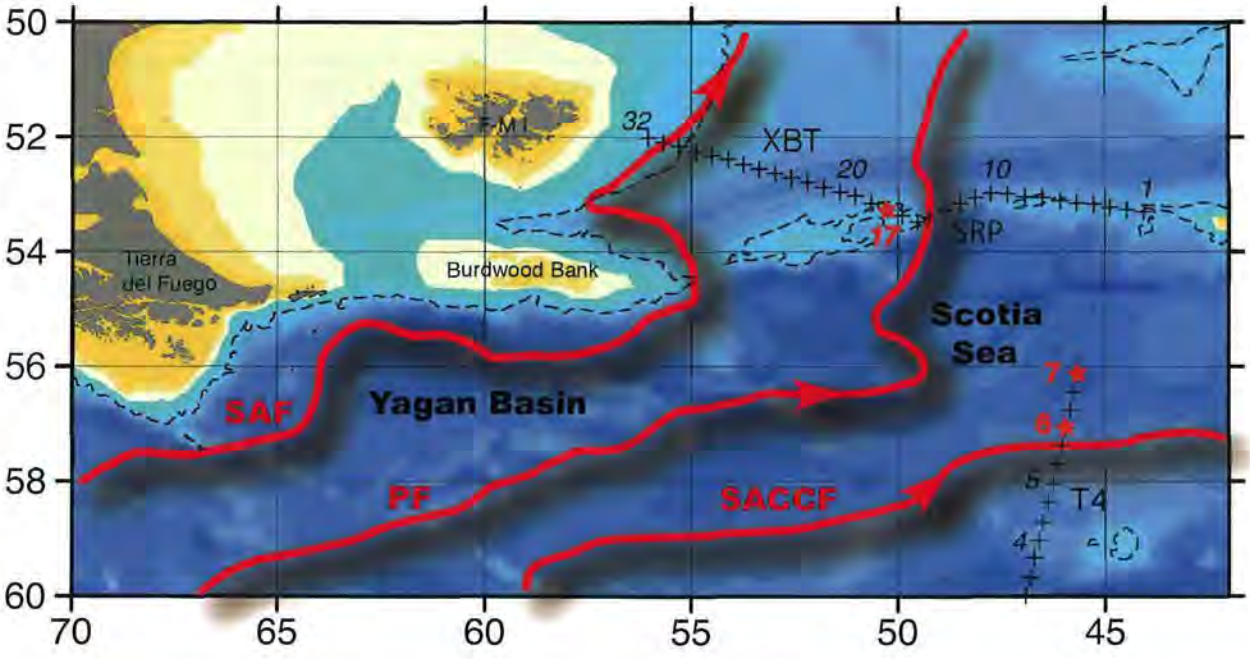

FIG. 1. – Topographic map of the southern southwest Atlantic (SSWA) depicting the Shag Rocks Passage (SRP). The red lines indicate the mean position of the sub-Antarctic Front (SAF), the Polar Front (PF) and the Southern Antarctic Circumpolar Current Front (SACCF) as described in Orsi *et al.*, 1995). The XBT transect consisted of 32 launches and was carried out on 21-22 Feb 2003. Transect T4 consisted of CTD casts and XBT launches. XBT 17 and CTDs 6 and 7 in T4 are indicated by the red stars. The dashed line is the 1500 m isobath.

rents and generate eddies, fronts and jets, which are significant contributors in the transport of properties such as heat, momentum and nutrients.

Mesoscale processes also have a large influence on the development and diversity of biological species at different trophic levels, from phytoplankton blooms to the life cycle of whales (Davis *et al.*, 2002). For instance, according to recent findings (Thatje and Fuentes, 2003), planktonic larvae from South America may have reached Antarctic waters by an intrusion of Subantarctic warm-water rings across the ACC fronts. Moreover, mesoscale phenomena are crucial to our understanding of ocean circulation and climate change, and to a large extent may determine the location and variability of fisheries. Here we present evidence that mesoscale turbulence in the SSWA may play a substantial role in the transport of properties within and across major currents of the ACC system, such as the Falkland-Malvinas Current (FMC). This evidence comes from observations at sea and from remote sensing.

The main ocean current in the SSWA (Fig. 1) is the FMC, a cold stream linked to the Subantarctic Front. To place the FMC in context, it carries about 40 to 70 Sv (1 Sv = 1×10^6 m^3 s^{-1}, Peterson, 1992; Vivier and Provost, 1999), or 200 times the outflow of the Amazon River, and in concert with the Patagonian shelf tides, it constitutes the dominant oceanographic signal in the SW South Atlantic, which is a distinct biogeochemical province (Longhurst, 1995). The FMC originates in the northern Drake Passage as a branch of the ACC associated with the SAF, and then flows northward, around the Burdwood Bank, steered by the edge of the Patagonian shelf (Piola and Gordon, 1989).

Further south, the ACC tends to be concentrated in frontal jets steered by the bottom topography (Nowlin *et al.*, 1977; Pollard *et al.*, 2002). The input of eastward momentum by the wind stress that generates the ACC is transferred vertically to the deep ocean, where it is dissipated by bottom friction, and hence the system is dynamically balanced (see Gent *et al.*, 2001 and references therein). This transfer of momentum is possible due to the generation of transient and standing eddies caused by the presence of topographic barriers in the path of the ACC, and is a form of interfacial stress set up by the eddies (McWilliams *et al.*, 1978; Wolff *et al.*, 1991).

Satellite altimetry shows that the SSWA is a region of enhanced eddy activity east of the Drake Passage (Gille *et al.,* 2000), where eddies might be generated by topographic features partially blocking the ACC (Wolff *et al.*, 1991). The continental shelf extending south from Tierra del Fuego, submarine ridges and seamounts are probably inducing the relatively high surface eddy kinetic energy observed downstream of Drake Passage in the northwest Scotia Sea.

This paper addresses the need to characterise mesoscale eddies in the SSWA, given their significant influence in the regional circulation and their potential for the transport of properties. We present examples that indicate agreement between remote sensing and in situ observations, and point out the potential of using continuous real-time satellite altimetry for detecting, monitoring and improving our understanding of mesoscale phenomena in a remote region that is beyond the present coverage of microwave-derived sea surface temperature and is often covered by clouds, which obscure visible and infrared imagery.

OBSERVATIONS

Extraordinary evidence of complex mesoscale patterns in the SSWA comes from images taken by SeaWiFS (Sea-viewing Wide Field-of-view Sensor). The example shown in Figure 2 illustrates complex non-linear patterns of stretching and folding of streaklines evolving around eddies and dipole vortices, indicating that eddies indeed play a significant part in the dynamics of the FMC. The FMC itself is visible as a lighter band of colour along the shelf slope to the east of the Falkland-Malvinas Islands. Note the counter-clockwise eddy of the same colour that appears to have detached from the current and drifted to the east. Notably, north of about 50°S the

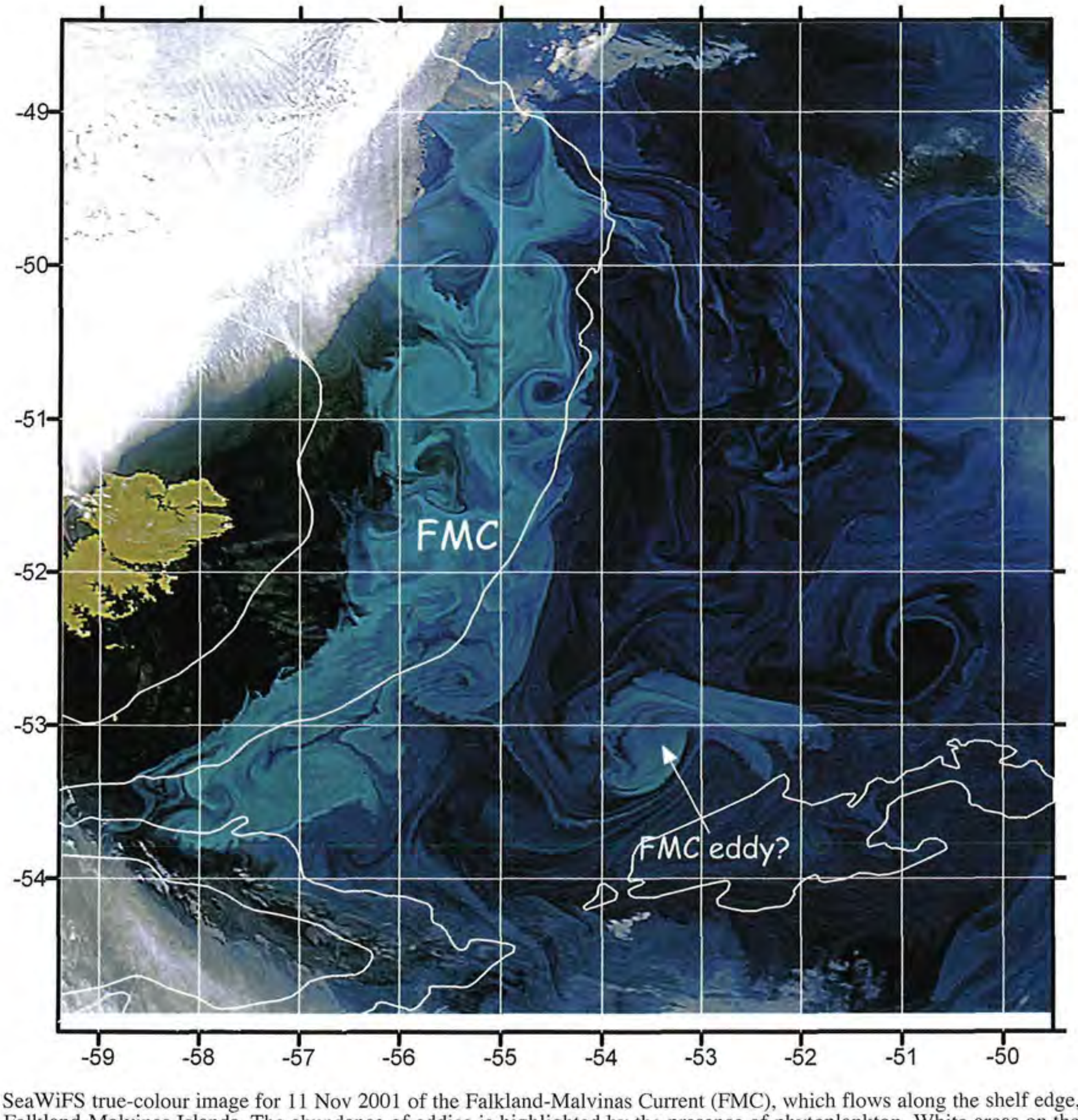

FIG. 2. – SeaWiFS true-colour image for 11 Nov 2001 of the Falkland-Malvinas Current (FMC), which flows along the shelf edge, offshore from the Falkland-Malvinas Islands. The abundance of eddies is highlighted by the presence of phytoplankton. White areas on the top- and bottom-left of the image are clouds. The white contours are the 200 m and 1500 m isobaths. Image provided by the SeaWiFS Project, NASA/Goddard Space Flight Center, and Orbimage.

FMC appears as a very low eddy energy region (Goni and Wainer, 2001), suggesting that the current stabilises downstream, presumably as it is steered by the steep bottom topography along the western edge of the Argentine Basin.

CTD (Conductivity-Temperature-Depth) data collected by the Fisheries Department of the Falkland Islands on a crisscross grid across the FMC in July 1999 gave a first indication of the presence of eddies embedded in the current (Glorioso, 2002). The extent of these eddies down into the water column has been described by performing a water mass analysis using the Optimum Multi-Parameter (OMP) method (Tomczak, 1981). The results obtained from this analysis have indicated that the observed FMC eddies reached the full water depth (more than 1000 m) and upwelled deep water to the surface layer of the ocean. Thus, the FMC eddies may play a significant role in the vertical redistribution of properties, supplying nutrients and other substances to the upper ocean.

Figure 3 presents expendable bathythermograph (XBT) data taken on 21-22 Feb 2003 at 32 positions every 15 nm, along a transect (see location in Fig. 1) that was designed to sample the underlying structure of eddies detected in satellite altimetry maps. In this figure, the relatively warm Antarctic Intermediate Water (AAIW) close to the continental shelf to the west is in sharp contrast with the colder Circumpolar Deep Water (CDW, carried by the ACC) to the east. Both water masses appear below a warmer surface layer due to seasonal heating.

This XBT section gives a fairly synoptic view of the eddies that were encountered. Eddy locations were monitored with sea surface height (SSH) anomaly fields produced by blending altimeter data from, for example, the TOPEX/Poseidon and ERS-2 satellites (Leben *et al.*, 2002) to accurately map the ocean mesoscale variability. Satellite altimeters measure changes in SSH due to the redistribution of the water column integrated mass and changes in water density, i.e. the barotropic and baroclinic components.

XBT positions 9 to 15 covered the Shag Rocks Passage (SRP in Fig. 1), transecting the mean path of the Polar Front (PF). In the vertical temperature

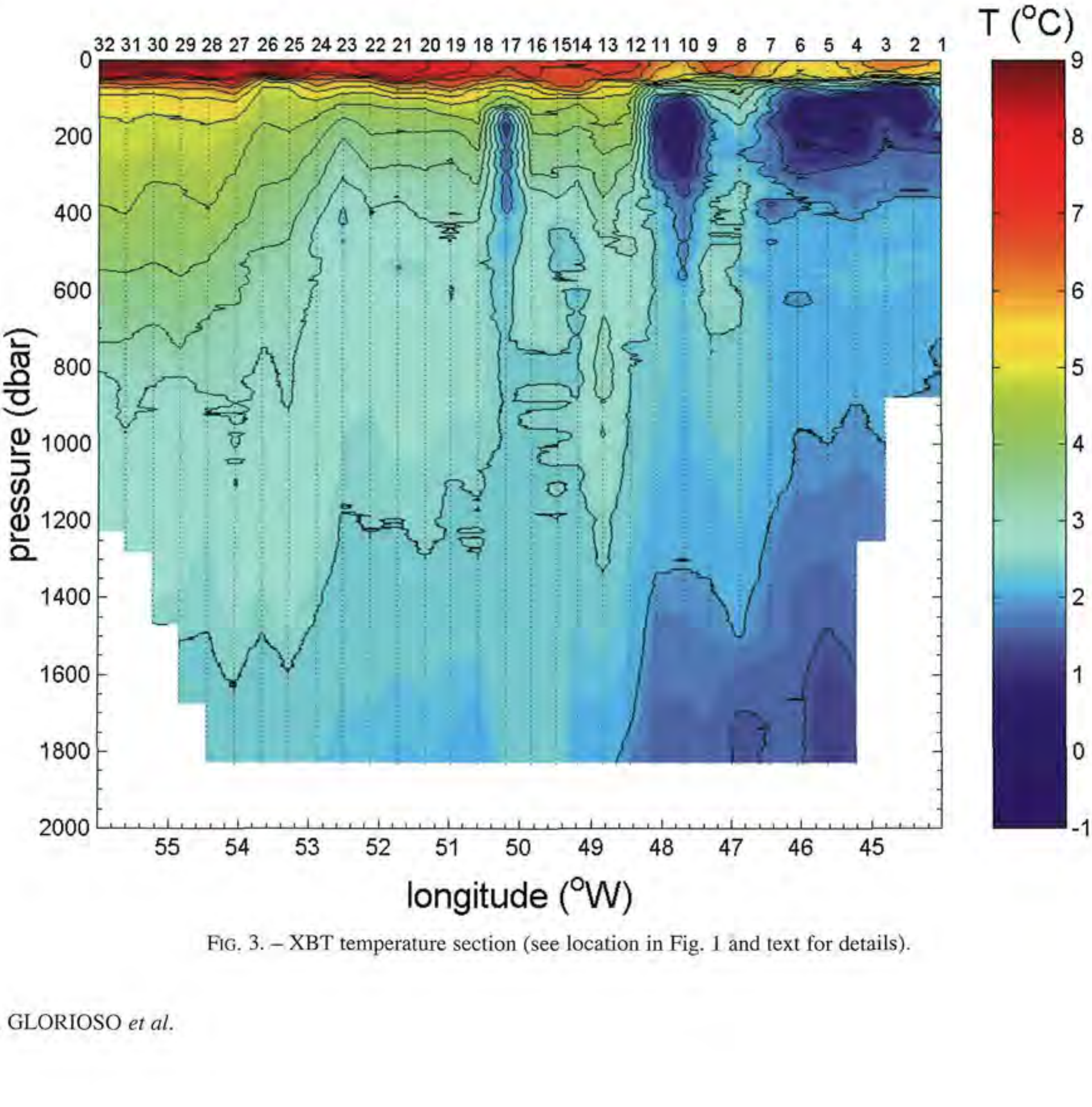

FIG. 3. – XBT temperature section (see location in Fig. 1 and text for details).

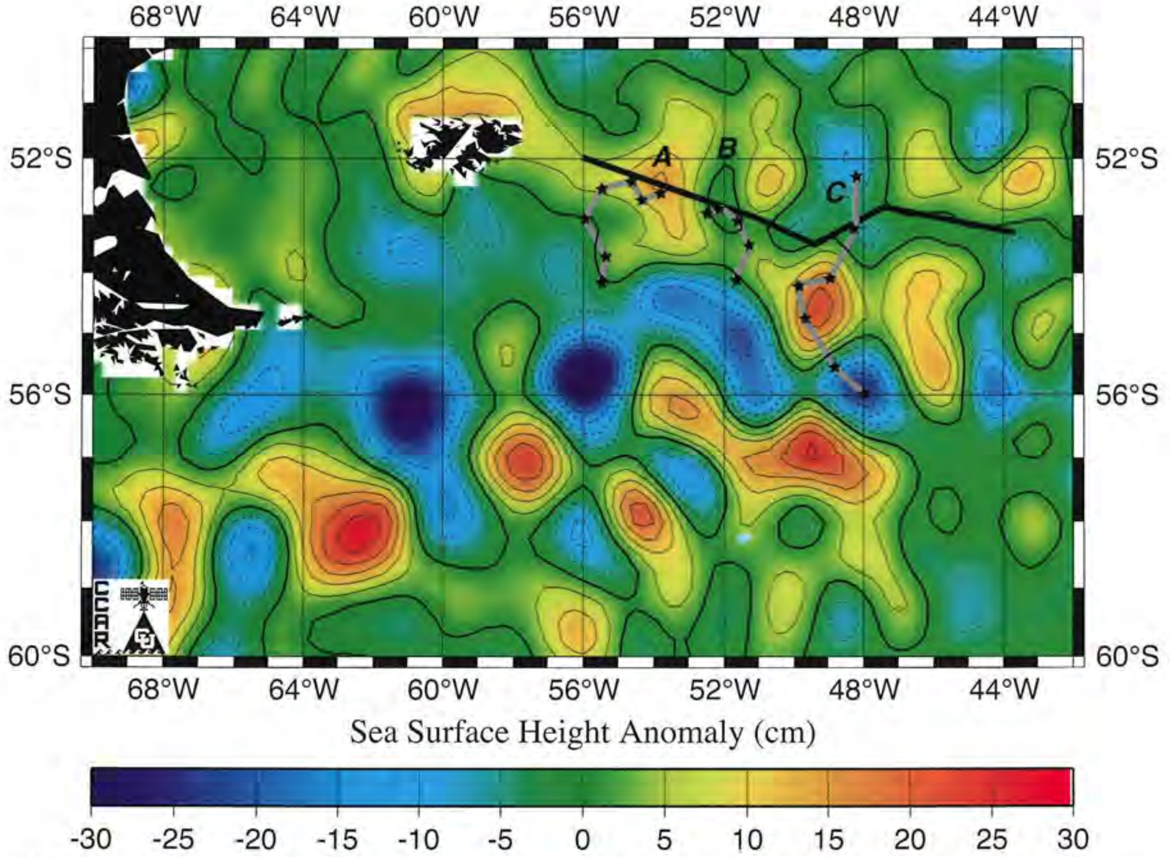

FIG. 4. – TOPEX/JASON/ERS-2/GFO altimetry analysis map for 22 Feb 2003 showing clockwise (anticlockwise) eddies with lower (higher) sea surface height (SSH) anomaly in blue (red). The heavy contour is the zero SSH anomaly. The XBT transect is indicated in the figure by the black line. Eddies labelled A, B and C are referred to in the text and their tracks, from 01 December 2002 to 12 March 2003, are depicted by the gray lines (black stars indicate where the eddies were clearly identified) as they moved north.

section (Fig. 3), the PF is seen as the strong horizontal gradient between XBTs 11 and 12, shallower than 400 m. Further west, the isotherms slope downward from XBTs 23 to 25, particularly at depth, suggesting the location here of the ACC jet associated with the SAF, whose mean position (see Fig. 1) would locate it closer to position 31. XBT 17 is located over the North Scotia Ridge, about 40 km west of the Shag Rock Passage, where the ACC jet associated with the Polar Front permeates through the ridge (Fig. 1). The 3 °C isotherm rises from about 450 m at XBT 18 to <150 m at XBT 17, but the thermocline located at about 80 m depth is nearly flat, and there is no surface signature of this eddy (Fig. 3). The vertical structure of low temperature centred at XBT 17, with a minimum of < 1.5 °C located at about 200 m depth, suggests that this cold eddy may have been shed from the PF, as it interacts with the bottom topography. This temperature distribution is similar to that found further north along 51°S (Arhan *et al.*, 2002).

The upward sloping of isotherms around XBT 23 associated with lower sea surface temperature (SST) similarly to the eddy observed at XBT 17, is interpreted as a clockwise rotating eddy, whose evolution was followed in a sequence of altimetry maps similar to the one shown in Figure 4. The mesoscale SSH anomaly map of 22 February 2003 shown in Figure 4 was constructed by blending Topex/POSEIDON and Jason data within ± 10 days with ERS and Geosat follow-on (GFO) data within ± 17 days. These "hindcast" maps depict the mesoscale eddy field for retrospective studies better than the "nowcast" maps produced in near real-time that only use along-track data collected before the analysis date. Both hindcast and nowcast maps are based on along-track data that have been high-pass filtered to retain mesoscale wavelengths, as described in Leben *et al.* (2002). The location of the XBT transect is indicated on this map, as well as the track of three eddies (A, B and C). These tracks start from the south on 01 Dec 2002 and end on 12 Mar 2003 following a general northerly direction. The black marks on the tracks indicate where these eddies were clearly identified throughout this period, even though their signature changed with time, perhaps due to changes in

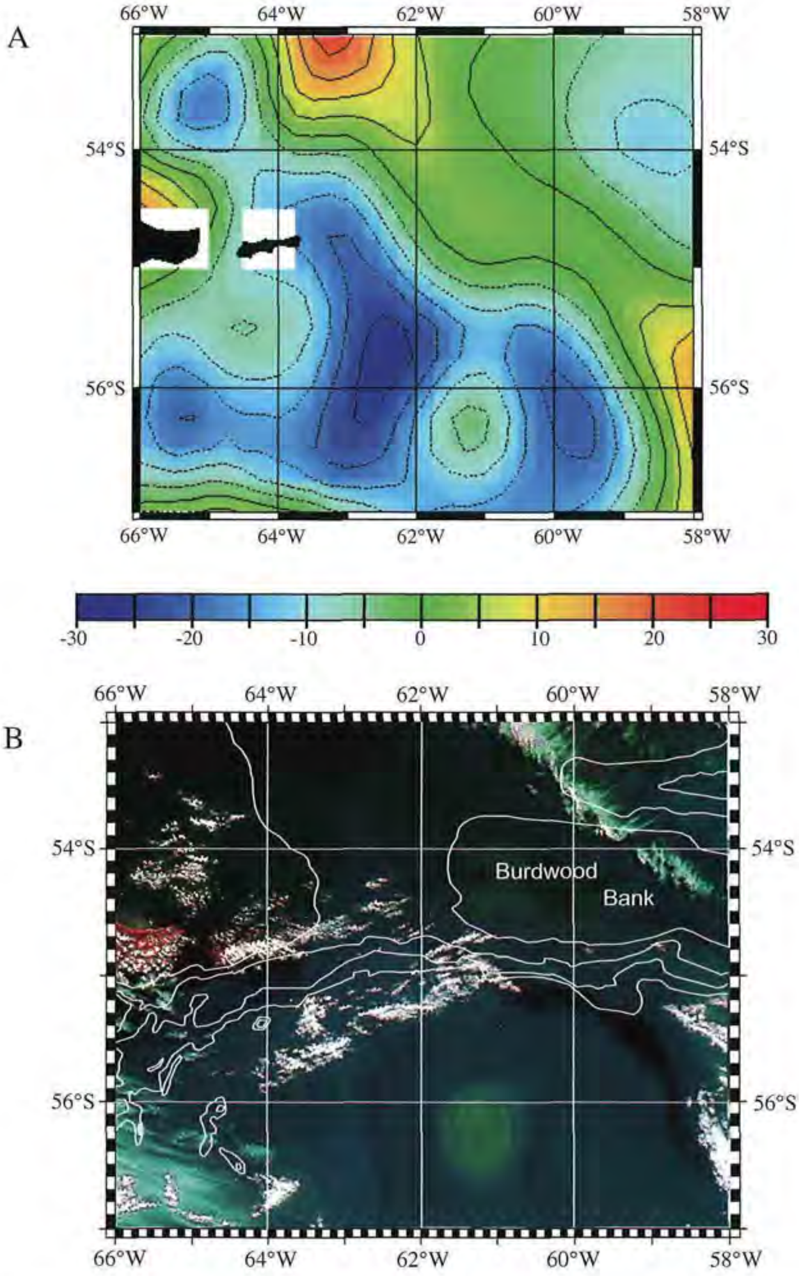

FIG. 5. – (A) TOPEX/ERS-2 altimetry analysis map and (B) enhanced true-colour SeaWiFS image (provided by the SeaWiFS Project, NASA/Goddard Space Flight Centre, and Orbimage) for 04 Mar 1998. The white contours in B are the 200, 1000, 2000 and 3000 m isobaths.

their strength and/or variations in sampling associated with the altimeter coverage. The sequence of altimetry maps (not shown here) indicated, for instance, that the eddy in the middle (B), which appears in Figure 4 with its centre of lower SSH anomaly at 52°W and 53°S, was stationary at that location for about two months. The relatively intense, small-scale eddy at XBT 17 (Fig. 3), which presumably detached from the Polar Front Zone, is also apparent in Figure 4 at 50°W, 53°S.

Further south, the eddy field revealed by the sea surface height anomaly maps is substantially more intense, with surface signatures greater than 30 cm. These large eddies found east of the Drake Passage might be generated by the partial blocking of the ACC by the tip of the continental shelf south of Tierra del Fuego. This hydrodynamic generation mechanism would agree with numerical experiments (Wolff *et al.*, 1991). After being generated, these major eddies interact with each other and follow a

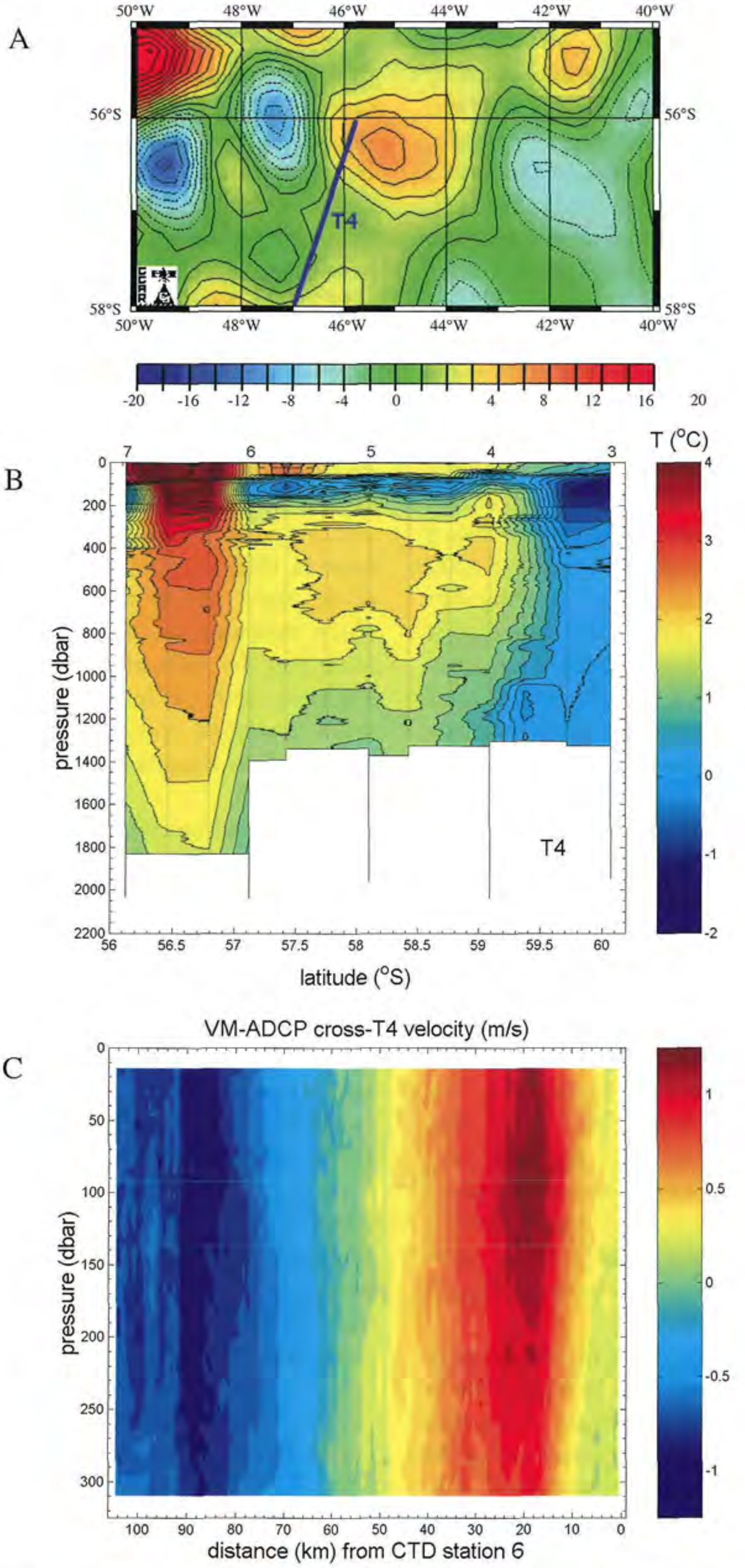

FIG. 6. – (A) Altimetry map for 24 Jan 2003, where T4 indicates the section surveyed by the RRS *James Clark Ross* referred to in the text. (B) Vertical distribution of temperature along T4, where numbers along the sea surface indicate CTD stations and dashed vertical lines indicate XBT launches. (C) Contours of horizontal velocity across T4, between CTD stations 6 and 7, measured by the vessel-mounted ADCP plotted as a function of distance to CTD 6. Positive eastward (red) and negative westward (blue) velocities indicate the anticlockwise rotation of the eddy.

general path towards the NE. However, they are nearly stationary for several weeks, allowing jet flows concentrated between the counter-rotating adjacent eddies to produce strong meridional and westward (i.e. against the ACC) currents. Measurements taken during repeated transects at the Drake Passage and spectral analysis of SSH anomaly TOPEX data indicate that these large eddies have time scales of about 40 days and spatial scales of between 150 and 200 km (Sprintall *et al.*, 1997, and subsequent work by these authors).

A combination of altimetry and SeaWiFS satellite data (Fig. 5) provides evidence of the evolution of another kind of eddy, which was formed on the continental slope and may have entrained water from the Patagonia shelf to the south, across the SAF and into the Yagan Basin. The feature has a radius of about 40 km and shows a positive SSH anomaly of the order of 20 cm relative to the surrounding waters. There is remarkable correspondence between the two remote sensing data products, in terms of the location, size and sense of rotation of this eddy, while the SeaWiFS image indicates that it contains higher phytoplankton biomass than the surrounding water.

Even though these anticlockwise Yagan eddies do not appear to be very common in an examined four-year time series (1999 to 2002) of altimetry maps, their occurrence might be significant to the transfer of properties across the shelf edge and the SAF. Because the southern Patagonia shelf shows the peak of biological production in February (Longhurst, 1998), this eddy may be advecting shelf organisms into the Yagan Basin. In addition, the eddy dynamics may act to further enhance the biological activity locally, for instance by upwelling nutrient-rich Subantarctic Zone waters into the photic layer. In this particular case, this eddy travelled south and back to the north, across isobaths, after reaching as far south as its position shown in Figure 5.

A similar example was detected in late January 2003 further east, at about the same latitude. This is shown in Figure 6a, where the larger eddy that appears in the centre of this altimetry map has higher SSH anomaly and therefore rotates anticlockwise. The eddy radius as determined from the altimetry is about 95 km and the SSH anomaly is 25 cm higher at the centre than around the edges. The blue line depicts the end section of transect T4, which was part of a survey by the RRS *James Clark Ross* that crisscrossed the Scotia Sea in the austral summer of 2003. Data from this transect are used here to characterise this eddy.

Figure 6b is the vertical section of temperature corresponding to transect T4, where numbers along the sea surface indicate CTD stations (3 to 7) in between which two XBT probes were launched (locations indicated by the vertical dashed lines). This temperature distribution shows the contrast between relatively warmer water associated with the ACC and colder water from the Weddell Sea. A subsurface temperature minimum (T < 0°C) located at 120-150 m depth is observed everywhere in T4, except between CTD stations 6 and 7, suggesting that the SACCF is located north of station 7, and of its mean climatological position (see Fig. 1 and Orsi *et al.*, 1995). The temperature maximum between stations 6 and 7, extending from the sea surface to beyond 1800 m, characterises the vertical structure of the eddy, which may have been generated by a sharp meander in the SACCF and drifted south. Note that the subsurface temperature minimum (< 1°C) near 150 m is interrupted by the eddy. Previous work described comparable cases with the aid of SST satellite images (García *et al.*, 2002; Meredith *at al.*, 2003).

The vessel-mounted RDI acoustic Doppler current profiler (ADCP) provided another source of data to characterise this energetic warm-core eddy. Figure 6c shows the cross-transect component of the velocity, where positive and negative values indicate eastward and westward flow respectively, between CTD stations 6 and 7. Despite the limited reach of the ADCP to about 300 m of depth, the anticlockwise rotation of the eddy is clearly seen. Rotational velocities are nil at the eddy core and rise beyond 1m s^{-1} at about 35 km from the centre, where the hydrographic section shows the largest horizontal temperature gradients. The rotational speed of the eastward flowing branch, shown in red, rapidly decreases to ~ 0.8 m s^{-1} at 400 m, in accordance with the decreasing horizontal temperature gradient with depth (Fig. 6b).

CONCLUSIONS

There is ample evidence that eddies are widespread phenomena in the southern southwest Atlantic. This comes from SeaWiFS colour images of the ocean surface, where phytoplankton acts as a tracer that displays a wide range of mesoscale structures, and also from maps produced by blending

TOPEX, Jason, ERS-2 and GFO altimetry data, an invaluable means of detecting and monitoring eddies and their associated currents in near-real-time, particularly for a remote region like the SSWA that is often covered by clouds and is located beyond the present coverage of microwave-derived sea surface temperature.

The most plausible mechanism involved in the generation of eddies in the SSWA is the partial blocking of the ACC by submarine topographic features, which would generate highly barotropic standing and transient eddies and eddy dipoles (Wolff *et al.*, 1991) similar to those we have observed. It is also possible that the amplification of instabilities, perhaps responding to atmospheric forcing, into sharp meandering and eddy spin-off from the ACC fronts east of the Drake Passage, may result in a cross-frontal exchange of water properties. In the Yagan Basin, continental slope eddies are likely to mix water properties between shelf and oceanic environments, moving across bathymetry as has been observed in the Gulf of Mexico (Ohlmann *et al.*, 2001), or to export water masses away from regions where they were generated.

The examples presented show that there is agreement between the sea surface signature of eddies in the SSH anomaly maps and the vertical structure revealed by the XBT and CTD measurements, and also between altimetry maps and SeaWiFS imagery. The evidence shown improves our understanding and encourages the use of altimeter data in future research of mesoscale eddies in the SSWA.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Diversity and endemism in cold waters of the South Atlantic: contrasting patterns in the plankton and the benthos*

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SUMMARY: In total, *ca.* 7000 zooplanktonic species have been described for the World Ocean. This figure represents less than 4% of the total number of known marine organisms. Of the 7000 zooplanktonic species world-wide, some 60% are present in the South Atlantic; about one third of the latter have been recorded in its Subantarctic waters, and *ca.* 20% south of the Polar Front. When compared with those of benthic animals, these figures indicate that proportions of the overall inventories that are present in the cold waters are almost two times higher among the zooplankton. In agreement with this pattern, the proportions of Antarctic endemics in the benthos are very significantly higher than those in the plankton. For the water-column dwelling animals, the Polar Front boundary is more important than the Tropical-Subtropical limit, but almost equivalent to the Subtropical-Transitional limit, and weaker in biogeographic terms than the Transitional-Subantarctic boundary. Some of the implications of these dissimilarities, both for ecological theory and for resource allocation strategies, are discussed.

Keywords: biodiversity, biogeography, zooplankton, benthos, Antarctic, Subantarctic.

RESUMEN: DIVERSIDAD Y ENDEMISMO EN LAS AGUAS FRÍAS DEL ATLÁNTICO SUR: CONTRASTES ENTRE EL PLANCTON Y EL BENTOS. – Para el Océano Mundial se ha descrito un total de 7000 especies de zooplancton. Esta cifra representa menos del 4% de los organismos marinos conocidos. De las 7000 especies zooplanctónicas del mundo, cerca del 60% está presente en el Atlántico Sur. De este 60%, alrededor de un tercio fueron registradas en aguas subantárticas, y ca. 20% al sur del Frente Polar. La comparación de estos valores con los de los animales bentónicos indica que, con respecto al total de especies descritas, en el zooplancton la proporción que habita las aguas frías duplica a las del bentos. En concordancia con ello, la proporción de endemismos es mucho más alta en el bentos que en el plancton. Para los animales que habitan la columna de agua la barrera del Frente Polar es más importante que el Límite Tropical-Subtropical, pero casi igual que el Límite Subtropical-Transición, y menos importante en términos biogeográficos que el Límite Transición-Subantártico. Se discuten algunas implicaciones de estas diferencias en términos de teoría ecológica y de las estrategias de distribución de los recursos.

Palabras clave: biodiversidad, biogeografía, zooplancton, bentos, Antártida, subantártico.

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DATA

Zooplanktonic species numbers and distribution ranges presented in this paper are chiefly based on the extensive compilations produced for the recent review "South Atlantic Zooplankton" (Boltovskoy, 1999a). The two volumes of this work included a total of 28 holo- and meroplanktonic taxa, but due to differences in the current knowledge of these animals, the degree and detail of coverage varied significantly. Most estimates and comparisons discussed use 15 of these 28 groups (encompassing 1305 species), whose distribution patterns between the equator and 60°S are reasonably well defined, and whose life cycle is restricted to the water column (holozooplankton). Conclusions rely heaviest on data summarised by Alder (1999) (Tintinnoinea), Angel (1999) (Ostracoda), Boltovskoy (1999b) (Radiolaria Polycystina), Casanova (1999) (Chaetognatha), Esnal (1999) (Appendicularia), Esnal and Daponte (1999) (Salpida), Gibbons *et al.* (1999) (Euphausiacea), Kemle-von Mücke and Hemleben (1999) (Foraminifera), Kling and Boltovskoy (1999) (Radiolaria Phaeodaria), Murano (1999) (Mysidacea), Nesis (1999) (Cephalopoda), Pugh (1999) (Siphonophorae), Spoel and Dadon (1999) (Pteropoda), Thuesen and Fernández Álamo(1999) (Polychaeta), and Vinogradov (1999) (Amphipoda).

It should be emphasised that the latitudinal distribution ranges tabulated are in some cases rather rough estimates based on ancillary and interpolated information. This introduces some uncertainty in the figures presented, for which reason most numbers should be considered as preliminary estimates. Nevertheless, with the framework of the comparisons drawn, we contend that the general patterns presented and contrasts with the benthic realm are valid.

BIODIVERSITY OF MARINE PLANKTON AND BENTHOS: THE WORLD OCEAN AND THE ANTARCTIC TODAY

So far, the World Ocean has yielded approximately 7000 species of zooplankton (Boltovskoy *et al.*, 2003; see Table 1), and 4000 of phytoplankton (Sournia *et al.*, 1991).

Table 1 illustrates the distribution of the zooplanktonic taxa with estimated figures for the World Ocean and for the South Atlantic. On the basis of subsets of selected groups we also calculated how many of the species recorded in the South Atlantic as a whole (0 to 60°S, American to African coasts) are present in its warm waters (Tropical or Equatorial and/or Subtropical, approximately between 0 and 35°S), in the Subantarctic domain (approximately 45-50°S; excluded are the Transitional waters, roughly between 35 and 45°S), and in the Antarctic waters (south of 47 to 60°S, depending on longitude). We anticipate that for most of these groups the precision of the numbers shown is around ±20%.

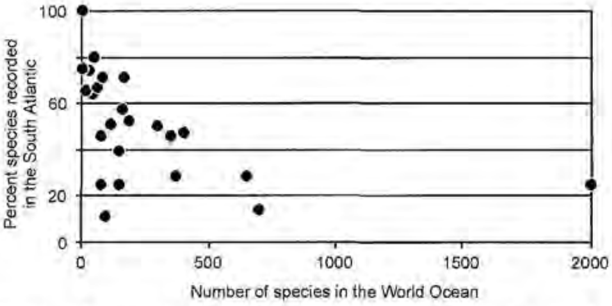

FIG. 1. – Proportions of species recorded in the South Atlantic for 26 zooplanktonic groups as a function of their overall totals known for the World Ocean (based on data from Table 1).

Estimates of the presence of world species in the South Atlantic are very preliminary because the data are significantly biased by two factors: (1) differences in the natural diversity of the groups encompassed, and (2) the degree of knowledge on them in the South Atlantic. In general terms, lower precision is associated with higher diversity values because of the higher effort needed to cover the more speciose groups. This is clearly shown in Figure 1, where a marked trend of lower percentages with higher overall species numbers is seen. The degree of coverage of the various groups in the South Atlantic, in turn, also introduces a significant bias: although some South Atlantic plankton taxa, like the Foraminifera, have been well covered by both local and international experts for many years, many others (e.g. Acantharia, Phaeodaria, Ciliophora, Nemertina and Mysidacea) have very seldom been investigated in these waters. Thus, while the overall average of World species recorded in the South Atlantic is around 37% (Table 1), when the groups are sorted according to their (subjectively perceived) degree of coverage in the South Atlantic the figures range between as high as 80% for the very well known Foraminifera to as low as 35% for the very poorly known taxa.

These considerations suggest that the "real" proportion of World Ocean zooplanktonic species that inhabit the South Atlantic is significantly higher than the figure shown in Table 1, probably around 60-70%.

TABLE 1. – Estimated numbers of marine zooplanktonic species for the World Ocean and for the South Atlantic (modified from Boltovskoy, 2000). Biogeographic boundaries indicated are from Boltovskoy *et al.* (1999) and references therein.

Group	Number of species worldwide	Number of species [and percentage of World total] in the South Atlantic	Percentage of South Atlantic species present in warm waters (Tropical and/ or Subtropical) (*)	Percentage of South Atlantic species present in Subantarctic waters (*)	Percentage of South Atlantic species present in Antarctic waters (*)	Degree of knowledge in the South Atlantic
Foraminifera	49	39 [80]	97	28	19	Very good
Acantharia	150					Very poor
Radiolaria Polycystina	350	160 [46]	90	26	23	Poor
Radiolaria Phaeodaria	350	158 [45]	70	33	43	Very poor
Ciliophora	150	58 [39]				Very poor
Tintinnida	300	151 [50]	60	17	16	Fair
Hydromedusae	650	185 [28]				Fair
Siphonophora	190	98 [52]	92	41	28	Fair
Scyphozoa	150	38 [25]				Poor
Ctenophora	80	20 [25]				Poor
Nemertini	97	11 [11]				Very poor
Polychaeta	120	61 [51]	87	33	31	Poor
Heteropoda	35	26 [74]				Fair
Pteropoda	160	91 [57]	86	16	9	Good
Cephalopoda	370	103 [28]	92	18	8	Very poor
Cladocera	8	8 [100]				Good
Ostracoda	169	120 [71]	95	37	21	Fair
Copepoda	2000	505 [25]				Poor
Mysidacea	700	96 [14]	66	38	8	Very poor
Amphipoda	400	188 [47]	89	26	23	Very poor
Euphausiacea	86	61 [71]	88	12	7	Good
Larvae of Brachyura	--	197				Poor
Chaetognatha	80	37 [46]	88	31	16	Good
Appendicularia	64	43 [67]	84	63	40	Good
Pyrosomatida	8	6 [75]				Very poor
Doliolida	17	11 [65]				Fair
Salpida	45	29 [64]	79	24	17	Very good
TOTAL	6778	2500 [37]				

(*) Figures based on subsets of the data including only those species for which distributional information is sufficient to allow these estimates.

When one compares the overall diversity of plankton with that of other communities, the first major contrast that strikes one's attention is the wide differences in biodiversity. As noticed above, zooplankton comprises around 7000 species, whereas non-planktonic marine animals, chiefly the benthos, range from 180,000 to 200,000 species (Zenkevitch, 1960; Briggs, 1996), with some estimates running into the millions (e.g. Grassle and Maciolek, 1992). The Antarctic benthos alone includes over 3000-4000 recorded species (Arntz *et al.*, 1997; Clarke and Johnston, 2003), with estimates of up to 11,000-17,000 expected species for the continental shelf alone (Gutt *et al.*, 2004).

A second interesting contrast between the plankton and the benthos is found in the proportions of overall species that are present south of the Polar Front. Using historical data for selected benthic invertebrates showing the highest species richness in the Southern Ocean, Clarke and Johnston (2003) estimated that Antarctic waters host between 17.5% (Pycnogonida) and 1% (Gastropoda) of the world totals. The average for their values was around 7% (Fig. 2). A similar analysis for 15 zooplanktonic groups considering Antarctic waters of the Atlantic sector alone yields an average of 10%, with values ranging between 27% (Appendicularia) and 1% (Mysidacea) (Fig. 2).

These figures, as well as other distributional traits (see below), strongly suggest that detachment from the bottom results in wider geographic ranges and lower degrees of endemism. Interestingly, for the planktonic groups illustrated in Figure 2, Cephalopoda and Mysidacea show the lowest proportions of species in Antarctic waters; planktonic Cephalopoda are largely comprised by the free-drifting paralarvae of benthic adults (Nesis, 1999), whereas most Mysidacea are benthopelagic organisms (Murano, 1999). The Amphipoda, in which some degree of association with the bottom is also common (Vinogradov, 1999), are also located on the right hand of the graph (Fig. 2).

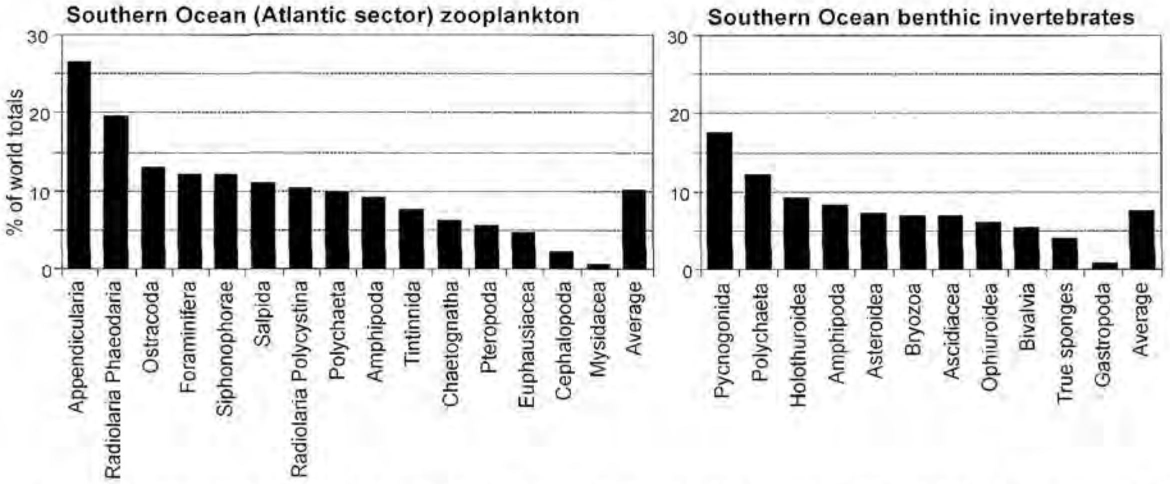

FIG. 2. – Zooplanktonic species described for the Southern Ocean (Atlantic sector) as a fraction of the world totals, as compared with similar values for the benthic invertebrate taxa, showing the highest species richness in the Southern Ocean (benthic invertebrate data from Clarke and Johnston, 2003).

It should be emphasised that association with the substrate affects not only the proportion of Antarctic species but also the geographic ranges of distribution worldwide. Of the approximately 700 mysid species known, only 96 (14%) have been recorded in the South Atlantic (Murano, 1999 and pers. comm.; see Table 1). Comparison of mysid vs. euphausiid world wide distribution patterns also points to the same trend where the chiefly coastal and shallow water mysids have much more circumscribed geographic ranges than the predominantly pelagic, open-ocean euphausiids (Angel, 1996). It is suggested that links with the bottom makes mysid ranges depend as much on currents and water masses, as on topographic features, resulting in more constrained areal dispersion patterns. A similar trend is also shown by the Hydromedusae, whose life cycle includes a benthic stage. Over 75% of the 197 species recorded in the South Atlantic inhabit shelf or slope waters and many of them are unable to cross the Atlantic. Of the 109 species present along the Atlantic coasts of Africa, 45 (41%) are absent on the American side of this ocean, whereas 77 (55%) of the 141 American species have not been recorded on the eastern side (Bouillon, 1999). Benthic stages in their life cycle are also probably responsible for the fact that South Atlantic waters host less than 30% of the inventory of the Hydromedusae of the World Ocean (Bouillon, 1999) (as opposed to *ca.* 60% for zooplankton as a whole, see above).

As opposed to terrestrial and freshwater habitats, the oceanic realm is typically characterised by few and often diffuse distributional barriers. To some degree this applies to all marine biotopes, although communities associated with the bottom can be affected by small-scale changes in the type of substrate, sill and bottom depth, etc., which in turn results in smaller areas and better defined biogeographic divisions and higher chances for reproductive isolation. Communities that dwell in the water column, on the other hand, typically lack these physical discontinuities, to the point that the process of speciation in the plankton itself, which has been the subject of interest and debate for at least half a century (e.g. Hutchinson, 1961), is still a largely unresolved issue. This is not only a practical problem with important implications for sampling strategy and design, but also a major issue in ecological theory. The tenets of modern ecology, including competitive exclusion and forced extinction and speciation, which have been formulated for physically structured, typically terrestrial ecosystems, are often not applicable to marine plankton (Venrick, 1986). The fact that, in the entire (epipelagic) Pacific Ocean, an area spanning over 180 million square kilometres, only 8 distinct planktonic provinces are recognised (McGowan, 1974) is a result of both the scarcity of species and the homogeneity of their makeup over vast areas (Bé and Tolderlund, 1971; Pierrot-Bults and Spoel, 1979; Hemleben *et al.*, 1989; McGowan and Walker, 1993; Angel, 1996).

BIODIVERSITY OF MARINE PLANKTON AND BENTHOS: FUTURE TRENDS FOR THE WORLD OCEAN AND THE ANTARCTIC

The above reviewed specific inventories are almost exclusively based on morphological criteria, which underestimate the true diversity of the organisms concerned. Indeed, for many marine planktonic protists with fossilizable remains (coccolithophorids, diatoms, foraminifers, radiolarians) circum-global distributions and very long stratigraphic ranges have been reported, which conflicts with their often very high turnover rates. The sequencing of various genes has shown that many of these morphological species are, in fact, monophyletic assemblages of sibling species which diverged several million years ago (De Vargas *et al.*, 2004). In some instances these siblings have been found to depict allopatric distribution ranges either temporally or geographically. A very nice example of cryptic speciation in the marine plankton was recently published by De Vargas *et al.* (1999). These authors found that one of the most distinctive planktonic foraminifers, *Orbulina universa*, which has always been regarded as a single species, is in fact a complex of three cryptic species whose distribution is correlated to hydrographic provinces, and particularly to the concentration of chlorophyll *a*.

Morphologically cryptic, but genetically distinctive, species of zooplankton are being found with increasing frequency (e.g., Bucklin *et al.* 1996, 2003, Goetze 2003) and will probably prove to be the norm across a broad range of taxa. Many putative cosmopolitan species may comprise morphologically similar, genetically distinct sibling species, with discrete geographic distributions, but how many cryptic species are present is currently unknown, even for well-known zooplankton groups (CMarZ, 2004).

Future work, however, will not always tend to enlarge existing inventories. While new species will be erected through genetic studies, many currently known ones will be invalidated as a result of them being synonymised. This will most probably affect speciose groups whose taxonomic systems are in a serious state of disarray, like the radiolarians (polycystines and pheodarians), the acantharians, and the tintinnids. The literature on these organisms is plagued with synonyms, to the point that in many cases binary names alone have little or no meaning (Boltovskoy, 1998; Boltovskoy *et al.*, 2003). This is partly due to problems arising from the use of poorly preserved materials and the analysis of skeletal (radiolarians, acantharians) or lorical (tintinnids) features only (Boltovskoy, 2000).

Nevertheless, the general consensus is that current zooplanktonic inventories are likely to increase rather than to shrink. However, even if every known species proves to be an assemblage of 3 or 4 morphologically cryptic siblings, the overall number of zooplanktonic species in the World Ocean will still remain below 20,000-30,000, which is at least one order of magnitude lower than the number of already described marine non-planktonic species (see above). Moreover, if benthic inventories are corrected for morphologically cryptic, so far undescribed species (e.g. see Held, 2005), the unbalance between biodiversity in the plankton and in the benthos will increase several-fold.

A useful approach to predicting the development of specific inventories is the analysis of the temporal trends in species descriptions, whereby rapidly climbing curves could indicate an incompletely documented fauna, whereas flat curves may suggest that the proportion of undescribed species is low (Costello *et al.*, 1996; Paxton, 1998; Clarke and Johnston, 2003). We compared such curves for two conspicuous and very well-researched groups of vertebrates (Primates and Reptilia), 1599 zooplanktonic species (several groups) recorded in the South Atlantic, and three groups of Antarctic benthic invertebrates (Fig. 3). As expected, the vertebrates show very flat curves because over 70% of the current inventories were reached by 1829 (Reptilia) to 1863 (Primates). The zooplankton depicts an intermediate shape with a significant decrease in species description rates after around 1910, when 70% of the inventory was attained. Finally, the Antarctic benthic invertebrates show typically climbing curves, with no indication of an imminent saturation.

These results confirm the above conclusion that differences between species richness in the plankton and in the benthos are not an artefact due to unbalanced knowledge, and that the gap is likely to increase as we get closer to accounting for the overall biodiversity of the marine fauna.

THE POLAR FRONT AS A BIOGEOGRAPHIC BOUNDARY AND ANTARCTIC ENDEMISM

The Polar Front is one of the most characteristic features of the Southern Ocean. Its position may be defined by the northern boundary of cold (-1.5 to 2°C) near-surface waters formed by winter cooling (Peterson and Stramma, 1991), or by the northern extent of the 2°C isotherm at 2000 m (Botnikov, 1963). At the surface, this circumpolar, meandering feature, characterised by a very sharp (2-3°C in 10-20 miles) temperature gradient, separates the Subantarctic zone from the Antarctic zone. This front is

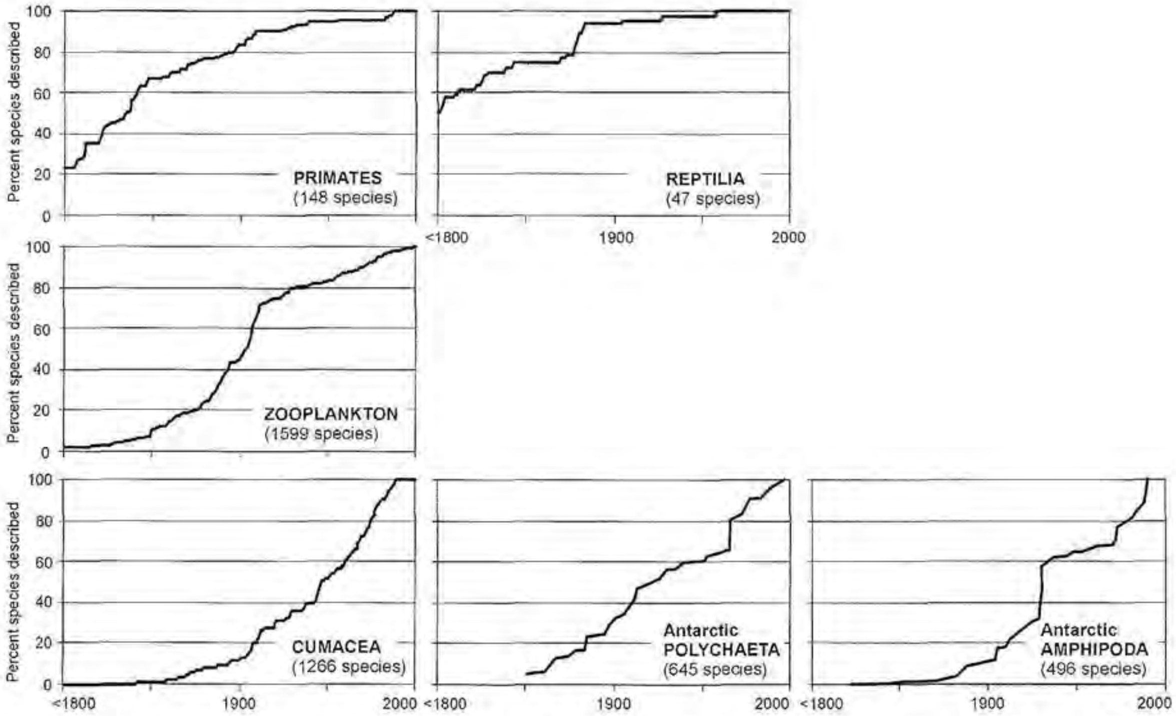

FIG. 3. – Cumulative percentage curves of species description rates for several animal groups. Data sources are, Primates: Groves (1993), Reptilia: Noreña (1999, reptiles from the Iberian Peninsula), zooplankton: Boltovskoy (1999a), Cumacea: Bacescu (1988, includes 4 families from the World Ocean), Antarctic Polychaeta and Amphipoda: Clarke and Johnston (2003).

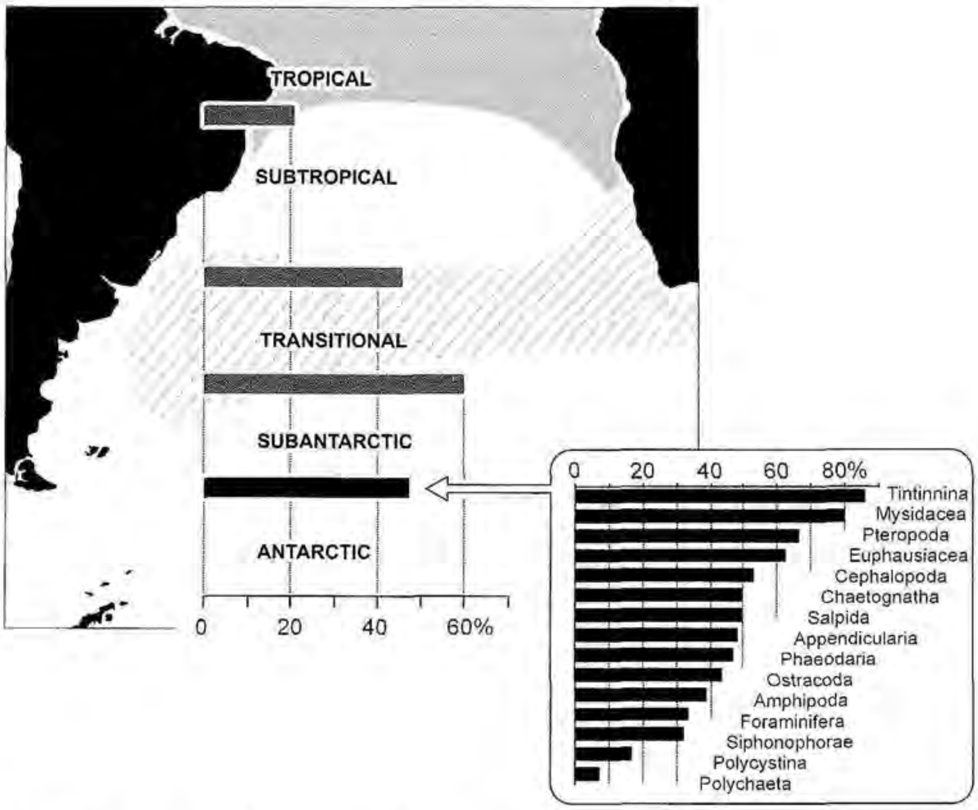

FIG. 4. – Species restricted to either side of each of the major biogeographic boundaries as a proportion of the totals recorded for the South Atlantic. Inset graph shows same figures for the Subantarctic-Antarctic limit broken down by major taxonomic group. Data from Boltovskoy (1999a).

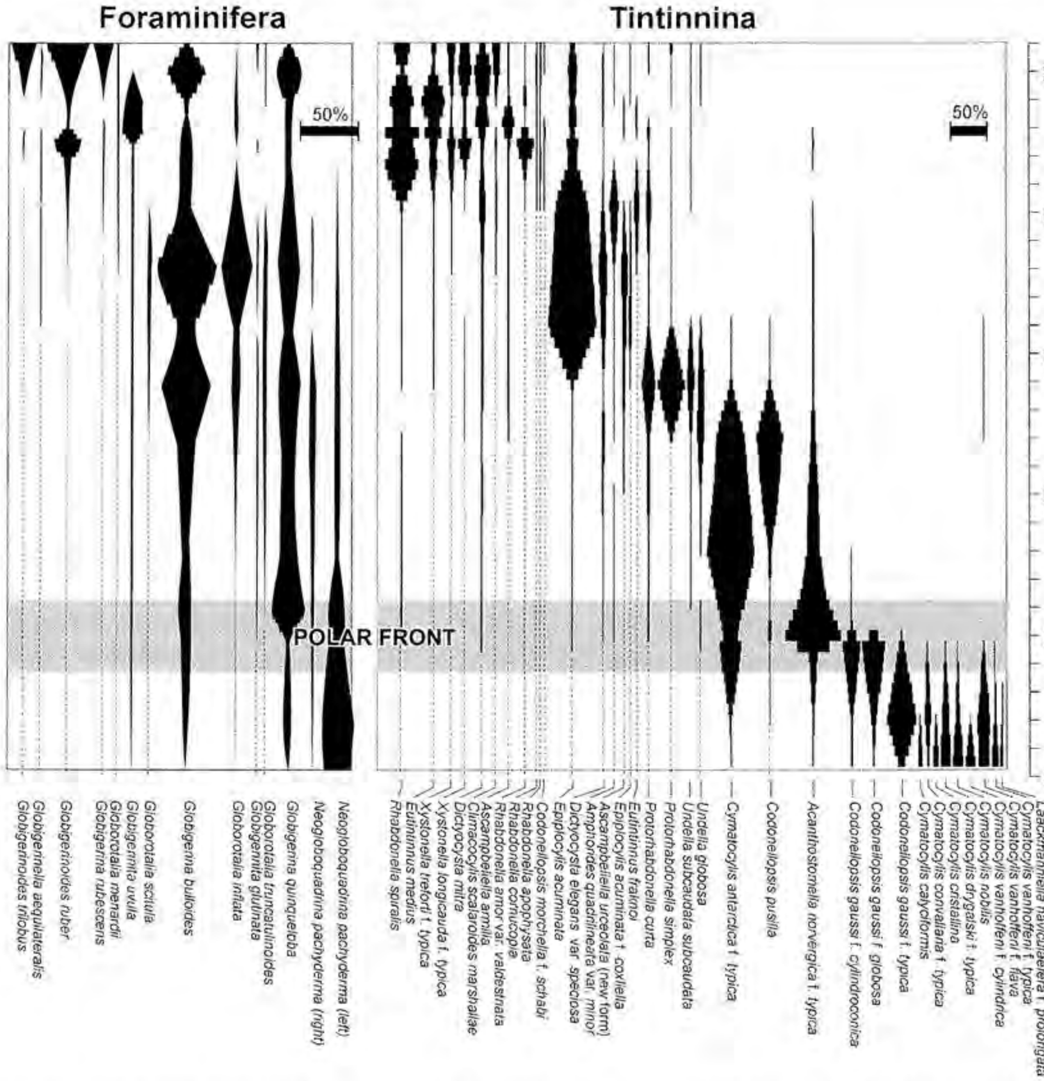

FIG. 5. – Latitudinal distribution of planktonic foraminifers and tintinnids along a transect of plankton samples (integrated data for vertically stratified tows down to 100 m from 22 stations between 34 and 60°S, along 51-56°W, in November 1994). Data from Boltovskoy *et al.* (2000, Foraminifera) and Thompson *et al.* (1999, Tintinnina).

often regarded as one of the sharpest and best defined biogeographic barriers in the World Ocean.

For benthic invertebrates, reported degrees of Antarctic endemism vary greatly between groups, but are usually high. Arntz *et al.* (1997) found values between 35% (scleractinian corals) and *ca.* 90% (pycnogonids). Other taxa show intermediate values (e.g., De Broyer and Jazdzewski, 1996; Brandt *et al.*, 1999; De Broyer and Rauschert, 1999). The distribution of zooplanktonic species, on the other hand, is much less affected by this boundary. Figure 4 illustrates the numbers of species whose latitudinal distribution ranges are interrupted by the Polar Front as a proportion of the species present on either side of it. For comparative purposes, the same figure is also given for the other three major faunal boundaries in the South Atlantic.

Two interesting observations emerge from these data. First, contrary to prediction on the basis of benthic data, the Polar Front boundary is more important than the Tropical-Subtropical Limit, but almost equivalent to the Subtropical-Transitional Limit, and weaker in biogeographic terms than the Transitional-Subantarctic. In other words, Antarctic and Subantarctic waters share about as many species as the Subtropical and the Transition zones, and are more alike than the Transitional and the Subantarctic areas. Second, the degree to which different groups are affected by this front is extremely variable: none of the species of pelagic Foraminifera that inhabit the cold waters of the South Atlantic (Subantarctic and/or Antarctic) are restricted to either side of this boundary, whereas among the Tintinnina *ca.* 90% of the cold water species do not

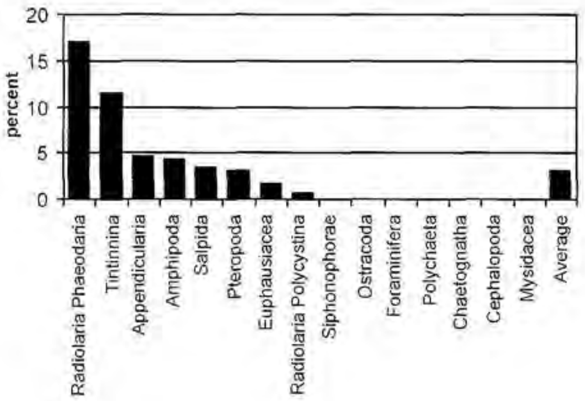

FIG. 6. – Approximate proportions of Antarctic endemic species in selected zooplanktonic groups. No column means no endemics known. Data from Boltovskoy (1999a, Atlantic sector only).

cross this limit (Fig. 5). This trend, in addition to contrasts between the various groups considered, is illustrated by data shown in Figure 6.

It should be mentioned that the above perception of the low degree of isolation of Antarctic zooplankton is probably somewhat biased by the fact that our records include not only the core areas of the species, but also their expatriation areas. The former are restricted to regions where the species reproduce and are able to maintain self-sustaining populations, whereas expatriation regions, where the animals merely survive, can be significantly larger (Beklemishev, 1969). Although benthic organisms are not free from this error either, we anticipate that the naturally much higher mobility of plankton can enhance this bias. Better coverage of the seas around the often poorly sampled Southern Ocean will decrease the proportions of Antarctic endemics. While this is true for both the benthos and the plankton, figures for the former will change more because benthic animals have typically smaller areas.

CONCLUSIONS

In this review we tried to show that marine zooplanktonic species are comparatively very few in number, and that a large proportion of them have already been discovered, partly because their geographic ranges are very wide.

Since its inception as an issue of major international interest at the National Forum on BioDiversity in Washington, DC, in 1986, the notion of biodiversity has had many formal definitions (Clarke and Johnston, 2003), yet for most of them assessment of the numbers of species is a key component of the concept. Aside from their theoretical and conceptual interest, precise estimates of the numbers of species awaiting discovery have a fundamental practical value insofar as they are a key consideration for the allocation of resources. However, in these discussions absolute numbers are rarely placed in context, which makes comparisons equivocal. Despite the fact that oceans cover over 70% of the earth's surface, they host only about 200,000 of the *ca.* 1,800,000 species described (Grassle, 2001). The plankton, in turn, occupies over 99% of the space available to marine creatures, and although a very large proportion of the few planktonic species have the largest distributional areas on the planet, they only represent a minor percentage (<5%) of the oceanic biodiversity. These contrasts suggest that at least some of the mechanisms important in structuring life and driving evolutionary processes in other communities are not applicable to the plankton, and that the ecological relevance of plankton is not paralleled by its diversity. Furthermore, the fact that marine planktonic inventories are probably better documented than those of several terrestrial and freshwater habitats may yield the wrong notion that we have a better understanding of them as a whole.

This is clearly not the case. Aside from the fact that for several zooplanktonic groups classification systems are in a very serious state of disarray, distributional and ecologic data are very scarce for almost all planktonic organisms. There are entire classes for which there is not a single species whose world wide distribution in the plankton has been mapped (e.g. Acantharia, Polycystina, Phaeodaria). Our current understanding of vertical distribution and abundance patterns, trophic relationships, consequences of marine planktonic bioinvasions, plankton-mediated global elemental cycles and patterns of endemism is still in its very infancy. Some of the overarching questions posed over 30 years ago, such as how planktonic distributional patterns arose, how they are maintained, and how rare species survive (e.g. McGowan, 1974) are still largely unresolved. The problem of rare species is particularly relevant because, while comprising the vast majority of the oceanic biodiversity (e.g. McGowan and Walker, 1993), they are the most vulnerable to both natural and human disturbance and extinction (Angel, 1996). These rare species are also the ones that are most incompletely accounted for in our current inventories. Thus, our understanding of the biodiversity (in the broad sense) of the marine pelagial is not better than that of terrestrial or freshwater communities, but the approaches that will be required in order to improve this knowledge are different from those necessary for other plant and animal groups.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Mesozooplankton assemblages in two bays in the Beagle Channel (Argentina) during January 2001*

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SUMMARY: This paper describes the composition and abundance of mesozooplankton of Bahía Ushuaia and Bahía Golondrina. These small bays are located in the northern Beagle Channel. Sampling was carried out from January 20 to 23, 2001 and samples were collected from the upper layer at nine stations. This study is the first research on mesozooplankton in this part of the Beagle Channel. Due to their dominance in the mesozooplankton community, we compared our Copepoda data with those reported by other authors from Antarctic coastal environments. By applying cluster analysis, we found two station groups in both bays: one in slightly polluted zones and the other in undisturbed external zones. Four assemblages in Bahía Ushuaia and two in Bahía Golondrina were determined by using non-metric multidimensional scaling (MDS) and cluster analysis. Mesozooplanktonic assemblages showed a certain resemblance in zones with and without anthropogenic influence. Most of the copepod species in our samples are typical of the sub-Antarctic region. *Oithona similis* (=*O. helgolandica sensu* Ramírez, 1966), *Oncaea curvata*, and *Ctenocalanus citer* show either similar or higher abundances at Antarctic coastal sites, including the upper layer in oceanic areas, in comparison with sub-Antarctic coastal localities. This suggests that, in agreement with other findings, the Polar Front is probably not a major geographic boundary for the distribution of these species.

Keywords: mesozooplankton, copepods, Beagle Channel, assemblage, *Oithona*, *Oncaea*, *Ctenocalanus*, Antarctic.

RESUMEN: ASOCIACIONES MESOZOOPLANCTÓNICAS EN BAHÍA USHUAIA Y BAHÍA GOLONDRINA (CANAL BEAGLE, ARGENTINA) DURANTE ENERO DE 2001. – Se describe la composición y abundancia mesozooplanctónica en Bahía Ushuaia y Bahía Golondrina, pequeñas bahías ubicadas al norte del Canal Beagle. El muestreo se realizó del 20 al 23 de enero de 2001 y las muestras se colectaron en el estrato superficial en nueve estaciones. Este estudio constituye la primera investigación realizada sobre el mesozooplankton, en las dos bahías del Canal Beagle. Debido a su dominancia en la comunidad mesozooplanctónica, los datos de copépodos fueron comparados con datos de otros autores para ambientes costeros de la Antártida. Los análisis de cluster y MDS revelaron dos grupos de estaciones en ambas bahías, uno en zonas levemente contaminadas y el otro en zonas más externas no perturbadas. Los mismos análisis permitieron determinar cuatro asociaciones de especies en Bahía Ushuaia y dos en Bahía Golondrina. Las asociaciones encontradas en ambas bahías presentaron una cierta semejanza en zonas con y sin influencia antrópica. La comparación del grupo Copepoda mostró que la mayoría de las especies de nuestras muestras son típicas de la región subantártica. Los copépodos *Oithona similis* (=*O. helgolandica sensu* Ramírez, 1966), *Oncaea curvata* y *Ctenocalanus citer* presentan similar o mayor abundancia en los ambientes costeros de la Antártida, incluyendo el estrato superficial de áreas oceánicas, que en los sitios costeros subantárticos. En coincidencia con otros hallazgos, el Frente Polar no parece ser una importante barrera geográfica para la distribución de dichas especies.

Palabras clave: mesozooplancton, Copepoda, Canal Beagle, asociaciones, *Oithona*, *Oncaea*, *Ctenocalanus*, Antártida.

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INTRODUCTION

The mesozooplankton of the Magellan Straits, the Chilean channels and fjords, and the Beagle Channel have been studied with certain detail in relation to the oceanographic and bio-ecological conditions (Mazzocchi *et al.*, 1995; Antezana *et al.*, 1997; Antezana, 1999; Sabatini *et al.*, 2001; Thatje *et al.*, 2003). In these areas, different assemblages constituted by a variable proportion of holoplanktonic and meroplanktonic forms have been observed (Defren-Janson *et al.* 1999; George and Schminke, 1999; Hamamé and Antezana, 1999; Pagès and Orejas, 1999). However, only a few zooplankton studies on different aspects have so far been carried out in the eastern Beagle Channel (Lovrich, 1999; Pagès and Orejas, 1999; Sabatini *et al.*, 2001; Thatje *et al.*, 2003). The coastal embayments near the most populated area on the channel coast such as Bahía Ushuaia (BU) and Bahía Golondrina (BG) are a poorly studied region. Particularly in these two bays, this is the first study on the mesozooplankton.

From a zoogeographical point of view, the Fuegian district (Lovrich, 1999) is part of the Magellan Province (Hamamé and Antezana, 1999) belonging to the sub-Antarctic neritic domain (Boltovskoy *et al.*, 1999). As such, it is an area of great interest on account of its very recent relationship with both the Atlantic and Pacific fauna since the environment has been marine only for the last 9000 years (Rabassa *et al.* 1986). In addition, the faunal exchange between the Antarctic and South America appears to be greater than that between any other pair of continents, despite the isolation caused by the independent evolution of the fauna of those two continents (Lovrich, 1999). The geographical proximity probably makes the relationship between the Magellan Province and the Antarctic more evident. Furthermore, the findings about the Antarctic plankton in the sub-Antarctic (Magellan) domain (Antezana, 1999; Mazzocchi *et al.*, 1995) and vice-versa (Thatje and Fuentes, 2003) demonstrate a planktonic exchange of certain forms in agreement with what Lovrich (1999) inferred in relation to anomuran and brachyuran decapod larvae. In the present study, we assume a possible link between the small-sized copepods from the Antarctic and those from the Fuegian district.

This study is the first contribution of a larger survey aimed at the study of the structure and dynamics of zooplankton in the two bays. To this end, we describe the mesozooplankton assemblages of the upper layer in BU and BG during mid-summer (January, 2001). In order to test the above-mentioned hypothesis, we compare our results on Copepoda with similar data from the coastal Antarctic embayments during the same season.

MATERIAL AND METHODS

The study area was restricted to Bahía Ushuaia and Bahía Golondrina (Tierra del Fuego, Argentina), which are two small embayments located on the northern coast of the Beagle Channel (54°79'–54°85'S and 68°22'–68°36'W).

Sampling was carried out from January 20 to 23, 2001 (Fig. 1). Nine stations were sampled (6 in BU and 3 in BG). The samples were collected in the daytime, usually between 9 am and 4 pm (local time). At each station, an oblique tow was performed at 0-5 m depth using a Nansen open net (with a Kahlsico® flowmeter) with a 0.53 m mouth diameter and a 0.2 mm mesh size. Small individuals, such as meroplankton and copepod eggs, naupliar, and the youngest copepodite stages, were not sampled quantitatively due to the relatively large mesh size used. However, due to their high abundances, their distribution pattern is included. Tow duration was 10-15 min, and towing speed was approximately 3.7 km h^{-1}. Samples were preserved in 4% sodium borate-buffered formalin. Data on the physical and chemical variables of this campaign in BU and BG were reported by Esteves *et al.* (2003).

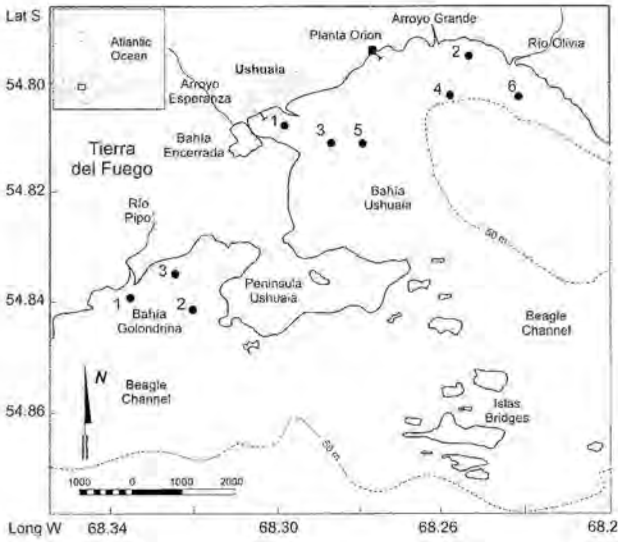

FIG. 1. – Map of the study area showing the location of sampling stations.

In the laboratory, the mesozooplankton was identified to the lowest possible taxonomic level under a stereoscopic microscope. In each sample, at least 100 individuals of the most abundant species were counted. Adult copepods were identified to species level, while copepodite stages, nauplii, and eggs were pooled together. In Argentinean waters, *Oithona similis* has not been cited as such but as *Oithona helgolandica* (Ramírez, 1966, 1970a,b). There is a synonymy problem with this species. Therefore, in this paper we decided to cite it as *Oithona similis* (=*O. helgolandica sensu* Ramírez, 1966). Although in this study we registered *Ctenocalanus citer* according to Heron and Bowman (1971), Sabatini *et al.* (2001) reported *C. vanus* for stations near our study area. Considering that these congeneric species closely resemble each other, further studies would be needed in order to verify the presence of the two species in the area. Abundance is reported in number of individuals per cubic metre. The percentage of occurrence was calculated taking into account the number of stations in which each taxon was present. The filtered volume was calculated from the number of revolutions of the flowmeter, the mouth area, and the flowmeter constant (0.27 m rev^{-1}).

Statistical parametric tests were used to test differences between the two bays. Statistical multivariate analyses were carried out with the PRIMER software package (Clarke and Warwick, 1994). Non-metric multimensional scaling (MDS) (Kruskal and Wish, 1978) was applied to order stations and species in a two-dimensional plot. Square root transformed data and the quantitative Bray-Curtis index were used. Hierarchical agglomerative clustering under the same conditions and an average linking were also used to determine the groups to be superimposed on the MDS plots when their stress values were <0.2 and >0.1. The same clustering technique was used to classify the stations according to depth, temperature, and chlorophyll *a*. These variables were utilised with the permission of Esteves *et. al* (2003).

STUDY AREA AND ENVIRONMENTAL FEATURES

Bahía Ushuaia and Bahía Golondrina display different physical and hydrological features. Both their size and their bathymetry are highly different. BU is 9 km long while BG is 2.2 km long. BU is deeper eastwards and towards the Beagle Channel, reaching 130 m depth, whereas BG is shallower (20 m approx.). The two bays also differ in the type of bottom. BG displays a soft-bottom surface whereas BU has a more consolidated soft bottom with stones and shells (Comoglio, 1994). Balestrini *et al.* (1998) report for the Bahía Golondrina and Bridges Island areas permanent currents flowing from the southwest with maximal velocities of 2.6 and 15.6 cm sec^{-1} respectively. In BU a permanent strong current moves west along the northern coast of the bay at 2 cm sec^{-1}, and then progresses to the southeast along the southern coast at 16.3 cm sec^{-1} (Balestrini *et al.*, 1998). Both bays receive effluents from Ushuaia city and the industries situated in the surroundings. As a result, coastal waters are slightly polluted (Amín *et al.*, 1996; Commendatore and Esteves, 2001). In the stations considered in this study, depth varied from 4 to 33 m (BU) and from 2.7 to 5 m (BG); temperature ranged from 8.5 to 9.9°C (BU) and from 8.8 to 11.7°C (BG). Chlorophyll *a* concentration ranged from 2.3 to 15.2 mg m^{-3} (BU) and from 0.68 to 1.59 mg m^{-3} (BG) (Fig. 2).

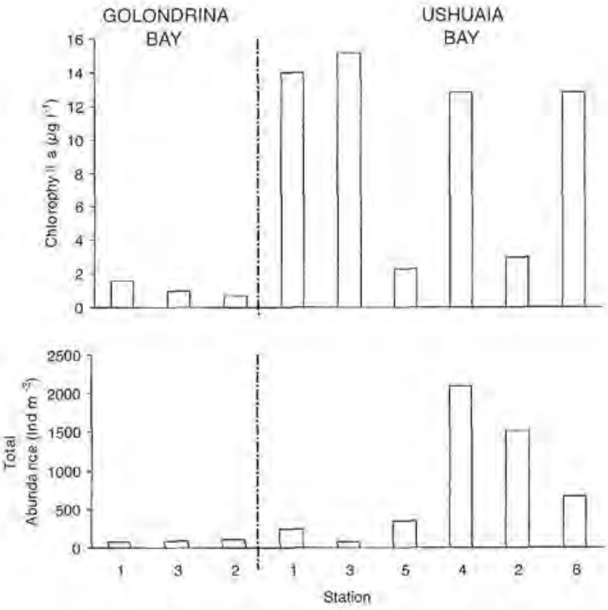

FIG. 2. – Chlorophyll *a* (after Esteves *et al.*, 2003) and total mesozooplankton abundance at each station of Bahía Ushuaia and Bahía Golondrina.

RESULTS

Total mesozooplankton abundance per station varied from 77 to 2087 ind m^{-3} in BU and from 68 to 109 ind m^{-3} in BG (Fig. 2). The differences observed

TABLE 1. – Taxa list at Bahía Ushuaia and Bahía Golondrina. Mean: mean abundance (Ind. m^{-3}). SE: standard error. O%: percentage of occurrence in all samples. L: larvae

Taxa	BAHIA USHUAIA Mean	BAHIA USHUAIA SE	BAHIA USHUAIA O %	BAHIA GOLONDRINA Mean	BAHIA GOLONDRINA SE	BAHIA GOLONDRINA O %
Calanus australis	0.17	0.17	16.66	-	-	-
Centropages brachiatus	0.67	0.42	33.33	0.67	0.33	66.66
Drepanopus forcipatus	4.50	2.99	50	4.00	1.73	100
Clausocalanus brevipes	18.33	11.26	83.33	1.33	0.67	66.66
Acartia tonsa	17.17	12.87	83.33	5.00	1.73	100
Eurytemora americana	7.33	4.70	66.66	0.33	0.33	33.33
Paracalanus parvus	1.17	0.79	50	0.33	0.33	33.33
Ctenocalanus citer	38.33	20.79	100	4.00	2.52	100
Calanoida copepodids	480.00	264.23	100	26.00	11.60	100
Calanoida nauplii	61.67	38.58	100	3,00	1.53	66.66
Calanoida eggs	58.00	29.43	100	-	-	-
Oncaea curvata	1.50	1.31	33.33	-	-	-
Oithona similis	94.33	46.38	83.33	8.67	2.91	100
Tisbe varians	0.33	0.33	16.66	0.67	0.67	33.33
Harpacticus furcatus	0.83	0.48	50	1.33	1.35	33,33
Parathalestris clausi	0.17	0.17	16.66	-	-	-
Harpacticoida spp.	0.33	0.21	33.33	0.33	0.33	33.33
Monstrilloida sp.	0,17	0.17	16.66	-	-	-
Podon leuckarti	6.17	2.40	83.33	0.33	0.33	33.33
Bosmina longirostris	-	-	-	0,33	0,33	33.33
Amphipoda	0.17	0.17	16.66	-	-	-
Decapoda (L)	1.33	1.33	16.66	-	-	-
Euphausiacea (L)	0.20	0.17	16.66	-	-	-
Cirripedia spp. (L)	5.00	2.97	50	2.00	0.58	100
Bryozoa (L)	1.83	1.25	66.66	4.00	1.00	100
Polychaeta	1.33	1.33	16.66	0.33	0.33	33.33
Polychaeta (L)	0.50	0.34	33.33	20.67	17.7	100
Autolytus sp.	-	-	-	0.33	0.33	33.33
Bivalvia (L)	-	-	-	1.33	0.33	100
Obelia sp.	21.33	12.70	100	3.67	2.67	100
Total	801.53			84.98		

in the mesozooplankton abundance in the two bays were statistically significant (t =2.24, p<0.05). Calanoid copepodids were the dominant taxon, with mean abundances of 480 ind m^{-3} (BU) and 26 ind m^{-3} (BG) (Table 1). The other most abundant taxa were *O. similis* (94.33 ind m^{-3}) and calanoid nauplii (61.67 ind m^{-3}) in BU and polychaete larvae (20.67 ind m^{-3}) and *O. similis* (8.67 ind m^{-3}) in BG.

Thirty mesozooplankton taxa were recorded (Table 1). Nineteen taxa were common to both bays, 8 were present in BU only, and 3 were found in BG only. A higher number of taxa were encountered in Ushuaia Bay than Golondrina Bay (27 and 22 respectively).

In both bays, holoplankton represented more than 50% of the taxa observed in the present study, whereas the remaining percentage was constituted by meroplankton and tychoplankton (organisms carried into the plankton by dynamic factors). Within the holoplankton, calanoid copepods predominated the total abundance followed by the cyclopoid copepod *Oithona similis*. In BU, the medusa *Obelia* and the cladoceran *Podon leuckarti* also occurred in relatively high numbers. In both bays, copepodite stages of calanoid copepods, mainly corresponding to *Drepanopus forcipatus, Clausocalanus brevipes* and *Ctenocalanus citer* (unpubl. data), occurred in the highest abundances (Table 1). Meroplankton was represented by bryozoan cyphonautes, cirriped nauplii and cypris, decapod zoeae, and benthic polychaete nectochaets. In BU only nine taxa presented the highest occurrence: *C. citer*, *Obelia* sp. and copepodids, nauplii and eggs of Calanoida (100%), and *C. brevipes*, *A. tonsa*, *O. similis* and *P. leuckarti* (83%). In contrast, in BG almost half of the taxa presented 100% occurrence.

The stations within each bay were arranged by cluster analysis according to the abundance and presence of mesozooplanktonic taxa (Fig. 3a, b). In BU, the presence of two groups (1 and 2) was determined at the 50% similarity level. Group 1 (G1) was constituted by Sts. 2, 4, and 6 (eastwards) and group 2 (G2) by Sts. 1, 3, and 5 (westwards) (Fig. 3a). In BG, two groups were observed: group 1 (G1) with Sts. 1 and 2 and group 2 (G2) with only Stn. 3 (Fig. 3b). The arrangement of the stations relative to depth, surface temperature and chlorophyll *a* values

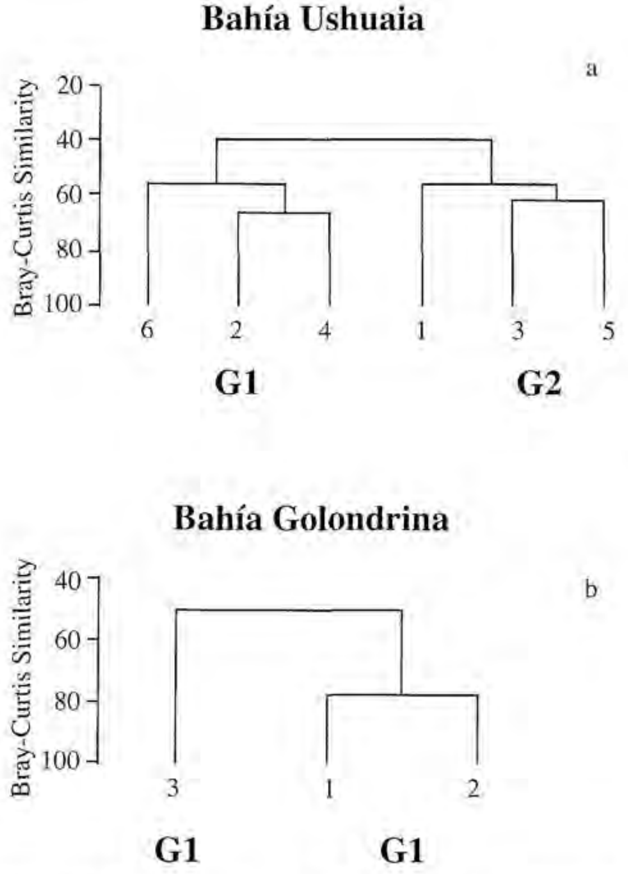

FIG. 3. – Clusters showing the station groups for Bahía Ushuaia (a) and Bahía Golondrina (b).

showed a slightly different pattern, but it was not possible to infer any relationship between these variables and the mesozooplankton distribution pattern. This was probably due to the absence of clear gradients of such variables but also to the low number of observations.

MDS plots revealed the existence of 4 mesozooplanktonic assemblages (A, B, C, and D) in BU (Fig. 4a) and 2 assemblages (A and B) in BG (Fig. 4b), with stress values of 0.14 and 0.08 respectively. These assemblages were also identified through cluster analysis at the 20% similarity level. In BU, assemblage A represented the most abundant taxa which mainly occurred at all stations (calanoid copepodids and nauplii, *C. citer*, and *O. similis*), but also DL, P and Oc were present with low abundances (Table 1 and 2). Assemblage B included low abundance taxa mainly occurring at Sts. 1, 3, 5 (G2) with the exception of bryozoan larvae and *C. brachiatus*. Assemblages C and D included taxa with low abundances. C presented only one species (*P. clausi*), which was found only at Sts. 1, 3, 5, whereas D presented two taxa (Amphipoda and *C. australis*) occurring only at Sts. 2, 4, 6 (G1). If a similarity level of 10% was considered, A, B and C would form only one assemblage. In BG, assemblage A represented all taxa occurring at Sts. 1 and 2 (G1), some of which were also found at Stn. 3 (G3), mainly those which were found in higher numbers. Assemblage B represented taxa which were observed only at Stn. 3 (Table 1 and 3).

From the results of the multivariate analysis it was possible to detect the relevant taxa characterising different zones (station groups) within each bay (Table 2 and 3). In BU, calanoid copepodids and *O. similis*, which comprised 65 and 11% of the total abundance respectively, were indicators of group 1. The same

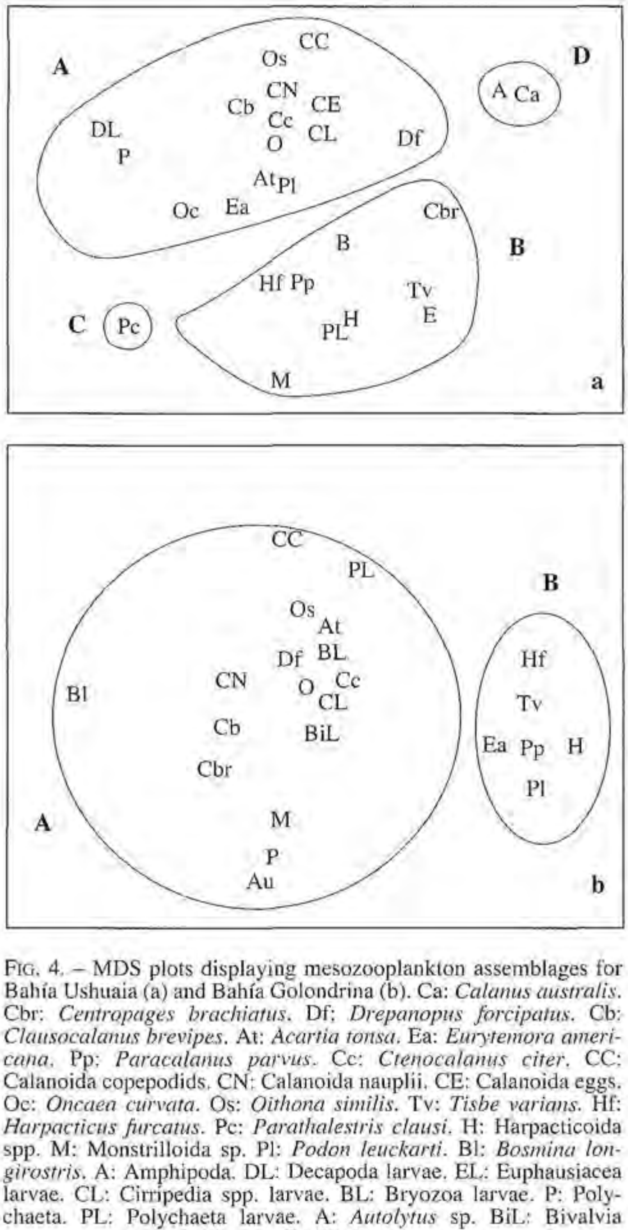

FIG. 4. – MDS plots displaying mesozooplankton assemblages for Bahía Ushuaia (a) and Bahía Golondrina (b). Ca: *Calanus australis*. Cbr: *Centropages brachiatus*. Df: *Drepanopus forcipatus*. Cb: *Clausocalanus brevipes*. At: *Acartia tonsa*. Ea: *Eurytemora americana*. Pp: *Paracalanus parvus*. Cc: *Ctenocalanus citer*. CC: Calanoida copepodids. CN: Calanoida nauplii. CE: Calanoida eggs. Oc: *Oncaea curvata*. Os: *Oithona similis*. Tv: *Tisbe varians*. Hf: *Harpacticus furcatus*. Pc: *Parathalestris clausi*. H: Harpacticoida spp. M: Monstrilloida sp. Pl: *Podon leuckarti*. Bl: *Bosmina longirostris*. A: Amphipoda. DL: Decapoda larvae. EL: Euphausiacea larvae. CL: Cirripedia spp. larvae. BL: Bryozoa larvae. P: Polychaeta. PL: Polychaeta larvae. A: *Autolytus* sp. BiL: Bivalvia larvae. O: *Obelia* sp.

TABLE 2. – Mean abundance (Ind. m^{-3}), standard error (SE) and abundance percentage (%) of each taxon in the different assemblages (A, B, C and D) and at each station group present in Bahía Ushuaia. In bold, highest percentages of abundance.

		Group 1 (Stn. 2, 4, 6)			Group 2 (Stn. 1, 3, 5)		
	Taxa	Mean	SE	(%)	Mean	SE	(%)
A	Calanoida nauplii	102.33	75.86	7.19	21.00	6.82	9.43
	Ctenocalanus citer	70.00	33.87	4.92	6.67	3.49	2.99
	Oithona similis	160.00	78.57	**11.25**	28.67	16.77	**12.87**
	Obelia sp.	30.33	25.94	2.13	12.33	7.34	5.54
	Clausocalanus brevipes	34.33	19.36	2.41	2.33	1.86	1.05
	Calanoida eggs	57.33	41.38	4.03	58.67	51.24	**26.35**
	Calanoida copepodids	931.67	380.7	**65.49**	28.33	17.44	**12.72**
	Cirripedia spp. larvae	-	-	-	10.00	4.36	4.49
	Podon leuckarti	3.00	2.52	0.21	9.33	3.53	4.19
	Eurytemora americana	10.00	10.01	0.70	4.67	1.77	2.10
	Acartia tonsa	3.33	2.40	0.23	31.00	25.14	**13.92**
	Drepanopus forcipatus	8.67	5.21	0.61	0.33	0.34	0.15
	Polychaeta	2.67	2.67	0.19	-	-	-
	Decapoda larvae	2.67	2.67	0.19	-	-	-
	Oncaea curvata	2.67	2.67	0.19	0.33	0.34	0.15
B	*Harpacticus furcatus*	-	-	-	1.67	0.66	0.75
	Paracalanus parvus	-	-	-	2.33	1.34	1.05
	Polychaeta larvae	-	-	-	1.00	0.58	0.45
	Harpacticoida spp.	-	-	-	0.67	0.34	0.30
	Bryozoa larvae	2.67	2.67	0.19	1.00	0.00	0.45
	Monstrilloida	-	0	-	0.33	0.34	0.15
	Euphausiacea larvae	-	0	-	0.33	0.34	0.15
	Tisbe varians	-	0	-	0.67	0.66	0.30
	Centropages brachiatus	0.67	0.66	0.05	0.67	0.66	0.30
C	*Parathalestris clausi*	-	0.00	-	0.33	0.34	0.15
D	*Autolytus* sp.	0.33	0.34	0.02	-	-	-
	Calanus australis	0.33	0.34	0.02	-	-	-

TABLE 3. – Mean abundance (Ind. m^{-3}), standard error (SE) and abundance percentage (%) of each taxon in the different assemblages (A and B) and at each station group present in Bahía Golondrina. In bold, highest percentages of abundance.

		Group 1 (Stn. 1, 2)			Group 2 (Stn. 3)	
	Taxa	Mean	SE	%	Abundance	%
A	*Obelia* sp.	5.0	3.27	5.65	1	1.12
	Ctenocalanus citer	5.0	3.27	5.65	2	2.25
	Cirripedia spp. larvae	2.0	0.82	2.26	2	2.25
	Bryozoa larvae	5.0	0.00	5.65	2	2.25
	Drepanopus forcipatus	5.5	1.23	6.21	1	1.12
	Calanoida nauplii	4.5	0.41	5.08	-	-
	Oithona similis	11.0	2.45	**12.43**	4	4.49
	Acartia tonsa	5.0	2.45	5.65	5	5.62
	Clausocalanus brevipes	2.0	0.00	2.26	-	-
	Centropages brachiatus	1.0	0.00	1.13	-	-
	Bivalvia larvae	1.5	0.41	1.69	1	1.12
	Polychaeta larvae	3.0	0.82	3.39	56	**62.92**
	Calanoida copepodids	36.5	6.95	**41.24**	5	5.62
	Bosmina longirostris	0.5	0.41	0.56	-	-
	Polychaeta	0.5	0.41	0.56	-	-
	Autolytus sp.	0.5	0.41	0.56	-	-
B	*Harpacticus furcatus*	-	-	-	4	4.49
	Tisbe varians	-	-	-	2	2.25
	Podon leuckarti	-	-	-	1	1.12
	Harpacticoida spp.	-	-	-	1	1.12
	Paracalanus parvus	-	-	-	1	1.12
	Eurytemora americana	-	-	-	1	1.12

taxa (both with 13%), calanoid eggs (26%) and *A. tonsa* (14%) characterised group 2. In BG, calanoid copepodids and *O. similis* comprised 41 and 12% respectively and characterised group 1. Polychaete larvae (63%) were the best indicator of group 2.

DISCUSSION

Despite the physical and hydrological differences between Bahía Ushuaia (BU) and Bahía Golondrina (BG), Esteves *et al.* (2003) found no important dif-

TABLE 4. – Summarised Copepoda data of Bahía Ushuaia and Bahía Golondrina Bay (Beagle Channel) and data of studies in Antarctic areas. N: number of samples. In bold, taxa cited for the Antarctic region; in normal type, for the sub-Antarctic region of South America and underlined for both regions. * These authors observed more copepod species without month specification

Region (Authors)	Year	N	Mesh (mm)	Depth (m) (haul)	Copepods	Mean (Ind. m^{-3})	Total Zooplankton Mean
Bahía Ushuaia and Bahía Golondrina (Beagle Channel) 54°79'-54°85'S 68°22'-68°36'W (present study)	2001	9	0.2	0-5 (oblique)	*Oithona similis*	65.77	541.89
					Ctenocalanus citer	26.88	
					Acartia tonsa	13.11	
					Clausocalanus brevipes	12.66	
					Eurytemora americana	5	
					Drepanopus forcipatus	4.33	
					Oncaea curvata	1	
					Paracalanus parvus	0.88	
					Centropages brachiatus	0.66	
					Calanus australis	0.11	
					Tisbe varians	0.44	
					Harpacticus furcanus	1	
					Parathalestris clausi	0.11	
					Harpacticoida spp.	0.33	
					Monstrilloida sp.	0.11	
					Calanoida nauplii	42.11	
					Calanoida copepodids	328.66	
					Calanoida eggs	38.66	
Ezcurra Inlet, Admiralty Bay (King George Island, South Shetland Islands) 62°09'S 58°28'W (Chojnacki and Weglenska, 1984)	1978	17	0.203	0-75 (vertical)	*Oithona similis*	>50%	10.6
					Oithona frigida		
					Oncaea spp.		
					Drepanopus pectinatus		
					Calanoides acutus		
					Calanus propinquus		
					Rhincalanus gigas		
					Metridia lucens		
					Metridia longa		
					Metridia gerlachei		
					Metridia curticauda		
					Calanus simillimus		
					Scolecithricella glacialis		
					Euchaeta antarctica		
					Pleuromamma robusta		
					Harpacticoida spp.		
					Copepoda nauplii		
Potter Cove (King George Island, South Shetland Islands) 62°15'S 58°39'W (Elwers and Dahms, 1998)*	1996 1997	6	0.055	0-38 (vertical)	*Oithona similis*	69.37	85.83
					Oncaea curvata	< 10	
					Ctenocalanus citer	< 10	
West coast Antarctic Peninsula and Shetland Islands 62°14'-64°52' S 58°44'-63°36' W (Hoffmeyer and Schiel, unpubl. data.)	1998	7	0.3	0-20 (oblique)	***Calanoides acutus***	< 0.1	0.35
					Calanus propinquus	< 0.1	
					Rhincalanus gigas	< 0.1	
					Subeucalanus longiceps	< 0.1	
					Microcalanus pygmaeus	< 0.1	
					Ctenocalanus citer	< 0.1	
					Metridia gerlachei	< 0.1	
					Paraeuchaeta antartica	< 0.1	
					Paralabidocera antartica	< 0.1	
					Oithona similis	<1.0	
					Oithona frigida	< 1.0	
					Oncaea curvata	< 0.1	
					Harpacticoida spp.	< 0.1	

ferences in the surface temperature except that chlorophyll *a* was different in the two bays in January 2001. They also observed a higher nutrient concentration, except for ammonia, as well as a lower chlorophyll *a* concentration in BG. In our study, mesozooplankton abundance showed an inverse trend with respect to that of chlorophyll *a* at most of the stations of both bays. However, in BU the values corresponding to both variables (abundance and chlorophyll *a*) were an order of magnitude higher than those of BG. This could be due to the higher ammonia concentration supply due to anthropogenic activities and freshwater flow in BU (particularly waste-water effluents) than in BG (Esteves *et al.*, 2003).

Pelagic copepods were the most abundant group in BU and BG. This is in agreement with studies carried out in the Magellan region and western Beagle Channel (Defren-Janson *et al.*, 1999), the Antarctic Peninsula (Chojnacki and Weglenska, 1984, among others), and the Santa Cruz and Tierra del Fuego coasts (Sabatini *et al.*, 2001). Of 45 species found in the Magellan Straits at all depths (Mazzocchi *et al.*, 1995), nine occurred in our study area in the upper 5 m of the water column. Eight of them (*Centropages brachiatus*, *D. forcipatus*, *C. brevipes*, *Acartia tonsa*, *Paracalanus parvus*, *C. citer*, *Oncaea curvata* and *O. similis*) were recorded in both bays whereas *Calanus australis* was only recorded in BU. At some stations of the eastern Beagle Channel, which is close to the study area, Sabatini *et al.* (2001) observed that the most important species was *D. forcipatus* in autumn and spring while *C. vanus* was abundant only in spring. In the present study, *D. forcipatus*, *C. brevipes*, and *C. citer* copepodids were dominant in January in both bays. *Calanus australis* was poorly represented in BU and was absent in BG. However, Sabatini *et. al.* (2001) recorded this species in spring at the station nearest to BU with approximately 50 ind m^{-3}. The presence at station 1 of BG of *Bosmina longirostris*, a casual and typically fresh-water cladoceran, could be due to the discharge from Río Pipo. Among the cnidarians mentioned by Pagès and Orejas (1999), *Obelia* sp. was found between Ballenero Channel and the stations located on the eastern mouth of the Beagle Channel. This taxon, which was more abundant in BU than in BG, was the only Cnidarian found in our samples.

Although they were not taxonomically examined in detail, a high diversity of both meroplankton and tychoplankton (in particular benthic harpacticoids) was noticeable in the samples. This phenomenon and its high occurrence in both bays might be indicative of the existence of an important benthopelagic coupling as reported by Antezana (1999) and Cattaneo-Vietti *et al.* (1999) for the Magellan Straits and western Beagle Channel. BU and BG, however, are shallower than the above studied sites. The contribution of meroplankton, which is completely different in the two bays (1% and 33.33% of total mean abundance in BU and BG respectively), could be a consequence of depth differences. However, such values are similar in magnitude (15%) to those reported by Defren-Janson *et al.* (1999) for a deep station (270 m) located to the west of the Beagle Channel in the "Victor Hensen" Campaign in November 1994. At this station, as well as in others located in the mouth of the Beagle Channel (30-100 m depth), Thatje *et al.* (2003) recorded mean abundances of Bryozoa, Cirripedia, Bivalvia, and Polychaeta which were higher than those found in the present study. Defren-Janson *et al.* (1999) and Thatje *et al.* (2003) obtained zooplankton samples through vertical hauls from the seafloor to the surface. Thatje *et al.* (2003) observed a high diversity of decapod larvae (17 taxa) and a great variability in abundance (7-12,300 ind.m^{-3}). Lovrich (1999) found five taxa with an average density ranging between less than 10 and almost 100 ind 10 m^{-3} in samples collected from bottom to surface in the Beagle Channel (i.e. including BU and BG) during January. We found only one type of decapod larvae at Stn. 2 (BU) but with a similar density (8 ind m^{-3}). These abundance-diversity differences may be due to the type and date of sampling.

In the two bays, the station groups defined by cluster analysis may reflect different environment conditions and water quality. In BU, G1 was distributed in an area relatively more external and apparently with less anthropogenic influence. Conversely, G2 was located in a port area that receives effluents with a high organic content (Esteves *et al.*, 2003). The mesozooplankton assemblages found in this bay correspond basically to the following two types: a) those that include the majority of holoplanktonic taxa with either highest or lowest abundance (A and D), and b) those that group meroplankton and tychoplankton (B and C) that characterise G1 and G2 respectively. In BG, G1 was located in a slightly more external area than G2. It could be under the influence of both Río Pipo (Stn. 1) and the area adjacent to the Beagle Channel (Stn. 2). Group 2 (Stn. 3) was distributed near *Macrocystis* (kelp), which would favour the presence of harpacticoid copepods. Although the assemblages found in BG share some taxa with those of BU, they are different in composition and abundance. However, in both bays, mesozooplankton assemblages from zones with or without anthropogenic influence show a certain resemblance.

The taxa recorded in the present study are, in general, indicative of sub-Antarctic and Antarctic coastal waters of South America (Pallares, 1968; Boltovskoy, 1981; Schnack-Schiel and Mujica, 1994; Mazzocchi *et al.*, 1995; Bradford-Grieve *et al.*, 1999; Thatje *et al.*, 2003). Among the 15 copepod taxa found (developmental stages of Calanoida not included), *A. tonsa*, *P. parvus*, *C. brachiatus*, *C. australis*, *C. brevipes*, *T. varians*, *H. furcatus*, Harpactocoida spp., and Monstrilloida spp. are described from the sub-Antarctic to the Tropical neritic domain (e.g. Pallares, 1968; Ramírez, 1969, 1970, 1971; Björnberg, 1981; Mazzocchi *et al.*, 1995; Boltovskoy, 1999). *Drepanopus forcipatus* has been cited by Mazzocchi *et al.* (1995) for the Magellan Straits, but this species is distributed not only on the southern Argentinean and Chilean shelves in the Atlantic and Pacific oceans respectively, but also within a small area around South Georgia Island (Heron and Bowman, 1971; Hülsemann, 1985; Sabatini *et al.*, 2001). The copepod *Eurytemora americana,* typical of the estuaries and coasts of the northern hemisphere (Heron, 1964; Kos, 1977; Miller, 1983), probably develops a short planktonic pulse in these bays during summer. This species, which is considered accidentally introduced in ballast water, was previously detected in Bahía Blanca estuary with a temperature range from 8-9 to 16-17°C during its planktonic pulse (Hoffmeyer *et al.*, 2000; Hoffmeyer, 2004).

Our findings of the presence of *O. similis*, *C. citer*, and *O. curvata* in BU and BG agree with those of Mazzocchi *et al.* (1995), who recorded these species in the Magellan Straits. Among the copepods found in our study, the above-mentioned species are the only ones found in both the Antarctic and sub-Antarctic domains. In the Antarctic region, these small sized copepods are distributed in oceanic areas down to 1000 m depth as well as in coastal ones (Atkinson and Peck, 1988; Metz, 1996; Atkinson and Sinclair, 2000), although *O. similis* prefers the upper 200 m (Schnack *et al.*, 1985). They are important because of their high density and biomass and their trophic role within the system (Fransz and González, 1995; Metz, 1995; 1996; Atkinson and Sinclair, 2000). *Oithona similis* extends from the Antarctic (e.g. Schnack *et al.*, 1985; Zmijewska, 1988) to tropical domains (Ramírez, 1970a, b; 1971; Mazzocchi *et al.*, 1995; Bradford-Grieve *et. al*, 1999; Marrari *et al.,* 2004). On the other hand, *C. citer* and *O. curvata* only extend from Antarctic (Hopkins, 1985; Montú and Oliveira, 1986) to southern sub-Antarctic waters (Mazzocchi *et al.*, 1995). It is important to note that the latter author found more Antarctic copepod species in the Straits of Magellan, which were not observed in our study. This could be because we sampled only the upper 5 m of the water column.

Due to the numerical importance of copepods, we compared their occurrence and abundance in BU and BG with those reported from some Antarctic coastal sites. We used Elwers and Dahms' (1998) data collected from Potter Cove (King George Island, South Shetland Islands), Chognacki and Weglenska´s (1984) data collected from Ezcurra inlet, Admiralty Bay (South Shetland Islands), and Hoffmeyer and Schiel's (unpubl. data) data collected at coastal stations of the Antarctic Peninsula and the Shetland Islands (between 62-64°S and 58-63°W). It is evident that most of the species recorded are restricted to the Antarctic domain (Table 4). However, *O. similis* and either *O. curvata* or *Oncaea* spp. are present at all the sites considered in the present survey. *C. citer* and Harpacticoida spp. also occurred at all the sites except for Ezcurra Inlet and Potter Cove. *O. similis* abundance in BU and BG (Beagle Channel) is similar to that found in Potter Cove, and is higher than that at the other sites. The highest abundance of *C. citer* occurs in BU and BG. *Oncaea curvata* shows, in BU and BG, values which are comparable with those of Potter Cove and which are lower than those off the Antarctic Peninsula and the South Shetland Islands. The wide distributional range of *O. similis*, *O. curvata* or *Oncaea* spp., and *C. citer* (40-70°S) is in agreement with Atkinson and Sinclair (2000), indicating that the Polar Front is not exactly a biogeographical barrier to them. Moreover, their highest concentrations have been found in the Polar Front area itself (Hopkins, 1971; Franz and Gonzales, 1997; Atkinson, 1998). Antezana (1999) also coincides with these authors, who claim that the presence of some Antarctic zooplankton groups in sub-Antarctic waters results from several mechanisms of seawater circulation. Conversely, Thatje and Fuentes (2003) detected the presence of two decapod crustacean larval morphotypes, Hippidae and Pinnotheridae, as well as the copepod genus *Acartia*, which are exclusively sub-Antarctic, in Antarctic waters (Maxwell Bay, sample taken on 28 March, 2002). These authors conclude that this phenomenon could be due to an intrusion of Subantarctic water masses into the Antarctic environment.

Though preliminary, the results from the present study are relevant considering the scarce knowledge on zooplankton in Bahía Ushuaia and Bahía Golondrina. On the other hand, the finding in these bays of *O. curvata*, *C. citer*, and *O. similis*, which are common species in the Antarctic, confirms our hypothesis that their distribution extends into sub-Antarctic waters. This finding, among others, together with the records of Thatje and Fuentes (2003), suggests the existence of an important pelagic exchange—in both directions—between the Antarctic and sub-Antarctic domains.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

The role of zooplankton in the pelagic-benthic coupling of the Southern Ocean*

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SUMMARY: Zooplankton contributes in different ways to pelagic-benthic coupling: Their faecal material is a major route of energy flow and the vertical migrations of many species as well as the production of pelagic larvae by benthic organisms represent different paths to link the two subsystems. Antarctic particle fluxes have been shown to be highly variable in size and composition within a given region and even at the same site from year to year. There are also differences throughout the water column, where particle fluxes close to the sea floor beyond the continental shelf break do not normally show seasonal variation within shallow environments. Commonly, at depths shallower than 500 m, the most evident feature is that more than 90% of the annual fluxes occur during a short period of the spring-summer. This event is masked near the seabed at greater depths due to resupension and lateral advection of particles. Faecal material of various origins is one of the main constituents of the biogenic matter flux. It usually reaches its maximum in February once the early phytoplankton bloom has developed. However, the presence of faecal pellets is ubiquitous during the months of the year when there is enough light to support primary production. At this stage more research is needed to elucidate the particular role of distinct taxa—including among others salps, krill, copepods and protozoans—in the transport of organic matter to the benthos, and their contribution to the biogeochemical cycles of carbon, nitrogen, phosphorus and silicon. Aggregation of particles is another important process controlling the development and dynamics of pelagic-benthic coupling due to its influence on the sinking velocity of particles and the enhancement of organic matter utilisation by members of the microbial loop in the upper layers of the water column. Also in shallow waters, aggregation favours the transfer of high-quality organic matter to the benthic realm. At greater depths resuspended aggregates and single particles from shallow environments may constitute a considerable fraction of the "fresh" biogenic flux. Submarine canyons accelerate and cause more efficient transfer of energy to the deep-sea benthos. Both faecal pellets and aggregation increase the original sinking velocity of individual particles and reduce their residence time in the water column, thus creating rich organic mats over the seabed in shallow environments. In the Southern Ocean these rapid organic matter transfers are important since they allow the accumulation of highly nutritive material, which may fuel the benthos during the dark months due to constant resuspension by tidal currents. Several factors control the particle fluxes in the Southern Ocean, such as size and composition of phytoplankton blooms, currents, seasonality, depth, and ice coverage. Due to this complexity, despite many efforts there is still a long way to go before the pathway of this ecologically important link can be fully understood and described. Our knowledge of the pelagic-benthic coupling in the Magellan region is still extremely limited and offers many opportunities for future scientific research. The same holds true for the production of meroplanktonic larvae in the Southern Ocean.

Keywords: particle flux, faecal pellets, vertical migration, meroplankton, pelagic-benthic coupling.

RESUMEN: El zooplancton contribuye de diferentes maneras al acoplamiento pelago-béntico: El hundimiento de su material fecal representa un flujo de energía muy importante y las migraciones verticales de muchas especies así como la producción de larvas pelágicas por organismos bénticos son dos ejemplos de conexión entre ambos subsistemas. En la Antártida, se ha detectado que los flujos de partículas varían en magnitud y composición dentro de una región e incluso en el mismo sitio entre año y año. También hay diferencias a lo largo de la columna de agua siendo que, generalmente, los flujos cerca del fondo marino más allá de la plataforma continental no presentan la variación temporal medida en ambientes más someros. Comúnmente, a profundidades menores a 500 m, la característica más evidente es que más del 90% del total del flujo anual de par-

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tículas ocurre durante un período corto de la temporada primavera-verano. Cerca del lecho marino este evento queda enmascarado debido a la resuspensión y el aporte lateral. El material fecal es uno de los constituyentes principales del flujo de material biogénico. Generalmente alcanza el valor máximo en Febrero, cuando el florecimiento temprano de fitoplancton se ha desarrollado. Sin embargo, los paquetes fecales son omnipresentes durante los meses del año en que hay luz suficiente para mantener la producción primaria. En este punto, se necesita intensificar la investigación para identificar la importancia de cada grupo taxonómico, por ejemplo, salpas, krill, copépodos y protozoarios, en el transporte de material orgánico al bentos y su participación en los ciclos biogeoquímicos del carbono, nitrógeno, fósforo y sílice. La adsorción de partículas es otro mecanismo importante en el control del desarrollo y la dinámica del acoplamiento pelago-béntico debido a la influencia que ejerce sobre la velocidad de hundimiento de las partículas y la utilización de la materia orgánica por los miembros de la comunidad microbiana en las capas superiores de la columna de agua. La adsorción de partículas en aguas someras también favorece la transferencia de material orgánico con buena calidad nutritiva al ambiente béntico. Paralelamente, los cañones submarinos aceleran y hacen más eficiente el transporte de energía al bentos del mar profundo. A mayor profundidad, la resuspensión de agregados y partículas individuales provenientes de ambientes someros puede constituir una fracción considerable del flujo de material biogénico "fresco". Los paquetes fecales y la adsorción de partículas aumentan la velocidad original de hundimiento de partículas individuales y reducen su tiempo de residencia en la columna de agua, creando en ambientes someros alfombras ricas en material orgánico sobre el lecho marino. En el Océano Austral la transferencia rápida de material orgánico al fondo del mar es especialmente importante ya que permite la acumulación de material orgánico con alto contenido nutritivo que servirá para alimentar al bentos durante los meses de oscuridad gracias a la resuspensión constante por corrientes de marea. Varios factores controlan el flujo de partículas en el Océano Austral, por ejemplo, el tamaño y la composición de las proliferaciones de fitoplancton, las corrientes, la variación estacional y la profundidad y la extensión del área cubierta por hielo. Esta complejidad hace que, a pesar de muchos esfuerzos, aún quede mucho por estudiar para conocer completamente las rutas de este importante vínculo ecológico. Nuestro conocimiento del acoplamiento pelago-béntico en la región del Estrecho de Magallanes es aún extremadamente limitado por lo que este tema ofrece productivas oportunidades de investigación, lo mismo es válido para la producción de larvas meroplanctónicas en el Océano Austral.

Palabras clave: flujos de partículas, paquetes fecales, migración vertical, meroplancton, acoplamiento pelago-béntico.

INTRODUCTION

The knowledge of the vertical flux of particulate material from the euphotic zone and its chemical and taxonomic composition is essential for the understanding of marine biogeochemical cycles. This pelagic-benthic coupling is a major route for energy flow. Zooplankton play a major role within the pelagic-benthic coupling, contributing in various ways to the energy flow, as their nitrogenous excretion is a major source of nutrients for algal growth and their faecal material, carcasses and exuvia sink and settle onto the seabed. Many holoplankton organisms perform diel and ontogenetic migrations covering the whole water column, connecting sea surface and sea bottom. Due to a downward migration, these species may come close to the sediment and provide a food source for benthic invertebrates. Benthic organisms often reproduce via planktonic larvae (meroplankton), which may seasonally contribute in high abundances to the zooplankton community.

Particle flux

Between <10 and 70% of the primary production of the euphotic layer reaches the benthic realm, depending on the region and the time of the year (Hargrave, 1973; Joint and Morris, 1982). A strong correlation between sedimentation of phytoplankton and benthic macro-faunal biomass/production has been observed worldwide (Joint and Morris, 1982; Billet *et al.*, 1983; Smetacek, 1984; Albertelli *et al.*, 1998; Gili *et al.*, 2001). However, sedimentation of phytoplankton cells is a complex process, and interactions between the pelagic and benthic systems are related to hydrographical and biological controls (Smetacek, 1984). The hydrographical controls are determined by the local wind, current regime, lateral advection and resuspension (Wassmann, 1984; Leventer and Dunbar, 1987; Jaeger *et al.*, 1996; Baldwin *et al.*, 1998; Dunbar *et al.*, 1998; Isla *et al.*, 2001; Povero *et al.*, 2001; Palanques *et al.*, 2002a; Baldwin and Smith, 2003), and in polar seas also by the ice dynamics (Leventer and Dunbar, 1996, Dunbar *et al.*, 1998; Pusceddu *et al.*, 1999; Palanques *et al.*, 2002b). The biological factors influencing sedimentation are the sinking of individual cells (Billet *et al.*, 1983; Wassmann, 1984; Fukuchi *et al.*, 1988; Bathmann *et al.*, 1991), the formation of aggregates and marine snow (Fowler and Knauer, 1986; Riebesell *et al.*, 1991; Karl *et al.*, 1991; Smith *et al.*, 1999; Kiørboe, 2001) and grazing by herbivores such as euphausiids and salps, which result in the transportation of packed phytoplankton cells and organic debris via faecal pellets to deeper water layers (Bishop *et al.*, 1977; Brulander and Silver, 1981; Urrère and Knauer, 1981; Joint and Morris, 1982; Fowler and Knauer, 1986; Emerson and Roff, 1987; Noji *et al.*, 1991; Dagg *et al.*, 2003; Huiskin *et al.*, 2004). Faecal pellet quality varies among zooplankton species and this is reflected in the quality of organics exported from the euphotic layer. For example, the food is thoroughly shredded in

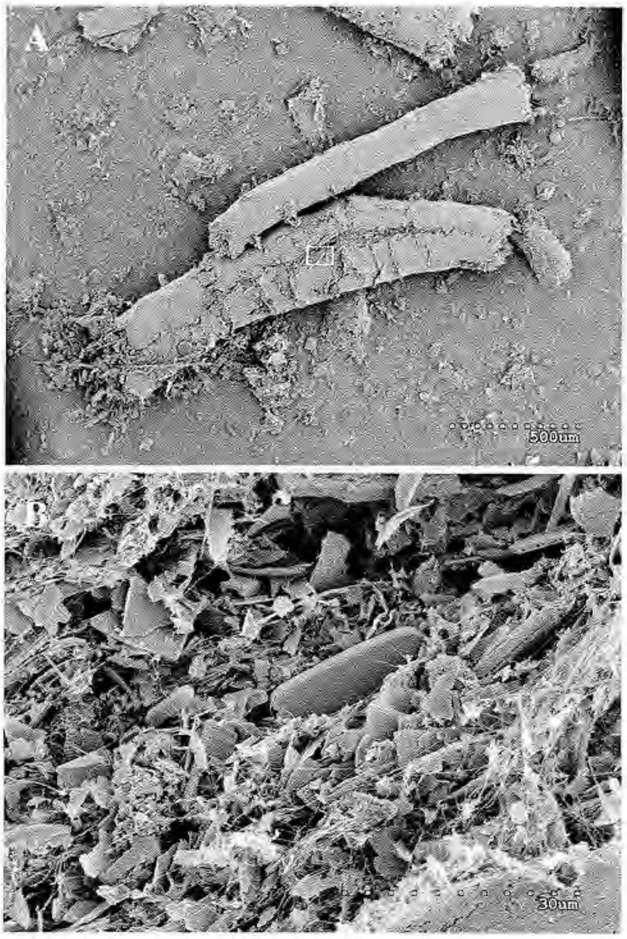

FIG. 1. – Scanning electron microscope images of faecal pellets collected with sediment traps, 30 metres above the bottom at 480 m depth on the eastern Weddell Sea shelf, showing, A) faecal pellets and B) empty diatom frustules and debris. The white rectangle in A corresponds to the area of image B.

euphausiids, and hence only a few intact phytoplankton cells and frustules occur in their faeces (Fig. 1). In contrast, numerous intact cells and unbroken frustules have been found in the faecal matter of salps (Peinert *et al.*, 1989), which presented C:N ratios close to the values of living phytoplankton (Bruland and Silver, 1981). Hence, salp faeces represent an important source of high quality food for the benthic realm. Faecal matter consists of both organic and inorganic material, which is more or less densely packaged and constitutes between <1% and almost 100% of the material collected with sediment traps (Urrère and Knauer, 1981; Bodungen *et al.*, 1987; Karl *et al.*, 1991; Accornero and Gowing, 2003). A reduced contribution of faecal pellets to settling material has been interpreted as the result of coprophagy, mechanical breakage and microbial attack (Paffenhöfer and Knowles, 1979; Turner and Ferrante, 1979; Hoffmann *et al.*, 1981; Noji *et al.*, 1991; Kiørboe, 2000). The role of attached prokaryotes converting large, rapidly sinking particles, into small, non-sinking particles of 0.3-0.6 μm was proposed by Cho and Azam (1988). It is now well established that zooplankton faecal pellets, especially those with small sizes, are grazed in the water column (Turner and Ferrante, 1979; Paffenhöfer and Knowles, 1979; Bishop *et al.*, 1980, Hoffmann *et al.*, 1981; Emerson and Roff, 1987; González and Smetacek, 1994). The sedimentation rate of the pellets depends on their content, shape, size, and the presence or absence of a peritrophic membrane (Cadée *et al.*, 1992). For example, the smaller the producers, the smaller the amount of pellets reaching the sea floor. Faecal pellets produced by larger zooplankton (such as euphausiids) sink rapidly throughout the water column (Komar *et al*, 1981; Lorenzen and Welschmeyer, 1983; Fowler and Knauer, 1986), and may exert a positive influence on the magnitude of benthic production. The arrival on the sea floor of faecal pellets with high nutritive value (e.g. rapid sinking pellets of salps) is welcomed by benthic organisms such as hydrozoans, corals and glass sponges, which feed directly on them and benefit from their organic contents (Orejas *et al.*, 2000; Duineveld *et al.*, 2004; Leys *et al.*, 2004).

The magnitude and pattern of biogenic export are considered to be related to the planktonic food web structure in the euphotic layer, i.e. by the size structure of primary production and the match/mismatch between primary production and grazing. Hence, when algal production and herbivorous consumption are in phase, most algal cells are packaged as faecal material before sinking out. On the other hand, when algal production and herbivore consumption are out of phase, a probably large proportion of algae sink directly to the ocean floor (Billet *et al.*, 1983; Legendre and Le Fèvre, 1989; Legendre and Rassoulzdegan 1996). In contrast, Rivkin *et al.* (1996) concluded from their studies in the Gulf of St. Lawrence that sedimentation processes are independent of the main trophic mode and are not related to the dominance of herbivorous or microbial trophic pathways. Fluxes of chlorophyll and mesozooplankton faecal pellets from the euphotic zone were 1 to 21 times greater and 2 to 6 times smaller during and after the phytoplankton bloom respectively. However, fluxes of POC and PON were similar in the two seasons. Thus, the POC fluxes were similar during the spring phytoplankton bloom, when herbivory dominated, and during postbloom conditions, when microbial and omnivorous food webs prevailed.

Water depth is another important controlling factor on the quality of biogenic particle fluxes. Vertical fluxes of particles throughout relatively shallow depths are exposed to short residence times in the water column, which results in them arriving at the seafloor in a relatively fresh condition (Isla *et al.*, 2001; Baldwin and Smith, 2003). Furthermore, the upper 100 m of the water column has been identified as an "aggregation" layer, whereas in the region below decomposition dominates biogenic particle transformation (Boyd *et al.*, 1999). Thus, due to the direct sinking of autotrophs, shallow areas receive rapid sedimentary pulses of high-quality organic matter. This scenario is mainly typical of the spring and summer periods with low standing stocks of zooplankton (Peinert *et al.*, 1989). Fluff layers derived from settled phytoplankton were also observed at deep-sea sites in all oceans where it also appeared to be a seasonal phenomenon (Beaulieu, 2002).

In polar seas the period of high primary productivity in the water column is short, and hence particle flux is characterised by high seasonality which displays an episodic signal including significant metabolic responses in benthic organisms (Matsuda *et al.*, 1990; Fabiano *et al.*, 1997). Much of the sedimented material seems to be utilised immediately by the large stocks of epibenthic suspension feeders (Gili *et al.*, 2001). However, deposits of phytodetritus on the shelves of the Weddell, Lazarev and Bellingshausen Seas indicate heavy sedimentation of phytoplankton largely unutilised by the benthos (Barthel, 1997; Gutt *et al.*, 1998; Isla *et al.*, unpubl.).

Vertical migration

Many zooplankton species perform daily vertical migrations, but in high latitudes seasonal or ontogenetic migrations are probably more important. Classically, during diel migration patterns the organisms migrate actively upwards from the deeper waters towards the surface layers at night when they feed, and they descend again to their daytime depths at dawn. The seasonal/ontogenetic migration pattern is characterised by the occurrence of different developmental stages at different depths in different seasons (reviewed by Longhurst, 1976). These vertical migration patterns are another example of pelagic-benthic coupling resulting in a downward transfer of organic material. On the one hand, faecal pellets are produced by migrants at depth from material gathered near the surface; on the other hand, the migrants become potential food for deeper living and benthic predators (Angel, 1989).

Meroplanktonic larvae

Pelagic-benthic coupling also occurs in the opposite direction, from the benthos to the pelagial via meroplanktonic larvae of benthic animals. Meroplanktonic larvae occur in many neritic parts of the oceans, at high latitudes. However, a general trend towards non-pelagic development and the predominance of brooding benthic species due to the unsecurity of prolonged larval life in the pelagial, where primary production is restricted to a short period each year, was assumed by Thorson (1950). This is known as "Thorson`s rule". The relative absence of pelagic larvae has been discussed extensively, and recently an increased number of benthic species with pelagic larvae have been identified. Some of these even have planktotrophic larvae, which raises doubts on the general validity of this rule. However, meroplanktonic larvae are still not as common in the Antarctic as would be expected from the high number of benthic species (reviewed by Arntz *et al.*, 1994; Arntz and Gili, 2001). In contrast to the Southern Ocean, high abundances of invertebrate larvae occur in the Magellan region (Antezana, 1999; Defren-Jason *et al.*, 1999; Thatje *et al.*, 2003).

PELAGIC-BENTHIC COUPLING IN THE ANTARCTIC PARTICLE FLUX

Modes of particle transportation

Phytoplankton material leaves the surface layers primarily as large aggregates or via sinking faecal pellets (Bodungen *et al.*, 1987; 1988; Wefer *et al.*, 1988; Leventer, 1991; Dunbar *et al.*, 1998, Smith and Dunbar, 1998; Frignani *et al.*, 2000; Anadón *et al.*, 2002; Accornero and Gowing, 2003). The exceptions include mass fallout of diatom cells (particularly *Thalassiosira antarctica*) from blooms in shallow coastal water (Bodungen *et al.*, 1986; Matsuda *et al.*, 1987; Fukuchi *et al.*, 1988; Handa *et al.*, 1992).

In the Southern Ocean, spring particulate matter that is transported from the surface into deeper waters consists mainly of material of phytoplanktonic origin, and high fluxes are commonly linked to the presence of marginal ice or post-bloom conditions (Bodungen *et al.*, 1986; Frignani *et al.*, 2000). During non-bloom conditions, downward fluxes are generally low and often made up of amorphous, unidentifiable material (Schnack, 1985; Anadón *et al.*, 2002). During this time of the year, material of zooplankton origin is seldom found in sediment traps, which probably mirrors the low density of zooplankton near the surface. Hence, this phytoplankton pulse occurs before the herbivorous zooplankton massively graze on the algal community, and represents a rapid, highly-rich organic matter transfer to the sea floor. In summer, faecal material of zooplankton seem to be the major vector for vertical transportation of particulate organic matter throughout the water column to the sea floor (Bodungen, 1986; Wefer *et al.*, 1988; Palanques *et al.*, 2002 a; b). Faeces of euphausiids in particular, and probably those of other large zooplankton such as salps, are important in summer, when they reach their highest concentrations. Local mass fluxes of faecal strings from krill have been observed during krill swarms (Bodungen, 1986; Bodungen *et al.*, 1987; Wefer *et al.*, 1988; Cadée, 1992). In the absence of krill swarms, the significance of small faeces increases (Bodungen *et al.*, 1988).

The faecal pellets of the various taxa differ in shape and size and are hence characteristic of each taxon. Different morphology types such as round, spherical, ellipsoidal, oval, cylindrical, triangular and elongated are recorded from trap material in the Southern Ocean. However, the producers of the various pellet types are not always easy to identify. Protozoans such as heterotrophic dinoflagellates and radiolarians are supposed to produce small round, ellipsoidal to spherical pellets (Nöthig and Bodungen, 1989; Buck *et al.*, 1990; González, 1992a;b; Thomas *et al.*, 2001). Ellipsoidal pellets are attributed to copepods (González *et al.*, 1994) and cylindrical pellets (also often called faecal strings) to euphausiids (Bodungen, 1986; Cadée *et al.*, 1992). However, the producers of many pellet types are still uncertain (see Accornero and Gowing, 2003).

The size of the pellets depends on the producer size, and hence pellets range in size from a few micrometres ("minipellets") produced by protozoans (3-50 μm) (Gowing and Silver, 1985; Nöthig and Bodungen, 1989; Buck *et al.*, 1990; González, 1992a) to several millimetres in length produced by large zooplankton organisms such as the Antarctic krill, *Euphausia superba*. Krill produce faeces as large as 660 μm in diameter and usually 1 to 5 mm in length (Marchant and Nash, 1986; González, 1992b).

Faecal pellets are found to be important contributors to the downward particle flux in all studied regions of the Southern Ocean and the highest contributions were observed during most periods of maximum sedimentation (Bodungen *et al.*, 1987; 1988; Fischer *et al.*, 1988; Dunbar *et al.*, 1998). Pellet contributions to carbon flux are reported to range from 4 to 59% in the Ross Sea (Accornero and Gowing, 2003) and up to 90% at the marginal ice zone in the Scotia Sea (Cadée *et al.*, 1992) and in the Bransfield Strait (Bodungen, 1986, Bodungen *et al.*, 1987; Wefer *et al.*, 1988). The high contributions in the latter two regions are attributed to the faecal strings of *Euphausia superba*, which were the most important carrier of particles.

The content of krill faecal strings is finely shredded and rarely contains intact cells (Bodungen, 1986; Gersonde and Wefer, 1987). According to Bodungen *et al.* (1987) and Wefer *et al.* (1988), the vertical flux was not related to phytoplankton standing stock and primary production, but to the abundance of krill. Krill swarms consume the majority of the phytoplankton in the upper water layers, and enhance the downward transport of biogenic particles such as diatom frustules also in addition to lithogenic particles in their large fast-sinking faecal strings. Hence, loss of organic matter from the illuminated surface layer is almost entirely mediated by krill. This is in sharp contrast to the Ross Sea, where faecal strings of euphausiids are only rarely found in trapped material (Dunbar *et al.*, 1989; Fabiano *et al.*, 1997; Asper and Smith, 1999; Langone *et al.*, 2000), coincident with the low abundances of krill (Dunbar *et al.*, 1998). High fluxes in the Ross Sea late in the season are carried out by the pteropod *Limacina helicina*, and the contribution of pteropod shells can reach nearly 50% of the total flux. The tests of the pteropods were mainly empty and were not considered to be "swimmers", which had actively migrated into the traps but directly settled after death (Dunbar, 1984; Collier *et al.*, 2000). It has been speculated by Gardner *et al.* (2000) that the reason for the crash could also have been the naked pteropod *Clione limacina*, which feeds specifically on *Limacina helicina*.

Similarly, Baldwin and Smith (2003) did not consider the highly abundant copepods during winter/early spring in the sedimented traps in Port Foster/Deception Island as "swimmers" due to the fact that they were partially decomposed. The high amount of copepods in the traps coincided with a change in the pelagic community. King and LaCasella (2003) and Kaufmann *et al.* (2003) observed an anomalous increase in the calanoid

TABLE 1. – Selected annual total flux data and occurrence of peak flux.

	Trap depth (m)	Total flux g m^{-2} yr^{-1}	Peak flux		Reference
			month	% of total	
Oceanic					
Polar Front (Atlantic)	700	38.3	Jan-Feb	89	Wefer and Fischer (1991)
Maud Rise (Atlantic)	4456	7.9	Feb-May	59	Wefer *et al.* (1990)
	360	33.7	Jan-May	91	Wefer and Fischer (1991)
Northern Weddell Sea (Atlantic)	863	0.4	Feb-Mar	90	Fischer *et al.* (1988)
Polar Frontal Zone (Pacific)	982	33.5	Dec-Jan	64	Honjo *et al.* (2000)
Antarctic Polar Front (Pacific)	1003	56.9	Nov-Mar	93	Honjo *et al.* (2000)
Antarctic Circumpolar Current (Pacific)	1031	80.6	Nov-Mar	90	Honjo *et al.* (2000)
Ross Gyre, Antarctic Zone (Pacific)	937	27.6	Jan-Feb	83	Honjo *et al.* (2000)
Neritic					
King George I., Bransfield Strait (Atlantic)	494	120.0	Jan	77	Wefer *et al.* (1988)
	1588	107.7	Dec-Jan	97	Wefer *et al.* (1988)
	693	11.9	Dec	96	Wefer *et al.* (1990)
	687	36.6	Nov-Dec	95	Wefer *et al.* (1990)
Livingston I., Bransfield Strait (Atlantic)	500	4.1	Nov-Jan	99	Palanques *et al.* (2002a;b)
	1000	1326.0	Aug-Sep	25	Palanques *et al.* (2002a;b)
Joides Basin, Ross Sea (Pacific)	211	3.9	Jan	99	Langone *et al.* (2000)
	540	30.0	Dec-Feb	88	Langone *et al.* (2000)
Joides Bay, Ross Sea (Pacific)	200	16.7	Mar-Apr	51	Collier *et al.*(2000)
Southcentral Ross Sea (Pacific)	206	33.2	Feb-May	92	Collier *et al.*(2000)
	481	84.5	Jan-Jun	90	Collier *et al.*(2000)
	465	69.3	Feb-Jun	90	Collier *et al.*(2000)
Southwestern Ross Sea (Pacific)	230		Feb	96	Dunbar *et al.* (1998)
	719		Jan-Mar	72	Dunbar *et al.* (1998)
Central Ross Sea (Pacific)	230		Feb-Mar	86	Dunbar *et al.* (1998)
	519		Feb-Mar	80	Dunbar *et al.* (1998)
Northwestern Sea (Pacific)	230		Feb-Mar	85	Dunbar *et al.* (1998)
	493		Jan-Mar	84	Dunbar *et al.* (1998)

copepod *Metridia gerlachei* as well as of the predatory ctenophore *Callianira* spp. Hence, the crash of the copepod population was coincident with the occurrence of the predator. However, metazooplankton remains such as carcasses and moults are only rarely recorded in sediment trap material (Angel, 1984). This is probably due to their rapid degradation (Small and Fowler, 1973) or ingestion before reaching greater depth (Fowler and Knauer, 1986). Yet another reason could be that they are perhaps produced by deep water animals (Wishner, 1980) dwelling just over the traps (Honjo *et al.*, 1982).

The planktic foraminifer *Neogloboquadrina pachyderma* is also reported from sedimented material in various Southern Ocean regions, including ice-covered areas, and accounts for most of the calcium carbonate flux (Fukuchi and Sasaki, 1981; Wefer *et al.*, 1982; Bodungen *et al.*, 1986; Wefer *et al.*, 1990; Wefer and Fischer, 1991; Collier *et al.*, 2000; Langone *et al.*, 2000).

Annual particle flux

Long-term time-series sediment trap studies have shown that particle flux is related to biological processes in the surface layer. Total annual flux rates in offshore areas in the Southern Ocean vary greatly between sites (Table 1). The lowest annual particle flux (0.371 g m^{-2} yr^{-1}) yet observed in the world ocean was found by Fischer *et al.* (1988) in 1985/86 in the north-central Weddell Sea at 863 m depth. About 80% of the total flux was biogenic opal, while 17% was organic matter. Slightly elongated faecal pellets of about 0.5 mm in diameter and of unknown origin played the most important role in the vertical transport of the material, and about 94,000 pellets m^{-2} yr^{-1} were counted (Wefer *et al.*, 1990). Diatom frustules were the major constituent of the pellets. Spring sea-ice thaw events rather than the occurrence of larger open seas seemed to be responsible for the great seasonal variability of particle flux (Fischer *et al.*, 1988). Fluxes as high as 56.9 and 80.6 g m^{-2} yr^{-1} were observed in the oceanic region of the Antarctic Polar Front and the Antarctic Circumpolar Current respectively (Honjo *et al.*, 2000). The annual total flux in neritic regions of the Antarctic also shows a high variability (Table 1). In the deep but neritic Bransfield Strait, Antarctic Peninsula, sediment traps deployed in mid-water layers between 494 and 687 m depth south of King George Island recorded total annual values of 120 (1983/1984), 11.9 (1984/1985), and 36.6 g m^{-2} yr^{-1}

(1985/1986). Hence, the annual value was 3 to 10 times higher in 1984/1985 than in the other years (Wefer and Fischer, 1991). The annual flux of organic carbon varied between 7.7, 0.35 and 1.1 gC m^{-2} yr^{-1} in the respective years, and hence carbon was 7 to 22 times greater than the values in 1983/1984. However, the most striking feature in the Southern Ocean is that particle export is characterised by high seasonality and is restricted to a short period of the year (Platt, 1979; Matsuda *et al.,* 1987; Fischer *et al.,* 1988; Wefer *et al.* 1988; Wefer and Fischer, 1991; Cripps and Clarke, 1998; Dunbar *et al.*, 1998; Accornero *et al.,* 1999; Collier *et al.*, 2000; Langone *et al.,* 2000; Palanques *et al.*, 2002 a; b).

Sedimentation is often confined to two to four months in the austral spring and summer when sea ice starts to melt and over 80% of the total annual flux occurs (Table 1). In the Ross Sea a time delay of 2 to 12 weeks between the ice retreat and the peak export of particles was observed (Dunbar *et al.*, 1998), whereas in the northern central Weddell Sea it lasted for 10 weeks (Fischer *et al.*, 1988).

During the winter, particle fluxes are extremely low under the ice-covered sea surface (Fischer *et al.*, 1988; Wefer *et al.*, 1990; Cripps and Clarke, 1998; Dunbar *et al.*, 1998; Accornero *et al.*, 1999; Collier *et al.*, 2000; Honjo *et al.*, 2000; Langone *et al.*, 2000). Contrastingly in the layer near the seabed, due to lateral advection and resuspension, total mass fluxes can be higher in winter than in summer (Berkman *et al.*, 1986; Palanques *et al.,* 2002a; b; Baldwin and Smith, 2003).

Daily flux rates

Short-term studies on flux rates, mainly carried out in austral spring and summer in neritic Antarctic regions, revealed daily flux rates ranging from approximately 10^2 to 10^3 mgC m^{-2} (Karl *et al.*, 1991). However, a high temporal and spatial variability in the amount and composition of trapped matter has been recorded throughout the Southern Ocean (Schnack, 1985; Bodungen *et al.*, 1986; Matsuda *et al.*, 1987; Bathmann *et al.*, 1991; Fischer *et al.*, 1991; Karl *et al.*, 1991; Nelson *et al.*, 1996; Dunbar *et al.*, 1998; Smith and Dunbar, 1998; Frignani *et al.*, 1999; Schloss *et al.*, 1999; Serret *et al.*, 2001).

Short-term sediment trap deployments at shallow depths in various coastal sites indicate that loss rates are generally low (Palanques *et al.*, 2002b). With a few exceptions, higher rates were found mainly when euphausiid faeces dominated trap collections (Schnack, 1985; Bodungen *et al.*, 1987; 1888; Cadée, 1992).

Spatial and temporal variability

Spatial differences were observed in many areas of the Southern Ocean. Intensive studies on particle flux carried out over several years in the Ross Sea have shown quite variable quantities and compositions among different sites and years (Leventer and Dunbar, 1996; Nelson *et al.,* 1996; Dunbar *et al.,* 1998; Smith and Dunbar, 1998; Asper and Smith, 1999; Collier *et al.,* 2000; Gardner *et al.,* 2000). Carbon flux is highest in the southwestern and southeastern-central Ross Sea (65.4 and 74.8 mgC m^{-2} day^{-1} respectively) and lowest in the northwestern part (8.2 mgC m^{-2} day^{-1}). In the southwest, tabular aggregates and faecal pellets accounted for 69% of the total mass flux at 230m depth, but only 11% at 719 m depth. The traps also included small ellipsoidal pellets (possibly from copepods), which on average represented 2% of the total flux. The traps at the northwestern site received the highest fluxes of diatom tests, which were dominated by the pennate diatoms *Fragilariopsis curta* and *F. cylindrus*. In the southeastern-central Ross Sea, pellets and aggregates represented a much smaller percentage of the total mass flux (38 and 4% at 230 and 519 m depth respectively). Small ellipsoidal faecal pellets accounted for less than 3%. Algal diversity was very high, with high numbers of the prymnesiophyte *Phaeocystis*, dinoflagellates and the diatoms *Fragilariopsis* and *Thalassiosira*. In the northern Ross Sea large tabular aggregates and pellets represented the smallest percentage of all sites (<15%). Large cylindrical pellets, probably from euphausiids, were only observed there. Within the diatom flux, *F. curta* comprised >70% (Jaeger *et al.*, 1996; Leventer and Dunbar, 1996; Nelson *et al.*, 1996; Dunbar *et al.*, 1998).

The Gerlache Strait at the Antarctic Peninsula seems to be an area of higher spring-summer sedimentation than other Antarctic regions. Serret *et al.* (2001) and Anadón *et al.* (2002) observed a high carbon export in the high chlorophyll, diatom-dominated Gerlache Strait (390-800 mgC m^{-2} d^{-1}) as compared with the low chlorophyll, microflagellate-dominated Bransfield Strait and Drake Passage (115-237 mgC m^{-2} d^{-1}). At low-chlorophyll stations dominated by flagellates, the sediment trap samples consisted mainly of unidentified amorphous material, while at high-chlorophyll stations dominated by diatoms the sediment trap samples showed a large amount of diatoms and euphausiid faeces. The number of faecal pellets varied extremely between stations: 0 - 0.2 x 10^6 m^{-2} d^{-1} at low-chlorophyll stations and between 0.2 and 1.3 x 10^6 m^{-2} d^{-1} at high-chlorophyll stations (Anandón *et al.*, 2002). However, despite the marked differences in phytoplankton biomass and species composition no differences in the calculated phytoplankton biomass growth and loss rates were observed between regions (Serret *et al.*, 2001; Anadón *et al.*, 2002). Hence, no significant differences in daily loss rates occurred between high- and low-chlorophyll *a* stations, which support the idea of Rivkin *et al.* (1996) that sedimentation processes are independent of the main trophic mode.

In the same region, spatial and temporal differences were observed by Karl *et al.* (1991) from December 1986 to March 1987, when a nearly constant downward flux of particulate matter was found in shallow waters off Livingston and Low islands (Bransfield Strait) and in deep waters of the Drake Passage, with POC and PON fluxes varying by a factor of <3. In contrast, two stations, one in a deep basin in the central Bransfield Strait and the other in coastal waters of the Gerlache Strait, both with a significant phytoplankton bloom followed by the coupled cessation of particle production and flux, showed a marked seasonal variation of 1-2 orders of magnitude. The highest flux was recorded in January and very low values in March. Resting spores of *Chaetoceros* dominated the sediment trap samples at all stations except in the Drake Passage, where *Nitzschia kerguelensis*, characteristic of the Antarctic circumpolar current, was most abundant (Leventer, 1991). The high-phytoplankton-bloom stations contained substantial amounts of faecal pellets, mostly from krill, indicating grazing activities (Karl *et al.*, 1991). However, seasonally integrated total mass fluxes were essentially identical for the entire four months of observations at all five stations, and hence the overall flux over the region seems to be similar despite the substantial differences in primary production in the euphotic layer. One consequence of these differences in the seasonal particle flux patterns is that the benthic habitats would receive a more well-defined and more concentrated pulse of organic matter, which may influence the timing of reproduction and growth of benthic organisms.

Relatively high daily sedimentation rates were recorded on the eastern shelf of the Weddell Sea in January-February 1985 (18 and 135 mgC m^{-2} d^{-1}, Bodungen *et al.*, 1988) and in the same months in 1988 (3 and 112 mgC m^{-2} d^{-1}, Bathmann *et al.*, 1991). In 1985, the sediment trap samples were dominated by faecal material of different origin, and the most abundant pellets were round, ellipsoidal or triangular (Nöthig and Bodungen, 1989). Two size classes of faecal pellets were encountered. The smallest (<150 μm) ranged from 9 to 8,600 x 10^3 m^{-2} d^{-1}, constituting between 50 and 99% of the total faeces settled in the traps, and were supposedly produced by protozoans (ciliates, radiolarians, heterotrophic dinoflagellates and foraminifers). The largest (>150 μm) (2 to 252 x 10^3 m^{-2} d^{-1}) were nearly round and represented a mean of 64% by volume of the vertical pellet flux. These pellets were of unknown origin but were probably produced by metazoans. All faecal pellets were filled with intact but empty diatom frustules. Copepod faecal pellets occurred rarely but steadily in the traps, whereas krill faeces were only occasional. However, daily vertical fluxes were highest where krill faeces were present in the traps (Bodungen *et al.*, 1988). Bathmann *et al.* (1991) observed three distinct sedimentation pulses in 1988. Empty diatoms and small faecal pellets were most numerous during the first pulse, but krill faeces packed with ice-associated diatoms contributed about 64% of the sedimented carbon. This indicates heavy grazing of krill in the vicinity of sea ice in mid-January. The second pulse in early February consisted again of round pellets together with minipellets, small planktonic aggregates containing many empty diatom frustules. This change in composition is assumed to be induced by Warm Deep Water sweeping onto the shelf resulting in unfavourable growing conditions for diatoms (Bathmann *et al.*, 1991). Large full cells of *Corethron criophilum* were the dominants of the third pulse. *C. criophilum* also dominated the greenish-grey fluff observed during box core studies at 600 m depth in a trough on the eastern shelf of the Weddell Sea in February 1996, and gave evidence of massive sedimentation events. However, the fluff consisted almost exclusively of frustules and only a few cells were still intact (Barthel, 1997).

Vertical variability

In shallow areas and mid-water depths most of the material collected in the traps during the spring and summer is of biogenic origin (Asper and Smith., 1999; Palanques *et al.*, 2002b). However, in deeper traps the lithogenic component can be extremely high due to lateral advection and resuspension

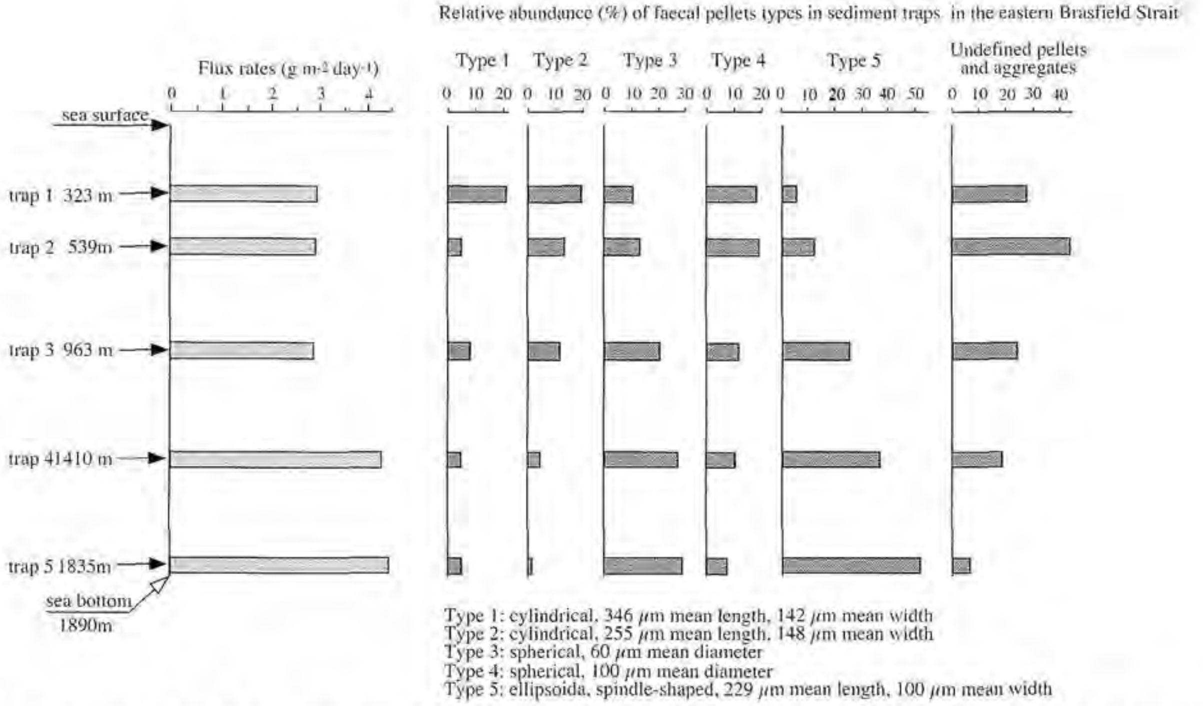

FIG. 2. – Flux rates (a) and relative abundance of different faecal pellets (b) in sediment traps in five different depths in November-≠December 1983 in the eastern Bransfield Strait (after Gersonde and Wefer, 1987).

(Platt, 1979; Domack and Mammome, 1993; Collier *et al.*, 2000; Langone *et al.*, 2000; Isla *et al.*, 2001; Palanques *et al.*, 2002a; b; Baldwin and Smith, 2003). The total mass flux in Johnson`s Dock, a shallow bay at Livingston Island with a water depth of 24 m, varied between 23,235 and 89,073 mg m^{-2} d^{-1} in a trap installed 4.5 m above bottom in summer 1997/1998, when lithogenic components accounted for more than 95% (Isla *et al.*, 2001). In Port Foster at Deception Island (water depth: 160 m), the flux increased in mid-winter, and was positively correlated with local wind speed. Lithogenic material was a major component found in the samples, showing the importance of wind-induced resuspension events on particle fluxes (Baldwin and Smith, 2003). The sedimentation in deeper waters seems to be more linked to the hydrodynamics of the area than to the production in surface waters (Frignani *et al.*, 2000).

In the Bransfield Strait south of Livingston Island in 1995-1996, a deep sediment trap installed at 1000 m (30 m above seafloor) recorded a 322 times higher annual total mass flux than that at 500 m depth during the same sampling period (1326 and 4.11 g m^{-2} yr^{-1} respectively). The near bottom flux was very high throughout the year (between 1178 and 5321 mg m^{-2} d^{-1}), without showing a seasonal signal as the shallower trap above it did. Mid-depth fluxes were largely biological and controlled mainly by settling of diatom frustules in spring or faecal material in summer, whereas near-bottom fluxes were mainly controlled by resuspension and lateral transport of material. It is important to mention that the deep trap collected several truly pelagic polychaetes such as *Tomopteris* sp. and *Pelagobia lonvirrata*, benthic diatoms (*Amphora*, *Cocconeis*, *Grammatophora*) and also littoral diatom species such as *Actinocylus actinochilus*, *Navicula directa*, *Thalasiosira antarctica*, and *Fragilariopsis kerguelensis*, indicating resuspension and lateral basinward transport (Palanques *et al.*, 2002a, b).

In the Bransfield Strait south of King George Island in 1983-1984 the total annual flux at 494 and 1588 m differed only slightly between the two depths (120 and 107.7 g m^{-2} yr^{-1}, and a distinct seasonal variability was evident in both depth strata (Wefer *et al.*, 1988). In short-term sediment trap deployments in December 1983, Gersonde and Wefer (1987) recorded vertical differences in the total flux but also in the composition of faecal pellets (Fig. 2). The total mass flux ranged between 2.9 g m^{-2} d^{-1} at 323 m and 4.4 g m^{-2} d^{-1} at 1835 m. The higher flux at depth was caused by a strong admixture of resuspended lithogenic material. The estimated pellet flux was 4 x 10^{5} pellets m^{-2} d^{-1} in the upper trap at 323 m, and 6 x 10^{5} pellets m^{-2} d^{-1} in the two lower traps at 1410 and 1835 m. Cylindrical pellets decreased with depth, while the total number of faecal pellets increased with depth (Fig. 2).

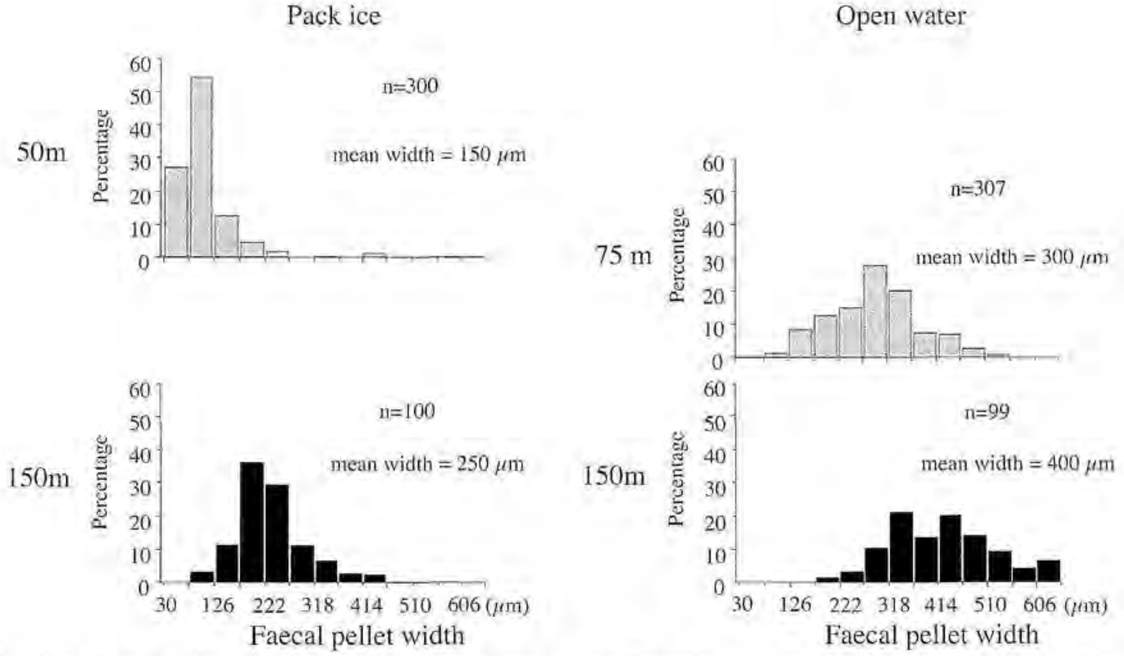

FIG. 3. – Size of krill faecal strings in shallow and deep sediment traps in December 1988 under ice cover (a) and in the melting ice zone (b) (after Cadée *et al.*, 1992).

Diatom frustules in the different faeces were finely shredded into small particles of 1 to 10 μm. Disintegration seems to be most pronounced between 300 and 1000 m water depth. Thus, mid-water bacterial breakdown of faecal material may be largely enhanced (Gersonde and Wefer, 1987). In situ repackaging by zooplankton feeding in deeper water, as described by Urrère and Knauer (1981), may lead to a modification of sinking faeces, originally occurring in the upper part of the water column. Evidence of this process in the Bransfield Strait is the increased flux of densely packed, ellipsoidal faecal pellets collected in the deeper traps. The apparent decrease with depth of krill faeces within the carbon flux could be explained by the combined effect of these processes.

Differences in pellet numbers and the length of krill strings in two depth layers were found in the Weddell-Scotia Confluence west of the South Orkney Islands in November-December 1988 (Cadée *et al.*, 1992). The krill strings were larger in the deeper trap at 150 m than in the shallower one (Fig. 3), indicating that the smallest strings do not leave the upper mixed layer. Besides size, zooplankton diet and pellet shape also seem to influence the vertical distribution and settling velocity of faeces. The highest settling velocities were observed when krill mainly fed on diatoms, whereas after feeding on flagellates the settling velocity decreased (Cadée *et al.*, 1992). Krill strings occurred in higher numbers in shallow traps (116-220 strings m^{-2} d^{-1} at 50-75 m depth) than in deeper ones (45 to 205 strings m^{-2} d^{-1} at 150 m depth); contrastingly, small oval pellets of unknown origin found in trap material occurred in greater numbers in deeper layers (4-90 and 110-270 pellets m^{-2} d^{-1} respectively). This is probably due to higher compaction and lower resistance to sinking of the oval pellets (Cadée *et al.*, 1992).

Particle flux from sea ice

The number of organisms living in the sea ice may exceed that in the water column, and ice algae blooms increase the biomass in the sea ice considerably before primary production in the open water starts (Lizotte, 2003; Schnack-Schiel, 2003 as reviews). However, the role of sea ice within the pelagic-benthic coupling has rarely been studied (Fukuchi and Sasaki, 1981; Matsuda *et al.*, 1987; Dunbar *et al.*, 1989; Pusceddu *et al.*, 1999; Thomas *et al.*, 2001). Ice algae tend to form aggregates, whose sinking rates are three orders of magnitude higher than those of dispersed ice algae, and hence they contribute greatly to the vertical flux (Riebesell *et al.*, 1991). In the eastern Weddell Sea, sedimentation of ice algae on the continental shelf (<500m depth) directly from the sea ice represent an important organic matter flux to the benthic realm during the austral spring and summer (Isla *et al.*, unpubl.). This phytoplankton pulse occurs before the herbivorous zooplankton massively graze on the algal community and represents a rapid, rich organic matter transfer to the sea floor.

Later in season, in February 1998, the settled material collected under a well-developed platelet ice layer in Drescher Inlet in the Riiser Larsen ice shelf, eastern Weddell Sea, was predominantly composed of faecal pellets (Thomas *et al.*, 2001). The sediment traps were deployed at 10 m (just under the platelet layer), 115 m (above the thermocline), 230 m (below the thermocline) and 360 m (close to the sea floor). The highest fluxes of faecal pellets but also of chlorophyll *a* and phaeopigments were collected at 230 m, just below the thermocline. POC occurred in higher amounts in the traps at both sides of the thermocline (Fig. 4). The faecal pellets were of undefined shape or very compact spherical pellets. More than 50% of the pellets in all traps were smaller than 97 μm in diameter and were probably produced by protists. The bottom trap had the greatest proportion of large pellets, and up to 20% of the pellets were more than 244 μm in diameter. They were probably produced by amphipods, which were collected in the traps at all depths together with calanoid and cyclopoid copepods. Regardless of the size of the faecal pellets, the contents were almost exclusively frustules of the ice-diatom genus *Fragilariopsis*, and mostly *F. cylindrus* and *F. curta*. Most striking was that the diatoms were largely intact and often in chains several cells long (Thomas *et al.*, 2001).

VERTICAL MIGRATION OF ZOOPLANKTON

Diel vertical migration is known for e.g. the Antarctic copepod *Metridia gerlachei* (e.g. Rudyakov and Voronina, 1974; Lopez and Huntley, 1995; Hernández-Léon *et al.*, 2001; King and LaCasella, 2003) and the euphausiids *Euphausia superba* and *E. crystallorophias* (e.g. Siegel and Kalinowsli, 1994; Hernández-Léon *et al.*, 2001; Kaufmann *et al.*, 2003). Krill aggregations were found close to the seafloor (<2 m) at 400-500 m depth in the eastern Weddell Sea shelf in January 1988 (Gutt and Siegel, 1994). This epibenthic behaviour was also observed in shallow waters (40 m depth) of Lützow-Holm Bay where krill were feeding on detrital matter on the seabed, and was suggested to be an overwintering strategy of *E. superba* (Kawaguchi *et al.*, 1986). Overwintering in deep water layers is also known for other Antarctic zooplankton species (Smith and Schnack-Schiel, 1990). Seasonal downward migrating species may arrive close to the bottom to hibernate and provide a rich, seasonally predictable food source for benthic invertebrates. For example, the copepod *Calanoides acutus*, which undergoes such ontogenetic seasonal vertical migrations, was found in higher numbers in the guts of the echinoderm *Astrotoma agassizii* later in summer on the eastern shelf of the Weddell Sea (Fig. 5, Dahm, 1994), and salp *Salpa thompsoni* of 1 to 5 cm in length were found in the stomachs of the anthozoan *Anthomastus bathyproctus* in summer off the Antarctic Peninsula (Orejas *et al.*, 2001).

PLANKTONIC LARVAE (MEROPLANKTON) OF BENTHIC ORGANISMS

Arntz *et al.* (1994) and Arntz and Gili (2001) summarised 20 meroplanktonic larvae types, eight as planktotrophic, four as lecitrophic and eight as not exactly known. Spawning of benthic organisms producing planktotrophic larvae, and hence feeding larvae, should be triggered by a seasonal control so the larvae appear at the same time as the phytoplankton bloom occurs, while species with

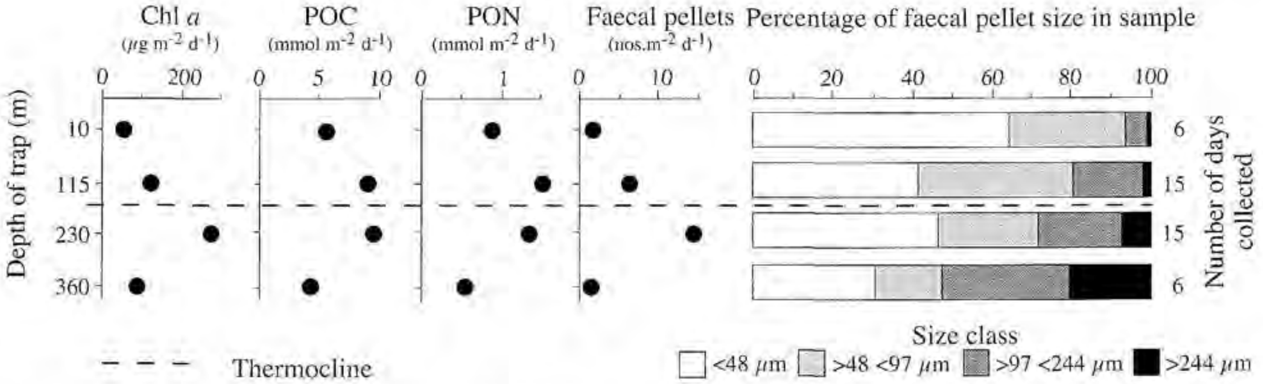

FIG. 4. – Chlorophyll *a*, particulate organic carbon (POC) and nitrogen (PON), and size distribution of faecal pellets in sediment traps in different depth layers in February 1998 under a platelet-ice layer/fast ice at Drescher Inlet in the eastern Weddell Sea (after Thomas *et al.* 2001).

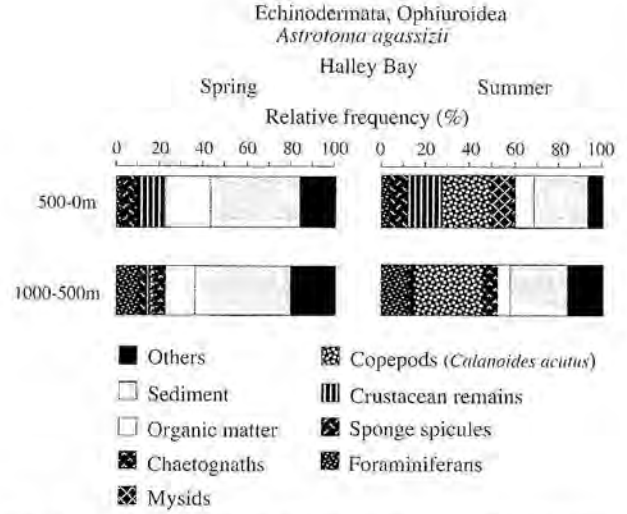

FIG. 5. – Relative abundance of food in the guts of the echinoderm *Astrotoma agassizii* in summer (after Dahm, 1994).

lecithotrophic larvae are weakly coupled to phytoplankton production. In shallow Antarctic waters, a relatively large number of planktotrophs occurs among the benthic species. Thus, it seems to be of advantage to have a dispersive larval phase in unstable environments with high disturbance conditions (Poulin *et al.*, 2002).

In McMurdo Sound, Pearse *et al.* (1991) yielded 12 meroplanktonic larvae within shallow-water asteroid, only two of which were brooders. However, only three of the larvae were feeding, whereas the others had pelagic lecithotrophic larvae. In the Bellingshausen Sea, 12 larvae types from seven phyla were described by Shreeve and Peck (1995). By far the highest number of different pelagic larval forms (131) was detected by Stanwell-Smith *et al.* (1999) in a two year study at Signy Island, Scotia Sea. However, the overall abundance of the larvae was very low compared to temperate and tropical areas. The number of larval types is low taking into account the great species richness in the Antarctic benthos (Clarke and Johnston, 2003). The meroplanktonic larvae occurred throughout the year but with different seasonal patterns (Fig. 6). Echinoderm and gastropod larvae occurred in the highest numbers in winter, mollusc and annelid larvae in summer. However, up to now the feeding mode is not known for most larvae. Hain and Arnaud (1992) studied the reproductive modes of 66 molluscan species in the Weddell Sea and observed planktotrophic or lecithotrophic larval stages in 27 bivalves. However, only two species of meroplanktonic gastropod larvae ("Echinospira" and "Limacosphaera" of the families Capulidae and Lamellariidae respectively) are relatively often found in plankton samples from the epipelagial (Boysen-Ennen, 1987; Piatkowski, 1987; Schiel, unpubl.). In contrast, the bivalve larvae seem to live demersally. Pelagic larval stages are also known from benthic shrimps (Boysen-Ennen, 1987; Piatkowski, 1987) and barnacles (Foster, 1989). Up to now only little is known about the duration of the meroplanktonic lavae in the pelagial. Decapod larvae seem to spend only an extremely short period in the water column, whereas Limacosphaera larvae can live for more than a year in the pelagial (Arntz and Gili, 2001).

A relatively well-studied species is the common bivalve *Adamussium colbecki*. The flux in summer induces relevant changes in body weight and gonad-somatic index of *A. colbecki* (Albertelli *et al.*, 1998). Hence, this species is able to take advantage of the short but intense food supply, storing energy for spawning. This species produces unprotected planktotrophic larvae, which feed in the water column (Berkman *et al.*, 1991).

PELAGIC-BENTHIC COUPLING IN THE MAGELLAN REGION

Our current knowledge of pelagic-benthic coupling in the Magellan region is extremely limited. Up to now there are only a few references to parti-

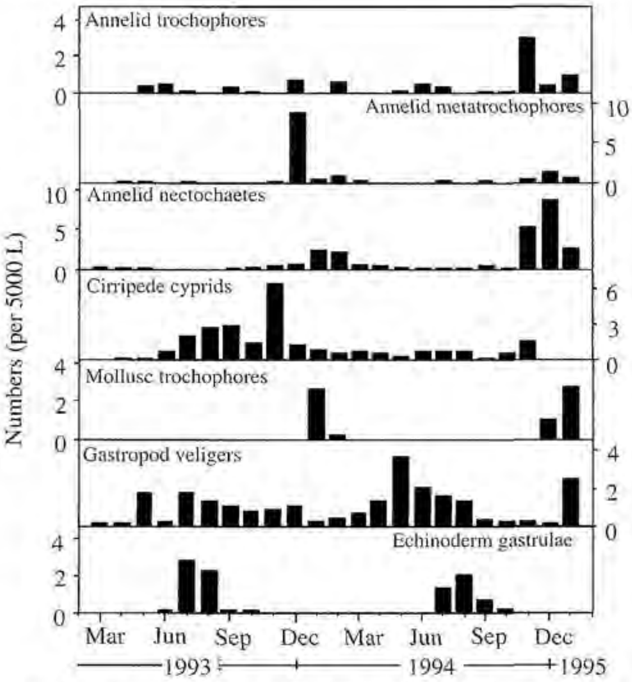

FIG. 6. – Abundance of selected larval groups at Signy Island in November 1992 to February 1995 (after Stanwell-Smith *et al.*, 1999).

cle flux in this region (see e.g. Antezana, 1999; Cattaneo-Vietti *et al.*, 1999). The hydrographic regime is very complex and shows great spatial variability in geomorphology, currents, temperature, salinity, phytoplankton biomass and production as well as in composition and origin of particulate organic matter (Hamamé and Antezana, 1999; Cattaneo-Vietti *et al.*, 1999). According to Antezana (1999), pelagic-benthic coupling is particularly important in the Magellan region, and a strong link between phytoplankton, vertical migrations of zooplankton and the benthos is evident. In spring the plankton is dominated by large diatoms, suggesting a short food chain, where most of the phytoplankon bloom may sink to the seafloor (Antezana, 1999). Greenish mats, which frequently cover the seafloor in spring indicate heavy sedimentation of phytodetritus largely unutilised by the benthos (Gutt and Schiekan, 1996). In summer, chlorophyll concentrations are much lower than in spring. Pico- and nanoplankton predominate and a more complex food web develops (Antezana, 1999). The few studies on benthic communities in this region show that the communities are poor and less structured than those in many parts of the Antarctic. Deposit feeders, scavengers and omnivores dominate (Cattaneo-Vietti *et al.*, 1999), whereas epibenthic suspension feeders are dominant in the high Antarctic (Brey and Gerdes, 1997; 1999). Cattaneo-Vietti *et al.* (1999) suggested that one reason may be the high inorganic material from glaciers in the Straits of Magellan, which can impede and damage the filtering structures of the suspension feeders. Despite previous efforts within the first IBMANT symposium in 1997, the study of benthic community differences between the high- and sub-Antarctic still offers a great opportunity to increase our knowledge in polar and particularly Antarctic ecology.

The euphausiid *Euphausia vallentini* is the most abundant krill in the Magellan region, where it is often found in dense swarms, performing intense vertical migrations between the upper 50 m and the stratum overlying the seabed (Guglielmo *et al.*, 1997). In comparison with the Antarctic krill, *Euphausis superba*, it is likely that the sinking of the faecal strings of *E. vallentini* contributes substantially to the vertical flux in this area. This species can also fuel carnivorous benthos organisms due to its vertical migrations.

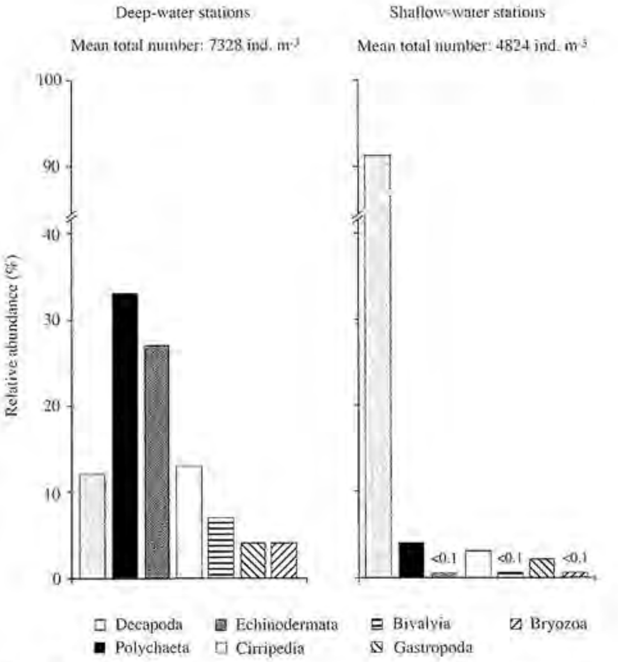

FIG. 7. – Relative abundance of meroplankton in the Magellan region in November 1994 (after Thatje *et al.*, 2003).

The amount of meroplanktonic larvae is much higher in the Magellan region than in the Antarctic. In the upper 50 m of the water column, meroplankton (mainly pluteus and zoea larvae) contributed numerically between 6 and 42% of the total zooplankton (Hamamé and Antezana, 1999). Thatje *et al.* (2003) observed differences between the deep-water stations south of the Straits of Magellan and shallow-water stations in the Beagle Channel. At the deep stations, the composition of the meroplankton was more heterogeneous and larvae of polychaetes and echinoderms were most abundant. In contrast, decapod larvae formed the bulk of the meroplankton at the shallow stations (Fig. 7). These high abundances of meroplanktonic larvae occurred in spring, and hence coincided with spring bloom conditions, which implies a strong pelagic-benthic coupling (Antezana, 1999).

CONCLUDING REMARKS

Pelagic-benthic coupling in the Southern Ocean is highly seasonal and most evident in the transport of energy within zooplankton faecal pellets. These particles and diatom aggregates transport most of the organic matter, which fuels the underlying benthos. However, there apparently exists much activity throughout the autumn-winter months, when benthic larval releases and resuspension may feed zooplankton migrating close to the seabed. Thus, zooplankton migrations strengthen the coupling between the two environments, emphasising the important role of zooplankton in the Southern Ocean pelagic-benthic coupling.

Sedimentation processes have received considerable attention in the Antarctic since the first IBMANT congress in 1997, and many investigations have been carried out in the Ross and Weddell Seas and west of the Antarctic Peninsula (Dunbar *et al.*, 1998; Pusceddu *et al.*, 1999; Isla *et al.*, 2001; Serret *et al*, 2001; Smith *et al.*, 2001; Thomas *et al.*, 2001; Anadón *et al.*, 2002; Palanques *et al.*, 2002a; b; Badwin and Smith, 2003). However, the role of zooplankton within the processes of pelagic-benthic coupling is not yet fully understood. The identification of faecal pellet material is still problematic, and should be improved to evaluate the contribution of dominant micro-, meso- and macrozooplankton taxa to the coupling between both environments.

More detailed sedimentation experiments should be conducted underneath different sea ice types (e.g. pack, fast, platelet) as well as underneath permanent ice cover. Very little is known about the quantitative importance of the microbial-microzooplankton food web in the Southern Ocean and the significance of these organisms for particle fluxes, pelagic-benthic coupling and marine biogeochemical cycles (already pointed out 20 years ago by Clarke, 1985).

Increasingly we are discovering that there are more planktonic larvae in Southern Ocean waters. This trend is likely to continue with the development of proper methods and better sampling gear such as pumps and nets handled by divers. Annual seasonal studies will also help to elucidate these issues. General studies on all aspects of pelagic-benthic coupling during different seasons are still required for the Magellan region.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Marine research in the Latitudinal Gradient Project along Victoria Land, Antarctica*

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SUMMARY: This paper describes the conceptual framework of the Latitudinal Gradient Project that is being implemented by the New Zealand, Italian and United States Antarctic programmes along Victoria Land, Antarctica, from 72°S to 86°S. The purpose of this interdisciplinary research project is to assess the dynamics and coupling of marine and terrestrial ecosystems in relation to global climate variability. Preliminary data about the research cruises from the R/V "Italica" and R/V "Tangaroa" along the Victoria Land Coast in 2004 are presented. As a global climate barometer, this research along Victoria Land provides a unique framework for assessing latitudinal shifts in 'sentinel' environmental transition zones, where climate changes have an amplified impact on the phases of water.

Keywords: Latitudinal Gradient Project, Victoria Land, Antarctic, global climate change, interdisciplinary cooperation.

RESUMEN: INVESTIGACIONES MARINAS A LO LARGO DE VICTORIA LAND. – Este trabajo describe el marco conceptual del proyecto "Gradiente latitudinal" que ha sido implementado por los programas antárticos de Nueva Zelanda, Italia y EE.UU. a lo largo de Victoria Land (Antártida), 72°S-86°S). El objetivo de este proyecto es evaluar la dinámica y el acoplamiento de ecosistemas marinos y terrestres con relación a los cambios climáticos globales. Se presenta información preliminar acerca de los cruceros científicos de los buques R/V "Italica" y "Tangaroa" a lo largo de la costa de Victoria Land en el año 2004. Como un barómetro climático global, esta investigación provee un marco de trabajo único para observar y evaluar cambios latitudinales en zonas de transición medioambiental, donde los cambios climáticos tienen un impacto amplificado en las fases del agua.

Palabras clave: Proyecto Gradiente Latitudinal, Victoria Land, Antártida, cambio climático global, cooperación interdisciplinaria.

INTRODUCTION

Coastal zones of continents and oceans—where terrestrial and marine ecosystems interact—are regions of high biological and physical diversity, which are generally heavily utilized by human populations. Distinguishing natural and anthropogenic impacts in coastal zones and throughout the Earth system is a major challenge of science in our global society (Berkman, 2002). The Antarctic coastal zone, while utilized by humans to a limited extent, is among the most pristine regions on the planet for unambiguously assessing such global changes. The purpose of this paper is to review the results of the

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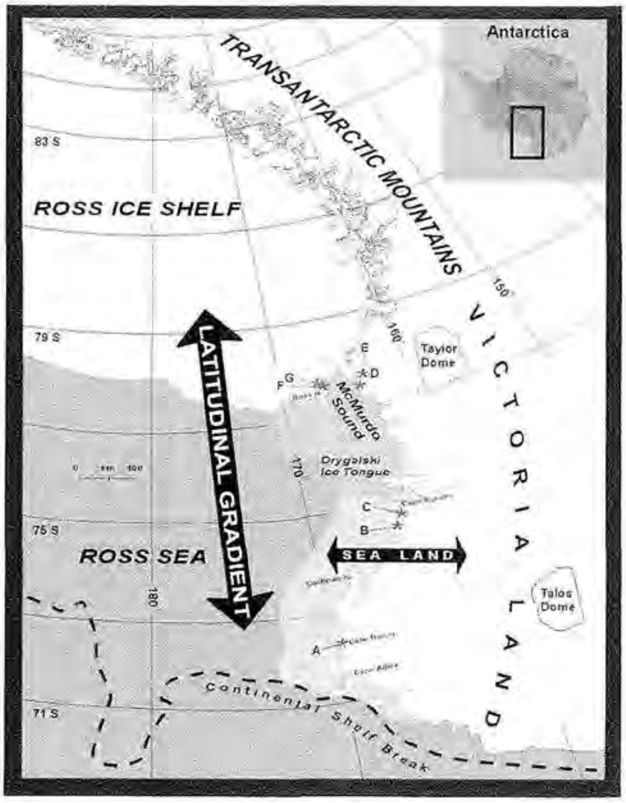

FIG. 1. – Spatial context of the Latitudinal Gradient Project along Victoria Land, Antarctica, from approximately 72°S to 86°S in the Ross Sea region. The principal research zones, which are recognized to have decreasing water vapour exchange between the ocean and land, from north to south are the: **Open-Water Zone** (south of Cape Adare to the Drygalski Ice Tongue in the Terra Nova Bay region); **Fast-Ice Zone** (south of the Drygalski Ice Tongue to McMurdo Sound and the edge of the Ross Ice Shelf; and **Ice-Shelf Zone** (south of the Ross Ice Shelf edge). National research stations, which represent the logistic centres for research along Victoria Land, are from north to south: **A** Cape Hallett (New Zealand and United States, summer only); **B** Gondwana (Germany, unoccupied); **C** Mario Zuchelli Station (Italy, summer only); **D** Marble Point (United States, summer only); **E** McMurdo Long-Term Ecological Research sites (United States, summer only); **F** McMurdo Station (United States, year-round); and **G** Scott Base (New Zealand, year-round). The map shading along Victoria Land represents the approximate boundaries between the open-water, fast-ice and ice-shelf zones that reflect the increasing duration of ice cover over the ocean and decreasing availability of water vapor.

Latitudinal Gradient Project (http://www.lgp.aq/) along the coast of Victoria Land, Antarctica, with emphasis on the marine research.

The Victoria Land coastal biome is defined by the complex of adjacent terrestrial and marine ecosystems that occupy permanently ice-free oases and outcrops on land, as well as periodically open-water and ice-covered habitats in the ocean, from approximately 72°S to 86°S (Fig. 1). Across this latitudinal gradient, ecosystems are operating at the liquid margin of life where climate changes have an amplified impact on the phases of water. This latitudinal gradient parallels the predominant trend of ice-sheet expansion and retreat associated with global climate changes (Conway *et al.*, 1999). Consequently, in an experimental context, Victoria Land provides a spatial gradient for evaluating environmental and ecosystem variability that otherwise would be recognised only through time. These features frame the rationale and activities in the Victoria Land Latitudinal Gradient Project that began emerging in 1999 under the coordination of Antarctica New Zealand, the Italian Programma Nazionale di Richerche in Antartide and the United States Antarctic Programme (Berkman and Everett, 2001).

The Latitudinal Gradient Project along Victoria Land is complemented by the Regional Sensitivity to Climate Change programme that is being sponsored by the Scientific Committee on Antarctic Research to assess terrestrial ecosystem responses to environmental and climate changes in the south polar region (http://www.riscc.aq). Together, the marine and terrestrial components of these latitudinal gradient research programmes are contributing to our understanding of species, community and ecosystem responses to global changes (Walther *et al.*, 2002).

RESEARCH FRAMEWORK FOR THE LATITUDINAL GRADIENT PROJECT

The climate-driven dynamics and coupling of marine and terrestrial environments and ecosystems along Victoria Land are influenced strongly by different forms of ice (Table 1). As the solid phase of water, ice represents aspects of the hydrological cycle that impact: moisture exchanges; marine, freshwater and terrestrial ecosystem dynamics; and the basic availability of liquid water for terrestrial life. In particular, sea ice has a pronounced influence on the dynamics of marine and terrestrial ecosystems as one of the most integrated natural phenomena in the Antarctic region. Because of diverse hydrological, glaciological, oceanographic and meteorological feedbacks, there also are numerous gradients and thresholds in the types and distribu-

TABLE 1. – Ice along Victoria Land, Antarctica.

Habitats	Types of Ice
Marine	snow, sea ice, ice tongues, ice shelves, icebergs, anchor ice
Freshwater	snow, lake ice, glaciers, permafrost
Terrestrial	snow, glaciers, permafrost, land ice, ice sheets

tions of sea ice along Victoria Land today. For example, from west McMurdo Sound to the Drygalski Ice Tongue there is landfast sea ice that is associated with supercooled water moving northward from under the Ross Ice Shelf. In contrast, annual sea ice occurs in east McMurdo Sound and north of the Drygalski Ice Tongue, which also influences the open-water region of the Terra Nova Bay polynya. These features of ice formed the basis for the following collaboration topics in the Victoria Land Latitudinal Gradient Project:

Collaboration Topic 1: Environmental thresholds across the latitudinal gradient of Victoria Land (e.g. continental shelf break, Drygalski Ice Tongue and Ross Ice Shelf) have a significant influence on the complexity of associated marine and terrestrial ecosystems.

Collaboration Topic 2: Across the latitudinal gradient of the Victoria Land system, ecological responses to land-air-sea interactions associated with climatic variability are amplified by ice (Table 1) and the availability of liquid water.

Collaboration Topic 3: Marine-terrestrial coupling across the Victoria Land system varies over time and space in relation to transfers of mass (sediments, salts, gases, water, nutrients, organic matter and organisms), momentum (currents and winds) and energy (latent heat).

In effect, collaborative topics #1 and #2 provide alternative hypotheses that could be tested and modelled to interpret ecosystem and environmental variability along the latitudinal gradient of Victoria Land (Fig. 2). In addition, the ice dynamics along Victoria Land lead to the identification of three zones (Fig. 1) that are distinguished by the duration of ice cover in the ocean:

Open-Water Zone: annual sea-ice retreat and exposure of open water.

Fast-Ice Zone: episodic retreat of sea ice every few years.

Ice-Shelf Zone: continuous ice coverage on the ocean over millennia.

MARINE ECOSYSTEM FEATURES ALONG VICTORIA LAND

Marine ecosystems along Victoria Land are known to vary across the latitudinal gradient in terms of maximum sea-surface temperatures; sea-ice extent, productivity and species assemblages. Oceanographic surveys indicate that maximum sea-surface temperatures are greater than 2°C north of the Drygalski Ice Tongue but are less than 0°C in McMurdo Sound to the south (Jacobs and Giulivi, 1998). Sea-ice along the coast of Victoria Land also varies with current patterns, harbours and embayments, katabatic wind regimes and ice-tongues. Generally, in west McMurdo Sound there is multi-year sea ice, which can increase in thickness to nearly 6 metres depth over periods longer than six years. On the other end of the extreme are open-water areas, like the Terra Nova Bay and Ross Sea polynyas. Responding to their environments, marine species along Victoria Land may vary in terms of their distributions and abundances; life history patterns, morphologies and energetics; and biochemical and physiological adaptations.

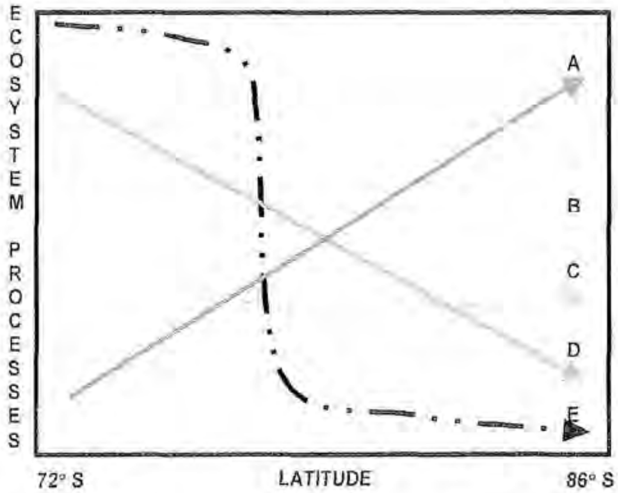

FIG. 2. – Alternative explanations for the variability in comparable ecosystem processes in marine, freshwater and terrestrial habitats (Table 1) across the latitudinal gradient of Victoria Land, Antarctica: **A** and **D** (linear ecosystem changes associated with environmental phenomena such as solar radiation and photo-periods); and **B, C and E** (non-linear ecosystem changes associated with environmental phenomena such as the number of freeze-thaw cycles and ice-tongue thresholds). From Berkman and Everett (2001).

Most of our understanding about benthic marine communities along Victoria Land is limited in geographic scope to McMurdo Sound (which has been extensively surveyed by the United States and New Zealand Antarctic programmes) and Terra Nova Bay (which has been extensively surveyed by the Programma Nazionale di Ricerche in Antartide). It is known that benthic algae are luxuriant in the Terra Nova Bay region, with vibrant stands at depths of less than 20 metres, whereas they are virtually absent in most areas in west McMurdo Sound.

These benthic macroalgae also include extensive coverage of coralline red algae on virtually all rocks in shallow water in the Terra Nova Bay region while they are rare in McMurdo Sound. This distribution of calcareous benthic algae is, in part, related to the warmer sea-surface temperatures and decreased solubility of calcium carbonate in the Terra Nova Bay region. Current New Zealand research is utilising these natural gradients in environmental conditions and productivity along the latitudinal gradient encompassed by the Victoria Land Coast; to investigate how variation in sea ice cover and primary production sources effects the structural and functional biodiversity of coastal benthic ecosystems. Climate-related environmental processes will influence the community dynamics and spatial structure of benthic populations, and hence there is potential for regional climate variability to impact ecosystem structure and function.

Among the benthic macroinvertebrates, species like the circum-Antarctic scallop (*Adamussium colbecki*) provide experimental templates for comparing and contrasting environmental conditions between habitats. For example, as in the distribution of coralline algae, *Adamussium* shells are significantly thicker in Terra Nova Bay than in McMurdo Sound, with stable isotope signatures that further reflect the relative seawater temperatures and production levels between these regions (Berkman *et al.*, 2004). There are also indications that *Adamussium* are releasing their gametes later in the austral summer and producing larger planktonic larvae in Terra Nova Bay than in McMurdo Sound (Chiantore *et al.*, 2000). In addition, there are marked differences in the abundance and depth distributions of both *Adamussium* and *Sterechinus neumayeri* (urchin) between McMurdo Sound and Terra Nova Bay (Chiantore *et al.*, 1998, 2001).

At the upper trophic levels, fish species have been an important research focus along Victoria Land because of their accessibility and utility for assessing adaptive responses to environmental variability. Fish trawls have provided important baselines for characterizing marine community structures, diversities and distributions in relation to oceanographic conditions along Victoria Land, with additional sites proposed from south to north (Eastman and Hubold 1999):

Erebus Basin as a baseline for high-latitude deep-water locality.

Sponge beds as sites of topographic and trophic complexity leading to high fish diversity.

Crary or Mawson banks as sites of high diversity surrounded by deep water areas.

Drygalski Trough as site of deepest and largest inner shelf depression in the Ross Sea.

Cape Adare as a continental shelf transition zone.

Iselin Seamount as a site of faunal transition and dispersal into the Ross Sea.

Antarctic fish are unique among vertebrates as the only fauna to have species (family Channichthyidae) without haemoglobin in their blood. Glycoprotein antifreezes, as well as other biochemical and physiological adaptations, reflect additional adaptive responses at the extreme of cold seawater temperatures. Relatively subtle increases in seawater temperatures could alter the physiological and biochemical processes among Antarctic fish faunas. Moreover, seawater temperature increases could lead to the incursion of species not generally found in the high latitudes that would further alter fish community compositions, interactions and dynamics.

Environmental conditions and suitable habitats similarly influence the distribution of avian faunas in the Ross Sea region. For example, the distribution of penguin rookeries is closely coupled with sea-ice coverage because of their required access to open-water areas where they forage. Today, the largest Adélie penguin (*Pygoscelis adelie*) rookery in Antarctica occurs in Cape Adare, with most southern rookeries along Victoria Land in the vicinity east of McMurdo Sound, where there is direct coastal access to open water every year. Guano deposits from these penguin rookeries, which include remains of their prey as well as organic materials for radiocarbon dating (Emslie *et al.*, 2003), provide information for assessing their past distributions and palaeo-environmental conditions.

Among the marine mammals, the southernmost seal species on Earth is the Weddell seal (*Leptonychotes weddellii*). This seal species, which is adapted to fast-ice environments, occurs throughout the coastal region of Victoria Land but with larger abundances in areas where there are cracks through the sea-ice and there is underwater access. In connection with the Antarctic Pack Ice Seal (APIS) programme in the 2000 austral summer, monitoring of seal populations revealed an apparent latitudinal gradient in crabeater seal (*Lobodon carcinophagus*) density along four north-south transect lines in the Ross Sea. Long-term population measurements of seal populations in McMurdo Sound further reveal potential connections with inter-annual and inter-decadal oscillations in the global atmosphere.

The corresponding history of ecosystem development along Victoria Land, which only became possible after habitats were no longer covered by ice sheets, is reflected by Holocene deposits in marine sediments, emerged beaches, terrestrial lakes, terrestrial ecosystems, penguin rookeries and ice cores. In particular, beginning around 6000 years ago, the Ross Sea region entered a new phase in ecosystem dynamics in conjunction with global climate conditions and local environmental changes in sea-ice coverage (Emslie *et al.*, 2003). These ecosystem changes are reflected by the geochemistry of the ice sheet in the terrestrial zone, occurrence of marine species in the coastal transition zone and deposition of phytoplankton species in the marine zone along Victoria Land (Berkman *et al.*, 2004). This period, from the mid-Holocene to the present, is most relevant to understanding ecosystem dynamics today.

LATITUDINAL GRADIENT RESEARCH CRUISES IN THE ROSS SEA IN 2004

The first ship-based marine campaigns in the framework of the Victoria Land Latitudinal Gradient Project were conducted in early 2004 on board the R/V "Italica" (3-22 February) and R/V "Tangaroa" (3 February - 7 March). The principal sites investigated by the R/V "Italica" were Cape Adare, Cape Hallett, Coulman Island, and Cape Russell. Contemporaneously to this Italian expedition, a 'sister' cruise by the R/V "Tangaroa" from New Zealand explored the marine benthic biodiversity and mapped the seabed of the northwestern Ross Sea and Balleny Islands.

The R/V "Italica" cruise involved extensive sampling in deeper environments along the Victoria Land Coast to enable both latitudinal and depth-related comparisons of the benthic communities and habitats. At each location, sampling was conducted along along depth gradients, with stations at nominal depths of 500, 400, 300, 200 and 100 m. Preliminary benthic community characteristics are shown in Table 2.

In addition, scientists from the Seafloor Mapping Lab from California State University Monterey Bay performed high-resolution acoustic remote sensing (multibeam and sidescan sonar) along with remotely operated vehicle video mapping. All sites were investigated with these remote survey tools, with the exception of Coulman Island, where a heavy sea-ice cover extended from shore out over the 400 m depth contour (Table 3). The multibeam imagery revealed extensive ice scouring that varied with location, depth and expo-

TABLE 2. – Benthic community characteristics along Victoria Land, Antarctica, from the 2004 R/V "Italica" cruise (Fig. 3).

Site	Latitude (S)	Longitude (E)	Station	Depth (m)	Substrate	Assemblage	Relative Biodiversity	Percent Dry Weight (mainly $CaCO_3$)
Cape Adare	71°15.5'	170°42.2'	A1	515-476	sand, cobbles	Ophiuroid community	LOW	69
Cape Adare	71°17.3'	170°39.2'	A2	430-421	sand	Stylasterinids	LOW	
Cape Adare	71°18.7'	170°33.5'	A3	312-305	sand, rocks	Stylasterinids	MEDIUM	36
Cape Adare	71°18.4'	170°28.9'	A4	235- 223	sand, cobbles	Tube-like ascidians	HIGH	47
Cape Adare	71°18.8'	170°26.7'	A5	139-124	sand, cobbles	Foliose ascidians	HIGH	41
Coulman I.	73°24.5'	170°23.2'	C1	480-474	mud, cobbles	Ophiuroid community	HIGH	94
Coulman I.	73°22.7'	170°06.9'	C2	410-372	mud, cobbles	Pterobranchia community	HIGH	85
Cape Hallett in	72°16.7'	170°09.8'	H-in 2	408-391	mud, cobbles	Gorgonian community	MEDIUM	79
Cape Hallett in	72°17.2'	170°12.3'	H-in 3	369-312	mud, sand, cobbles	Tube-like ascidians	HIGH	35
Cape Hallett in	72°17.7'	170°12.2'	H-in 4	266-228	mud, sand	Ophiuroids	LOW	43
Cape Hallett in	72°17.1'	170°14.0'	H-in 4bis	196		Botriform ascidians	HIGH	
Cape Hallett in	72°17.6'	170°12.8'	H-in 4tris	156-152	mud	Polychaetes	LOW	
Cape Hallett in	72°17.2'	170°17.9'	H-in 5	84		Botriform ascidians	HIGH	70
Cape Hallett out	72°15.5'	170°28.3'	Hout 1	537-475	mud, cobbles	Bryozoans + gorgonians	LOW	
Cape Hallett out	72°17.1'	170°29.9'	H-out 2	388-353	mud, sand	Flustridae	HIGH	77
Cape Hallett out	72°16.3'	170°24.9'	Hout 2bis	337-332	cobbles	Bryozoans	HIGH	
Cape Hallett out	72°17.5'	170°26.1'	Hout 3	289-246	sand, cobbles	Bryozoans	HIGH	
Cape Hallett out	72°17.2'	170°23.9'	Hout 4	235-195	cobbles	Bryozoans (Celleporinidae)	HIGH	84
Cape Hallett out	72°16.9'	170°17.0'	Hout 5	106-103	sand, cobbles	Mixed community	HIGH	61
Cape Russell	74°49.0'	164°18.1'	R 2	364		Bryozoans	MEDIUM	71
Cape Russell	74°49.8'	164°12.9'	R 3	330-307	sand, cobbles	Gorgonians	HIGH	64
Cape Russell	74°50.2'	164°05.5'	R 4	216-174	sand, cobbles	Bryozoans and Pterobranchia	MEDIUM	74
Cape Russell	74°49.9'	164°05.3'	R 4bis	156-135	sand, cobbles	Gorgonians	MEDIUM	
Terra Nova Bay	74°43.6'	164°13.6'	SMN	366-363	sand, cobbles	Polychaetes	LOW	75

TABLE 3. – Multibeam surveys along Victoria Land, Antarctica, from the 2004 R/V "Italica" cruise (Fig. 3).

Site	Survey lines	Linear distance (km)	Total area (km^2)	Total soundings
Cape Hallett	92	197.0	37.27	20,418,059
Cape Adare	27	96.9	23.78	8,389,464
Cape Russell	22	72.6	11.30	7,564,900
TOTAL	141	366.5	72.35	36,372,423

sure. A wide variety of ice disturbance features were clearly visible from shallow scrapes less than 1 m deep to broad gouges 100 m wide with more than 8 metres of vertical relief from trough to berm (Fig. 3).

In general, the preliminary multibeam results reveal a subtidal landscape dominated by a mosaic of disturbance patches stratified by depth and in various stages of recovery. Habitats at depths of 200-300 m and unprotected by topographic highs are exposed to the massive impact of tabular icebergs hundreds to thousands of metres in horizontal dimensions that come from the 300 m thick Ross Ice Shelf. The scours made by these giants are unmistakable due to the depth range in which they occur, and the characteristically broad and extremely flat "road-like" appearance of the features. In the 40-150 m depth range, the scours tend to be narrower, carved by more pointed ice keels ending in a terminal pit.

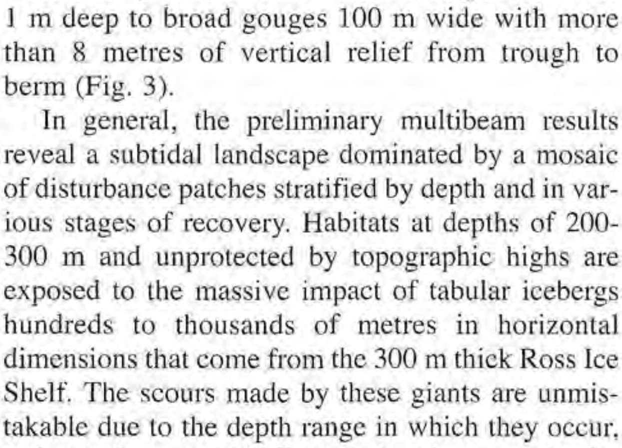

FIG. 3. – Representative shaded relief multibeam image of the marine bottom in the Cape Hallett area along the Victoria Land Coast of Antarctica in the vicinity of 72°18'S and 170°16'E at 40-50 m depth. Topographic Position Index (TPI) analysis was applied to a 2 m Digital Elevation Model (DEM) grid of the same area and "tuned" to detect troughs (black) and berms (dark gray). These results indicate that 28.95% (12.72% troughs and 16.23% berms) of the 1,376,328 m^2 area was scoured by icebergs. The multibeam surveys on the R/V "Italica" cruise were produced by the Seafloor Mapping Lab from California State University Monterey Bay.

Antarctic benthic communities are strongly influenced by iceberg disturbance (Gutt, 2001), but to date there have been few investigations on the spatial extent to which this occurs (or its frequency) in the coastal Ross Sea region (Lenihan and Oliver, 1995). Preliminary investigations of shallow water benthos (<30 m) on the R/V "Italica" cruise indicated striking differences in abundance and diversity of macroalgae, and biogenic habitats in the northwestern Ross Sea compared with McMurdo Sound. This cruise has provided valuable insights into the relative importance of different environmental variables that structure communities in the coastal Ross Sea region and how they might change with latitude (e.g. iceberg disturbance, sea ice cover, light regime and primary production sources), which will be assessed with future sampling.

A major objective of the *R/V Tangaroa* voyage was to collect information on the diversity of benthic macroinvertebrate and fish communities, and habitat types, along the northern Victoria Land coast and around the Balleny Islands. Phytoplankton productivity of the overlying water, physical disturbance of the bottom by icebergs, and the complexity of habitat-forming species in affecting faunal distribution and biodiversity also were investigated. Together, these data provide baseline information to assess ecosystem and environmental impacts from the growing human presence in Antarctica.

Five across-shelf (generally aligned SW-NE) transects from the 50 m bottom depth to the shelf edge (approx. 750 m) were multibeamed to establish bathymetry, and benthic sampling was conducted within three depth strata (750-500, 500-250, 250-50 m). The transects ran roughly perpendicular to the shoreline and were evenly spread from Cape Adare down to Cape Hallett. A wide variety of gear types was deployed (bottom trawl, beam trawl, epibenthic sled, and grabs) to sample different assemblages and provide a much greater appreciation of macrofaunal diversity than would be gained from using just one or two types of gear (e.g. Arntz, 1999). Camera deployment further added to information on the nature of benthic habitats, and information on sediment characteristics (e.g. particle size, organic carbon, and chlorophyll content) was also collected. Preliminary results indicate marked differences in species composition between the Ross Sea and Balleny Island locations. In addition, the sessile fauna was dominated by sea squirts and corals in offshore (deeper) areas, and by sponges inshore.

CONCLUSIONS

Research along the Victoria Land Coast goes back to the end of the 18th century, with the first winter-over expedition in Antarctica (Borchgrevink, 1901). The 2004 research cruises of the R/V "Italica" and R/V "Tangaroa" are part of this rich history.

The Latitudinal Gradient Project along Victoria Land provides an interdisciplinary umbrella for compiling and integrating data, maps, figures, tables, geographic information systems and publications that have been collected for more than a century regarding the components, dynamics and chronologies of terrestrial and marine ecosystems and environments over diverse time and space scales in Antarctica. These interdisciplinary data involve the geology, limnology, meteorology, glaciology, oceanography and ecology associated with the southernmost ecosystems on Earth. For the future, this research on the coupling and dynamics of marine and terrestrial ecosystems along Victoria Land provides a unique framework for assessing latitudinal shifts in 'sentinel' environmental transition zones (Fig. 1), as a global barometer that reflects climate dynamics.

ACKNOWLEDGEMENTS

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Changing chain: past, present and future of the Scotia Arc's and Antarctica's shallow benthic communities*

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SUMMARY: The Scotia Arc links Patagonia to the Antarctic Peninsula. This island chain has changed considerably since Antarctica's geographic and thermal isolation from other land and water masses. Now its rates of air, land and fresh-water climate change are among the highest measured. This review examines work on the shallow water benthos of this region in the context of climate change. In summer, primary productivity is as intense as anywhere, whilst in winter the water reaches unprecedented clarity. Suspension feeders may eat for just a few months but others feed all year. Growth and reproduction are up to 50x slower than non-polar rates. Life here is in the slow lane. There is intense summer disturbance from ice-scour and wave action. This has erased shore zonation and created it below the surface. In contrast to summer disturbance, the winter is among the calmest and most thermally stable environments, when the area is overlain by fast ice. Whilst few animal phyla or species are represented on land, phyletic richness—and in some groups species richness—rivals that of tropical regions. Data showing clines in benthic richness at several taxonomic levels across the Patagonia-South Georgia-Signy Is.-Adelaide Is. chain and 50 years of ice-sheet retreat are presented.

Keywords: polar benthos, zonation, metabolism, suspension-feeding, growth, reproduction.

RESUMEN: UNA CADENA CAMBIANTE: PASADO, PRESENTE Y FUTURO DE LAS COMUNIDADES BENTÓNICAS SOMERAS DEL ARCO DE SCOTIA Y ANTÁRTIDA. – El Arco de Scotia conecta la Patagonia con la Península Antártica. Esta cadena de islas ha cambiado considerablemente desde el aislamiento geográfico y térmico de la Antártida respecto de otras masas de agua y tierra. Actualmente, esta área tiene las tasas de cambios climáticos más elevadas, tanto en aire, tierra y aguas continentales. En esta revisión, se examinan los estudios en las comunidades bentónicas de aguas someras en el contexto del cambio global. La productividad primaria es, durante el verano, tan intensa como en otras áreas, mientras que en invierno las aguas alcanzan una claridad sin precedentes. Los suspensívoros pueden alimentarse por apenas unos pocos meses, pero otros se alimentan durante todo el año. El crecimiento y la reproducción son hasta 50 veces más lentos que en los organismos no polares. La vida aquí está en el "carril lento". Durante el verano, existe un disturbio intenso debido al raspaje del hielo y la acción de olas. Estos factores han eliminado la zonación costera y la generaron debajo de la superficie del agua. En contraste al disturbio de verano, el invierno está entre los ambientes más calmos y térmicamente estables, cubierto por la banquisa de hielo. Mientras que sólo unos pocos phyla o especies animales están representados en tierra, la riqueza filética y en algunos grupos la riqueza específica, equipara la de las regiones tropicales. Se presentan datos evidenciando gradientes en la riqueza bentónica en varios niveles taxonómicos a través de la cadena Patagonia - Islas Georgias del Sur - Isla Signy - Isla Adelaida, además de 50 años de retracción glaciaria.

Palabras clave: bentos polar, zonación, metabolismo, suspensívoros, crecimiento, reproducción.

ENVIRONMENTAL CHARACTERISTICS

When the ancient supercontinent of Gondwana disintegrated and the fragments drifted apart to form continents, Antarctica became very isolated over the geographic south pole. From its former near-subtropical forests, Antarctica has become the coldest, windiest, driest and highest continent that is almost entirely covered with ice sheets several kilometres thick. The Circumpolar Current that developed in

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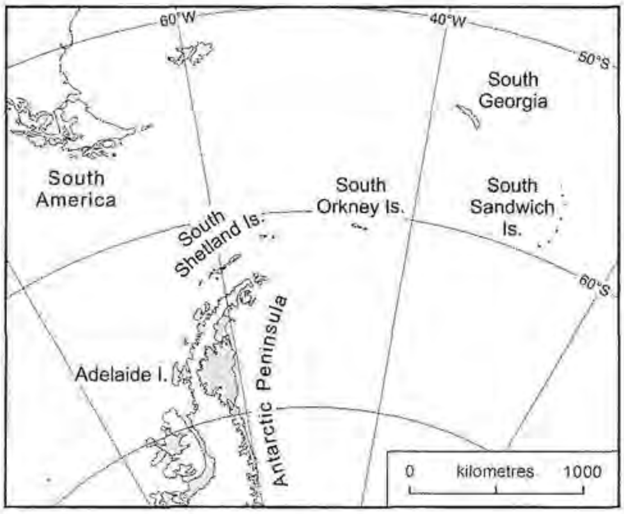

FIG. 1. – The Patagonia-Scotia Arc-Antarctic Peninsula region of the South Atlantic and Southern Ocean. The major study islands discussed are named.

the deep basins surrounding the cooling continent and the Polar Frontal Zone (PFZ) became a major oceanic barrier between the southern parts of the Atlantic, Indian and Pacific Oceans and the Southern Ocean. At its narrowest point it covers almost 10 degrees of latitude (53-63°S), which is almost entirely ocean, except for a few small islands and archipelagos. Several of these archipelagos, South Georgia, the South Sandwich Islands and the South Orkney Islands (Fig. 1), are the tips of an almost continuous subsurface mountain chain linking the Andes and the Antarctic Peninsula. These mountains, the Scotia Arc, are the only connection between Antarctica and another continent apart from deep abyssal plains. At the most northerly and ice free (and thus most convenient) parts of the continent, islands such as the South Shetlands have become important centres for science and other anthropogenic activities. Convenience aside, the Patagonia-Scotia Arc-Antarctic Peninsula has for many reasons become a crucial region of the globe for biological and climatological research.

For examination of nearshore benthic systems, the Patagonia-Scotia Arc-Antarctic Peninsula offers the only possibility for investigating the continuity of trends across latitude at southern high latitudes. It also represents the mostly likely point for invasions of terrestrial and marine habitats. Although some parts of the Scotia Arc, the South Sandwich Islands, are very poorly known (Baker *et al.*, 1964; Holdgate and Baker, 1979), the Scotia Arc and Antarctic Peninsula region have increasingly become hotspots for cold water research. In the 1970s, much of the groundbreaking polar research was focused at McMurdo Sound in the high Antarctic (e.g. Dayton *et al.*, 1970; 1974). The last decade, however, has seen a proliferation of science in the west Antarctic region, including significant progress in the understanding of colonisation (e.g. Rauschert, 1991), growth (e.g. Klöser *et al.*, 1993), larval development (Peck, 1993), reproduction (e.g. Brêthes *et al.*, 1994), feeding (e.g. Barnes and Clarke, 1995), food availability (Clarke and Leakey, 1996), metabolism (e.g. Ahn and Shim, 1998) and specific dynamic action (e.g. Robertson *et al.*, 2001) in the nearshore benthic environment. Important discoveries of ice shelf disintegration (Doake and Vaughan, 1991), high shelf benthic richness (Barnes and Brockington, 2003), great age and records of atomic bomb tests in animal shells (Peck and Brey, 1996), warming of air (King and Harangozo, 1998) and lake temperatures (Quale *et al.*, 2002) have also focused on western Antarctica. In this review many features of the environment and shallow benthic faunas are compared, such as disturbance, zonation, recruitment, diversity and mortality along this link between the continents. Of crucial importance and background to such discussions is the context of the southern polar environment and how it contrasts with elsewhere.

The relative positions and amounts of land and water in the south and north polar regions are very different; at Scotia Arc latitudes the southern hemisphere is virtually all water, whereas it is nearly all land in the northern hemisphere. At 55-70°N Subarctic and Arctic seas have massive fresh water input over summer periods as major rivers discharge on all sides from the surrounding continents. The ocean around the Scotia Arc is virtually all fully saline (Antarctica has no rivers). Some of the Scotia Arc islands (e.g. the South Sandwich Archipelago) may be young but the region is old, whilst the entire Arctic environment is young. There are, however, many similarities between the Scotia Arc region of Antarctica and equivalent northern hemisphere latitudes, particularly in terms of climate. For matched latitudes there is the same light climate, becoming more seasonal polewards. This imparts a strong seasonal influence on sea surface temperatures, fast-ice (frozen sea surface) formation and breakup, disturbance and primary productivity (and therefore, secondary productivity). Sea surface temperatures change abruptly across the PFZ with those south of it, typically reaching nearly -2°C in winter and barely +2°C in summer (Table 1). In addition to the glaciations, the relatively long period of cold southern polar sea temperatures has removed much of

TABLE 1. – Comparison of marine environments from Patagonia to the Antarctic Peninsula in terms of physical, biological, climatic and anthropogenic factors of change. Decreased ozone is shown as '$\Downarrow O_3$'.

factor	Patagonia	South Georgia	South Orkneys	South Shetlands	Antarctic Peninsula
sea temp	0°C to12°C.	-2°C to >4°C.	-2°C to 2°C.	-2°C to 2°C	-2°C to 4°C
ice scour	occasional around glaciers	occasional around glaciers	seasonal major factor	seasonal major factor	seasonal major factor
fast ice	rare	occasional, short period	seasonal, up to 9 months	seasonal, up to 8 months	seasonal, up to 8 months
radiation	seasonal. $\Downarrow O_3$ for days	seasonal. $\Downarrow O_3$ for days	seasonal. $\Downarrow O_3$ for days	seasonal. $\Downarrow O_3$ for weeks	seasonal. $\Downarrow O_3$ for weeks
climate change	glacial retreat, air temps	glacial retreat, air temps	highest lake warming, air temps	air temps	ice shelf changes, air temps
organism invasions	terrestrial/ marine	terrestrial / lake	terrestrial	terrestrial/ marine?	terrestrial
persistent debris	abundant	abundant	common	common	rare
tourism and ship traffic	high	high	low	moderate	low
science presence	moderate	low	low	high	low

the terrestrial and intertidal biota. This, and the relative constancy of this low-temperature environment, have left biota which are highly stenothermal and an austral fauna with a strong pattern of temperature-dependent biogeography (Peck, 2002; Pörtner, 2002a,b,c). The influence of temperature in the polar realm has been of fundamental interest for half a century and even now its effect on fertilisation or enzyme kinetics (Vetter and Buchholz, 1998) and rates of protein synthesis (Fraser *et al.*, 2002) have become important topics. Clarke (1988) described the seasonal pattern of sea surface temperature at Signy Island as typically being a long period at -1.85 °C followed by a sharp rise to positive temperatures, then a few months later a sharp fall back to -1.85 °C. Sahade *et al.* (1998) have found this pattern to be little different in the South Shetland Islands, and indeed it is similar further down the Antarctic Peninsula at 68°S (Adelaide Island). In contrast, south of the Antarctic Peninsula, around the continental margins, the annual change in sea surface temperature has been reported to be as little as a tenth of a degree (Dayton *et al.*, 1970). Therefore, Antarctic sea temperatures, compared with those in Patagonia and elsewhere (even the high arctic), are characterised by depressed levels and relative constancy.

DISTURBANCE

All environments experience disturbance, but the frequency, scale and patchiness of events differ enormously. It is not, however, merely the intensity of destruction which dictates the effect on the biota: the capability of communities to recover governs the diversity and structure of ecosystems. Forests experience small-scale (in time and space) events ranging from tree falls to massive land slides (Garwood *et al.*, 1979; Borkaw, 1985). Nearshore marine environments are typically exposed to chemical, biological and physical disturbance. In coastal water this is often from sedimentation, fresh water runoff, pollution, anoxia or currents and wind-driven wave action. Of these, currents and wave action are likely to be most important in the Scotia Arc region. This sort of disturbance ranges from the smallest ripples, which are only likely to effect meiofauna, to benthic storms, hurricanes and tsunamis. The average wind speed and wave height is reasonably predictable across the globe by latitude (Fig. 2A,B): the most heavily disturbed latitudes are those at the level of the Scotia Arc.

Shallow seas also experience a wide range of mechanical disturbance, incuding bioturbation by organisms, bashing by drift logs (Dayton, 1971), digging by Gray whales (Nerini and Oliver, 1983) and hurricanes (Wulff, 1995). None of these agents of disturbance are as severe in either impact force or frequency as ice scour, which like wave height is predictable to some extent by latitude (Fig. 2C). The polar and sub-polar regions occupy a major proportion of the globe (nearly a third), but ice scour also occurs adjacent to glaciers at lower latitudes (Pugh and Davenport, 1997). Nevertheless, in terms of non-anthropogenic disturbance an averaged mean

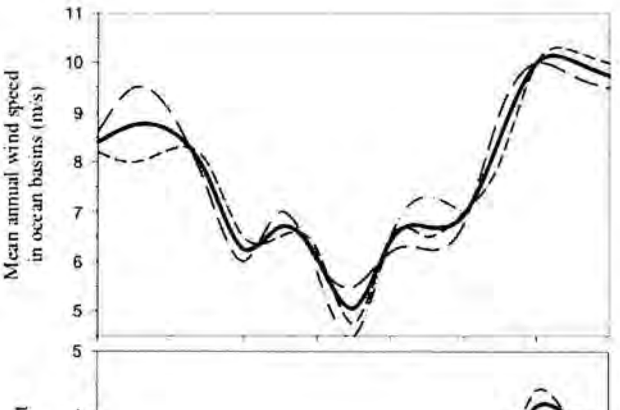

FIG. 2. – Shallow water disturbance with latitude and ocean basin. Mean surface wind speed and wave height from Barnes (2002a) drawn from data in Bentamy *et al.* (1996); solid line is mean across different oceans. Ice scour data from satellite imagery of floating ice prevalence.

across latitude is likely to show massive levels at polar latitudes compared with anywhere else. In periods of open water billions of pieces of floating ice collide with the sea floor, almost denuding the intertidal zone around an entire continent (Hedgepeth, 1969; Shabica, 1972). Below the littoral bigger icebergs are able to hit (Fig. 3A)—the biggest scrape the bottom at several hundred metres (Lien *et al.*, 1989; Gutt *et al.*, 1996) and are amongst the most destructive natural forces (Dayton, 1990). In the Scotia Arc one of the major influences of ice-scour on hard substrata is a marked pattern of sublittoral zonation (Shabica, 1972; Zamorano, 1983; Gallardo, 1987; Gambi *et al.*, 1994; Barnes 1995a; Nonato *et al.*, 2000; Gutt, 2001; Barnes and Brockington, 2003). The same is also true at many Arctic and Subarctic localities (Ellis and Wilce, 1961; Bolton, 1983; Dowdswell *et al.*, 1993; McCook and Chapman, 1997; Conlan *et al.*, 1998). In mud and silt ice, gouging can even wipe out most of the meiofauna (Peck *et al.*, 1999, Lee *et al.*, 2001a) and resuspend huge volumes of sediment (Rearic *et al.*, 1990). These plough furrows and other ice scour features have been preserved in rock, giving important clues to pre-present aquatic ice patterns and processes (Dionne, 1977; Vogt *et al.*, 1994). The recolonisation time in sediments begins in days, with the more mobile forms, particularly scavengers, returning to feast on the previous destruction (Peck *et al.*, 1999; Lee *et al.*, 2001a,b). Thus, as theorised for deep sea environments (Dayton and Hessler, 1972; Grassle and Sanders, 1973), this disturbance promotes wider scale diversity by increasing surface heterogeneity (Fig. 3B) and the dominance of fauna from place to place (Gutt and Piepenburg, 2003). On hard substrata too, encrusting, competitively-dominant species are prevented from monopolising space by periodically being wiped out (Barnes, 2002a). Poorly ranked competitors (usually pioneers) are often highly abundant in shallow polar habitats, as can also happen at some lower latitude sites promoted by disturbance (Dayton, 1971; Paine, 1979; Karlson, 1983) or keystone species abundance (Paine, 1974). In the Patagonia-Scotia Arc-Antarctic Peninsula region there is likely to be a trend of increased levels of ice scour with latitude, but any signal from such a cline would be complex for several reasons:

The latitude of the PFZ, and therefore freezing water, varies in time and space. The ANDEEP (Fütterer *et al.*, 2003) and LAMPOS (Arntz and Brey, 2003) cruises of the Polarstern have, for example, collected data suggesting the PFZ to occasionally be south of South Georgia. If this is the case, the PFZ may wander hundreds of miles in the South Georgia region.

Complexity is also generated by other forms of disturbance, such as wave action (Fig. 2B), ice-foot and anchor ice formation, also changing with latitude.

The prevalence and duration of freezing surface waters (fast ice) increases with latitude. When fast-ice forms it effectively locks up icebergs so that they are immobilised, reducing scouring to already grounded ice, and even this to only the location where they are.

Anchor ice (formed by supercooled water nucleating around organisms or objects) is rare in the Sco-

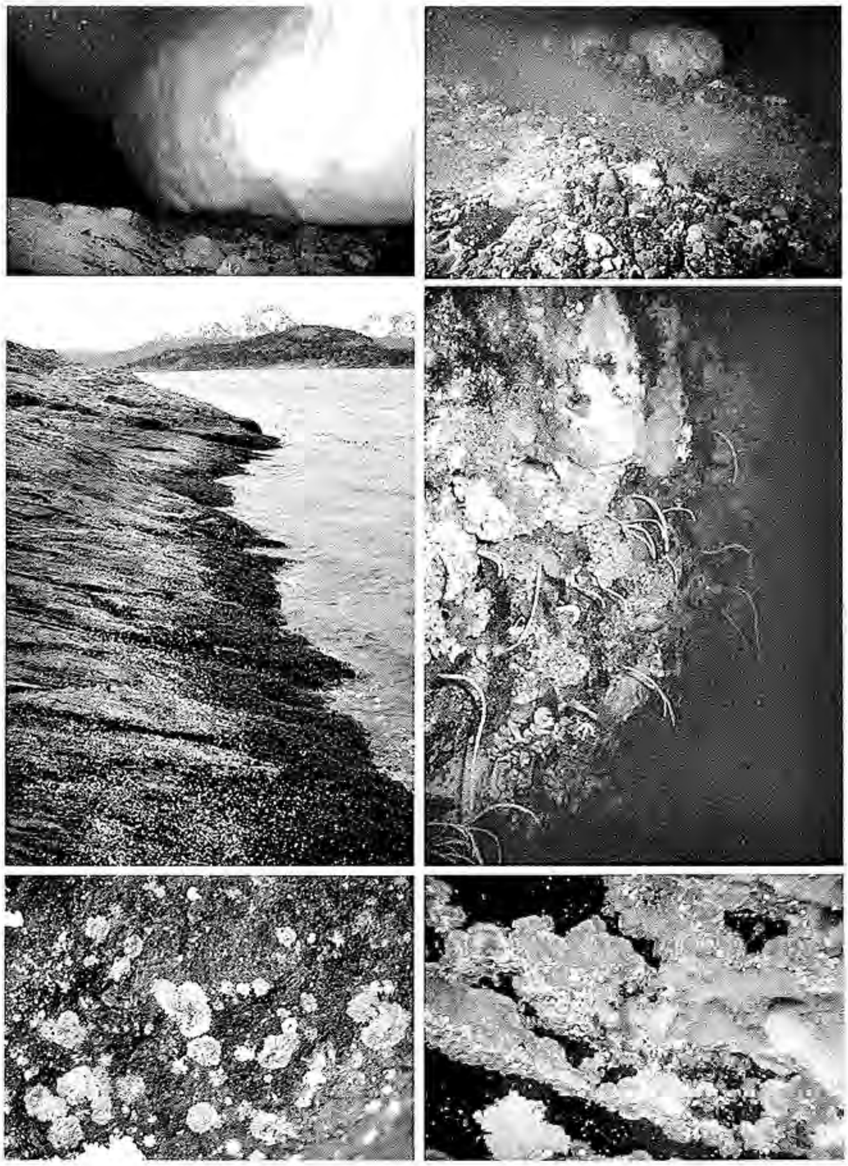

FIG. 3. – Disturbance and colonisation. Ice in the process of scouring the seabed (top left); ice scour path left after iceberg has scraped the seabed (top right); southernmost shore zonation in Tierra del Fuego (middle left); rich benthos on a wall at 20 m, Signy Island (middle right); first year colonisation on a boulder at Adelaide Island (bottom left); colonisation after ~ a decade (bottom right).

tia Arc or along the Antarctic Peninsula, and even in the high Antarctic below 30 m (Dayton *et al.*, 1970; 1974). Much of Antarctica's coastline lies at 67-72 °S, but we still know little of the relative balances of disturbance and community structuring at these latitudes. Only at the Vestfold Hills and Adelaide Island has shallow shelf sea bed and fauna even been studied in moderate detail in the context of ice disturbance (Kirkwood and Burton, 1988; Tucker, 1988; Barnes and Brockington, 2003). There is, however, no littoral or even shallows around much of the high Antarctic, as floating ice sheets extend out from the continent. In the SE Weddell Sea the only 'shallows' are sea-mounts rising to within 100 m of the surface.

Ice is clearly one of the most severe natural disturbance events. Only in recent years, however, has the impact of anthropogenic disturbance—particularly fishing—begun to be evaluated and realised. Fishing has massively changed benthic (and other) ecosystems across the globe by systematically removing the uppermost trophic level (Jackson *et al.*, 2001). In warm waters sharks and large predatory fish, such as tuna, have been gradually been reduced to smaller populations of smaller fish (Myers and Worm, 2003), with ultimately a smaller ecological role. These authors suggest that large predatory fish have been reduced to just 10% of their number, causing catastrophic changes cascading along trophic levels. In the Scotia Arc this is now happening to the Patagonian Toothfish *Dissostichus* and the commercially fished squid populations (Collins *et al.*, 2003). In the case of these Southern Atlantic and Southern Ocean fisheries, as with whales, the problem is acute, as adults take a long time to grow and mature. Furthermore, the fishing methods have resulted in by-catches of seabirds and have been crippling populations of another top predator—albatrosses (Schiavini *et al.*, 1998). Previously the Southern Ocean, particularly around the Scotia Arc, was the centre for one of the largest scale changes of an ecosystem. Over just a few decades the large populations of the most massive animals ever to have occurred on earth were reduced to near ecological extinction. In size-successive order man removed the Blue, Fin, Sei and other baleen whales from the ecosystem—their bones lie scattered around many bays of the Scotia Arc islands (e.g. South Georgia and Signy Island). It seems that even the scale of the reduction of the great whales themselves is still being underestimated (Roman and Palumbi, 2003).

The effects of demersal fishing in some ways mimic those of ice scour. Some areas are being 'scoured' by trawls many times a year (Collie *et al.*, 2000, Thrush and Dayton, 2002), though this is rare within the Scotia Arc. The type of destruction resembles ice scour in many ways, such as in the type, effect and frequencies involved. Acoustic methods are increasingly being used to evaluate the impact of fishing on benthic communities and this method is likely to be an increasingly powerful tool for investigating polar ice scouring. In the Patagonia-Scotia Arc-Antarctic Peninsula, ice is probably the major structuring influence to coastal benthic communities above ~100 m depth, and in some areas even below this (Gutt, 2001). In the intertidal this is principally mediated by ice-foot encasement during the winter and by ice-scour during summer open-water periods (seasonally in Patagonia (Fig. 3A,B)). In the shallow subtidal, ice-scour starts overtaking wave action as of most influence at about 52-56 °S and anchor ice likewise starts becoming the most important influence south of 73-75 °S (Barnes and Brockington, 2003). In deeper polar water it is clear that scouring occurs commonly (in places) even at several hundred metres depth, in both the Antarctic and the Arctic (Gutt *et al.*, 1996; McCook and Chapman, 1997; Gutt and Starmans, 2001). Therefore, ice effects have pronounced clines with latitude, bathymetry and season, but are most apparent in the strong zonation created.

ZONATION

Zonation has for more than a century been an important concept for understanding distributions of organisms. Many environmental gradients exist in space and time but those that marine biologists particularly associate with zonation are tidal, geographical, topographical and exposure. Nowhere is this more obvious than on temperate shores as a clear series of 'belts': superabundance of particular animals, algae or lichens are obvious across a vertical plane spanning just a few meters. On the southernmost shores of South America, Africa and Australasia littoral zonation is striking, yet around the Antarctic and high Arctic coastlines this banding disappears (Dayton, 1990). In the Atlantic, Tristan da Cunha (37°S), Gough (41°S) and the Falkland/Malvinas Is. (51°S) are amongst the most southerly islands. On these shores littoral zonation is clear amongst algae and macrofauna (see de Vil-

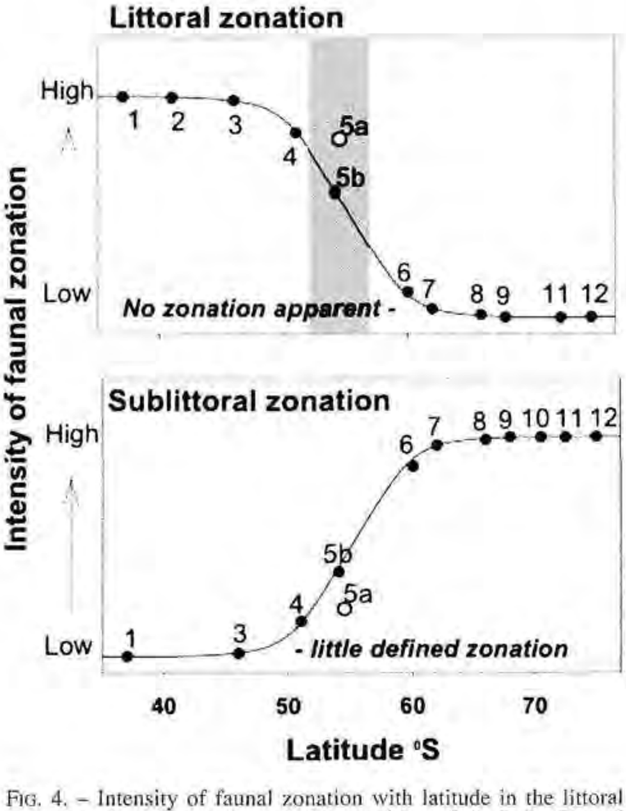

FIG. 4. – Intensity of faunal zonation with latitude in the littoral (upper) and sublittoral (lower). The position of the Polar Frontal Zone is shown as a grey shaded bar. Schematic diagram modified from Barnes and Brockington (2003) suggesting a change of intensity of zonation based on the strength of littoral and sublittoral macrobiota patterns at sites at latitudes indicated by 1. Tristan da Cunha, 2. Gough Is., 3. Prince Edward Archipelago, 4. Falkland Islands, 5a. Ushuaia (Tierra del Fuego), 5b. South Georgia, 6. Signy Island, 7. South Sandwich Archipelago, 8. Haswell Is., 9. Adelaide Is., 10. Weddell Sea seamount at 71°S, 11. Vestfold Hills, 12. McMurdo Sound.

liers, 1976). Around the margins of the Polar Frontal Zone, though, there is a dramatic change: the only sign of shore zonation is the banding of macroalgae. This is largely the case in the Subantarctic islands of the Prince Edward archipelago, Kerguelen and South Georgia (de Villiers, 1976; Pugh and Davenport, 1997). Beyond these latitudes, in the South Sandwich, South Orkney and South Shetland archipelagos, even macro-algae are absent from shores. As zones are entirely biologically defined, that is they are largely the visible patterns of a few such dominant species (Underwood and Kennelly, 1990), the phenomenon of zonation in the littoral disappears south of about 54°S - except at the southern tip of South America. The most southerly shores around Cape Horn at about 55°S are permanently north of the PFZ and do show (reduced) faunal and algal zonation (Fig. 3C). Thus, there is a cline in the strength of zonation with latitude, which can be seen by comparing shores of islands from the South Atlantic to those along the Antarctic Peninsula (Fig. 4).

Increased levels of floating ice, the scouring that this causes, and winter freezing are thought to be the driving factors behind the disappearance of abundant littoral macrobiota and zonation. For decades it was considered that life was virtually absent from the Antarctic littoral zones, but there are a few—mainly marine—species that colonise during summer open-water periods (see Hedgepeth, 1969; Shabica, 1972; Barnes *et al.* 1996; Kim, 2001; Barnes and Brockington, 2003). However, ice scour, primarily responsible for the reduction of shore biota and zoning, starts becoming a major structuring force in the sublittoral at similar latitudes. Only fast-growing pioneer species (a few gastropods, bivalves, tubicolous polychaetes, encrusting bryozoans and hydroids) are found in the top 5-10 m on hard rocky bottoms at Signy Island in the South Orkney Archipelago (60°S) (Barnes, 1995b). The different faunas between 25 m (Fig. 3D) and 6 m at Signy Island are, however, apparent even in the differential species recruiting to newly available substrata (Stanwell-Smith and Barnes, 1997). Experimental panels immersed for nearly 2 years at 6 m at Signy Island were only colonised by the few pioneers (spirorbid worms and a few species of bryozoans) that are typical of encrusting communities at that depth. Similar panels immersed at the same place for the same period but at 25 m revealed a much richer colonising fauna. In the upper-most islands of the Antarctic Peninsula region, zonation is a prominent feature, and has been documented from a variety of islands, especially around the South Shetland Archipelago (62°S). As with temperate shore zonation, this probably takes the form of a series of slightly differing species distributions, but 3-4 zones are characteristically described, based on the distributions of the most abundant species. One of the earliest descriptions (from the South Shetland Archipelago), by Gruzov and Pushkin (1970), trisplit the shallow subtidal into an upper surf zone, a middle kelp zone and a deeper (15-30 m) fauna zone. More detailed accounts of biota horizons in the shallow waters around King George Island have been given by Zielinski (1981), Rauschert (1991), Klöser *et al.* (1993), Arntz *et al.* (1994), Arnaud *et al.* (1998), Jazdzewski (1998), Sahade *et al.* (1998), and most recently by Nonato *et al.* (2000) and Bromberg *et al.* (2002). The upper zone (0-4 m), though variable from place to place, seems to be mainly depauperate of fauna (apart from amphipods) and comprises the algae *Desmarestia*, *Himantothallus* and *Leptsomia*. Below this, to about 15-18 m polychaetes, the limpet *Nacella concinna*, serolid isopods and the bivalve *Laternula elliptica* become abundant. In the deeper zones to 25 m and beyond the fauna becomes richer and resembles a typical shallow-water Antarctic Peninsula fauna, e.g. the echinoid *Sterechinus neumayeri*, the nemertean *Parborlasia corrugata* and the isopod *Glyptonotus antarcticus*, among others. Meiofaunal patterns seem to be similar to those in the macrofauna (increases in abundance and diversity) with respect to depth (Skowronski *et al.*, 1998; Vanhove *et al.*, 2000; Lee *et al.*, 2001a,b).

Though less well described, the benthic zonation appears to be more delineated at the Palmer Archieplago (Zamorano, 1983) and the Haswell Islands (66°S) (Propp, 1970) and at Adelaide Island (Barnes and Brockington, 2003). At Adelaide Island Barnes and Brockington (2003) report that the trilevel zonation can even be distinguished by characteristics within populations of single species: the size of *Sterechinus neumayeri* varies significantly with depth. Furthermore, species such as *S. neumayeri*, and other grazers (e.g. *Nacella concinna*), can not only create zonation patterns by their own differential abundance but by their feeding intensify them through removal of recruits. Strong zonation has been found at similar depths at other higher latitude sites around the Antarctic continent shelf (Gallardo 1987), or more specifically the Vestfold Hills (Kirkwood and Burton, 1988), Terra Nova Bay (Cattaneo-Vietti *et al.*, 2000) and McMurdo Sound (Dayton *et al.*, 1970; 1974; Dayton, 1979; Miller and Pearse 1991). The vertical zonation absent in the littoral zone south of the PFZ is therefore quite apparent in the shallow sublittoral and increases as an opposite trend to decreasing shore patterns (Fig. 4). A number of authors have, however, reported distinct sublittoral zonation along temperate Pacific shores, particularly along the Chilean fjords and Californian coast.

Ellis and Wilce (1961), and others since, have reported equivalent zonation patterns from the high Arctic. The littoral macrofauna and zonation patterns do become reduced with latitude, though there are still quite a number of species on some shores at 77-79°N (Spitsbergen) (Weslawski *et al.*, 1993). Both in the littoral and sublittoral, Arctic biota have strong additional forces of zonation. Run-off from surrounding continents, especially large inputs of fresh water, localised pollution and sedimentation (Holte *et al.*, 1996) or anoxia (Kvitek *et al.*, 1998) contribute substantially to faunal vertical distributions. Changes in zonation with latitude (mediated by ice scour) probably occur up coastlines into the Arctic as well as along the Patagonia-Scotia Arc. Zonation is clear in the high Arctic sublittoral (Dayton, 1990), though equivalent changes seem to occur at a much higher boreal (than anti-boreal) latitude. As in the southern polar region, these patterns in the sublittoral are due to the frequency of disturbance versus the potential of biota to colonise. Settlement and recruitment was therefore a key feature for the understanding of nearshore benthic community structure, yet until 1991 (when both Pearse and Pearse, and Rauschert reported studies), Dayton and Oliver's now famous (1977) experiment at McMurdo Sound was the only such study reported from the entire Southern Ocean.

RECRUITMENT

For a long time since the pioneering reproductive studies undertaken by Thorson and their wider interpretation (Mileikovsky, 1971), the idea of many polar taxa using pelagic larvae was against a strong paradigm. A couple of decades later it seemed that some taxa did not follow Thorson's rule (Pearse *et al.*, 1991; but see Arntz and Gili, 2001). Even in remote archipelagos like the South Orkney Islands, pelagic larvae from a wide range of taxa can be common (Stanwell-Smith *et al.*, 1998). Pelagic larvae may, however, be quite rare in large areas of the Southern Ocean, such as across the Weddell Sea (unpublished ANDEEP III cruise data). The timing, duration, abundance and mortality of recruits was completely unknown in the southern polar region before Dayton (1989) reported some strange recruitment patterns in the Ross Sea. This experiment had been running for about a decade and a rich fauna, with respect to cheilostome and cyclostome bryozoans, had colonised the panels (Moyano, 1984). Periodic macroscopic observation by divers had suggested almost no recruitment for a number of years followed by a massive recruitment later on in the experiment. This may, indeed, be evidence of considerable interannual variation, as suggested by Dayton (1989), but there are other interpretations. Early examination was by divers only, so it is not surprising that they were unable to see much because many pioneer species are small and translucent. Furthermore, for a number of years the panels were not examined at all, so while strong interannual variation in recruitment may have occurred, we cannot be certain that recruitment was more gradual, as has been measured elsewhere. In the same year the first of a number of settlement and recruitment studies in the Patagonia-Scotia Arc-Antarctic Peninsula were published. At 46°S López-Gappa (1989) showed that benthic recruitment in Magellanic shallow waters closely resembled that of the better-studied northern Atlantic with respect to space occupied, richness and other obvious factors. The first study in the Antarctic Peninsula region revealed the presence and importance of relatively fast-growing ascidians in early community development (Rauschert, 1991). Two back-to-back two-year studies (Barnes, 1996;

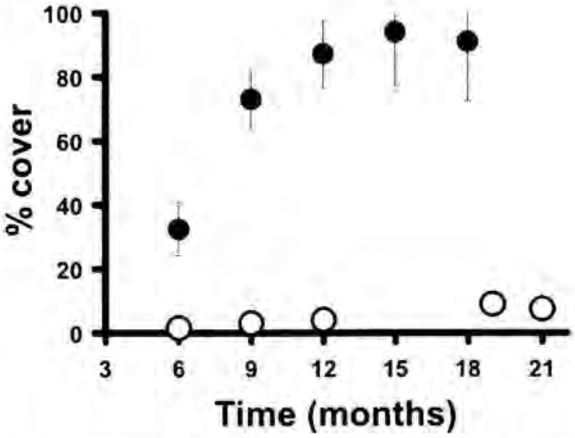

FIG. 5. – Coverage of artificial substrata (settlement panels) in temperate/tropical localities (filled symbols) vs southern polar localities. Adapted from Stanwell-Smith and Barnes (1997).

TABLE 2. – Recruitment to benthic environments, experiments with artificial substrata in the Scotia Arc and Antarctic. Two values for species richness and duration refer to the different sources given above.

factor	Patagonia	South Orkneys	South Shetlands	Antarctic Peninsula	high Antarctic
source	López Gappa, 1989; Barnes, unpublished	Barnes, 1996; Stanwell-Smith and Barnes, 1997	Rauschert, 1991	Bowden, unpubl.	Moyano, 1984; Dayton, 1989; Arntz *et al.* unpub.
% cover	75%	2-10%	>10%	40-80%	variable by year (<5%)
species richness	24 species, 19 species	22 species, 23 species	low	moderate	46 species
diversity	moderate	low	low	low	moderate
taxa	polychaetes, bryozoans, ascidians	polychaetes, bryozoans, ascidians	polychaetes, bryozoans, ascidians	polychaetes, bryozoans, sponges, ascidians	polychaetes, bryozoans
duration	9 months 4 months	21 months 21 months	3 years	2 years	10 years 3 years

Other southern polar studies include those of Pearse and Pearse (1991), who recorded very little on panels immersed for a year at McMurdo Sound, Davenport and Stevenson (1998), who recorded 3 species on panels at South Georgia, and Gerdes and Klages (unpublished data), who recorded 0 species after 1 year at 670 m in the Weddell Sea. A further study was set up in the South Shetland Is. more than 4 years ago but remains to be retrieved (Arntz pers. comm.).

Other northern polar studies include those of DePalma (1969), who recorded 8 species (7 at any one time) in Newfoundland, and Schoener et al. (1978), who recorded 8 species (8 at any one time) in southern Alaska and 10 species (7 at any one time) in Washington. The most recent experiment is the fouling over 2-3 years on Arctic moorings but is yet to be published (Arntz pers. comm.).

Stanwell-Smith and Barnes, 1997) at Signy Island in the South Orkney Islands were the first to report seasonal data. Both studies showed very low levels of colonisation compared to temperate or tropical studies (Fig. 5, Table 2). Whether or not rarity of pelagic larvae contributes to depressing colonisation rates is debatable, as many colonists at low latitudes are those with benthic larvae. Benthic recruitment studies also emphasise the disturbance in shallow water: both Rauschert (1991) and Barnes (1996) lost panels to ice and wave action. Schoener *et al.* (1978) had shown, despite site and year variability, that latitude was a major factor in explaining recruitment differences in northern hemisphere sites from the tropics to the Subarctic. Although most of Antarctica's coastline lies between 67 and 72°S, at no site within this latitudinal span had hard substratum recruitment been investigated until recently. The preliminary results of a new shallow water study by David Bowden at Rothera, Adelaide Island, suggests that colonisation rates were low compared to those at low-latitude sites but not nearly to the extent found by the two studies at Signy Island. The depressed colonisation values found by Barnes (1996) and Stanwell-Smith and Barnes (1997) may owe as much to the isolation of the South Orkney Islands as to their polar latitude. If this is true, it contrasts with a lack of strong isolation effects in other austral, but lower-latitude, recruitment studies (e.g. Holmes *et al.*, 1997). To date no large-scale nested studies of recruitment, such as those performed across the Great Barrier Reef (Hughes *et al.*, 1999), have included high latitude sites—this needs to be done to determine the scale at which we can really apportion variability.

Dayton (1989) considered that ice occasionally providing uplift for benthic larvae was important in shallow soft sediment environments in the Ross Sea. Such events might support the interannual variability he and co-workers reported of recruits to panels. Certainly ice patterns do seem to show short 4-8 year patterns as well as those on larger and smaller (seasonal) scales (Murphy *et al.*, 1995). Although many features of sediments have been well studied in the Scotia Arc and Antarctic Peninsula region, little is still known of recruitment to such habitats. Among rooted bryozoans, Winston (1983) found that many of the young colonies had grown from fragments of older ones, so much 'recruitment' was vegetative rather than from sexual origins. In soft sediment habitats, settlement in and invasion of scours, that is the recolonisation of ice denuded areas, has probably been the most studied aspect of recruitment. In deep waters the recruitment of pioneer species to scours has now been well documented in the Arctic (Conlan *et al.*, 1998) and Antarctic (Gutt and Piepenburg, 2003). In shallow waters bimodal distributions of bivalves (e.g. *Yoldia eightsi*) have been found in well-scoured sediments with entire cohorts missing (Peck and Bullough, 1993).

Recruitment into soft sediments occurs through both migration in and settlement onto surface muds. Peck *et al.* (1999) found that recruitment to new scours varied considerably between taxa: the more mobile elements of both macro- and meio-fauna were quickest. Recruitment of meiofauna, as with much of the ecology of this important fraction of the benthos, is poorly known, but work by a few teams is starting to rectify this (e.g. Skowronski *et al.*, 1998; Lee *et al.*, 2001a,b).

DIVERSITY AND RICHNESS

Half a decade of northern hemisphere work has led to a long and complex argument as to the cause of a 'global' latitudinal cline in biodiversity (see Pianka, 1966; Gray, 2001; Allen *et al.*, 2002). It is frequently referred to as the most recognised diversity pattern, despite the fact that such a trend has never been established in the southern hemisphere (Clarke, 1992). Investigations of global geographic diversity trends in bivalves (Stehli *et al.*, 1967; Crame, 2000) and corals (Stehli and Wells, 1971), for example, have found longitudinal components to be as strong as latitudinal. In gastropods (Roy *et al.*, 1998) and bryozoans (Clarke and Lidgard, 2000) strong pole-ward declines have been established, but their data were restricted to particular northern coasts only. Recently complex but broadly poleward declines have been described in decapods around South America (Astorga *et al.* 2003) and on North American coastlines (Boschi, 2000). A number of taxa, however, not only show no such decline in the southern hemisphere but even may have raised polar values. These include the brachiopods (Foster, 1974), bryozoans (Hayward, 1995; López Gappa, 2000), pycnogonans (Clarke and Johnston, 2003) and even molluscs (Valdovinos *et al.*, 2003). For such work the coastline of North America conveniently stretches from the tropics to the high Arctic, but the Patagonia-Scotia Arc-Antarctic Peninsula chain has an even greater latitudinal span. For investigation and explanation of large-scale trends in the distribution or characters of organisms, the Patagonia-Scotia Arc-Antarctic Peninsula link offers the best opportunity to evaluate latitude in the southern hemisphere. Early expeditions and collections revealed striking differences between the biota of the southernmost continent and its surrounding ocean, not least the near absence of some taxa, unusual abundance of others, extremely high endemism (see Arntz *et al.*, 1997), minute land fauna and, conversely, gigantism in some marine fauna. Exploring the continuity of such macro-ecological/evolutionary trends has, however, been heavily dominated by work around Europe and North America.

The many confounding problems of using historical data have again placed emphasis on ecological, multiple small-scale sampling across wide latitudinal ranges. For many decades surveys of shallow water benthos have been undertaken from the scientific bases of most nationalities in the Scotia Arc-Antarctic Peninsula region (see Arntz *et al.*, 1994; 1997). This information is very patchy in shallow waters. A number of detailed studies have addressed diversity patterns along the Chilean coast (Santelices and Marquet, 1998; Rivadeneira *et al.*, 2002), but few have been undertaken along Argentina and the Falkland/Malvinas (López Gappa 2000) or South Georgia islands and none (to the author's knowledge) in the South Sandwich archipelago. Studies in the South Orkney Archipelago have focused on just one island, Signy (Barnes, 1995a; Barnes *et al.*, 1996), whilst the sublittoral around the South Shetland and Palmer archipelagos in the northern Antarctic Peninsula are probably as well studied as some European and North American coasts (Gruzov and Pushkin, 1970; Zamorano, 1983; Rauschert, 1991; Arnaud *et al.*, 1998; Jazdzewski, 1998; Sahade *et al.*, 1998; Nonato *et al.*, 2000). Antarctic Peninsula sites can be highly speciose, as well as having high biomass and abundance values relative to those in the Arctic or even temperate regions (Brey and Clarke, 1993; Arntz *et al.*, 1997). Some of the highest values recorded have been at Adelaide Island at 68°S (Barnes and Brockington, 2003), but vertical surfaces at other locations, such as Signy Island (Fig. 3D), also clearly have high values. At Adelaide island 75 species were found in a total sample area of just 7.5 m^2 and 9 species were found in the intertidal—rich by Antarctic standards. Hard substratum samples taken within similar areas (about 4x 0.25 square m) at several depths at 5 sites along the Patagonia-Scotia Arc-Antarctic Peninsula are reported in the current paper for the first time (see Gerdes *et al.*, 1992 for a comparison of soft sediment and latitude within the Southern Ocean). Diversity was highest at the deeper depths (12-35 m) and patterns were similar both between sites and between the taxonomic levels used (Fig. 6). Thus higher taxon surrogacy for pattern analysis does seem valid for these data, albeit a

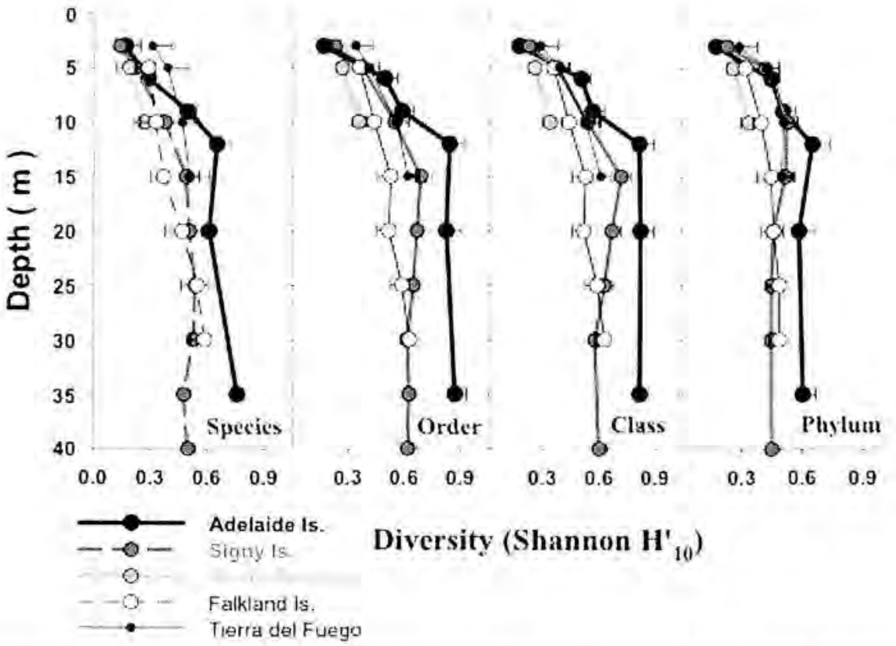

FIG. 6. – Benthic diversity (Shannon H' base 10) with site and depth in the Patagonia-Scotia Arc-Antarctic Peninsula region. South Georgia and Signy Is. occur in the Scotia Arc at 54°S and 60°S respectively. Adelaide Is. occurs at 68°S in the Antarctic Peninsula. Data from Barnes (1995b), Barnes and Brockington (2003) and author's unpublished collections.

small set. The lowest diversity (Shannon H') values were in the shallowest depths and in the Falkland/Malvinas and South Georgia. Thus, as with recruitment to settlement panels, low values are associated with isolated islands, but diversity at Signy Island, also in an isolated archipelago, was as high as at Tierra del Fuego.

Elsewhere in the world comparable methods have been used at similar, though northern latitudes. Maughan and Barnes (2000), in the subtidal zone of SW Ireland (51°N), found uniformly fewer (range 10-67, mean 43) species at 3-18 m depth in mean sample areas of 2.747 m^2. On the west Atlantic seaboard (Maine), Ojeda and Dearborn (1989) encountered just 60 species from sampling an area 14 times the size of the areas sampled here in the rocky subtidal. At a lower latitude, e.g. Milos Is., a site of established regional (Mediterranean Sea) benthic richness (Morri *et al.*, 1999), numbers of hard substratum shallow benthic species were comparable with SW Ireland and lower than at Tierra del Fuego, Signy and Adelaide islands. In contrast, typical temperate and tropical species richness in the littoral zone is probably an order of magnitude higher (e.g. McGuiness, 1990; Maughan and Barnes, 2000). The taxon richness values at the Patagonia-Scotia Arc-Antarctic Peninsula sites studied here are very high in comparison with typical Arctic sites (see Dayton, 1990; Arntz *et al.*, 1994). Just 3-42 species m^2 have been found at similar depths by a number of studies in the high Arctic from 10 x the sample area (author's unpublished data, Holte *et al.*, 1996; Sjer *et al.*, 2000). There are, however, highly improverished subtidal faunas in the Scotia Arc and along the Antarctic Peninsula, such as the South Sandwich Islands and the wind- and wave-swept Snow Island (Barnes and Arnold, 2001a,b). At some isolated Subantarctic localities, such as Marion Island, considerable sublittoral species richness (64-106 species in 0.4 m^2 area, 203 species in 4 m^2) has been reported (Becley and Branch, 1992). Although they are not completely barren, intertidal zone species richness and diversity on Antarctic shores is substantially reduced. In Tierra del Fuego, and to a lesser extent the Falkland/Malvinas, a wide range of animals and animal taxa are still common on sheltered shores. Pugh and Davenport (1997) did report a number of colonists on some littoral areas of South Georgia, but typically these shores have a very reduced presence of algae and animals. Further south, Rauschert (1991) and Barnes and Arnold (2001a,b) found 5 or fewer littoral species in large sample areas at Signy Island and various Antarctic Peninsula islands. Only at Thorgerson Is. (Palmer Archipelago) and Adelaide Island were as many as 9 littoral species found. The most common hard substratum species are generally the copepod *Tigriopus angulatus*, the limpet *Nacella concinna*, cheilostome bryozoans (e.g. *Inversiula nutrix*) and amphipods (e.g. *Hippomedon kergueleni*). On soft sediment shores (which are rare) amphipods and a variety of worms, such as sipunculans (e.g. *Golfingia margaritacea*) and priapulans (e.g. *Priapulus tuberculatospinosus*) are typical. The species richness of southern polar shores may be poor but most of them also represent different phyla. This mirrors the substantial higher taxon richness of the subtidal: 16 animal phyla and 25 classes were represented in 10 m^2 at Adelaide Island. The combination of high space coverage, densities and richness in the subtidal zone and the fact that the system is almost certainly less complex than those at lower latitudes, should have made this region ideal for investigations of major ecological concepts such as competition for resources.

COMPETITION

It has long been thought that competition and predation are more severe with decreasing latitudes whilst environmental factors become more severe (see McGuiness, 1990). Such a difference between temperate and tropical regions has been hard to demonstrate because of confounding issues such as variability between sites, localities or regions and differences between taxa, basin ages and other variables. The vigourous research in polar regions has not yet, however, spread to competition in either polar marine realm. This may in part be due to the historical assertion that resources need to be limiting for competition to occur (Connell, 1978) and the assumption that in polar seas disturbance is high and empty space is common in young communities (Fig. 3E). However, many areas, such as cliffs, overhangs, crevices and caves are ice-sheltered, competition can be intense on assemblages a few years old (Fig. 3F) and there is virtually no free space on those unscoured for decades (Fig. 3D). In the ecological literature there is an abundance of studies in cool temperate North America and NW Europe. Much discussion has focused on the outcomes of competition, such as the importance of tied vs decided interactions (Schmidt and Warner, 1986), reversals in outcome between competitor pairs (Chornesky, 1989) and levels of transitivity (how hierarchical an assemblage is) (Russ, 1982; Tanaka and Nandakumar, 1994). How competition is structured on hard surfaces is of fundamental importance to recovery from disturbance and generation of diversity: in a strict hierarchy an ultimate dominant species should emerge and monopolise most space. This has been found to happen in a number of hard substratum environments. In such places diversity can be maintained either by mechanical or biological disturbance removing clumps of fauna and exposing space. Dayton (1971) found that floating logs smashed gaps in mussels which otherwise smothered the coast and Paine (1974) found that a keystone predator, *Pisaster*, acted similarly, opening up opportunities for competitive inferiors. This is equivalent to pioneer trees growing in the clearings made from the destructive fall of competitively superior trees. On Atlantic (Jackson, 1979) and Indo-West Pacific coral reefs (Chornesky, 1989), intransitive networks prevail in competition—resulting in so many ties or reversals in outcome that large numbers of species can exist side-by-side. Work in Patagonia (López Gappa, 1989), the Scotia Arc (Barnes and Arnold, 2001a) and the Antarctic Peninsula (Barnes and Clarke, 1998) showed that high latitude assemblages were more hierarchical than any other assemblages previously measured. The clashes between the encrusting animals of these southern polar communities rarely resulted in ties and the competitive dominant species overgrew any competitor encountered on virtually all occasions. Only in vertebrate intraspecific battles for status had such hierarchies previously been established (Clutton-Brock *et al.*, 1979; Wagnon *et al.*, 1996). There thus seems to be a latitudinal cline in the structure of competition, and therefore in the mechanism of succession in shallow marine environments (Barnes, 2002a). An obvious note of caution, though, is that there are comparatively few tropical data, so the low values of the few low latitude studies may be driving the significance of the relationship. The cline is still supported, though, even when just the southern polar data are examined (Fig. 7). The significance of this trend in competition as a

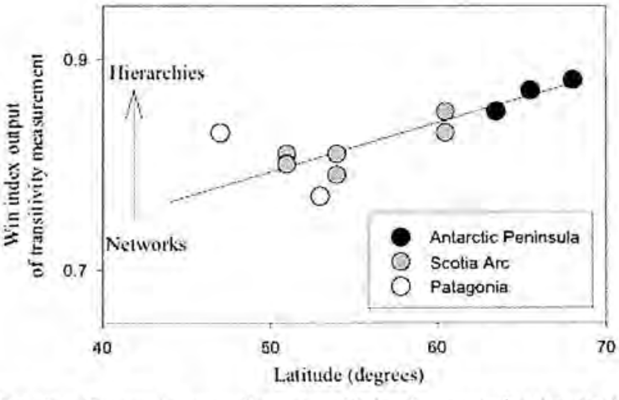

FIG. 7. – Change in assemblage transitivity (in encrusting benthos) with latitude in the Patagonia-Scotia Arc-Antarctic Peninsula region. Y axis is assemblage score on Tanaka and Nandakumar's (1994) index. Plot adapted from Barnes (2002a).

structuring force is that typically in the tropics no environmental disturbance is required to maintain high levels of local diversity. At polar latitudes, in contrast, without disturbance, competitive dominants would monopolise vast areas of shallow benthic space (on hard substratum) and poorer competitors would be shut out completely. With current (high) levels of disturbance, diversity and richness is also low as assemblages are numerically dominated by fast growing pioneer species (Barnes and Clarke, 1998). Thus, with extremely high or low disturbance only one or two species prevail in an environment which at mid-levels (on the larger boulders, see Barnes *et al.*, 1996) can support tens of species in just a square metre. As such, this system represents one of the best examples of the intermediate disturbance hypothesis (Connell, 1978; Huston, 1979) at local scales for hard substrata. Examples of poor competitors dominating assemblages are known from elsewhere in the world (Karlson, 1980; 1983; Paine, 1979), but in the Antarctic this phenomenon occurs along vast areas of hard bottom coastline. Therefore, although only small areas of space are occupied in very shallow waters around the Scotia Arc-Antarctic Peninsula, competition is common and severe. Only the regularity and catastrophic nature of disturbance enables pioneer species; the fast dispersers dominate what little space the fauna occupies. This 'rapid' colonisation of new space does involve adult movement as well as larvae recruiting into it, but speedy physical movement of animals in this entire region is unusual.

METABOLISM AND ACTIVITY

One of the most striking features of southern polar shallow water communities to an *in situ* observer is how little movement there is, despite (in places) high densities, biomass and richness. Sessile or sedentary suspension feeders and deposit feeders often comprise the major part of communities (see e.g. Gruzov and Pushkin, 1970; Winston and Heimberg, 1988; Gerdes *et al.*, 1992; Barnes, 1995a) and are increasingly seen as playing a fundamental role in food webs (Gili and Coma, 1998). Even invertebrate predators such as nemertean worms, certain gastropods, pycnogonans and asteroids can still have moved less than a metre in a week. Greatly speeded up film has revealed some remarkable nemertean chases of limpets and burrowing and wriggling of bivalves over actual periods of many hours (Peck, pers. com.). The success of some fauna in such areas as polar seas and abyssal plains has been based on their living life in the slow lane (Emson, 1985). Certainly many of the highly successful fauna (e.g. bryozoans, brachiopods, echinoderms and hexactinellids [now placed in the phylum Symplasma]) are mainly bone and do not move or move only slowly. Even southern polar fish are usually fairly sluggish. They more than any other taxa have been important for larger scale comparisons of latitude and temperature on physiology such as muscle oxidative capacity (Johnston *et al.*, 1998) and metabolic scaling (Clarke and Johnston, 1999). Again, the Scotia Arc and Antarctic Peninsula has been the focus for virtually all analysis of activity and metabolic rates, and how these link with environmental factors such as temperature. The normal oxygen consumption or resting metabolic rate has now been measured in quite a wide variety of animals (Fig. 8). Two decades ago almost nothing was known about the 'tick-over' of polar invertebrates but in the last two decades we have gained insight into oxygen use in a wide variety of taxa. Typical values stretch over approximately an order of magnitude (30-300 $\mu g\ O_2.g\ AFDM^{-1}.h^{-1}$) and seem to vary as much within as between taxa and lifestyles. For example, the highest and lowest values to date are both in sessile bryozoans. Though some of this work has been undertaken in places such as Kerguelen Island (Féral and Magniez, 1988), most has arisen from studies in the Scotia Arc and Antarctic Peninsula. When the values of these southern polar species in any group are compared with values for low latitude representatives (in those for which this comparison is possible), polar animals seem to have depressed metabolic rates but not metabolic cold adaptation (Peck, 1998; 2002).

Cold water does of course hold more gas than warm water, which in combination with great wave action and cold, dense surface water sinking means that southern polar waters are well oxygenated. After decades of argument and guesswork, oxygen availability has proved to be fundamentally linked to animal size (Chapelle and Peck, 1999). The idea of 'polar gigantism' inspired by huge isopods (e.g. *Glyptonotus antarcticus*) and pycnogonans (*Decalopodium australis*), amongst other animals, is simply an artefact of the high oxygen in cold polar waters. Predominantly Southern Ocean benthos such as molluscs, amphipods and isopods are small (see Hain, 1990; De Broyer and Jazdzewski, 1993; Brandt, 1999, respectively). Hain (1990) reports that

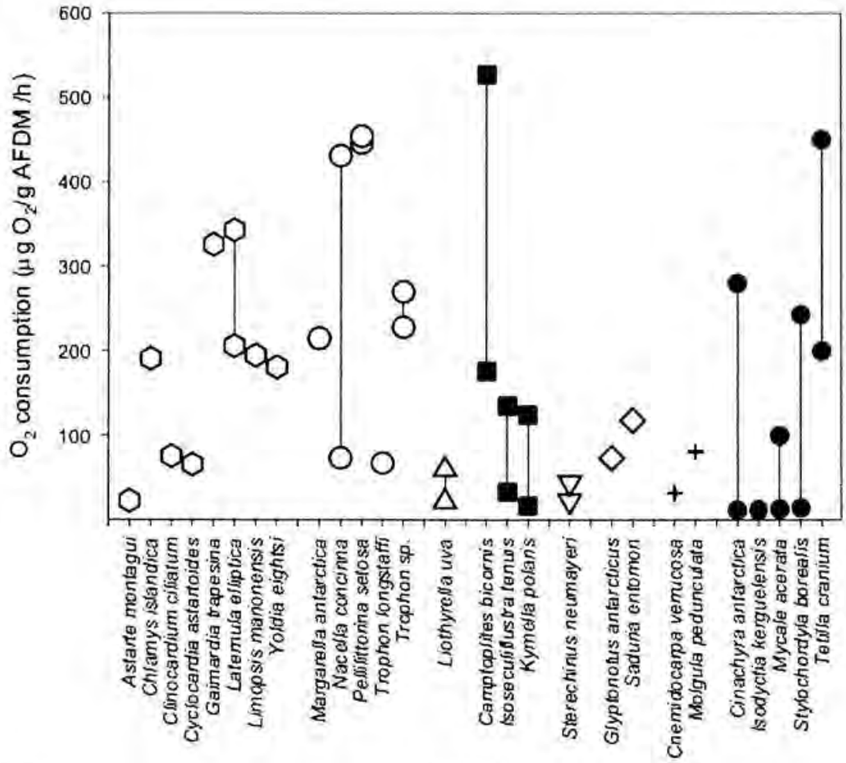

FIG. 8. – Mass-specific oxygen consumption measures ($\mu g\ O_2.g\ AFDM^{-1}.h^{-1}$) in a range of polar marine invertebrates. The taxa are bivalves (hexagons), gastropods (open circles), a brachiopod (triangles up), bryozoans (filled squares), an echinoid (triangles down), isopods (diamonds), ascidians (crosses) and sponges (filled circles). Figure modified from Harper and Peck (2003) with data for bryozoans, echinoid, isopods, ascidians and sponges added. Data from Ralph and Maxwell (1977), Houlihan and Allan (1982), Davenport (1988), Schmid (1996), Peck *et al.* (1997), Ahn and Shim (1998), Pörtner *et al.* (1999), Gatti *et al.* (2000), Gatti and Orejas (2000), Brockington (2001), Kowalke *et al.* (2001), Robertson *et al.* (2001) and Peck and Barnes (2003). Lines show ranges of data for a given species.

55% of molluscs are smaller than 10 mm, for example. Nevertheless, because of the high oxygen levels in southern polar waters, giants occur. These include the largest bryozoan colonies and sponges (1.5 m high or long), ctenophores (50 cm long) and nudibranch molluscs (30 cm long) (all pers. obs.). This strikes a strong contrast with not only the true terrestrial fauna, which are tiny (the largest are mites a few mm in size), but also typical animals in very shallow or deep waters. In the subtidal biota are so frequently hit by ice that populations are frequently formed of small (and young) individuals (Peck and Bullough, 1993; Urban and Campos, 1994; Barnes and Clarke, 1998; Urban and Mercuri, 1998; Brockington, 2001). The great size achieved in some taxa as a feature of this extreme environment was merely one of a number of major curiosities and themes of research into the growth of polar ectotherms.

SEASONALITY OF FEEDING, GROWTH AND REPRODUCTION

Investigations into feeding, growth and reproduction of polar invertebrates are necessarily also studies of seasonality. Seasonality is a major feature of shallow benthic communities across much of the globe and comparable responses of organisms can be seen in environments as seemingly dissimilar as the Mediterranean Sea and the Southern Ocean (Coma *et al.*, 2000). The extreme nature of the light climate in the water column is further exaggerated by formation of sea-ice and overlying snow further decreasing light penetration in autumn or spring. Thus, abundant food availability to primary consumers is highly restricted to just a few months a year (Clarke, 1988). However, rather than all suspension feeders closing down and 'hibernating' for the majority of the year (see e.g. Gruzov, 1977), there is clearly a range of strategies varying from feeding for a couple of months to throughout the year (Barnes and Clarke, 1995). Feeding for long periods is possible in some taxa because they feed on the smaller nanophytoplankton (ciliates and flagellates), rather than the larger diatoms which dominate typical Southern Ocean blooms (Clarke and Leakey, 1996). Resuspension of particles, by currents or iceberg scouring, may also be important for non-summer feeding—benthic diatoms have, for example, been found in the stomachs of brachiopods during winter (Peck *et al.* unpublished data). As in several areas of ecology, in just a decade we have moved from a situation of almost no hard data to one in which we now have established the seasonal patterns of feeding for representatives from a wide variety of taxa. Even taxa traditionally regarded as difficult to examine feeding in, such as sponges and ascidians (see Gatti and Orejas, 2001; Kowalke, 1999; Tatián *et al.*, 2002; Sahade *et al.*, 2004 respectively), are beginning to be tackled. Typical seasonal patterns of plankton availability and feeding by a gastropod, an echinoid, an ascidian and a bryozoan are shown in Figure 9. Of course, nanoplanktonic food is not the dominant food for all of these or many other suspension feeders and the narrow feeding windows of some taxa, such as the holothurians (Barnes and Clarke, 1995), may be due to a reliance on the highly seasonal diatom abundance. One of the potential sources of food that we know little about and we should, perhaps, be making an effort to study is the bacterial picoplankton. Overall we probably now have good data for feeding of Antarctic suspension feeder communities and this has allowed comparisons between other areas for which there has been a large body of work, such as the Mediterranean Sea (Coma *et al.*, 2000; Gili and Coma, 1998). They suggest strong similarities between tropical/subtropical and polar suspension feeders, which are predominantly feeding in clear waters in contrast to those in temperate regions with high particulate run-off even far from the coast.

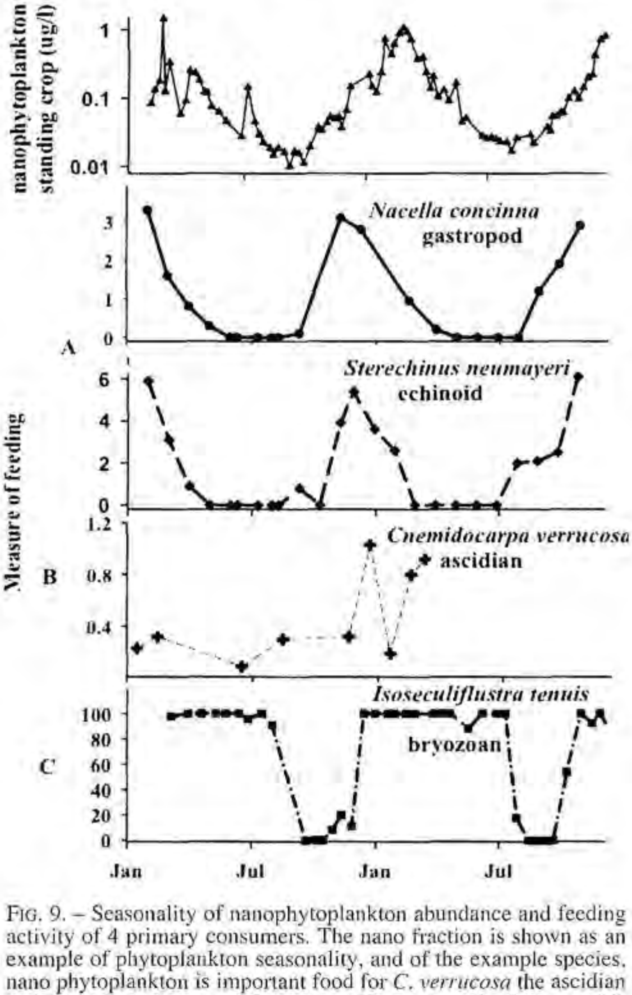

FIG. 9. – Seasonality of nanophytoplankton abundance and feeding activity of 4 primary consumers. The nano fraction is shown as an example of phytoplankton seasonality, and of the example species, nano phytoplankton is important food for *C. verrucosa* the ascidian and *I. tenuis* the bryozoan. In contrast *N. concinna* the limpet and *S. neumayeri* the echinoid feed on benthic material and larger particles. The axes are faecal egestion [faeces mg.individual dry mass $(g)^{-1}$](A), gut content dry mass.g (B) and per cent colonies feeding (C). Data are from Fraser *et al.* (2002), Brockington *et al.* (2001), Tatian *et al.* (2002) and Peck and Barnes (2003).

In contrast to the work on feeding, which has focused on the Scotia Arc and Antarctic Peninsula (but see Gatti and Orejas, 2001), that on growth has been going on right round the Southern Ocean and is now one of the best known aspects of the Antarctic benthos (Arntz *et al.*, 1994). Historically, much investigatory study has focused on fish (e.g. Wohlschlag, 1961; Burchett, 1983; Everson, 1984), due to obvious potential commercial applications, but here I will discuss progress on other taxa. Work on the duration, timing of initiation and cessation of feeding has helped interpret the patterns of growth, such as the establishment of growth check lines of some animals as annual (Barnes, 1995b). The production of growth check lines in taxa such as the molluscs (Lutz and Rhodes, 1980), bryozoans (Winston, 1983), brachiopods (Brey *et al.*, 1995a) and echinoids (Brey *et al.*, 1995b) is a major source of information. This provides not only the extent of annual growth (and so annual variability), age (and so variability with age) but also—by comparison to local primary productivity—relationships between the duration of food availability and growth. Use of stable isotopes has shown some high Antarctic bivalve, brachiopod and bryozoan growth check lines to be annual (Brey and Mackensen, 1997; Brey *et al.*, 1999a,b). However, one the most common shallow water brachiopods produces growth check lines at a frequency of 1.8 years and has decoupled reproductive and somatic growth (Peck and Brey, 1996). These authors showed that shells of species, e.g. *Liothyrella uva*, living to great age are an environmental archive recording such events as atomic bomb tests decades ago. Most taxa do not, however, produce obvious 'readable' growth check lines. Early assessment of a taxon, the crustaceans, seemed to suggest slow growth (Littlepage, 1965; Oliver, 1979), which now seems to be typical for southern polar benthos (Arntz *et al.*, 1994). It has

TABLE 3. – Growth and reproductive tempo in benthic Antarctic animals in comparison with non-polar taxa. The symbols are Antarctic Peninsula (AP) and Scotia Arc (AC).

taxon	growth tempo	reproduction	location	source
sponges	slow, very few fast		Ross Sea	Dayton *et al.* 1974, Dayton 1979, 1989; Gatti *et al.* 2002
cnidarians		slow	Ross Sea	Oliver 1979, Orejas *et al.* 2002
nemerteans		slow	SA, Ross Sea	Dearborn 1965, Peck 1993
annelids		highly diverse strategies	Magellan Weddell Sea	Pearse *et al.* 1986, Gambi *et al.* 2000; 2001
crustaceans	slow	slow	South Georgia, AP, Ross Sea	Littlepage 1965, Dearborn 1967, White 1970, Oliver 1979, Luxmore 1982, Clarke 1985, Marinovic 1987, Wägele 1987
molluscs	slow to very slow	slow	SA, AP Macquarie Is Ross Sea	Shabica 1974, Ralph and Maxwell 1977, Simpson 1977, Richardson 1979, Stockton 1984, Berkmann 1990, Peck and Bullough 1993, Brêthes *et al.* 1994, Urban and Mercuri 1998, Powell 2001
brachiopods	slow to very slow	slow	SA, Weddell Sea	Brey *et al.* 1995a, Peck *et al.* 1997, Peck and Brey 1996
bryozoans	slow to comparable	slow	AP, Patagonia, Ross Sea, Weddell Sea	Winston 1983, López Gappa 1989, Barnes 1995b, Stanwell-Smith and Barnes 1997, Brey *et al.* 1999a,b, Barnes and Arnold 2001b, Cancino *et al.* 2001
echinoderms	slow	slow	SA, AP Kerguelen Is Macquarie Is Ross Sea, Weddell Sea	Pearse 1965, Simpson 1982, Magniez 1983, Yakovlev 1983, Bosch *et al.* 1987, McClintock and Pearse 1987, McClintock *et al.* 1988, Pearse *et al.* 1991, Gutt *et al.* 1992, Brey *et al.* 1995b
ascidians	moderate - fast		AP	Rauschert 1991, Kühne 1997, Sahade *et al.* 1998, Kowalke *et al.* 2001, Sahade *et al.* 2004
fish	slow	slow	SA, AP, Antarctica	Wohlschlag 1961, Burchett 1983, Everson 1984, di Prisco *et al.* 1991

now been widely reported both that typical organic growth is slow and that there are exceptions (Dayton, 1989; Rauschert, 1991). Some Antarctic pioneer species have been reported as having tempos of growth which were 'fast' or comparable to low-latitude species (Barnes, 1995a; Dayton, 1989; Rauschert, 1991), but this is really only relative to typical temperate values. If the fastest polar species are compared with the fastest low-latitude species, i.e. pioneers compared with pioneers (like with like), growth seems universally slower in the polar realm. However, many polar animals are growing for only a short period, if the tempo of growth whilst actually growing is compared between polar and non-polar environments, growth may indeed be comparable (Barnes, 1995a). Here I would stress the importance of linking knowledge of precise food taken, its duration of abundance, feeding behaviour and allocation between somatic and reproductive development.

The tempo of reproduction, like growth, seems to be typically slow (Table 3). This is easiest seen in rates of larval development. Compared to temperate species echinoderms take up to 10x longer (Bosch *et al.*, 1987; Hoegh-Guldberg and Pearse, 1995; Stanwell-Smith and Peck, 1998), bivalves take up to 15x longer (Powell, 2001) and brachiopods take up to 50x longer (Peck and Robinson, 1994). Again, like work establishing patterns of Antarctic invertebrate growth, reproductive strategies represent some of the earliest ecological work right around the shores of Antarctica. Even before the establishment of Thorson's rule (Mileikovsky, 1971), ecologists were intrigued by reproduction in cold water (Dearborn, 1965; 1967; Pearse, 1965). Several decades of study later, it remains true that molluscs have a high proportion of brooders and direct developing young and that some brooding taxa, such as the isopods, amphipods and pycnogonans, have achieved a high level of success (see Arntz *et al.*, 1994 for general review). Pelagic larvae of many taxa have, in places, been found to be abundant in Antarctic waters and can be released into the water column at various times (Stanwell-Smith *et al.*, 1998). Conversely, Arntz and Gili (2001) suggest that in comparison with temperate latitudes pelagic larvae are comparatively rare in open-ocean areas south of the PFZ. There are certainly taxa that arguably (see Arntz and Gili, 2001) do not seem to follow Thorson's rule (Pearse *et al.*, 1991) and on investigation some have a remarkable diversity of strategies (Gambi *et al.*, 2000; 2001). One of the most important perspectives to emerge recently is the contrast between evolutionary vs ecological success of particular reproductive strategies. Amongst the echinoids, for example, most extant Antarctic shallow water species are brooders but the super-successful Echinidae are broadcast spawners (Poulin *et al.*, 2002). Similarly amongst the molluscs, despite the prevalence of brooding, many of the most successful species (e.g. the limpet *Nacella concinna*) are also broadcast spawners with planktotrophic larvae. Poulin *et al.* suggest that this is due to selective extinction of those with pelagic larvae, probably during times when expanding ice sheets bulldozed fauna off the shelves into deeper water. Those pelagic spawners that did survive are much more able to quickly colonise shallow water environments, especially habitats with high rates of ice-scour disturbance where populations of adults are regularly destroyed. Alternatively, Pearse and Bosch (1994) argue that the nature of the circum-polar current might favour selective speciation of brooders (rather than selective extinction of broadcast spawners). There may be a middle ground between these ideas in which both selective extinction of broadcast spawners and selective speciation of brooders explains the current situation (Pearse and Lockhart, in press). The new emphasis on the importance of long-term data sets in marine biology is filtering through to the polar scientific community. Now that multiyear data sets exist for comparison of feeding, growth and reproductive patterns for a number of species, these could prove to be vital evidence in marine organism response to climate change.

SEAS OF CHANGE

Scientists across the world are quantifying all manner of changes in the biosphere at the current time, but then to our knowledge, many things have always been changing—it is the pace that differs. The large predators are disappearing from the world ocean environment to be replaced by man at the top of each food web (Jackson *et al.*, 2001; Myers and Worm, 2003). Nowhere is this fishing depletion more obvious than in the Southern Ocean, where huge populations of the largest animals to ever populate the planet, the *Balaenoptera* whales, have been reduced to mere thousands of individuals (Roman and Palumbi, 2003). In terms of benthic habitats, though, those around the Antarctic continent must be amongst those least affected, as large vertebrates (such as teleost fish [though these can be major consumers of benthos], sharks, marine reptiles and mammals) have little structuring influence compared with elsewhere. Over the last century, when much of the fishing damage has been done, the earth's climate has warmed by about 0.6°C. Across habitats there has been a major phenological (timing of activity) response from organisms, such as earlier flowering, migrant arrival and breeding (Walther *et al.*, 2002). In the Arctic and west Antarctic, however, the temperature rise has—regionally at least—proved even more dramatic (Quadfasel *et al.*, 1991). Both the highest increases of air temperatures (King and Harangozo, 1998) and lake temperatures (Quale *et al.*, 2002) have been measured around the Scotia Arc-Antarctic Peninsula region. Quale *et al.* (2002) described this as nearly 1°C in the lakes of Signy Island in just a decade. The signal in the sea is not as clear and model estimates of 2°C change over the next 80 years have associated errors as large as the predicted values of change (Murphy and Mitchell, 1995). The rapid retreat and disintegration of ice shelves is suggested as a sign of drastic warming along coastal Antarctica (Doake and Vaughan, 1991). In just over half a century the ice shelf adjacent to the British Antarctic Survey Station of Rothera has retreated 2 km but the majority of this has occurred in just the last decade (Fig. 10). Similar retreats are being quantitatively marked in Patagonia and elsewhere in the world (though perhaps not in the high Antarctic). Considering that so many of the Southern Ocean's benthos is known to be highly stenothermal, they are an obvious group of organisms to act as indicators of biotic response. To have a massive effect on the biota, temperatures almost certainly do not need to rise to the point of killing animals through thermal shock but merely to functional limits whereby animals are not capable of feeding, reproducing or adequately defending themselves.

Generally associated biotic responses to changing temperatures are altitudinal and latitudinal range shifts, but also in the context of isolated Antarctic biota there is an increased possibility of invasions or survival of propagules. Unlike all other marine (and all terrestrial) environments, the Southern Ocean is

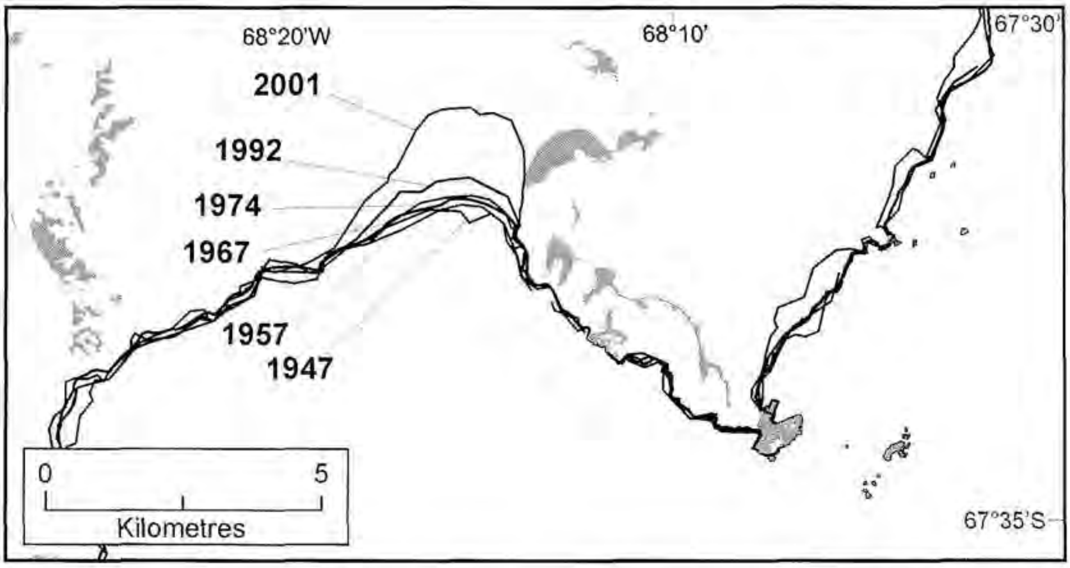

FIG. 10. – Coastline changes (ice sheet retreat) at Adelaide Island, Antarctic Peninsula over half a century. Data courtesy of Alison Cook (Mapping and Geographic Information Centre, BAS).

the only realm in which no invasive species are yet known. However, a few larvae of some decapod crustaceans and adults of others have recently been found around the South Shetland Islands (Thatje and Fuentes, 2003; and Tavares and Melo, 2004 respectively). Anomuran (lithodid) crabs, long known from South Georgia, are now present in deep water (200+ m) off the Antarctic Peninsula (Boschi and Gavio, 2003), though whether they have recently invaded this habitat or been there a while is unknown. In the Arctic lithodid crabs introduced to the Barents Sea have certainly undergone a major migration west across Subarctic Norway in just the last decade (Fletcher and Gollasch, 2003). It seems that it is only a matter of time before the first marine invaders establish a breeding population in the Southern Ocean. The region's best protection, sea temperatures barely above freezing in summer and nearly –2°C in winter, may be on their way up if the predictions of the Hadley Centre model are born out (Murphy and Mitchell, 1995). We should be concerned, not only because Antarctic seas are the only ones left without known invaders but also because the fauna there has levels of endemism of ~75-90%—higher than anywhere else (Arntz *et al.*, 1997). These values may appear very high partly because the Southern Ocean is big, and clearly the larger the area considered the higher its endemism (at m scale it is ~0% and at global scale 100%). Also, with increasing research some Antarctic species may have wider distributions, thus reducing the level of southern polar endemism. Nevertheless, it is likely that the real values of Antarctic endemism are indeed high. Endemics, frequently the species that are out-competed or eaten by introduced species, are gone forever if lost because, by definition, they occur nowhere else.

One of the most likely potential mechanisms of marine invasions is in ship ballast water or due to fouling hulls. Although shipping in general is not on the increase, those carrying scientists and particularly tourists to the Scotia Arc and Antarctic Peninsula regions certainly are. However, there is another source of transport to fouling organisms more numerous than ships, increasing faster and travelling to any shore: plastic debris. In the last two decades this has been increasing dramatically on even remote southern Atlantic islands (Ryan and Moloney, 1993) and reaching Southern Ocean islands before people have even set foot on them (Convey *et al.*, 2002). By the early 1980s Subantarctic and Antarctic island shores right round the continent had plastics, tars and other debris washing up on them (Gregory *et al.*, 1984; Torres and Gajardo, 1985; Ryan, 1987; Eriksson and Burton, 2001). Some of the longest data sets anywhere for the build-up of sea plastics are in the Scotia Arc-Antarctic Peninsula region (see e.g. Torres and Gajardo, 1985; Torres and Jorquera, 1996). With no longer any forests and only rare volcanic activity there are very few natural agents of flotsam within the Polar Frontal Zone, so the increase has been proportionally greater here than anywhere else. Of course, drifting macroalgae have probably been carrying float-

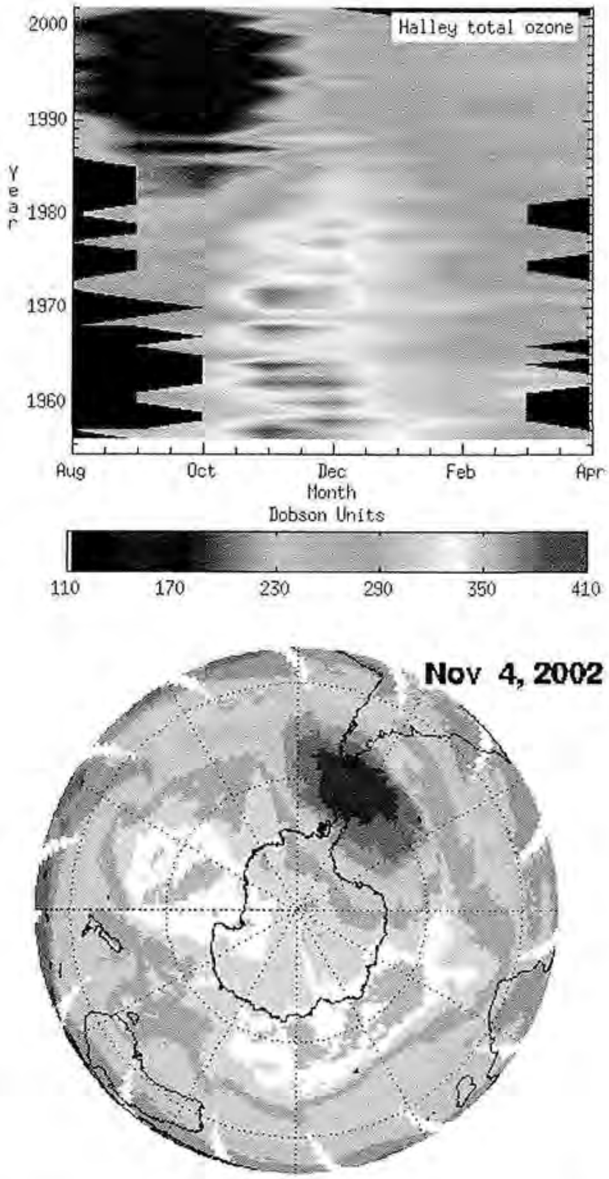

FIG. 11. – Stratospheric ozone changes with season and year, over nearly half a century, over the East Ronnie Ice Shelf (upper) and the geographic extent of the 'ozone hole' on Nov 4th, 2002. Data from Shanklin (2001) and NOAA.

ing biota for considerable periods of time, but they break down more quickly (in wave action or UV light), are now much rarer than artifacts, and many organisms preferentially settle on plastic (Barnes, 2002b). Just half a century ago plastics and other artefacts were rare at sea or on any islands; now it is rare for anywhere to be without them and a large proportion may carry attached biota (Barnes, 2002b). Recently just a single piece of floating plastic was found with 10 species from a total of 5 phyla washed onto an Adelaide Island shore, showing that, as in the tropics, diverse assemblages of animals can raft in the Southern Ocean (Barnes and Fraser, 2003). Worryingly, this seems to be an increasingly likely method of non-native species entering Antarctic waters, as the amount of material entering the seas keeps growing.

Production of waste has had another (though indirect), much better-known, influence on the polar regions: halogenated carbon molecules and other compounds of anthropogenic origin react in the stratosphere attacking ozone molecules. In the mid-1980s large total losses of stratospheric ozone were discovered (Farman *et al.*, 1985). The seasonal opening up of an 'ozone hole', which exposes organisms to higher doses of UV irradiation, has increased in intensity since its discovery (Fig. 11 upper). The area of depleted ozone is mobile and sometimes spans southern Patagonia to the northern Antarctic Peninsula (Fig. 11, lower). Penetration of UV into the water column is poor but is likely to have strong effects on the already fragile intertidal and shallow subtidal (Häder *et al.*, 1998), and the impact on terrestrial ecosystems in the region and elsewhere has already been reported (Rozema, 1999; Newsham *et al.*, 2002). The change from complete UV shielding to full exposure with retreat of snowpack in spring meltback is likely to be dramatic to the 'life on the edge' in the intertidal as it is to terrestrial organisms (Cockell *et al.*, 2002).

CONCLUSIONS

The Patagonia-Scotia Arc-Antarctic Peninsula has proved to be an important place for scientific research in the last half century and particularly so in the last decade. The density of scientific stations is greater than anywhere else in Antarctica, as is the increase in the influence of man, most noticeably with the rapid rise of tourist vessels and marine flotsam. It seems to be a pivotal place for various aspects of climate change as well as studies on biogeography and biodiversity. Some of Antarctica's longest environmental data sets occur there and some of the key recent scientific advances in understanding scale, pattern and process in Southern Ocean benthic ecology have been made there. The sampling is patchy within this region but levels of knowledge are now approaching those for other shelf environments elsewhere in the world. There remain adjacent areas which are still very poorly known, however, like the Bellingshausen Sea. The next decade should see a strong push in expansion from predominantly organism and population work to work ranging from the subcellular level, through organism and populations, to ecosystems, with emphasis on the importance of each scale of evolution and ecology in Antarctica's benthos. We have some crucial questions to answer; many involve the past, such as when exactly did the Drake Passage open sufficiently for the circumpolar current to develop in deep water? As ice-shelves have started to retreat now can we interpret the patterns of colonisation with a view to explaining how recolonisation may have happened in the past? When ice-shelves expanded and bulldozed shallow faunas to the shelf-edges (Clapperton and Sugden, 1988), were their refuge shelf areas that were not covered and can we link these periods in time to extinctions and subsequent radiations? Are larvae and/or adults crossing the Polar Frontal Zone regularly and are they doing so naturally or aided by man? How frequently do icebergs scour the seafloor and how does this change with depth and geography? How will sea temperature, circulation and ice-scour alter, and how will the biota react in the face of climate change? There are many questions to be answered and most will have a profound impact on our understanding of the world north of the PFZ. As just one example, the range of latitude covered by Patagonia, the Scotia Arc and the Antarctic Peninsula make it the only location for examining whether the northern diversity-latitude relationship really holds true in the southern hemisphere. Scientists in the Patagonia-Scotia Arc-Antarctic Peninsula in the last 10 years have played a major role in shaping the concepts and current paradigms in benthic ecology—it will be important not to lose this momentum.

DEDICATION

The author would like to dedicate this paper to Kirsty Brown, who lost her life in July 2003 when attacked by a Leopard seal at the British Antarctic Survey's Rothera research station. She was undertaking cutting-edge work trying to measure how often and when ice actually scrapes the seabed. Kirsty was a dynamic, enthusiastic and extremely popular scientist with a bright future: she will be a big loss to the southern polar scientific community.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
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Distribution patterns of Chilean shallow-water sea anemones (Cnidaria: Anthozoa: Actiniaria, Corallimorpharia), with a discussion of the taxonomic and zoogeographic relationships between the actinofauna of the South East Pacific, the South West Atlantic and the Antarctic*

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SUMMARY: The first complete zoogeographical analysis of Chilean shallow water sea anemones (Actiniaria and Corallimorpharia) and their taxonomic relations with neighbouring faunas is provided, based on extensive recent sampling in combination with a literature review. Between 1994 and 2004, we collected more than 1000 specimens of 32 distinct species of Actiniaria and Corallimorpharia at more than 100 sites along the Chilean coast between Arica (18°30'S; 70°19'W) and the Straits of Magellan (53°36'S 70°56'W). Sampling was done in the intertidal during low tides and in the subtidal by means of SCUBA diving down to depths of 40 m. The northern part of the Chilean fjord region showed the highest number of species (23). Our results contradict an abrupt general change in the marine faunal composition at 42°S, instead showing the continuation of species of the exposed coast and the joining of fjord species due to the availability of additional habitats in the richly structured fjord region south of 42°S, and also to eurybathy. The southern distribution limits of the species we found in northern and central Chile show only one significant concentration around the Peninsula Taitao (approx. 48°S). This either indicates a zoogeographic barrier for shallow water species at the Peninsula Taitao, or is a sampling artifact caused by poor data from the region between the Peninsula Taitao and the Straits of Magellan. According to the literature, 18 of the 63 described Chilean sea anemones (Pacific Ocean) can also be found in Argentina (Atlantic Ocean) and 13 in the Antarctic. However, many records and statuses of the common species of the South East Pacific and the South West Atlantic/Antarctic are uncertain or doubtful and need revision or confirmation.

Keywords: Actiniaria, Corallimorpharia, species list, zoogeography, distribution, benthos, Chile, Argentina.

RESUMEN: PATRONES DE DISTRIBUCIÓN DE ANÉMONAS DE MAR CHILENAS DE AGUAS SOMERAS (CNIDARIA: ANTHOZOA: ACTINIARIA, CORALLIMORPHARIA); CON UNA DISCUSIÓN DE LAS RELACIONES TAXONÓMICAS Y ZOOGEOGRÁFICAS DE LA ACTINOFAUNA DEL PACÍFICO SUDORIENTAL, EL ATLÁNTICO SUDOCCIDENTAL Y LA ANTÁRTIDA. – La presente publicación provee un primer análisis zoogeográfico completo de las anémonas de mar (Actiniaria y Corallimorpharia) de las aguas someras a lo largo de la costa chilena y de sus relaciones con faunas vecinas, basando en un extenso muestreo en los últimos años en combinación con revisiones de la literatura. Desde 1994 hasta 2004 obtuvimos mas de 1000 ejemplares pertenecientes a 32 especies de Actiniaria y Corallimorpharia. Se muestrearon mas de 100 lugares enclavados en el intermareal y el submareal hasta 40 metros de profundidad, a lo largo de la costa chilena entre Arica (18°30'S 70°19'W) y el Estrecho de Magallanes (53°36'S 70°56'W). La parte norte de la región de los fiordos chilenos presenta el máximo número de especies (23). Nuestros resultados muestran la continuación de especies características de costas expuestas y la agregación de especies típicas de los fior-

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dos, lo cual se contradice con el concepto arraigado del cambio brusco y general en la composición de la fauna marina a partir de 42ºS. Los límites de distribución sureña de especies que encontramos en la región del centro-norte de Chile muestran solamente una concentración significativa alrededor de la Península Taitao (aprox. 48ºS). Esto bien indica una barrera zoogeográfica para especies de aguas someras en la Península Taitao o también puede ser debido a un artefacto de muestreo causado por la falta de datos que existe de la región entre la Península Taitao y el Estrecho de Magallanes. Según la literatura, 18 de las 63 especies de anémonas de mar descritas para Chile (Pacífico Sudoriental) han sido también citadas en Argentina (Atlántico Sudoccidental) y 13 en la Antártida. Sin embargo muchos registros y estatus taxonómicos de las especies comunes del Pacífico Sudoriental y del Atlántico Sud-occidental/Antártida son dudosos y requieren revisión y confirmación.

Palabras clave: Actiniaria, Corallimorpharia, lista de especies, zoogeografía, distribución, bentos, Chile, Argentina.

INTRODUCTION

The coast of continental Chile extends over almost 4200 km and flanks a large part of the South East Pacific. While the coastline between Arica (18°20'S) and Chiloé Island (approx. 42°S) is poorly contoured, the region between Chiloé and Cape Horn (approx. 56°S) is highly structured and presents a large number of islands, channels and fjords. An increased number of species can be observed there (Fernández *et al.*, 2000, own observation), probably due to the highly heterogeneous coast with a large variety of habitats (Ward *et al.*, 1999), the occurrence of marked differences within short distances (Antezana, 1999) and the existence of refugia in the Chilean fjord region during glaciation (Valdovinos *et al.*, 2003).

During the last three decades, a large number of papers have dealt with the biogeography of Chilean benthic invertebrates. While most studies have included only one taxonomic group (Sebens and Paine, 1979; Moyano G., 1991; Desqueyroux-Faúndez, 1994; Ojeda *et al.*, 2000; Montiel *et al.*, 2005), some have summarised available data on the biogeography of various taxa and oceanographic processes (Viviani, 1979; Brattström and Johanssen, 1983; Castilla *et al.*, 1993; Lancellotti and Vásquez, 1999; Fernández *et al.*, 2000; Camus, 2001). Most studies have proposed two main biogeographic regions within Chile: the Peruvian or warm-temperate Province between the Peninsula Illescas (or Bayovar) (approx. 6°S) and Chiloé Island (42°S) and the Magellan or cold-temperate Province between Chiloé Island and Cape Horn (56°S) (Fig. 1), which extends into Argentina to the Rio de la Plata (36-38°S) (Riemann-Zürneck, 1986; Zamponi *et al.*, 1998a). Several authors have recognised a transitional area somewhere between 30 and 42°S where both faunas occur (e.g. Stuardo, 1964; Desqueyroux-Faúndez, 1994). Pickard (1973) subdivided the Magellan Province into three regions, the North Zone (42°S to approx. 46.5°S), the central zone (46.5°S to approx. 53°S) and the southern zone (S of approx. 53°S) due to different oceanographic conditions. Viviani (1979) and Stuardo and Valdovinos (1992) suggested the same sub-regions based on the distribution pattern of benthic invertebrates and called them Northern, Central and Southern Patagonia. A recent study including a wide set of invertebrates from the intertidal to 100 m depth. (Lancellotti and Vásquez, 1999) negates the widely assumed faunal break at 42°S and proposes a transitional temperate region between 35 and 48°S where a gradual but important change in the species composition occurs.

Many benthic organisms, especially those of shallow water, show population fluctuations in sea-

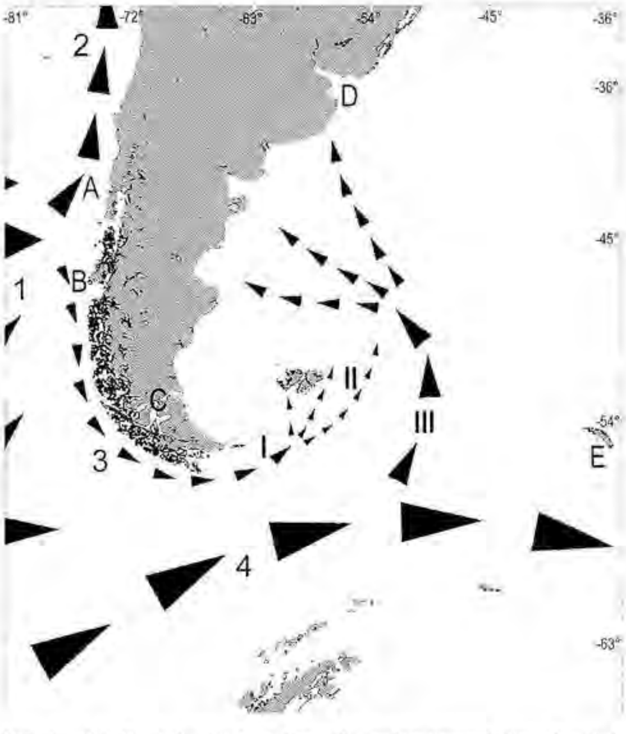

FIG. 1. – Southern South America with major currents (numbers): 1 Westwind Drift, 2 Humboldt Current, 3 Cape Horn Current, 4 Circumpolar Current; I Burdwood Bank, II Falkland Plateau, III Shag Rock Passage; zoogeographic barriers for benthic invertebrates: A Assumed limit between Peruvian and Magellan Province, B Peninsula Taitao and Golfo de Penas, C Straits of Magellan, D Rio de la Plata, E South Georgia.

sonal or several year cycles. Sea anemones with a—for invertebrates—comparably long life span are less susceptible to short term environmental changes and their populations show comparably few annual fluctuations. These conspicuous sessile marine invertebrates are present in almost all marine habitats; especially in higher latitudes they can be abundant or even dominating. These characteristics make them an excellent taxonomic group for long-term monitoring and detection of general zoogeographic patterns and trends (Riemann-Zürneck, 1986). Since the large vessel-based expeditions to the sea off Chile between 1850 and 1950 (Verrill, 1869; Hertwig, 1882; Carlgren, 1899 (for 1898); McMurrich, 1904; Carlgren, 1927; 1959), the Chilean actinofauna, although quite abundant, has received very little attention. While for many benthic invertebrates the data from the Lund University Chile Expedition created a good basis for subsequent taxonomic and zoogeographic work (e.g. Garth, 1957; Pawson, 1969), Oscar Carlgren died before he could finish his publication about the sea anemones of the Lund University Chile Expedition. As a consequence, the publication is incomplete and the existing descriptions are very short and preliminary (see Carlgren, 1959). Since the middle of the 20th century only a very small number of papers with restricted topics (Carter, 1965; Stotz, 1979; Brace, 1981; Riemann-Zürneck and Gallardo, 1990; Zamponi and Excoffon, 1995; Dayton *et al.*, 1995; Häussermann and Försterra, 2001; Häussermann, 2003; Häussermann and Försterra, 2003; Häussermann, 2004b; 2004a; 2005) have been dedicated to the Chilean actinofauna. Sebens and Paine (1979) published the first biogeographic study of the Chilean Actiniaria and Corallimorpharia, mainly based on literature. Despite some recent expeditions to the Chilean fjord region (Joint Magellan "Victor Hensen" Campaign 1994; several Cimar Fiordos expeditions between 1995 and 2004), no papers have yet been published on the sea anemone fauna collected during these expeditions, nor have the specimens been identified.

Between 1997 and 2004, we sampled sea anemones in shallow water to 40 m depth along the Chilean coast between Arica and Punta Arenas. To date we have described one new species (Häussermann and Försterra, 2001), re-described four (Häussermann, 2003; 2004b; 2005) and reported a colonial one (Häussermann and Försterra, 2003). In this paper, we describe the distribution of the collected species and discuss the agreement of the distribution ranges with the traditionally assumed biogeographic provinces. We list all species described for Chile and discuss the taxonomic overlaps and the biogeographic connections with the actinofauna of the South East Pacific, the South West Atlantic and Antarctica.

MATERIAL AND METHODS

Between 1994 and 2004, we observed, collected, examined and preserved more than 1000 specimens of 32 clearly distinguishable shallow-water Actiniaria and Corallimorpharia at more than 100 sites along the Chilean coast from Arica (18°30'S 70°19'W) to Fuerte Bulnes, Straits of Magellan (53°36'S 70°56'W) [for a detailed list of sampling sites of northern and central Chile see the online Appendix of Häussermann and Försterra (2001) at http://www.senckenberg.uni-frankfurt.de/odes/ and for a list of sampling sites of southern Chile see the online appendix of Häussermann (in press) at http://dx.doi.org/10.1007/s00300-004-0637-x (restricted access); for a map of the sampling sites of north and central Chile see Häussermann (2003), for a map of sampling sites of southern Chile see Försterra and Häussermann (2003)]. We kept the distance between neighbouring study sites less than 200 km with the exception of the region between Puerto Chacabuco (45°27'S 72°48'W) and Puerto Natales (51°44'S 72°30'W), where we could not access the coast due to logistic constraints. We studied and photographed specimens in situ by means of SCUBA-diving to depths of 25 m in northern and central Chile and to 40 m in the fjords. We kept some specimens of each species for several days in aquaria for detailed examinations and documentation. *Oulactis coliumensis* was dredged off Dichato by the research vessel Kay-Kay from the Universidad de Concepción from approx. 20 m depth. *Dactylanthus antarcticus* was found at several sites in the Chilean fjord region by Carlos Viviani (in litt., 2003) and we took additional distribution data from Dayton *et al.* (1995). For preservation, we relaxed the specimens with menthol crystals for 45-180 min and fixed them in 10-15% seawater formalin. For the histological examinations, we embedded parts of specimens in paraffin, sectioned them at 8-9 μm, and stained them with Azocarmin triple staining (Humason, 1967). We examined fired and unfired cnidae from living and preserved specimens with a light microscope (1000x oil immersion), drew or photographed and measured them.

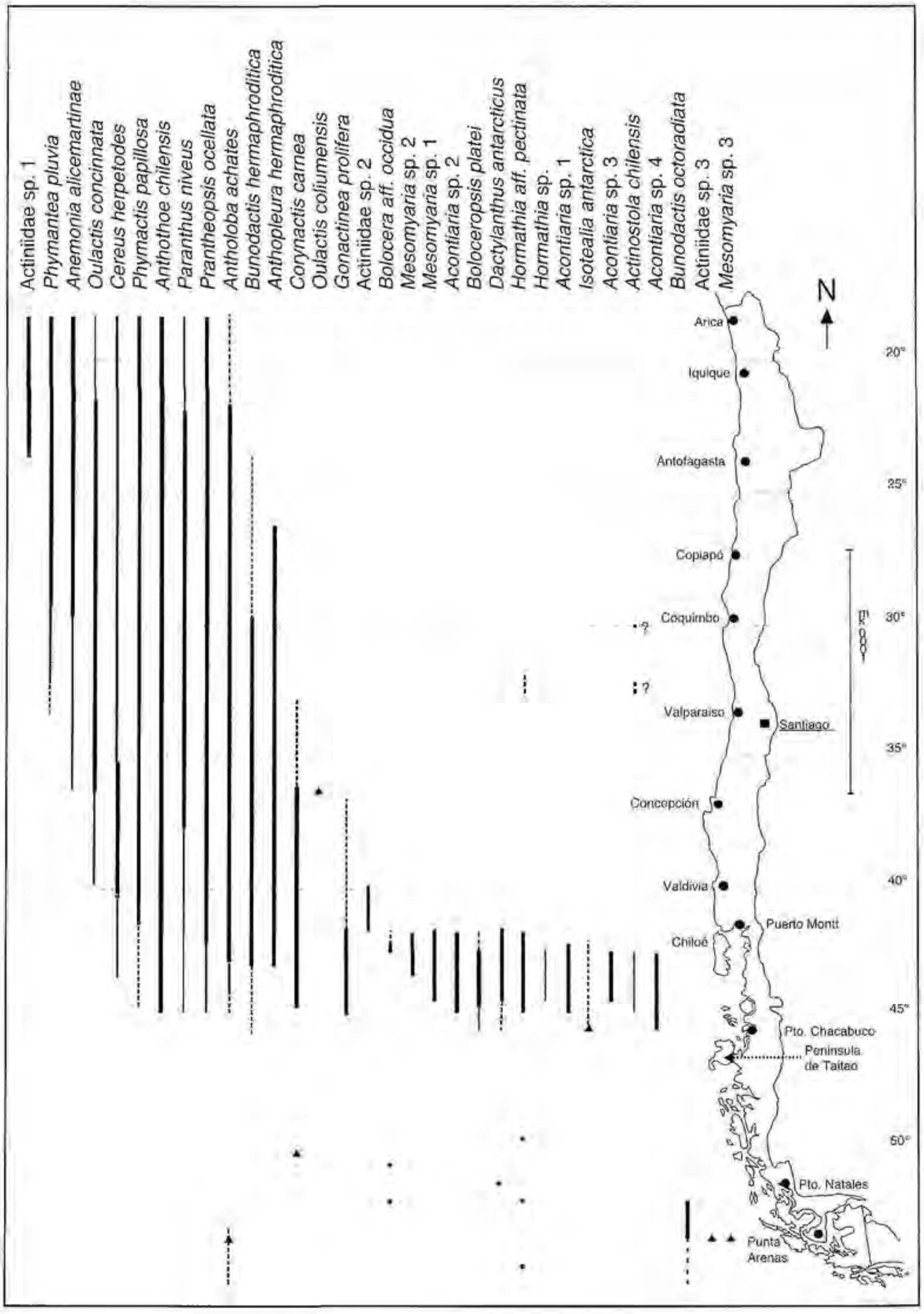

FIG. 2. – Distribution of sea anemones examined in the present study; complete lines and triangles: own findings, interrupted lines and squares: data from other authors.

RESULTS

From the 32 shallow-water sea anemone species collected along the Chilean coast, we identified 19 to the species level and three to the genus level; ten species have not yet been identified (Fig. 2). We found 16 species along the exposed coast of northern and central Chile between Arica (18°S) and Puerto Montt (42°S). From these 16 species, five species had their northern distribution limit and four species their southern distribution limit between Antofagasta (23°S) and Valdivia (40°S), and nine had their southern distribution limit south of Puerto Montt within the fjord region. *Antholoba achates* was found along the

TABLE 1. – List of sea anemones described from the coast of continental Chile.

Order Corallimorpharia
Family Corallimorphidae Hertwig, 1882
Corynactis carnea Studer 1878
Corynactis chilensis Carlgren, 1941 =? *C. carnea*
Corallimorphus profundus Moseley, 1877
Corallimorphus rigidus Moseley, 1877

Order Actiniaria
Suborder Endocoelantheae Carlgren, 1925
Family Halcuriidae Carlgren, 1819
Halcurias pilatus McMurrich, 1893

Suborder Nynantheae Carlgren, 1899
Tribe Athenaria Carlgren, 1899
Family Edwardsiidae Andres, 1881
Edwardsia intermedia McMurrich, 1893
Edwardsiella ignota (Carlgren, 1959)
Family Galatheanthemidae Carlgren, 1956
Galatheanthemum profundale Carlgren, 1956 (deep sea)
Family Halcampidae Andres, 1883
Cactosoma chilensis (McMurrich, 1904)
Halcampa abtaoensis Carlgren, 1959
Family Halcampoididae Appelöf, 1896
Scytophorus striatus Hertwig, 1882
Family Haloclavidae Verrill, 1899
Peachia chilensis Carlgren, 1934
Family Octineonidae Fowler, 1894
Octineon chilense Carlgren, 1959
Tribe Thenaria Carlgren, 1899
Subtribe Acontiaria Stephenson, 1935
Family Aiptasiidae Carlgren, 1924
?Aiptasia sp. McMurrich, 1904 (probably belongs to another species)
Family Aiptasiomorphidae Carlgren, 1949
Aiptasiomorpha elongata Carlgren, 1951
Family Hormathiidae Carlgren, 1932
Actinauge chilensis Carlgren, 1959
Amphianthus lacteus (McMurrich, 1893)
?Chondrophellia nodosa var. coronata (Verrill, 1883) (a northern hemispheric species) = *?Actinauge verrilli* McMurrich, 1893 = (probably another species *sensu* Carlgren, 1949) = *Actinauge fastigata* McMurrich, 1893
Hormathia pectinata (Hertwig, 1882) = *?Phellia spinifera* Hertwig, 1882
Phelliactis pelophila Riemann-Zürneck, 1973
?Stephanauge nexilis (Verrill, 1883) (a northern hemispheric species)
Family Sagartiidae Gosse, 1858
Anthothoe chilensis (Lesson, 1830) = *?Sagartia (Actinia) nymphaea* (Drayton in Dana, 1846)
Cereus herpetodes (McMurrich, 1904)
Choriactis impatiens (Couthouy in Dana, 1846)
Choriactis laevis (Carlgren, 1899)
? Actinothoe lobata (Carlgren, 1899) = ? *Metridium parvulum* McMurrich, 1904 = ? *M. senile* subsp. *lobatum*
Phellia exlex (McMurrich, 1904)
Subtribe Endomyaria Stephenson, 1921
Family Actiniidae Rafinesque, 1815
Anemonia alicemartinae Häussermann and Försterra, 2001 = *Actinia* sp. (*sensu* Sebens and Paine, 1979)
Anthopleura hermaphroditica (Carlgren, 1899)
Bolocera occidua McMurrich, 1893 *? *B. patens* (Hertwig, 1882) =? *B. kerguelensis*
Boloceropsis platei McMurrich, 1904
Bunodactis hermaphroditica (McMurrich, 1904)
Bunodactis octoradiata (Carlgren, 1899) =? *Parantheopsis cruentata*
Condylanthus magellanicus Carlgren, 1899
?Bunodactis elongata (McMurrich, 1904) (probably belongs to another species)
?Bunodactis eydousii (Milne Edwards, 1857) (probably belongs to another species)
Epiactis georgiana Carlgren, 1927
?Gyrostoma incertum McMurrich, 1904
Isosicyonis alba (Studer, 1879)
Isotealia antarctica Carlgren, 1899 =? *Leiotealia badia* McMurrich, 1893
Oulactis coliumensis (Riemann-Zürneck and Gallardo, 1990)
Oulactis concinnata (Drayton in Dana, 1846) = *Isoulactis chilensis* Carlgren, 1959
Parantheopsis cruentata (Drayton in Dana, 1846)
Parantheopsis ocellata (Lesson, 1830) = *Bunodes ocellata* (Lesson, 1830) = *?Nemactis (Actinia) rubus* (Drayton in Dana, 1846) = ? *Sagartia (Actinia) nymphaea* (Drayton in Dana, 1846)
Phymactis papillosa (Lesson, 1830) = *P. clematis* (Drayton in Dana, 1846) =? *Phlyctenactis tuberculosa* sensu Zamponi and Excoffon, 1995
Phymanthea pluvia Carlgren, 1959
Family Liponematidae Hertwig, 1882
Liponema multipora Hertwig, 1882
Subtribe Mesomyaria Stephenson, 1921
Family Actinoscyphiidae Stephenson, 1920
Actinoscyphia plebeia (McMurrich, 1893)
Family Actinostolidae Carlgren, 1932
Actinostola chilensis McMurrich, 1904 = p.p. A. intermedia Carlgren, 1899
Actinostola crassicornis (Hertwig, 1882)
Anthosactis excavata (Hertwig, 1882)
Antiparactis lineolatus (Drayton in Dana, 1846)
Antholoba achates (Couthouy in Dana, 1846)
Ophiodiscus annulatus Hertwig, 1882
Ophiodiscus sulcatus Hertwig, 1882
Paranthus crassa (Carlgren, 1899)=? P. niveus
?Paranthus ignotus (McMurrich, 1904)
Paranthus niveus (Lesson, 1830)
Pseudoparactis tenuicollis (McMurrich, 1904)

Suborder Prothantheae Carlgren, 1891
Family Gonactiniidae Carlgren 1893
Gonactinia prolifera (Sars, 1835)

Suborder Ptychodacteae Stephenson, 1922
Family Preactiidae England in England and Robson, 1984
Dactylanthus antarcticus (Clubb, 1908)

Dubious species with uncertain classification: *?Polyopsis striata* Hertwig, 1882 and *?Aulorchis paradoxa* Hertwig, 1888.
Legend: "?": dubious species; "=?": uncertain/possible synonymy.

entire Chilean coast to Tierra del Fuego; *Corynactis carnea* was found between Valparaíso (32°S) and 50°S; and *Oulactis coliumensis* was only dredged at one location in this area (Häussermann, 1998 (unpublished); Häussermann and Försterra, 2001; Häussermann, 2003; Häussermann and Försterra, 2003; Häussermann, 2004b; 2005) (Fig. 2).

Thirteen species had their northern distribution limit near Puerto Montt (42°S) at the northern end of the fjord region; only three of them were found at one or a few sites south of the Peninsula Taitao by other authors. However, one or two of them (the taxonomic accordance of Doumenc's *Actinostola intermedia* with *A. chilensis* is uncertain) were dredged

TABLE 2. – Taxonomic relationships of the South East Pacific, the South West Atlantic and the Antarctic actinofauna.

Species in common South East Pacific/Antarctic:
Corallimorphus profundus [1]
Actinoscyphia plebeia
Actinostola crassicornis (in Chile [2]*)*
Bolocera occidua (= B. kerguelensis?) [3, 4]
Choriactis laevis [5] (in Chile [2])
Condylanthus magellanicus [1] (in Chile [2])
Dactylanthus antarcticus
Edwardsia intermedia [6]
Epiactis georgiana [3]
Galatheanthemum profundale [1] (in Chile [2])
Isosicyonis alba [3]
Isotealia antarctica [3, 7]
Liponema multipora [1]

Species in common South West Atlantic/Antarctic:
Actinostola crassicornis
Bolocera tuediae subsp. *occidua (=B. kerguelensis?)*[4]
Condylanthus magellanicus[1] (in Chile [2])
Isosicyonis alba [11]
Epiactis georgiana [3, 11]

Species in common Magellan region/northern Scotia-Arc:
Corynactis carnea=Sphincteractis sanmatiensis (*sensu* Riemann-Zürneck, 1979) [12]
Amphianthus aff. *lacteus* [13]
Antholoba achates [1]
Anthothoe chilensis [14]
Bunodactis octoradiata [2]
Choriactis laevis [5]
Condylanthus magellanicus (in Chile [2])
Parantheopsis cruentata [1, 10]

Species in common South East Pacific/South West Atlantic:
Corynactis carnea [12]
Actinostola crassicornis (in Chile [2])
Amphianthus aff *lacteus* [13]
Antholoba achates [1]
Anthothoe chilensis [14]
Bolocera occidua (=?*B. tuediae* subsp. *occidua)*
Bunodactis octoradiata [2]
Choriactis laevis [5] (in Chile [2])
Condylanthus magellanicus[1] (in Chile [2])
Epiactis georgiana [3, 11]
Hormathia pectinata [8, 11]
Isosicyonis alba [3, 11]
Isotealia antarctica [3]
Metridium senile subsp. *lobatum* [9]
Parantheopsis cruentata [1, 10]
Paranthus crassa =?P. niveus
Phellia exlex
Phelliactis pelophila
NON *Phymactis papillosa*
(probable *Choriactis impatiens* [2])

Species distributed around southern South America:
Antholoba achates [1]
?*Isosicyonis alba* [3]
?*Metridium senile lobatum* [9]

[1] Wide distribution.
[2] Only reported for Magellan region.
[3] For Chile only mentioned once based on one (*B. occidua*) and two (*I. antarctica, E. georgiana, I. alba*) badly preserved specimens.
[4] The South American *Bolocera* species were synonymised with *B. kerguelensis* based on preserved material (Fautin, 1984). Since they are extremely variable and the preserved specimens present very few distinctive characteristics, the synonymisations should be reconsidered based on examination of *in vivo* material.
[5] Taxonomic status of species uncertain *sensu* Fautin (2003).
[6] Found at two non-Chilean sites: on Scotia Arc (1 spec.) and on Antarctic Peninsula (2 spec.) (Carlgren, 1927); identification of Carlgren's (1959) specimens uncertain.
[7] Identification of Antarctic specimens (McClintock and Baker, 1997; Bryan *et al.*, 1998; Amsler *et al.*, 1999) cannot be verified.
[8] Specimens found by Carlgren (1959) in Chilean fjords differ in size and cnidae from the type specimen described for the Magellan region and from the Argentinean specimens examined by Riemann-Zürneck (1973; 1986).
[9] Despite extensive sampling, we could not confirm the existence of this species along the Chilean coast.
[10] We still could not assign any Chilean specimens to this species.
[11] Disjunct distribution along the Argentinean coast (cold water areas).
[12] Taxa very poorly studied: since variability is very high, this species might represent a species complex.
[13] Identification of Argentinean species uncertain (Riemann-Zürneck, 1986).
[14] Not found south of the Peninsula Taitao in Chile. In the Atlantic, this species is cited for Mar del Plata to Rio de Janeiro, South Georgia and South Africa (Zamponi *et al.*, 1998a; Zamponi *et al.*, 1998b; Excoffon *et al.*, 1997). However, the agreement of specimens from the Scotia Arc and from Argentina with specimens from Chile has to be confirmed since *A. chilensis* is very variable, even within Chile, and thus might represent a species complex.

in deep water off central Chile by Doumenc (1984). We found three species only in the Magellan region (Fig. 2). Along the Chilean coast, the greatest number of species in shallow water exists in the northern part of the Patagonian fjord region (23 species).

The literature review yielded the following results:

Including deep-water species, 63 species of sea anemones have been described for the Chilean coast (Table 1), 86 for the Antarctic (E. Rodriguez, in litt., 2004) and approximately 50 for the Argentinean coast. Based on the literature, 18 of the sea anemones (Actiniaria and Corallimorpharia) described for the South East Pacific are also reported from the South West Atlantic and 13 from the Antarctic; seven are described for all three regions. However, reports for 12 of the 18 species that Chile shares with Argentina and reports for eight of the 13 species that Chile shares with the Antarctic contain major taxonomic uncertainties or the localities are of minor zoogeographical value (see Table 2 and discussion). Fifteen of the 18 species (exceptions: *Anthothoe chilensis, Bunodactis octoradiata, Parantheopsis cruentata*) that Chile has in common with Argentina and all that it has in common with the Antarctic have their main vertical distribution in deeper waters (>50 m). Only one, or possibly three species show a continuous distribution around the southern tip of South America (Riemann-Zürneck, 1986) (Table 2). Most species that inhabit the central Patagonian zone (sensu Pickard, 1973; Viviani, 1979; Stuardo and Valdovinos, 1992) were not found at the west coast of Tierra del Fuego, south of the Straits of Magellan (Riemann-Zürneck, 1986). Three of the Argentinean deep-water species show a conspicuous disjunct distribution with registrations east and north of the Falkland (Malvinas) Islands (47-52°S), and off Rio de la Plata at the Subtropical Convergence (approx. 38°S) (Riemann-Zürneck, 1991) (Table 2). Eight species that inhabit the southern Patagonian zone are also found along the northern part of the Scotia Arc to South Georgia (Table 2).

DISCUSSION

Distribution of sea anemones along the Chilean coast

Former studies

Sebens and Paine (1979) provided the first distribution map of 31 species of Chilean Actiniaria and Corallimorpharia. Sampling was carried out at 33 sites along the Chilean coast between Iquique (20°16'S 70°08'W) and Ushuaia, Argentina (54°50'S 68°12'W). Very little sampling was done in the northern fjords, and no study sites were situated in the Central and South Patagonian Zone between 43°14'S and 53°02'S. The high number of species appearing on their distribution map around Chiloe Island coincides with the high sampling effort of the Lund University Chile Expedition (Carlgren, 1959) in this area. In the collection deposited by Sebens and Paine at the Naturalis Museum in Leiden (Netherlands), only nine common species from northern and central Chile possess name tags while the other specimens of this collection do not seem to have been identified and thus cannot have contributed to the distribution map presented by Sebens and Paine (1979: 223).

The northern and central Chilean coast

The northern limit of the Peruvian Province is situated at Paita, Peru (approx. 5°S), where the Humboldt current turns westward towards the Galapagos Islands (Strub *et al.*, 1998); its southern limit is situated somewhere between Valparaiso (33°S) and Puerto Montt (42°S), depending on the author (see Brattström and Johanssen, 1983; Camus, 2001). Only four of the northern Chilean shallow-water sea anemones found in this study have a distribution range within the limits of the Peruvian Province (Fig. 2); their southern distribution limits are spread over more than 1000 km. Most of the species found in north and central Chile extend clearly south of Puerto Montt into the fjord region (Fig. 2). Of the three species that have their northern distribution limit between Valparaiso (33°S) and Valdivia (40°S), two can also be found in the fjords (up to 45°S). The observed pattern suggests neither the existence of a sea anemone fauna that is characteristic of the Peruvian Province nor a transitional zone north of Puerto Montt. Instead, a gradual replacement of warm water species through cold water species can be observed along the coast.

One of the species of north and central Chile, *Anemonia alicemartinae*, either strongly increased in abundance or was introduced, and has continuously spread southward until it reached Concepción (37°S) (Häussermann and Försterra, 2001). Its distribution coincides precisely with the horizontal and bathymetrical extension of the southward *Chile Coastal Countercurrent* (Häussermann and Försterra, 2001).

The Patagonian fjord region

Eleven of the 23 species we observed in shallow water of the fjords have a clear northern distribution limit near Puerto Montt (42°S), where the fjord region ends. Two have also been reported from deep water off central Chile (Doumenc, 1984); however, the accordance of Doumenc's *Actinostola intermedia* with *A. chilensis* is uncertain. Ten species extend further north along the exposed coast. The species found in the fjords belong to three different faunal elements: a) shallow water species that are clearly restricted to fjord- and channel-specific habitats (e.g. *Acontiaria* sp. 1, *Mesomyaria* sp. 2); b) representatives of a deep water emergence (eurybathy) fauna (e.g. *Actinostola chilensis*, *Bolocera* aff. *occidua*) that is characteristic of shallow water of northern Chilean fjords, but can also be found in deeper water further north (e.g. *Hormathia* aff. *pectinata*); and c) the fauna of the exposed coast that is more present in the channels and islands than in the inner fjords and extends further north (e.g.

Antholoba achates, *Cereus herpetodes*, *Parantheopsis ocellata*). The observed pattern contradicts the classical hypothesis of a general faunal break at 42°S (Brattström and Johanssen, 1983; Camus, 2001). Only the faunal element that is restricted to fjord region specific habitats has a clear-cut northern distribution limit due to the abrupt lack of suitable niches further north. This confirms and completes the hypothesis of Riemann-Zürneck (1986) and Brattström and Johanssen (1983) that the South Chilean fauna possesses a high percentage of endemic species. The coexistence and merging of these three faunistic elements caused by an abrupt diversification of coast morphology south of 42°S due to the splitting up of the straight coastline into numerous channels and fjords results in an increased species number and thus characterises the fjord region as a biodiversity hotspot. The first studies in the northern Patagonian fjords revealed high species diversity on steep rocky substrata even in strongly fresh water influenced areas, especially right below the influence of the Low Salinity Layer (Försterra and Häussermann, 2003; Carvalho *et al.*, 2005). While reaching farther north, the Patagonian cold-water fauna might be displaced to greater depths, where it can be found e.g. off Concepción (e.g. Schrödl, 2003; Cairns *et al.*, 2005) or off Coquimbo (Doumenc, 1984), and is overlain by the northern warm water fauna.

South of the Taitao Peninsula (46-47°S), the South Patagonian Icefield is moulding the hydrographic conditions of the inner fjords (Pickard, 1973): the region is characterised by low salinities and high sedimentation (Pickard, 1973). A reported poverty of species along the South Patagonian Icefield south of Golfo de Penas (47-48°S) (Thatje and Mutschke, 1999) has been explained by the strong fresh water influence in this region (Pickard, 1971; Pickard, 1973; Strub *et al.*, 1998). Due to technical restrictions, the expeditions to this area carried out with large vessels generally could only sample on soft bottoms and pebble ground, mainly at greater depth. Since most sea anemones settle on hard substrata, low anthozoan diversity along the South Patagonian Icefield might therefore be a sampling artifact due to general low sampling effort in this zone and especially due to soft bottom biased sampling (Thatje and Mutschke, 1999; Montiel *et al.*, 2004). Due to logistic constraints, we could not sample between 46 and 52°S. There are only four species of sea anemones that are reported both from the northern fjords and from one or a few sites south of the Taitao Peninsula (Fig. 2); all of them have their main vertical distribution in deeper waters and only *Corynactis carnea* extends to water shallower than 30 m. The detected distribution pattern supports the hypothesis of a zoogeographic barrier at the Taitao Peninsula, as proposed by Lancellotti and Vásquez (1999): at 47°S, fjords and channels are interrupted by the Taitao Peninsula, which lies north of the Golfo de Penas and extends far into the Pacific Ocean (Fig. 1). This latitude also marks the southernmost oscillation (40-45°S) of the water masses of the *West Wind Drift*, which hit the continent and are split up into a northward and a southward component (Johnson *et al.*, 1980; Castilla *et al.*, 1993; Strub *et al.*, 1998). It is plausible that the Peninsula, together with the Golfo de Penas, the changing oceanographic conditions and the parting of currents, form a biogeographic barrier, at least for shallow water species that are limited to protected habitats or the inner fjords. However, due to the poor data from the central and southern Patagonian zone, the southern distribution limits of most species found in the northern Patagonian fjord region still have to be traced.

Relations of the South-East Pacific actinofauna with neighbouring areas

Overlaps between the western Patagonian and the eastern Patagonian actinofauna

It can be inferred from the literature that 18 of the 63 species reported from Chile (29%) are also mentioned for the South West Atlantic. However, a detailed look at the reports reveals that of these 18 species, six are either of uncertain taxonomic status or the relevant records are doubtful; one species is restricted to the Magellan area, three more are described from the Argentinean shelf and extend into the (Chilean) Straits of Magellan, and two might represent species complexes (see Table 2). Since the Straits of Magellan are situated at the limit between the South East Pacific and the South West Atlantic, species with distribution limits in the Straits of Magellan cannot be interpreted as common species of eastern and western Patagonia.

Riemann-Zürneck synonymised the Chilean species *Metridium parvulum* McMurrich, 1904 and *Sagartia lobata* Carlgren, 1899 with *Metridium senile* and created the subspecies *M. senile lobatum*. She then cited it for the Argentinean coast (Riemann-Zürneck, 1975; 1986). This species inhabits the shallow water around the Peninsula Valdes (own observation) and around Buenos Aires (D. Lauretta, in litt., 2004). Fautin *et al.* (1989) do not accept this synonymisation and leave the two species *Actinothoe lobata* (Carlgren, 1899) and *Metridium parvulum* McMurrich, 1904 separate and purely Chilean. Based on the literature, the species is found at depths between 8 and 35 m between Coquimbo, northern Chile, and Calbuco at the northern limit of the fjord region. However, despite intensive field work and extensive information from local divers, fishermen and scientists, we could not confirm the presence of a species of *Metridium* along the Chilean coast.

The hydrographic situation at the southern tip of South America (Fig. 1) leads one to expect a comparably low overlap of Pacific and Atlantic shallow water species. The southern part of the Patagonian fjord region, south of Taitao Peninsula, lies under the influence of southward flowing water masses (Cape Horn Current), which flow around the southern tip of South America through the Drake Passage (Pickard, 1973; Brattström and Johanssen, 1983; Riemann-Zürneck, 1986; 1991; Castilla *et al.*, 1993; Strub *et al.*, 1998). The relatively shallow layer of water rounding the South American continent turns north or north-east, partly sweeps over the Burdwood Bank and the Falkland Shelf (Riemann-Zürneck, 1991) and then crosses the Falkland Plateau (Fig. 1). Due to strong eastward currents around the southern tip of South America, sessile shallow water species can spread from Chile to Argentina, but vice-versa it is almost impossible (Riemann-Zürneck, 1986) because adults as well as larvae are supposed to be unable to move against these strong currents. However, even the eastward crossing of the Straits of Magellan is difficult due to the lower salinity of the surface water, the relatively high temperature differences between the Pacific and the Atlantic opening and the existence of deep-sea basins (Riemann-Zürneck, 1986). To enter the Atlantic Ocean rounding Cape Horn, larvae have to withstand temperatures around 6°C (Riemann-Zürneck, 1986). Although it has been regularly assumed in the literature (Semenov and Berman, 1977; Zamponi *et al.*, 1998a), there is no evidence for a northward near-shore current on the Atlantic side south of 41°S (Piola and Georgi, 1982). The lack of such a current could explain the rarity of South East Pacific shallow-water sea anemones along the coast of Argentina.

Overlaps between the South East Pacific and the Antarctic actinofauna

The faunal overlap of Chilean and Antarctic sea anemone species that can be inferred from the literature should also be interpreted cautiously. From the 13 species mentioned in the literature for Chile and the Antarctic (21% of the Chilean species), five are based on uncertain records or doubtful identifications, one is a deep-sea species, and three are—for Chile—only reported from the Magellan area (one of these is also of uncertain status) (see Table 2). Eight Magellanic species are reported along the northern part of the Scotia Arc to South Georgia, but not for the Antarctic. Plausible reasons for a relatively low overlap of the South Chilean fauna with the Antarctic can be found in the hydrographic situation: the Scotia Arc connects South America with the Antarctic and presents Magellanic aspects in its northern part and Antarctic aspects in its southern part (Arntz and Brey, 2003). The Antarctic Convergence lies approximately at the latitude of South Georgia, oscillating in a way that leaves this island either north or south of it (Arntz and Brey, 2003). The eastward direction of the strong *Circumpolar Current* facilitates the dispersion of larvae from the southern tip of South America and from the Antarctic towards South Georgia, but hinders a westward spread from South Georgia.

Unusual distribution pattern of some Argentinean sea anemones

The unusual, disjunct distribution pattern of three Argentinean sea anemone species (see Table 2) (Riemann-Zürneck, 1973; 1986) is already known from other benthic coelenterates that inhabit the Argentinean continental shelf, e.g. the siphonophore *Rhodalia miranda* (Riemann-Zürneck, 1991). These species are found south and east of the Falkland (Malvinas) Islands, at the Malvinas Canyon and off Rio de la Plata, south of the Subtropical Convergence (Riemann-Zürneck, 1991). These distribution patterns can be explained by the special hydrographic situation of the South West Atlantic. A stable and constant flow of cold circumpolar water swashes over the Shag Rock Passage at 48°W, crosses the South Atlantic Basin and rises along some of the large canyons on the Argentinean shelf. The conditions around the Falkland Islands, which are under permanent influence of Subantarctic water masses, seem to be more similar to those in southern Chile than to those in southern Argentina (Riemann-Zürneck, 1986; Moyano, 1991; Desqueyroux-Faúndez, 1994). The described current patterns limit Subantarctic benthic species to regions that constantly offer stable cold conditions.

Zoogeographic patterns found in other invertebrate taxa

The zoogeographical limit between the Peruvian and the Magellan Province at 40 to 42°S has been described for sponges (Desqueyroux-Faúndez, 1994), crustaceans (Garth, 1957), asteroids (Bernasconi, 1964), fish (Mann, 1954; Ojeda *et al.*, 2000), foraminiferans (Balech, 1954) and bryozoans (Moyano, 1991). Some of the mentioned papers additionally subdivide the Peruvian Province into a North Chilean and a Central Chilean Sub-Province (e.g. Balech, 1954; Bernasconi, 1964; Desqueyroux and Moyano, 1987). In contrast, the Chilean polychaete fauna is characterised by a gradual replacement of warm-water species by cold-water species along the Chilean coast and no abrupt change at 42°S can be observed (Montiel *et al.*, 2004, 2005). For polychaetes, Montiel *et al.* (2005) suggest a sub-division into a Pacific and an Atlantic part of the Magellan Province since the species overlap is only 10%. Thus, the distribution pattern of polychaetes coincides quite well with that of sea anemones. Several authors also reported a longitudinal zoogeographic barrier for benthic taxa of the South East Pacific at the eastern mouth of the Straits of Magellan (Stuardo and Valdovinos, 1992; Strub *et al.*, 1998), while others consider the Straits of Magellan to be a latitudinal zoogeographical barrier for Chilean species (Balech, 1954; Stuardo, 1964; Riemann-Zürneck, 1986). However, the latter may also be a sampling artifact (Riemann-Zürneck, 1986), since the known distribution patterns often reflect the range of sampling activities. Among nudibranchs, on the other hand, most species that are described for southern Argentina can also be found in southern Chile (Schrödl, 2003). Schrödl (2003) reports that cold-water species from the Straits of Magellan have been observed up to Concepción (37°S); while warm-water species from the central Chilean coast have generally not been described for the region south of Chiloé Island (42°S). However, most invertebrate sampling has been quite scarce along the exposed islands even of the northern fjord region (Guaitecas and Chonos Archipelago and west coast of Chiloé Island), so this might also be a sampling artifact. The number of Magellanic shelled gastropods and nudipleurans shared with areas south of the Antarctic Convergence is very low (Linse, 2000; Schrödl, 2003); remarkably, the percentage of Magellanic bivalves in these southern waters is much higher (Linse, 2000).

CONCLUSIONS

Abrupt diversification of the coast morphology south of 42°S increases the number of habitats and allows the overlap of three different shallow water faunal elements in the northern Patagonian zone: a) shallow water species that depend on fjord habitats; b) emerged deep water species; and c) shallow water species from the exposed coast of north and central Chile. This strongly increases overall species number and diversity in the fjords.

A southern limit of the Peruvian Province close to Puerto Montt cannot be confirmed from the available distribution data of sea anemones.

There is a distribution limit from south to north at 42°S for shallow water species that are restricted to fjord- and channel-specific habitats.

We hypothesise that, due to splitting of currents and different oceanographic conditions, the Taitao Peninsula together with the Golfo de Penas (47-48°S) form a zoogeographic barrier, at least for shallow-water species of the inner fjords.

The percentage of western Patagonian sea anemone species that also occur in eastern Patagonia lies between 10 and 22%.

The percentage of South East Pacific sea anemones that also occur in the Antarctic lies between 8 and 14%.

Conspicuousness, life style, reproduction, abundance, longevity and population dynamics make sea anemones a potentially perfect taxonomic group for general zoogeographic surveys. However, the poor effort that has been dedicated to sea anemones in the southern oceans, their generally difficult taxonomic situation, the problems in identification of living animals (Häussermann, 2004a), and the general lack of voucher material for uncertain distribution data still leave many gaps and doubts. More refined zoogeographic conclusions will be possible after more sampling on hard substrata, especially in the central and southern Patagonian zones in depths right below the low salinity layer.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Scotia Arc bryozoans from the LAMPOS expedition: a narrow bridge between two different faunas*

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SUMMARY: The 78 bryozoan species collected by the German R/V "Polarstern" during the LAMPOS cruise in April 2002, encompassing the Scotia Arc archipelagos between Tierra del Fuego and the Antarctic Peninsula, were studied to discern the biogeographical patterns of the Magellan region of South America, the Scotia Arc archipelagos and the Antarctic. The resulting dendrogram shows three clusters: an isolated one with the three easternmost archipelagos and the other two linking some of the northern and southern Scotia Arc archipelagos with Tierra del Fuego. A more comprehensive analysis using all the species previously recorded from the Scotia Arc archipelagos and adjacent areas (214 spp.) produced a clearer zoogeographical pattern without isolated clusters of localities. The Antarctic Peninsula plus the Scotia Arc archipelagos form a large cluster distinct from the Magellan-Falkland Subantarctic area. A third analysis making use of 78 genera present in the study area plus Australia and New Zealand reinforces this pattern, showing two clusters: one uniting South America and the Australian-New Zealand realm and the other linking the Scotia Arc archipelagos with the Antarctic Peninsula. These results indicate that the Scotia Arc archipelagos represent merely a very narrow bridge connecting two different bryozoan faunas with only a few bryozoan species in common between the study areas.

Keywords: Scotia Arc, bryozoans, zoogeography.

RESUMEN: Bryozoa de la Expedición LAMPOS al Arco de Scotia: un puente estrecho entre dos faunas diferentes. – Se estudiaron 78 especies de briozoos recolectados por el B/I alemán "Polarstern" durante el crucero LAMPOS realizado desde Tierra del Fuego a la Antártida, incluyendo los archipiélagos del Arco de Scotia, para discernir las conexiones zoogeográficas existentes. El dendrograma resultante muestra tres conjuntos de localidades: uno desconectado de los otros y que agrupa a Shag Rocks y los archipiélagos más orientales y los otros dos unen el área de las Malvinas con las Shetland y la Isla Elefante. Un nuevo análisis más amplio usando todas las 214 especies previamente registradas en el Arco de Scotia y áreas adyacentes produjo un patrón zoogeográfico más claro sin localidades o grupos de ellas aislados. En éste la Península Antártica y los archipiélagos del Arco de Scotia forman un gran conjunto antártico que se opone a otro formado por el área magallánica y las Malvinas. Finalmente se realizó un tercer análisis utilizando los 78 géneros a los que pertenecen las especies estudiadas y que también se hallan en el área australo-neozelandesa. Este tercer dendrograma viene a reforzar al segundo mostrando dos grandes agrupaciones: una que liga a Sudamérica con el área australo-neozelandesa y la otra que agrupa a los archipiélagos del Arco de Scotia con la Península Antártica. Estos resultados sugieren que la fauna de briozoos del Arco de Scotia simplemente un puente muy estreco que conecta dos faunas diferentes, con sólo unas pocas especies comunes de las dos áreas estudiadas.

Palabras clave: Arco de Scotia, briozoos, zoogeografía.

INTRODUCTION

The known Magellan bryozoans total more than 220 species. Those of the Antarctic Peninsula also reach a similar total. Endemism of the former is about 55%, whereas that of the latter is higher, varying from 65% to more than 90% (Moyano, 1991; Hayward, 1995).

The physical links between the two bryozoan faunas are the Scotia Arc archipelagos, which might constitute stepping stones between South America and the Antarctic for dispersal and interchange of

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TABLE 1. – LAMPOS expedition collecting stations yielding bryozoans.

	Localities	Date	Latitude	Longitude	Depth
St 145	Burdwood Bank	05.04.02	54°2,00'S	62°0.52'W	272 m
St 153	Burdwood Bank	06.04.02	54°33,23'S	56°10.12'W	297 m
St 164	Shag Rocks	09.04.02	53°24'S	42°43'W	178 m
St 207	South Sandwich Islands	16.04.02	57°40' S	26°27'W	210 m
St 217	East of Drygalski Seamount	18.04.02	59°55.24'S	32°26.46'W	518 m
St 238	South Orkneys	23.04.02	61°11.05'S	45°43.76'W	324 m
St 251	Off Elephant Island	25.04.02	61°23.91' S	55°27.62'W	293 m
St 252	Off Elephant Island	25.04.02	61°23.14'S	55°27.66'W	268 m
St 253	Off Elephant Island	25.04.02	61°22.32'S	55°31.51'W	211 m

faunal elements (Crame, 1999; Gorny, 1999; Moyano, 1996, 1999, 2000; Barnes and De Grave, 2000).

This, and other issues concerning the role of the Scotia Arc archipelagos in interactions between the Antarctic and Subantarctic ecosystems, led to the German LAMPOS cruise on board RV "Polarstern" in April-May 2002 (ANT XIX/5; Arntz and Brey, 2003). The bryozoan collection gathered included some 80 species.

The species collected were dominated in mass by large flexible colonies of flustriform and cellariiform bryozoans, whereas the encrusting species were less abundant, forming calcareous sheets on small pebbles. A new genus and species were discovered among the former and a new species in the latter.

Preliminary results of the German LAMPOS expedition plus previously published data from several authors are employed in this work to assess the role of bryozoans in linking the Magellan and Antarctic ecosystems.

MATERIALS AND METHODS

Table 1 gives station data for the LAMPOS expedition of RV "Polarstern", which yielded bryozoans. Samples were collected by means of an Agassiz trawl and stored in an aqueous ethanol solution of at least 90%. In the Universidad de Concepción Bryozoology Laboratory they were transferred to 70% ethanol to be sorted and identified.

Colony pieces to be photographed by SEM were boiled in a NaClO solution, rinsed with tap water, dried from 70% ethanol and finally coated with gold.

Analysis of the zoogeographical affinity between Antarctic and Subantarctic bryozoan faunas from the Magellan area to the Antarctic Peninsula through the Scotia Arc archipelagos was performed primarily using the bryozoan faunal list obtained from the LAMPOS expedition and subsequently in combination with other faunal lists by Hastings (1943), Hayward (1995) and López de la Cuadra and García Gómez (2000).

Dendrograms were constructed by the UPGMA mode (Crisci and López, 1983) using the Kulczinsky-2 index (Sibouet, 1979) to assess zoogeographical affinity (Moyano, 1982).

RESULTS

The species collected during the LAMPOS cruise are shown in Table 2 and the dendrogram comparing different Subantarctic and Antarctic stations on the basis of their bryozoans is shown in Figure 1. The number of species per station varied between 5 and 21, with an average of 12. The richest station was that at Burdwood Bank (south of Falkland Islands – Islas Malvinas) with 21 spp. and the poorest stations were stns. 207 and 217 off South Sandwich with only 5 spp. each. The last three stations, near Elephant island are very close, so the real number of species should be some 29.

The 78 species of Table 2 belong to ten different zoarial forms. Most frequent were the encrusting species (32%), followed by the flustriform ones (15.4%). The erect (50 spp.), rigid (18 spp.) and flexible (32 spp.) forms constitute the largest number in comparison with the encrusting (32 spp.) and the irregular plurilaminar celleporiform forms (3 spp.). The flustriform species predominate within the flexible forms and also in the number of zoaria and mass considering the whole set of species and samples.

The dendrogram (Fig. 1) shows two clear-cut sets of stations on the basis of their bryozoan species. The largest group includes 6 stations subdivided in turn into two clusters: Subantarctic stns. 145 and 153 and Antarctic stns 238, 251, 252 and 253. The two sets exhibit an affinity of only 5%. The

TABLE 2. – Bryozoa collected during the LAMPOS expedition between Punta Arenas and the northernmost tip of the Antarctic Peninsula.

					Stations					FZ
	145	153	164	207	217	238	251	252	253	
1. *Acanthophragma polaris ?*				x						I
2. *Adelascopora jeqolqa*						x	x			CE
3. *Adelascopora secunda*									x	F
4. *Amastigia* sp.	x									CE
5. *Antarcticaetos bubeccata*							x			CE
6. *Aspidostoma coronatum*					x					I
7. *Aulopocella brachyrhyncha*							x			V
8. *Austroflustra australis*	x	x								F
9. *Austroflustra gerlachi*	x	x								F
10. *Austroflustra vulgaris*								x	x	F
11. *Beania challengeri*		x								I
12. *Beania erecta*							x			I
13. *Beania magellanica*	x									I
14. *Bostrychopora dentata*							x			I
15. *Caberea darwini*		x								CE
16. *Carbasea curva*							x		x	F
17. *Carbasea ovoidea*								x		F
18. *Camptoplites giganteus*								x		BU
19. *Camptoplites tricornis*						x	x			BU
20. *Cellaria incula*						x	x			CE
21. *Cellaria malvinensis*	x									CE
22. *Cellaria tenuis*	x	x								CE
23. *Cellaria variabilis?*	x									CE
24. *Cellarinella* sp.						x	x			A
25. *Cellarinella watersi*						x	x	x		A
26. *Chaperiopsis* sp.			x	x						I
27. *Chartella notialis*	x									F
28. *Cornucopina polymorpha*						x	x	x	x	BU
29. *Cornucopina* sp.	x									BU
30. *Crisidia delicatissima*								x		CA
31. *Dakariella concinna*				x						I
32. *Disporella octoradiata*			x							I
33. *Escharella* sp.			x		x					I
34. *Exochella* sp.					x					I
35. *Fenestrulina rugula*								x		I
36. *Flustrapora magellanica*									x	F
37. *Foveolaria terrifica*	x	x								I
38. *Himantozoum antarcticumx*									x	F
39. *Hornera* sp.							x			V
40. *Hippothoa flagellum*			x	x						I
41. *Ichthyaria oculata*	x	x								BU
42. *Isoschizoporella secunda*									x	E
43. *Melicerita blancoae*	x									A
44. *Melicerita obliqua*						x			x	A
45. *Menipea* sp.	x									CE
46. *Micropora brevisima*			x							I
47. *Microporella hyadesi*	x	x								E
48. *Nematoflustra flagellata*						x				F
49. *Nevianipora sp.*	x									V
50. *Notoplites drygalskii*								x	x	BU
51. *Notoplites* sp.	x									BU
52. *Ogivalia elegans*	x									V
53. *Orthoporidroides erectus*	x									V
54. *Osthimosia bicornis*	x						x	x	x	Cel
55. *Osthimosia* sp.1	x									Cel
56. *Osthimosia* sp.2						x				Cel
57. *Paracellaria cellarioides*		x								Cel
58. *Parafigularia* sp. n.			x							I
59. *Platychelina planulata*		x								I
60. *Reteporella erugata*					x					RE
61. *Reteporella frigida*								x	x	RE
62. *Reteporella hippocrepis*							x			RE
63. *Reteporella magellensis*		x								RE
64. *Schizoporella ?* sp.		x								I
65. *Securiflustra bifoliata*		x								F
66. *Smittina antarctica*						x	x	x	x	E
67. *Smittina monacha ?*		x								I
68. *Smittina* sp. n.					x					I
69. *Smittinella* sp.			x							I
70. *Smittoidea pugiuncula*			x							I
71. *Smittoidea conspicua*							x			I

TABLE 2 (Cont.). – Bryozoa collected during the LAMPOS expedition between Punta Arenas and the northernmost tip of the Antarctic Peninsula.

	Stations									FZ
	145	153	164	207	217	238	251	252	253	
72. *Systenopora contracta*						x				A
73. *Talivittaticella frigida*	x								x	CA
74. *Toretocheilum turbinatum*			x							I
75. *Tricellaria* sp.		x								BU
76. *Trilochites biformatus*			x	x						I
77. *T. phylactelloides*								x	x	E
78. Flustridae n. gen. n. sp.		x								F
	21	17	10	5	5	11	16	12	13	

FZ = Zoarial forms:
A = adeoniform (6.4%)
Re = reteporiform (5.1%)
Bu = buguliform (10.25%)
Cel = celleporiform (3.85%)
F = flustriform (15.4%)
Ce = cellariiform (12.6%)
V = vinculariiform (6.4%)
E = eschariform (5.1%)
I = encrusting (32%)
Ca = catenicelliform (2.6%)

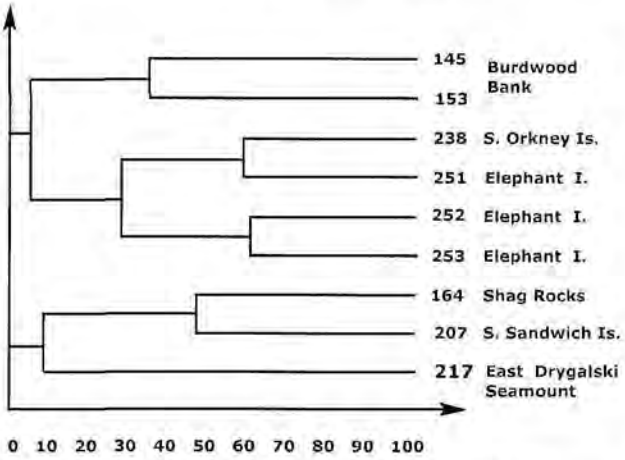

FIG. 1. – Dendrogram relating stations on the basis of their bryozoan fauna. Stations 145 and 153 are located between Burdwood Bank and Shag Rocks-South Georgia. Stations 164, 207, 217, 238, 251, 252 and 253 are situated east and south of South Georgia.

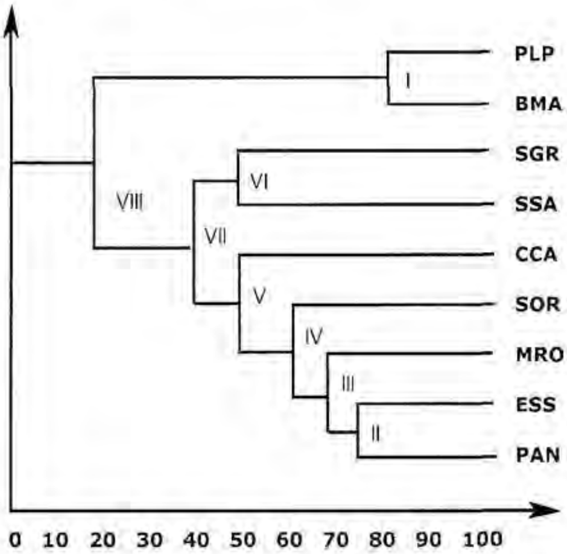

FIG. 2. – Dendrogram resulting from the geographical matrix for bryozoans (Table 4, Appendix 1). Localities: PLP: Patagonian shelf; BMA: Falklands-Malvinas and Burdwood Bank; SGR: South Georgia; SSA: South Sandwich; SOR: South Orkneys; ESS: Elephant I. and South Shetlands; PAN: Antarctic Peninsula; MRO: Ross Sea; CCA: Antarctic continental coasts.

station group 164, 207 and 217, which does not unite with the larger one, joins the most isolated places of the Scotia Arc in relation to South America and Antarctica.

As these primary results do not indicate a clear pattern of bryozoan distribution along the Scotia Arc archipelagos or the relationships between South America and the Antarctic, a larger set of data, compiled from the works of several authors published over the past 60 years, was analysed (Table 3, Figs. 2 and 3, Appendix 1).

In order to further test the zoogeographical pattern shown in the dendrogram in Figure 2, an analysis of the bryozoan genera present in the Scotia Arc archipelagos was carried out in comparison with the Subantarctic Magellan region and "Australasia" *sensu* Mawson (i.e. Australia and New Zealand

TABLE 3. – Scotia Arc bryozoans after Hastings (1944) (HS), Hayward (1995) (HY), López de la Cuadra and García Gómez (2000) (L-G) and Moyano (LAMPOS expedition 2002, this study) (LAM). Localities: PLP = Patagonian shelf; BMA= Falklands and Burdwood Bank; SGR = South Georgia - Shag Rocks; SSA = South Sandwich; SOR =South Orkneys; ESS = Elephant-South Shetland; PAN = Antarctic Peninsula; MRO = Ross Sea; CCA = Antarctic continental coasts.

Authors				Localities								
HS	HY	L-G	LAM	PLP	BMA	SGR	SSA	SOR	ESS	PAN	MRO	CCA
23	145	85	78	48	51	94	43	66	117	89	79	38

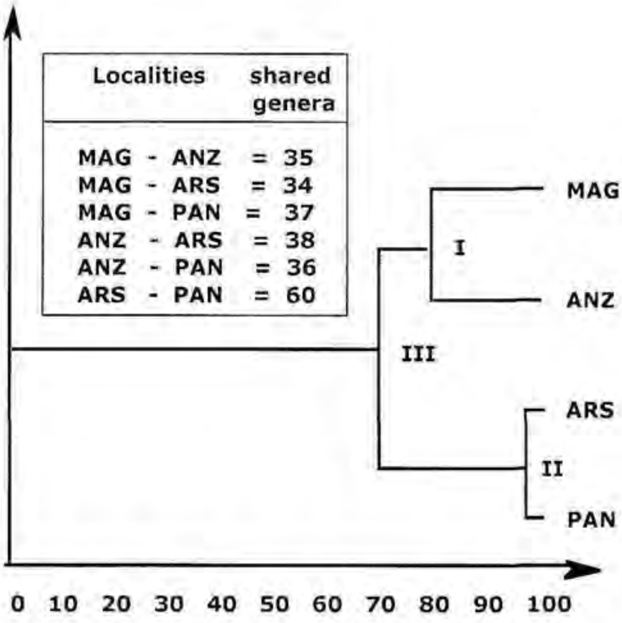

FIG. 3. – Dendrogram showing the relationships among the Scotia Arc with Subantarctic and Antarctic areas on the basis of the shared bryozoan genera (Table 5, Appendix 2); MAG: Magellan area; ANZ: Australia – New Zealand realm; ARS: Scotia Arc archipelagos; PAN: Antarctic Peninsula.

(Table 5 and Fig. 3, Appendix 2). The list of bryozoan genera in Appendix 2 does not contain all the genera known to exist south of the Antarctic Convergence, but certainly more than 85% of them. Other endemic Antarctic genera are *Cellarinelloides, Eminoecia, Dendroperistoma* and *Filaguria*. There are also some Subantarctic genera not listed here like *Sclerodomus*.

The dendrogram in Figure 3 exhibits the same pattern as Figure 2, this time on the basis of bryozoan genera, showing the Scotia Arc closely united with the Antarctic Peninsula and joining the Magellan region with New Zealand and Australia.

TABLE 5. – Geographical distribution of 72 cheilostomatid bryozoan genera from the Scotia Arc archipelagos in Antarctic and Subantarctic areas after the data by López de la Cuadra and García Gómez (2000) and Moyano (this study). MAG = Magellan area including Patagonian shelf; ANZ = Australian and New Zealand areas; ARS = Scotia Arc archipelagos; PAN = Antarctic Peninsula. Information on bryozoan genera from New Zealand and Australia after Gordon (1984, 1986, 1989) and Moyano (1996)

	MAG	ANZ	ARS	PAN
Nunber of genera	46	42	63	60

DISCUSSION

The role of the Scotia Arc archipelagos in the interactions between Antarctic and Subantarctic ecosystems stimulated the LAMPOS cruise on board the German research vessel "Polarstern" in April-May 2002. The bryozoan collection gathered included some 80 species that belong to two completely different groups: a Subantarctic group to the west and north of Shag Rocks and an Antarctic group originating from east and south of that archipelago.

Both groups are dominated by large flexible bryozoan colonies, namely flustriform, buguliform and cellariiform, plus some rigid forms such as eschariform and reteporiform. The encrusting species are less abundant, forming calcareous sheets on small pebbles. Most species were previously known except for two new ones. One of them belongs to a new flustrine genus and the other to the cribriline genus *Parafigularia*.

Systematically the links of Antarctic and Subantarctic Bryozoa are more at the generic than at the specific level although, as demonstrated above, the highest generic affinity appears between the Scotia Arc and the Antarctic Peninsula. There are some

TABLE 4. – Geographical matrix for the bryozoans of the Scotia Arc, based on Appendix I. Values above the diagonal represent Kuczinsky-2 indices. Values below the diagonal are the number of species shared between localities. Localities (Lc): PLP = Patagonian shelf; BMA= Falklands-Malvinas and Burdwood Bank; SGR = South Georgia - Shag Rocks; SSA = South Sandwich; SOR =South Orkneys; ESS = Elephant-South Shetland; PAN = Antarctic Peninsula; MRO = Ross Sea; CCA = Antarctic continental coasts. Number of species per locality (Sp) appearing above and left of localities after Hastings (1944), Hayward (1995), López de la Cuadra and García Gómez (2000) and Moyano (this study).

Sp		48	51	94	43	77	117	89	79	38
	Lc	PLP	BMA	SGR	SSA	SOR	ESS	PAN	MRO	CCA
48	PLP		77	32	20	19	19	16	5	5
51	BMA	38		27	19	12	16	15	3	2
94	SGR	20	18		44	38	35	44	36	26
43	SSA	9	9	26		36	40	43	38	35
77	SOR	11	9	32	20		65	59	50	33
117	ESS	13	11	36	25	60		71	60	56
89	PAN	10	10	40	25	49	72		67	49
79	MRO	3	2	31	21	39	57	56		58
38	CCA	2	1	14	14	17	32	26	30	

species, mostly from shallow waters, like *Celleporella bougainvillei, Inversiula nutrix* and *Beania inermis,* living in Magellan South America and at the Antarctic Peninsula (See Moyano, 1999, Moyano and Cancino, 2002). More abundant are vicariant species such as *Parafigularia magellanica* and *P. discors, Aulopocella petiolata* and *A. brachyrhyncha, Adelascopora stellifera* and *A. secunda, Austroflustra australis* and *A. vulgaris*. However, more abundant are species endemic to each fauna. These statements result from a comprehensive analysis of all known bryozoan species, both Magellan and Antarctic.

In the bryozoans collected during the LAMPOS cruise, connections between the two faunas are almost non-existent, probably due to the collecting depths of more than 200 m. In this context, all archipelagos showed a typical Antarctic bryozoan fauna. The limit between the two faunas seems to be situated not too far off Shag Rocks, probably coinciding with the Antarctic Convergence boundary.

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APPENDIX 1. – Bryozoans from Scotia Arc and adjacent Subantarctic and Antarctic areas, after Hastings (1944) (HA), Hayward (1995)(H) López de la Cuadra and García Gómez (2000) (LG) and Moyano (this study) (MO). Localities: PLP: Patagonian shelf; BMA: Falkland Is. - Is. Malvinas and Burdwood Bank; SGR: South Georgia; SSA: South Sandwich; SOR: South Orkney; ESS: Elephant I. and South Shetland; PAN: Antarctic Peninsula; MRO: Ross Sea; CCA: Antarctic continental coasts.

		PLP	BMA	SGR	SSA	SOR	ESS	PAN	MRO	CCA
1.	*Acanthophragma polaris ?*				MO				H	
2.	*Adelascopora jeqolqa*					H/MO	MO	H	H	
3.	*Adelascopora secunda*					LG	H/MO	H		
4.	*Aimulosia antarctica*			H/LG		H	LG		H	H
5.	*Aimulosia australis*	H	H	H	H	H/LG	H	H		
6.	*Amastigia sp.*	MO								
7.	*Amastigia gaussi*	HA	H	H/LG		HA		HA		H
8.	*Amphiblestrum georgensis*	H		H/LG						
9.	*Amphiblestrum inermis*				H	H	LG	H	H	H
10.	*Andreella uncifera*	H	H			H				
11.	*Antarcticaetos bubeccata*				H	H	MO	H	H	H
12.	*Apiophragma hyalina*						H	H		
13.	*Arachnopusia aquilina*						H			H
14.	*Arachnopusia aviculifera*			H/LG		LG				
15.	*Arachnopusia decipiens*						H/LG	H		
16.	*Arachnopusia ferox*						H			
17.	*Arachnopusia inchoata*	H		H/LG	H/LG	H/LG	H/LG			
18.	*Arachnopusia monoceros*	MO	MO	LG						
19.	*Arachnopusia tubula*						H			
20.	*Aspericreta georgensis*			H						
21.	*Aspidostoma coronatum*				MO	LG				
22.	*Aspidostoma giganteum*	MO	H				H			
23.	*Aulopocella brachyrhyncha*						MO	H	H	
24.	*Aulopocella stenorhyncha*					LG	H	H	H	
25.	*Austroflustra australis*	MO	MO							
26.	*Austroflustra gerlachi*	MO	MO							
27.	*Austroflustra vulgaris*			LG		LG	H/MO			
28.	*Beania challengeri*		MO							
29.	*Beania erecta*				H/HA	H	H/MO	H	H	H
30.	*Beania erecta livingstonei*			LG		LG	LG	HA		
31.	*Beania inermis*	H						MO		
32.	*Beania magellanica*	MO	MO							
33.	*Bostrychopora dentata*						MO	H	H	H
34.	*Brettiopsis triplex*			H						H
35.	*Buffonellodes antarctica*					H			H	
36.	*Bugulella klugei*						H		H	H
37.	*Caberea darwini*	MO	MO	LG	HA	LG	LG	HA		
38.	*Camptoplites angustus*					H	HA	H	HA	HA
39.	*Camptoplites areolatus*						HA			HA
40.	*Camptoplites asymmetricus*	H		H/HA						
41.	*Camptoplites bicornis*	HA		H		HA	HA	H	HA	H
42.	*Camptoplites giganteus*			H			MO	H	H	HA
43.	*Camptoplites latus*			H/HA					H	
44.	*Camptoplites retiformis*				H		H/HA	H	HA	HA
45.	*Camptoplites tricornis*			H		MO	MO	H	H	HA
46.	*Carbasea curva*			H/LG		LG	LG/M	H		
47.	*Carbasea ovoidea*	H	H				H/LG	MO		
48.	*Cellaria aurorae*			H	H		H	H	H	H
49.	*Cellaria diversa*				LG	H	H/LG	H	H	H
50.	*Cellaria incula*					MO	MO		H	H
51.	*Cellaria malvinensis*	H/M	H/M	H/LG						
52.	*Cellaria moniliorata*					LG	H	H	H	H
53.	*Cellaria sobrinoi*						LG			
54.	*Cellaria tenuis*	MO	MO							
55.	*Cellaria variabilis?*	MO	MO							
56.	*Cellarinella anomala*			H		LG				
57.	*Cellarinella sp.*					MO	MO			
58.	*Cellarinella latilaminata*			LG			H/LG		H	
59.	*Cellarinella nutti*					LG	LG			
60.	*Cellarinella rogickae*					LG	LG			
61.	*Cellarinella terminata*						H			
62.	*Cellarinella virgula*						H			
63.	*Cellarinella watersi*			H		H/LG	MO	H	H	
64.	*Celleporella alia*			H	H	H	H	H		
65.	*Celleporella antarctica*					H/LG	H/LG			
66.	*Celleporella bougainvillei*	H	H	H/LG	LG	LG	H/LG	H		
67.	*Celleporella dictyota*					H	H			
68.	*Celleporella discreta*	H	H	H						
69.	*Chaperiopsis sp.*			MO	MO					
70.	*Chaperiopsis galeata*	H	H	H	H					
71.	*Chaperiopsis orbiculata*			H						

APPENDIX 1 (Cont.). – Bryozoans from Scotia Arc and adjacent Subantarctic and Antarctic areas, after Hastings (1944) (HA), Hayward (1995)(H) López de la Cuadra and García Gómez (2000) (LG) and Moyano (this study) (MO). Localities: PLP: Patagonian shelf; BMA: Falkland Is. - Is. Malvinas and Burdwood Bank; SGR: South Georgia; SSA: South Sandwich; SOR: South Orkney; ESS: Elephant I. and South Shetland; PAN: Antarctic Peninsula; MRO: Ross Sea; CCA: Antarctic continental coasts.

		PLP	BMA	SGR	SSA	SOR	ESS	PAN	MRO	CCA
72.	*Chaperiopsis protecta*				H			H		
73.	*Chaperiopsis rotundata*			H						
74.	*Chartella notialis*	MO	MO							
75.	*Cornucopina ovalis*	H		H/HA						
76.	*Cornucopina pectogemma*	H	H	H/HA	H/HA		H/LG			
77.	*Cornucopina polymorpha*			H	H	MO	H/LG	H	HA	HA
78.	*Cornucopina sp.*		MO							
79.	*Crisidia delicatissima*						MO	MO		
80.	*Dakariella concinna*				MO				H	
81.	*Dakariella dabrowni*			H					H	
82.	*Dendroperistoma projecta*			H/LG	H	LG	H	H	H	
83.	*Disporella octoradiata*			MO						
84.	*Electra longispina*	H		H						
85.	*Ellisina antarctica*		H	H		H	LG			
86.	*Eminoecia carsonae*					H		H	H/MO	
87.	*Escharella mamillata*			H	H		H		H	
88.	*Escharella watersi*			H/LG				H	H	
89.	*Escharella sp.*			MO	MO					
90.	*Escharoides praestita*			H/LG				H	H	
91.	*Escharoides torquata*			H						
92.	*Escharoides tridens*					H		H		
93.	*Exochella elegans*						H/LG			
94.	*Exochella hymanae*			H/LG		H		H		
95.	*Exochella umbonata*						H/LG			
96.	*Exochella sp.*				MO					
97.	*Fenestrulina antarctica*					LG	LG	H	H	
98.	*Fenestrulina exigua*			H/LG				H	H	
99.	*Fenestrulina fritilla*		H	H/LG						
100.	*Fenestrulina jocunda*			H/LG						
101.	*Fenestrulina proxima*						H	H		
102.	*Fenestrulina rugula*			H		H/LG	LG/M	H		
103.	*Filaguria spatulata*			LG			H	H	H	H
104.	*Flustrapora magellanica*	MO	MO							
105.	*Foveolaria terrifica*	MO	MO							
106.	*Galeopsis bullatus*			H						
107.	*Harpecia spinosissima*			H	LG	H	LG	H	H	
108.	*Himantozoum antarcticum*			H	LG	HA	LG/M	H	H	H
109.	*Hippadenella inerma*						H	H	H	
110.	*Hippomonavella pellucidula*			H/LG						
111.	*Hippomonavella ramosae*			LG						
112.	*Hippothoa flagellum*	H	H/MO	MO	MO		LG	H	H	
113.	*Hornera sp.*						MO			
114.	*Icelozoon dichotomum*						H			H
115.	*Ichthyaria oculata*	MO	MO							
116.	*Inversiula nutrix*	H	H	H	H	H	H/LG	H		
117.	*Isoschizoporella secunda*					H/L	LG/M	H	H	
118.	*Isoschizoporella similis*					H		H	H	
119.	*Isoschizoporella tricuspis*					LG	LG			
120.	*Isoseculiflustra rubefacta*					H	H/LG			
121.	*Isoseculiflustra tenuis*						H	H		H
122.	*Isoseculiflustra thysanica*						H	H		
123.	*Klugeflustra antarctica*			H	H		HA		H	HA
124.	*Klugeflustra onychocelloides*				H					H
125.	*Klugeflustra vanhoffeni*						H	H		
126.	*Klugerella antarctica*						H	MO	H	
127.	*Klugerella olasoi*			LG						
128.	*Kymella polaris*					LG	LG	H	H	H
129.	*Lacerna eatoni*	H	H			H	LG	H		
130.	*Lacerna hosteensis*	H	H	H/LG	H	H	H			
131.	*Lacerna watersi*						H	H	H	
132.	*Larvapora mawsoni*			H		LG	LG	H		
133.	*Macropora georgensis*			LG						
134.	*Melicerita blancoae*	MO	MO							
135.	*Melicerita flabellifera*						H			
136.	*Melicerita latilaminata*					LG	H/LG	H	H	
137.	*Melicerita obliqua*					H/MO	H	H	H	H
138.	*Menipea sp.*	MO	MO							
139.	*Menipea patagonica*	H	H	H/HA						
140.	*Micropora brevisima*			H/L/M		LG	H/LG	H	H	H
141.	*Micropora notialis*	H		H/LG				H		
142.	*Microporella hyadesi*	MO	MO	LG						
143.	*Microporella stenoporta*				H			H	H	
144.	*Nematoflustra flagellata*			H/LG		LG/M	LG	H		

APPENDIX 1 (Cont.). – Bryozoans from Scotia Arc and adjacent Subantarctic and Antarctic areas, after Hastings (1944) (HA), Hayward (1995)(H) López de la Cuadra and García Gómez (2000) (LG) and Moyano (this study) (MO). Localities: PLP: Patagonian shelf; BMA: Falkland Is. - Is. Malvinas and Burdwood Bank; SGR: South Georgia; SSA: South Sandwich; SOR: South Orkney; ESS: Elephant I. and South Shetland; PAN: Antarctic Peninsula; MRO: Ross Sea; CCA: Antarctic continental coasts.

	PLP	BMA	SGR	SSA	SOR	ESS	PAN	MRO	CCA
145. *Nevianipora sp.*		MO							
146. *Notoplites sp.*		MO							
147. *Notoplites antarcticus*			H			HA	H		
148. *Notoplites crassiscutus*			H/HA						
149. *Notoplites drygalskii*			H	HA		LG/M	H	H	H
150. *Notoplites tenuis*			H	HA			H	H	H
151. *Ogivalia elegans*	MO	MO							
152. *Orthoporidra compacta*					H/LG	H/LG	H	H	
153. *Orthoporidroides erectus*	MO	MO							
154. *Osthimosia bicornis*	H/MO	H	H/LG		LG	LG/M	MO	H	
155. *Osthimosia sp.1*		MO							
156. *Osthimosia sp.2*					MO				
157. *Osthimosia clavata*				H	H		H	H	
158. *Osthimosia curtioscula*			H/LG						
159. *Osthimosia fusticula*						H			
160. *Osthimosia malingae*					H/LG	H/LG		H	
161. *Osthimosia milleporoides*			H/LG	H	H/LG	H/LG		H	
162. *Osthimosia notialis*				H	H/LG	H	H	H	
163. *Osthimosia phalacrococraca*			H					H	
164. *Paracellaria calveti*		H				H			
165. *Paracellaria cellarioides*	MO	MO							
166. *Paracellaria elephantina*						H			
167. *Parafigularia sp. n.*			MO						
168. *Pemmatoporella marginata*					LG				
169. *Platychelina planulata*	MO	MO							
170. *Plesiothoa calculosa*						H		H	
171. *Polirhabdotos inclusum*						H		H	H
172. *Relepria conforma*			H						
173. *Reteporella antarctica*			H		LG	LG	H	H	
174. *Reteporella erugata*			LG	MO					
175. *Reteporella frigida*					LG	H/MO	H	H	
176. *Reteporella hippocrepis*					LG	MO			
177. *Reteporella lepralioides*					LG				
178. *Reteporella magellensis*	MO	MO							
179. *Reteporella protecta*			H/LG			H	H		
180. *Rhynchozoon fistulosum*			H						
181. *Romancheina asymmetrica*						H	H	H	
182. *Schizoporella ? sp.*		MO							
183. *Securiflustra bifoliata*		MO							
184. *Smittina abditavicularis*			H					H	
185. *Smittina alticollarita*			H			H	H	H	
186. *Smittina antarctica*			LG		H/MO	MO	H	H	
187. *Smittina exertaviculata*					H			H	
188. *Smittina incernicula*			H		LG	H/LG		H	
189. *Smittina monacha ?*	MO	MO							
190. *Smittina sp. n.*				MO					
191. *Smittina obicullata*					H		H	H	
192. *Smittina pocilla*						H			
193. *Smittina rogickae*						H		H	H
194. *Smittinella sp.*			MO						
195. *Smittinella rubrilingulata*			H	H		H	H	H	
196. *Smittoidea conspicua*						MO			
197. *Smittoidea malleata*						H	H	H	
198. *Smittoidea pugiuncula*			MO			H		H	
199. *Smittoidea rhynchota*		H	LG	H					
200. *Stomhypselosaria watersi*	H			H	H	LG	H	H	H
201. *Swanomia brevimandibulata*						LG	MO	H	A
202. *Swanomia membranacea*				H			H	H	H
203. *Systenopora contracta*					MO	H	H	H	H
204. *Talivittaticella frigida*	H	MO				H/MO	H		
205. *Toretocheilum turbinatum*			MO		H			H	
206. *Tricellaria sp.*		MO							
207. *Tricellaria aculeata*	H	H	H/HA						
208. *Trilaminopora trinervis*			H			LG	H		H
209. *Trilochites biformatus*			H/MO	H/MO		H	H		
210. *Thrypticocirrus phylactelloides*					LG	MO	H	H	
211. *Turritella cribrata*			H				H	H	
212. *Valdemunitella lata*			H		LG	LG	H		
213. *Flustridae n. gen. n. sp.*		MO							
214. *Xylochotridens rangifer*						H			
	48	51	94	43	77	117	89	79	38

APPENDIX 2. – Cheilostomatous bryozoan genera from the Scotia Arc archipelagos after López de la Cuadra and García Gómez (2000) and Moyano (LAMPOS 2002, this study); MAG = Magellan area; ANZ = Australia and New Zealand with bryozoan genera after Gordon (1984,1986, 1989); ARS = Scotia Arc; PAN = Antarctic Peninsula. Endemism: the endemic Antarctic genera including those present in Scotia Arc archipelagos appear in **bold.** * = One Subantarctic species and seventeen Antarctic species. ** = North Atlantic genus represented in the southwest Atlantic by only one species. *** = Subantarctic Magellan genera located around the southern tip of South America. 5.**** = New flustriform genus collected during the LAMPOS expedition off Shag Rocks in Subantarctic waters (because all other species in the sample were typically Subantarctic).

	MAG	ANZ	ARS	PAN		MAG	ANZ	ARS	PAN
1. *Acanthophragma*	-	-	x	x	39. ***Isoseculiflustra***	-	-	x	x
2. *Adelascopora*	x	-	x	x	40. *Klugerella*	-	x	x	x
3. *Aimulosia*	x	x	x	x	41. ***Kymella***	-	-	x	x
4. *Amastigia*	x	x	x	x	42. *Lacerna*	x	x	x	x
5. *Amphiblestrum*	-	x	x	x	43. ***Larvapora***	-	-	x	x
6. ***Antarcticaetos***	-	-	x	x	44. *Macropora*	-	x	x	-
7. *Arachnopusia*	x	x	x	x	45. *Melicerita*	x	x	x	x
8. *Aspidostoma*	x	x	x	x	46. *Menipea*	x	x	-	-
9. *Aulopocella*	x	x	x	x	47. *Micropora*	x	x	x	x
10. *Austroflustra*	x	-	x	x	48. *Microporella*	x	x	x	x
11. *Beania*	x	x	x	x	49. ***Nematoflustra***	-	-	x	x
12. ***Bostrychopora***	-	-	x	x	50. *Ogivalia*	x	x	-	-
13. *Caberea*	x	x	x	x	51. *Orthoporidra*	-	x	x	x
14. *Carbasea*	x	-	x	x	52. *Orthoporidroides* ***	x	-	-	-
15. *Camptoplites*	x	x	x	x	53. *Osthimosia*	x	x	x	x
16. *Cellaria*	x	x	x	x	54. *Paracellaria*	x	-	x	x
17. *Cellarinella* *	x	-	x	x	55. *Parafigularia*	x	-	x	x
18. *Chaperiopsis*	x	x	x	x	56. ***Pemmatoporella***	-	-	x	x
19. *Celleporella*	x	x	x	x	57. *Platychelina* ***	x	-	-	-
20. *Chartella* **	x	-	-	-	58. *Reteporella*	x	x	x	x
21. *Cornucopina*	x	x	x	x	59. *Securiflustra*	x	x	x	-
22. ***Dakariella***	-	-	x	x	60. *Smittina*	x	x	x	x
23. ***Dendroperistoma***	-	-	x	x	61. *Smittoidea*	x	x	x	x
24. *Ellisina*	x	x	x	x	62. *Stomhypselosaria*	x	x	x	x
25. *Escharella*	x	x	x	x	63. ***Swanomia***	-	-	x	x
26. *Escharoides*	-	x	x	x	64. ***Systenopora***	-	-	x	x
27. *Exochella*	x	x	x	x	65. *Talivittaticella*	x	x	x	x
28. *Fenestrulina*	x	x	x	x	66. ***Toretocheilum***	-	-	x	x
29. ***Filaguria***	-	-	x	x	67. *Tricellaria*	x	x	x	x
30. *Flustrapora* ***	x	-	-	-	68. ***Trilaminopora***	-	-	x	x
31. *Foveolaria*	x	x	-	-	69. ***Trilochites***	-	-	x	-
32. ***Harpecia***	-	-	x	x	70. ***Trypticocirrus***	-	-	x	x
33. *Himantozoum*	x	x	x	x	71. *Valdemunitella*	-	x	x	x
34. *Hippomonavella*	-	x	x	x	72. Flustridae n. gen. ****	x	-	-	-
35. *Hippothoa*	x	x	x	x					
36. *Ichthyaria*	x	x	-	-	72 = **19**/53	46	42	63	60
37. *Inversiula*	x	x	x	x	100% = **26**%/72%				
38. ***Isoschizoporella***	-	-	x	x					

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

The bivalves from the Scotia Arc islands: species richness and faunistic affinities*

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SUMMARY: Species richness of the shallow-water bivalves from the Scotia Arc islands was studied on the basis of new collections and by reviewing extant information. Seventy-three species are recognised from the entire area. South Georgia, the South Orkney Islands and the South Shetland Islands were similar in species richness to the Antarctic Weddell sector. New records for 51 bivalve species are provided and the presence of 18 undescribed species is reported. The faunistic similarity of the islands of the Scotia Arc to the Magellan region and the Antarctic Weddell sector is re-examined. These islands show a high similarity to the Antarctic Weddell sector (49 to 85%) and a low similarity to the Magellan region (12 to 32%). Evidence from bivalves clearly supports the placement of the Scotia Arc islands within the Antarctic region.

Keywords: diversity, biogeography, molluscs, Bivalvia, Scotia Sea, Antarctic.

RESUMEN: DIVERSIDAD Y SIMILITUDES FAUNÍSTICAS DE LOS BIVALVOS DE LAS ISLAS DEL ARCO DE SCOTIA. – La diversidad de bivalvos que habitan en las aguas someras del Arco de Scotia fue estudiada sobre la base de recientes colecciones desarrolladas en el área y por la revisión de la información preexistente. Un total de 73 especies fueron reconocidas para el área; el número de especies hallado en las islas Georgias del Sur (49), Orcadas del Sur (43) y Shetland del Sur (42) resultó similar al actualmente conocido para el cuadrante antártico de Weddell (41 especies). Se proporcionan nuevas citas para 51 especies de bivalvos y se informa sobre la existencia de 18 especies aún no descriptas. Las similitudes faunísticas de las islas del Arco de Scotia con la región magallánica y con el cuadrante antártico de Weddell fueron reanalizadas. Estas islas mostraron una elevada similitud con el cuadrante antártico de Weddell (49 a 85%, dependiendo del archipiélago) y una baja similitud respecto a la región magallánica (12 a 32%). Las evidencias procedentes de los bivalvos claramente soportan el emplazamiento de las islas del Arco de Scotia dentro de la región antártica.

Palabras clave: diversidad, biogeografía, moluscos, Bivalvia, Mar de Scotia, Antártida.

INTRODUCTION

Four archipelagos forming the Scotia Arc are located between the southernmost South American mainland and the Antarctica. According to their geological origin and history, two groups of islands are recognised: the first one comprises the old archipelagos originated as a consequence of the fragmentation process of the Gondwana supercontinent, 37 to 20 Ma (i.e. South Georgia, the South Orkney Islands and the South Shetland Islands); the second is a series of younger islands originated by volcanic processes that started about 1-10 million years ago: the South Sandwich archipelago (Dalziel and Elliot, 1971; Birkenmajer, 1984; Gambôa and Maldonado, 1991; Ramos, 1996; Udintsev *et al.*, 2000). The islands of the Scotia Arc provide an outstanding opportunity to study the origin and evolutionary radiation of their fauna, taking into account the intermediate geographic position between South

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America and the Antarctica. Moreover, the study of the fauna from these islands could provide a basis for the understanding of the present faunistic similarities between South America and Antarctica, two continents linked during the Mesozoic and presently geographically separated and isolated by deep water and marine current systems (Dalziel and Elliot, 1971; Crame, 1999).

Based on data from different invertebrate taxa, the Scotia Arc islands were usually included in the Antarctic region (e.g. De Broyer and Jazdzewski, 1993: Amphipoda; Mühlenhardt-Siegel, 1999: Cumacea; Gorny, 1999: Decapoda) but also considered as a member of the Subantarctic region (e.g. Casteló, 1999: Isopoda). A particular situation is found with South Georgia, which has been considered as related either to the Magellan (Linse, 1997: Mollusca) or the Antarctic regions (Carcelles, 1953: Mollusca), as representing a transitional area between these regions (Linse *et al.*, 2003: Mollusca; Schrödl, 1999, 2003: Nudibranchia), or as a distinctive biogeographic unit (Linse, 2002: Mollusca; Powell, 1951: Gastropoda; De Broyer and Jazdzewski, 1993: Amphipoda). Canteras and Arnaud (1985) argued for faunistic affinities of South Georgia with the Kerguelen Islands and Crozet Islands. The sets of data analysed by several authors were heterogeneous; furthermore, the available information on species diversity and their geographical distribution is still fragmentary and in many cases needs revision before it can be included in a biogeographic analysis. Both of these facts seem to be the origin of discrepant interpretations.

Knowledge on the species richness of bivalves from the Scotia Arc islands is fragmentary. The most important contributions for the area were provided by the Discovery, Discovery II and William Scoresby expeditions (Dell, 1964 and 1990). Relevant studies on the fauna from South Georgia were provided by Martens (1885) and Martens and Pfeffer (1886). Dall (1914), David (1934), Soot-Ryen (1951) and Carcelles (1953) provided new localities for some species within the archipelago, and Zelaya and Ituarte (2002, 2003) described three new species from these islands. The fauna of the South Orkney Islands was studied by the Scottish National Antarctic Expedition (Melvill and Standen, 1907), from the R/V "Polarstern" and R/V "Walther Herwig" cruises (Mühlenhardt-Siegel, 1989). Preston (1916), Soot-Ryen (1951), Arnaud *et al.* (1986), Mühlenhardt-Siegel (1989), Arnaud *et al.* (2001), and Narchi *et al.* (2002) contributed to the knowledge of the fauna from the South Shetland Islands.

Carcelles (1953) and Powell (1960) provided checklists of the Antarctic bivalves (including the Scotia Arc islands), but subsequent studies conducted in Antarctic waters (Dell, 1964, 1990; Hain, 1990; this study) strongly suggest that the information contained in published lists needs to be revised. In this paper the species richness of the shallow water bivalves from the Scotia Arc islands was studied on the basis of recent collections and by reviewing extant information, in order to reanalyse the current biogeographic status of these islands and their relationships with the Magellan region and adjacent Antarctic waters.

MATERIAL AND METHODS

Sources of information

The main sources of information for this study were the bivalves collected by R/V "Polarstern" during the "Latin American Polarstern Study" (ANT XXI-5, LAMPOS) in 2002. Sampling took place at 17 sampling stations along the Scotia Sea (for details on stations see Arntz and Brey, 2003). Additional information came from 30 sampling stations off South Georgia worked on the R/V "Eduardo L. Holmberg" during the 1995, 1996, 1997 cruises, and 20 sampling stations in Patagonia (Beagle Channel, Straits of Magellan and east of Tierra del Fuego) visited by the A.R.A. "Alférez Sobral". Other sources of information were molluscs from the following museum collections: Museo de La Plata, La Plata (MLP), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN) and Museo Nacional de Historia Natural, Santiago, Chile (MNHN). Moreover, published information on bivalves from all these areas, as well as that from the Antarctic Weddell sector, was critically reviewed and added to the present analysis.

Terminology

Throughout this article, the term "Scotia Arc islands" is used to refer to the Scotia Sea archipelagos, i.e. South Georgia, the South Sandwich Islands, the South Orkney Islands and South Shetland Islands. "Antarctic Weddell sector" comprises the Antarctic Peninsula and the Weddell Sea. "Patagonia" is used to refer to the southern tip of South

TABLE 1. – List of bivalve species and their geographic distribution. X: this study; X^1: new records from this study; *: literature records; ?: presence uncertain; P, Patagonia; M/F, Malvinas / Falkland Is.; SG, South Georgia; SS, South Sandwich Is.; SO, South Orkney Is.; SSH South Shetland Is.;WS, Antarctic Weddell sector.

Family	Species	P	M/F	SG	SS	SO	SSH	WS
Solemyidae	*Acharax patagonica* (Smith, 1885)	X						
Nuculidae	*Ennucula eltanini* Dell 1990	X						
	Ennucula georgiana Dell, 1964			X				
	Ennucula grayi (d'Orbigny, 1846)	X	?					
	Nucula falklandica Preston, 1912	X	*			?		?
	Nucula pseudoexigua Villarroel and Stuardo, 1998	X						
Nuculanidae	*Nuculana* (?) *inaequisculpta* (Lamy, 1906)					X	X	*
	Nuculana sulculata (Couthouy in Gould, 1852)	X	*					
	Propeleda longicaudata (Thiele, 1912)	X		X		X	X	*
Malletiidae	*Malletia cumingi* (Hanley, 1860)	X	*					
	Malletia magellanica (Smith, 1875)	X						
Tindariidae	*Tindaria virens* Dall, 1889	*						
Yoldiidae	*Yoldia eightsi* (Couthouy in Jay, 1839)	?	?	X		X	X	X
	Yoldia woodwardi Hanley, 1860	X	X					
	Yoldiella antarctica (Thiele, 1912)				X	X	X	
	Yoldiella ecaudata (Pelseneer, 1903)							*
	Yoldiella granula Dall, 1908	X						
	Yoldiella cf. *indolens* Dall, 1908	X						
	Yoldiella oblonga (Pelseneer, 1903)							*
	Yoldiella valettei Lamy, 1906	?	X		X^1	*	X^1	*
	Yoldiella sp.	X						
Siliculidae	*Silicula patagonica* Dall, 1908	X						
	Silicula rouchi Lamy, 1910			?		X	X	*
Limopsidae	*Limopsis hirtella* Mabille and Rochebrune, 1889	X	X					
	Limopsis jousseaumi (Mabille and Rochebrune, 1889)	X						
	Limopsis lillei Smith, 1915			X		*	*	*
	Limopsis cf. *marionensis* Smith, 1885				X	*	*	*
	Limopsis scotiana Dell, 1964			X	X^1	X	X	
	Limopsis sp.				X			
	Lissarca cf. *miliaris* (Philippi, 1845)	X	*	*		*	X	X
	Lissarca notorcadensis Melvill and Standen,1907		X^1	X	X	X	X	X
Philobryidae	*Adacnarca limopsoides* (Thiele, 1912)					?	*	*
	Adacnarca nitens Pelseneer, 1903			*	X	X	X	*
	Adacnarca n. sp.			X^1				
	Philobrya atlantica Dall, 1895	*	*	*				
	Philobrya capillata Dell, 1964		*					*
	Philobrya crispa Linse, 2002	X						
	Philobrya cf. *kerguelensis* Smith, 1885			*				
	Philobrya magellanica (Stempell, 1899)	X						
	Philobrya multistriata Lamy, 1908	?	X					
	Philobrya olstadi (Soot-Ryen, 1951)					*	*	X^1
	Philobrya quadrata (Pfeffer in Martens and Pfeffer, 1886)	?		X		*		?
	Philobrya sublaevis Pelseneer, 1903			X	X	X	X	*
	Philobrya wandelensis Lamy, 1906		?	X	X^1	*	*	*
	Philobrya n. sp. 1		X^1					
	Philobrya n. sp. 2		X^1					
	Philobrya n. sp. 3	X^1						
Mytilidae	*Aulacomya atra* (Molina, 1782)	X	*					
	Crenella magellanica Linse, 2002	X	X^1					
	Dacrydium cf. *albidum* Pelseneer, 1903				X^1		*	*
	Mytilus chilensis Hupé, 1854	X	*	?				
	Perumytilus purpuratus (Lamarck, 1819)	X	X^1					
Limidae	*Acesta patagonica* Dall, 1902	X						
	Limatula hodgsoni (Smith, 1907)			X	X	X	X	*
	Limatula ovalis (Thiele, 1912)						*	X
	Limatula pygmaea (Philippi, 1845)	X	X	?				
	Limatula simillima Thiele, 1912					*		*
	Limatula n. sp.	X^1	X^1					
Pectinidae	*Adamussium colbecki* (Smith, 1902)				*	X	*	*
	Chlamys tehuelchus (d'Orbigny, 1846)	X						
	Semipallium natans (Philippi, 1845)	X						
	Zygochlamys patagonica (King and Broderip, 1832)	X	X					
Propeamussiidae	*Cyclopecten falklandicus* Dell, 1964	*	X					
	Cyclopecten gaussianus (Thiele, 1912)							*
	Cyclopecten multistriatus Linse, 2002	X						
	Cyclopecten pteriola (Melvill and Standen, 1907)					*		?
	Cyclopecten n. sp. 1		X^1					
	Cyclopecten n. sp. 2		X^1					
	Cyclopecten n. sp. 3				X^1			
	Cyclopecten n. sp. 4			X^1				
	Cyclopecten n. sp. 5			X^1				

TABLE 1 (Cont.). – List of bivalve species and their geographic distribution. X: this study; X^1: new records from this study; *: literature records; ?: presence uncertain; P, Patagonia; M/F, Malvinas / Falkland Is.; SG, South Georgia; SS, South Sandwich Is.; SO, South Orkney Is.; SSH South Shetland Is.;WS, Antarctic Weddell sector.

Family	Species	P	M/F	SG	SS	SO	SSH	WS
Lucinidae	*Epicodakia falklandica* Dell, 1964	X	*	X^1		X^1		
	Lucinoma lamellata (Smith, 1881)	X	*					
Thyasiridae	*Genaxinus* (?) *debilis* (Thiele, 1912)	?	?	X	X	X	X	*
	Thyasira bongraini (Lamy, 1910)					X	*	*
	Thyasira falklandica (Smith, 1885)		X	?		?	?	
	Thyasira fuegiensis (Dall, 1889)	X						
	Thyasira magellanica Dall, 1901	X						
	Thyasira n. sp. 1	X^1						
	Thyasira n. sp. 2			X^1			X^1	
	Thyasira n. sp. 3			X^1		X^1		
Astartidae	*Astarte longirostris* d´Orbigny, 1846	X	X	*				
	Astarte antarctica Thiele, 1912						X	*
Carditidae	*Carditella naviformis* (Reeve, 1834)	X	*					
	Carditella pallida (Smith, 1881)	X						
	Cyclocardia astartoides (Martens, 1878)	?		X	X	X	*	*
	Cyclocardia compressa Reeve, 1843	X	X^1					
	Cyclocardia thouarsi (d´Orbigny, 1846)	*	X					
	Venericardia velutina (Smith, 1881)	X	*					
Condylocardiidae	*Carditopsis flabellum* (Reeve, 1843)	*	*					
	Benthocardiella n. sp. 1	X^1						
	Benthocardiella n. sp. 2	X^1						
Lasaeidae	*Kellia* cf. *magellanica* Smith, 1881	X	*					
	Kellia simulans Smith, 1907						*	*
	Kellia sp. 1	X						
	Kellia sp. 2			X				
	Kellia sp. 3					X		
	Lasaea adansoni (Gmelin, 1791) [following Coan *et al.*, 2000]	X	X	*		*		
	Montacuta (?) *nimrodiana* (Hedley, 1911)			X^1		X^1	*	*
	Mysella (?) *arthuri* (Cooper and Preston, 1910)		X					
	Mysella (?) *miniuscula* (Pfeffer in Martens and Pfeffer, 1886)			X	*	*	*	*
	Pseudokellya cardiformis (Smith, 1885)		*	X	*		*	*
	Pseudokellya georgiana Dell, 1964			X				
	Pseudokellya gradata Thiele, 1912					*	*	*
	Pseudokellya inexpectata Dell, 1964			X		*		
	Rochefortia charcoti (Lamy, 1906)	?		*		*	X	*
	Rochefortia mabillei Dall, 1908	X	X^1					
	Rochefortia rochebrunei Dall, 1908	X						
Galeommatoidea	*Waldo parasiticus* (Dall, 1876)	X		X		X^1	*	
	Waldo trapezialis Zelaya and Ituarte, 2002			X		X^1		
Cyamiidae	*Cyamium antarcticum* Philippi, 1845	X	X					
	Cyamium falklandicum Melvill and Standen, 1898		*					
	Cyamium iridescens Cooper and Preston, 1910		*					
	Cyamium willii Pfeffer in Martens and Pfeffer, 1886			*				
	Cyamiocardium crassilabrum Dell, 1964	X	*					
	Cyamiocardium dahli Soot-Ryen, 1957	X						
	Cyamiocardium denticulatum (Smith, 1907)	?	?			X^1	X	*
	Cyamiocardium n. sp.			X^1				
	Cyamiomactra laminifera (Lamy, 1906)		?	X	*	*	*	*
	Gaimardia adamsorium Osorio and Arnaud, 1984		*					
	Gaimardia bennetti (Preston, 1913)	X^1	X					
	Gaimardia trapesina (Lamarck, 1819)	X	X	X				
	Gaimardia sp.	X						
	Kidderia bicolor (Martens, 1885)			*				
	Kidderia pusilla (Gould, 1845)	X	*					
	Kidderia subquadrata (Pelseneer, 1903)						X	X
	Kidderia sp. 1	*						
	Kidderia sp. 2		X					
	Ptychocardia vanhoeffeni Thiele, 1912							*
Neoleptonidae	*Neolepton amatoi* Zelaya and Ituarte, 2004	*						
	Neolepton cobbi (Cooper and Preston, 1910)	X	X					
	Neolepton concentricum (Preston, 1912)	X^1	*					
	Neolepton falklandicum Dell, 1964	X^1	X					
	Neolepton georgianum Zelaya and Ituarte, 2003			*				
	Neolepton holmbergi Zelaya and Ituarte, 2003			*				
	Neolepton hupei Soot-Ryen, 1957	X	X					
	Neolepton yagan Zelaya and Ituarte, 2004	*						
	Neolepton n. sp.	X^1						
	Puyseguria n. sp.	X^1						
Cardiidae	*Trachycardium delicatulum* (Smith, 1915)		*					

TABLE 1 (Cont.). – List of bivalve species and their geographic distribution. X: this study; X^1: new records from this study; *: literature records; ?: presence uncertain; P, Patagonia; M/F, Malvinas / Falkland Is.; SG, South Georgia; SS, South Sandwich Is.; SO, South Orkney Is.; SSH South Shetland Is.;WS, Antarctic Weddell sector.

Family	Species	P	M/F	SG	SS	SO	SSH	WS
Veneridae	*Eurhomalea exalbida* (Dillwyn, 1817)	X	*					
	Gomphina foveolata (Cooper and Preston, 1910)	X	*					
	Protothaca antiqua (King and Broderip, 1832)	X						
	Tawera gayi (Hupé in Gay, 1854)	X	?					
Petricolidae	*Petricola dactylus* G. B. Sowerby I, 1823 [sensu Coan, 1997]	X						
Tellinidae	*Macoma georgiana* Dell, 1964			*				
	Macoma inornata (Hanley, 1844)	X	*					
Pharidae	*Ensis macha* Molina, 1789	X	X					
Mactridae	*Darina solenoides* (King and Broderip, 1832)	X	*					
	Mulinia (?) *edulis* (King and Broderip, 1832)	X						
Myidae	*Mya antarctica* Melvill and Standen, 1914	X^1	*					
	Sphenia hatcheri Pilsbry, 1899	X						
Hiatellidae	*Hiatella meridionalis* d' Orbigny, 1846	X	*	X				
	Hiatella sp.	X	X		*			
Teredinidae	*Bankia martensi* Stempell, 1899	*						
Pandoridae	*Pandora cistula* Gould, 1850	*						
	Pandora patagonica (Dall, 1915)	X						
Lyonsiidae	*Lyonsia* cf. *arcaeformis* Martens, 1885	X^1		X	X^1	X	*	*
	Lyonsia fretalis Dall, 1915	*	*					
Thraciidae	*Thracia meridionalis* Smith, 1885	?	X	X	*	X	X	*
	Thracia sp.	X						
Laternulidae	*Laternula elliptica* (King and Broderip, 1832)			X	*	*	X	*
Cuspidariidae	*Cardiomya simillima* Smith, 1915	X	*					
	Cuspidaria concentrica Thiele, 1912		X^1	X^1				
	Cuspidaria minima (Egorova, 1993)					*	X^1	
	Cuspidaria tenella Smith, 1907	*	*	X	*	*	*	*
	Cuspidaria sp.1	X	X	X	X	X	X	
	Cuspidaria sp. 2			X				
Verticordiidae	*Lyonsiella radiata* Dall, 1889	*						
Poromyidae	*Poromya adelaidis* (Hedley, 1916)		X	X^1	X^1	X^1	X	
Total number of species		93	67	49	25	43	42	41

America, between Peninsula Valdés (~ 43°S) in the Atlantic Ocean, and 42ºS in the Pacific Ocean. The reference to the Islas Malvinas/Falkland Islands also includes the Burdwood Bank.

This study was restricted to the bivalve faunas from shelf waters. In the case of the South Sandwich Islands (where a shelf does not exist) the 600 m isobath was considered as the depth limit. Those species characteristic of Argentine and Peruvian Provinces that occasionally reach the northern limit of the Magellan region were not considered in this study.

The high level classification of bivalves follows Coan *et al.* (2000). "Endemics" refers to species only known from one of the archipelagos or any of the above mentioned areas (e.g. Patagonia or the Antarctic Weddell sector), which are mentioned in each particular case.

Analysis of similarity

Degrees of faunistic affinity among the areas were evaluated by using the Simpson similarity coefficient (SI). This coefficient moderates the bias caused by different sampling efforts (Cheetham and Hazel, 1969). The percentage of similarity, referred to as "similarity" in the text, was determined as SI x 100.

RESULTS

Table 1 lists the 170 species recognised as present in the study area and shows their geographic distribution. Specimens of 147 species were examined during this study, 18 of which are still undescribed. In addition, another 23 species known from literature records were regarded to be distinct species with a reasonable certainty. Seventy-three of the 170 listed species were present in the Scotia Arc islands, while the remaining 97 species only occurred in Patagonia, Islas Malvinas/Falkland Islands or the Antarctic Weddell sector. The South Georgia, South Orkney and South Shetland islands accounted for a similar number of species (49, 43 and 42 species respectively), a species richness sim-

TABLE 2. – Simpson similarity coefficient values (SI) for the analysed areas.

	Patagonia	Malvinas/Falkland	South Georgia	South Sandwich	South Orkney	South Shetland	Weddell Sector
Patagonia	1						
Malvinas / Falkland	0.70	1					
South Georgia	0.24	0.29	1				
South Sandwich	0.16	0.32	0.68	1			
South Orkney	0.18	0.21	0.67	0.80	1		
South Shetland	0.12	0.21	0.57	0.88	0.81	1	
Weddell Sector	0.10	0.17	0.49	0.72	0.71	0.85	1

ilar to that of the Antarctic Weddell sector (41 species) but clearly lower than that of Patagonia and the Islas Malvinas/Falkland Islands (93 and 67 species respectively). The lowest number of species was found off the South Sandwich Islands, where only 25 species of bivalves were recognised.

The South Sandwich Islands showed a high faunistic similarity to the South Shetland Islands (88%) and a lower similarity to the South Orkney Islands (80%) and South Georgia (68%) (Table 2). South Georgia showed a moderately high similarity to the South Orkney Islands (67%) and the South Shetland Islands (51%). Similarity values between the South Orkney Islands and the South Shetland Islands were high (81%) (Table 2). Comparisons made between each component of the Scotia Arc islands and the remaining areas showed high similarity to the Antarctic Weddell sector (49 to 85%, depending on the archipelago) and low similarity to Patagonia and the Islas Malvinas/Falkland Islands (12 to 29%) (Table 2).

Of the 73 species from the Scotia Arc islands, 26 (36%) were endemic to the Scotia Sea, 28 were shared with the Antarctic Weddell sector and 11 were shared with Patagonia or the Islas Malvinas/Falkland Islands; the remaining 8 species were widespread, and present in the Scotia Arc islands, the Islas Malvinas/Falkland Islands, Patagonia and the Antarctic Weddell sector. The contribution of the "endemic" species to the total species number of each archipelago was: Islas Malvinas/Falkland Islands, 12 species (18%); South Georgia, 14 species (29%); South Sandwich Islands, 2 species (8%); South Orkney Islands, 2 species (7%); and South Shetland Islands, 0 species. At a larger regional scale, Patagonia showed 43 species (446% of the total) that were not found in the Scotia Arc islands or the Antarctic Weddell sector, and the Antarctic Weddell sector contributed 4 species (10%) that were not found in the Scotia Arc islands or Patagonia.

A genus-level analysis showed that the generic richness in South Georgia (35 genera) was greatest among the Scotia Arc islands and the Antarctic Weddell sector (Table 3). However, this diversity is smaller than values from Patagonia (61 genera) and the Islas Malvinas/Falkland Islands (46 genera).

Of the 73 genera recognised in this study, 33 occurred only in Patagonia and the Islas Malvinas/Falkland Islands; 5 genera were present only in Patagonia, the Islas Malvinas/Falkland Islands and South Georgia, and a further 5 genera also extended to other islands of the Scotia Arc. Eight genera were shared only by the Scotia Arc islands and the Antarctic Weddell sector and one genus (*Ptychocardia*) was found only in the Antarctic Weddell sector (Table 3). The remaining 21 genera were widely spread and represented in the Scotia Arc islands, the Antarctic Weddell sector and Patagonia. No endemic genera were found for the Scotia Arc islands.

The genus *Philobrya* accounted for the largest number of species (13), followed by *Neolepton* (9), *Cyclopecten* (9), *Yoldiella* (7) and *Thyasira* (7) . *Limopsis* and *Kellia* were represented by six and five species each, and the remaining genera by a lower number of species, usually one or two.

DISCUSSION

The present study revealed the existence of a widely diversified bivalve fauna in the Scotia Arc islands and adjacent waters, reporting 18 still undescribed species and providing new records for 51 species. The total number of species reported in this study for the Scotia Arc islands (73) is higher than the numbers previously reported by Carcelles (1953) and Powell (1960) for the same area (45 and 35 species respectively). This difference clearly reflects the increase in the knowledge of bivalve diversity in the last 40 years. The same occurs in the Weddell Sea, where several recent specific studies also resulted in a considerable increase in the total number of species for the area. Conversely, the number of species reported here for the Magellan region

TABLE 3. – Geographic distribution of bivalve genera.

GENERA	Patagonia	Malvinas/ Falkland Is.	South Georgia	South Sandwich Is.	South Orkney Is.	South Shetland Is.	Antarctic Weddell sector
Acesta	x						
Acharax	x						
Adacnarca			x	x	x	x	x
Adamussium				x	x	x	x
Astarte	x	x	x			x	x
Aulacomya	x	x					
Bankia	x						
Benthocardiella	x						
Carditella	x	x					
Cardiomya	x	x					
Carditopsis	x	x					
Chlamys	x						
Crenella	x	x					
Cuspidaria	x	x	x	x	x	x	x
Cyamiocardium	x	x	x		x	x	x
Cyamiomactra		?	x	x	x	x	x
Cyamium	x	x	x				
Cyclocardia	x	x	x	x	x	x	x
Cyclopecten	x	x	x	x	x		x
Dacridium				x		x	x
Darina	x	x					
Ennucula	x	?	x				
Ensis	x	x					
Epicodakia	x	x	x		x		
Eurhomalea	x	x					
Gaimardia	x	x	x				
Genaxinus	?	?	x	x	x	x	x
Gomphina	x	x					
Hiatella	x	x	x	x			
Kellia	x	x	x		x	x	x
Kidderia	x	x	x			x	x
Lasaea	x	x	x		x		
Laternula			x	x	x	x	x
Limatula	x	x	x	x	x	x	x
Limopsis	x	x	x	x	x	x	x
Lissarca	x	x	x	x	x	x	x
Lucinoma	x	x					
Lyonsia	x	x	x	x	x	x	x
Lyonsiella	x						
Macoma	x	x	x				
Malletia	x	x					
"Montacuta"			x		x	x	x
"Mulinia"	x						
Mya	x	x					
"Mysella"		x	x	x	x	x	x
Mytilus	x	x	?				
Neolepton	x	x	x				
Nucula	x	x			?		?
Nuculana	x	x			x	x	x
Pandora	x						
Perumytilus	x	x					
Petricola	x						
Philobrya	x	x	x	x	x	x	x
Poromya		x	x	x	x	x	
Propeleda	x		x		x	x	x
Protothaca	x						
Pseudokellya		x	x	x	x	x	x
Ptychocardia							x
Puyseguria	x						
Rochefortia	x	x	x		x	x	x
Semipallium	x						
Silicula	x		x		x	x	x
Sphenia	x						
Tawera	x	?					
Thracia	x	x	x	x	x	x	x
Thyasira	x	x	x		x	x	x
Tindaria	x						
Trachycardium		x					
Venericardia	x	x					
Waldo	x		x		x	x	
Yoldia	x	x	x	x	x	x	x
Yoldiella	x	x		x	x	x	x
Zygochlamys	x	x					
Total number of genera	61	46	35	21	30	29	29

was lower than those listed by Carcelles (1950), Carcelles and Williamson (1951) and Linse (1999), who included several names which are actually synonymous or have been erroneously reported for the area (Zelaya, unpubl. inf.). The list of species given by Linse (1999) also includes deep-water species, which are not the focus of the present paper.

The values of faunistic similarity among components of the Scotia Arc islands ranged from 57 to 88%, accounting for a relatively homogeneous species composition of the bivalve fauna. The highest similarity values were found among components of the southern branch of the Scotia Arc, i.e. in the couples South Sandwich–South Orkneys, South Sandwich–South Shetland and South Orkneys–South Shetlands. The lowest similarity was found when comparing the northern and southern branches of the Scotia Arc (i.e. the couples South Georgia – South Shetland Islands and South Georgia – South Orkney Islands). Although species richness was similar in these archipelagos, the composition of their assemblages was found to be somewhat different. This fact originates from the high number of endemic species occurring in South Georgia (14 species, 29% of the total). Moreover, South Georgia has a greater number of Magellanic components than the South Orkney and South Shetland islands, whose faunas are of predominantly Antarctic origin.

The biogeographic position of South Georgia has been the focus of controversial opinions. Based on evidence coming from different invertebrate taxa, authors have proposed its placement either in the Antarctic or Magellan regions (Arnaud, 1964; Clarke, 1996; Hasting, 1943; Hedgpeth, 1969; Linse, 1997; Winkler, 1994; Zelaya, 2000). South Georgia bivalve assemblages included representatives from both the Magellan and Antarctic faunas. A similar mixed origin was previously reported for other invertebrate groups, such as Cumacea (Mühlenhardt-Siegel, 1999), Sipuncula (Saiz-Salinas and Pagola-Carte, 1999) and Nudibranchia (Schrödl, 1999). This led researchers to consider the biogeographic position of South Georgia as transitional between the Magellan and Antarctic regions. This fact might be related to the convergence in the area of two water masses of different origins: the Weddell Gyre and the West Wind Drift. However, for bivalves it is important to note that the similarity between South Georgia—and other Scotia Arc islands—and the Antarctic Weddell sector were high, ranging from 49 to 88%. Conversely, the similarity found between the Scotia Arc islands and Patagonia and the Islas Malvinas/Falkland Islands were low (12 to 32%). Hence, South Georgia and the other Scotia Arc islands appear to be a group that is well differentiated from the Magellan region, justifying their biogeographic placement within the Antarctic region as far as bivalves are concerned.

Based on the biogeographic scheme assumed above and analysing the geographic distribution of the 170 species listed in Table 1, 93 species (54%) were present in the Magellan region and not in the Antarctic region, 57 species (34%) were present in the Antarctic region and not in the Magellan region, and only 20 of the total of 170 species (12%) were present in both areas. The same analysis at genus level revealed 33 Magellan genera and 7 Antarctic genera.

The differences in the composition of bivalve assemblages reported here for the Magellan and Antarctic regions can be related to the geological history of these areas, which started to separate in the Oligocene (37-23 Ma.) and suffered an intense latitudinal zonation of the shallow-water fauna no later than the Miocene (10-12 Ma) (Crame, 1999). At this time, according to Crame (1999), the development of the Polar Frontal Zone, "one of the strongest natural boundaries in the world ocean", induced some profound biological changes along its course by producing significant vicariant evolutionary processes. Carcelles (1953) suggested that the deep waters of the Drake Passage could also be responsible for differences presently found between the Magellan and Antarctic faunas.

Within this historical scheme, the South Sandwich Islands, an archipelago of volcanic origin, is the youngest among the Scotia Arc islands (1-10 Ma., Ramos, 1996; Udintsev *et al.*, 2000). This fact, together with the great distance from both South America and the Antarctic, could also explain their low species and genera richness. However, it is important to note that the low species and genera richness in the South Sandwich Islands could also originate from the paucity of studies conducted in the archipelago. Furthermore, sampling during the LAMPOS cruise showed that the volcanic bottoms around the South Sandwich Islands, consisting mostly of pumice and lava, may not be an ideal substrate for bivalve molluscs. Also, the values of similarity reported here for South Sandwich are likely to overestimate the actual affinities.

The effects of the West Wind Drift together with the Weddell Gyre might explain the high similarities found between the Scotia Arc islands and the

Antarctic Weddell sector. Algal rafting represents an effective dispersal mechanism for species living on algae (e. g. *Gaimardia trapesina* and some species of *Philobrya*), which distribute eastward following the West Wind Drift. Additionally, transport by fishes has been reported as a dispersal mechanism: *Rochefortia charcoti*, withstanding passage through the digestive tract of fishes, is passively dispersed in Antarctic environments (Domaneschi *et al.*, 2002). Above all, the West Wind Drift could be potentially contributing to the distribution of species having a planktonic larval stage, a condition so far only reported for a few Antarctic bivalves (e.g. Pearse *et al.*, 1991), but inferred from protoconch morphology for a few other species (Hain and Arnaud, 1992). Some cases such as *Limatula hodgsoni* are controversial, having been reported as planktotrophic (Pearse *et al.*, 1991) or lecithotrophic with demersal development (Linse and Page, 2003).

Although the molluscan fauna from the Scotia Arc Islands has been studied since the 19th century, new species of bivalves have recently been described (e.g. Zelaya and Ituarte, 2002, 2003) and several undescribed species have been reported for the area (present study). This, together with the fact that several species are difficult to recognise from their original descriptions and that a significant number of species were not collected again after those descriptions, reveal the need to undertake new and revisive work on the bivalve fauna from the Scotia Arc islands, in order to improve our knowledge of the Antarctic molluscan fauna.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Distributional patterns of shallow-water polychaetes in the Magellan region: a zoogeographical and ecological synopsis*

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SUMMARY: The zoogeography of polychaete annelids was described for the Magellan region. This work considered information available from 19 expeditions carried out in the last 124 years of polychaete taxonomic research around the southernmost tip of the South American continental shelf. The polychaete fauna of the Magellan region comprised a total of 431 species belonging to 108 genera and 41 families. MDS and ANOSIM analyses showed the Magellan region to be divided into two subregions, one on the Pacific side of the tip of South America and one on the Atlantic side. These subregions showed a low percentage of "endemic species" (< 10%) whereas > 70% of the species recorded for the whole Magellan region showed a wide distribution range, and there were especially high affinities with Antarctic and Subantarctic areas. We suggest that the opening of the Straits of Magellan created a new pathway for enhanced exchange of faunal elements between the Pacific and the Atlantic. Transport of larvae via easterly directed currents of the West Wind Drift plays an important role in current distribution patterns of polychaete fauna around the tip of South America.

Keywords: polychaete zoogeography, Antarctic affinities, species composition, Magellan region.

RESUMEN: PATRONES DE DISTRIBUCIÓN DE LOS POLIQUETOS DE AGUAS SOMERAS EN LA REGIÓN MAGALLÁNICA: UNA SINOPSIS ZOOGEOGRÁFICA Y ECOLÓGICA. – Se describe la biogeografía de los poliquetos anélidos para la región de Magallanes, haciéndose referencia a la información disponible de 19 expediciones realizadas durante los últimos 124 años de investigación taxonómica en la plataforma del cono sur de Sudamerica. La fauna de poliquetos de la región de Magallanes esta constituida por un total de 431 especies pertenecientes a 108 géneros y 41 familias. El análisis de MDS y ANOSIM mostró que la región de Magallanes se puede dividir en dos subregiones biogeográficas, una del lado pacífico y otra del lado atlántico del cono sur de Sudamérica. Estas entidades biogeográficas se caracterizaron por un bajo porcentaje de especies endémicas (< 10%). Aproximadamente el 70% de las especies registradas en ambas subregiones mostró un amplio rango de distribución, especialmente se encontró una alta afinidad con áreas antárticas y subantárticas. Esto sugiere que la apertura del Estrecho de Magallanes creó un nuevo pasaje de intercambio de especies entre el Pacífico y el Atlántico. Además se sugiere que la dispersión vía transporte larvario a través de la Corriente de Deriva del Oeste estaría jugando un rol preponderante en el actual patrón de distribución de la fauna de poliquetos en la región de Magallanes.

Palabras clave: zoogeografía de poliquetos, afinidades antárticas, composición de especies, región de Magallanes.

INTRODUCTION

Polychaetes have been considered for zoogeographical analysis in South America only in the last decade (Lancellotti and Vásquez, 1999; Fernández *et al.*, 2000; Camus, 2001; Glasby and Alvarez, 1999). They are thought to be inadequate indicators for zoogeographical purposes because of their wide geographical range at all taxonomic levels, and especially because of their long-distance dispersal

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capabilities. Paradoxically, polychaetes constitute worldwide a large portion of the total macrofauna of soft bottoms (Hutchison, 1998), and with more than 16,000 species known so far, they are the fourth major group of marine invertebrates (Blake, 1995; Bouchet, 2000). Although, with the exception of a few poorly-known ones, polychaete families occur in all oceans and at all depths, overview studies on species level, which would be required for zoogeographic analysis, are scarce in the polychaete literature, and the Magellan region is by no means an exception (e.g. Hartmann-Schröder and Hartmann, 1974; Knox and Lowry, 1977). According to Knox (1957) more than 40% of the southern hemisphere polychaete species are thought to be cosmopolitans, but the poor knowledge of polychaete taxonomy and the low level of quantitative data might well be one reason for this unusually high percentage.

The zoogeography of the Magellan region has been reviewed several times, but despite these studies the gain of knowledge has remained comparatively poor. Balech (1954) was the first to propose a scheme for the Magellan region, subdividing it into 5 districts: two on the Atlantic side (Santacruceño and Chubutiano), two on the Pacific side (Valdiviano and Chiloense) and the Fueguino district, which connects both sides at the tip of South America. Fifty-six years later and after several reviews (Viviani, 1979; Brattström and Johanssen, 1983; Carreto, 1983; Stuardo and Valdovinos, 1992; Lancellotti and Vásquez, 1999), Camus (2001) questioned whether the Magellan region as a zoogeographic province should be extended into the Atlantic area off the South American coast.

Based on oceanographic and phytoplankton data, only two divisions at the tip of South America were considered by Longhurst (1998): the Humboldt Current Coastal Province, stretching northwards over the entire Chilean Pacific coast, and the Falkland Coastal Province on the Atlantic side. From the zoogeographical point of view, the discussion about the limits between regions and provinces is still open, and for this reason we call the Magellan region a region and its subdivisions "subregions".

In this context the purpose of this investigation was, using all available polychaete data, to analyse whether the traditional subdivisions of the Magellan region are also recognisable on the basis of distribution patterns of polychaete species. Certainly the amount of information on polychaete distribution patterns is considerable and is based on almost 120 years of descriptive taxonomy. However, to our knowledge no one has ever tried to synthesize this bulk of data. This study checks the existing zoogeographical subdivisions in the Magellan region by using polychaete data (presence/absence) of species in the different regions and analyses the zoogeographical affinities with the Antarctic.

MATERIAL AND METHODS

Study area

Based on oceanographic conditions and topography, the tip of South America can be divided into three major areas:

1) Numerous channels and fjords on the Pacific side structured by the last glaciation periods (Syvitski *et al.*, 1987) extend from about 42°S to 55°S in a section of the South American coastline with a wider shelf (Strub *et al.*, 1998). The mean width of the Pacific continental shelf is 6.54 km (Gallardo, 1984). This area is under the influence of the Humboldt Current and the Cape Horn Current, both of which are branches of the West Wind Drift Current (WWD). The Subantarctic water can penetrate into the inlets (Silva *et al.*, 1998), whose depth may locally exceed 1000 m. The hydrographical regime is characterised by a strong freshwater input due to high precipitation and concomitant runoff, both producing a strong and shallow pycnocline (Dávila *et al.*, 2002). Sediments are characterised by silt and clay (Murray, 1895), coarser sediments such as pebbles/gravel, and biogenic gravel from molluscs and barnacles which are also present at shallower depths (Brambati *et al.*, 1991). Three permanent ice fields, Campo de Hielo Norte (46-47 °S), Campo de Hielo Sur (48-52°S), and the Cordillera Darwin (54-55°S; Naruse and Aniya, 1992), are responsible for freshwater supply to the fjord system.

2) The Straits of Magellan (52°58´S, 70°55´W and 53°43´S, 70°17´W) are a natural seaway connecting the Pacific with the Atlantic Ocean. Water depths reach 1200 m at the western entrance on the Pacific side (Antezana *et al.*, 1992). Currents decrease from 1m s^{-1} on the Atlantic side of the Straits to 0.2 m s^{-1} in the Paso Ancho (Michelato *et al.*, 1991). Primary production ranges seasonally between 282 and 1000 mg C m^{-2} day^{-1} (Guglielmo and Ianona, 1997). Sediments mainly consist of sand and gravel with varying proportions of mud and shell debris; the distribution patterns appear rather heterogeneous, especially in the shallower parts of the Straits (Brambati *et al.*, 1991).

TABLE 1. – Chronological and synoptic list of expeditions carried out in Magellan waters. In the station list the following symbols represent the various kinds of gear used: D: Dredge; AGT: Agassiz Trawl; T: Trawl; McI: Mac Intyre grab; MG: Multibox corer; PG: Petersen grab; VV: Van Veen grab. (*) Information on species per station or station georeference not available.

Campaign	Research Vessel	No. of stations	Gear	Source
HMS Challenger	"Challenger"	6	D	McIntosh, 1885
Swedish Antarctic Expedition	"Antarctic"	28	*	Hartman, 1953
Discovery Expedition	"Discovery"	1	D, T	Monro, 1930-36
Discovery Expedition	"William Scoresby"	112	D, T	Monro, 1930-36
Lund Univ. Chile Expedition	"Arauco II" and „Galvarino"	95	D	Wesenberg-Lund, 1962
Mission du Cap Horn	"Romanche"	23*	*	Fauvel, 1941
Mar Chile I	"Chipana"	6	D	Hartmann-Schröder, 1965
USNS Eltanin	"Eltanin"	26	D, T, PG	Hartman, 1967
Akademic Knipovich	"Akademic Knipovich"	20	*	Averince, 1972
Akademic Knipovich	"OB"	4*	*	Averince, 1972
Walther Herwig 15th,36th and 76th	"Walther Herwig"	71	D, T	Hartmann-Schröder, 1983
Allan Hancock Pacific Expedition	"Vema"	25*	T	Maurer and William, 1988
Italian Oceanographic expedition	"Cariboo	16	D, VV	Gambi *et al.*, 1999
Shinkai Maru 4th, 5th, 10th and 11th	"Shinkai Maru"	22*	D, VV	Brémec *et al.*, 2000
CIMAR Fiordos	"Vidal Gormaz"	19	AGT	Montiel *et al.*, 2004
UMAG, data base.	"Lenga"	3	McI	Ríos *et al.*, 2003
Joint Magellan Campaign	"Victor Hensen"	20	MG	Present study
CIMAR Fiordos	"Vidal Gormaz"	18	MG	Present study
ANT XIII/4	"Polarstern"	4	MG	Present study

3) The Atlantic shelf of the Magellan region extends from the Rio de la Plata to Tierra del Fuego. This region between 38°S and 55°S comprises the Argentine Patagonian shelf and the Falkland/Malvinas plateau. The continental shelf widens to a maximum of about 850 km at 51°S (Piccolo, 1998). The hydrographic regime is structured by the confluence of the Falkland/Malvinas and Brazil currents. The mean annual winter temperature in the Falkland Current is 10°C and primary production varies between 150 and 500 mg C m^{-2} day^{-1} (Longhurst, 1995). The Brazil Current shows a higher annual mean temperature of 22°C with variations in the primary production between 115 and 830 mg C m^{-2} day^{-1} (Boltovskoy, 1999). In general, the bottom sediments are composed of sand (fine to median size) and silt (< 2 mm; Bastida *et al.*, 1981). The coarse fraction > 2 mm prevails near the coast (< 50 m depth). In the embayments of Peninsula Valdés, Bahía Blanca and San Matías, this fraction has high percentages of biogenic gravel of mollusc, brachiopod and barnacle shells (Bastida *et al.*, op.cit.).

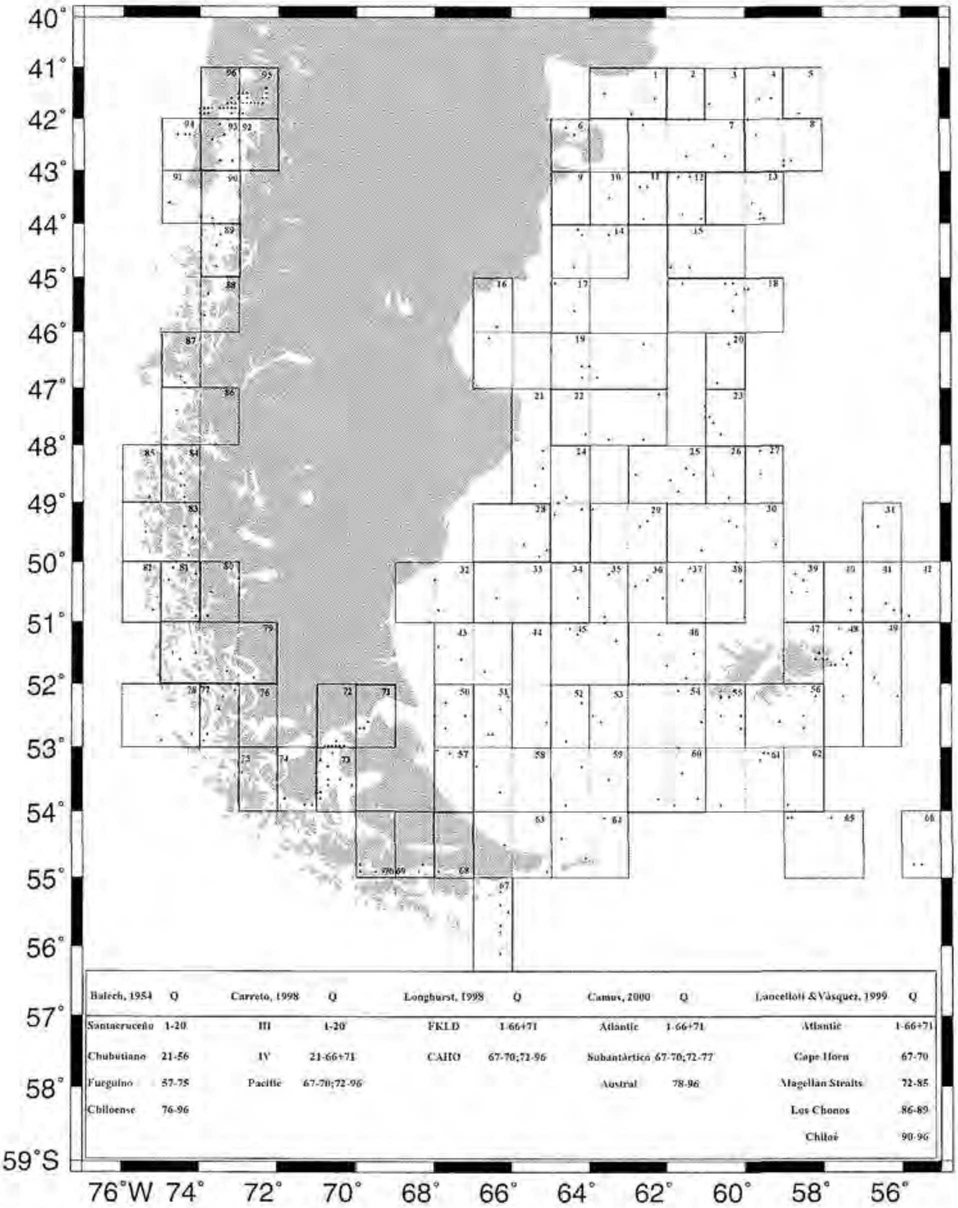
Origin of polychaete data

The zoogeographical analysis was based on data from 19 different expeditions, with a total of 445 sampling stations from continental shelf areas of the Magellan region. In total data from 519 stations provided the basis for our analysis. Forty-two of these stations were sampled personally during three expeditions with RVs "Victor Hensen" in 1994 (Arntz and Gorny, 1996), "Vidal Gormaz" in 1995 (Mutschke *et al.*, 1996) and "Polarstern" in 1996 (Fahrbach and Gerdes, 1997). The origin of the remaining data is summarised in Table 1.

Data treatment

The total number of polychaete species used for this data base includes all species records with exact geographical positions (latitude-longitude), and at least the presence of 1 individual per finding. The sea surface around the tip of South America was divided into 96 quadrants, each one degree longitude and one degree latitude in size. Quadrants without polychaete findings per station were not considered and quadrants with only one station were homologised with the neighbouring quadrants (Fig. 1). The quadrants were enumerated from the Atlantic to the Pacific direction; quadrants 1 to 66 plus quadrant 71 represented the Atlantic sector, quadrants 72-75 represent the Straits of Magellan, and quadrants 67 to 70 plus 76 to 96 represent the Pacific side.

To check whether or not polychaete distribution patterns coincide with the traditional (sub-)divisions of the Magellan region sensu Balech (1954), Carreto (1983), Longhurst (1998), Lancellotti and Vásquez (2000) and Camus (2001), analyses of similarities (ANOSIM) and a Multi-Dimensional Scaling (MDS) between groups of quadrants were carried out. ANOSIM and MDS were performed on the basis of 216 species records from 96 quadrants to



Balech, 1954	Q	Carreto, 1998	Q	Longhurst, 1998	Q	Camus, 2000	Q	Lancellotti & Vásquez, 1999	Q
Santacruceño	1-20	III	1-20	FKLD	1-66+71	Atlantic	1-66+71	Atlantic	1-66+71
Chubutiano	21-56	IV	21-66+71	CAHO	67-70;72-96	Subantártico	67-70;72-77	Cape Horn	67-70
Fueguino	57-75	Pacific	67-70;72-96			Austral	78-96	Magellan Straits	72-85
Chiloense	76-96							Los Chonos	86-89
								Chiloé	90-96

FIG. 1. – Grid of the sea surface off the tip of South America. Dots indicate sampling locations and quadrant numbers and traditional divisions of the Magellan region. **A**: Atlantic, **AU**: Austral, **C**: Chubutiano, **CAHO**: Cape Horn Province sensu Longhurst (1998), **CS**: Chiloense, **CE**: Chiloé, **CH**: Cape Horn sensu Lancellotti and Vásquez (1999), **CI**: Chonos Inlet, **F**: Fueguino, **FKLD**: Falkland Province, **MS**: Magellan Straits, **PI**: Pacific Inlets, **S**: Santacruceño, **SA**: Subantarctic (sensu Camus, 2001).

evaluate the dissimilarity between our quadrant groups and the traditional divisions. In the next step the similarity percentage breakdown analysis (SIMPER; Clarke, 1993) describes the contribution of each species to the dissimilarity between the obtained groups of quadrants. All analyses were carried out using the software PRIMER version 5.2.1 (Clarke and Warwick, 1994) with standardised presence/absence data.

The following acronyms were used by the authors for the traditional division of the Magellan region:

A: Atlantic, **AU**: Austral, **C**: Chubutiano, **CAHO**: Cape Horn Province sensu Longhurst (1998), **CS**: Chiloense, **CE**: Chiloé, **CH**: Cape Horn sensu Lancellotti and Vásquez (1999), **CI**: Chonos Inlet, **F**: Fueguino, **FKLD**: Falkland Province, **MS**: Magellan Straits, **PI**: Pacific Inlets, **S**: Santacruceño, **SA**: Subantarctic (sensu Camus, 2001). For comparison with the adjacent Subantarctic and Antarctic areas south and temperate areas north, additional acronyms (**ANTA** = Antarctic, **SANT** = Subantarctic and **HUMB** = Humboldt Current region respectively) were introduced according to Longhurst (1998).

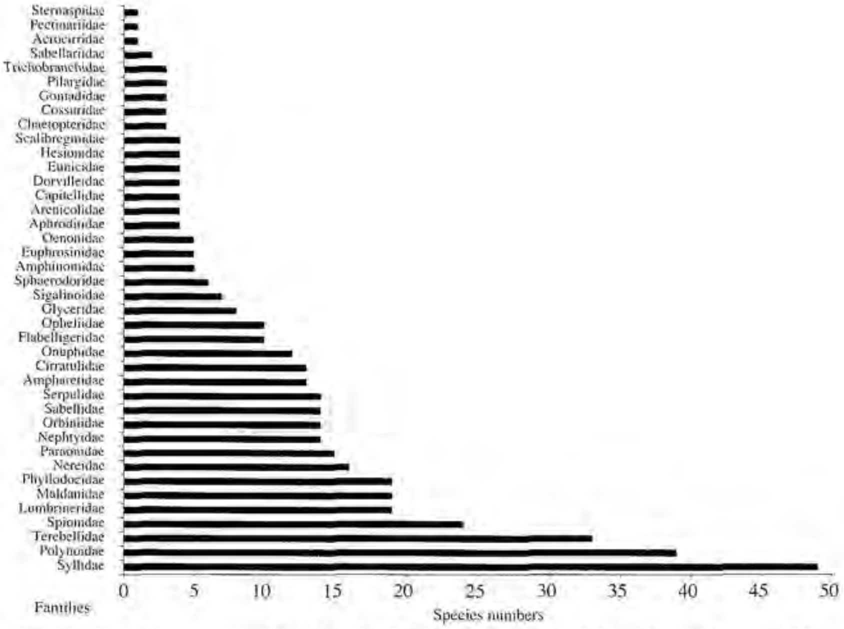


FIG. 2. – Total species number per polychaete family obtained from the study (n = 431).

Many of the polychaete species used as discriminators for subregions in the Magellan region also occurred in adjacent and other parts of the world ocean. Because of this, each species was categorised according to its distribution range, basing on the fundamental taxonomic studies of Hartman (1959 a, b) and Rozbaczylo (1985). In addition, the most recent taxonomical reviews for the species distribution of the eunicemorph polychaetes of Orensanz (1990), and the families Spionidae (Blake, 1983), Syllidae (Licher, 1999) and Glyceridae (Böggemann, 2002) were consulted.

RESULTS

Up to now a total of 431 polychaete species have been recorded for the Magellan region, summarising 124 years of polychaete research in this part of the world. These species were divided into 108 genera and 41 families. The most speciose families were Syllidae, contributing 11% to the total polychaete species, followed by Polynoidae (9%), Terebellidae (8%), Spionidae (6%) and Lumbrinereidae (4%), whereas other families were of minor importance (< 4%, Fig. 2).

Out of the 431 polychaete species, 104 species were reported without exact catch positions and another 111 species occurred as single findings, i.e. they were not considered for further analysis. The remaining 216 species thus provided the basis for the numerical and statistical analyses.

TABLE 2. – ANOSIM pairwise test of presence/absence data of polychaete species from quadrants according to the division by the different authors. **A**: Atlantic **AU**: Austral **C**: Chubutiano **CAHO**: Cape Horn Province **CS**: Chiloense **CE**: Chiloe **CH**: Cape Horn **CI**: Chonos inlet **F**: Fueguino **FKLD**: Falkland Province **MS**: Magellan Straits **PI**: Pacific Inlets, **S**: Santacruceño **SA**: Subantarctic.* significant difference. (R = Rank similarities; P = Probability values)

Hypothetical group *sensu* different authors	***R***	P (%)	Number ≥ observed
Balech, 1954			
S - C	0.2	0.2	1
S - F	* 0.321	0.1	0
S - CS	* 0.557	0.1	0
C - F	0.151	0.9	8
C - CS	* 0.564	0.1	0
F - CS	* 0.263	0.1	0
Lancellotti and Vásquez 2000			
A - CE	0.342	1.5	14
A - MS	* 0.455	0.1	0
A - CI	* 0.617	0.1	0
A - CH	* 0.86	0.1	0
CE - MS	0.329	2.9	28
CE - CI	0.026	51.4	18
CE - CH	0.476	0.6	2
MS - CI	0.244	7.5	74
MS - CH	* 0.524	0.1	0
CI - CH	0.31	3.3	11
Carreto 1988			
III - IV	0.179	0.4	3
PI - III	* 0.428	0.1	0
PI - IV	* 0.45	0.1	0
Camus 2001			
SA - AU	0.112	5.9	58
A - SA	* 0.353	0.1	0
A -AU	* 0.517	0.1	0
Longhurst 1998			
FKLD - CAHO	* 0.447	0.1	0
Present study			
PI - A	* 0.482	0.1	0
PI - MS	-0.034	5.3	52
A - MS	0.237	57.8	577

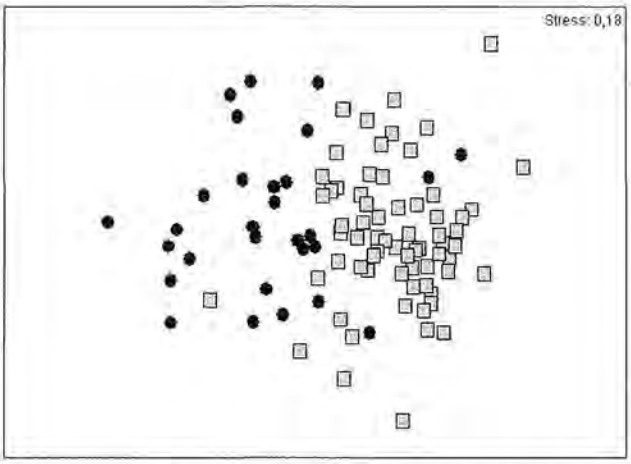


FIG. 3. – MDS ordination plot for the CAHO (circle) and FKLD (squares) regions.

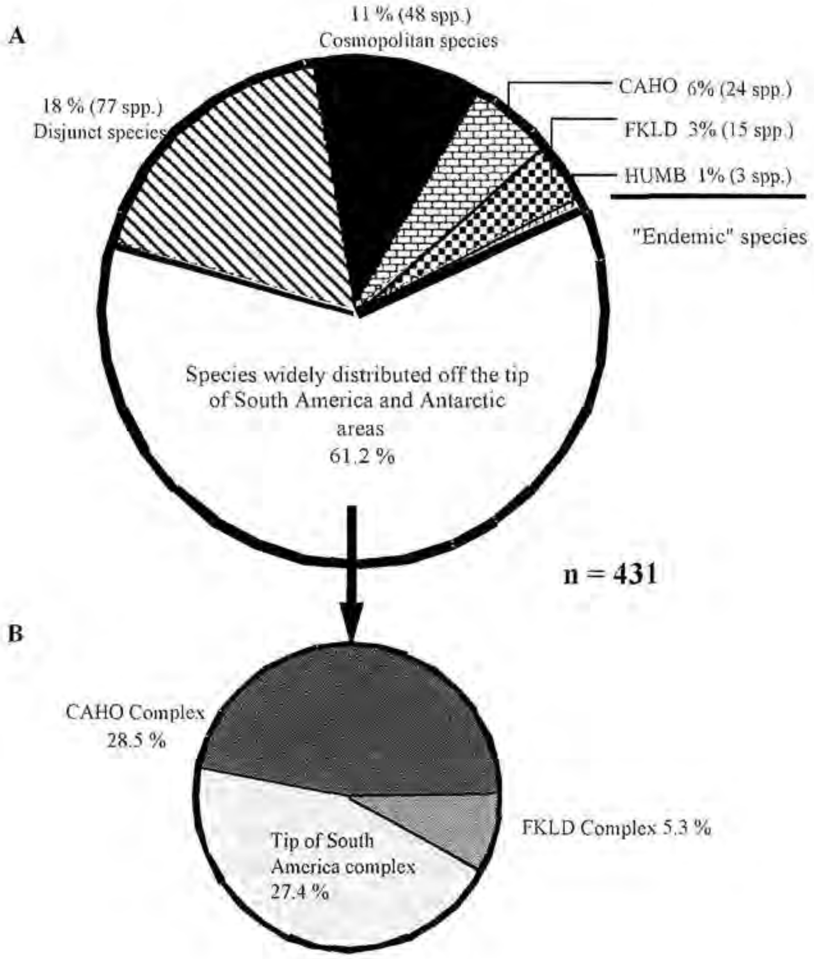
Agreement of polychaete distribution patterns with traditional patterns

The results of the ANOSIM analysis summarised in Table 2 show the subdivision of the Magellan region into two significant subregions: one on the Atlantic side (FKLD) and one on the Pacific shelf (CAHO). This result resembles that obtained by Longhurst (1998) on the basis of satellite pictures of phytoplankton in surface waters.

The ANOSIM between CAHO and FKLD data revealed a significant difference between the two subregions (R= 0.4, $P < 0.001$; Table 2). The MDS plot confirmed this (Fig. 3) and showed two distinct quadrant groups on the Pacific and the Atlantic shelves of the tip of South America.

TABLE 3. – Results of the SIMPER analysis of presence/absence data of polychaete species from the CAHO and FKLD quadrants. Species are listed in the order of their contribution to the average dissimilarity between both groups after Longhurst (1998). Diss: Dissimilarity; SD: Standard deviation.

Species	Mean Diss	Diss / SD	Contribution (%)	Cumulative contribution (%)
Idanthyrsus macropaleus	2.65	0.79	2.80	2.80
Serpula narconensis	2.38	0.75	2.51	5.31
Perkensiana antarctica	2.05	0.71	2.16	7.47
Chaetopterus variopedatus	1.77	0.61	1.87	9.34
Glycera capitata	1.72	0.62	1.81	11.15
Onuphis pseudoiridescens	1.60	0.63	1.69	12.84
Leanira quatrefagesi	1.57	0.68	1.66	14.50
Ninoe falklandica	1.55	0.56	1.64	16.14
Polyeunoa laevis	1.54	0.61	1.63	17.77
Eunice magellanica	1.52	0.53	1.61	19.38
Maldane sarsi	1.51	0.57	1.59	20.96
Aglaophamus praetiosus	1.49	0.60	1.57	22.54
Harmothoe spinosa	1.47	0.65	1.55	24.09
Nicon maculata	1.47	0.58	1.55	25.64
Platynereis australis	1.28	0.47	1.35	26.99
Melinna cristata cristata	1.27	0.52	1.34	28.33
Harmothoe magellanica	1.19	0.53	1.26	29.59
Abyssoninoe abyssorum	1.17	0.54	1.24	30.82
Perinereis nuntia vallata	1.16	0.39	1.22	32.05
Gymnonereis hartmannschroederae	1.15	0.53	1.22	33.27
Amphitrite kerguelensis	1.13	0.56	1.19	34.46
Eunereis patagonica	1.06	0.51	1.12	35.58
Syllis (Syllis) sclerolaenia	1.05	0.46	1.10	36.68
Kinbergonuphis dorsalis	0.92	0.45	0.97	37.65
Trypanosyllis gigantea	0.90	0.47	0.95	38.60
Glycinde armata	0.90	0.42	0.95	39.55
Sternaspis scutata	0.89	0.43	0.94	40.49
Harmothoe campoglacialis	0.88	0.45	0.92	41.41
Thelepus plagiostoma	0.85	0.43	0.90	42.31
Hyalinoecia artifex	0.85	0.33	0.89	43.21
Austrolaenilla antarctica	0.82	0.41	0.86	44.07
Typosyllis armillaris	0.78	0.36	0.83	44.90
Nereis eugeniae	0.78	0.48	0.83	45.72
Lumbrineris cingulata	0.77	0.52	0.82	46.54
Nothria anoculata	0.75	0.37	0.79	47.33
Nicolea chilensis	0.74	0.42	0.79	48.12
Lumbrineris magalhaensis	0.72	0.45	0.76	48.88
Autolytus charcoti	0.70	0.35	0.74	49.62
Marphysa aenea	0.70	0.30	0.74	50.36
Aphelochaeta cincinnata	0.69	0.39	0.73	51.09
Phylo felix	0.67	0.46	0.71	51.80
Aphrodita longicornis	0.65	0.29	0.69	52.49



CAHO Complex	Spp.	**Tip of South America complex**	Spp.	**FKLD Complex**	Spp.
HUMB-CAHO-SANT	2	CAHO-FKLD	42	FKLD-ANTA	1
HUMB-CAHO-SANT-ANTA	5	HUMB-CAHO	57	FKLD-SANT	5
CAHO-ANTA	12	HUMB-CAHO-FKLD	19	FKLD-SANT-ANTA	3
CHA-SANT	32			FKLD-CAHO-ANTA	2
CAHO-SANT-ANTA	72			FKLD-CAHO-SANT	5
				FKLD-CAHO-SANTA-ANTA	6
				FKLD-HUMB-CAHO-ANTA	1

FIG. 4. – Graph **A** shows the percentage of species numbers characterised by the geographical range distribution of each polychaete species in the Magellan region, including **CAHO**: Cape Horn subregion; **FKLD:** Falkland subregion, **HUMB**: Humboldt subregion; **C:** cosmopolitan; **D**: disjunct species and the percentage of an arbitrary group of species widely distributed off South America and in the Antarctic. Graph **B** shows further subdivisions of the arbitrary species group, including different combination of geographical range distribution of species numbers with affinity to the Subantarctic areas (**SANT**) and Antarctic areas (**ANTA**). Number in brackets shows absolute species number.

Considering these results, SIMPER was performed between the FKLD and CAHO data to identify the main contributor species for the average dissimilarity (average = 94.75) and the possible differences in species composition between these shelves off the tip of South America. In FKLD the main contributor species with highest occurrence were *Idanthyrsus macropaleus*, *Serpula narconensis*, *Perkensiana antarctica*, and *Chaetopterus variopedatus*, whereas in the CAHO group species such as *Glycera capitata*, *Onuphis pseudoiridescens*, *Leanira quatrefagesi* and *Ninoe falklandica* were better discriminators between the two subregions (Table 3).

Distribution patterns of polychaetes in the Magellan region and affinities with the Antarctic

The distribution patterns of the polychaete fauna are shown in Figures 4 a, b. These figures considered all 431 species known from the Magellan region.

Seventy-seven species (18%) appeared with disjunctive findings worldwide. Forty-eight species (11%) showed a cosmopolitan distribution. Only rather low percentages of the polychaete species of the present study were restricted to just one of the distinguished subregions: 4% to the Atlantic side and 6% to the southern Pacific side, whereas another 1% occurred exclusively along the Pacific coast of South America north of 42°S. Most of the remaining species (61%) showed an overlapping distribution pattern everywhere along the South American coasts and down to Antarctica. Because of the complexity and a high number of species with overlapping distribution patterns, we divided the remaining species into three arbitrary groups representing the best fit to our abovementioned results (Fig. 4b).

The biggest of these groups (123 species) showed close affinities to the CAHO area. The species were distributed along the Pacific coast of South America towards high Antarctic waters, and some species even extended their northern distribution limit over 42°S into more temperate regions.

The smallest group (5%) showed closest affinities between the FKLD area on the Atlantic side and waters south of the Antarctic Convergence. Another distinct group of species occurred in Atlantic and Pacific waters around the tip of South America, some of them even extending beyond 42°S latitude northwards.

DISCUSSION

Species numbers and structure of the polychaete fauna in the Magellan region

Based on the 431 species considered in this study, the polychaete fauna was dominated by the families Syllidae, Polynoidae, and Terebellidae. This dominance was described before in the classical polychaete reviews of Orensanz (1974) and Knox and Lowry (1977) on the basis of 397 and 223 species respectively. In our study Spionidae followed as the next important family in the fourth position, whereas Phyllodocidae occupied this rank in the studies of Orensanz (1974) and Knox and Lowry (1977). The latter sequence also resulted in the biodiversity review of Clarke and Johnston (2003) for the whole Southern Ocean and the study of Rozbaczylo (1985) for the southeastern Pacific coast.

Since the studies of Knox and Lowry and Orensanz in the mid-1970s, 32 new records and 2 new species have been described for the Magellan region (Gambi and Mariani, 1999; Hilbig and Montiel, 2000; Montiel and Hilbig 2004). This increase may be explained to some extent by new expeditions in the 1980s and 1990s. Many of these species, however, occurred as "single findings" or "disjunctive species", i.e. due to few and scattered records, wide distribution ranges, and/or uncertain taxonomical status they did not have much value for zoogeographical analyses. Therefore our database for the zoogeographical analysis consisted of fewer than the 431 species described for the Magellan region in total. Our results showed 111 species which occurred as single records at the tip of South America. This agrees with the analyses of the macroinvertebrate fauna along the Chilean coast (Lancellotti and Vásquez, 1999). These authors also described this area as a zone with a high number of single records of species, which may be a result of insufficient numbers of surveys in this region.

Zoogeographical patterns of the polychaete fauna

Based on the polychaete presence/absence data, the Magellan region can be subdivided into Pacific and Atlantic subregions. A similar pattern results from the satellite plankton discrimination of Longhurst (1998). Due to the composition of the plankton under the influence of the Humboldt Current system and the Cape Horn Current this area is called Humboldt Province. However, in our analysis species occurring in the Humboldt area were poorly represented, and we therefore propose a different name for this zoogeographic area, the Cape Horn subregion (CAHO).

In the last decade marine zoogeographical studies based on macroinvertebrates from the Pacific coast of South America have been performed exclusively with data from old literature (Fernández *et al.*, 2000, Lancellotti and Vasquez, 1999; Camus, 2001). These authors have given strong emphasis to the traditional zoogeographical barriers along the Chilean coastline, as proposed by Viviani (1979) and Brattström and Johanssen (1983)—for example the 42°S barrier between the Magellan region in the south and the adjacent temperate region to the north—and along the Atlantic coastline, as proposed by Balech (1954). However, this traditional barrier does not exist for many polychaete species, as is obvious from the high percentage of overlapping species with a wide range of distribution and the high number of common species north and south of 42°S. One reason could be an enormous ecological capacity and tolerance of polychaetes to very different environmental conditions, as is typical of organisms of phylogenetically old lineage (Fauchald, 1984). Another reason may be local oceanographic conditions (see below).

The marine realm is a dynamic system, i.e. fixed borderlines hardly occur. Absolute barriers in aquatic systems are almost impossible, and for many species borders probably act more as filters than as barriers, allowing species exchange in both directions (Dell, 1972; Scheltema, 1988; Hilbig, 1994; Boltovskoy, 1999).

Do our arbitrary groups (Fig. 4) correspond to polychaete distribution patterns and how could these patterns be explained? We distinguished two groups with species showing a high affinity to Antarctic waters and one group that was restricted to South American shelf areas. Within the first two groups one group contained 28.5% of the species, showing affinity between Pacific and Antarctic waters, and a smaller second group (5.3%) showed affinity between Atlantic and Antarctic waters. The processes and mechanisms behind these patterns are controversially discussed in the literature (Orensanz, 1990). Two different explanations are under discussion: a) common species in both areas (Pacific–Antarctic or Atlantic–Antarctic) occur due to the common history of the areas as parts of Gondwana (*vicariance*) and b) common species occur due to dispersion of meroplanktonic larvae (*dispersalism*). We suggest that dispersion of Antarctic species through larval transport via easterly directed currents of the West Wind Drift (WWD) plays an important role in the current distribution patterns of the fauna around the tip of South America. This hypothesis is supported by a higher proportion of species with higher Antarctic affinities to the Pacific coast as compared to the relatively small proportion of species with affinities to the Atlantic side. However, according to Bhaud (1998) the spreading potential of polychaete larvae does not necessarily predict the adult distribution. Key processes for the establishment of a successful population in a new habitat are especially the recruitment conditions and the substrate choice of settling larvae (Bhaud op. cit). The presence of common species on both sides of the Drake Passage provides strong evidence to argue that dispersion might be an important process for faunal exchange between the Magellan region and Antarctica. The Polar Front does not therefore function as a strict barrier for many species. In fact, several of the dominating polychaete species in the Magellan area as defined by the SIMPER analysis (*I. macropaleus, S. narconensis, C. variopedatus, L. quatrefagesi*) reproduce via meroplanktonic larvae (Giangrande, 1997). Another hypothesis includes the adjacent deep-sea areas as possible sources for shelf species. However, potential pathways of recolonisation of shelf communities from the deep sea are still under study and hardly understood. The results of the recent "ANDEEP" and "LAMPOS" expeditions (Fütterer *et al.*, 2003; Arntz and Brey, 2003) might be particularly important to present keystones in the overall Antarctic-Magellan puzzle.

Finally, we suggest that the last group restricted to the tip of South America and occurring exclusively in South American waters with its high number of common species on the Pacific and Atlantic side is the result of the glaciation history of the southern parts of South America. The southeastern Magellan region is a geologically young system (Pisano, 1990), which was ice-covered during the Last Glacial Maximum some 12,000 years BP (Clapperton *et al.*, 1995; Benn and Clapperton, 2000). All present polychaete species in Magellan waters recolonised this area from adjacent Atlantic and Pacific areas. Moreover, the Straits of Magellan have been an important corridor for species exchange between both sides since the opening 7,000 year BP (McCulloch and Davies, 2001). The oceanography of this area reflects the intrusion of oceanic waters from both sides of the continent and the mixture of these water masses in the Paso Ancho in the middle of the Straits. We suggest that the opening of the Straits of Magellan created a new pathway for enhanced exchange of faunal elements from the Pacific to the Atlantic and vice-versa.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Influence of biotic and abiotic sediment factors on abundance and biomass of harpacticoid copepods in a shallow Antarctic bay*

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SUMMARY: This study presents data of the first investigation on benthic harpacticoid copepods in Potter Cove, King George Island, Antarctica (62°14'S, 58°40'W) with special emphasis on spatial distribution and relation to environmental factors. In addition to the individual numbers that are normally given, the biovolume of the meiobenthic copepods was measured. It showed great variety due to changes in abundance and habitat preferences of the different species along the two studied transects in the inner cove and at the cove entrance. The distribution of the two species *Pseudotachidius jubanyensis* and *Scottopsyllus (S.) praecipuus* was studied in detail; their body volumes are given for developmental stages and adults, and their importance for the total biovolume at the different stations is discussed. Statistical analyses (Spearman rank, canonical correspondence analysis) indicate that the biovolume of harpacticoid copepods was related more to total organic matter than to the carbon:nitrogen ratio and chloroplastic equivalents or even grain size and depth. While *P. jubanyensis* was strongly connected to depth and to a lesser extent to small grain sizes, *S. (S.) praecipuus* showed a preference for sites with low chloroplastic equivalent values, but neither of them was related to total organic matter.

Keywords: meiofauna, Copepoda, size classes, biovolume, *Pseudotachidius jubanyensis*, *Scottopsyllus (S.) praecipuus*, King George Island, Antarctic.

RESUMEN: INFLUENCIA DE LOS FACTORES BIÓTICOS Y ABIÓTICOS SOBRE LA ABUNDANCIA Y BIOMASA DE COPÉPODOS HARPACTICOÍDEOS EN UNA CALA POCO PROFUNDA DE LA ANTÁRTIDA. – El presente estudio facilita los primeros datos sobre la distribución espacial de los copépodos harpacticoídeos bentónicos en la Caleta Potter, Isla Rey Jorge, Antártida (62°14'S, 58°40'W) y su relación con factores ambientales. Además del cálculo de abundancias se midió el biovolumen de los copépodos del meiobentos. Se detectó una variabilidad bastante elevada del biovolumen debido a las diferentes preferencias ecológicas de las especies a lo largo de los dos transectos muestreados, uno en la entrada de la cala y otro en su interior. La distribución de dos de las espécies encontradas, *Pseudotachidius jubanyensis* y *Scottopsyllus (S.) praecipuus*, fué estudiada en detalle. Se presentan datos del biovolumen de los diferentes estadios ontogenéticos y de los adultos de estas dos especies y se discute su importancia para el biovolumen total en las diferentes estaciones muestreadas. Análisis estadísticos (Spearman rank, análisis canónico de correspondencias) indican que el biovolumen de los copépodos harpacticoídeos está mejor correlacionado con el contenido orgánico total que con la relación carbono:nitrógeno y equivalentes de pigmentos cloroplásticos o incluso con parámetros granulométricos y profundidad. *P. jubanyensis* parece estar relacionado con la profundidad y, en menor medida, con sedimento de grano fino, mientras que *S. (S.) praecipuus* mostró preferencia por estaciónes con valores bajos de equivalentes de pigmentos cloroplásticos, pero ninguna de las especies está relacionada con el contenido total de materia orgánica.

Palabras clave: meiofauna, copépodos, clases de tamaño, biovolumen, *Pseudotachidius jubanyensis*, *Scottopsyllus (S.) praecipuus*, Isla Rey Jorge, Antártida.

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INTRODUCTION

Antarctic and Subantarctic shallow water meiofauna has been studied for many years and quite a few data sets and environmental details have been compiled. Studies normally focus on major meiofauna taxa such as nematodes, copepods, kinorhynchs and annelids and do not differentiate at species level (de Bovée and Soyer, 1977; Soyer and de Bovée, 1977; de Skowronski and Corbisier, 2002). This is partly due to the goals that have been set, such as the determination of meiofauna densities or the understanding of the relations between sediment structures and food availability on the one hand and meiofauna communities on the other (Bouvy and Soyer, 1989; de Skowronski and Corbisier, 2002). In these studies terms such as "meiofauna community structure" or "taxonomic diversity" are normally used to explain the interrelationships of individual numbers of higher taxa in a seasonal or regional context. Only recently, studies by Lee *et al.* (2001) and Vanhove *et al.* (1998; 2000) have given detailed information, in addition to the usual meiofauna data, on the genus- or species-level taxonomic structure of the most abundant meiofauna taxon, the nematodes.

The lack of ecological species-level studies for harpacticoid copepods in the Antarctic may be due to the lack of taxonomic descriptions of animals from these latitudes. A comparison of species numbers of known Harpacticoida from the Arctic and the Antarctic clearly shows the problem we are facing in the Antarctic: for the northern polar region about four times as many species of harpacticoids are described as for the Antarctic (Wells, 1986). Obviously, there is still a lot of taxonomic work to be done for the Antarctic.

This work presents a study on benthic harpacticoids from Potter Cove, King George Island, Antarctic. Although still far from the final aim of describing an Antarctic benthic copepod assemblage at species level, it gives additional accessible information on top of the mere comparison of individual numbers: the biovolume of benthic copepods. The biovolume of a meiofauna fraction can give important information on the suitability of a habitat for a certain taxon, or the habitat preferences of certain biotypes. For this study, the idea of taking the biovolume of the benthic copepods into account arose in order to investigate whether body size in Antarctic meiofauna was an additional means of differentiating between distinct sampling stations. Together with descriptions of new harpacticoid species from Potter Cove, this study should contribute to both the taxonomical and ecological investigation of the meiofauna of the Antarctic.

MATERIAL AND METHODS

Study site and sampling

This study was carried out in Potter Cove (62°14'S, 58°40'W) (Fig. 1), Maxwell Bay, on King George Island, South Shetland Islands, Antarctic where the German Dallmann Laboratory is located as an annex to the Argentinian Jubany Station. Klöser and Arntz (1994) gave a detailed description of the site. Two depth transects (5, 10, 20 and 30 m) were sampled during the Antarctic summer (02/01/1996 – 09/02/1996). The inner cove Transect 1 (perpendicular to the former Casa Bomba) is an unexposed area protected by a shallow ridge at its entrance. On Transect 1 muddy sediments predominate. The deeper sampling stations of this site are not affected by strong currents or disturbed by icebergs as frequently as on Transect 2. The latter (perpendicular to Punta Elefante) is located at the ridge between inner and outer cove, which—with a maximum depth of about 30 m —constitutes a natural barrier for big icebergs. Therefore, it is an exposed area with slightly sandier sediments at least at the uppermost stations. Strong near-bottom currents are always present.

Meiofauna samples were collected by scuba diving (01/02/1996 to 09/02/1996) along the two depth

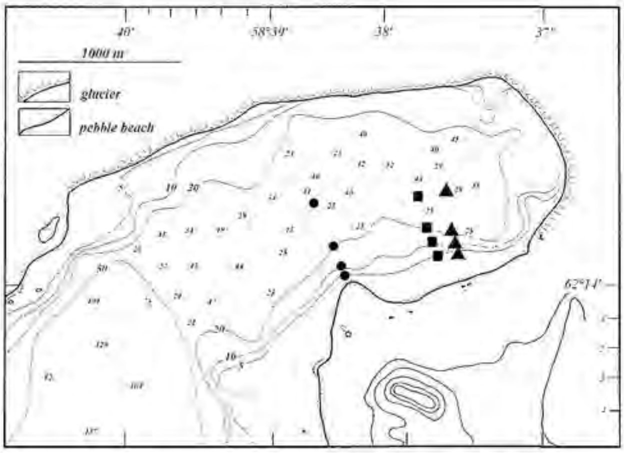

FIG. 1. – Map of Potter Cove, King George Island, Antarctic with bathymetric contours, additional single depths (modified after: Atlas Hidrografico, Chile) and transect locations. Black triangles: Transect 1, inner cove; black dots: Transect 2, cove entrance; black squares: transect sampled by Mayer (2000).

transects. At each station six sediment corers of 80 cm^2 each were randomly pushed into the sediment and brought to the surface as undisturbed as possible. The upper 3 cm of oxidised sediment layer of three sediment cores were split into four equal parts each and frozen for biochemical and grain size analysis (even the samples from stations with muddy sediment were deeply oxidised—no black reduced layer visible—because the sediment was very fluid). The resulting 12 parts provided 3 true replicate samples for each sediment analysis. The upper 3 cm sediment layer of the remaining three sediment cores was preserved in 5% formalin.

Abbreviations used in the text:
Stations: Transect 1, 30 m = 1.30;
Transect 2, 5 m = 2.05
Individuals per 10 cm^2 = Ind. 10 cm^{-2}

Sediment analyses

Grain size analysis was conducted with freeze-dried sediment samples for the inorganic sediment components. After a treatment with H_2O_2 and HCl to destroy organic matter and calcareous particles, the sediment was wet-sieved through a series of 2000, 630, 200, 63 and 20 μm meshes. The fine silt (< 20 μm) and clay (< 2 μm) fractions were determined by drying the rinsing water. The mean diameter Φ (Md), the inclusive graphic quartile deviation (QDI) and the inclusive graphic skewness (SkI) were determined graphically and calculated according to Folk (1974). Mean grain size was calculated from the mean diameter Φ after Giere *et al.* (1988).

The total organic matter (TOM) represented by the ash-free dry weight of the freeze-dried and homogenised sediment was determined by combustion at 500°C for four hours in a muffle furnace. Contents of organic carbon and nitrogen were measured from freeze dried, homogenised and HCl-treated sediment using a Fison C/N analyser and expressed as molar C/N. Chloroplastic pigments were extracted with acetone (90%) from defrosted homogenised sediment samples. Extinctions were measured photometrically (Shimadzu UV-1202) and chloroplastic equivalents (CPE), represented by the sum of chlorophyll *a* and phaeopigments, were calculated using the equations given by Greiser and Faubel (1988).

Meiofauna treatment

The fixed samples were washed using a 40 μm mesh sieve with tap water. Meiofauna and organic material were extracted from the remaining sand particles by centrifugation with a colloidal silica polymer (Ludox) as the flotation medium and kaolin to cover the heavier particles (McIntyre and Warwick, 1984). The centrifugation was repeated three times at 5000 rpm for five minutes each. After each centrifugation the floating matter was decanted and rinsed with tap water. This supernatant normally contains all organic material found in the sample. In this special case masses of particles of macroalgal detritus made sorting of the whole samples unrealistic and it was decided to split the samples in order to get manageable sample sizes.

Two centrifuged cores per sampling station were chosen. A meiofauna sample splitter after Jensen (1982) was used to obtain eight equal parts of each sample. The sample was filled up with tap water to a defined level and after splitting only equally divided samples were accepted, with the volume of all eight parts being the same. In order to ensure this, marks for the correct subsample volume were drawn on the outside of the transparent splitting chambers. When the splitting did not fulfil the prerequisites, the subsamples were unified again and the procedure was repeated. Finally, three subsamples per core were randomly selected and sorted. In total 6 parts representing altogether 60 cm^2 of sediment surface were investigated per station. Sample parts were stained with rose bengal for sorting and copepods were subsequently transferred to glycerine-lactate for clearing. The individual numbers were counted and the median values taken for further interpretation.

Body length and maximum width of 87 specimens of *Pseudotachidius jubanyensis* Veit-Köhler and Willen, 1999, 74 specimens of *Scottopsyllus (Scottopsyllus) praecipuus* Veit-Köhler, 2000 and 534 other harpacticoid copepods (adults and copepodid stages) were measured with the aid of a camera lucida. Per depth station on each transect, 100 other harpacticoids were randomly selected. When a station did not yield 100 specimens, all available animals were taken into account (Transect 1 = 223 specimens; Transect 2 = 311 specimens).

Body volumes were calculated using the body shape-dependent conversion factors C given by Warwick and Gee (1984):

$$\text{Body volume [nl]} = \text{length [mm]} \times (\text{width [mm]})^2 \times C$$

Biovolume was calculated using the station-dependent mean value of body volume per copepod and the median values of individual numbers per station. For the two distinctly larger species *P. jubanyensis* and *S. (S.) praecipuus*, sex- and developmental stage-dependent body volumes were calculated and considered according to abundance and distribution of sexes and stages in the samples.

Statistical analysis

For all variables of the different stations median rather than average values were used. This procedure was chosen because the calculation of mean values assumes the existence of a normal distribution of the data. Additionally, replicative sampling is required, which due to the necessary splitting of meiofauna samples was not given for this part of the study. Furthermore, outliers disproportionately influence mean values when applied to lower sample numbers.

With a Spearman rank test the correlations between individual numbers and biovolumes on the one hand and the environmental data on the other hand were tested. The Spearman rank was chosen because it can be applied to small data sets and even when the data are not distributed normally. To relate total harpacticoids and harpactiocid biovolume to grain size, TOM, C/N and CPE, the coefficient r_S was calculated. For the distributions and biovolumes of *P. jubanyensis* and *S. (S.) praecipuus*, as well as for all relations to water depth, the coefficient $r_{S.B}$ had to be used, as the coefficient r_S would have overestimated the correlations due to the occurrence of similar ranks in these data sets (Sachs, 1974).

For data interpretation a canonical correspondence analysis (CCA) was chosen, as this analysis allows animal data and environmental data to be compared at different sample sites at the same time. CCA was carried out after Ter Braak (1986), using the statistical package MVSP 3.1. No data transformations were carried out, as every transformation bears the risk of bias.

RESULTS

Sediment analyses

On both transects grain size of the upper 3 cm sediment layer shows a clear tendency towards smaller fractions with depth. While Transect 1 in the inner cove is characterised by the dominating silt and clay fraction (43.4% at 5 m; 80% at 30 m), Transect 2 at the cove entrance reveals a higher amount of fine sand (57.4% at 5 m; 49% at 20 m), which is exceeded by the silt and clay fraction at 2.30 of 58%. The data for the mean grain size as determined graphically and calculated from Md support these findings (Table 1). The apparent discrepancies between dominating sediment fraction and mean grain size are due to the very heterogeneous grain size distributions along both transects, as indicated by the very high QDI between 1.98 and 3.27, which stands for poorly to very poorly sorted sediments. The SkI values show that 1.05 has a symmetric grain size distribution. For the other stations negative SkI values indicate a displacement of Md and a preponderance of fine sediments. In contrast, at the three upper stations on Transect 2 positive SkI values show that, despite the relatively low Md, the coarser fractions prevail. Only at 2.30 are the sediment fractions symmetrically distributed.

TOM normally ranges between 4.40 and 5.48% for the upper 3 cm sediment layer along the two transects. Only 2.10 shows differing values: the

TABLE 1. – Median values of mean grain size, inclusive graphic quartile deviation (QDI), inclusive graphic skewness (SkI), total organic matter (TOM), molar carbon:nitrogen ratio (C/N), and chloroplastic equivalents (CPE) along Transect 1 in the centre of and Transect 2 at the entrance to Potter Cove; [1] = 5 m station of Transect 1 omitted from statistical analysis.

Station and depth [m]	Mean grain size [μm]	QDI	SkI	TOM [% dw]	C/N molar	CPE [μg (g^{-1}dw)]
Transect 1 Inner cove						
5[1]	27	3.27	-0.05	5.13	6.63	14.15
10	12	2.75	-0.3	5.23	7.20	3.96
20	11	2.42	-0.2	4.79	6.42	2.57
30	7	1.98	-0.16	5.48	6.52	3.25
Transect 2 Cove entrance						
5	40	2.32	0.16	4.40	7.23	7.84
10	22	2.47	0.22	6.15	8.36	20.60
20	32	2.4	0.56	5.13	7.99	9.94
30	15	2.5	-0.06	5.40	8.07	5.77

TABLE 2. – Median values of individual numbers and biovolumes of other Harpacticoida, *Scottopsyllus (S.) praecipuus*, and *Pseudotachidius jubanyensis* (biovolume weighed for developmental stages) along Transect 1 in the centre of and Transect 2 at the entrance to Potter Cove; ^{1} = 5 m station of transect 1 omitted from statistical analysis.

Station and depth [m]	Other Harpacticoids [Ind. 10 cm^{-2}]	*S. (S.) praecipuus* [Ind. 10 cm^{-2}]	*P. jubanyensis* [Ind. 10 cm^{-2}]	Other Harpacticoids [nl 10 cm^{-2}]	*S. (S.) praecipuus* [nl 10 cm^{-2}]	*P. jubanyensis* [nl 10 cm^{-2}]
Transect 1 Inner cove						
5^1	3	0	0	33.6	0	0
10	5	0	0	24.0	0	0
20	32	8	2	118.4	74.6	16.6
30	66	2	10	237.6	5.4	340.5
Transect 2 Cove entrance						
5	21	0	0	105.0	0	0
10	216	0	0	648.0	0	0
20	92	0	0	285.2	0	0
30	64	2	2	192.0	24.8	81.4

6.15% concentration of organic matter is higher than that of all other stations. This is due to the accumulation of macroalgal detritus in a depression at the sampling site (pers. observation).

C/N for the upper 3 cm sediment layer varies between 6.42 and 8.36. The values on the detritus-rich Transect 2 are higher than on Transect 1, supporting the visual findings: while sediments on Transect 1 were covered with living benthic diatoms, thus revealing comparatively more nitrogen, Transect 2 is characterised by higher amounts of dead organic material, especially macroalgal detritus originating from the kelp at the rocky sites of the bay.

CPE as the sum of chlorophyll *a* and phaeopigments in the upper 3 cm sediment layer clearly follows the findings of the other biotic sediment factors: higher amounts along Transect 2 are due to macroalgal detritus particles, especially at 2.10 with 20.60 μg/g dw. The high values at the 5 m station of Transect 1 are the effect of cyanobacteria mats (pers. observation), which emerged as a consequence of the nearby station drainage. As this situation differed greatly in its conditions from the other sites, 1.05 was excluded from further statistical analysis.

Copepod abundances and biovolume

Benthic copepods in the central Potter Cove show increasing abundances with depth (Table 2). Along Transect 1 median individual densities for the upper 3 cm sediment layer reach their maximum with altogether 78 Ind. 10 cm^{-2} at 30 m depth. On Transect 2 at the entrance to the inner cove, the highest copepod abundance overall is recorded from the 10 m station with 216 Ind. 10 cm^{-2}. A marked decrease in individual densities for the deeper stations was observed, although the 30 m station revealed approximately the same numbers as the deepest station of the inner cove transect.

Biovolume of benthic copepods was calculated by multiplying the station-dependent mean body volume by the median individual number per sta-

TABLE 3. – Geometrical size classes applied to the body volumes of benthic copepods sampled along two depth transects in the centre of and at the entrance to Potter Cove.

Geometrical size class	Biovolume [nl]
1	0.2 – 0.39
2	0.4 – 0.79
3	0.8 – 1.59
4	1.6 – 3.19
5	3.2 – 6.39
6	6.4 – 12.79
7	12.8 – 25.59
8	25.6 – 51.19
9	51.2 – 102.4

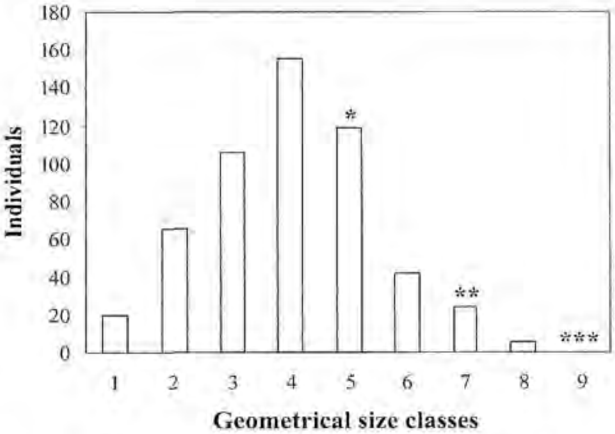

FIG. 2. – Distribution of 534 randomly selected "other" benthic harpacticoids from Potter Cove according to geometrical size classes based on body volumes (Table 3). Examples for size classes in which developmental stages of *S. (S.) praecipuus* and *P. jubanyensis* should be placed: * = C I *P. jubanensis*; ** = C VI F *S. (S.) praecipuus*; *** = C VI F *P. jubanyensis*.

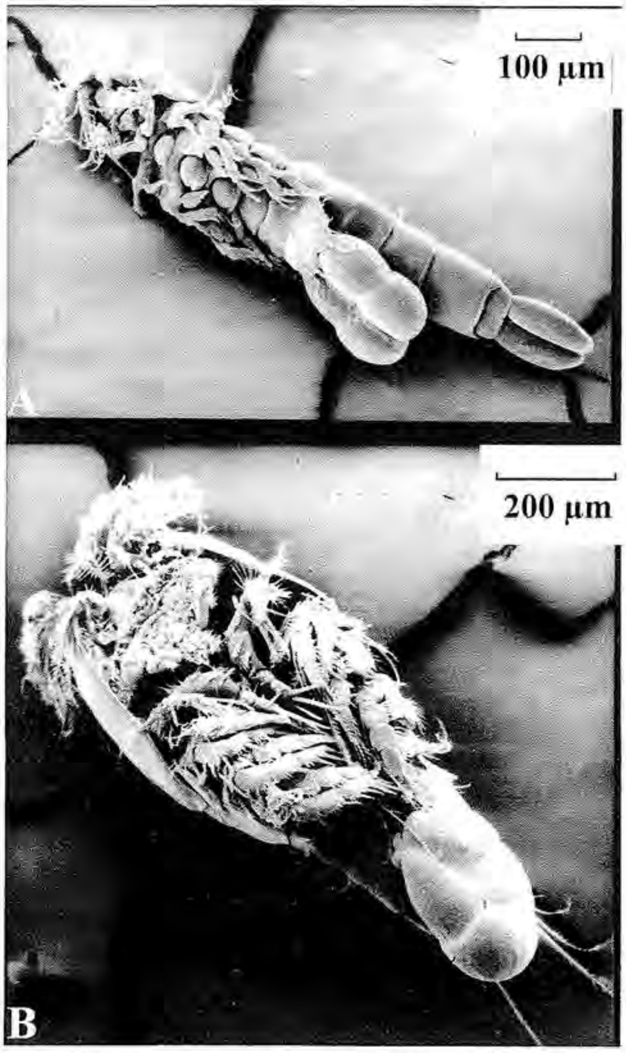

FIG. 3. – REM-photographs of adult, egg-sac carrying females (ventral views) of Copepoda Harpacticoida from Potter Cove: A. *Scottopsyllus (S.) praecipuus* Veit-Köhler, 2000 and B. *Pseudotachidius jubanyensis* Veit-Köhler and Willen, 1999.

tion. The mean body volume per copepod ranged between 3.0 and 5.0 nl for nearly all stations, but at 1.05 the very high mean individual body volume of 11.2 nl was detected for the few animals collected at this exceptional site, which was covered with cyanobacteria. Along a depth gradient on both transects (omitting 1.05) the mean biovolume of other harpacticoids decreased (1.10: 4.8 nl to 1.30: 3.5 nl; 2.05: 5.0 nl to 2.30: 3.0 nl).

When sorted for geometrical size classes (Table 3, Fig. 2), most of the measured benthic copepods in Potter Cove belonged to size class 4 (1.6-3.19 nl). Towards the lower and the higher size classes the numbers of individuals continuously decreased.

Pseudotachidius jubanyensis and *Scottopsyllus (S.) praecipuus*

The two species *Pseudotachidius jubanyensis* and *Scottopsyllus (S.) praecipuus* (Fig. 3) have been described from Potter Cove (Veit-Köhler, 2000; Veit-Köhler and Willen, 1999). Their adults are the largest harpacticoids to be found at the deeper stations of the transects (Tables 4, 5).

Adult females of the pyriform *P. jubanyensis* (conversion factor C = 400; Warwick and Gee, 1984) had an average body volume of 68.9 nl with an average body length of 1.03 mm. Adult males of the same species are still within size class 7 (Table 3), with an average body volume of 24.9 nl. Even first stage copepodids C I of *P. jubanyensis* had a biovolume that reached the average for "other" copepods from some of the transect stations. All in all, an adult female of *P. jubanyensis* increases its body volume twenty times with only five copepodid moults during its development.

Male and female adult *S. (S.) praecipuus* are represented by size classes 6 and 7. Although females of this species had about the same average body length (0.93 mm) as female *P. jubanyensis*, it is due to their cylindrical body shape and the resulting conversion factor (C = 750) that they attain only about a quarter of the body volume of the other species.

Abundance-dependent classification according to size classes was not performed for *S. (S.) praecipuus* and *P. jubanyensis*. However, three markers

TABLE 4. – Body volumes of developmental stages of *Pseudotachidius jubanyensis* (partly distinguished for males and females) measured and calculated according to Warwick and Gee (1984). C I – C V = Copepodid I – V; C VI = Copepodid VI (adult); F = Female; M = Male.

Pseudotachidius jubanyensis	No. Individuals measured	Mean body volume [nl]	Standard Dev. [nl]
C VI F	18	68.9	12.5
C VI M	16	24.9	4.6
C V F	4	52.6	21
C IV	6	23.5	9.2
C III	7	12.1	3
C II	13	5.6	1.3
C I	23	3.4	1

TABLE 5. – Body volumes of developmental stages of *Scottopsyllus (S.) praecipuus* (partly distinguished for males and females) measured and calculated according to Warwick and Gee (1984). C I – C V = Copepodid I – V; C VI = Copepodid VI (adult); F = Female; M = Male.

Scottopsyllus (S.) praecipuus	No. Individuals measured	Mean body volume [nl]	Standard Dev. [nl]
C VI F	10	17.9	1.1
C VI M	12	11.6	0.7
C V F	7	10.9	1.4
C V M	8	9.1	0.7
C IV F	7	6.6	1.9
C IV M	4	4.4	0.9
C III	7	3.1	0.8
C II	11	2.3	0.3
C I	8	1.6	0.3

TABLE 6. – Results of the Spearman rank analysis of environmental parameters versus animal data; [1] = data sets for which the correlation coefficient $r_{S.B}$ instead of r_S had to be calculated; ** = α: 0.05; * = α: 0.1 for the two-sided test.

Environmental parameters	Total number of harpacticoids	Total biovolume of harpacticoids	Number of *P. jubanyensis*[1]	Biovolume of *P. jubanyensis*[1]	Number of *S. (S.) praecipuus*[1]	Biovolume of *S. (S.) praecipuus*[1]
Depth[1]	0.330	0.477	0.827 **	0.859 **	0.704	0.697
Grain	0.107	- 0.143	-0.772 *	-0.726 *	-0.713	-0.647
TOM	0.607	0.786 **	0.238	0.294	0	-0.02
CPE	0.536	0.321	-0.713	-0.647	-0.772 *	-0.726 *
C/N	0.536	0.464	-0.475	-0.373	-0.535	-0.451

for developmental stages have been placed in Figure 2 in order to highlight the exceptional positions both species hold in their environment.

As shown in Table 2, both species can only be found at the deeper stations of the two transects. While they occur at 1.20 and 1.30, on Transect 2 they were only found at a depth of 30 m. Their abundances in the upper 3 cm sediment layer are very low, with *S. (S.) praecipuus* revealing a maximum of 8 Ind. 10 cm^{-2} at 1.20 and *P. jubanyensis* reaching its highest abundance with 10 Ind. 10 cm^{-2} at 1.30.

In order to calculate the biovolume for both species a stage-dependent approach was adopted. The data given in Table 2 are the median biovolumes found after all specimens for all sorted samples had been taken into account according to their sex and developmental stage. Despite their low densities of only a few specimens per station, both species obviously contribute to a large extent to the total biovolume at the sites where they are found. This is most strikingly apparent at 1.30: *P. jubanyensis* with only 10 individuals outranged the biovolume of 66 other copepods by over 100 nl. The average copepod at this site had a biovolume of 3.5 nl, the average *P. jubanyensis* 34 nl.

Taking into account *P. jubanyensis* and *S. (S.) praecipuus*, the mean biovolume per copepod increased drastically at the stations where they occurred: 2.30: 4.4 nl, 1.20: 5.5 nl, and at 1.30 even 7.5 nl.

Statistical analyses

Spearman rank analysis

Harpacticoid densities and biovolume along the two transects in Potter Cove can hardly be correlated with any of the environmental parameters (Table 6). Only the total biovolume of harpacticoids was correlated to the concentration of TOM at the 5% level of significance. For *P. jubanyensis* both individual densities and biovolume were connected positively with depth at the 5% level and negatively with grain size at the 10% level. *S. (S.) praecipuus* was related only to decreasing CPE-values at the 10% level. Although the main structure of the data becomes clear from the Spearman rank analysis, the CCA ordination diagram displays all at the same time.

Canonical correspondence analysis

A canonical correspondence analysis (CCA) for 6 variables (individuals and biovolume per 10 cm^2 of all Harpacticoida, *P. jubanyensis* and *S. (S.) praecipuus*) and 7 cases (2 transects with 3 and 4 stations respectively) was performed for the environmental data with 5 variables (depth, mean grain size, TOM, C/N and CPE). The ordination diagram of CCA displays sites and animal data as points and environmental variables as vectors (Fig. 4). The vector for depth decreases with the first axis (X), whereas CPE,

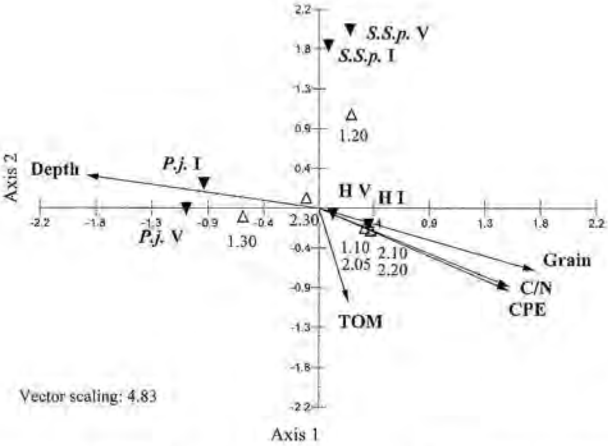

FIG. 4. – Canonical correspondence analysis of individual number (I) and biovolume (V) of *Pseudotachidius jubanyensis* (*P.j.*), *Scottopsyllus (S.) praecipuus* (*S.S.p.*) and other harpacticoids (H) (black triangles), and stations (white triangles; e.g. 2.10 = Transect 2; 10 m depth) according to environmental data (vectors: depth, mean grain size (Grain), total organic matter (TOM), carbon:nitrogen ratio (C/N), chloroplastic equivalents (CPE)).

C/N and grain size increase with this axis. TOM is more related to axis 2 and decreases along Y. For data interpretation the vectors can virtually be produced through the axis intersection. The ordination of data points in relation to environmental vectors is determined by projecting the data points at a right angle to the corresponding vector (Ter Braak, 1987).

The deepest stations of Transect 1 and, to a far lesser extent, of Transect 2 are positively related only to depth and inversely related to the other environmental variables. 1.20 and 1.30 are found in regions with decreasing TOM and especially 1.30 is shown to contribute very low values of CPE, C/N and grain size. All remaining shallower stations (1.10, 2.05, 2.10, 2.20) are only slightly related to increasing TOM, CPE, C/N and grain size. The same weak relation to environmental variables can be found for harpacticoid individual densities and harpacticoid biovolume. In contrast to the Spearman rank analysis in the CCA, the data point for harpacticoid individual density is higher in the order of projections onto the TOM vector than the harpacticoid biovolume.

P. jubanyensis and *S. (S.) praecipuus* reached their maximum abundance and biovolume at the three stations projected in quadrants I, III and IV of the diagram. *P. jubanyensis* is strongly related to depth and stations 1.30 and 2.30. It has a connection to small grain sizes as does *S. (S.) praecipuus*, which on the other hand is only to a far lesser extent related to depth. In contrast to *P. jubanyensis*, *S. (S.) praecipuus* can be found in relatively high abundance at 1.20, which is also expressed in the CCA by the proximity of the corresponding data points. Interpreting the CCA, TOM plays a more important role for *P. jubanyensis* than for *S. (S.) praecipuus*. CPE, C/N and grain size are negatively correlated with both species. Axes 1 and 2, however, explained 96.5% of the total variance, which may be due to the relatively low number of variables.

DISCUSSION

Harpacticoid densities and biovolume

Regarding the joint plot of the CCA (Fig. 4) and the Spearman rank analysis, it becomes obvious that only the combination and consideration of both procedures can lead to a suitable interpretation. Although in a CCA environmental variables with long arrows are more strongly correlated with the ordination axes than those with short arrows, and therefore are more closely related to the pattern of variation shown in the ordination diagram (Ter Braak, 1987), the Spearman rank analysis indicates that TOM, despite the short vector, is the only environmental factor that plays a significant role concerning the biovolume of harpacticoid copepods in Potter Cove. Furthermore, this significance is not very clearly expressed in the CCA, as the data point for harpacticoid individual density is higher in the order of projections onto the TOM vector than the harpacticoid biovolume. To clarify this problem it must be taken into account that Ter Braak (1987) states that the projection of a data point onto an environmental vector indicates the position of the data point within the distribution, "although approximately".

Therefore, total harpacticoid biovolume seems to be related to food supply in terms of carbon and nitrogen availability provided by benthic and pelagic primary production. Obviously, the quality of nutrition is not as important as the total amount of organic matter, as higher individual densities can be observed at locations with a higher content of TOM, but higher C/N ratios pointing to advanced degradation are observed at these stations as well.

In Potter Cove the highest abundance and biovolume of harpacticoids was found at 2.10, which is situated in a depression on the ridge between the inner and outer cove. This site was at that time loaded with macroalgal detritus, as can easily be recognised from the TOM, C/N and CPE values obtained there (Table 1). Although a statement about temporal changes at this site cannot be made, the huge masses of macroalgal remnants indicate a regular deposition of this material at the site. Physical disturbances such as iceberg scours are known to have a negative influence on individual density and community structure of benthic macrofauna, at least initially; the duration of the recovery process is not known (Gerdes *et al.*, 2003; Gutt and Piepenburg, 2003). For meiofauna, the recolonisation time after iceberg scouring in a shallow water habitat has been studied by Lee *et al.* (2001): only 30 days after the impact meiofauna abundance had reached control levels again, with copepods and ostracods being the pioneer colonisers. This might be an explanation why in Potter Cove the highest abundance of copepods was found at the most exposed site. The detritus-rich depression observed at 2.10 was probably the remnant of an iceberg scour, which served as a detritus trap in an environment characterised by strong near-bottom currents.

Mayer (2000) did an extensive survey on foraminiferans in the sediments of Potter Cove from October 1996 to December 1998. A comparison of summer data (January 1997 and 1998) from her transect with the February 1996 data from this study shows a great difference between the three transects. Her transect, which was placed between the two transects examined in this study (Fig. 1), was supposed to be more similar to Transect 1 of my study. Chloroplastic pigment content could not be checked due to different analysis procedures, but C/N ratios along Mayer's transect were higher than those of 1.05 and 1.10 and about the same as those of 1.30. The elevated content of dead organic material and a mean grain size of around 17 μm from 5 m down to 30 m indicate that this transect differs sedimentologically from Transects 1 and 2 of this study.

Mayer's (2000) data for the uppermost 3 cm were added up and compared to the copepod area data of this study (Ind. 10 cm^{-2} from the upper 3 cm sediment layer). Mayer mentions foraminiferans being the most abundant meiofauna and nematodes as the most abundant metazoan taxon in the sediments of Potter Cove. However, the copepod densities from Transect 2 of this study alone nearly double the total metazoan numbers of her 20 m station in both years and exceed the number of metazoans from her 30 m station in 1998. Copepod numbers from this study always exceeded half the metazoan numbers found by Mayer, not taking into account station 1.05 for the above-mentioned reasons. These are immense differences, although all three transects are located in Potter Cove. Obviously, there must be additional factors influencing meiofaunal abundances in Potter Cove because, despite the overall high TOM content and sufficient nutrient availability, meiofauna densities along Mayer's transect were relatively low.

The comparison of four samplings from three years, in direct vicinity to each other, shows how difficult it is to compare meiofauna studies and draw the right conclusions.

De Skowronski and Corbisier (2002) studied meiofauna densities at various 15 m deep stations close to Potter Cove in Martel Inlet, Admiralty Bay, King George Island. Total meiofauna abundance at the Martel Inlet stations ranged between 1,953 and 6,310 Ind. 10 cm^{-2}. With the average copepod share of about 9.5% given by them, a total amount of about 185 to 600 Ind. 10 cm^{-2} could be expected. The situation found in Martel Inlet is not easy to compare with the results obtained in this study, as de Skowronski and Corbisier integrated the upper 10 cm sediment layer. Following Mayer's findings (2000) from Potter Cove, most of the metazoan abundance was concentrated in the first 3 cm of sediment, although in Potter Cove she still found meiofauna metazoans at sediment depths of 10 to 16 cm. As mean grain size at all stations of this study with a maximum of 40 μm does not exceed the size of silt and clay, an interstitial life of meiofauna is not possible anywhere along the two transects. Therefore, a burrowing or epibenthic lifestyle must be assumed for all harpacticoid species (Schwinghamer, 1981; Warwick, 1984). This is particularly true for the deeper stations of the two transects, where very fluid sediments were observed. Thus, in the findings of de Skowronski and Corbisier (2002), the overall high individual numbers might be due to the mostly sandy sediments in Martel Inlet, which might provide meiofauna with more suitable interstitial habitats than they find on the Potter Cove transects. However, in this interpretation again uncertainty remains: their station with the highest individual density is a coarse silt station, which on the other hand revealed the highest organic matter content they found in Martel Inlet.

There are more reasons why comparisons with meiofauna data from other authors should be handled with care (Soyer and de Bovée, 1977). Firstly the mesh sizes used for sample treatment are different (see de Skowronski and Corbisier, 2002), and secondly the sampling methods are very diverse (corers placed by scuba divers: de

Skowronski and Corbisier, 2002; Vanhove *et al.*, 1998, 2000; Lee *et al.*, 2001; sub-samples from Reineck corer: de Bovée and Soyer, 1977; Soyer and de Bovée, 1977).

An additional difficulty for data discussion is the sampled sediment volume: although individual densities are compared per 10 cm^2, the sampled sediment volume due to the integration of different sediment depths varies greatly from author to author, or is not given at all (Lee *et al.*, 2001).

Lee *et al.* (2001), as mentioned above, investigated copepod densities at Signy Island in temporal and spatial proximity to an iceberg scouring event. Their control samples from December 1993 and June 1994 (two replicates at each date) revealed 38 and 51.9 Ind. 10 cm^{-2} respectively. The highest copepod abundance within the iceberg scour region was 472 Ind. 10 cm^{-2} (3 months after the event), whereas the lowest was 10.1 Ind. 10 cm^{-2} (4 months after the event). A comparison with the data from this study is not possible, because environmental factors were not measured.

Soyer and de Bovée (1977) sampled sediments in Morbihan Bay, Kerguelen Islands, and report from depths down to 30 m a maximum copepod density of 259 Ind. 10 cm^{-2} in fine sand integrating a sediment depth of 10 cm, although copepod numbers normally ranged between 3 and 43 Ind. 10 cm^{-2}. These data are quite within the range of this study, but as the sediment was collected with a Reineck corer and subsampled, a further comparison will not be undertaken.

Again at Signy Island, Factory Cove, Vanhove *et al.* (1998) sampled fine sands in January and February 1994, revealing very high copepod densities of 866 and 779 Ind. 10 cm^{-2} respectively (calculated from 0–3 cm depth and the taxon-percentages given). Meiofauna in Factory Cove is provided with an excess of food during the summer (C/N: 9–12 for the upper three centimeters, TOM: 2 and 4%) and copepods especially, due to highly reduced sediments, are confronted with only a few centimetres of suitable habitat. Also in Factory Cove, Vanhove *et al.* (2000) found correlations between harpacticoid copepods on the one hand and sediment bound pigments and organic nitrogen on the other.

Compared to Potter Cove, where even higher TOM and lower C/N indicating fresher and more abundant food should support higher numbers of harpacticoid copepods, again the only plausible reason for lower harpacticoid numbers is grain size and the lack of interstitial habitat.

The importance of species-related investigations

Pseudotachidius jubanyensis and *Scottopsyllus (S.) praecipuus* have been described from Potter Cove (Veit-Köhler and Willen, 1999; Veit-Köhler, 2000) due to their large size and interesting reproductive strategy. Until today these species have not been reported from elsewhere in the Antarctic or adjacent regions, but the genera are widely distributed in the polar and subpolar regions. George (1999) reported *Scottopsyllus* from the Magellan Straits and the Patagonian continental slope. *Pseudotachidius* has been found in the Magellan and Beagle areas (George and Schminke, 1999) and in the Weddell Sea (Willen, 1999).

A byproduct of the studies on *Pseudotachidius jubanyensis* and *Scottopsyllus (S.) praecipuus* was that there are copepod species, which despite better food availability in shallower areas prefer the calmer, undisturbed zones of the cove, as their distribution does not seem to be related to other environmental factors (Fig. 4). The biovolume data show that only small harpacticoids with a mean individual volume of about 3 nl seem to be adapted to the kind of environment available at these deeper sites. Adding up the total biovolume at 1.30 (Table 2), only 78 individuals have nearly the same biovolume as 216 individuals at the 10 m station of Transect 2, because of the presence of *P. jubanyensis*.

Harpacticoid biovolumes have not been published for polar regions. Due to the appearance of *P. jubanyensis* and *S. (S.) praecipuus*, total biovolume increases with depth, whereas the rest of the community experiences a decrease in mean biovolume with depth.

For the future, ecological studies will have to be combined with diversity studies on species level in order to elucidate relationships that up to now are unknown or neglected, and to verify the assumption that body size in Antarctic meiofauna is an additional means of differentiating between sites.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
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Sublittoral and bathyal Harpacticoida (Crustacea: Copepoda) of the Magellan region. Composition, distribution and species diversity of selected major taxa*

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SUMMARY: Two expeditions, undertaken in 1994 and 1996, provided quantitatively sampled material of sublittoral and bathyal meiobenthos from the Paso Ancho of the Straits of Magellan, the Beagle Channel, and the Patagonian continental slope (Chile). To investigate whether these distinct geographic areas might also be characterised by different harpacticoid assemblages, qualitative and quantitative analyses of Copepoda Harpacticoida were carried out. At supraspecific level 25 harpacticoid families were found, as well as several species that could not yet be assigned to any major harpacticoid taxon. Due to the high amount of collected Harpacticoida, detailed investigations at species level had to be restricted to six taxa, namely the Ancorabolidae, Argestidae, Cletodidae, Diosaccinae, Paramesochridae, and Paranannopinae. The corresponding specimens were assigned to 122 species in 52 genera. More than 80% of them are new to science. Qualitative comparisons of both species composition and species distribution allow the three areas to be distinguished in terms of species richness. However, statistical analyses confirm these results only partly. Similarity analyses applying non-metrical multidimensional scaling, as well as diversity analyses using the rarefaction method, suggest that the observed differences in distribution and diversity patterns are due to small-scale, local conditions, which may overlay possible large-scale ones.

Keywords: meiobenthos, similarity analysis, Harpacticoida, Chile, Straits of Magellan, Beagle Channel.

RESUMEN: HARPACTICOÍDEOS SUBLITORALES Y BATIALES (CRUSTACEA, COPEPODA) DE LA REGIÓN MAGALLÁNICA. COMPOSICIÓN, DISTRIBUCIÓN Y DIVERSIDAD ESPECÍFICA DE TAXONES MAYORES SELECCIONADOS. – Durante dos expediciones realizadas en 1994 y en 1996, se colectó una gran cantidad de material meiobentónico del sublitoral y batial en el Paso Ancho del Estrecho de Magallanes, del Canal Beagle y del talud continental patagónico (Chile). Posteriormente, se realizaron análisis cualitativos y cuantitativos de los copépodos harpacticoideos para verificar si estas diferentes áreas geográficas también se distinguen con respecto a la fauna harpacticoidea. A nivel supra-específico, se determinaron 25 familias diferentes, más varias especies desconocidas que no pudieron ser asignadas a ningún taxon harpacticoideo. Debido al gran número de harpacticoideos colectados, una evaluación a nivel de especies debió ser restringida a los representantes de solo seis familias, en particular a los Ancorabolidae, Argestidae, Cletodidae, Diosaccinae, Paramesochridae y Paranannopinae. Los especímenes respectivos corresponden a 122 especies que pertenecen a 52 géneros. Más del 80% de ellas puede ser considerado como nuevo para la ciencia. Un análisis cualitativo de la composición y distribución de especies permite diferenciar entre las tres áreas geográficas. Los análisis estadísticos de los datos cuantitativos confirmaron, sin embargo, este resultado sólo parcialmente. Sendos análisis de similaridad usando nMDS y de diversidad aplicando el método de "Rarefaction" indican que las diferencias observadas se deben principalmente a condiciones locales y de pequeña escala, las cuales posiblemente se superponen con condiciones de escala mayor.

Palabras clave: meiobentos, análisis de similaridad, Harpacticoida, Chile, Estrecho de Magallanes, Canal Beagle.

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INTRODUCTION

The disintegration of Gondwana and the related distribution of Gondwanan floral and faunal elements form the basis of biogeographical comparisons within the southern hemisphere. Since the early sixties, several biogeographic investigations have been carried out, focussing exclusively on macrofauna (e.g. Knox, 1960; 1963; 1977; Knox and Lowry, 1977; Lipps and Hickman, 1982; Brattstrøm and Johanssen, 1983; Brandt, 1992; Sieg, 1992; Winkler, 1994). In particular, the supposed high affinity between Antarctica and South America, as the two Gondwanan fragments that were last separated, calls for studies on the origin and spreading of recent Antarctic and Magellan flora and fauna and for potential correlation with latitudinal gradients in species diversity (Crame, 1994; Arntz, 1997, 1999). A number of recent investigations concentrated on different macrofaunal groups (e.g. Arntz and Gorny, 1996; Fahrbach and Gerdes, 1997 (macrofaunal major groups); Brandt, 1991; 1992; Winkler, 1994 (Isopoda); Linse, 1997 (Mollusca)), and were followed some years later by the first studies on meiofauna (Chen *et al.*, 1999; George, 1999; George and Schminke, 1999).

Faunistic investigations dealing with Harpacticoida from deeper waters (>100 m to ~1,000 m) at species level are rare (cf. George 1999). The present contribution is the first one to detect, describe and compare harpacticoid assemblages from deeper waters of different Magellan areas at species level, as a basis for future comparisons with corresponding Antarctic sublittoral and bathyal assemblages. Comparable investigations in general are rare. The detailed investigation of harpacticoid taxa had to be restricted to six families, which is justified by the enormous amounts of specimens and species found in the Magellan region.

MATERIAL AND METHODS

Sampling areas

The investigated material originates from two international sampling expeditions to the southern tip of South America:

The 1994 "Magellan Campaign" of RV "Victor Hensen" (17.10.-20.11.1994; Arntz and Gorny, 1996) provided quantitative sublittoral meiobenthic material of this region for the first time. In total, 62 hauls at just as many stations were taken with a Minicorer (MIC) in the Paso Ancho of the Straits of Magellan, as well as from the channels Magdalena, Cockburn, Brecknock, Ballenero and Beagle (Fig. 1), 17 of which provided sufficient material for further quantitative analyses. The MIC, which resembles a small Multiple corer (MUC) as developed by Barnett *et al.* (1984), samples up to four cores per haul simultaneously.

The 1996 expedition ANT XIII/4 of RV "Polarstern" in May, 1996 (Fahrbach and Gerdes, 1997) provided material from the Patagonian continental slope (Fig. 1). The MUC was used to sample 8 stations, 3 of which were useful for further analyses.

Sampling localities

For the analyses, material from 20 stations was available (Fig. 1, Table 1). Their distribution over the areas is as follows (depth ranges (m) in brackets):

- Straits of Magellan (79-550):
  - 9 stations at 5 localities
  - 24 MIC cores
- Beagle Channel (100-346):
  - 8 stations at 7 localities
  - 24 MIC cores
- Patagonian continental slope (101-1,168):
  - 3 stations at 3 localities
  - 21 MUC cores

Treatment of samples

The material was immediately fixed in 5% formaldehyde. For the posterior treatment of sam-

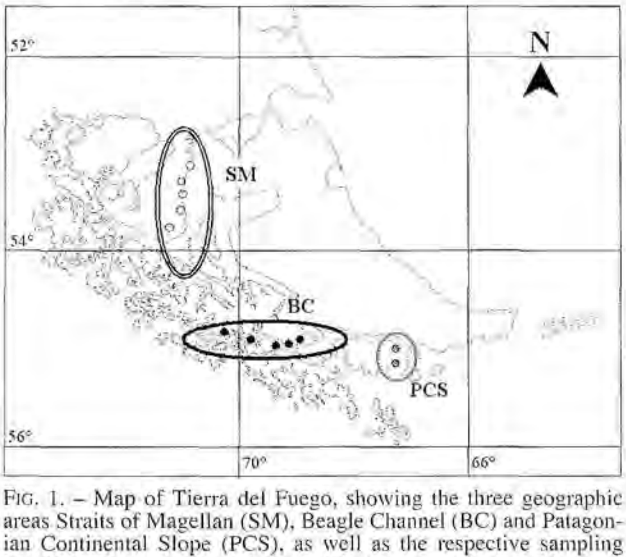

FIG. 1. – Map of Tierra del Fuego, showing the three geographic areas Straits of Magellan (SM), Beagle Channel (BC) and Patagonian Continental Slope (PCS), as well as the respective sampling localities. For station numbers and their geographical position, see Table 1.

TABLE 1. – Station list including sedimentological data: Granulometric data after Chen *et al.* (1999). "Median" describing median grain size (μm).

Geogr. area	Station	Locality	Depth (m)	Sand (%)	Silt (%)	Clay (%)	Median
SM	840	53°08.8'S/70°38.4'W	123	22.3	59.43	18.27	28.52
	847	53°21.2'S/70°42.7'W	200	50.99	39.85	9.16	65.4
	864	53°42.6'S/70°48.7'W	550	20.15	57.86	21.99	17.19
	866	53°51.8'S/70°54.6'W	440	11.87	65.17	22.96	12.97
	872	53°43.4'S/70°56.0'W	351	23.87	52.55	23.58	17.3
	877	53°41.5'S/70°56.5'W	227	-	-	-	-
	954	53°59.7'S/70°33.0'W	79	4.98	37.3	57.72	2.742
	956	53°59.9'S/70°32.9'W	80	0	33.88	66.12	2.082
	977	53°33.0'S/70°39.2'W	459	2.02	67.78	30.2	8.649
BC	1033	54°52.7'S/69°55.2'W	309	1.04	72.29	26.67	8.001
	1076	54°53.6'S/69°30.3'W	346	7.2	75.04	17.76	15.12
	1123	54°58.7'S/68°49.9'W	219	8.02	67.65	24.33	11.18
	1135	54°58.1'S/68°49.9'W	257	0	67.53	32.47	7.02
	1138	54°54.5'S/68°38.7'W	320	6.56	71.83	21.61	11.01
	1144	55°08.4'S/66°54.5'W	110	0	66.23	33.77	7.535
	1181	55°07.0'S/66°55.4'W	110	0	58.89	41.11	5.295
	1234	55°00.4'S/66°53.6'W	100	0	70.16	29.84	8.891
PCS	40/110	55°26.4'S/66°14.0'W	101	-	-	-	-
	40/111	55°29.0'S/66°04.4'W	1168	-	-	-	-
	40/116	55°27.8'S/66°09.1'W	336	-	-	-	-

ples and abiotic conditions, see Chen *et al.* (1999). Sedimentological data are summarised in Table 1. Species determination was realised using a Wild Heerbrugg M5 stereo microscope, a Leitz Dialux EB 22 phase contrast microscope, and a Leica DM LB interference contrast microscope, both equipped with a 100x objective. Taxa determination was done using identification keys (Lang, 1948; Wells, 1976-1985; Huys *et al.*, 1996) and original literature.

Abbreviations used in the text: BC = Beagle Channel, MR = Magellan region, SM = Straits of Magellan, PCS = Patagonian continental slope.

Selection of major harpacticoid taxa

Due to the high amounts of collected Harpacticoida, for detailed analyses at species level a restriction of the material was necessary. Ancorabolidae Sars, 1909, Argestidae sensu Por, 1986, Cletodidae sensu Por, 1986, Diosaccinae Sars, 1906, Paramesochridae Lang, 1944, and Parananopinae sensu Por, 1986 were selected because of the taxonomical expertise of the author in particular for these groups. However, as shown by George (1999), they reflect very well the overall abundance data and distribution patterns in the study area.

Similarity analysis

For a similarity analysis, non-metrical multidimensional scaling (nMDS) was applied using Cosine Similarity (Pfeifer *et al.*, 1996):

$$\cos(ob_x, ob_y) = \frac{\sum_{k=1}^{N} x_k y_k}{\sqrt{\sum_{k=1}^{N} x_k^2}\sqrt{\sum_{k=1}^{N} y_k^2}} = \cos(\vec{x}, \vec{y})$$

where ob_x and ob_y are considered as n-dimensional vectors $\vec{x} = [x_1, \ldots x_k, \ldots x_N]^T$ as well as $\vec{y} = [y_1, \ldots y_k, \ldots y_N]^T$. Consequently, the Cosine Similarity then corresponds to *cos* α between vectors $\vec{x}$ and $\vec{y}$ within a multidimensional ecological space. The dimensions are represented by the attributes, i.e. the species at each station. Comparison between two vectors (here: stations) considers both the single and common presence of species. This means that neither single nor common absences are taken into account. To avoid any original data manipulation, no transformation was carried out.

RESULTS

Composition of Harpacticoida at family level

With 91.9%, Harpacticoida clearly dominated the benthic copepod fauna (George, 1999). In total, 25 supraspecific harpacticoid taxa were determined, comprising a number of 5,493 adult individuals (Table 2). Ten families (40%) showed a distribution within the whole study area. Furthermore, both SM and PCS present exclusive taxa at family level (Adenopleurellidae and Harpacticidae in SM, Peltidiidae, Superornatiremidae and Tegastidae in PCS), while BC cannot be characterised by any

TABLE 2. – List of Harpacticoida collected in the Magellan region, sorted per station and supraspecific taxon. Family names written in capitals indicate selected families for investigations at species level.

					MS									BC					PCS				Presence/abcense	
Station	840	847	864	866	872	877	954	956	977	1033	1076	1123	1135	1138	1144	1181	1234	40110	40111	40116	Sum	MS	BC	PCS
Ameiridae	11	17	6	6	26	17	19	12	21	1	21	4	4	20	38	57	159	511	29	21	1000	+	+	+
ANCORABOLIDAE		2				8											1	30			41	+	+	+
ARGESTIDAE	4	2	1	6	8	3			28	3	19	15	4	36	1	8	5	2		2	147	+	+	+
"Canthocamptidae"		2		5	6	10						1		2	53	43	3	28	5	2	160	+	+	+
CLETODIDAE	14	4	12	22	19	22					1	34	13	9	66	83	102		2		403	+	+	+
DIOSACCINAE	9	33	24	74	109	59	10	17	31	4	15	25	11	28	12	14	17	212	15	48	767	+	+	+
Ectinosomatidae	14	41	43	78	84	121	8	8	65	16	6	63	24	87	169	157	365	207	56	26	1638	+	+	+
PARANANNOPINAE	1	10	12	23	9	15			12	11		6	2	3	8	18	30	1	1		162	+	+	+
Thalestridae		1	4			17	1		15	2		2	2	1	13	7		48	5		118	+	+	+
Tisbidae	1			9	27	4			15	12	25	12	5	7	4	10	4	14		6	155	+	+	+
(remaining specimens	8									12		14	15		12	12	23	24	3	2	125)			
Cerviniidae		3		4	6	2			6		11			43							75	+	+	
Normanellidae				5	11	12						2	5								35	+	+	
Huntemanniidae		1								3											4	+	+	
Cristacoxidae							1											1			2	+		+
Leptastacidae							47	20										19			86	+		+
PARAMESOCHRIDAE		1		2			16	10	1									337		29	396	+		+
Laophontidae												1					1	59	1		62		+	+
Tetragonicipitidae															5	2	24	1			32		+	+
Harpacticidae							1														1	+		
Adenopleurellidae	1			2		5			1												9	+		
Leptopontiinae																		36			36			+
Neobradyidae																			1		1			+
Peltidiidae																		1	1	1	3			+
Superornatiremidae																		29	1		30			+
Tegastidae																		5			5			+
Sum	63	117	102	236	305	295	103	67	195	64	98	179	85	236	381	411	734	1565	120	137	5493			

exclusive family (Table 2). It shares common taxa with at least one of the remaining areas, which indicates its possible role as a transitional area, connecting the northern and eastern Magellan region.

Six families can be considered as generally dominating the harpacticoid community in the study area: Ameiridae, Cletodidae, Diosaccinae, Ectinosomatidae, Paranannopinae and Paramesochridae. However, each geographic area shows at least minor differences in taxa composition, illustrated in Figure 2. Dominating taxa in the SM are Ectinosomatidae (31.4%) and Diosaccinae (24.8%), followed by three families exceeding 5% of relative abundance. Together, the five dominating taxa exceed 77% of the relative abundance, whereas the remaining 13 families collected in this area reach almost 23%. BC shows different dominance patterns. Although this area is also clearly dominated by Ectinosomatidae (42.2%), Diosaccinae (6.0%) play a secondary role only, while Cletodidae (14.7%) and Ameiridae (14.5%) show a higher relative abundance. Moreover, 11 additional families were recorded from this area, reaching 23% of relative abundance. PCS differs from both geographic areas in having Ameiridae (31.4%) as the dominating taxon, followed by a more interstitial group, the Paramesochridae (20.4%). Ectinosomatidae play only a minor role, not reaching 17%.

Distribution of genera

The Harpacticoida dealt with are distributed over 52 genera (Table 3). Compared with the results at family level, the number of taxa showing a distribution within the whole investigation area

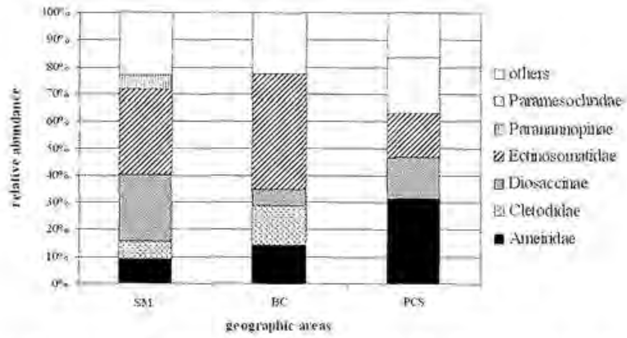

FIG. 2. – Harpacticoid composition of SM, BC and PCS. The relative abundance (%) of the dominating taxa Ameiridae, Cletodidae, Diosaccinae, Ectinosomatidae, Paranannopinae, and Paramesochridae is presented. The remaining families collected at SM (13), BC (11) and PCS (19) are summarised as "others".

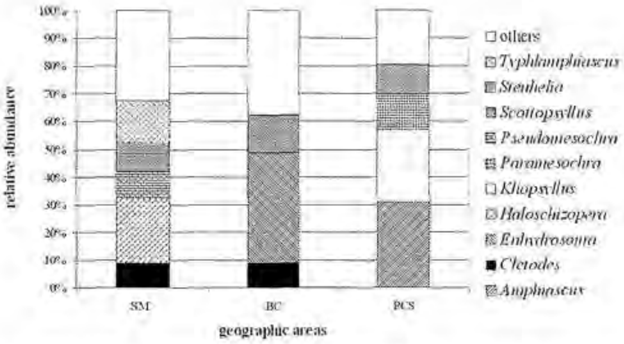

FIG. 3. – Harpacticoid composition of the SM, BC and PCS. The relative abundance (%) of the dominating taxa *Amphiascus*, *Cletodes*, *Enhydrosoma*, *Haloschizopera*, *Kliopsyllus*, *Paramesochra*, *Pseudomesochra*, *Scottopsyllus*, *Stenhelia*, and *Typhlamphiascus* is presented. The remaining genera collected at SM (31), BC (28) and PCS (23) are summarised as "others".

decreases. Only 9 genera (17%) were collected at SM, BC, and PCS. The number of taxa shared by SM and BC is 15 (28.8%), which is almost twice the common genera between SM and PCS (7 taxa = 13.5%). PCS and BC show no genus in common (Table 3). However, in contrast to the results at family level, each geographical area can be characterised by a certain number of exclusive genera. SM encloses 5, BC 7, and PCS 9 taxa. As shown in Figure 3, only a few genera seem to dominate each geographic area.

The differences between the areas increase remarkably at this taxonomic level. Whereas SM and BC shows at least two abundant genera (*Cletodes* and *Stenhelia*), PCS shows quite a different taxa composition. Between SM and BC there are also noteworthy differences. BC is characterised by a relatively high portion of genera (~38%) not reaching 5% of relative abundance, versus three dominant genera, with *Enhydrosoma* (39.7%) as the most abundant one. On the other hand, SM seems to present a generally higher variety, comprising five dominant genera (with *Haloschizopera* (23.4%) showing highest values) versus 31 taxa with a relative abundance below 5%. Finally, PCS is clearly dominated by *Amphiascus*, *Kliopsyllus*, *Parame-*

TABLE 3. – List of harpacticoid genera and their distribution within the Magellan region.

No.	Genus/area	SM	BC	PCS	No.	Genus/area	SM	BC	PCS
1	*Fultonia*	+	+	+	**25**	*Laophontodes*	+		+
2	*Cletodes*	+	+	+	**26**	Diosaccinae sp. 1	+		+
3	*Amphiascus*	+	+	+	**27**	*Paramphiascella*	+		+
4	*Bulbamphiascus*	+	+	+	**28**	*Kliopsyllus*	+		+
5	*Haloschizopera*	+	+	+	**29**	*Leptopsyllus*	+		+
6	*Robertgurneya*	+	+	+	**30**	*Paramesochra*	+		+
7	*Stenhelia*	+	+	+	**31**	*Scottopsyllus*	+		+
8	*Typhlamphiascus*	+	+	+	**32**	*Dendropsyllus*	+		
9	*Paradanielssenia*	+	+	+	**33**	Argestidae sp. 8	+		
10	Argestidae sp. 1	+	+		**34**	Diosaccinae sp. 2	+		
11	Argestidae sp. 2	+	+		**35**	Diosaccinae sp. 6	+		
12	Argestidae sp. 3	+	+		**36**	Paranannopinae sp. 1	+		
13	*Eurycletodes (O.)*	+	+		**37**	*Arthropsyllus*		+	
14	*Mesocletodes*	+	+		**38**	Argestidae sp. 4		+	
15	*Acrenhydrosoma*	+	+		**39**	Argestidae sp. 5		+	
16	*Enhydrosoma*	+	+		**40**	Argestidae sp. 6		+	
17	*Stylicletodes*	+	+		**41**	Diosaccinae sp. 4		+	
18	*Amphiascoides*	+	+		**42**	Diosaccinae sp. 5		+	
19	Diosaccinae sp. 3	+	+		**43**	Paranannopinae sp. 2		+	
20	*Carolinicola*	+	+		**44**	Argestidae sp. 7			+
21	*Jonesiella*	+	+		**45**	Diosaccinae sp. 7			+
22	*Paranannopus*	+	+		**46**	Diosaccinae sp. 8			+
23	*Psammis*	+	+		**47**	*Schizopera*			+
24	*Pseudomesochra*	+	+		**48**	Paramesochridae sp. 1			+
					49	Paramesochridae sp. 2			+
					50	Paranannopinae sp. 3			+
					51	*Diarthrodella*			+
					52	*Rossopsyllus*			+

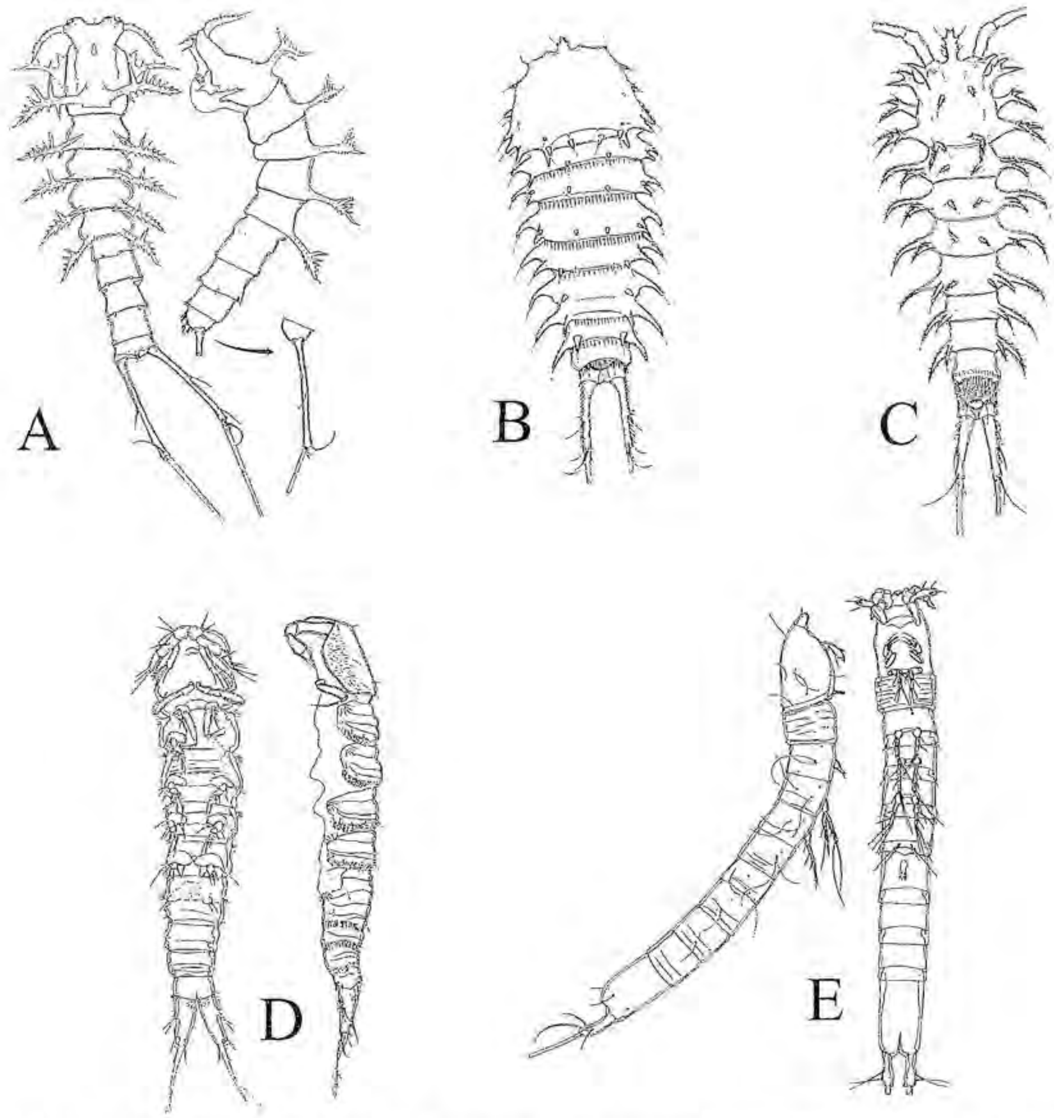

FIG. 4. – Some Harpacticoida of the Magellan region. A. *Dendropsyllus magellanicus* (Ancorabolidae Sars, 1909), B. *Breviconia australis* (Ancorabolidae), C. *Ancorabolus ilvae* (Ancorabolidae), D. *Laophontisochra maryamae* (Cristacoxidae Huys, 1990), E. *Isthmiocaris longitelson* (Canthocamptidae Sars, 1906). A after George and Schminke 1998, B after George 1998, C after George 2001, D after George 2002, E after George and Schminke 2003.

sochra and *Scottopsyllus*, the latter three confirming the general dominance of Paramesochridae in this area. The four mentioned taxa face a number of 23 remaining genera not reaching 20% of relative abundance.

Composition and diversity of harpacticoid species

Due to the high abundance, further analysis at species level was done on the representatives (= 1,916 adult specimens) of 6 selected taxa (Ancorabolidae Sars, 1909, Argestidae Por, 1986, Cletodidae sensu Por, 1986, Diosaccinae Sars, 1906, Paramesochridae Lang, 1944, Paranannopinae Por, 1986) (Table 2). They can be assigned to 122 different species, 103 of which (= 84.4%) must be considered as new to science (see Table 4 for species list). Recently, a few new species have been described (George, 1998; 2001; 2002; George and Schminke, 1998; 2003) (Fig. 4).

Specific composition indicates both similarities and differences between the geographic areas. A total number of six species (*Cletodes* sp. 2, *Stylicletodes longicautdatus* (Brady and Robertson, 1880), *Amphiascus* sp. 1, *Haloschizopera exigua* (Sars, 1906), *Stenhelia (D.)* sp. 2, *Typhlamphiascus* sp.) was recorded in the whole investigation area, again meaning a decrease of common taxa compared with the results at family and genus level. In addition,

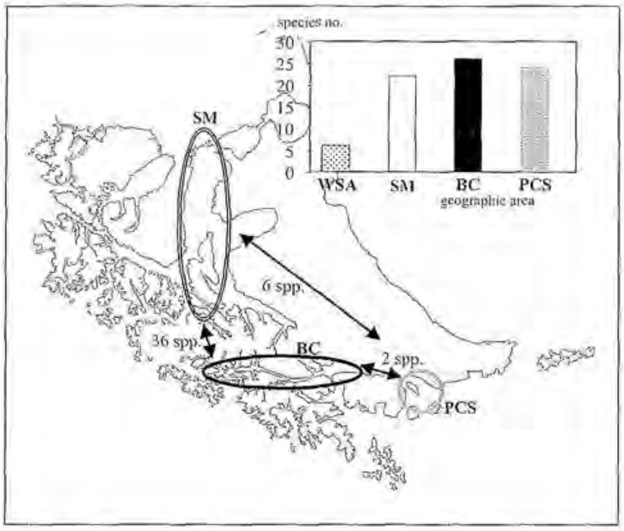

FIG. 5. – Numbers of harpacticoid species in common between the respective geographic areas (arrows with corresponding species (spp.) numbers). The graphic illustration shows the numbers of exclusive harpacticoid species reported from the respective geographical areas: WSA = Whole Study Area, SM = Straits of Magellan, BC = Beagle Channel, PCS = Patagonian Continental Slope.

each geographical area shares some species with one of the remaining areas (Fig. 5). SM and BC show a relatively high number of species in common, whereas adjacent BC and PCS share only few species, falling even below the value shown by distant SM/PCS.

Apart from similarities between the geographical areas due to common species, all of them can be characterised by several exclusive species (Fig. 5), thus confirming the distinction between the areas already indicated at family and genus level. To underline the results obtained, quantitative similarity and diversity analyses were done.

Similarity analysis

The ordination plot (Fig. 6A) (cf. Fig. 6B for Shepard diagram) indicates a general mixing of the stations, independent of their geographical location. Most of the SM, BC, and PCS stations form a big group on the right side of the plot. Only two small distinct groups are discernible, one formed by 2 stations of the SM and one enclosing 3 BC stations (dotted circles in Fig. 6). Both groups match the geographic locality of the corresponding stations. The SM group is located in the northern Paso Ancho and encloses stations 954 and 956. Both stations are unique in presenting the species Diosaccinae sp. 2 (Table 4). Moreover, they differ from all remaining SM stations in the presence of *Paramesochra* sp. 1, a species collected also from station 40/110 (PCS).

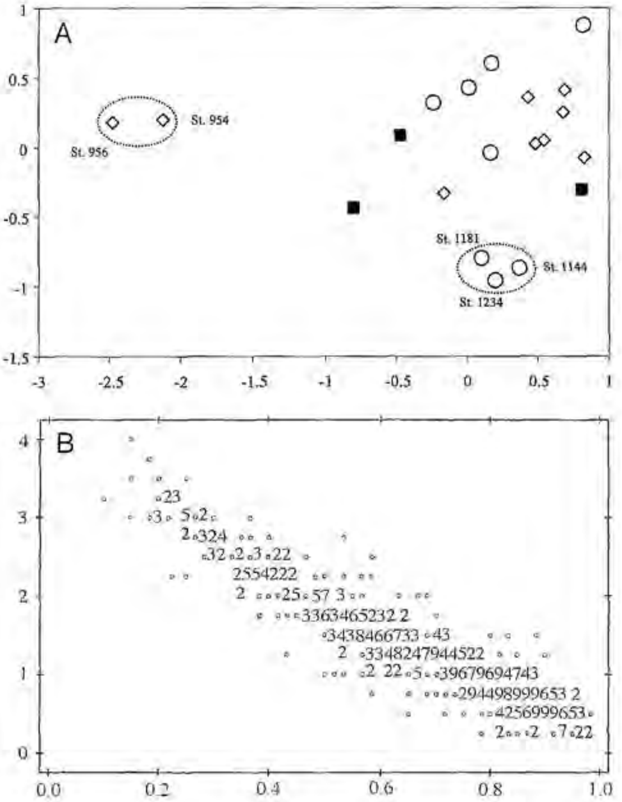

FIG. 6. – A, Ordination plot resulting from the similarity matrix using Cosine Similarity. Ordination is two-dimensional (monotonous, non-parametric regression, Stress 0,12). White rhomboid dots: SM stations, white circles: BC stations, black squares: PCS stations. B, Shepard diagram of the nMDS.

The BC group is located in the eastern BC, comprising stations 1144, 1181, and 1234. They share *Bulbamphiascus* sp. 2 (although single specimens were also collected at two SM stations) (Table 4) and *Paradanielssenia* sp. 1 (although in common

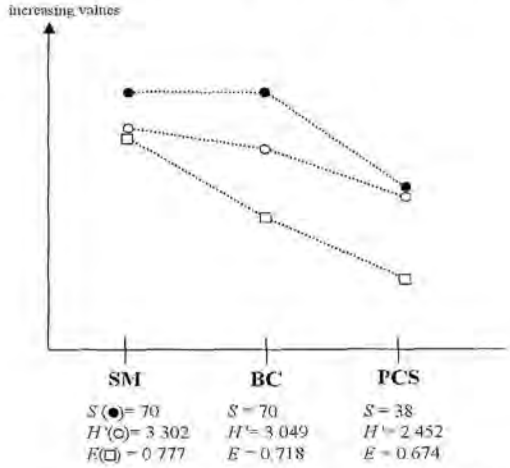

FIG. 7. – Illustration of the compared species numbers (*S*), species richness (*H'*), and evenness (*E*) values at the three investigated geographic areas Straits of Magellan (SM), Beagle Channel (BC), and Patagonian Continental Slope (PCS).

TABLE 4. – List of harpacticoid species collected in the Magellan region (individual numbers at corresponding stations).

No.	species\station	SM									BC								PCS			Sum
		840	847	864	866	872	877	954	956	977	1033	1076	1123	1135	1138	1144	1181	1234	40110	40111	40116	
1	*Arthropsyllus australis*																	1				1
2	*Dendropsyllus magellanicus*		1																			1
3	*Laophontodes* sp.1		1				8															9
4	*Laophontodes typicus*																		29			29
5	*Laophontodes whitsoni*																		1			1
6	Argestidae sp.1	1	1		1										1							4
7	Argestidae sp.2				1	1				2					6		5					15
8	Argestidae sp.3					2				7					1							10
9	Argestidae sp.4											5										5
10	Argestidae sp.5														3							3
11	Argestidae sp.6											1			1							2
12	Argestidae sp.7																				2	2
13	Argestidae sp.8			1																		1
14	*Eurycletodes (O.) abyssi*																	5				5
15	*Eurycletodes (O.) monardi*												4									4
16	*Eurycletodes (O.) oblongus*		1				2						4									7
17	*Eurycletodes (O.)* sp.1	1			1	1				9					3	1	3					18
18	*Eurycletodes (O.)* sp.2												1									1
19	*Eurycletodes (O.)* sp.3					2							3	1								6
20	*Fultonia bougisi*												1						2			3
21	*Fultonia sarsi*						1						1									2
22	*Fultonia* sp.1	1																				1
23	*Fultonia* sp.2	1													2							3
24	*Fultonia* sp.3				2					4					9							15
25	*Fultonia* sp.4										3											3
26	*Fultonia* sp.5											2										2
27	*Mesocletodes abyssicola*				1	1				4												6
28	*Mesocletodes soyeri*												1	1								2
29	*Mesocletodes* sp.1											10		1	3							14
30	*Mesocletodes* sp.2					1				2		1		1	7							12
31	*Acrenhydrosoma* sp.1			3	1									1	1			2				8
32	*Cletodes latirostris*				2	10	1															13
33	*Cletodes* sp.1	5	1	2	8		6						2									24
34	*Cletodes* sp.2	5		1	3	3	8					1	10	1			21	4		1		58
35	*Cletodes* sp.3						1															1
36	*Cletodes* sp.4						1							3	6							10
37	*Cletodes* sp.5												4									4
38	*Cletodes* sp.6												2									2
39	*Cletodes* sp.7													1								1
40	*Enhydrosoma hopkinsi*				4													2				6
41	*Enhydrosoma littorale*																	1				1
42	*Enhydrosoma* sp.1	1	1										1	5								8
43	*Enhydrosoma* sp.2			3		3	1															7
44	*Enhydrosoma* sp.3												2					2				4
45	*Enhydrosoma* sp.4					1							5	1		1						8
46	*Enhydrosoma* sp.5			3	3									1	1		2	4				14
47	*Enhydrosoma* sp.6															65	59	84				208
48	*Enhydrosoma* sp.7																1	3				4
49	*Stylicletodes longicaudatus*	3	1			1	3						7		1					1		17
50	*Stylicletodes oligochaeta*		1		1	1	1						1									5
51	Diosaccinae sp.1		1																1			2
52	Diosaccinae sp.2							9	17													26
53	Diosaccinae sp.3	4					3						1									8
54	Diosaccinae sp.4												1									1
55	Diosaccinae sp.5												1									1
56	Diosaccinae sp.6				4																	4
57	Diosaccinae sp.7																		1			1
58	Diosaccinae sp.8																		1			1
59	*Amphiascoides subdebilis*	1																		1		2
60	*Amphiascoides* sp.1														1							1
61	*Amphiascus minutus*																		4		1	5
62	*Amphiascus* sp.1	1										1	1			1			192		13	209
63	*Bulbamphiascus* sp.1							1												4		5
64	*Bulbamphiascus* sp.2			1		1										1	13	2				18
65	*Haloschizopera abyssi*			7	27	20																54
66	*Haloschizopera exigua*		18	1	33	20	21			1			6		1	4		2			22	129
67	*Haloschizopera* sp.1																				10	10
68	*Paramphiascella* sp.1					5	1												5			11
69	*Paramphiascella* sp.2					3																3
70	*Robertgurneya* sp.1	3																1				4
71	*Robertgurneya* sp.2																		3			3

TABLE 4 (Cont.). – List of harpacticoid species collected in the Magellan region (individual numbers at corresponding stations).

No.	species\station	SM									BC								PCS			
		840	847	864	866	872	877	954	956	977	1033	1076	1123	1135	1138	1144	1181	1234	40110	40111	40116	Sum
72	*Schizopera* sp.1																		5	1		6
73	*Stenhelia (D.)* sp.1		2													1						3
74	*Stenhelia (D.)* sp.2		7	3	1	3	2			2		14	13		6	3				2		56
75	*Stenhelia (D.)* sp.3			1	4	8	3			4					2							22
76	*Stenhelia (D.)* sp.4						2							1	2							5
77	*Stenhelia (D.)* sp.5						1															1
78	*Stenhelia (D.)* sp.6			5		6				2				4	14							31
79	*Stenhelia (D.)* sp.7													3	2							5
80	*Stenhelia (D.)* sp.8			2			1															3
81	*Stenhelia (D.)* sp.9				5									1			1	12				19
82	*Stenhelia (D.)* sp.10																			1		1
83	*Stenhelia (D.)* sp.11																			4		4
84	*Stenhelia (D.)* sp.12																			2		2
85	*Stenhelia (St.)* sp.1															1						1
86	*Typhlamphiascus* sp.		3	4		43	25			22	4		2	2							2	107
87	Paramesochridae sp.1																		15			15
88	Paramesochridae sp.2																		1			1
89	*Diarthrodella* sp.																		2			2
90	*Kliopsyllus* sp.1		1																15		1	17
91	*Kliopsyllus* sp.2							1														1
92	*Kliopsyllus* sp.3																		37		13	50
93	*Kliopsyllus* sp.4																		95			95
94	*Kliopsyllus* sp.5				2																	2
95	*Kliopsyllus* sp.6																				6	6
96	*Kliopsyllus* sp.7																		2		9	11
97	*Leptopsyllus* sp.1							7														7
98	*Leptopsyllus* sp.2																		9			9
99	*Paramesochra* sp.1							8	10										10			28
100	*Paramesochra* sp.2																		75			75
101	*Rossopsyllus* sp.																		3			3
102	*Scottopsyllus* sp.1																		73			73
103	*Scottopsyllus* sp.2									1												1
104	Paranannopidae sp.1				1																	1
105	Paranannopidae sp.2														1							1
106	Paranannopidae sp.3																		1			1
107	*Carolinicola* sp.1						1				2											3
108	*Carolinicola* sp.2										3											3
109	*Jonesiella* sp.	1					3			1					1		5	19				30
110	*Paradanielssenia* sp.1									1			1			4	7	9				22
111	*Paradanielssenia* sp.2										1									1		2
112	*Paranannopus* sp.1		6								5											11
113	*Paranannopus* sp.2		1																			1
114	*Paranannopus* sp.3		1											1								2
115	*Paranannopus* sp.4		1			1	2						1									5
116	*Psammis* sp.1				1									1		3		2				7
117	*Psammis* sp.2				1										1	2	6					10
118	*Pseudomesochra longifurcata*												2									2
119	*Pseudomesochra* sp.1		3		1		3						1									8
120	*Pseudomesochra* sp.2					3				1			1									5
121	*Pseudomesochra* sp.3			12	19	5	2			9												47
122	*Pseudomesochra* sp.4						4															4
	Sum	28	52	49	127	145	107	26	27	72	18	35	80	30	76	87	123	155	582	18	79	1916

with stations 977 and 1123), but in particular they are absolutely dominated by *Enhydrosoma* sp. 6. This species was collected in remarkably high individual numbers only from these three stations, reaching 84 specimens at station 1234 (Table 4).

Diversity analysis

SM and BC, both characterised by $S = 70$, may show the same species number, which is nearly twice the PCS value ($S = 38$). This trend is generally confirmed by Shannon's H' and Pielou's evenness E, which are considerably higher at SM and BC than at PCS (Fig. 7). The highest species richness was at SM, with higher H' and E values than at BC. To verify these results, a second diversity analysis was done, applying rarefaction to the three different areas. Comparison of the geographic areas revealed similar results to using diversity indices (Fig. 8A). SM and BC show a considerably higher species richness than PCS. However, in contrast with the results obtained from calculating the diversity

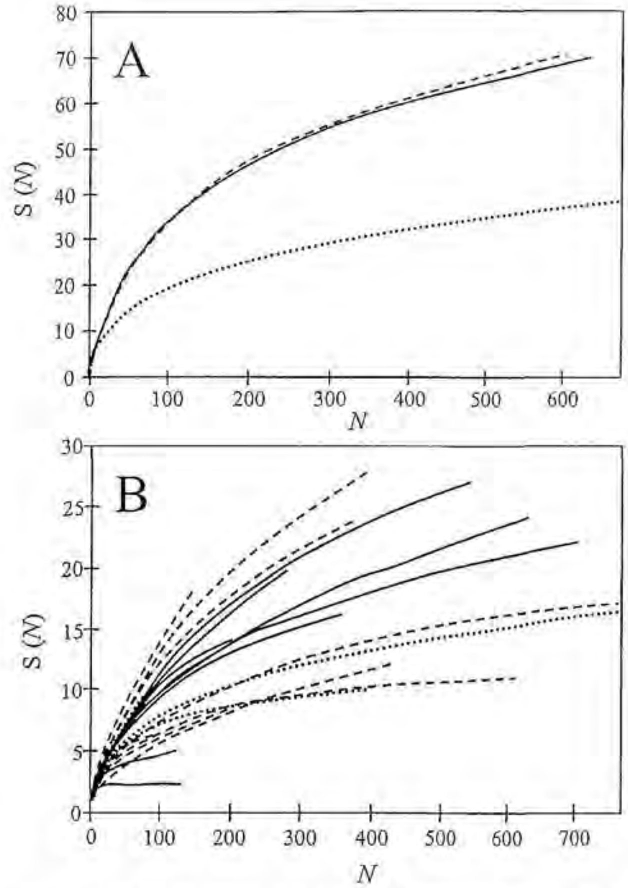

FIG. 8. – Rarefaction curves A. of the three geographic areas Straits of Magellan (SM; black line), Beagle Channel (BC; dark grey line), and Patagonian Continental Slope (PCS; light grey line). *S(N)* = number of estimated species, with *N* = individual numbers, B. of all single stations of the investigated region (SM=black lines, BC=dark grey lines, PCS=light grey lines). *S(N)* = number of estimated species, with *N* = individual numbers.

indices, rarefaction indicates a tendency of slightly higher species richness at BC than in SM. Due to this deviation, a second analysis was done, comparing all single stations. This analysis reveals a remarkable small-scale variability even between stations within the same geographic area (Fig. 8B), which may conceal probable large-scale influences.

DISCUSSION

The Magellan region is generally characterised by a high variability in topographic, sedimentological, hydrographical, oceanographic and climatological conditions (e.g. Brattstrøm and Johanssen, 1983; Artegiani *et al.*, 1991, Brambati *et al.*, 1991, Antezana *et al.*, 1996, Klöser, 1996). Therefore, the question arose whether the three geographically, topographically, and hydrographically distinct areas SM, BC and PCS might show differences also with respect to their inhabiting sublittoral and bathyal harpacticoid fauna. This question becomes particularly important for future comparisons with corresponding harpacticoid assemblages of Antarctica. Against the background of a supposed high affinity between the Antarctic and the South American (i.e. Magellan) fauna, it is of importance to know whether the Magellan region is characterised by geographically separated, clearly distinct faunas which may prohibit the consideration of the region as a whole for interregional faunistic comparisons, as has been done for macrofauna. The results obtained in this study indicate a remarkable variety of the Magellan region with respect to species composition and species diversity. Instead of being clearly distinct, the three studied areas show a considerable overlap of taxa composition and diversity, as shown by MDS and rarefaction. However, this overlap is due not to homogeneous but to heterogeneous distribution of taxa. This leads to the conclusion that for future comparisons with Antarctic harpacticoid associations, the MR should be considered as a whole.

The results presented here reveal an impressive harpacticoid diversity within the Magellan region. Wells (1986) presumed that at family level, Harpacticoida would show a world-wide distribution. For the Magellan region, his assumption was already confirmed by George and Schminke (1999), who presented a list of 19 families. However, it must be pointed out that the authors included Cerviniidae (George and Schminke, 1999, p. 135, Table 2), a taxon that was ignored in this contribution because it was represented exclusively by juveniles, which were not taken into account in the analyses.

The record of several specimens of Superornatiremidae Huys, 1996 was somewhat surprising. They are considered as being restricted to anchialine caves and showing an amphi-Atlantic/Mediterranean distribution (Huys, 1996). The specimens collected at station 40/110 (PCS) extend both the distribution and habitat preference considerably. All specimens belong to the same new species (George and Martínez Arbizu, in press).

In the past, several investigations concluded that for faunistic investigations it was sufficient to deal with taxa at higher taxonomic levels such as genera or even families (e.g. Hartmann, 1982; 1986; Heip *et al.*, 1988; Ray, 1992; Lambshead, 1993). The results of the qualitative comparison of the geographic areas SM, BC and PCS contradict this assumption. For example, families and genera show a much wider distribution than the species they enclose, clearly demonstrating the fact that families and even genera are united groups of different species with quite different ecological claims. Whereas a family (e.g. Ancorabolidae) may be distributed within the whole Magellan region, the corresponding species (e.g. *Breviconia*, *Dendropsyllus*) may be restricted to small areas. Therefore, although community analyses at higher taxonomic level may allow more taxa to be considered (here: all Harpacticoida), they undoubtedly generalise and bias real distribution patterns or community structure instead of describing almost real patterns. At family level, the geographical areas SM, BC and PCS show a relatively high degree of similarity (~40%), which decreases at generic level (~17%) and reaches at most ~5% at species level. Therefore, it is advisable to select the species level for community analyses, even if this inolves a restriction of the taxa dealt with.

The remarkably high number of 122 species reported from the six investigated harpacticoid families confirms the conclusion of Wells (1986) that the apparent poverty in species of the southern hemisphere reflects a lack of investigations rather than real species numbers. The report of 103 scientifically new species from the Magellan region means an increase of nearly 30% for the whole Southern Hemisphere compared with Wells' (1986) data. This points to the urgent need for further investigations in this region.

The qualitative comparisons allow three areas to be distinguished, each of which is characterised by exclusively collected species. It is surprising that BC and PCS show such little similarity in both species composition and species diversity. One would expect these areas especially to be more similar, due to a supposed continuous organism input into PCS from BC caused by predominating eastward currents. However, apart from some taxa showing a distribution in the whole study area, BC and PCS have no taxa in common, even at generic level. Still, as shown by quantitative analysis, a characterisation based only on presence and absence of species would be too superficial. Firstly, it is obvious that the non-registration of a species in an area may be an artefact of sampling; it does not necessarily reflect the distribution of the species. Secondly, the species composition of each area is quite complex, leading to similarities and differences between them. This complexity may already be indicated by the qualitative analysis, which apart from differences also revealed certain similarities between areas, due to species in common. The MDS approaches the actual conditions best. Just two small areas, one in the northern SM and one in the eastern BC, seem to be characterised by specific harpacticoid assemblages. The remaining study area shows a remarkable variety, with neither clear differences nor great similarities between the geographical areas SM, BC and PCS. On the other hand, stations of different areas often show greater similarity than stations of the same area. The same applies to the results of the diversity analysis. The results of rarefaction are favoured here because of its better "response" to smaller samples, paired with several general disadvantages of diversity indices (Hurlbert 1971, Achtziger *et al.* 1992). However, both methods applied to the geographical areas show that SM and BC have nearly the same species richness. The difference between the results of calculating H' and E, which estimated SM to be richer than BC, and rarefaction, which shows the opposite, may be neglected because of the relatively small database on which they are based. However, the results presented in Fig. 8B show clearly that, as in the similarity analysis, the study area also shows a considerable variety with respect to species richness, thus making it impossible to distinguish the three geographical areas SM, BC and PCS. In summary, it is concluded that both similarity and diversity analysis point towards a considerable influence of small-scale biotic and abiotic variables, leading to a high local variability in harpacticoid communities of the Magellan region.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
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The shallow-water Asellota (Crustacea: Isopoda) from the Beagle Channel: Preliminary taxonomic and zoogeographical results*

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SUMMARY: The shallow-water Asellota from the Beagle Channel were investigated, based on material collected at four localities in 2001-2002. A total of 3,124 asellotes were sorted, and three new species and 12 new records of distribution were reported. The Paramunnidae showed the highest species diversity and abundance (11 species and 1,463 specimens). The present research raises the number of species known from the Beagle Channel to 23; of these, 16 were previously reported from the Magellan Straits, representing 69% of similarity. Based on the present results and published data, the faunistic affinities for the shallow-water Asellota was 30% between the Magellan region and the Scotia Arc, and 26% between the Magellan region and the Antarctic Peninsula.

Keywords: Asellota, Isopoda, diversity, Beagle Channel, Magellan region.

RESUMEN: ASELLOTA (CRUSTACEA: ISOPODA) DE AGUAS SOMERAS DEL CANAL BEAGLE: PRIMEROS RESULTADOS TAXONÓMICOS Y BIOGEOGRÁFICOS. – Se estudiaron los isópodos Asellota colectados en cuatro localidades de aguas poco profundas del Canal Beagle en el 2001 y 2002. Se obtuvo un total de 3.124 ejemplares, se identificaron 3 especies inéditas y se dieron a conocer 12 registros nuevos de distribución. Paramunnidae fue la familia con mayor diversidad específica y abundancia (11 especies y 1.463 individuos). En el presente trabajo se elevó a 23 el número de especies conocidas para el Canal Beagle, 16 de las cuales son también conocidas del Estrecho de Magallanes (69% de similitud). A partir de los resultados del presente trabajo y datos bibliográficos, las afinidades faunísticas para los Asellota de aguas poco profundas fueron de 30% entre la región magallánica y el Arco de Scotia; y de 26% entre la región magallánica y la Península Antártica.

Palabras clave: Asellota, Isopoda, diversidad, Canal Beagle, región magallánica.

INTRODUCTION

The Beagle Channel is a narrow, elongated sound located at the southern tip of South America. Brandt *et al.* (1997) stated that this channel is one of the key areas for taxonomic, ecological and biogeographic research, and they suggested that it should be investigated faunistically in more detail.

Many isopod Asellota have been reported from the Magellan region, mainly by Nordenstam (1933), Menzies (1962), Winkler and Brandt (1993) and Winkler (1994a). Despite this, only seven species are known from the Beagle Channel up to now (Monod, 1926; Nordenstam, 1933; Brandt, 1999).

The aims of this study are to describe the taxonomic composition and abundance of the shallow-water Asellota from the Beagle Channel, and to ana-

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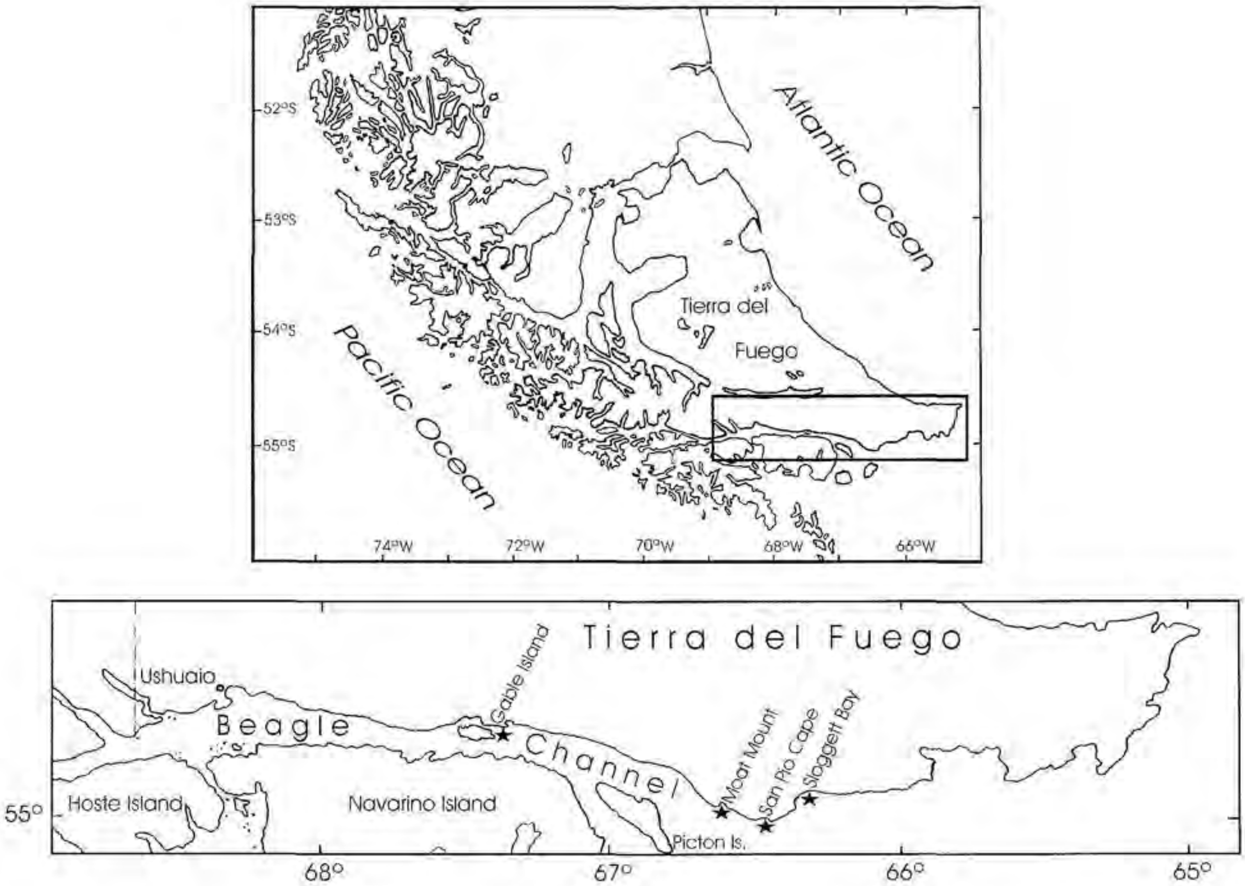

FIG. 1. – Locations of the sampling stations in the Beagle Channel.

lyze the faunistic affinities between this channel and the surrounding areas.

MATERIAL AND METHODS

The specimens studied were collected at four shallow-water localities, one in the Beagle Channel and the other three in front of its eastern mouth (Fig. 1, Table 1). For the sake of simplicity, all these localities are regarded as belonging to the Beagle Channel. Samples were dredged from the Argentine navy vessel "Alférez Sobral" at 15-35 m depth in February and May 2001 and September 2002. A 45 x 50 cm trawl fitted with a net of 2 mm mesh size was used. The material collected was fixed in 10% buffered formaldehyde solution and transferred to 70% ethanol. The Asellota were picked from the bulk samples and identified to species (or genus) level.

In this contribution the Magellan region has been defined as the Patagonian shelf south of 41°S on both the Pacific and Atlantic coasts (including the Malvinas/Falkland Islands); the Scotia Arc comprises the South Georgia, South Sandwich and South Orkney Islands; and the Antarctic Peninsula includes the South Shetland Islands.

The biogeographic analysis deals with the Asellota whose vertical distribution is restricted to depths < 200 m and those which were found at greater depths but also at < 200 m. In order to facilitate comparisons between areas, a list of all the Asellota collected in shallow waters from the Magellan region (including our data from the Beagle Channel), the Scotia Arc and the Antarctic Peninsula is provided (Table 3). Papers which were consulted to prepare this list are mentioned in Winkler (1994b). Other papers utilised include the following:

TABLE 1. – Localities sampled in the Beagle Channel.

Locality	Latitude	Longitude	Depth (m)	Date
Gable Island	54°54.0'S	67°21.0'W	15-20	11 May 2001
Moat Mount	55°01.5'S	66°41.7'W	15-25	09 Feb 2001
San Pio Cape	55°03.0'S	66°37.0'W	30-35	29 Sep 2002
Sloggett Bay	55°00.0'S	66°20.6'W	15-30	09 Feb 2001

Kussakin (1965), Richardson and Hedgpeth (1977), Branch *et al.* (1991), Teodorczyk and Wägele (1994), Wilson and Wägele (1994), Serov and Wilson (1995), Mariani *et al.* (1996), Lorenti and Mariani (1997), Brandt (1999), Castelló (1999, 2004), Cariceo *et al.* (2002), Lörz and Brandt (2003), and Just and Wilson (2004). For the faunistic analysis, the localities marked with one or two asterisks and the specimens identified as "*Paramunna* cf. *menziesi*", "*Sporonana* sp.", "*Austrofilius* sp. A", "*Ianiropsis* sp. A", "*Caecianiropsis* cf. *ectiformis*", "*Joeropsis* sp. A", "*Munna* sp." and "*Munna* spec." in Table 3 were excluded. Junior synonyms in Table 3 are mentioned only when these names were used for specimens collected in the Magellan/Antarctic/Subantarctic areas. Affinities between areas were estimated using Simpson's Coefficient of Similarity (C/N_1 x 100), where C = number of shared species and N_1 = total number of species reported from the smaller of the two groups being compared (see Cheetham and Hazel, 1969). The term "diversity" refers to the total number of species, and the term "abundance" to the total number of specimens.

RESULTS

Species composition and abundance in the Beagle Channel

A total of 3,967 isopods were sorted, the Asellota being the dominant group (3,124 specimens), followed by the Sphaeromatidae (790 specimens), Rectarcturidae (17 specimens), Gnathiidae (15 specimens), Serolidae (14 specimens), Idoteidae (6 specimens) and Aegidae (1 specimen).

Among the Asellota, 25 species belonging to six families were identified (Table 2). Three of these species are new to science and 12 are new records for the Beagle Channel. All these new records belong to species formerly found in the Magellan Strait or other localities of the Magellan region (Table 3).

Of the three new species reported herein, two belong to the genus *Austrosignum* and one to the genus *Paramunna*. Since the *Austrosignum*/*Munnogonium* complex is under revision (Jean Just and George D.F. Wilson, pers. comms.), the inclusion of the new species identified as "*Austrosignum* n. sp.

TABLE 2. – Number of Asellota isopods collected in the Beagle Channel during this study. (*) First record for the area.

	Gable Island	Moat Mount	San Pío Cape	Sloggett Bay
Paramunnidae				
Allorostrata ovalis Winkler, 1994 *			6	6
Antennulosignum elegans Nordenstam, 1933 *	4			
Austrosignum n. sp. 1 (unpublished)		3	30	401
Austrosignum n. sp. 2 (unpublished)				188
(?) *Paramunna dentata* Nordenstam, 1933 * (1)		2		11
Paramunna integra Nordenstam, 1933 *	5		41	216
(?) *Paramunna kerguelensis* Vanhöffen, 1914 * (1)		1		
(?) *Paramunna menziesi* Winkler, 1994 * (1)			2	7
(?) *Paramunna* cf. *menziesi* (1)			69	178
Paramunna n. sp. (unpublished)			15	
Pleurosignum magnum Vanhöffen, 1914 *			11	
Sporonana sp. A	171	3	92	1
Janiridae				
Austrofilius furcatus Hodgson, 1910	101		8	
Austrofilius sp. A		8		
Caecianiropsis cf. *ectiformis* (Vanhöffen, 1914)	3	1	1	1
Ianiropsis varians Winkler and Brandt, 1993 *	1	95		60
Ianiropsis sp. A		5		
Iathrippa menziesi Sivertsen and Holthuis, 1980 (= *I. chilensis* Menzies, 1962) *	1	33	14	2
Neojaera antarctica (Pfeffer, 1887)	41	10	127	10
Joeropsidae				
Joeropsis curvicornis (Nicolet, 1849) (= *J. patagoniensis* Richardson, 1909)	160	45	55	38
Joeropsis intermedius Nordenstam, 1933	192	18	187	17
Joeropsis sp. A	124		12	4
Munnidae				
Munna gallardoi Winkler, 1992 *			10	
Munna sp.	11	1	233	1
Santiidae				
Santia compacta Sivertsen and Holthuis, 1980 *		3	1	1
Acanthaspidiidae				
Ianthopsis laevis Menzies, 1962 *		1	25	

(1) not in *Paramunna* after Just and Wilson (2004).

TABLE 3. – Asellota collected in the Magellan region, the Scotia Arc and the Antarctic Peninsula at depths < 200 m. The species shared between the Beagle Channel and the Magellan Strait are in **bold**. Depths refer to the entire bathymetrical range of the species. BC, Beagle Channel; MS, Magellan Strait; OL, other localities.

	Magellan Region			Scotia Arc	Antarctic Peninsula	Depths (m)
	BC	MS	OL			
PARAMUNNIDAE						
Austrosignum n. sp. 1 (unpublished)	+					15-35
Austrosignum n. sp. 2 (unpublished)	+					15-30
Paramunna n. sp. (unpublished)	+					30-35
(?) *Paramunna* cf. *menziesi* (1)	+					15-35
Allorostrata ovalis Winkler, 1994	+	+				12-35
Paramunna integra sensu Winkler, 1994 (2)	+	+				10-70
(?) *Paramunna kerguelensis* Vanhöffen, 1914 (1)	+	+				0-25
(?) *Paramunna menziesi* Winkler, 1994 (1)	+	+	+			9-35
Pleurosignum chilense Menzies, 1962	+	+	+			0-50
Antennulosignum elegans Nordenstam, 1933	+		+			15-22
(?) *Paramunna dentata* Nordenstam, 1933 (1)	+		+			15-30
Sporonana sp. (3)	+	+		+		0-35
Pleurosignum magnum Vanhöffen, 1914	+		+		+	22-385
Allorostrata scutifrons Just and Wilson, 2004		+				9
Austrosignum dentatum Winkler, 1994		+				12
Austrosignum globifrons Menzies, 1962		+				intertidal
Magellianira serrata Winkler, 1994		+				10
Omonana brachycephala Just and Wilson, 2004		+				9
Omonana parasimplex (Winkler, 1994)		+				9
(?) *Paramunna magellanensis* Winkler, 1994 (1)		+				9-12
(?) *Paramunna patagoniensis* Winkler, 1994 (1)		+				12-21
Munnogonium tillerae (Menzies and Barnard, 1959)		+			+	10-361
Austrosignum falklandikum Nordenstam, 1933			+			22-150
Austrosignum latifrons Menzies, 1962			+			100
Omonana simplex (Menzies, 1962)			+			100
Paramunna integra Nordenstam, 1933			+			40-157
Austrosignum grande Hodgson, 1910 (= *A. glaciale* Hodgson, 1910)			+	+	+	0-743
Pleurosignum elongatum Vanhöffen, 1914			+		*	25-385
Palanana serrata (Richardson, 1908)			?		+	0-55
Paramunna rostrata complex (4)				+	+	6-107
(?) *Paramunna lunata* Hale, 1937 (1)				+	+	3-32
Coulmannia australis Hodgson, 1902				*	+	89-400
Austrimunna antarctica Richardson, 1906				+	+	12-107
Austrosignum escanellae Castelló, 2004					+	45
Austrosignum incisum (Richardson, 1908)					+	0-15
Austrosignum spinosum Kussakin, 1982					+	17
Coulmannia ramosae Castelló, 2004					+	124
Harrietonana subtriangulata (Richardson, 1908)					+	25
Palanana gaini (Richardson, 1913)					+	1-6
(?) *Paramunna gaussi* Vanhöffen, 1914 (1)					+	45-385
JANIRIDAE						
Austrofilius sp. A	+					15-25
Ianiropsis sp. A	+					15-25
Caecianiropsis cf. *ectiformis* (Vanhöffen, 1914)	+					15-35
Ianiropsis varians Winkler and Brandt, 1993	+	+				9-32
Iathrippa menziesi Sivertsen and Holthuis, 1980 (= *I. chilensis* Menzies, 1962)	+	+	+			5-300
Iathrippa longicauda (Chilton, 1884)	+	+	+	*		12-500
Iais pubescens (Dana, 1852) (= *I. hargeri* Bovallius, 1886)	+	+	+	+		0-5
Neojaera antarctica (Pfeffer, 1887)	+	+	+	+	+	1-700
Austrofilius furcatus Hodgson, 1910	+	+	+	+	+	0-190
Iathrippa multidens Menzies, 1962		+				intertidal
Ianiropsis chilensis Menzies, 1962		+	+			0-40
Ianiropsis perplexus Menzies, 1962			+			intertidal
Iathrippa sarsii (Pfeffer, 1887) (= *Notasellus australis* Hodgson, 1902)			*	+	+	0-700
Iathrippa trilobatus (Richardson, 1910)			+	+	*	13-410
Ectias turqueti Richardson, 1906				+	+	6-126
Austrofilius serratus Vanhöffen, 1914					**	170-385
JOEROPSIDAE						
Joeropsis sp. A	+					15-35
Joeropsis curvicornis (Nicolet, 1849) (= *J. patagoniensis* Richardson, 1909)	+	+	+			0-641
Joeropsis intermedius Nordenstam, 1933	+	+	+		**	3-641
Joeropsis bidens Menzies, 1962			+			0-300
Joeropsis antarctica Menzies and Schultz, 1968					+	45-1408

TABLE 3 (Cont.). – Asellota collected in the Magellan region, the Scotia Arc and the Antarctic Peninsula at depths < 200 m. The species shared between the Beagle Channel and the Magellan Strait are in **bold**. Depths refer to the entire bathymetrical range of the species. BC, Beagle Channel; MS, Magellan Strait; OL, other localities.

	Magellan Region			Scotia Arc	Antarctic Peninsula	Depths (m)
	BC	MS	OL			
MUNNIDAE						
Munna sp.	+					15-35
Munna gallardoi **Winkler, 1992**	+	+				9-41
Munna longipoda Teodorczyk and Wägele, 1994	+		+		+	15-285
Munna chilensis Menzies, 1962		+				intertidal
Munna lundae Menzies, 1962		+				intertidal
Uromunna nana (Nordenstam, 1933)		+	+			0-120
Uromunna schauinslandi (G. O. Sars, 1905)			+			intertidal
Munna neglecta Monod, 1931			+	+	+	0-215
Munna pallida Beddard, 1886			+		+	3-173
Munna affinis Nordenstam, 1933				+		6-15
Munna spec. Monod, 1931				+		20
Munna antarctica (Pfeffer, 1887) (= *Haliacris australis* Hodgson, 1902)				+	+	2-420
Munna bituberculata Nordenstam, 1933				+	+	15-310
Munna amphoricauda Teodorczyk and Wägele, 1994					+	104-234
Munna globicauda Vanhöffen, 1914					+	26-522
Munna jazdzewskii Teodorczyk and Wägele, 1994					+	10-45
SANTIIDAE						
Santia compacta **Sivertsen and Holthuis, 1980**	+	+				10-40
Santia hispida (Vanhöffen, 1914)		+	+		+	5-95
Santia mawsoni (Hale, 1937)		+	+		+	2-45
Santia dimorphis (Menzies, 1962)			+			0-80
Santia laevifrons (Menzies, 1962)			+			intertidal
Santia hofsteni (Nordenstam, 1933)				+		0-100
Santia marmorata (Vanhöffen, 1914)				+		0-54
Santia charcoti (Richardson, 1906)					+	0-305
ACANTHASPIDIIDAE						
Ianthopsis laevis **Menzies, 1962**	+	+	+			3-100
Ianthopsis bovalli (Studer, 1884)		+	+	+	**	12-457
Ianthopsis nasicornis Vanhöffen, 1914				+	+	3-887
Ianthopsis multispinosa Vanhöffen, 1914					+	98-385
STENETRIIDAE						
Tenupedunculus inflectofrons (Schultz, 1982)		+	*			82-586
Tenupedunculus acutus (Vanhöffen, 1914)			+		+	150-3397
DESMOSOMATIDAE						
Eugerdella falklandica (Nordenstam, 1933)			+		+	16-234
Desmosoma australis Nordenstam, 1933				+	+	64-410
Desmosoma brevipes Nordenstam, 1933				+	+	64-188
Desmosoma modestum Nordenstam, 1933				+	+	125-250
Desmosoma anversense Schultz, 1979					+	109-137
Pseudogerda latipes (Hansen, 1916)					+	163-1102
MUNNOPSIDAE						
Echinozone quadrispinosa (Beddard, 1886) (= *Notopais spicatus* Hodgson, 1910)				+	+	10-1500
Echinozone spinosa Hodgson, 1902				+	+	18-569
Coperonus frigidus (Vanhöffen, 1914)				*	+	36-399
Ilyarachna nordenstami Wolff, 1962				*	+	51-310
Coperonus gracilis Brandt, 1992					+	45-420
Coperonus pulcher Brandt, 1992					+	89-429
Coperonus vanhoeffeni Brandt, 1992					+	139
Echinozone bispinosa Kussakin and Vasina, 1982					+	65-460
Lionectes humicephalotus Wilson, 1989					+	58-659
Munopsurus australis (Vanhöffen, 1914)					+	173-649

* depth > 200 m.
** depth unknown.
(1) not in *Paramunna* after Just and Wilson (2004).
(2) includes *Paramunna integra* sensu Winkler (1994) and many specimens present in our samples.
(3) includes *Paramunna subtriangulata* sensu Monod (1926), Nordenstam (1933), Menzies (1962), Winkler (1994a), and many specimens present in our samples.
(4) includes *Austrimunna rostrata* sensu Richardson (1913) and *Paramunna rostrata* sensu Nordenstam (1933). Some of these specimens may belong to the genus *Pagonana* proposed by Just and Wilson (2004).

1" and "*Austrosignum* n. sp. 2" in Tables 2 and 3 should be taken as provisional.

At family level, the Paramunnidae showed the highest diversity (11 species) and abundance (1,463 specimens). Janiridae was the second family in diversity (7 species) and Joeropsidae the second family in abundance (852 specimens) (Table 2).

Faunistic affinities between the Beagle Channel and the Magellan Straits

Including the data herein reported, the number of shallow-water asellotes in the Beagle Channel and the Magellan Straits was 23 and 34 respectively (Table 3). Sixteen of the species of the Beagle Channel co-occur in the Magellan Straits, which represents 69% of similarity (Table 3).

The Beagle Channel and the Magellan Straits shared six of the eight families reported from the Magellan region: Paramunnidae, Janiridae, Joeropsidae, Munnidae, Santiidae and Acanthaspidiidae (Table 3). One species of Stenetriidae has been reported from the Magellan Straits but no specimens were found in our samples. No member of Desmosomatidae has been reported from the Magellan Straits, and our samples did not contain any species of this family either.

For both areas the Paramunnidae and Janiridae were the most diverse families (Table 3). For the Paramunnidae 11 species were found in the Beagle Channel and 14 in the Magellan Straits. Of these, only five species co-occur in both areas. For the Janiridae six species were found in the Beagle Channel and eight in the Magellan Straits, all the species recorded from the Beagle Channel being also present in the Magellan Straits.

Faunistic affinities between the Magellan region and the Scotia Arc and the Antarctic Peninsula

Table 3 lists all the Asellota recorded at depths < 200 m from the Magellan region, the Scotia Arc and the Antarctic Peninsula. Of the 89 species reported for the entire area, 58 were found in the Magellan region, 23 in the Scotia Arc, and 50 in the Antarctic Peninsula. The Magellan region shared 7 species with the Scotia Arc (30% of similarity) and 13 species with the Antarctic Peninsula (26% of similarity).

The Paramunnidae showed the highest diversity in the Magellan region and the Antarctic Peninsula, while the Janiridae was the most diverse family in the Scotia Arc (Table 3).

DISCUSSION

The examination of just a few samples yielded three new species and 12 new records for the Beagle Channel, which suggests that many species of Asellota still remain undiscovered in this coastal area.

Winkler (1994b) mentioned that the Paramunnidae was the most diverse family in the Magellan region, followed by the "Janiridae/Joeropsidae", a fact that is consistent with our results in the Beagle Channel.

Nordenstam (1933) erected the genus *Antennulosignum* (Paramunnidae) to include *A. elegans* from the Malvinas Islands. This species is reported herein for the second time after its original description (Table 2). Brandt (1999) described some specimens from the Beagle Channel as *Pleurosignum chilense* Menzies, 1962. However, it is likely that because of their peculiar antennule the specimens studied by Brandt belong to the genus *Antennulosignum*.

The genus *Caecianiropsis* (Janiridae) includes three species. Of these, only *C. ectiformis* (Vanhöffen, 1914) is found in the southern hemisphere. This species was previously known from the following Subantarctic islands: Kerguelen, St. Paul, and Marion/Prince Edward (Vanhöffen, 1914; Kensley, 1976; Branch *et al.*, 1991). Our finding of *C.* cf. *ectiformis* in the Beagle Channel widely extends the range of distribution of the genus *Caecianiropsis* in the southern hemisphere.

The genus *Munna* (Munnidae) is well represented in the Magellan region (Winkler, 1994b), as well as in Antarctic and Subantarctic waters (Teodorczyk and Wägele, 1994). Although six species were reported from the Magellan region (Nordenstam, 1933; Menzies, 1962; Winkler, 1992, 1994b; Teodorczyk and Wägele, 1994; Lorenti and Mariani, 1997) only one, *Munna gallardoi* Winkler, 1992, was identified from the Beagle Channel (Table 3). Most probably, among the specimens herein reported as "*Munna* sp." more than one species were included, but the poor condition of the available material has prevented us from identifying them.

The family Santiidae has a pronounced southern distribution, and its species occur at depths of less than 100 m (Wolff, 1989). Five species of *Santia* have been reported from the Magellan region (Winkler, 1994b; Lorenti and Mariani, 1997); in contrast, only one has been found in the Beagle Channel so far (Table 3).

Two species belonging to the family Acanthaspidiidae have been recorded from the Magellan region. *Ianthopsis laevis* Menzies, 1962, endemic for this region, was recorded herein from the Beagle Channel. On the other hand, *Ianthopsis bovallis* (Studer, 1884) was not reported from the Beagle Channel, despite its wide distribution in the southern seas (see Winkler, 1994b; Lorenti and Mariani, 1997).

The species of the genus *Tenupedunculus* (Stenetriidae) and those of the families Desmosomatidae and Munnopsidae are distributed mainly in deep-sea waters (Kussakin, 1973; Serov and Wilson, 1995). However, emergence has been postulated for many deep-sea Asellota, especially at higher latitudes (see Brandt *et al.*, 2004). This could explain the larger number of species found in the Scotia Arc/Antarctic Peninsula in comparison with the Magellan region (Table 3). Although no species of the three families mentioned above have been recorded from the Beagle Channel, *Eugerdella falklandica* (Nordenstam, 1933) and some species of *Tenupedunculus*, a genus that is distributed from around the southern tip of South America to the Antarctic, are likely to be found in future surveys carried out in the Beagle Channel.

Menzies (1962) recorded four species from Chile, viz., *Uromunna schauinslandi* (G. O. Sars, 1905) near 41°S, *Joeropsis bidens* Menzies, 1962 between 42 and 20°S, *Santia dimorphis* (Menzies, 1962) near 44°S and *Santia laevifrons* (Menzies, 1962) between 44 and 32°S. All these species were found slightly below 41°S and thus were listed in Table 3. Because zoogeographic regions cannot be neatly divided, the addition of these species to the Magellan fauna must be taken with caution.

Knowledge of the Magellan Asellota is still scarce and further taxonomic studies are strongly required. Although the results presented herein are preliminary, they will hopefully contribute to a better understanding of this faunal group.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Species richness and faunistic affinities of the Gammaridea and Corophiidea (Amphipoda) from shallow waters of southern Tierra del Fuego, Argentina: preliminary results*

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SUMMARY: Species richness and faunistic affinities of gammaridean and corophiidean amphipods from southern Tierra del Fuego were studied. The material was collected with dredges and grabs at 7 locations (15 sampling stations) in a range of 5 to 35 m depth. A total of 61 species belonging to 20 families and 43 genera were identified. The genera *Cephalophoxoides*, *Ceradocopsis* and *Photis* are reported for the first time from the Magellan region and 3 species belonging to *Atylus*, *Ischyrocerus* and *Photis* appear to be new to science. Most of the species collected belong to Phoxocephalidae, whereas most individuals were contained in the Stenothoidae and Lysianassidae s.l. The analysis of the faunistic affinities showed that 16 species (39%) are endemic to the Magellan region, 9 species (22%) extend to the south, 5 species (12.2%) to the north and 5 other species (12.2%) to both the north and south. In addition, 6 species extend beyond the Magellan region as far as Oceania.

Keywords: Magellan region, Beagle Channel, Amphipoda, diversity, distribution.

RESUMEN: – Riqueza de especies y afinidades faunísticas de Gammaridea y Corophiidea (Amphipoda) de aguas someras del sur de Tierra del Fuego. Argentina: resultados preliminares. – Se estudió la diversidad y las afinidades faunísticas de los anfípodos gammarideos y corophiideos del sur de Tierra del Fuego. El material fue recolectado utilizando rastras y dragas en 7 sitios (15 estaciones de muestreo) a un rango de profundidad entre 5 y 35 metros. Un total de 61 especies pertenecientes a 20 familias y 43 géneros fueron identificadas. Los géneros *Cephalophoxoides*, *Ceradocopsis* y *Photis* son citados por primera vez para la región magallánica, y 3 especies de los géneros *Atylus*, *Ischyrocerus* y *Photis* parecen ser nuevas para la ciencia. Phoxocephalidae resultó la familia con mayor número de especies, mientras que Stenothoidae y Lysianassidae s.l. fueron las más abundantes. El análisis de las afinidades faunísticas reveló que 16 especies (39%) son endémicas de la región magallánica, 9 especies (22%) se extienden hacia el sur, 5 especies (12,2%) hacia el norte y otras 5 (12,2%) están presentes en el norte y en el sur. Además, 6 especies se extienden más allá de la región magallánica alcanzando Oceanía.

Palabras clave: región magallánica, Canal Beagle, Amphipoda, diversidad, distribución.

INTRODUCTION

The gammaridean and corophiidean amphipods (Crustacea, Peracarida, Amphipoda) represent a widely diversified group of invertebrates in benthic communities from the Magellan region. Based on extensive collections along the Chilean coasts and data from the literature, a total of 206 species were listed by De Broyer and Rauschert (1999). In contrast, the amphipod fauna from the Argentine sector

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FIG. 1. – Sampling locations in southern Tierra del Fuego.

of the Magellan region still remains scarcely studied. Unfortunately, the main contributions for the area by Schellenberg (1931) and Barnard (1932) have overlooked important details in their descriptions of species, and most of them need revision and redescription. Recently, several species have been described from the provinces of Santa Cruz and Chubut, but the knowledge on the group is sparse in Tierra del Fuego, where only a few studies carried out by Alonso (1987a,b, 1989) and Alonso de Pina (1993a, 1997a) provided the description of 2 new species and the addition of 3 new records of distribution. The low number of species presently known from the Argentine waters of the Magellan region is probably due to the lack of extensive field surveys conducted in this area.

The present work provides the first results on the species richness and faunistic affinities of the Gammaridea and Corophiidea collected in southern Tierra del Fuego. The sampling area is not only of great biogeographic interest due to its proximity to the Subantarctic islands and the Antarctic, but also represents a transitional region between the Atlantic and Pacific oceans.

MATERIAL AND METHODS

Seven locations (comprising a total of 15 sampling stations) were established along the Beagle Channel and its eastern mouth, at the southern coast of Tierra del Fuego, Argentina (Fig. 1, Table 1). All stations were selected within a relatively homogeneous bathymetric range (5 to 35 m) in order to avoid depth-related effects. A total of 6 samples were obtained with a dredge of 45 x 50 cm mouth and 2 mm mesh. The dredge was pulled for 7 minutes at Isla Gable, Punta Moat, Cabo San Pío, Bahía Slogget, Bahía Aguirre and Bahía Buen Suceso (Fig. 1). In addition, the contents of grab samples (Snapper and Van Veen, 0.07 m^2) taken at 9 sampling stations in Bahía Ushuaia were received from colleagues and considered altogether for this study (Table 2).

The material was fixed in 10% formalin. Amphipods were sorted from the sediment under a stereoscopic microscope, preserved in 70% ethanol, and identified to the lowest taxonomic level. The taxonomic classification of the amphipods follows Barnard and Karaman (1991) and Myers and Lowry (2003).

TABLE 1. – Sampling locations

Locations	Date	Latitude	Longitude	Depth (m)	Sampler
Bahía Ushuaia					
Península Ushuaia	27/10/96	54° 51' S	68° 19' W	5-10	Van Veen Grab
Bahía Golondrina	12/2/97	54° 50' S	68° 20' W	5	Snapper Grab
Bahía Golondrina	12/2/97	54° 50' S	68° 19' W	5	Snapper Grab
Bahía Golondrina	12/2/97	54° 50' S	68° 14' W	5	Snapper Grab
Bahía Golondrina	10/2/97	54° 49' S	68° 14' W	12	Snapper Grab
Bahía Golondrina	10/2/97	54° 50' S	68° 16' W	30	Snapper Grab
Bahía Golondrina	10/2/97	54° 49' S	68° 17' W	30	Snapper Grab
Isla Lucas	10/12/97	54° 50' S	68° 19' W	17	Snapper Grab
Pozo Angel	12/2/97	54° 52' S	68° 15' W	23	Snapper Grab
Isla Gable	11/5/01	54° 54' S	67° 21' W	15-20	Dredge
Punta Moat	2/9/01	55° 02' S	66° 42' W	15-25	Dredge
Cabo San Pío	29/9/02	55° 03' S	66° 37' W	30-35	Dredge
Bahía Slogget	2/9/01	55° 00' S	66° 21' W	15-27	Dredge
Bahía Aguirre	2/2/00	54° 54' S	65° 57' W	30-35	Dredge
Bahía Buen Suceso	8/2/01	54° 47' S	65° 14' W	12	Dredge

The number of species and specimens were determined for each locality.

For the analysis of the faunistic affinities, the following areas were considered:

a) Magellan region: comprising the Malvinas (Falkland) Islands, the Argentine coast south of Península Valdés and the Chilean coast south of Isla Chiloé; the southern limit is Cape Horn (Boschi, 2000).

b) "North of the Magellan region": embracing the coasts north of Península Valdés (Atlantic Ocean) and Isla Chiloé (Pacific Ocean), including the Brazilian, Uruguayan, Peruvian and northern Argentinean and Chilean waters.

c) "South of the Magellan region": includes the Scotia Arc islands (South Georgia, South Sandwich Islands, South Orkney Islands and South Shetland Islands), the Subantarctic islands (Kerguelen, Crozet, Campbell, Macquarie, Auckland, Prince Edward and Marion Islands) and the Antarctic.

Data for these areas were obtained from Schellenberg (1931), K. H. Barnard (1932), Lowry and Bullock (1976), González (1991), De Broyer and Jazdzewski (1993), Wakabara and Serejo (1998) and De Broyer and Rauschert (1999). In the analysis of faunistic affinities, the new species and those reported as "sp." or "cf." were not considered.

RESULTS

Species richness of amphipods

A total of 3,928 specimens were examined during this study and 41 species were identified (Table 2); another 20 species (reported as "sp." or "cf." in Table 2) were recognised as different taxa. In total, 61 species belonging to 43 genera and 20 families were reported (Table 2). The present study provides the first records of the genera *Cephalophoxoides*, *Ceradocopsis* and *Photis* from the Magellan region and of 18 species from the Beagle Channel. Moreover, 3 species belonging to *Atylus*, *Ischyrocerus* and *Photis* appear to be new to science (Table 2).

Among the twenty families recognised, Phoxocephalidae had the highest number of species (7). Ten families had 3 to 6 species, and nine families only 1-2 species (Table 2). A high number of genera also had a low number of species: 34 genera were only represented by 1 species each; three genera (*Atyloella*, *Atylus* and *Iphimedia*) by 2 species each; and four genera (*Liljeborgia*, *Probolisca*, *Pseudiphimediella* and *Seba*) by 3 species each. *Gammaropsis* and *Gondogeneia* had 4 and 5 species each respectively (Table 2).

Stenothoidae and Photidae were the families that accounted for the highest number of specimens (887 and 797 respectively), followed by Lysianassidae s.l. (575) and Eusiridae s.l. (458). The remaining 16 families were consistently less abundant (Table 2). Among the Stenothoidae, *Probolisca nasutigenes* was the most abundant species (545 specimens), followed by *P. ovata* (189 specimens) and *P. elliptica* (153 specimens). Among the Photidae, *Gammaropsis deseadensis* was the most abundant species (485 specimens). All other species were represented by fewer than 300 specimens, including 41 species that were represented by fewer than 35 specimens each (Table 2).

Tryphosites chevreuxi was the most frequent species, being present at all locations, whereas *Phoxorgia sinuata* was found at 6 out of 7 locations (Table 2). The highest number of species (29) was found in the sample from Bahía Slogget, followed by those from Punta Moat (28 species) and Bahía Ushuaia (26 species), whereas the highest abundance (1,211 specimens) was found at Cabo San Pío (Table 2).

Faunistic affinities

For the 41 amphipod taxa identified at species level in this study, 16 species (39%) are known only from the Magellan region (Table 3) and the ranges of 24 species extend beyond this region: 9 (22%) to the south, 5 (12.2%) to the north, and 5 (12.2%) to both the north and the south (Fig. 2). Another 6 species extend beyond the Magellan region, reaching Oceania: 2 of them (*Bircenna fulva* and *Seba typica*) are known only from this allopatric distribution; *Jassa alonsoae* is also present in South Georgia and the Subantarctic islands; *Eusirus antarcticus* is also present in the Scotia Arc islands, Subantarctic islands and Antarctica; *Probolisca ovata* is also distributed north of the Magellan region; and *Eusiroides monoculoides* is found in the Magellan region, Subantarctic islands, South Africa, and Oceania (Lowry and Bullock, 1976; De Broyer and Jazdzewski, 1993; De Broyer and Rauschert, 1999).

For the 14 species extending south of the Magellan region, 5 (*Fuegiphoxus fuegiensis*, *Liljeborgia octodentata*, *Pariphimedia normani*, *Phoxorgia sinuata* and *Seba subantarctica*) reach only the Scotia Arc islands, 6 (*Amphilochus marionis*, *Gammarop-*

TABLE 2. – List of species of Gammaridea and Corophiidea collected in southern Tierra del Fuego. Total number of species and specimens for each location; •: new records for the Magellan region; **X**: new records for the Beagle Channel. Locations = BU: Bahía Ushuaia, IG: Isla Gable, PM: Punta Moat, CP: Cabo San Pío, BS: Bahía Slogget, BA: Bahía Aguirre, BB: Bahía Buen Suceso. Distribution = M: Magellan region, S: south of the Magellan region, N: north of the Magellan region, O: other localities.

Species				Locations				Distribution
	BU	IG	PM	CP	BS	BA	BB	
Ampeliscidae								
Ampelisca sp.						29		
Amphilochidae								
Amphilochus marionis Stebbing, 1888			3	27				MS
Aoridae								
X *Lembos argentinensis* Alonso de Pina, 1992	2	5	8	1	11			M
Corophiidae								
Corophium sp.	2							
X *Haplocheira barbimana robusta* K.H. Barnard, 1932	9	7	96	66	6			M
Dexaminidae								
Atylus (Atylus) sp. n.						3	9	M
Atylus (Atylus) cf. *villosus* Bate, 1862		50		5	25	1		
X *Paradexamine nana* Stebbing, 1914			2					M
Eophliantidae								
X *Bircenna fulva* Chilton, 1884			1					MO
Eusiridae s. l.								
X *Atyloella dentata* K.H. Barnard, 1932		6		35	2			M
Atyloella magellanica (Stebbing, 1888)	1	54	61	98	48			MNS
X *Eusiroides monoculoides* (Haswell, 1879)	1	1	3	3	1			MSO
Eusirus antarcticus Thomson, 1880		10		1				MSO
Paramoera cf. *fissicauda* (Dana, 1852)			39		94			
Gammarellidae								
Austroregia regis (Stebbing, 1914)	3							M
Gondogeneia cf. *antarctica* (Chevreux, 1906)			5					
Gondogeneia gracilicauda (Schellenberg, 1931)			1					M
Gondogeneia cf. *macrodon* (Schellenberg, 1931)							1	
X *Gondogeneia patagonica* Alonso, 1986			3		1			M
Gondogeneia cf. *thurstoni* Alonso, 1989					20	50	42	
Gammaridae s.l.								
• *Ceradocopsis* sp.			1					
Maera sp.				77				
Iphimediidae								
X *Iphimedia magellanica* Watling and Holman, 1980			10		1			M
Iphimedia multidentata (Schellenberg, 1931)	1		10	2				M
Pariphimedia normani (Cunningham, 1871)			5		2			MS
Pseudiphimediella glabra (Schellenberg, 1931)	1							M
X *Pseudiphimediella nodosa* (Dana, 1852)				4	1			M
Pseudiphimediella sp.	1							
Ischyroceridae								
Ischyrocerus sp. n.			24		26			M
Jassa alonsoae Conlan, 1990					21			MSO
Notopoma sp.				4				
Ventojassa georgiana (Schellenberg, 1931)			64	4	85			MS
Liljeborgiidae								
Liljeborgia cf. *macrodon* Schellenberg, 1931	2	24			3			
Liljeborgia octodentata Schellenberg, 1931	1	2	6	2	2			MS
Liljeborgia sp.		1						
Lysianassidae s. l.								
X *Erikus dahli* Lowry and Stoddart, 1987	56		118	21	71			M
Tryphosella schellenbergi (Schellenberg, 1931)	9	5			19			MN
Tryphosites chevreuxi Stebbing, 1914	89	78	16	17	27	32	6	MN
X *Uristes serratus* Schellenberg, 1931	10							M
Stomacontion sp.				1				
Oedicerotidae								
Oediceroides cf macrodactylus Schellenberg, 1931	12							
Photidae								
X *Gammaropsis (Gammaropsis) deseadensis* Alonso, 1981		42	43	399	1			M
Gammaropsis (Gammaropsis) longitarsus (Schellenberg, 1931)					16			MS
Gammaropsis (Paranaenia) dentifera (Haswell, 1879)		37	78	143	28			MS
Gammaropsis sp.					4			
• *Photis (Photis)* sp. n.			2			2	2	M
Phoxocephalopsidae								
X *Phoxocephalopsis zimmeri* Schellenberg, 1931						6	5	MN
Phoxocephalidae								
• *Cephalophoxoides* sp.	1						1	
Fuegiphoxus fuegiensis (Schellenberg, 1931)	4	1		3				MNS
Heterophoxus videns K. H. Barnard, 1930	2							MNS

TABLE 2 (Cont.). – List of species of Gammaridea and Corophiidea collected in southern Tierra del Fuego. Total number of species and specimens for each location; •: new records for the Magellan Region. **X**: New records for the Beagle Channel. Locations = BU: Bahía Ushuaia, IG: Isla Gable, PM: Punta Moat, CP: Cabo San Pío, BS: Bahía Slogget, BA: Bahía Aguirre, BB: Bahía Buen Suceso. Distribution = M: Magellan Region, S: south of the Magellan Region, N: north of the Magellan Region, O: other localities.

Species	Locations							Distribution
	BU	IG	PM	CP	BS	BA	BB	
Microphoxus cornutus (Schellenberg, 1931)	57							MN
X *Parafoxiphalus longicarpus* Alonso de Pina, 2001	45					32		M
X *Phoxorgia sinuata* (K. H. Barnard, 1932)	20	19	9	20	14		2	MNS
Proharpinia stephenseni (Schellenberg, 1931)	6						1	M
Sebidae								
Seba saundersii Stebbing, 1875	16							MS
Seba subantarctica Schellenberg, 1931	1							MS
X *Seba typica* (Chilton, 1884)					1			MO
Stenothoidae								
Probolisca elliptica (Schellenberg, 1931)		97	3	50	3			MS
X *Probolisca nasutigenes* (Stebbing, 1888)		342	13	177	13			MNS
Probolisca ovata (Stebbing, 1888)	2		4	50	133			MNSO
Urothoidae								
X *Urothoe falcata* Schellenberg, 1931			3	1		27	21	MN
Total number of species	26	18	28	25	29	9	10	
Total number of specimens	354	781	631	1211	679	182	90	

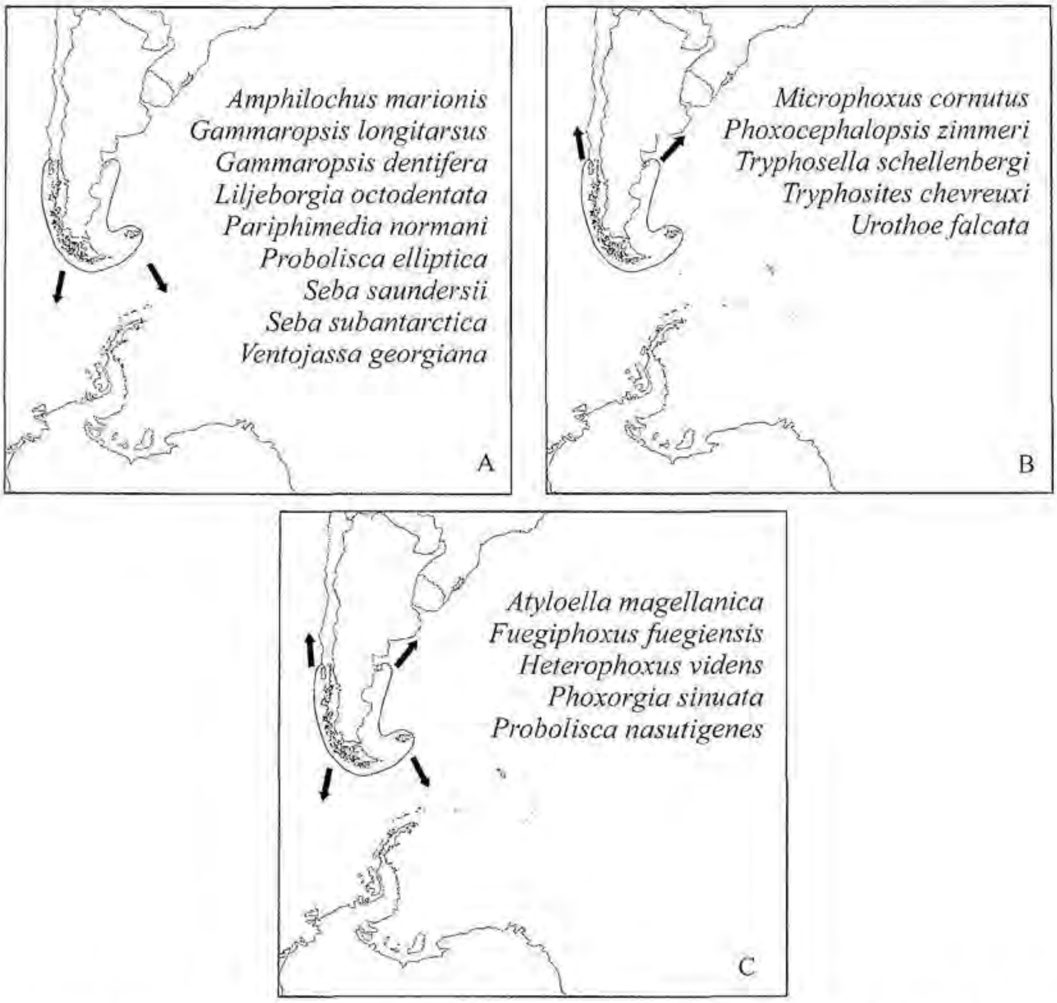

FIG. 2. – Distribution of species from southern Tierra del Fuego. A: Magellan species distributed towards the south; B: Magellan species distributed towards the north; C: Magellan species distributed towards both the north and the south.

TABLE 3. – Distribution of the species collected during the present study in southern Tierra del Fuego known hitherto only from the Magellan region. PO, Pacific Ocean; SM, Straits of Magellan; AO, Atlantic Ocean.

Species	PO	SM	AO
Atyloella dentata			X
Austroregia regis	X	X	X
Erikus dahli	X		
Gammaropsis (Gammaropsis) deseadensis			X
Gondogeneia gracilicauda			X
Gondogeneia patagonica			X
Haplocheira barbimana robusta			X
Iphimedia magellanica			X
Iphimedia multidentata	X	X	X
Lembos argentinensis			X
Paradexamine nana		X	X
Parafoxiphalus longicarpus			X
Proharpinia stephenseni		X	X
Pseudiphimediella glabra	X	X	X
Pseudiphimediella nodosa		X	
Uristes serratus		X	X

sis dentifera, *G. longitarsus*, *Probolisca elliptica*, *P. nasutigenes* and *Seba saundersii*) extend to the Subantarctic islands and 3 (*Atyloella magellanica*, *Heterophoxus videns* and *Ventojassa georgiana*) reach the Antarctic continent.

Table 3 shows the geographic distribution of the 16 species collected during this study that were known exclusively from the Magellan region: 8 of them are also present in the Atlantic Ocean, 1 in the Straits of Magellan and 1 in the Pacific Ocean, 3 in the Straits of Magellan and the Atlantic Ocean, and 3 in the Straits of Magellan and also in the Atlantic and Pacific oceans. None of the species was endemic to the Beagle Channel.

DISCUSSION

The present study provides new information on the species richness of the shallow-water amphipod fauna from southern Tierra del Fuego, giving the first records of 3 genera from the Magellan region and reporting 18 species for the first time from the Beagle Channel. In addition, 3 probable new species are reported.

De Broyer and Rauschert (1999) listed 206 gammaridean and corophiidean species from the Magellan region. The present contribution adds to this list: two species described by Alonso de Pina (1993b and 1997c) and 2 records reported by Alonso de Pina (1997b) that were omitted by De Broyer and Rauschert; 4 new species described from the area by Alonso de Pina (2000, 2001, 2003); and the records from this study (2 species belonging to the genera *Ceradocopsis* and *Cephalophoxoides* and 3 apparently undescribed species). These additions increase the species number of the Magellan region to 219. Sixty-one out of these species (27.9%) were found in southern Tierra del Fuego during this study. The relatively low number of species in this area as compared to the entire Magellan region could be a consequence of the few samples examined and the narrow bathymetric range considered herein. In fact, although Stenothoidae is the most speciose family in the Magellan region (more than 36 species were listed by De Broyer and Rauschert, 1999), only 3 species were collected during this study. This low number is probably due to the deep-water habitat of most stenothoids and to the relatively large mesh size used. The higher number (7 species) of phoxocephalids found (the most speciose family in this study) seems to be related to their sand-burrowing habit and a different sampling method: most of the phoxocephalid species and specimens were collected from Bahía Ushuaia, where a grab was used as the sampling device.

Gammarellidae, Lysianassidae s.l. and Eusiridae s.l., which have high species diversity in the Magellan region, were also well represented in southern Tierra del Fuego. Six out of 8 iphimediid species reported for the whole Magellan region were collected in southern Tierra del Fuego during this study. This fact is probably related to the low sampling depth since iphimediids are predominantly shallow-waters inhabitants.

Although dredge samples are not strictly quantitative, they provide a large amount of material with a relatively low effort (Arntz *et al.*, 1999). For this reason, they are useful for taxonomic studies, but the number of specimens caught should be considered only a crude estimate of abundance. The total number of species collected in Bahía Aguirre (9) and Bahía Buen Suceso (10) was lower than at the remaining locations, probably due to the faster speed of the sampling vessel that resulted in an inappropriate performance of the dredge. Moreover, the high number of species and the low number of specimens found at Bahía Ushuaia seems to be related to the sampling method used: grabs frequently capture a lower number of specimens than dredges, but they can penetrate more deeply into the substrate, thus obtaining more infaunal species.

The occurrence of Magellanic species present also at localities north of the Magellan region is probably related to the Malvinas, Patagonic and

Humboldt currents, three water masses which run northward reaching Brazil and Buenos Aires (Bastida *et al.*, 1992; Piola and Rivas, 1997), and Peru and Ecuador respectively (Brattström and Johanssen, 1983). Similarly, the presence of Magellanic species in the Scotia Arc islands, Subantarctic islands and Oceania is favoured by the West Wind Drift/Antarctic Circumpolar Current, regarded as a means of dispersion of other groups of invertebrates (Fell, 1962; Dell, 1972; Helmuth *et al.*, 1994; Castilla and Guiñez, 2000).

This study provides preliminary results on the species richness of the shallow amphipod fauna living in southern Tierra del Fuego. Additional samples are needed to confirm the taxonomic status of the 20 amphipods reported as sp. or cf. in this study and to improve the knowledge on the diversity and faunistic affinities of this region. Further investigations are also required in the southwest Atlantic Ocean, in order to determine the current distribution of the amphipods present in the Magellan region.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Cryptic speciation in the giant Antarctic isopod *Glyptonotus antarcticus* (Isopoda: Valvifera: Chaetiliidae)*

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SUMMARY: The genus *Glyptonotus* is most commonly regarded as monospecific, with *Glyptonotus antarcticus* Eights 1852 being its only constituent. Two more forms (*G. acutus, G. antarcticus var. obtusus*) that had been described based on morphological evidence have received little attention in the literature, though no formal attempt to evaluate their taxonomic status has been undertaken. In a survey of within-species genetic diversity, 23 specimens of the benthic Antarctic isopod *Glyptonotus antarcticus* from three sampling areas around the Antarctic had a high genetic variability in their mitochondrial LSU (16S) gene. Eleven unique mitochondrial haplotypes were found, two at the Antarctic Peninsula (AP), two in the Ross Sea (RS) and seven in the Eastern Weddell Sea (EWS). Average haplotype variation within sampling areas (AP, RS, EWS) was one order of magnitude less than between sampling areas. In the EWS, however, two highly differentiated haplotypes co-exist. These four groups of haplotypes may represent cryptic, but reproductively isolated species rather than a single species.

Keywords: sibling species, molecular systematics, biogeography, Antarctic benthos.

RESUMEN: ESPECIACIÓN CRÍPTICA EN EL ISÓPODO GIGANTE ANTÁRTICO *GLYPTONOTUS ANTARCTICUS* (ISOPODA, VALVIFERA, CHAETILIIDAE). – En una investigación sobre diversidad genética intra-específica se registró variabilidad en el gen mitocondrial LSU (16S) de 23 especímenes del isópodo bentónico antártico *Glyptonotus antarcticus* de tres áreas antárticas. Se encontraron once haplotipos mitocondriales únicos, dos en la Península Antártica (AP), dos en el Mar de Ross (RS) y siete en el Mar de Weddell (EWS). La variación media de los haplotipos dentro de las áreas (AP, RS, EWS) fue un orden de magnitud menor que entre ellas. Sin embargo, en el EWS coexisten dos haplotipos altamente diferenciados. Estos cuatro grupos de haplotipos pueden representar especies crípticas reproductivamente aisladas, más que una única especie como se asumía anteriormente.

Palabras clave: especies hermanas, sistemática molecular, biogeografía, bentos antártico.

INTRODUCTION

The giant isopod *Glyptonotus antarcticus* was one of the first isopods described from Antarctic waters (Eights, 1852). It can grow to up to 9 cm long and is one of the most conspicuous and locally abundant components of the High Antarctic megazoobenthos.

Because it is ecologically important and relatively easy to catch and maintain in aquaria, it has become a model organism in several fields of Antarctic biology, including ecology, physiology and biochemistry (Arnaud, 1970; Clarke, 1979, 1982; Dearborn, 1967; Janssen and Hoese, 1993;

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Key and Barnes, 1999; Luxmoore, 1984; Martin, Jaros, Chaigneau and Meyer-Rochow, 1995; Rakusa-Suszczewski and McWhinnie, 1976; Starmans, 1997; Whiteley, Taylor, Clarke and El Haj, 1997; White, 1970, 1975).

Two more species or variants of *Glyptonotus* have been put forward based on morphological characters. Richardson (1906) described *Glyptonotus acutus* from the shallow waters around Wincke and Booth-Wandel islands (Antarctic Peninsula). It differs from *G. antarcticus* mainly by a longer, more acute pleotelson and different proportions. Comparing numerous individuals from both forms, Tattersall (1921) came to the conclusion that many differences between them are a function of body size and age of the individual rather than consistent differences between species. He recommended treating *G. acutus* as a mere variety of *G. antarcticus*. Sheppard (1957) went even further than Tattersall by stating that "...it is impossible to separate *G. acutus*, even as a variety, from *G. antarcticus*".

Another variety, *G. antarcticus* var. *obtusus*, was described by Meyer-Rochow (1980), also based on distinctive features of pleotelson shape and proportions found in a population from the Ross Sea. A more detailed account of the taxonomic history of the genus will be given in a revision of *Glyptonotus* (Held, in prep.), but today the synonymy of all forms described so far is widely accepted among taxonomists (Brandt, 1990; Kussakin, 1982; Wägele, 1991). *Glyptonotus antarcticus* sensu lato is recorded around the High Antarctic shelf and some Subantarctic islands in waters ranging from the shallow subtidal down to more than 600 metres depth.

Molecular data have recently indicated that another widely distributed Antarctic isopod, *Ceratoserolis trilobitoides*, may represent more than one species (Held, 2003), and complimentary morphological data support this interpretation (Held, in prep.). To investigate the taxonomic status and genetic variability of nominate *Glyptonotus antarcticus*, 23 specimens were collected around the Antarctic and a 516 bp fragment of their mitochondrial large subunit gene (16S) was sequenced.

In particular, the following questions were addressed: (1) Is there cryptic speciation in *Glyptonotus antarcticus*? (2) If so, how many species of *Glyptonotus* are present? and (3) How can divergent populations of a single species be separated from several reproductively isolated species?

MATERIAL AND METHODS

Sample collection

Specimens of *Glyptonotus* were collected during the expeditions ANT XIII/3 to the Eastern Weddell

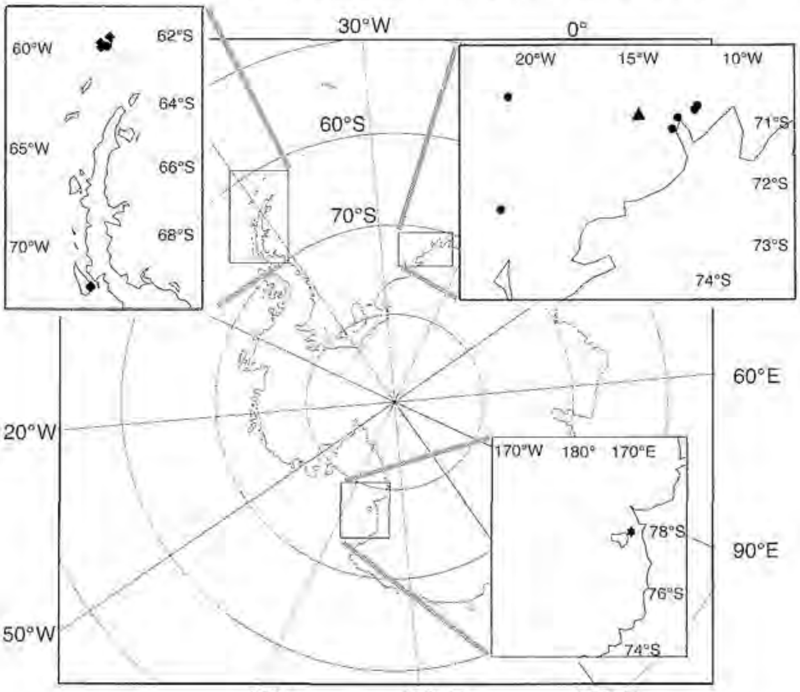

Fig. 1. – The sampling locations of nominate *Glyptonotus antarcticus* in the Southern Ocean The four mitochondrial haplotypes, possibly representing four species, are: Antarctic Peninsula (◆), Eastern Weddell Sea group A (●), Eastern Weddell Sea group B (▲), Ross Sea (✱).

TABLE 1. – Individual codes, GenBank accession numbers and sampling location for the specimens of *Glyptonotus* used in this study. The last column indicates the occurrence of each of the 11 unique 16S haplotypes.

specimen code	accession	region	station	latitude	longitude	depth (m)	haplotype
B088	AM086466	Antarctic Peninsula	Elephant Island	61°11'S	55°58'W	130	H2
B101	AM086464	Antarctic Peninsula	Elephant Island	61°15'S	55°37'W	87	H1
B201	AM086467	Antarctic Peninsula	Elephant Island	61°02'S	55°52'W	148	H1
B233	AM086465	Antarctic Peninsula	Elephant Island	61°01'S	55°07'W	143	H1
B311	AM086468	Antarctic Peninsula	Rothera	67°34'S	68°08'W	10	H1
B312	AM086469	Antarctic Peninsula	Rothera	67°34'S	68°08'W	10	H1
C040	AM086470	Antarctic Peninsula	Anchorage Isl.	67°36'S	68°13'W	10	H1
A126	AM086473	Eastern Weddell Sea	Kapp Norvegia	71°08'S	11°32'W	123	H4
A127	AM086474	Eastern Weddell Sea	Kapp Norvegia	71°08'S	11°32'W	123	H5
A145	AM086475	Eastern Weddell Sea	Kapp Norvegia	71°32'S	12°26'W	504	H6
A146	AM086476	Eastern Weddell Sea	Vestkapp	73°18'S	21°10'W	468	H5
A148	AM086477	Eastern Weddell Sea	Kapp Norvegia	71°19'S	12°17'W	170	H4
A149	AM086479	Eastern Weddell Sea	Vestkapp	73°23'S	21°11'W	338	H4
A151	AM086480	Eastern Weddell Sea	Vestkapp	73°18'S	21°10'W	468	H4
A152	AM086471	Eastern Weddell Sea	Vestkapp	73°18'S	21°10'W	468	H3
A154	AM086481	Eastern Weddell Sea	Drescher Inlet	72°01'S	19°00'W	413	H7
A155	AM086482	Eastern Weddell Sea	Kapp Norvegia	71°03'S	11°26'W	462	H8
A156	AM086472	Eastern Weddell Sea	Kapp Norvegia	71°03'S	11°26'W	462	H3
A157	AM086478	Eastern Weddell Sea	Kapp Norvegia	71°08'S	11°32'W	123	H4
A147	AM086483	Eastern Weddell Sea	Kapp Norvegia	71°23'S	14°20'W	634	H9
A150	AM086484	Eastern Weddell Sea	Kapp Norvegia	71°23'S	14°20'W	622	H9
B359	AM086485	Ross Sea	Arrival Heights	77°49'S	166°39'E	10	H10
B360	AM086486	Ross Sea	Arrival Heights	77°49'S	166°39'E	10	H11

Sea (Arntz and Gutt 1997) and ANT XIV/2 to the Antarctic Peninsula (Kattner, 1998). The catch from towed gear (bottom trawl, Agassiz trawl, Rauschert dredge) was hand-sorted. Specimens were fixed in 80-96% ethanol. To minimize enzymatic degradation of DNA, the ethanol was pre-chilled to -20°C and freshly fixed material was kept at temperatures between -30 and 4°C until the DNA was extracted (Held, 2000a).

Additional material, collected by scuba diving, was kindly made available from the Ross Sea by J. McClintock and co-workers and from the Antarctic Peninsula by M. White, L. Peck and K. Linse. Details about the sampling locations are given in Figure 1 and Table 1.

DNA extraction and sequencing

Sequence data were determined for a total of 23 specimens of *Glyptonotus*. Muscle tissue was dissected from walking legs and transferred to sterile microfuge tubes. Exoskeleton was avoided because of contamination risks with DNA from bycatch organisms (Held, 2000a). The muscle tissue was digested overnight with Proteinase K, and genomic DNA was extracted using spin columns (Qiagen QiaAmp DNA mini) following the animal tissue protocol of the manufacturer. The DNA was finally eluted in 35 μl AE buffer.

Amplification of the mitochondrial 16S ribosomal (LSU) gene was carried out in 25 μl volume (one unit Qiagen Taq polymerase, 2.5 μl 10x PCR buffer, 5 μl Q-buffer, 2.5 μl dNTPs, 0.5-1 μl DNA template, filled to 25 μl with sterile H_2O) as described in Held (2003) using the primers 16Sar 5'-CGCCTGTTTATCAAAAACAT-3' and 16Sbr 5-CCGGTCTGAACTCAGATCACGT-3' (Palumbi *et al.*, 1991). The temperature profile of the amplification on an MWG Primus cycler was as follows: 5 min 94°C initial denaturing, 35 cycles of 45 s 94°C, 45 s 52°C, 80 s 72°C, followed by 7 min final extension. PCR products were column purified (Qiagen Qiaquick) and checked on a 1% ethidium-bromide stained agarose gel for purity, concentration and possible contamination.

Between 0.5 and 1 μl of the purified PCR products were sequenced directly in a dideoxy cycle sequencing reaction on Techne Progene cycler (94°C 2 min initial denaturing, 30 cycles of 25 s 94°C, 25 s 48°C, 35 s 70°C) following the recommendations of the manufacturer (Amersham), except that the reaction volume was reduced to 13 μl. After denaturation (30 s 94°C), the samples were kept on ice and 1.5 μl was loaded and run on an automated sequencer (LiCor models 4000 and 4200). Sequence reads were proofread and contigs from both strands were assembled in the program AlignIR 1.2 (LiCor). The corrected sequences were

TABLE 2. – Maximum-likelihood estimates of pairwise genetic distances (lower triangle) and observed genetic distances (upper triangle) between the 11 unique mitochondrial haplotypes in the LSU gene of *Glyptonotus* in this study. The specimens and sampling localities of each haplotype are given in Table 1. Details about the LRT and the model used are described in the text. Observed distance values should be regarded as rough approximations only because no corrections for multiple substitutions are made. Lower variability within sampling regions was indicate in *italics* and the higher divergence of haplotype H9 in **bold**.

	Ant. Peninsula		Eastern Weddell Sea							Ross Sea	
	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11
H1	*	*2*	45	45	43	45	45	45	39	47	46
H2	*0.004091*	*	43	43	41	43	45	43	39	47	46
H3	0.143933	0.133679	*	*4*	*8*	*10*	*6*	*5*	**31**	45	44
H4	0.141898	0.131807	*0.008328*	*	*4*	*6*	*2*	*1*	**30**	44	43
H5	0.133389	0.123621	*0.017215*	*0.008222*	*	*2*	*6*	*5*	**26**	42	41
H6	0.143289	0.133080	*0.022098*	*0.012662*	*0.004071*	*	*8*	*7*	**27**	44	43
H7	0.141898	0.143592	*0.012983*	*0.004129*	*0.012812*	*0.017547*	*	*3*	**29**	43	42
H8	0.141898	0.131807	*0.010504*	*0.002006*	*0.010368*	*0.014903*	*0.006250*	*	**31**	45	44
H9	0.119653	0.121103	**0.086915**	**0.082364**	**0.069076**	**0.073204**	**0.078026**	**0.085804**	*	27	26
H10	0.160591	0.162994	0.145323	0.139167	0.130666	0.140538	0.133283	0.143414	0.072751	*	*1*
H11	0.153961	0.156249	0.139241	0.133283	0.124995	0.134582	0.127591	0.137426	0.068643	*0.002039*	*

aligned with ClustalX (Thompson *et al.*, 1997) using the default parameters. On the basis of secondary structure information from *Drosophila melanogaster* (GenBank accession number X53506) as stored in the ribosomal RNA database (Gutell *et al.*, 1993), the alignment was corrected resulting in a final alignment length of 505 bp. No data had to be excluded because of alignment difficulties. The alignment is available from the first author upon request.

Data analysis

The number of unique mitochondrial haplotypes was determined with the computer program DnaSP 4 (Rozas *et al.*, 2003). To ensure a choice of a model of nuceotide substitution which describes the data accurately, a likelihood-ratio test was carried out with the program Modeltest 3.06 (Posada and Crandall, 1998). The model with the best fit was HKY, with a transition/transversion ratio of 3.7369, gamma distributed rates (shape parameter alpha = 0.2026) and no invariant positions. This model was then used to calculate maximum-likelihood estimates of pairwise genetic distances in Paup 4b10 (Swofford, 1998).

RESULTS

The 23 *Glyptonotus* large ribosomal subunit sequences varied in length between 494 and 505 bp. Among the LSU sequences, 11 unique mitochondrial haplotypes were distinguished (Table 1). Pairwise haplotype differences ranged from one to 47 observed substitutions over the length of the alignment (Table 2). Table 2 also shows distance estimates corrected for multiple substitutions.

Observed, i.e. uncorrected, distances may be a poor estimate of the true number of substitutions, because the identity of the substituted nucleotides is not taken into account. Two pairs of sequences can be separated by an identical number of observed substitutions. If one pair of differences were predominantly due to theoretically rare substitutions, the probability of undetected multiple substitutions is higher than differences due to the most frequently occurring substitution types. For this reason two sequence pairs featuring an identical number of substitutions may not have an identical corrected distance value, particularly at higher degrees of divergence (Table 2, e.g. H6/H10; H3/H11; H8/H11). Therefore, the observed values are only a rough estimate of true genetic divergence.

The largest haplotype diversity was among the *Glyptonotus* from the Eastern Weddell Sea. The two haplotype pairs from the Ross Sea and the Antarctic Peninsula differ only by one and two substitutions respectively. In the Eastern Weddell Sea there are more haplotypes present (7 haplotypes). These show corrected differences of up to 0.022098 (10 substitutions) when haplotype H 9 is ignored and up to 0.086915 (31 substitutions) when H 9 is considered.

For many, but not all, haplotypes the genetic distance scales with the geographic distances between sampling locations. Typically, the haplotypes which are found within each of the three sampling regions (AP, EWS, RS) are about an order of magnitude less divergent than genetic variation between sampling areas (indicate in italics in Table 2).

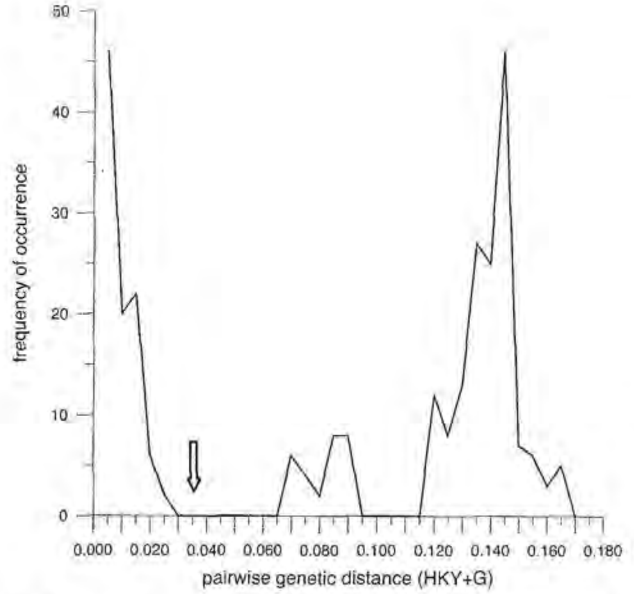

Fig. 2. – Maximum-likelihood estimates of pairwise genetic distances corrected for multiple hits, the mode choice is based on a likelihood-ratio test (for details see text). The arrow marks the smallest interspecific distance in the homologous region of the mitochondrial LSU (16S) gene between the species of marine isopods in Held (2003).

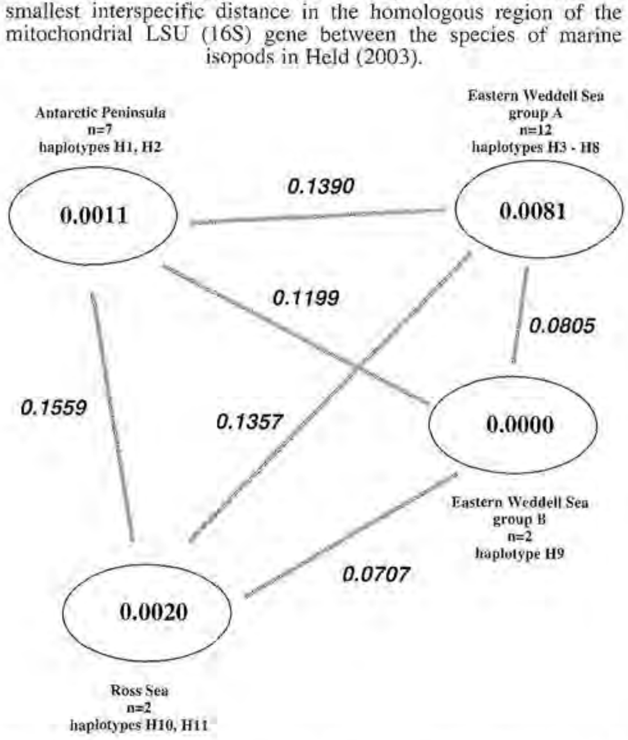

Fig. 3. – Average pairwise genetic distances (HKY + G) within and between four groups of 16S mitochondrial haplotypes of nominate *Glyptonotus antarcticus*; n denotes the number of sequences in the group, Hx indicates unique haplotypes as listed in Table 1.

This is not true, however, for *Glyptonotus* haplotypes in the Eastern Weddell Sea when haplotype 9 is included. The haplotype 9 versus haplotype 3 to 8 distances are in the lower range of values typical of trans-regions several thousand kilometres apart (bold values in Table 2).

The absence of a continuous spectrum of inter-haplotype differences is noteworthy (Fig. 2). Haplotypes are either similar (≤ 0.02210 corrected distance) or different (≥ 0.0691), with no intermediate values. If haplotype H 9 from the Eastern Weddell Sea is ignored, the gap is even more pronounced (≤ 0.02210 vs. ≥ 0.123621).

Only if haplotype H 9 is recognised as a fourth group in addition to the remaining haplotypes grouped according to their region of occurrence a clear pattern emerges.

Within the four groups, the genetic divergence is on average an order of magnitude smaller than any of the average between-group divergence values (Fig. 3).

DISCUSSION

The unexpectedly high genetic variability in nominate *Glyptonotus antarcticus* poses the question whether some or all of the genetic variability is an indication of cryptic speciation, or random, or reflects only locally adaptive differences within one species. There are four sharply distinct groups of mitochondrial haplotypes in *Glyptonotus*, which in the absence of samples connecting the three largely disjunct sampling areas (AP, EWS, RS) could be interpreted as either reproductively isolated species or populations of a single species.

Held (2000b, 2003) developed a set of criteria to provide evidence for cryptic speciation of serolid isopods on the high Antarctic shelf: (1) bimodal distribution of pairwise distance measures with no intermediate values, (2) differentiation at a level known for this gene from other undisputed species pairs closely related to the studied species, and (3) persistence of high levels of genetic differentiation in sympatry.

The *Glyptonotus* data fulfil the first criterion although without further analyses it remains uncertain which of the two gaps in Figure 2 can be regarded as separating the intra- and interspecific distances (see below). Because all distance values between 0.069 and 0.087 in Figure 2 are related to haplotype H9, this amounts to the question of the specific status of the two specimens bearing haplotype H9.

The *Glyptonotus* sequences presented in this study are differentiated at a level that surpasses the other isopods reported by Held (2003) and are in the upper range of typical inter-specific differentiation for this gene in other Crustacea (France and Kocher, 1996; Schubart, Neigel and Felder, 2000 and references therein). By induction from the data for other taxa, the threshold indicating the break between intra- and interspecific values can be assumed to lie between 0.02210 and 0.0691 corrected sequence divergence (position of arrow in Fig. 2).

It should be noted that the last criterion for distinguishing cryptic speciation from genetic plasticity is rigid. In particular, it is not a necessary criterion because different specific status is also possible in allopatric populations.

In the Eastern Weddell Sea specimens with haplotype H9 were caught in two different, but closely spaced, trawls which were situated approximately halfway between locations that were dominated by other haplotypes (Fig. 1). Two of these other haplotypes (H3 and H4) occurred both east and west of the stations where haplotype H9 was caught (Table 1). Although the sampling density—especially further away from the coast—is too low to give a conclusive answer at this time, this can be taken as evidence that haplotype H9 occurs sympatrically or at least in close proximity to other haplotypes while still maintaining a high degree of genetic dissimilarity, which was otherwise only observed between the major sampling areas in this study (AP, RS, EWS).

It is unclear what processes lead to the coexistence of the two putative species of *Glyptonotus* in the Eastern Weddell Sea, but the concept of geographic separation is strongly anthropocentric. France and Kocher (1996) presented data for the giant amphipod *Eurythenes gryllus*, demonstrating that surprisingly little separation in the vertical (a few hundred metres) can yield a genetic separation that is normally associated with horizontal distances, which are many orders of magnitude larger (thousands of kilometres). In *Glyptonotus* haplotype H9 occurs in close proximity to the haplotypes H3 to H8, though both specimens with H9 were the only *Glyptonotus* that were caught deeper than 600 metres (Table 1). It is possible that H9 occurs next to H3-8, but is separated from them vertically.

The molecular data strongly suggest that the four groups of haplotypes, including H9 as a separate group, are candidates for cryptic species, which in the past have been regarded as a single species with a wide distribution range.

Although the present analysis cannot prove the existence of cryptic speciation, it indicates patterns of variation that are not expected in a single species, even in the presence of local differences. In other words, this procedure provides necessary, but not entirely sufficient evidence for cryptic speciation. Nevertheless, it provides a useful starting point for subsequent systematic work aiming to reconcile the existing morphological and molecular data.

It is possible that many accounts of *Glyptonotus antarcticus* in the literature are the result of misidentifications and may refer to reproductively isolated species of the genus. The true distribution range of the putative species of *Glyptonotus* can therefore not be reconstructed from the literature but must refer to museum collections and newly collected material.

We therefore assume that the specimens B088, B101, B201 and B233 which were sampled at the original type locality (King George Island, South Shetlands) represent the species originally described by Eights in 1852. According to this interpretation, *Glyptonotus antarcticus* sensu strictu occurs along the Antarctic Peninsula, with two more species being present in the Eastern Weddell Sea and another in the Ross Sea. It is beyond the scope of this paper to ascertain the identity of one of the other haplotype groups (if any) with the other available names (*G. acutus* and *G. obtusus*). A revision of *Glyptonotus* based on morphological and molecular data from different genes with a formal (re)description of the species and a key is under preparation (Held, in prep.).

These results, if confirmed, also have significant ramifications outside taxonomy and biogeography because *G. antarcticus* is an abundant and conspicuous species of the high Antarctic benthos. It plays a major role as a model organism in ecological, biochemical and physiological studies (see introduction for references). If it comprises four or more species, then previous comparative studies of *G. antarcticus* could have been flawed. In particular, studies dealing with differences in adaptation to environmental parameters such as temperature and seasonality would need to be re-examined.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Distribution, reproductive and energetic conditions of decapod crustaceans along the Scotia Arc (Southern Ocean)*

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SUMMARY: Studies on decapod distribution patterns and reproductive and energetic conditions were carried out along the islands and shallows of the Scotia Arc (Southern Ocean) during the RV "Polarstern" LAMPOS expedition (ANT XIX/5) between April and May 2002. A clear biogeographic zonation was found. The Subantarctic Magellan-South Atlantic decapod fauna consisting of both "natant" (caridean) and "reptant" (astacidean, anomuran, and brachyuran) decapods appeared along the northern branch of the Scotia Arc to South Georgia, where Subantarctic and Antarctic faunas were found overlapping. An impoverished caridean shrimp fauna was found along the islands of the southern branch, from the South Sandwich Islands to the Antarctic Peninsula. Differences in the reproductive traits of the two most abundant species were detected. The reproductive cycle of *Notocrangon antarcticus* at South Georgia was more advanced than that at the South Orkney Islands, probably due to temperature differences between the two locations. Although the oogenesis and the reproductive cycle of *Munida subrugosa* seem to be in phase at Burdwood Bank and in the Beagle Channel, the oocyte number is probably lower at the former location. A new index was used to measure the energy devoted to reproduction by relating the energy contents of the egg mass/ovary plus hepatopancreas and the energy content of the whole body. This index revealed that the energy investment in reproduction was (1) independent of the sampling location, (2) species-specific, and (3) larger in caridean shrimps than in galatheid crabs.

Keywords: biogeography, Antarctic, *Munida*, *Notocrangon*, *Campylonotus*, *Nematocarcinus*.

RESUMEN: Distribución, condiciones reproductivas y energéticas de crustáceos decápodos en el Arco de Scotia (Océano Austral). – En abril y mayo de 2002, durante la expedición LAMPOS (ANT XIX/5) a bordo del BIO "Polarstern" se realizaron estudios sobre la distribución y condiciones reproductivas y energéticas en aguas someras del Arco de Scotia (Océano Austral). Se encontró una clara zonación biogeográfica: sobre la rama septentrional del Arco de Scotia hasta las Islas Georgias del Sur prevalece fauna de decápodos subantárticos –de la Provincia Magallanica y del Atlántico Sur– constituida por "Natantia" (carideos) y "Reptantia" (astacideos, anomuros y braquiuros). En las Islas Georgias del Sur las faunas subantárticas y antárticas se superponen. En la rama meridional, desde las Islas Sandwich del Sur hasta la Península Antártica, se encontró una fauna limitada a los camarones. Se hallaron diferencias en aspectos reproductivos de dos de las especies más abundantes. El ciclo reproductivo de *Notocrangon antarcticus* en las Islas Georgias del Sur estaba avanzado en comparación con el de la población de las Islas Orcadas del Sur, probablemente debido a la diferencia de temperaturas entre ambas localidades. A pesar que la oogenesis y el ciclo reproductivo de *Munida subrugosa* parecieran estar en fase en el Banco Burdwood y en el Canal Beagle, el número de oocitos es probablemente menor en la primera localidad. Se utilizó un nuevo índice que relaciona el contenido energético entre la masa de huevos/ovario más el hepatopancreas y el contenido energético del animal completo. Este índice reveló que la inversión energética en reproducción fue (1) independiente de la localidad, (2) especie-específica y (3) más alta en camarones que en cangrejos galateidos.

Palabras clave: biogeografía, Antártida, *Munida*, *Notocrangon*, *Campylonotus*, *Nematocarcinus*.

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INTRODUCTION

Southern Ocean benthic decapods are among the best marine biological examples for a clear zoogeographic separation of the Antarctic from the Subantarctic or antiboreal provinces, such as the Magellan region of South America (Hedgpeth, 1969; Gorny, 1999). This is demonstrated by a rich Subantarctic decapod fauna including various "reptant" (Astacidea, Anomura, and Brachyura) and "natant" (Caridea) families, in comparison with a strongly impoverished caridean shrimp fauna and a few lithodid crabs left in Antarctic waters south of the Polar Frontal system (Gorny, 1999; Thatje and Arntz, 2004). The reasons for this impoverishment in decapod diversity towards polar seas in general are numerous, but have been principally attributed to physiological constraints and a lack of life history adaptations to polar conditions (for discussion see Frederich *et al.*, 2001; Thatje *et al.*, 2003; 2005).

The Magellan region is the geographically closest Subantarctic Province to Antarctica (Hedpgeth, 1969). Both regions probably remain geographically connected by the islands and shallow waters of the Scotia Arc (Fig. 1). From a biogeographic point of view, this submarine extension of the South American Andes may constitute a transitional biogeographic area for decapods from either side—the Antarctic and the cold-temperate waters (Arntz *et al.*, 1999). Hence, the Scotia Arc can be considered as a key zone for the study of changes in decapod life history and distribution, indicating both evolutionary pathways and changes in the marine biota through geological times (Crame, 1999; Thatje *et al.*, 2005).

The reproductive effort (RE) is a suitable parameter for elucidating energy investment in reproduction (Clarke, 1987) but is rarely used in decapods (Fernández *et al.*, 2000; Brante *et al.*, 2003). So far, the RE has been a difficult parameter to measure, because it involves a great deal of detailed physiological work. In fact, this parameter considers the cost of activity associated with reproduction, the associated respiratory cost, gonad production and the energy assimilated (Clarke, 1987). The reproductive output (RO) has been commonly used as a proxy parameter for RE, especially in marine invertebrates (Hughes and Roberts, 1980; Hines, 1982; Havenhand and Todd, 1989). The RO is calculated as the ratio between gonad and body masses (Clarke, 1987), and particularly in decapods as the ratio between egg and body masses (Hines, 1982). The RO is an inadequate estimator of RE in the case of brooding species, because the energy allocated to brood care is not considered (Fernández *et al.*, 2000; Brante *et al.*, 2003). However, given the

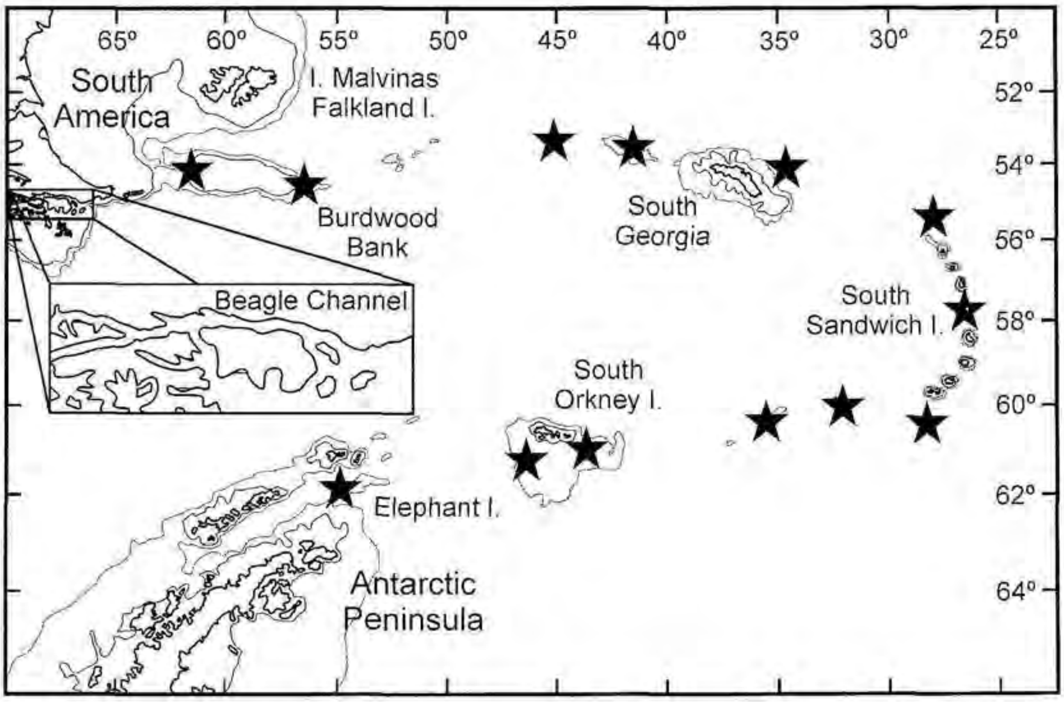

FIG. 1. – Area under investigation, with indication of sampling stations (stars), from the Subantarctic Magellan region of South America along the Scotia Arc islands to the Antarctic Peninsula.

logistic limitations to accessing good quality samples from polar seas, the RO may still be considered as an approximation which allows comparisons of energy investment in reproduction in related species at the same phase of their reproductive cycle.

Energetic costs of reproduction in high latitudinal decapods have been widely restricted to comparisons of lipid and fatty acid contents of eggs in relation to fecundity and female size (Clarke, 1979, 1983) as a measure of ecological fitness (Graeve and Wehrtmann, 2003; Thatje *et al.*, 2004). Whereas early studies suggested clines in energy contents of eggs as an indicator for latitudinal changes in environmental conditions, mainly temperature and food availability (e.g. Wehrtmann and Kattner, 1998), a recent study indicated no substantial difference in polar shrimp eggs compared to those of related taxa from temperate and tropical regions (Graeve and Wehrtmann, 2003).

Even if the decapod composition at either side of the Antarctic Convergence is different, we expect energy content to change in response to varying environmental conditions. In this context, energetic and reproductive parameters are supposed to reflect the ecological fitness of species living at their distributional limits. In this paper, we describe the reproductive status, the reproductive output and the energy content of the most abundant decapods along the Scotia Arc. We introduce a new index, including the hepatopancreatic energy, which measures the energy devoted to egg production, and thus allows a comparison between populations or species desynchronised in their reproductive cycle.

MATERIALS AND METHODS

Sampling of decapod material

Decapods were collected during the XIX/5 (LAMPOS) expedition of RV "Polarstern" along the Scotia Arc between 3 April and 5 May 2002 (Fig. 1). Samples were collected with an Agassiz trawl (AGT) and a fish bottom trawl. Detailed cruise information has been published by Arntz and Brey (2003).

In order to compare reproductive and energetic conditions along latitude/longitude, additional material of three decapod species was sampled in the Beagle Channel (Fig. 1). In March, May and July 2002, and May 2003, samples of *Munida subrugosa*, *Campylonotus vagans* and *C. semistriatus* were obtained. Sampling was done using an epibenthic trawl operated with an inflatable dinghy (see Tapella *et al.*, 2002 for details).

In each sampling, all decapods were separated from the catch, placed on ice and identified to species level according to Boschi *et al.* (1992) and Retamal (2000). Animals were sorted by sex, counted, and their carapace length (CL) was measured with a digital caliper to the nearest 0.01 mm. Sex was differentiated from differences in pleopod morphology or presence of eggs. The proportion of ovigerous females was evaluated from the presence of eggs attached to the pleopods. At least 20 females of frequently occurring species from each haul were randomly selected and dissected. Gonads were sorted into different developmental stages according to their general appearance (colour, gonad and oocyte sizes, c.f. Tapella *et al.*, 2002). Gonads, hepatopancreas and eggs were removed, dried separately to constant weight at 55°C and pelletised. The caloric content of each sample was obtained by burning pellets of 20-200 mg in an adiabatic calorimeter (Parr model 1425). Energy values were calculated using standard equations (Parr Instrument Company, 1993). The values obtained were corrected for ash and acid content and expressed as $kJ \cdot g^{-1}$ ash free dry mass (AFDM). Differences in the energy content of ovaries or egg mass and hepatopancreas were analysed using one-way analysis of variance (ANOVA, Sokal and Rohlf, 1995).

The reproductive status was studied using several parameters. Oocyte diameter was measured using a binocular microscope and a gridded eyepiece with a precision of ±0.17 mm. The gonado-somatic index was estimated as the ratio between ovary and whole body dry mass. The reproductive output (RO) was calculated as the ratio between the egg mass and body dry mass. The energy condition associated with reproduction (reproductive investment) was estimated using two different indices. Indices were calculated as ratios between the energy contents (EC) of (a) ovary or egg clutch and the whole female (EI_a), as compared to the RO, or (b) ovary or egg clutch plus the hepatopancreas and the whole female (EI_b). In all cases, the body mass or energy in the denominator of the calculations included all the body parts, e.g. the ovary. We decided to incorporate the energy content of the hepatopancreas in EI_b because this organ stores energy in the form of lipids just before or during the ovarian development and is the main energy supply to the ovary during the secondary vitellogenesis (Chapelle, 1977; Mourente

TABLE 1. – Species list of benthic decapod crustaceans collected along the Scotia Arc during the cruise ANT XIX/5 (LAMPOS) in April/May 2002. Numbers represent the total specimens caught per species. References: Shag-Georgia refers to Shag Rocks and South Georgia; Banks refers to Herdman and Discovery Banks.

Infraorder	Family	Species	Localities					
			Burdwood Bank	Shag-Georgia	South Sandwich Islands	Banks	South Orkney Islands	Elephant Island
Caridea		Undetermined Caridea	1		1			
	Nematocarcinidae	*Nematocarcinus lanceopes*			10			
	Hippolytidae	*Chorismus antarcticus*		2				
		Undetermined sp. 1			3			
	Crangonidae	*Notocrangon antarcticus*		401			253	3
	Campylonotidae	*Campylonotus semistriatus*		10				
		Campylonotus vagans	1					
		Campylonotus arntzianus			2			
		Undetermined sp. 2	1					
	Palaemonidae	Undetermined sp. 3			2	1		
Astacidea	Nephropsidae	*Thymops birsteini*	2					
Anomura	Galatheidae	*Munida subrugosa*	238					
		Munida spinosa	10					
	Paguridae	*Pagurus comptus*	3					
		Pagurus forceps	3					
	Lithodidae	*Paralomis spinosissima*		4				
		Lithodes confundens	3	3				
Brachyura	Majidae	*Eurypodius latreillei*	27					
		Eurypodius longirostris	6					
		Eurypodius sp.	1					
Species number			12	5	5	1	1	1

and Rodríguez, 1991; Haefner and Spaargaren, 1993). This approach is particularly useful for comparing species in different reproductive states imposed by variable environments, climate zones or latitude. Hence, the EI_b index would better show changes in the reproductive effort of species in different reproductive statuses.

Differences in the EI_b index, EC of ovary or egg mass, and EC of hepatopancreas among crustaceans were analysed using one-way analysis of variance (ANOVA). The assumptions of normality and homogeneity of variances were tested in all cases with the Kolmogorov-Smirnov and Bartlett tests respectively (Sokal and Rohlf, 1995). Unplanned comparisons were done when significant differences were found. Null hypotheses of equality of reproductive parameters between Anomura and Caridea were tested with a one-way ANOVA and orthogonal contrasts.

RESULTS

Species composition and distribution of benthic Decapoda along the Scotia Arc

Sampling stations close to the South American continent showed the highest species richness when compared with the stations sampled along the Scotia Arc (Table 1). At Burdwood Bank, a predominance of the galatheid crab *Munida subrugosa*, an abundant species of the channels and fjords of Tierra del Fuego, was found. The most abundant species following *M. subrugosa* were majid species of the genus *Eurypodius*, the only brachyuran crab in our samples. The first faunistic change in Magellan Province fauna was observed at Shag Rocks, close to South Georgia, where lithodid crabs were still present, but represented by different species than in the Magellan region and at Burdwood Bank (Table 1). However, the caridean shrimp *Campylonotus semistriatus*, typical of Magellan and south-west Atlantic waters, still constituted a faunistic element of Shag Rock waters. South of South Georgia, the decapod fauna was only represented by Antarctic shrimp species, being dominated by *Notocrangon antarcticus* (Table 1). Further south, the shallow waters off the Sandwich Islands revealed an extremely poor decapod fauna. Off South Orkney and Elephant Islands, *N. antarcticus* was the only representative of decapod shrimps, where decapodid and juvenile stages (3 individuals of 2.0, 2.3 and 3.3 mm CL) were also caught for the first time.

Reproductive condition

All female *Munida subrugosa* captured at Burdwood Bank were non-ovigerous (Table 2) and

TABLE 2. – Reproductive traits of six species of decapod crustaceans from the Beagle Channel and different locations of the Scotia Arc. GSI: gonadosomatic index; DM: dry mass; RO: reproductive output; EC: energy content; EI_a and EI_b , reproductive energy indices; OF: proportion of ovigerous females; $_{O-E}$: ovary or egg clutch; $_B$: body; $_H$: hepatopancreas. Indices in bold were calculated with the energy content of the egg clutch instead of ovaries (in regular font). N_1 and N_2 indicate sample sizes for reproductive traits and proportion of ovigerous females respectively.

Species	Site	GSI (DM_O/DM_B)· 100	RO (DM_E/DM_B · 100)	Energy Indices EI_a (EC_{O-E}/EC_B · 100)	 EI_b [($EC_{O-E}+EC_H$)/ EC_b · 100]	EC total (kJ · g^{-1} AFDM)	N_1	OF% (N_2)
Anomura								
Munida subrugosa	Beagle Channel (July)		**10.75 ± 2.81^{a}**	**14.60 ± 4.39^{a}**	**20.11 ± 6.13**	**17.42 ± 1.42**	12	100 (12)
Munida subrugosa	Beagle Channel (March and May)	2.80 ± 1.77		3.25 ± 1.98^{b}	20.58 ± 6.56	20.26 ± 1.17	19	0 (19)
Munida subrugosa	Burdwood Bank	1.54 ± 0.72		3.12 ± 1.88^{b}	15.30 ± 7.04	18.23 ± 1.74	39	0 (131)
Munida spinosa	Burdwood Bank		**8.57 ± 2.53^{a}**	**12.89 ± 2.51^{a}**	**19.96 ± 5.02**	**18.08 ± 1.30**	4	80 (5)
Caridea								
Campylonotus vagans	Beagle Channel		**15.29 ± 8.44**	**17.65 ± 3.69**	**24.43 ± 3.54^{a,b,c}**	**22.09 ± 0.93**	9	69 (13)
Campylonotus semistriatus	Beagle Channel		**17.29 ± 2.73**	**22.85 ± 5.06**	**29.64 ± 4.82^{b,c}**	**22.39 ± 0.92**	3	50 (6)
Notocrangon antarcticus	South Georgia		**14.19 ± 3.31**	**18.03 ± 4.00**	**21.12 ± 5.43^{a}**	**21.64 ± 1.33**	33	98 (115)
Notocrangon antarcticus	S. Orkney Is.	8.54 ± 2.20		10.18 ± 2.17	21.83 ± 4.31^{a,c}	22.88 ± 1.58	41	26 (119)
Nematocarcinus lanceopes	S. Sandwich Is.	10.00 ± 0.26		10.77 ± 1.09	31.22 ± 3.45^{b}	27.00 ± 1.74	3	0 (7)

showed a wide size range (Fig. 2). Particularly small specimens (<8 mm CL) occurred at this site, a pattern similar to populations at greater depths of the Beagle Channel, > 90 m depth (c.f Tapella, 2002). In the Beagle Channel females and males attain physiological maturity at 9.9 and 8.0 mm CL respectively (Tapella *et al.*, 2002). Accordingly, at Burdwood Bank 5.6 and 18.6% of females and males respectively were immature. In April, gonads of *M. subrugosa* from the Burdwood Bank were less developed than those in the Beagle Channel. In the former location, the gonado-somatic index was significantly lower than in the Beagle Channel (Table 2), but the oocyte diameter was identical (Burdwood Bank: 0.22 ± 0.01 mm; Beagle Channel: 0.22 ± 0.02 mm). In *M. spinosa* from Burdwood Bank the majority of females were carrying undifferentiated eggs in April (Table 2), whereas in *M. subrugosa* in the Beagle Channel egg extrusion occurs in July (Tapella *et al.*, 2002). However, both species of *Munida* showed comparable reproductive outputs at the two different locations: the RO, and EI_a of *M. subrugosa* from the Beagle Channel recorded in July were similar to those of *M. spinosa* from the Burdwood Bank in April (Table 2).

Clear differences in the reproductive condition were detected in the two geographically separated populations of *Notocrangon antarcticus*. At South Georgia, 98% of female *N. antarcticus* were ovigerous (Table 2; Fig. 2), carrying undifferentiated eggs with non-developed ovaries (Fig. 3). In contrast, off the South Orkney Islands only 26% of all captured females were egg-carrying (Table 2; Fig. 2), though non-ovigerous individuals showed relatively well-developed gonads (Fig. 3; Table 2). Hence, these females were assumed to be close to egg-extrusion. Differences between the GSI at the South Orkney Islands and the RO at South Georgia, along with differences in EI_a at both locations, indicate that the reproductive cycle in *N. antarcticus* is delayed at the South Orkney Islands (Table 2). The smallest ovigerous females occurring in our samples were 11.9 and 15.4 mm CL at South Georgia and the South Orkney Islands respectively (Fig. 2), indicating differences in size at gonadal maturity in both populations. Size frequency distributions also differed between locations (Fig. 2). On average, female *N. antarcticus* at South Georgia were smaller (14.6 ± 1.2 mm CL) than those from the South Orkney Islands (16.6 ± 1.3 mm CL). Size frequency distributions of males were more dispersed (Fig. 2) and their mean sizes were 12.2 ± 3.3 and 13.3 ± 2.6 mm

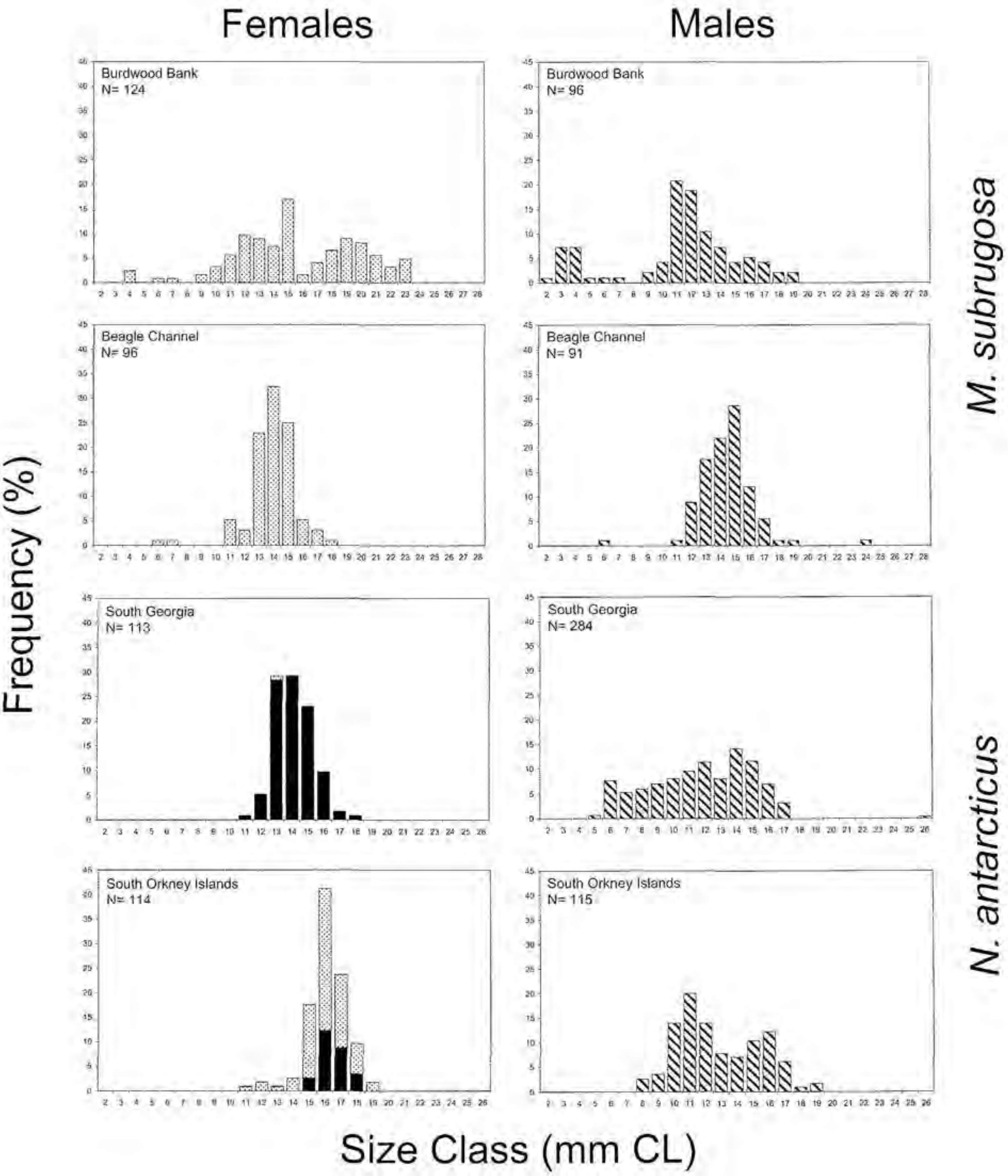

FIG. 2. – Size frequency distributions for male and female *Munida subrugosa* from the Burdwood Bank and the Beagle Channel, and *Notocrangon antarcticus* from South Georgia and the South Orkney Islands. Ovigerous females are represented by black bars. N = sample size.

CL at South Georgia and the South Orkney Islands respectively.

The RO was different in the two decapod groups (Table 2). Principally, anomurans showed significantly lower values of RO than carideans (F_{ANOVA} =4.1; p=0.005; $F_{contrasts}$ =14.1; p<0.001). Among caridean shrimps, RO variability was relatively high, even within the same genus, as for example in *Campylonotus* (Table 2). When the reproductive investment is expressed as the energy content of the ovary in relation to that of the body (EI_a), differences became less evident (Table 2, bold numbers). The highest, although statistically non-significant, values of EI_a were those of species from the Beagle

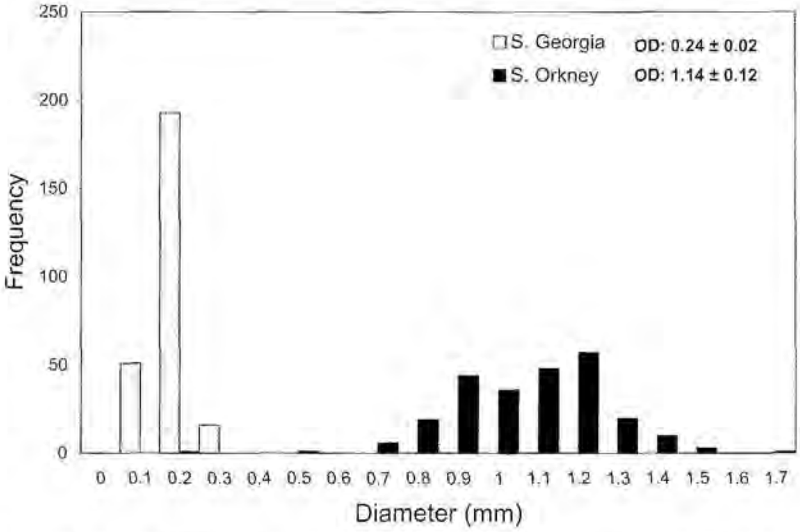

FIG. 3. – Size frequency distribution of oocyte diameter in *Notocrangon antarcticus* in waters off South Georgia (grey bars) and the South Orkney Islands (black bars). Average oocyte diameter (OD) and one standard deviation are indicated at the top right.

Channel, namely *M. subrugosa* and *C. semistriatus*. Among the species with ovigerous females, the lowest EI_a was shown by *M. spinosa* at Burdwood Bank (Table 2).

In those species of which two populations were sampled, comparisons between GSI and RO, and between EI_a, indicated geographic differences in the oogenesis process. In *M. subrugosa* the GSI at Burdwood Bank in April corresponded to 14% of the RO in the Beagle Channel in July just after egg extrusion. Likewise, EI_a at both locations at Burdwood Bank (in April) and in the Beagle Channel (in March and May) reached about 20% of the maximum value found in the Beagle Channel in July. Hence, in April 2002, the secondary vitellogenesis of *M. subrugosa*, i.e. lipid accumulation in the ovary, was starting in both locations. In *N. antarcticus* off the South Orkney Islands, the EI_a represented 56% of values found at South Georgia, where eggs were recently extruded. This suggests that in the South Orkney Island population the secondary vitellogenesis was advanced and the oocytes were close to extrusion (c.f. Fig. 3).

Energy condition

Table 2 summarises the total energy content by species and sampling site. EC was higher in caridean than in anomuran species (F_{ANOVA} =47.6; p<0.001; $F_{contrasts}$ =207.1; p<0.001). Among *Munida* spp. the total and ovarian energy contents (ECs) were similar among the different sampling locations (Table 2; Fig. 4). The only observed difference in energy conditions of *M. subrugosa* was a lower hepatopancreatic EC at Burdwood Bank than in the Beagle Channel (Tukey test p<0.001; Fig. 4). Among carideans, total EC differed significantly (Table 2; Fig. 4). Differences were due to the high EC of *N. lanceopes*, reflected by a significantly high EC of ovaries and hepatopancreas. In *N. antarcticus*, the hepatopancreatic EC was significantly lower at South Georgia than at the South Orkney Islands (Tukey test p<0.001; Fig. 3).

A typical reproductive energy index that involves the energy contents of egg or ovaries and the somatic energy (EI_a) was useless for comparison between species at different stages of their reproductive cycle, because delays in the ovarian development due to geographic differential distribution were not reflected (Table 2). For example, *M. subrugosa* with developing ovaries sampled during the secondary oogenesis (March-May) showed lower EI_a than individuals with already extruded eggs (July). Likewise, in *Notocrangon antarcticus* from South Georgia with recently extruded eggs, the EI_a was higher than in those off the South Orkney Islands, where oocytes were in the final phase of development. Conversely, when the hepatopancreas was included in the index, EI_b values were more comparable in measuring the reproductive output among the species in a different reproductive status (Table 2). The EI_b was similar among Anomura, i.e. *Munida* spp. (F=1.81; p=0.17), and different among caridean species (F=5.56; p<0.001). This difference was due to *N. lanceopes* from the South Sandwich Islands, which showed a significantly higher EI_b than *N. antarcticus* from the

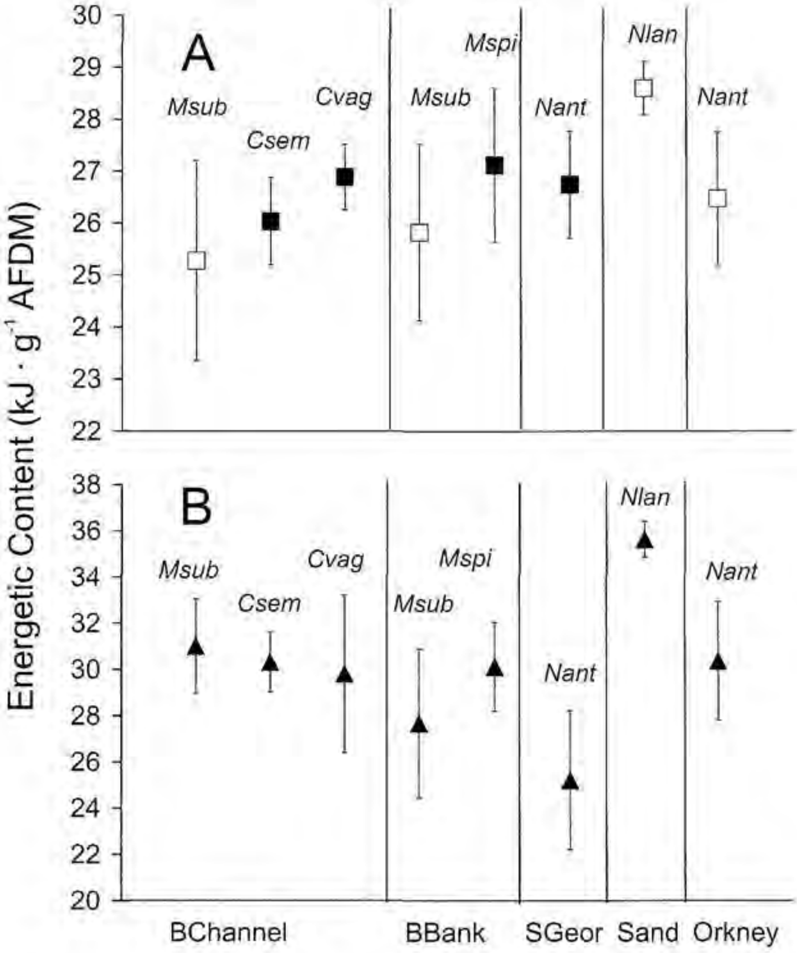

FIG. 4. – Average energy content (kJ · g^{-1} AFDM) ± 1 standard deviation of (A) ovary or egg mass (full and empty squares respectively), and (B) hepatopancreas from decapod species in the Beagle Channel and along the Scotia Arc. References: *Msub: Munida subrugosa; Mspi: M. spinosa; Csem: Campylonutus semistriatus; Cvag: C. vagans; Nant: Notocrangon antarcticus; Nlan: Nematocarcinus lanceopes;* BChannel: Beagle Channel; BBank: Burdwood Bank; SGeor: South Georgia; Sand: South Sandwich Islands; Orkney: South Orkney Islands.

South Orkney Islands and South Georgia (Table 2). The two populations of *N. antarcticus* showed a similar EI_b.

DISCUSSION

Decapod biogeography along the Scotia Arc

We found an extension of the Magellan fauna towards South Georgia along the shallows of the northern branch of the Scotia Arc. At least for the decapod fauna, South Georgia has been formerly considered to be part of the Antarctic biogeographic region (Gorny, 1999). However, the coexistence of typically Subantarctic lithodids (see Thatje and Arntz, 2004 for a review) and shrimps such as *Campylonotus semistriatus* with Antarctic shrimps *Chorismus antarcticus* and *Notocrangon antarcticus* probably justifies considering this area as transitional for decapod distribution. Currents associated with the dominant West Wind Drift, e.g. the Cape Horn and Malvinas-Falklands currents, may disperse planktonic larvae of species occurring off the southern tip of South America (Antezana, 1999). Planktonic larvae of most benthic decapods occurring in southern South America—even those typically intertidal species such as *Halicarcinus planatus*—were also found at Burdwood Bank (Bacardit, 1986). However, given the distributional depth limits of both Anomura and Brachyura (Gorny, 1999), their presence along the northern branch of the Scotia Arc is probably only possible in the scattered shallows, which serve as biogeographic stepping stones and local refuges. However, few data are available for the deep waters of the Scotia Arc and future research should explore their role in faunal exchange. In particular the deep-sea trenches east off the Scotia Arc could be pathways of interchange for some benthic decapod species (Thatje and Arntz, 2004) if physiological constraints imposed by low water temperatures could be overcome (Thatje *et al.*, 2005).

Reproductive conditions

The scarcity of decapods sampled from different populations does not allow for generalisations about decapod reproductive patterns along the Scotia Arc. Nevertheless, we detected differences in the reproductive cycle of the two most abundant species. The oogenesis and therefore the reproductive cycle of *Munida subrugosa* from the Burdwood Bank seems to be in phase with that of those from the Beagle Channel, since the oocyte diameter and the relative energy of the ovary were similar. However, the GSI and the energy content of the hepatopancreas in *M. subrugosa* from the Burdwood Bank were lower, contrasting with the similar RO, EI_b and hepatopancreas energy content of *M. subrugosa* from the Beagle Channel and *M. spinosa* from the Burdwood Bank. *Munida subrugosa* inhabits the cold temperate waters off the southern tip of South America (Matthews, 1932; Retamal, 1981; Boschi *et al.*, 1992). This study extends the geographical distribution of *M. subrugosa* southeast to the Burdwood Bank (c.f. Rayner, 1935; Boschi *et al.*, 1992), and this site probably constitutes a marginal habitat for this species. During the secondary oogenesis, the ovarian quality, i.e. mass and energy contents, of *M. subrugosa* is determined by the food type (Romero, 2003). Hence, food availability and poor environmental conditions, reflected by a low hepatopancreatic energy content, probably constrain ovarian development, resulting in a low GSI. This indicates that oocytes will probably be less numerous though they contain the same energy content as in areas in which *M. subrugosa* is a dominant faunistic element, like the Beagle Channel (Gutt *et al.*, 1999; Pérez-Barros *et al.*, 2004).

The most important difference in the reproductive cycle and associated energy parameters was found in *Notocrangon antarcticus*. The reproductive cycle at South Georgia was advanced in comparison with that at the South Orkney Islands. This is probably due to higher temperatures north of the Antarctic Convergence. Bottom temperature was 2.2 and –0.15°C off South Georgia and the South Orkney Islands respectively (Grabbert *et al.*, 2003). In ectotherm invertebrates, temperature is the main exogenous factor which determines the extent of oogenesis and growth (e.g. Bergstrom, 1991; Pearse and Mc Clintock, 1991; Calcagno *et al.*, 2005) and is likely to be responsible for the differences in ovarian development rate and female maturity size between South Georgia and the South Orkney Islands. Differences in reproductive timing of *N. antarcticus* between the same locations were also reported by Makarov (1970). Females attain size at maturity earlier and fecundity is higher in waters off South Georgia than at the South Orkney Islands (Makarov, 1970).

Lipid mobilization between the hepatopancreas and ovaries, and eventually to the eggs, justifies the inclusion of the hepatopancreas energy in the (EI_b) index. During the oocyte lipid deposition, i. e. secondary vitellogenesis, events that involve the energy flux can be summarised as follows. Prior to ovarian growth, lipids accumulate in the hepatopancreas during a variable period of time. Then, lipids are transported to and deposited in the oocytes, with the increase in energy in the ovary and the concurrent decrease in the hepatopancreatic energy. During and shortly after egg intrusion, both the ovary and the hepatopancreas have low energy contents, and finally the hepatopancreas recovers by re-building its energy reserves (Harrison, 1990; Mourente and Rodríguez, 1991; Haefner and Spaargaren, 1993; Styrishave and Andersen, 2000; Albessard *et al.*, 2001; Wen *et al.*, 2001).

The inclusion of the hepatopancreatic energy into an index (EI_b) allowed us to make comparisons between species with differences in the timing of their reproductive cycle. Oocyte extrusion of *Notocrangon antarcticus* in the South Orkney Islands was later than at South Georgia, where females were mostly ovigerous, with a very recently spent ovary and had a hepatopancreas with a lower energy content than those from the South Orkney Islands (Fig. 4B). The difference between the maximum ovary size and a developing ovary is the difference between the RO at South Georgia and the GSI at the South Orkney Islands. We interpret that the higher energy value in the hepatopancreas of *N. antarcticus* at the South Orkney Islands occurs because this energy is still to be transferred to ovary growth. The index (EI_b) revealed that the energy allocated to egg production plus that stored in the hepatopancreas is similar at the two locations. *Nematocarcinus lanceopes* exhibited ripe gonads and the GSI represented 63% of the maximum GSI reported by Gorny and George (1997), which is comparable to 60% of the GSI:RO ratio for *N. antarcticus* at the two sample sites. Hence, we assume that during April 2002 *N. lanceopes* were in the final phase of the secondary vitellogenesis, suggesting that egg extrusion would occur at the same time as in *N. antarcticus* off the South Orkneys. Therefore, the EI_b is comparable among all Caridea sampled for this study.

Our results show that this new index EI_b is species-specific and independent of the sampling location and reproductive status. The EI_b does not reflect a clear trend along the Scotia Arc. For example, in *Notocrangon antarcticus* from different localities, EI_b values and thus the reproductive investment are the same, regardless of whether females are in the secondary oogenesis or carrying eggs. Our results of higher EI_b in *N. lanceopes* than in *N. antarcticus* are consistent with the higher egg lipid content in the former species (Graeve and Wehrtmann, 2003), and justify the inclusion of hepatopancreatic energy into the index. The Subantarctic shrimp *C. semistriatus* shows higher EI_b than *N. antarcticus*, both near the Antarctic Convergence (South Georgia) and in the Antarctic waters off the South Orkneys. Although the EI_b index does not consider the cost of egg-care (c.f. Brante *et al.*, 2003), this approximation allowed us to obtain a reliable estimation of investment in egg production, and is useful for comparing species with a different reproductive status obtained from a single sampling period, or for making latitudinal comparison without a time series. If this period coincides with—or is close to—egg extrusion, this index could be useful for comparing the energy investment in egg production between related species or different populations of a single species.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

On the distribution of decapod crustaceans from the Magellan Biogeographic Province and the Antarctic region*

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SUMMARY: The distribution of decapod crustaceans in the southernmost areas of South America and the Antarctic is assessed considering the Magellan Biogeographic Province instead of the antiboreal region. Possible associations between decapod crustaceans from the Magellan Biogeographic Province and those from the Antarctic region are analysed. Species records were assigned to seven geographic regions that were clustered using multivariate analyses based on species presence/absence and Bray-Curtis similarity. The results showed two well-established clusters, one of which included the Pacific and Atlantic areas of the Magellan Province, the southern tip of South America and the Kerguelen Arc islands, with the highest similarity between the southern tip and the Atlantic area. Another cluster was well separated and included the Antarctic and South Georgia with the highest similarity index. Earlier studies and results obtained here suggest that the faunas of southern Chile and southern Argentina are biogeographically related. There is a low level of association among decapod species from the circum-Antarctic region and the Magellan Province.

Keywords: decapod crustaceans, Magellan Biogeographic Province, circum-Antarctic distribution.

RESUMEN: SOBRE LA DISTRIBUCIÓN DE LOS CRUSTÁCEOS DECÁPODOS DE LA PROVINCIA BIOGEOGRÁFICA MAGALLÁNICA Y LA REGIÓN ANTÁRTICA. – Se estudió la distribución de los crustáceos decápodos en las áreas más australes de Sudamérica, considerando la Provincia Biogeográfica Magallánica en lugar de la región antiboreal. Se analizó la posible asociación entre los crustáceos de la Provincia Magallánica y los de la región antártica. Las especies registradas fueron asignadas a siete regiones geográficas, las que fueron agrupadas utilizando análisis de agrupamientos basado en presencia/ausencia de especies. Se utilizó el índice de similitud de Bray- Curtis. Los resultados mostraron dos grupos bien definidos de los cuales uno incluyó las áreas pacífica y atlántica de la Provincia Magallánica, la del extremo más austral de Sudamérica y las islas del Arco de Kerguelen. El otro grupo estuvo separado del anterior e incluyó la Antártida y las Islas Georgias con el índice de similitud más alto. Estudios anteriores y los resultados obtenidos en éste, sugieren que las faunas del sur de Chile y sur de Argentina se encuentran relacionadas. Existe baja asociación entre las especies actuales de crustáceos decápodos con distribución circumantártica y las de la Provincia Magallánica.

Palabras clave: crustáceos decápodos, Provincia Biogeográfica Magallánica, distribución circumantártica.

INTRODUCTION

Our knowledge on the distribution of decapod crustaceans from the Southern Ocean and Subantarctic areas has increased considerably in the past years, and some studies have been concentrating on faunal connections of the Magellan and Antarctic decapod fauna (Arntz *et al.*, 1999; Gorny, 1999; Thatje and Arntz, 2004).

A common feature of previous studies is that the

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Magellan region is referred to as the South American antiboreal region, between the Subtropical and the Antarctic Convergence (Ekman, 1953). Holthuis (1952) identified Chiloé Island in the Pacific Ocean as the northern boundary of the South American antiboreal region. In the Atlantic, the Río de La Plata was the limit considered in other studies. Zarenkov (1968) recognised the Antarctic Convergence as the limit of the Antarctic decapod fauna. Boschi (1979b) proposed using the term "South American Notal" for the southern hemisphere instead of "antiboreal", and recognised that the fauna from southern Chile and southern Argentina are related (Boschi, 2000a).

The distribution and biodiversity of decapods on the continental shelves of North and South America were divided into sixteen biogeographic provinces by Boschi (2000a, b), who defined a province as "part of the neritic zone with a relatively narrow range of temperatures where the fauna shows certain homogeneity". It should be mentioned that species can be present in more than one province. The Maguellan Biogeographic Province extends from northern Chiloé Island on the Eastern Pacific Ocean south to the Maguellan and Tierra del Fuego region through Cape Horn, and reaches the coastal area of the southwestern Atlantic Ocean off the Patagonian region. It includes the Islas Malvinas/Falkland Islands, and ends north at the Península Valdés (Boschi, 2000a, b). The Province extends off the continent at 43°-44°S stretching north to reach 35°S at a distance of 100-150 km from the coast and 60-200 m water depth. In the southwestern Atlantic, the Argentinean Biogeographic Province includes the coastal waters off Patagonia from 43-44°S to 23°S (see Boschi, 2000a). Between 43-44°S and 35°S, both provinces occupy the same latitudinal range (see Boschi, 2000a, b; Fig. 1).

The determination of regions in the oceans (Ekman, 1953) and provinces on the continental shelves (Boschi, 2000a) follow oceanographic characteristics, temperature being one of the main determinants in the distribution of crustaceans. However, the distribution of the circum-Antarctic decapod fauna studied by other authors also considered ecological features such as productivity and habitat (Gorny, 1999), and most recently ecological and physiological limits in crustaceans (for a review see Thatje and Arntz, 2004). In studies in which the boundaries of the South American antiboreal region were considered, a number of species were placed in different biogeographic provinces such as the Magellan or the Argentinean. Boschi (2000a) concluded that at that time the number of species present in the Magellan Province was 79, of which 19 were endemic. Since then, new records have been published (Thatje, 2000, 2003, Thatje and Gerdes, 2000).

The aim of this study is to determine whether there is a biogeographic association between decapod crustaceans from the Magellan Biogeographic Province and those from the Antarctic region, and to compare our results with those of previous studies in which species with circum-Antarctic distribution were also considered.

MATERIAL AND METHODS

The database utilised here includes species from the Magellan Province compiled by Boschi (2000a), and those with circum-Antarctic distribution and new species updated from the literature (Arntz and Gorny, 1991; Arntz *et al.*, 1999; Boschi *et al.*, 1992; Retamal, 2000; Zarenkov, 1968; Gorny, 1999; Kirkwood, 1984; Macpherson, 1988; Thatje and Gerdes, 2000; Thatje, 2000, 2003; Yaldwyn, 1965). The Magellan Province includes species present on both coasts, only in the Pacific or only in the Atlantic. In biogeographic terms, the southernmost boundary reaches Cape Horn, and therefore, species present north of 55°S belong to the Magellan Province.

Considering the limits of the Magellan Biogeographic Province and species distribution, for this study we assigned species to the following geographic areas: [1] the Magellan Atlantic (north of 55°S), [2] the Magellan Pacific (north of 55°S), [3] the Southern tip of South America (south of 55°S), [4] the Antarctic (continental shelf and islands off the Antarctic Peninsula), [5] South Georgia, [6] the Kerguelen Arc Islands, and [7] South American deep fauna.

The geographic regions were clustered using PRIMER 5.2 multivariate cluster analysis based on species presence/absence. The Bray-Curtis similarity index was used. South American deep-sea species contained in the species list were not included in the analysis.

RESULTS

In the Magellan Province (Atlantic and Pacific sides, southern tip and deep species), there is a much

TABLE 1 – Species list and geographic distribution of decapods in the Magellan Biogeographic Province and the Antarctic region. (MA: Atlantic Magellan, MP: Pacific Magellan, ST: Southern tip of South America, A: Antarctic, SG: South Georgia, K: Kerguelen Arc Islands, DS: South American deep species).

Infraorder	Family	Species	MA	MP	ST	A	SG	K	DS
Anomura	Chirostylidae	*Uroptychus parvulus* (Henderson, 1885)		*					
	Coenobitidae	*Coenobita compressus* (H. Milne Edwards, 1837)		*					
	Diogenidae	*Paguristes weddelli* (H. Milne Edwards, 1848)		*					
	Galatheidae	*Munida gregaria* (Fabricius, 1793)	*	*	*			*	
		Munida spinosa (Henderson, 1885)	*		*			*	
		Munida subrugosa (White, 1847)	*	*	*			*	
		Munidopsis aspera (Henderson, 1885)		*					
	Hippidae	*Emerita analoga* (Stimpson, 1857)	*	*					
	Lithodidae	*Lithodes confundens* (Macpherson, 1988)	*	*					
		Lithodes santolla (Molina, 1782)	*	*	*				
		Lithodes turkayi (Macpherson, 1988)	*	*	*				
		Lithodes murrayi, Henderson, 1888				*		*	
		Paralomis aculeatus Henderson, 1888						*	
		Paralomis anamerae (Macpherson, 1988)	*						
		Paralomis formosa (Henderson, 1888)	*				*		
		Paralomis granulosa (Jaquinot, 1847)	*	*	*				
		Paralomis spinosissima (Birstein y Vinogradov, 1972)	*		*	*	*	*	
		Paralomis tuberipes (Macpherson, 1988)		*					
	Paguridae	*Pagurus comptus* (White, 1847)	*	*	*				
		Propagurus gaudichaudii (H. Milne Edwards, 1836)	*	*	*				
	Parapaguridae	*Sympagurus dimorphus* (Studer, 1882)	*	*	*			*	
	Porcellanidae	*Liopetrolisthes mitra* (Dana, 1852)		*					
		Petrolisthes laevigatus (Guérin, 1835)		*					
		Petrolisthes violaceus (Guérin, 1831)		*					
Astacidea	Nephropidae	*Thymops birsteini* (Zarenkov and Semenov, 1972)	*	*	*				*
Brachyura	Atelecyclidae	*Peltarion spinosulum* (White, 1843)	*	*	*				
	Bellidae	*Bellia picta* H. Milne Edwards, 1848		*					
		Acanthocyclus albatrossis Rathbun, 1898	*	*					
		Corystoides abbreviatus A. Milne Edwards, 1880	*	*					
	Cancridae	*Cancer coronatus* Molina, 1782		*					
		Cancer edwardsi Bell, 1835		*					
		Cancer polyodon Poeppig, 1836		*					
	Corystidae	*Gomeza serrata* Dana 1852		*					
		Pseudocorystes sicarius (Poeppig, 1836)		*					
	Epialtidae	*Taliepus dentatus* (H. Milne Edwards, 1834)		*					
	Geryonidae	*Chaceon notialis* (Manning and Holthuis, 1989)	*						
	Grapsidae	*Cyrtograpsus affinis* (Dana, 1851)	*						
		Cyrtograpsus altimanus (Rathbun, 1914)	*						
		Cyrtograpsus angulatus (Dana, 1851)	*	*					
		Hemigrapsus crenulatus (H. Milne Edwards, 1837)		*					
		Planes cyaneus (Dana, 1852)		*					
	Hymenosomatidae	*Halicarcinus planatus* (Fabricius, 1775)	*	*	*			*	
	Inachidae	*Eurypodius latreillei* Guerín, 1828)	*	*	*				
		Eurypodius longirostris Miers, 1886		*					
	Inachoididae	*Inachoides microrhynchus* H. Milne Edwards and Lucas, 1842		*					
		Leurocyclus tuberculosus (H. Milne Edwards and Lucas, 1843)	*	*					
	Leucosiidae	*Leucosia planata* (Fabricius, 1793)	*						
	Majidae	*Leucippa pentagona* H. Milne Edwards, 1833	*	*					
		Libidoclaea granaria H. Milne Edwards and Lucas, 1842	*	*					
		Libidoclaea smithi (Miers, 1886)		*					
	Pinnotheridae	*Pinnaxodes chilensis* (H. Milne Edwards, 1837)	*	*					
		Pinnixa valdiviensis Rathbun, 1907)		*	*				
		Pinnotherelia laevigata H. Milne Edwards and Lucas, 1843		*					
	Pisidae	*Pisoides edwardsii* (Bell, 1835)		*					
		Rochinia gracilipes H. Milne Edwards, 1875	*						
	Portunidae	*Coenophthalmus tridentatus* H. Milne Edwards, 1879	*						
		Ovalipes trimaculatus (De Haan, 1833)	*	*					
	Xanthidae	*Eurypanopeus crenatus* (H. Milne Edwards and Lucas, 1843)		*					
		Gaudichaudia gaudichaudi (H. Milne Edwards, 1834)		*					
		Homalaspis plana (H. Milne Edwards, 1834)		*					
		Pilumnoides hassleri A. Milne Edwards, 1880	*						
		Pilumnoides perlatus (Poeppig, 1836)		*					
Caridea	Alpheidae	*Betaeus truncates* Dana, 1852	*	*	*				
		Synalpheus spinifrons (H. Milne Edwards, 1837)		*					
	Campylonotidae	*Campylonotus semistriatus* Bate 1888	*	*	*				
		Campylonotus arntzianus Thatje, 2003				*			
		Campylonotus vagans Bate, 1888	*	*	*	*	*		
		Campylonotus capensis Bate, 1888						*	*

TABLE 1 (Cont.). – Species list and geographic distribution of decapods in the Magellan Biogeographic Province and the Antarctic region. (MA: Atlantic Maguellan, MP: Pacific Maguellan, ST: Southern tip of South America, A: Antarctic, SG: South Georgia, K: Kerguelen Arc Islands, DS: South American deep species).

Infraorder	Family	Species	MA	MP	ST	A	SG	K	DS
Caridea	Crangonidae	*Notocrangon antarcticus* (Pfeffer, 1887)	*	*	*	*	*		
	Hippolytidae	*Chorismus antarcticus* (Pfeffer, 1887)	*	*	*	*	*	*	
		Chorismus tuberculatus Bate, 1888	*		*		*	*	
		Latreutes antiborealis Holthuis, 1952		*					
		Nauticaris magellanica (A. Milne Edwards, 1891)	*	*	*			*	
		Nauticaris marionis Bate, 1888		*				*	
		Lebbeus antarcticus Hale, 1941			*	*			
		Eualus kinzeri Tiefenbacher, 1990				*			
		Eualus dozei (A. Milne Edwards, 1891)		*	*				
	Nematocarcinidae	*Nematocarcinus lanceopes* Bate, 1888			*			*	
		Nematocarcinus longirostris Bate, 1888						*	
	Oplophoridae	*Acanthephyra pelagica* (Risso, 1816)	*			*			
		Hymenodora gracilis Smith, 1886				*			
	Pandalidae	*Austropandalus grayi* (Cunningham, 1871)	*	*	*				
		Pandalopsis ampla Bate, 1888			*	*			
	Pasiphaeidae	*Pasiphaea acutifrons* Bate, 1888	*	*	*	*	*		
		Pasiphaea dofleini Schmitt, 1932		*					
Palinura	Polychelidae	*Stereomastis suhmi* (Bate, 1878)		*	*				
Penaeoidea	Benthesicymidae	*Benthesicymus brasiliensis* Bate, 1881	*						
	Penaeidae	*Artemesia longinaris* Bate, 1888	*						
	Solenoceridae	*Pleoticus muelleri* (Bate, 1888)	*						
Sergestoidea	Sergestidae	*Sergestes arcticus* Krøyer, 1855	*	*	*				
	Sergestidae	*Sergia potens* (Burkenroad, 1940)	*						
Thalassinidea	Callianassidae	*Notiax brachyophthalma* (A. Milne Edwards, 1870)	*	*					
		Notiax santarita Thatje, 2000			*				
	Ctenochelidae	*Anacalliax argentinensis* (Biffar, 1971)	*						
	Upogebiidae	*Upogebia australis* Thatje and Gerdes, 2000			*				

higher number of species than those currently recognised for the Antarctic. The Anomura (22 species), Brachyura (37 species) and Caridea (19 species) are well represented in the Magellan Province (Table 1), whereas the only taxa present in the Antarctic, the Caridea (10 species incl. SG) and Anomura Lithodidae (3 species incl. SG), are low in species numbers. The total number of species cited for the whole study area is 95. In the Magellan Province, 16 species were present only in the Atlantic and 33 only in the Pacific, with 32 present in both oceans (Table 1).

At the southern tip, 32 non-endemic species were recorded that are also present either in the Atlantic or the Pacific area of the Magellan Province north of 55°S (Table 1). Four of them, *Campylonotus vagans* (but see Thatje, 2003), *Notocrangon antarcticus, Chorismus antarcticus* and *Paralomis spinosissima,* are also found in the Antarctic and South Georgia. The distribution range of two Antarctic species, *Lebbeus antarcticus* and *Pandalopsis ampla,* stretches to the southern tip of South America. Four anomuran species, *Munida gregaria, M. subrugosa, M. spinosa and Paralomis spinosissima,* and four carideans, *Chorismus antarcticus, C. tuberculatus, Nauticaris magellanica,* and *N. marionis,* are found in both the Magellan Province and the Kerguelen Arc.

The dendrogram shows two clusters (A and B) (Fig. 2). Cluster A involves the Pacific and Atlantic areas of the Magellan Province and the southern tip, with the highest similarity index between the southern tip and the Atlantic area. The islands of the Kerguelen Arc are mostly associated with the South American fauna. Cluster B includes the Antarctic and South Georgia, with a high similarity index (Table 2).

DISCUSSION

The biogeography of crustacean decapods from the Magellan Province and the Antarctic follows different patterns. The distribution of thirteen species overlaps in the Magellan Province and the circum-Antarctic area (Table 1). Ten species out of 95 recorded for the study are present in the Antarctic, only five of them also being found in waters off South Georgia, and two of them (*Chorismus*

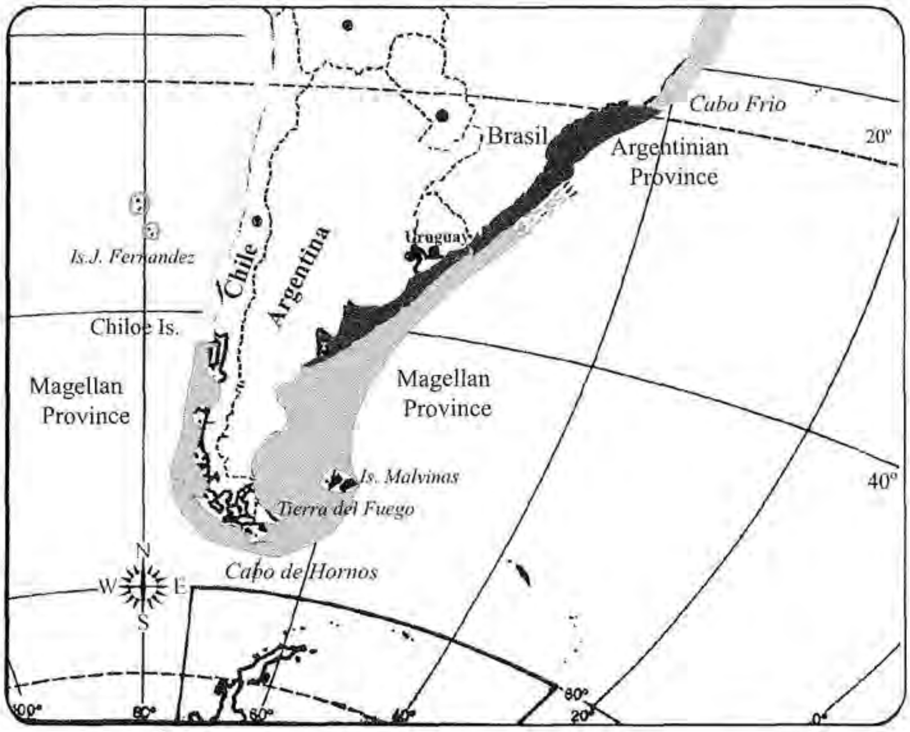

FIG. 1. – Extension of the Magellan Province around the southern tip of South America.

TABLE 2. – Bray-Curtis similarity matrix of geographic regions based on the distribution of decapod species.

	Magellan Atlantic	Magellan Pacific	Southern tip of S. America	Antarctic	South Georgia
Magellan Pacific	56.14				
Southern tip of S. America	59.25	49.48			
Antarctic	19.35	10.25	31.11		
South Georgia	25.00	11.11	30.76	60.00	
Kerguelen Is.	28.57	17.72	43.47	22.22	28.57

antarcticus and *C. tuberculatus*) in the Kerguelen Arc (Table 1). *Halicarcinus planatus* is the only brachyuran crab present in the Magellan Province; it has a range that extends to the Kerguelen Arc and the genus is of circum-Antarctic distribution (Gorny, 1999). However, *H. planatus* has never been recorded at South Georgia (Gorny, 1999), and its presence in the South Orkney Islands, as reported by other authors, is uncertain due to probably mislabelled material (Thatje and Arntz, 2004).

The decapod fauna along the Pacific and Atlantic ocean coasts of the Magellan Province is similar. In terms of species number it is the largest group compared to the Antarctic and circum-Antarctic areas. The numbers presented here are slightly higher than those reported by Boschi (2000a), due to the updated information included in Table 1. Despite the high degree of similarity, the cluster analysis separates the Pacific area from the Atlantic and the southern tip of South America (Fig. 2).

Gorny (1999) studied the biogeography and ecology of the Southern Ocean decapod crustaceans and concluded that brachyurans should be included in the Antarctic decapod fauna. Our results and conclusions differ from those obtained by Gorny in two aspects: 1) concerning the biogeographic regions considered, and 2) with regard to the database used in the analysis. As in this study we considered the limits of the Magellan Biogeographic Province, which are different from those of the Magellan region, the species arrangement changed. For example, *Chaceon notialis* was included in the antiboreal and temperate regions of Argentina (Gorny, 1999) although it is only present in the Magellan Province

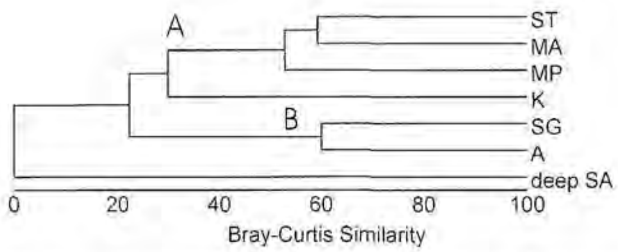

FIG. 2. – Cluster analysis of geographic regions. Cluster A shows a high similarity index between the Magellan Atlantic, the southern tip of South America and the Magellan Pacific. The Kerguelen Arc Islands are associated with the Magellan Province. Cluster B includes South Georgia and the Antarctic. Cluster A and B show great dissimilarity. ST: Southern tip of South America, MA: Magellan Atlantic, MP: Magellan Pacific, K: Kerguelen Arc Islands, SG: South Georgia, A: Antarctic, deep, SA: South American deep species.

(Boschi, 2000a, b). On the other hand, the anomuran *Pachycheles chubutensis* was included in the antiboreal region (Gorny, 1999), while this species is only present in the Argentinean Province (Boschi 2000a, b). This interpretation of the distribution of species along the Argentinean coast is due to the use of "antiboreal regions" instead of "biogeographic provinces", whose distributional ranges overlap in this case (Boschi, 2000a, b).

Acha *et al.* (2004) recognised six marine zones that cover all neritic ecosystems of austral South America. The "Patagonian cold estuarine" zone encircles the tip of South America and connects both the Pacific and Atlantic oceans. The authors propose that the southward currents from Chiloé Island, reaching the cold estuarine front of Atlantic Patagonia and the Atlantic shelf-break front, could be a transport system for organisms into the Argentinean Magellan Province (Acha *et al.,* 2004). Several authors (Knox, 1960; Stuardo, 1964; Boschi, 1966, 1976, 1979a, b, 2000a; Boschi *et al.*, 1981, 1992) argue that the faunas of southern Chile and southern Argentina are related. This is confirmed by our study and we conclude that there is little similarity between decapod species from the Antarctic and the Magellan Province, which is obviously the result of the impoverished Antarctic decapod fauna in general (Thatje and Arntz, 2004).

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Biodiversity of Antarctic echinoids: a comprehensive and interactive database*

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SUMMARY: Eighty-one echinoid species are present south of the Antarctic Convergence, and they represent an important component of the benthic fauna. "Antarctic echinoids" is an interactive database synthesising the results of more than 100 years of Antarctic expeditions, and comprising information about all echinoid species. It includes illustrated keys for determination of the species, and information about their morphology and ecology (text, illustrations and glossary) and their distribution (maps and histograms of bathymetrical distribution); the sources of the information (bibliography, collections and expeditions) are also provided. All these data (taxonomic, morphologic, geographic, bathymetric...) can be interactively queried in two main ways: (1) display of listings that can be browsed, sorted according to various criteria, or printed; and (2) interactive requests crossing the different kinds of data. Many other possibilities are offered, and an on-line help file is also available.

Keywords: sea urchins; Antarctic; biodiversity, database.

RESUMEN: BIODIVERSIDAD DE EQUINOIDEOS: UNA BASE DE DATOS AMPLIA E INTERACTIVA. – Al sur de la Convergencia Antártica existen 81 especies de equinodermos, que representan una componente importante de la fauna bentónica en la zona. "Antarctic echinoids" es una base de datos interactiva que sintetiza los resultados de más de 100 años de expediciones antárticas y contiene informaciones de todas las especies de equinodermos existentes. Incluye claves ilustradas para la determinación de las especies e informaciones sobre su morfología y ecología (texto, ilustraciones y glosario); su distribución (mapas e histogramas de distribución batimétrica); y además presenta fuentes de informacion (bibliografía, colecciones y expediciones). Todos estos datos (taxonómicos, morfológicos, geográficos, batimétricos...) pueden ser obtenidos interactivamente de dos formas principales: (1) Indicación de listados que ofrecen la posibilidad de ser observados, ordenados según diversos criterios o impresos; (2) Preguntas interactivas combinando los diferentes tipos de datos. Otras posibilidades son ofrecidas, y hay disponibilidad de una seccion "on-line"de ayuda.

Palabras clave: equinoideos, antártico, biodiversidad, base de datos.

INTRODUCTION

Although sporadic samplings had been made in the Magellan region previously, Antarctic echinoids were first collected during the British "Challenger" expedition (1873-76), and almost simultaneously by the German "Gazelle" expedition (1874-76). Subsequently, they were regularly collected by successive expeditions that probed Antarctic and Subantarctic waters. After those pioneering voyages, oceanographic explorations delineated the main geographic areas around Antarctica, and collected abundant new echinoid species. The Antarctic Peninsula and, to a lesser extent, the Weddell Sea were the most

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extensively explored areas. On the other side of the continent, the eastern Ross Sea area (Balleny Island and Victoria Land) was also repeatedly investigated. Subantarctic waters were largely explored in the areas where islands are plentiful, that is to say in the Weddell and Enderby quadrants. Since the Second World War, the installation of scientific bases and the appearance of modern oceanographic ships have triggered numerous supplementary explorations. However, the previous imbalance between the principal zones around Antarctica has continued to prevail, though new and deeper zones have also been investigated.

ANTARCTIC ECHINOID BIODIVERSITY

Among the 19 post-Palaeozoic echinoid orders, nine have been reported in the Antarctic, among which four are known only in the fossil record, and two are exclusively recent (Hotchkiss, 1982; McKinney *et al.*, 1988; Pawson, 1994; Néraudeau *et al.*, 2000). These nine orders are on the whole represented by 15 families, with few variations in the number of taxa over time. However, there are rather important changes in the composition of the fauna at the order and family levels. For example, only two orders are present from the Mesozoic to the Recent, while four others, known in the fossil record, survive today only outside Antarctica (David *et al.*, 2005). Recent Antarctic echinoids are widely distributed from onshore environments to the deep sea. Although they are not vastly diversified (there are only 79 species), they represent nine families and seven disparate orders, and display highly diverse morphologies from pencil urchins with smooth, cylindrical, spatulate, or strongly thorned spines to strange, bottle-shaped deep-sea forms and the almost cylindrical *Dermechinus*. In addition, Antarctic sea urchins are distinguished by some of their unusual life-history traits, including the fact that there are more brooding than broadcasting forms (Poulin and Féral, 1996). Adaptations to this reproductive pattern lead to unique features such as the bizarre, internal brooding system of *Antrechinus* (David and Mooi, 1990; Mooi and David, 1993).

THE DATABASE

Gathering and ordering the data about recent Antarctic echinoids led us to build a database and to conceive the idea to make this database a powerful tool for extracting and crossing synthetic information about Antarctic echinoid fauna. The main aim of this database is to provide a tool for anyone (ecologists, biogeographers…) interested in Antarctic fauna, but not necessarily for specialists of echinoids.

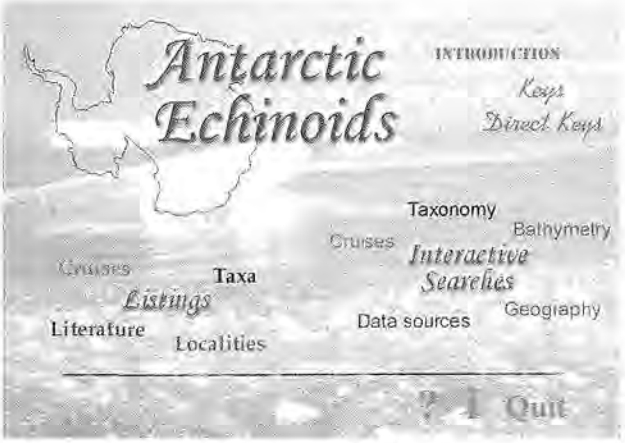

FIG. 1. – Home page of the database

"Antarctic echinoids" is an interactive database synthesising the results of more than 130 years of Antarctic expeditions. Data from 59 oceanographic cruises, starting in 1872, and from museum and private collections have been revisited, and have led to a systematic revision of the Antarctic echinoid fauna.

The core of the information stored in the database includes: (i) taxonomy, encompassing determination keys, morphological diagnoses, illustrations and a glossary; (ii) geographic and bathymetrical distributions; and (iii) cruises and data sources, including museum collections. The database can be interrogated in two ways that are available from the home page (Fig. 1):

- A static query allowing a simple browsing of the data and displaying listings of taxa, geographic records, cruises, literature and collections, with the possibility of sorting and printing. In this part, a system of illustrated dichotomic keys allows one to advance step by step in the determination of families, genera and species.
- An interactive query allowing connections and combined queries between taxonomy, geography, bathymetry, cruises and data sources. This query makes full use of the relational aspect of the database.

The database comprises information about 81 specific or subspecific taxa gathered into 30 genera, 9 families and 7 orders. For every taxon, the database provides illustrations, diagnosis, a geographic distribution map (Fig. 2) and a histogram of bathy-

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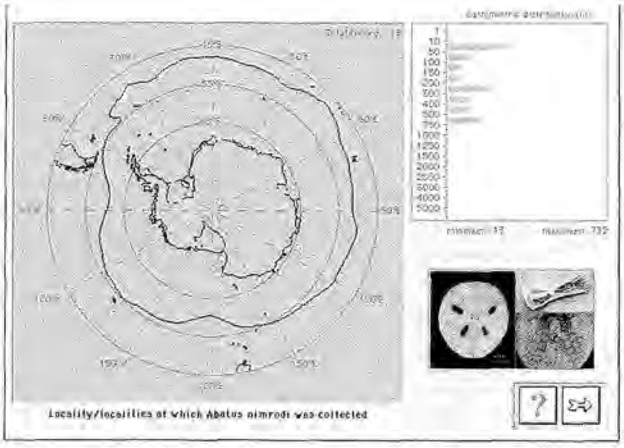

FIG. 2. – Geographic distribution of a selected taxon

metrical distribution. Localities are divided into quadrats of 5° latitude and 10° longitude in conjunction with depth. Only the localities situated south of the Antarctic Convergence were considered. Two maps are available for geographic queries, one with cells corresponding to the quadrats, and one with several sets of larger cells (including the four classical Antarctic quadrants, and rings of latitudinal range). A glossary of echinoid terminology is available to help people who are not familiar with echinoids to read the diagnoses. It includes 139 terms with precise illustrated definitions. In addition, general documents dealing with the history of Antarctic cruises that have searched for echinoids, the Antarctic tectonic and climatic evolution, and an extensive part on the biology of echinoids are provided. For each step, a help screen is available in order to guide the user through the system and give explanations.

CONCLUSIONS

Availability

The database allows one to make numerous types of queries, therefore answering biogeographic as well as ecological questions in a rapid and user-friendly way. It was built with the 4D™ software but is available in a compiled form which does not require 4D to be installed on the user's computer. It works on Apple Macintosh computers, and is also available for Windows.

If you use the database, please quote this paper.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Ascidians (Tunicata, Ascidiacea): species distribution along the Scotia Arc*

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SUMMARY: Ascidians are found in all the oceans. The Polar Front is considered a strong barrier, especially for benthic organisms, separating the Southern Ocean from other oceans. Its influence on ascidian species present at the boundary of the Magellan and Antarctic regions along the Scotia Arc and on the species composition at each station is inferred from the samples taken during the "LAMPOS" cruise. Ascidians were collected by Agassiz (AGT) and bottom (GSN) trawls at depths between 250 and 587 m on different types of substrate. Of 25 identified species/morphospecies one is new and eight were found in new localities, enlarging the known range of five of these species. Muddy bottoms were found to support higher species richness than hard bottoms, and the South Georgia Islands are found to be the northern limit for Antarctic species and the southern limit for Magellan ones. Affinity between the ascidian fauna of the Magellan region and the Antarctic is slightly stronger than was previously considered; there is also a species gradient along the Scotia Arc, which can be regarded as a bridge between the two regions.

Keywords: Tunicata, Scotia Arc, Polar Front, biogeography.

RESUMEN: ASCIDIAS (TUNICATA, ASCIDIACEA): DISTRIBUCIÓN ESPECÍFICA A LO LARGO DEL ARCO DE SCOTIA. – Las ascidias habitan todos los mares. Considerado como una barrera especialmente para los organismos del bentos, el Frente Polar separa al Océano Austral del resto de los océanos. A partir de la composición de especies colectadas en cada estación durante el crucero "LAMPOS", se infiere la influencia del Frente Polar sobre las especies de ascidias presentes en el límite entre las regiones magallánica y antártica a lo largo del Arco de Scotia. Los ejemplares fueron colectados mediante rastra Agassiz y red de fondo entre 250 y 587 m, en tipos diferentes de sustrato. De un total de 25 especies/morfoespecies identificadas, una es nueva mientras que ocho fueron encontradas en nuevas localidades extendiendo el rango de distribución conocido para cinco de ellas. Se encontró una mayor riqueza de especies sobre fondos lodosos que sobre fondos duros. Las islas Georgias del Sur constituyen el límite norte para las especies antárticas y el límite sur para las magallánicas. Las afinidades entre la ascidiofauna de las regiones magallánica y antártica son ligeramente mayores de lo que se consideraba, existiendo un gradiente a lo largo de las islas del Arco de Scotia, las cuales constituirían un puente biogeográfico entre dichas áreas.

Palabras clave: Tunicata, Arco de Scotia, Frente Polar, biogeografía.

INTRODUCTION

Ascidians occur in all the oceans, from the intertidal to the abyssal plain. There are several studies on ascidian biodiversity in the Southern Ocean (Herdman, 1882, 1886; Sluiter, 1906; Hartmeyer, 1912; Ärnbäck-Christie-Linde, 1938, 1950; Millar, 1960; Kott 1969a, b, 1971), the most important recent study being that of Monniot and Monniot (1983). According to these authors, affinities between the ascidian fauna from the tip of South America and the Antarctic are low. A look at the Scotia Arc suggests that it might be a bridge between these two areas, in spite of the geographic distance, currents and the

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presence of the Polar Front. The Polar Front (Antarctic Convergence) is an irregular but permanent barrier (Hedgpeth, 1969; Boltovskoy, 1981) which contributes to the isolation of the fauna of Antarctic waters, limiting the migration from and into northern areas. For pelagic fauna this front may rather represent a transitional area (Clarke and Crame, 1989). The distribution of benthic sessile fauna depends on dispersal abilities of larval or even pre-larval stages such as gametes, eggs and embryos, which in turn can be affected by various factors: hydrology (salinity, temperature, currents and suspended material), depth and bottom type (Clarke, 1996). The influence of the Polar Front on the dispersal of sessile species like ascidians, characterised by short-lived and lecithotrophic larvae, is still unknown. While many ascidian species disappear just at the Polar Front, there are several species with a range extending across the Polar Front such as *Aplidium falklandicum* (Sahade *et al.*, 2003). New records on the Scotia Arc must improve the knowledge on ascidian biodiversity and distribution, contributing to the biogeography of the study area.

MATERIALS AND METHODS

Samples were taken during the "LAMPOS" cruise (ANT XIX/5) of RV "Polarstern" in April 2002. Ascidians were collected by Agassiz (AGT) and bottom (GSN) trawls at depths between 250 and 587 m on different types of substrate (Table 1). For the gear characteristics see the LAMPOS cruise report (Arntz and Brey, 2003). Living animals were photographed to record their colour, which is lost on fixation. Animals were relaxed in seawater and later fixed in buffered formalin-seawater 4%. Species were examined with a stereoscope and a compound microscope. The reproductive status of colonial species was recorded, including the presence of larvae. The examined material is in the Museo de Zoología, Facultad de Ciencias Exactas Físicas y Naturales, Universidad Nacional de Córdoba, Argentina.

Multivariate analyses were used to determine species affinity between localities. Classification was performed using the UPGMA clustering method (Bray-Curtis similarity). In addition, our data were pooled with previous data reported by Monniot and Monniot (1983), corresponding to the species distribution in the sampling area at depths of up to 1,000 m. A similarity matrix was constructed with the pooled dataset, using the Kulczynski-2 index (Monniot and Monniot, 1983).

RESULTS AND DISCUSSION

Species recorded

25 species/morphospecies were found at the different stations sampled during the cruise, solitaries being slightly more abundant than colonial forms. One species is new, and eight were found in new

TABLE 1. – Stations sampled during the cruise.

Nº Station / Gear	Locality	Lat / long	Depth	substrate
145/AGT	Burdwood Bank	54º 1.36´ S/ 62º 1.33´ W	272 m	gravel
150/AGT	Burdwood Bank	54º 30.22´ S/ 56º 8.20´ W	286 m	gravel
153/GSN	Burdwood Bank	54º 31.22´ S/ 56º 8.93´ W	296 m	gravel
160/AGT	Burdwood Bank	53º 23.75´ S/ 44º 45.12´ W	435 m	gravel
164/AGT	Shag Rocks	53º 23.8´ S/ 42º 42.03´ W	313 m	gravel
167/GSN	Shag Rocks	53º 23.68´ S/ 42º 42.23´ W	306 m	gravel
174/GSN	South Georgia	54º 24.47´ S/ 35º 36.81´ W	278 m	mud
182/AGT	South Georgia	54º 27.63´ S/ 35º 41.33´ W	249 m	mud
187/AGT	South Sandwich	55º 56.08´ S/ 28º 7.51´ W	255 m	volcanic stones
194/AGT	South Sandwich	57º 40.55´ S/ 26º 25.14´ W	309 m	volcanic stones
196/GSN	South Sandwich	57º 40.6´ S/ 26º 25.42´ W	301 m	volcanic stones
207/AGT	South Sandwich	57º 40.36´ S/ 26º 27.89´ W	587 m	volcanic stones
208/GSN	South Sandwich	57º 40.25´ S/ 26º 27.97´ W	630 m	volcanic stones
214/AGT	South Sandwich	59º 42.55´ S/ 27º 57.02´ W	332 m	pebbles
217/AGT	Herdman Bank	59º 54.98´ S/ 32º 28.33´ W	521 m	pebbles
223/AGT	Discovery Bank	60º 8.16´ S/ 34º 55.59´ W	374 m	pebbles
229/GSN	Discovery Bank	60º 8.77´ S/ 34º 54.83´ W	371 m	pebbles
231/AGT	South Orkneys	60º 59.19´ S/ 43º 27.42´ W	402 m	mud
238/AGT	South Orkneys	61º 10.81´ S/ 45º 42.72´ W	322 m	mud
241/GSN	South Orkneys	61º 11.15´ S/ 45º 43.84´ W	323 m	mud
252/AGT	Elephant Is.	61º 23.45´ S/ 55º 26.82´ W	285 m	mud
253/GSN	Elephant Is.	61º 23.40´ S/ 55º 26.99´ W	282 m	mud

TABLE 2. – Known distribution range of the species found (including only distribution from Antarctic Peninsula to Magellan through the Scotia Arc) and new records. * From Monniot and Monniot (1983). APS: Antarctic Peninsula, South Shetland Islands and Elephant I.

Species	Distribution range*	New records
Aplidium falklandicum Millar, 1960	Widely, from APS to Magellan	
Aplidium globosum (Herdman, 1886)	South Orkneys, South Sandwich	Elephant I., Burdwood Bank
Aplidium polarsterni n. sp.		Burdwood Bank
Synoicum adareanum (Herdman, 1902)	APS, South Orkneys	
Synoicum georgianum Sluiter, 1932	APS to Magellan	
Polyclinidae sp.		Burdwood Bank
Protoholozoa pedunculata Kott, 1969	South Orkneys	
Cystodytes antarcticus Sluiter, 1912	APS	Burdwood Bank
Tetrazona glareosa (Sluiter, 1906)	APS, South Sandwich	Burdwood Bank
Distaplia cylindrica (Lesson, 1830)	Widely, from APS to Magellan	
Polysyncraton trivolutum (Millar, 1960)	APS, South Georgia, Magellan	S. Orkneys
Tylobranchion speciosum Herdman, 1886	Widely, from APS to Magellan	
Cibacapsa gulosa Monniot and Monniot, 1983		S. Sandwich
Caenagnesia bocki Ärnbäck-Christie-Linde, 1938	APS, South Sandwich, South Georgia	
Ascidia meridionalis Herdman, 1880	South Georgia, Magellan	
Styelidae sp.		Shag Rocks
Cnemidocarpa verrucosa (Lesson, 1830)	Widely, from APS to Magellan	
Cnemidocarpa drygalskii (Hartmeyer, 1911)	APS	Herdman, Discovery and Burdwood Bank
Pyura bouvetensis (Michaelsen, 1904)	APS, South Orkneys	
Pyura discoveryi (Herdman, 1910)	APS, South Orkneys, South Georgia	
Pyura georgiana (Michaelsen, 1898)	South Georgia	
Pyura squamata Hartmeyer, 1911	APS, South Orkneys	Shag Rocks
Molgula pedunculata Herdman, 1881	From APS to South Georgia	
Molgula hodgsoni Herdman, 1910	APS, South Orkneys, South Georgia	
Eugyrioides polyducta Monniot and Monniot, 1983	APS, South Sandwich, South Georgia	

localities, extending the known range of five of these species (Table 2). Ascidians were a commonly collected group, being present in more than 80% of the captures; however the abundance was low, with usually only a few individuals per sample. 11 families were found, the most common being Polyclinidae (6 species) and Pyuridae (4 species). Muddy bottoms were found to support higher species richness than hard bottoms such as gravel, pebbles and volcanic stones.

List of species

Order APLOUSOBRANCHIA Lahille, 1887
Family POLYCLINIDAE Verrill, 1871

Aplidium falklandicum Millar, 1960

Aplidium falklandicum Millar, 1960: 34, Pl. I 3-4, Fig. 3 A-H; Monniot and Monniot, 1983: 15 (synonymy).

Examined material: St. 182: 14 colonies; St. 231: 13 colonies; St. 253: 2 colonies.

The morphology of the colonies and zooids agrees with Millar (1960), although he observed a maximum of seven stomach folds, whereas our specimens have up to eight. The most relevant feature, not reported before, is the intense yellow-lemon colour seen in live colonies, which is replaced by a dark grey colour after preservation. Larvae were present; according to Millar (1960), this species breeds throughout the year.

Aplidium globosum (Herdman, 1886)

Amaroucium globosum Herdman, 1886: 219, Pl. 24, Fig. 1-5; Monniot and Gaill, 1978: 143, Fig. 3 C, D (type revision); Monniot and Monniot, 1983: 17 (synonymy).

Examined material: St. 145: 3 colonies; St. 153: 2 colonies; St. 252: 7 colonies.

Zooids reach a large size (up to 1.3 cm) with an atrial languet, two- or three-lobed. The stomach folds vary in number from six to eight. Larvae were present. A parasitic copepod was observed in the atrial cavity of one of the zooids.

Aplidium polarsterni n. sp.
(Fig. 1 A, B, C)

Type locality: Burdwood Bank (St. 145), 54°2'S 62°0,5'W; 272 m, 5/IV/02. Holotype: (MZUC VIIIa 00001) Museo de Zoología, Facultad de Ciencias Exactas Físicas y Naturales, Universidad Nacional de Córdoba, Argentina.

Etymology: from "Polarstern" research vessel of the Alfred Wegener Institute, Germany.

Examined material: St. 145: 2 colonies.

Description: The round shaped colonies are thinner at the base, with one short stalk or sessile. The colonies have only one head. The colour in life and

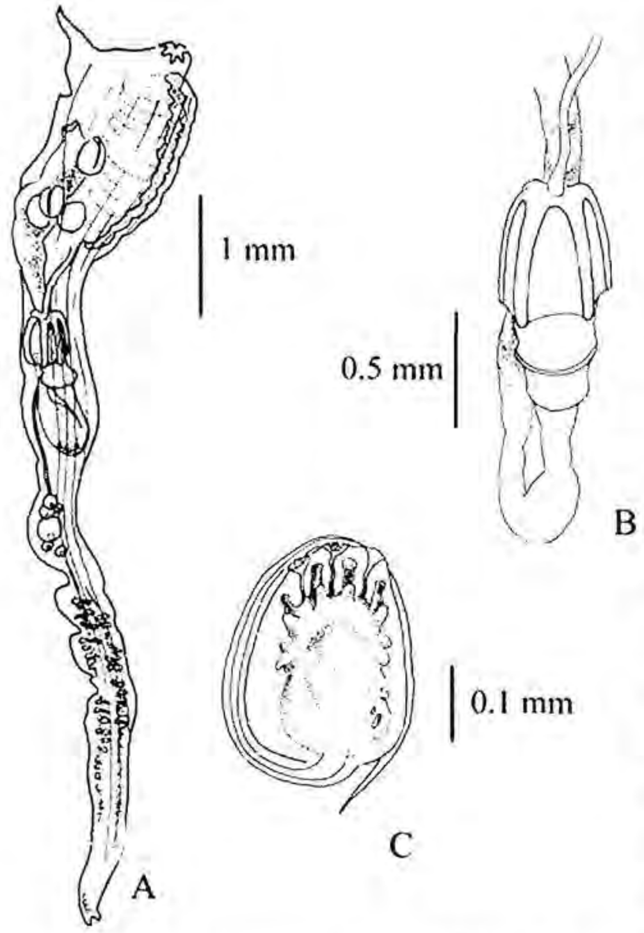

FIG. 1. – *Aplidium polarsterni* n. sp. A: zooid. B: larva. C: gut.

after fixation is transparent. The tunic is smooth, gelatinous and soft. Particles of sand (most of them coarse, quartz-like particles) are dispersedly arranged, internally and externally, but are mostly at the base. There are epibionts (bryozoans and small corals) attached to the base of the colony. The length of the colonies reaches 2.5 cm.

The zooids, evident through the tunic, are large, pale orange in colour and not arranged in clear systems, the common cloacal apertures not being evident. The total length of the zooids, when they are not contracted, reaches 10 mm. The thorax and abdomen are of approximately the same length: the thorax varies from 1 to 3 mm, the abdomen from 1 to 2.5 mm. The post-abdomen is of variable length, from 1.5 to 5 mm. The musculature is well developed with about eight longitudinal strong muscle bands, which run along either side of the body from the thorax to the posterior end of the post-abdomen, where they are still conspicuous. The oral siphon is terminal, with six sharp lobes. The atrial siphon is a small aperture situated at the level of the first or third stigmata row, which is provided by a long atrial languet from the anterior border of the opening, single or with two or three lobes (with the central lobe more developed). The branchial sac is narrow, with a total of 12-13 stigmata rows, with at least 12 stigmata per row on each side. The oesophagus is slender and very long; the stomach, situated in the middle of the abdomen, is cylindrical or trapezoidal, with five or six deep folds which continue along the whole length of the stomach. There is a marked post-stomach provided by a post-stomachal disc; situated on or very close to the intestinal loop, there is a stilted mid-intestine. The anus lies just at the level of the seventh or eighth stigmata row. The gonads are located in lateral widening of the post abdomen, at a short distance from the intestinal loop or even very far from it, at the middle of the post-abdomen. The ovary has a variable number of follicles of different size, depending on the colony and zooid. The testis follicles are arranged in single or double rows along the extension of the post-abdomen.

Colonies were full of larvae, reaching up to 15 larvae in the peribranchial cavity of a single zooid. The ovoid trunk is 0.3–0.5 mm long and 0.2–0.3 mm wide. A long tail extends nearly the whole distance around the body. There are three long anterior adhesive papillae provided by slender stalks alternating with four broad median ampullae. There is also a crown composed of at least four pairs of lateral ampullae. Both ocellus and otolith are present.

Remarks: This species has affinities with *Aplidium undulatum* Monniot and Gaill (1978), which also has colonies embedded in sand particles and zooids with a similar number of stigmata rows and stomach folds. Nevertheless, the zooids of *A. undulatum* do not have strong thoracic muscle bands. The oral siphon shows small lobes, and the aperture of the atrial siphon is wide, extending up to the sixth stigmata row. The post-stomach is absent or poorly marked. The species *Aplidium globosum* has a similar appearance in shape, colour and size to *A. polarsterni*, but the colonies do not include sand particles. In *A. globosum* the zooids are arranged in systems around a common cloaca. They also have small oral lobes, their stomach folds are discontinuous, and teh testis follicles are always arranged in a single row.

Synoicum adareanum (Herdman, 1902)

Polyclinum adareanum Herdman, 1902: 194; Monniot F., 1978: 4 (synonymy); Monniot and Monniot, 1983: 31; Monniot and Monniot, 1994: 18; Tatián *et al*., 1998a: 148; 1998b: 112, Fig. 2 B.

Examined material: St. 253: 3 colonies.

The larvae are present and arranged in brood pouches enclosed in the internal test, as was described by Kott (1969a). This species was previously found at shallower depths, between 5 and 90 m (Herdman, 1902; Monniot F., 1970, 1978; Monniot and Monniot, 1974; Vasseur, 1974a, b).

Synoicum georgianum Sluiter, 1932

Synoicum georgianum Sluiter, 1932: 11, Fig. 9-10; Monniot and Monniot, 1983: 32 (synonymy).

Examined material: St. 253, 5 colonies.

Sand particles, algae and bryozoans are attached to the colonies. There is a high variability in the shape of the stomach: in our specimens the stomach is cubic, rhomboid, oval or enlarged longitudinally, always big and with the wall smooth or striated transversally. No larvae were found.

Polyclinidae sp.

Examined material: St. 145: 2 colonies; St. 153: 1 colony; St. 231: 1 colony.

The colonies are cushion-shaped, with one or two heads. They are up to 3 cm high and 4 cm wide. The tunic is firm and tough. The colour is transparent to ochre. The zooids are distinguishable through the tunic, arranged in parallel rows at different levels along the colony. No common cloaca is evident. There are sand particles and shell fragments attached to the base of the colony.

The zooids were immature or in dormant stage, between 0.2 and 10 mm length, with the body divided into thorax, abdomen and post-abdomen. Apertures, branchial sac, digestive tract and gonads were not developed.

Family POLYCITORIDAE Michaelsen, 1904

Protoholozoa pedunculata Kott, 1969

Protoholozoa pedunculata Kott, 1969a: 35, Fig. 17-20; Monniot and Monniot, 1982: 103, Pl. 1 C, Fig. 3 (type revision); Monniot and Monniot, 1983: 36, Pl. V A (synonymy).

Examined material: St. 217: 5 colonies; St. 223: 5 colonies.

The zooids had larvae, which reached a size of up to 0.5 cm; presence of embryos was previously reported in October (Kott, 1969a). Species show a wide bathymetric distribution, from 374 m (the present finding) down to abyssal depths (2818-5000 m Kott, 1969a).

Cystodytes antarcticus Sluiter, 1912

Cystodytes antarcticus Sluiter, 1912: 460; Monniot and Monniot, 1983: 36 (synonymy).

Examined material: St. 150: 2 colonies.

With larvae, up to 2 mm size.

Tetrazona glareosa (Sluiter, 1906)

Distoma glareosa Sluiter, 1906: 6, Pl. 1, Fig. 1-4. Monniot and Monniot, 1983: 37 Pl. III G, Fig. 6 E-G (synonymy).

Examined material: St 145: 2 colonies.

Fresh colonies are red-indigo, colour becomes transparent in preservation. The tunic has calcaric spicules of variable shape. In most cases larvae were bigger than zooids. This finding enlarges the bathymetric range for the species (previously up to 100 m).

Family HOLOZOIDAE Berril, 1950

Distaplia cylindrica (Lesson, 1830)

Holozoa cylindrica Lesson, 1830: 439 ; Monniot and Monniot, 1983: 36 (synonymy); Tatián *et al*., 1998a: 149 ; 1998b: 113, Fig. 2 E.

Examined material: St. 174: 1 colony; St. 182: 1 colony; St. 241: 7 colonies.

In many colonies zooids are male, female and undifferentiated (young or in relapse posterior to sexual period). Larvae were present.

Family DIDEMNIDAE Giard, 1872

Polysyncraton trivolutum (Millar, 1960)

Didemnum trivolutum Millar, 1960: 58, Fig. 12; Monniot and Monniot, 1983: 43, Pl. IV A-D; Fig. 8 A-H (synonymy); Monniot and Monniot, 1994: 18.

Examined material: St. 182: 5 colonies; St. 231: 3 colonies.

The colonies are incrusted on little rocks, bryozoans and sponges. The maximum size of the lateral spreading is 13 cm. The tunic is about 4 mm thick and is embedded with spicules, mainly in the superficial layer and around the zooids, these parts of the colony turning white. Spicules have a size of 18 to 24 μm: their form is stellate, with no more than 20 conical rays in a medial plane, rounded or bluntly pointed. There were larvae (up to 2 mm size).

Order PHLEBOBRANCHIA Lahille, 1887

Family CIONIDAE Lahille, 1887

Tylobranchion speciosum Herdman, 1886

Tylobranchion speciosum Herdman, 1886: 157, Pl. XXII 1-17; Monniot and Monniot, 1983: 50, Pl. IV F, I (synonymy); Monniot and Monniot, 1994: 119; Tatián *et al.*, 1998a: 149; 1998b: 113, Fig. 2 F.

Examined material: St. 194: 3 colonies; St. 196: 1 colony.

The colonies are attached to little rocks and gorgonians, with epibiotic algae and hydrozoans.

Family OCTACNEMIDAE Herdman, 1888

Cibacapsa gulosa Monniot and Monniot, 1983

Cibacapsa gulosa Monniot and Monniot, 1983: 50, Pl. IV G, H, Fig. 10; Monniot and Monniot, 1994: 28.

Examined material: St. 207: 3 specimens.

This is a species known from the Ross and Weddell Sea and South of Kerguelen (Monniot and Monniot, 1983, 1994). The present is the first record for the Scotia Arc (South Sandwich Islands).

Family AGNESIIDAE Huntsman, 1912

Caenagnesia bocki Ärnbäck-Christie-Linde, 1938

Caenagnesia bocki Ärnbäck-Christie-Linde, 1938: 41, Pl. 2 Fig. 20-22; Monniot and Monniot, 1983: 60, Fig. 11 G (synonymy).

Examined material: St 252: 1 specimen.

The tunic is uniformly covered with sand, mud, bryozoans, foraminifers and gastropods.

Family ASCIDIIDAE Adams, 1858

Ascidia meridionalis Herdman, 1880

Ascidia meridionalis Herdman, 1880: 465; Monniot and Monniot, 1983: 62, Fig. 12 A-E (synonymy).

Examined material: St. 150: 2 specimens; St. 153: 5 specimens; St. 160: 2 specimens; St. 164: 4 specimens.

The specimens show epibionts: bryozoans, polychaete tubes and algae. They are also covered by inorganic material, sponge spicules and sand particles. The gonads are composed of rounded testis follicles, joined or separate, covering the stomach, mainly in the posterior 2/3 of the body. The ovary follicles are small and yellow, arranged in irregular rows on the intestinal loop. Full gonoducts revealed the advanced reproductive state of the individuals (spawning). Renal vesicles are arranged around the gonads and the digestive tract.

Order STOLIDOBRANCHIA Lahille, 1887

Family STYELIDAE Sluiter, 1895

Styelidae sp.

Examined material: St. 164: 1 specimen.

The identification of the main characters was possible, but the gonadal structure was not. Epibiont of *Ascidia meridionalis*, the sole specimen collected at Shag Rocks may be a young specimen because of the small size (0.5 cm height, 0.8 cm width) and the little development of the gonads and the digestive tract.

Cnemidocarpa verrucosa (Lesson, 1830)

Cynthia verrucosa Lesson, 1830: 151; Monniot and Monniot, 1983: 68, Pl. VII A-C (synonymy); Monniot and Monniot, 1994: 32. Tatián *et al.*, 1998a: 149; 1998b: 113, Fig. 2 I.

Examined material: St. 174: 2 specimens; St. 182: 1 specimen; St. 187: 1 specimen.

There was a high variability in shape and colour among specimens collected at South Georgia and South Sandwich. The former are of large size (up to 20 cm), whitish, with both apertures very developed, the oral situated anteriorly. The tunic is provided with spines ending in multiple points. The specimen collected in South Sandwich was red-orange alive, brown-red when preserved. Apertures are both sessile and located at the same level. The tunic has rounded conical papillae.

Cnemidocarpa drygalskii (Hartmeyer, 1911)

Tethyum drygalskii Hartmeyer, 1911: 452, Pl. 45, Fig. 6; Monniot and Monniot, 1983: 69, Fig. 13 C, D (synonymy).

Examined material: St. 153: 1 specimen; St. 217: 2 specimens; St. 229: 1 specimen.

Family PYURIDAE Hartmeyer, 1908

Pyura georgiana (Michaelsen, 1898)

Boltenia georgiana Michaelsen, 1898: 364; Monniot and Monniot, 1983: 88, Pl. VI D, Fig. 19 A (synonymy).

Examined material: St. 182: 4 specimens.

The present record extends the bathymetric range of this endemic species from the South Georgia Islands to 300 m depth. Variable epibionts include hydrozoans, bryozoans and algae; particles of sand were also observed on the tunic.

Pyura bouvetensis (Michaelsen, 1904)

Boltenia bouvetensis Michaelsen, 1904: 216, Pl. 10, Fig. 6. Monniot and Monniot, 1983: 88 Pl. VI E, F, Fig. 18 D (synonymy); Monniot and Monniot, 1994: 33. Tatián *et al.*, 1998a: 150; 1998b: 113: Fig. 2 L.

Examined material: St. 231: 3 specimens; St. 241: 1 specimen; St. 252: 4 specimens; St. 253: 14 specimens.

Pyura discoveryi (Herdman, 1910)

Halocynthia discoveryi Herdman, 1910: 9; Monniot and Monniot, 1983: 96 (synonymy); Monniot and Monniot, 1994: 34. Tatián *et al*., 1998a: 150; 1998b: 113, Fig. 2 K.
Examined material: St. 174: 1 specimen ; St. 182: 5 specimens.

The specimens have epibionts at the base of the body: hydrozoans, bryozoans, bivalve shells, algae. There are sand particles adhered mainly to the base and close to the apertures.

Pyura squamata Hartmeyer, 1911

Pyura squamata Hartmeyer, 1909-1911: 1337 (nomen nudum); 1911: 439, Pl. 45 12, Pl. 50 1-5; Monniot and Monniot, 1983: 95 Fig. 20 A (synonymy); Monniot and Monniot, 1994: 34.

Examined material: St. 164: 1 specimen.

Although this specimen had five branchial folds at each side of its body, the published number of folds for this species is five well developed ones with a rudimentary sixth fold (Millar, 1960; Monniot and Monniot, 1983).

Family MOLGULIDAE Lacaze-Duthiers, 1877

Molgula pedunculata Herdman, 1881

Molgula pedunculata Herdman, 1881: 234; Monniot and Monniot, 1983: 98 (synonymy); Monniot and Monniot, 1994: 35; Tatián *et al*., 1998a: 150 Fig. 2 b, 3 a-c; 1998b: 113.

Examined material: St. 174: 2 specimens; St. 182: 2 specimens; St. 253: 1 specimen.

Specimens with epibionts: hydrozoans and algae.

Molgula hodgsoni Herdman, 1910

Molgula hodgsoni Herdman, 1910: 11, Pl. 3 Fig. 7B; Monniot and Monniot 1983: 99, Pl. VII G (synonymy); Monniot and Monniot, 1994: 34.
Examined material: St. 174: 4 specimens; St. 182: 5 specimens; St. 231: 1 specimen.

Description: The shape is nearly spherical, reaching a height of 1.3 to 2.4 cm and a width of 1.2 to 2 cm. The colour is transparent, the tunic is slender but resistant, showing abundant extensions similar to hairs. Algae, polychaetes, sponge spicules, foraminifers and sand particles are adhered mainly to the right side of the tunic. Both siphons are situated at the same level in the corners of the anterior part of the body. Some are conspicuous and others not. The mantle is thin. It is possible to see the internal organs by transparence. The musculature is strong: 16 to 20 longitudinal bands radiate from each aperture onto both sides of the body; they are interrupted at the anterior middle of the body (at the level of the visceral mass in the left side). Transverse bands are thinner, abundant in the siphons; some intercrossed in the body wall. The oral siphon is six-lobed, the cloacal siphon is four-lobed, both apertures have an internal velum. There are 15-16 oral tentacles in three different sizes, placed between and branched in three orders. The dorsal tubercle is C-shaped, opening to the left side, sometimes with curved horns, always inward. The dorsal lamina is short and narrow with a smooth margin or large with transverse grooves, wider in the posterior part. The branchial sac has a variable number of folds: in specimens from 1.5 to 2.3 cm height we found 7 folds on each side, but only 6 folds on the right side in specimens from 1.3 to 2.4 cm, and finally a total of 6 folds on both sides in one specimen of 2.2 cm. Folds located dorsally are mainly elevated, the ventral ones flat and arranged close to one another. There are 4-13 longitudinal vessels in the folds and 1-7 between folds. Some are branched. In one specimen (2.4 cm height) it was possible to observe the following arrangement of folds and longitudinal vessels:

On the right side: DL 5 (8) 6 (9) 5 (9) 6 (10) 6 (8) 5 (8) 2 (9) 2 E

On the left side: DL 1 (11) 6 (12) 5 (7) 5 (9) 6 (11) 5 (10) 5 (7) 2 E

There are transverse vessels at each side of the body separated by some thinner ones, and discontinuous parastigmatic vessels. The stigmata are straight, 5-7 per mesh. In some parts (at the base of the folds, in the joint of the folds and close to the wider transverse vessels) stigmata were lightly curved, not forming infundibula. The digestive tract is placed along the major part of the left side, with a long and narrow esophagus and a round or oval stomach covered by hepatic diverticula. The intestine is close to the endostyle, making a closed primary loop and a secondary curve very pronounced, followed by a very long rectum which is overlapped by the stomach, finishing in one smooth anus. Both hermaphrodite gonads are joined to the kidney and the intestine, respectively, by their posterior tip. The ovary is central and composed of small round follicles, yellow colour, covered by bigger and pyriform testis follicles, white colour, joined in many bunches. The oviduct is short, conspicuous and situated at the dorsal tip of the gonad; the sperm duct, less developed, opens beside the ovary. The kidney is transparent, sometimes curved.

Remarks: This species has been confused with small specimens of *Molgula pedunculata* (Millar, 1960; Kott, 1969a). Published literature always described the presence of seven folds on each side (Herdman, 1910; Ärnbäck-Christie-Linde, 1938; Millar, 1960; Monniot C., 1978). In some of our specimens there are only six, independent of the animal size. Monniot and Monniot (1983) saw "6 clean folds", but described a total of seven folds when they showed the number of longitudinal vessels. Some authors have seen infundibula (Kott, 1969a; Monniot and Monniot, 1983), whereas Herdman (1910) did not.

Eugyrioides polyducta
Monniot and Monniot, 1983

Eugyrioides polyducta Monniot and Monniot, 1983: 115, Pl. VII H, Fig. 24 D; Monniot and Monniot, 1994: 35.

Examined material: St. 252: 17 specimens

The tunic is covered by sand and mud particles and epibionts such as sponges and hydrozoans. The ovary is constituted by rounded follicles, while the testis follicles are arranged at the dorsal ridge of the ovary. The kidney is small and inconspicuous.

Biogeography

Species composition of the stations sampled was related to substrate type: cluster analysis divided the stations into 4 groups (Fig. 2). Group A and B contained samples from South Sandwich stations (volcanic stones, hard bottoms) that were characterised by a low number of species which caused the separation of the other groups. Group C comprised stations belonging to the Antarctic and Magellan banks (hard substrates). Group D included soft substrate stations from South Georgia, South Orkney and South Shetland Islands. Sub-groups clustered samples of close localities, i.e. Burdwood Bank and Shag Rocks (c_1), Herdman and Discovery Banks (c_2); South Orkney and South Shetland (d_1) and South Georgia and South Sandwich (d_2). Stations were grouped mainly by substrate type and then by geographical distance or region. Substrate type appears to be an important factor in ascidian distribution. Molgulids usually settle on soft substrates (Monniot and Monniot, 2001), and the same is true for some widely distributed Antarctic species such as *Distaplia cylindrica* or *Caenagnesia bocki* (Van Name, 1945; Millar, 1960; Kott, 1969a); these species, together with the molgulids *Molgula pedunculata, Molgula hodgsoni* and *Eugyrioides polyducta,* were found exclusively on muddy bottoms.

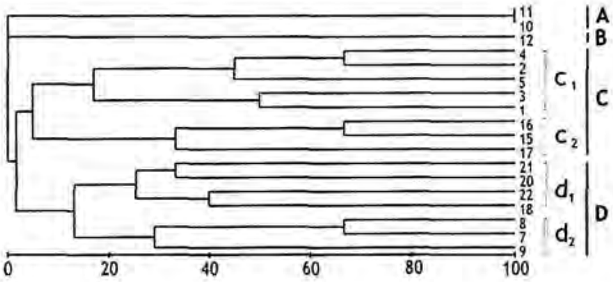

FIG. 2. – Cluster analysis of species at different localities. Groups formed are indicated with capital letters; sub-groups, indicated in lower-case letters (stations: 1-5: Burdwood Bank, Shag Rocks; 7-8: South Georgia; 9-12: South Sandwich; 15-17: Herdman and Discovery Banks; 18-20: South Orkneys; 21-22: South Shetland). Stations without ascidians were not included in the analysis.

The second cluster included previous data (Monniot and Monniot, 1983) and those from the present study (Fig. 3). It showed 2 main groups: group A included Antarctic localities (South Georgia, South Sandwich, South Orkney and South Shetland), and group B included samples from the Magellan Province. Sub-groups clustered samples of close localities: South Sandwich and South Georgia Islands (a_1) and South Shetland and South Orkney Islands (a_2). In this case with more samples and species, biogeographic region and distance seems to better explain the cluster analyses. Faunistic affinities using the pooled data-set (our data plus previous data) among different localities were compared with those calculated by Monniot and Monniot (1983). Table 3 reveals a gradient from Magellan to Antarctica along the Scotia Arc, in terms of their ascidian fauna. Nevertheless, the addition of six species to Magellan situated this area closer to the islands of the Scotia Arc than had been previously considered.

Stations belonging to the Magellan Province (Burdwood Bank, Shag Rocks) were similar. Only 3 species (*Aplidium globosum,* Polyclinidae sp. and *Cnemidocarpa drygalskii*) from a total of 9 found at these stations were also found in other localities.

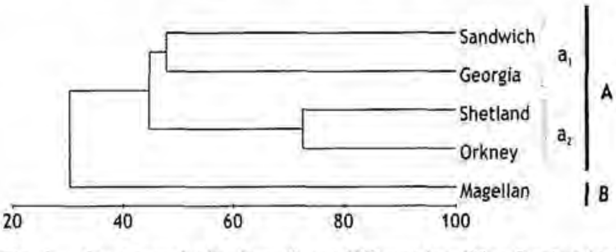

FIG. 3. – Cluster analysis of species at different localities. Pooled data from the present study and those from Monniot and Monniot (1983). Groups are indicated in upper case, sub-groups in lower case.

TABLE 3. – Similarity index between different localities. APS: pooled data from Antarctic Peninsula, South Shetland Islands and Elephant I. Ts: similarities calculated in this study; Ps: similarities calculated in a previous study by Monniot and Monniot (1983).

	Magellan		S. Georgia		S. Sandwich		S. Orkneys	
	Ts	Ps	Ts	Ps	Ts	Ps	Ts	Ps
S. Georgia	45%	42%	-	-	-	-	-	-
S. Sandwich	29%	25%	47%	49%	-	-	-	-
S. Orkney	35%	27%	45%	44%	41%	43%	-	-
APS	33%	27%	48%	47%	45%	44%	69%	65%

Some Subantarctic species are replaced in the Polar Front: *Ascidia meridionalis* is distributed along the Patagonian shelf to the South Georgia Islands, were it is replaced by *Ascidia challengeri*, which is absent in South American waters (Millar, 1960; Kott, 1969a; Monniot and Monniot, 1983).

The Polar Front seems to be an effective barrier to the dispersal of ascidians and the Scotia Arc islands could be a bridge for the colonisation of Antarctica (or vice-versa), as also suggested for other faunal groups (Clarke and Crame, 1989). Particularly interesting is the position of the South Georgia islands, since they represent the northernmost limit of exclusively Antarctic species and the southernmost of Magellan species, showing similar affinities to both the Antarctic and the Magellan region (Table 3). These distribution patterns, following the stepping stone model, suggest a fluctuating position of the Polar Front. Thus, as observed during the LAMPOS cruise but in contrast to most publications on the subject, the South Georgia Islands may be at the north of the Polar Front. This alternating position may cause considerable instability for shallow-water benthos.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Zoogeographical relationships of the littoral ascidiofauna around the Antarctic Peninsula, in the Scotia Arc and in the Magellan region*

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SUMMARY: Three Spanish Antarctic research cruises (Ant-8611, Bentart-94 and Bentart-95) were carried out in the South Shetland Archipelago (Antarctic Peninsula) and Scotia Arc (South Orkney, South Sandwich and South Georgia archipelagos) on the continental shelf and upper slope (10-600 m depth). They have contributed to our knowledge about ascidian distribution and the zoogeographical relationships with the neighbouring areas and the other Subantarctic islands. The distribution of ascidian species suggests that the Scotia Arc is divided into two sectors, the South Orkney Archipelago, related to the Antarctic Province, and the South Georgia Archipelago (probably including the South Sandwich Archipelago), which is intermediate between the Antarctic Province and the Magellan region.

Keywords: ascidians, Antarctic, Scotia Arc, Magellan, biogeography.

RESUMEN: RELACIONES ZOOGEOGRÁFICAS DE LA ASCIDIOFAUNA LITORAL EN LA PENÍNSULA ANTÁRTICA, ARCO DE SCOTIA Y REGIÓN MAGALLÁNICA. – Tres campañas antárticas españolas (Ant-86, Bentart-94 y Bentart-95) en el Archipiélago de las Shetland del Sur (Península Antártica) y Arco de Scotia (Archipiélagos de las Órcadas del Sur, Sandwich del Sur y Georgia del Sur), sobre fondos de la plataforma continental y parte superior del talud (profundidades entre 10 y 600 m), han contribuido a ampliar el conocimiento de la distribución de las ascidias en estas zonas, y sus relaciones biogeográficas con las áreas vecinas y otras islas subantárticas. Desde el punto de vista de la ascidiofauna, el Arco de Scotia se divide en dos sectores, por un lado las Órcadas del Sur más relacionadas con la Provincia Antártica; y por otro el Archipiélago de las Georgias del Sur (y probablemente las islas Sandwich del Sur) que ocupa una posición intermedia entre la Provincia Antártica y la región magallánica.

Palabras clave: ascidias, Antártida, Arco de Scotia, Magallanes, biogeografía.

INTRODUCTION

The Antarctic Province represents one of the most clearly defined biogeographic divisions in the world. Its northern limit is defined by the Antarctic Convergence (Ekman, 1967, Hedgpeth, 1969; Briggs, 1974; Knox, 1994; Crame, 1999). However, there are several hypotheses about the subdivisions of the Antarctic region, and their relationships with the Scotia Arc and the Magellan region. Ekman (1967) and Briggs (1974) consider two main subdivisions (subregions of Ekman, and provinces *sensu* Briggs). The latter proposed: i) a high Antarctic subregion or South Polar Province containing the continental coastal area and adjoining islands (including the South Shetland, South Orkney and South Sandwich archipelagos); and ii) a low Antarctic subregion or South Georgia Province containing the

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South Georgia Archipelago and the Shag Rock Bank. Dell (1972) opposed this hypothesis on the relationships of the Antarctic benthic fauna, emphasising that there is little evidence to warrant biogeographic subdivisions. Recently, Knox (1994), following Hedgpeth's scheme (1969), considered the Subantarctic region to be divided into the Magellan and Kerguelen Provinces or subregions; the Antarctic region in the western Antarctic, with the Antarctic Peninsula and the Scotia Arc (with the South Georgia district); and the Continental Antarctic. Longhurst (1998), basing his conclusions on plankton ecology, proposed that the Scotia Arc and the South Georgia Archipelago be included in the Austral Polar Province (Antarctic continent and adjoining islands). Arntz (1999) stressed the necessity of more effort in taxonomy to improve knowledge on floral and faunal relationships between the Antarctic and Magellan regions.

From a biogeographical point of view, the ascidians represent an excellent taxon for studying possible affinities between zones (Kott, 1969; Millar, 1971; Monniot and Monniot, 1983; Ramos-Esplá, 1991), and they have a high percentage of endemisms in the Antarctic region (about 34-38% in the Antarctic and Subantarctic regions in Monniot and Monniot, 1983). In terms of numbers and biomass, ascidians represent one of the main sessile benthic groups on the Antarctic continental shelf (Kott, 1969; Monniot and Monniot, 1983; Arnaud *et al.,* 1998), and they play an important role in the structure of filter-feeding communities (Gallardo, 1987; Jazdzewski *et al.*, 1986; Dayton, 1990; Galéron *et al.*, 1992; Arntz *et al.*, 1994, 1997; Sahade *et al.*, 1998; Kowalke, 1999; Gili *et al.*, 2001).

The Antarctic ascidiofauna has been well studied (see references in Van Name, 1945; Millar, 1960; Kott, 1969; Monniot and Monniot, 1983), and recent studies have focused on the South Shetland Archipelago and Weddell Sea (Rauschert, 1991; Monniot and Monniot, 1994; Luján and Ramos-Esplá, 1996; Tatián *et al.,* 1998; Varela and Ramos-Esplá, 2003). Also, the Scotia Arc and the Magellan region have been the subject of recent ascidian studies (Sanamyan and Schories, 2003). (Tatián and Sahade in Arntz and Brey, 2003). This study explores the biogeographical relationships of the Antarctic Peninsula and Scotia Arc with the Antarctic continent, Magellan region and the Subantarctic islands from the point of view of littoral ascidiofauna.

MATERIAL AND METHODS

Ascidians were collected (Table 1) on three Spanish Antarctic cruises: Ant-8611 (Scotia Arc and Elephant Island) with the fisheries vessels 'Pescapuerta IV' and 'Nuevo Alcocero'; and Bentart-94 (Livingston and Deception Islands) and Bentart-95 (Livingston, Deception and Trinity Island, and Bransfield Strait) with the RV 'Hespérides'. The samples were taken from the continental shelf and from upper slope locations, between 10 and 600 m depth, by SCUBA diving and remote sampling gears (Agassiz trawl, rocky and anchor dredges and Van Veen grab). Macrobenthos ($\varnothing \geq 1$mm) was sorted by sieve and the ascidians were separated, anaesthetised in menthol, and fixed/preserved in neutral formalin (10% in sea water with borax).

With regard to the ascidian distribution, we considered the following zones: i) the Antarctic region separating the Antarctic Peninsula (Graham and Palmer Lands, and adjoining islands, including the South Shetland Archipelago) from the Antarctic Continent; ii) the Scotia Arc, including the South Orkney, South Sandwich and South Georgia archipelagos; iii) the Magellan region, south of a line from Chiloé Island (at 42°S) to the mouth of the Rio de la Plata (at 35°S); and iv) the Subantarctic islands (Bouvet, Prince Edwards, Marion, Crozet, Kerguelen, Heard, MacDonald, Macquarie). For the purpose of distributional analysis we considered the shore or littoral ascidiofauna extending from the surface down to 500 m depth. This arbitrary depth was selected because the Antarctic ascidian fauna is rather uniform over this range (Briggs, 1974) and some deep Antarctic ascidian species such as *Cibacapsa gulosa* reach 500-600 m depth (Monniot and Monniot, 1983, 1994).

The presence/absence data were aggregated by the Bray-Curtis similarity index, and the analysis of the relationships between species and zones was carried out by hierarchical agglomerate (group average) clustering for the species and multidimensional scaling analysis (MDS) for the zones indicated above: the Antarctic Continent (AC), the Antarctic Peninsula (AP), the South Orkney (SO), South Sandwich (SS) and South Georgia (SG) archipelagos, the Magellan region (MR) and the Subantarctic islands (SAI), using the PRIMER software package (Clarke and Warwick, 1994). With regard to the ascidian distribution, we followed mainly the work of Monniot and Monniot (1983: Table IV) and completed it with recent data.

TABLE 1. – Ascidians recorded on the Spanish Antarctic cruises (Ant-8611, Bentart94 and Bentart95). Depth range: (1) 0-100 m; (2) 101-200 m; (3) 201-500 m; (4) 500-800 m.

Cruises (date)	Ant-8611 (22/11/86-05/02/87)						Bentart-94 (24/01-11/02/94)			Bentart-95 (16/01-04/02/95)								Total
Area	S. Georgia Is.		S. Sandwich Is.		S. Orkney Is		South Livingston Is.			Deception Is.		Livingston Is.			Antarctic Peninsula			Ind/col.
Latitude (S)	53°22'-55°28'		56°14'-59°00'		60°26'-61°53'		62°38'-62°45'			62°49'-62°59'		62°01'-62°46'			63°56'-63°59'			
Longitude (W)	34°21'-42°07'		26°14'-27°33'		43°03'-47°12'		60°21'-60°44'			60°32'-60°40'		60°19'-60°40'			60°41'-60°59'			
Depth range (n° ascidian samples)	2 (15)	3 (23)	2 (3)	3 (1)	3 (14)	4 (1)	1(27)	2 (12)	3 (2)	1 (2)	2 (6)	1 (7)	2 (5)	3 (7)	1 (1)	2 (1)	3 (2)	
Aplidium cyaneum Monniot and Monniot, 1983	.	.	.	.	.	.	6	1	.	.	.	1	.	.	.	.	.	8
Aplidium falklandicum Millar, 1980	7	2	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	19
Aplidium imbutum Monniot and Monniot, 1983	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
Aplidium loricatum F. Monniot, 1970	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	2
Aplidium meridianum (Sluiter 1906)	2	1	1	.	1	.	15	.	.	.	.	1	.	.	.	.	10	31
Aplidium millari Monniot and Monniot, 1994	.	.	.	.	.	.	19	.	.	.	.	.	.	.	.	.	.	19
Aplidium radiatum (Sluiter, 1906)	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	3
Synoicum adareanum (Herdman, 1902)	19	11	4	1	3	.	130	64	.	.	14	177	30	11	1	15	31	511
Synoicum ostentor Monniot and Monniot, 1983	.	.	.	.	.	.	70	20		.	.	.	.	.	.	.	.	90
Cystodytes antarcticus Sluiter, 1912	.	.	.	.	.	.	2	.	.	.	.	.	1	.	.	.	.	3
Distaplia colligans Sluiter, 1932	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1
Distaplia cylindrica (Lesson, 1830)	2	5	.	.	1	.	1	1	.	.	.	2	3	3	.	.	.	18
Sycozoa georgiana (Michaelsen, 1907)	.	.	.	.	.	.	12	.	.	.	.	.	.	.	.	.	.	12
Polysyncraton trivolutum (Millar, 1960)	.	.	.	.	.	.	5	.	.	.	3	31	.	.	.	.	.	39
Tylobranchion speciosum Herdman, 1886	.	.	.	.	.	.	122	4	2	.	.	10	.	.	.	.	.	138
Corella eumyota Traustedt, 1882	.	.	.	.	.	.	9	3	.	.	.	8	3	.	.	.	.	23
Agnezia biscoei (Monniot and Monniot, 1983)	.	.	.	.	5	.	94	.	52	.	.	80	.	.	.	.	.	231
Caenagnesia bocki Ärnback, 1938	.	.	.	.		.	126	.	.	.	9	.	.	.	.	.	.	135
Caenagnesia schmitti Kott, 1969	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	2
Ascidia challengeri Herdman, 1882	.	3	.	.	.	1	29	7	.	.	3	183	3	.	.	1	.	230
Cnemidocarpa drygalskii (Hartmeyer, 1911)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3
Cnemidocarpa pfefferi (Michaelsen, 1898)	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	2	4
Cnemidocarpa verrucosa (Lesson, 1830)	.	8	.	.	4	2	8	1	.	4	22	6	.	3	2	2	2	64
Dicarpa insinuosa (Sluiter, 1912)	.	.	.	.	.	.	.	1	.	.	2	.	.	.	.	1	.	4
Styela glans Herdman, 1881	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
Styela wandeli (Sluiter, 1911)	3	.	.	.	.	.	55	.	.	.	.	16	.	.	.	.	.	71
Bathypera splendens Michaelsen, 1904	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1
Pyura bouvetensis (Michaelsen, 1904)	1	6	.	.	5	.	.	.	.	.	1	7	.	5	19	14	16	69
Pyura discoveryi (Herdman, 1910)	38	80	.	.	2	1	5	.	.	.	.	.	.	1	1	1	3	132
Pyura georgiana (Michaelsen, 1898)	4	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15
Pyura legumen (Lesson, 1830)	1	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Pyura lycoperdon Monniot and Monniot, 1983	.	.	.	.	.	.	16	17	.	.	.	9	.	.	.	.	.	42
Pyura obesa Sluiter, 1912	.	.	.	.	2	.	12	.	.	.	.	11	2	1	.	.	.	28
Pyura setosa (Sluiter, 1905)	.	.	.	.	.	.	.	3	.	.	.	1	1	.	.	1	9	15
Pyura squamata Hartmeyer, 1909	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Eugyrioides polyducta Monniot and Monniot, 1983	.	.	.	.	.	.	22	.	.	.	3	5	15	.	.	.	.	45
Molgula enodis (Sluiter, 1912)	.	.	.	.	.	.	24	.	.	.	1	6	.	.	.	.	.	31
Molgula hodgsoni Herdman, 1910	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	5	.	1
Molgula marioni Millar, 1960	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Molgula mortenseni (Michaelsen, 1922)	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
Molgula pedunculata Herdman, 1881	1	9	.	.	2	.	93	5	.	140	338	107	10	8	.	.	.	713
Paraeugyrioides arnbackae (Millar, 1960)	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
N° colonies or individuals	80	154	5	1	28	4	890	128	54	144	397	664	70	32	23	40	76	2790
N° species	11	14	2	1	11	3	27	13	2	2	11	19	11	7	4	8	8	42

RESULTS AND DISCUSSION

Species groups

On the three Spanish Antarctic cruises Ant-8611, Bentart-94 and Bentart-95, forty-two species (Table 1) with about 2800 specimens were identified. Some species have enlarged their distribution zones: i) *Synoicum adareanum, Styela wandeli, Pyura bouvetensis, P. legumen, P. squamata, Molgula marioni* and *M. mortenseni* in South Georgia; ii) *Aplidium millari* and *Synoicum ostentor* in the South Shetlands (Antarctic Peninsula); iii) *Synoicum adareanum* and *Aplidium meridianum* in the South Sandwich Islands; and iv) *Agnesia biscoei, Cnemidocarpa pfefferi* and *Pyura obesa* in the South Orkney Islands.

The species cluster analysis (Fig. 1) from the sampled ascidians, with the records (Table 2) of different authors (Millar, 1960; Kott, 1969, 1971; Monniot and Monniot, 1983; 1994; Sanamyan and Schories, 2003), discriminates two main groups of species (similarity < 40%): I) the South Georgia-Magellan group (4 spp, 9.5% of the total), *Pyura legumen, Molgula marioni* and *M. mortenseni*, and *Pyura georgiana* (an endemic species to South Georgia); and II) species with Antarctic distribution (38 spp., 90.5% of the total), some of them present in the Magellan region, the Scotia Arc and/or the Subantarctic islands.

In this second group three subgroups can be distinguished:

IIa) Species only found in the Antarctic Peninsula: *Aplidium radiatum, Cystodytes antarcticus* and *Pyura lycoperdon*.

IIb) Species found off the Antarctic Continent, the Antarctic Peninsula, the South Orkney and/or the South Sandwich archipelagos: *Aplidium cyaneum, A. loricatum, Aplidium millari, Synoicum ostentor, Agnesia biscoei, Caenagnesia schmitti, Pyura obesa, P. setosa,* and *Molgula enodis* and *Paraeugyroides arnbackae,* with *Styela glans* and *Bathypera splendens* (euribathyc species also reported in the Magellan region).

IIc) Species present in the Antarctic Region, the Scotia Arc, including South Georgia Archipelago (*Caenagnesia bocki, Cnemidocarpa pfefferi, Dicarpa insinuosa, Syela wandeli, Pyura discoveryi, Eugyroides polyducta* and *Molgula hodgsoni*), and some of them with a wide distribution in the Magellan Region and/or in the rest of the Subantarctic islands (*Aplidium falklandicum, A. imbutum, A. meridianum, Synoicum adareanum, Distaplia colligans, D. cylindrica, Sycozoa georgiana, Polysyncraton trivolutum, Tylobranchion speciosum, Corel-*

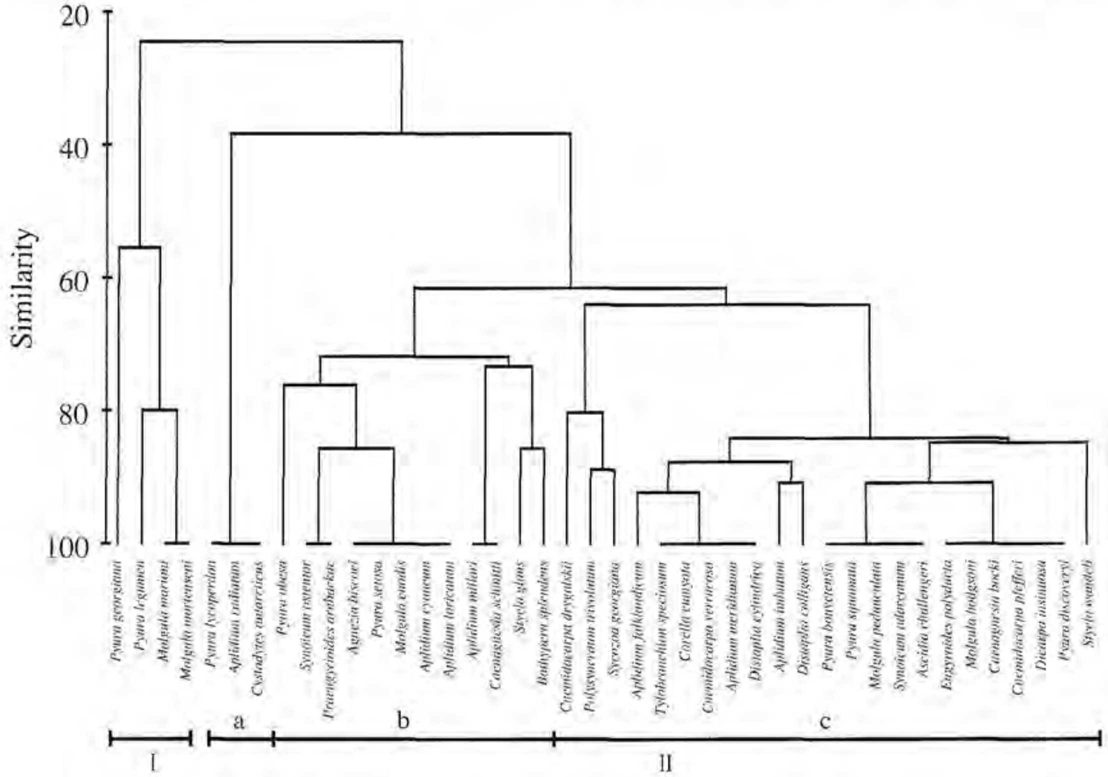

FIG. 1. – Cluster dendrogram of the sampled ascidian species with regard to the biogeographical affinities.

TABLE 2. – Distribution of the Antarctic and Subantarctic ascidiofauna: (AC) Antarctic continent; (AP) Antarctic Peninsula; (MR) Magellan region; (SAI) Subantarctic islands (Gough, Bouvet, Prince Edward, Marion, Crozet, Kerguelen, Heard, McDonald, Macquarie); (SG) South Georgia Is.; (SO) South Orkney Is.; (SS) South Sandwich Is., (Dr) depth range: (1) 0-200 m; (2) 201-500 m; (3) 501-1000 m); (4) > 1000 m. (AZ) other zones: (1) Chile (<42°S), Peru (>17°S); (2) New Zealand sector (<50°S); (3) Tasmania, Southern Australia; (4) South Africa, Namibia; (5) Cosmopolitan.

	MR	SG	SS	SO	AP	AC	SAI	Dr	AZ
Fam. Polyclinidae Verrill, 1871									
Aplidiopsis discoveryi Millar, 1960	+	.	.	.	.	.	.	1	2
Aplidiopsis pyriformis Herdman, 1886	.	.	.	.	.	.	+	1	.
Aplidium acropodium Monniot and Gail, 1978	.	.	.	.	.	.	+	1	.
Aplidium annulatum Sluiter, 1906	.	.	.	.	+	.	.	1	.
Aplidium aurorae (Harant and Vernières, 1938)	.	.	.	.	.	+	.	1-2	.
Aplidium balleniae Monniot and Monniot, 1983	.	.	.	.	.	+	.	1	.
Aplidium bilinguae Monniot and Monniot, 1983	.	+	.	.	.	+	.	1-2	.
Aplidium circumvolutum (Sluiter, 1900)	+	+	.	.	+	.	+	1-2	1
Aplidium cyaneum Monniot and Monniot, 1983	.	.	.	+	+	+	.	1-4	.
Aplidium didemniformis Monniot and Gail, 1978	.	.	.	.	.	.	+	1	.
Aplidium falklandicum Millar, 1960	+	+	.	+	+	.	+	1-2	.
Aplidium fuegiense Cunninghan, 1871	+	+	.	+	+	+	+	1-3	1
Aplidium globosum (Herdman, 1886)	.	.	+	+	.	.	+	1-3	.
Aplidium gracile Monniot and Monniot, 1983	+	.	.	.	.	.	.	1-3	.
Aplidium hians Monniot and Gail, 1978	.	.	.	.	.	.	+	1	.
Aplidium imbutum Monniot and Monniot, 1983	+	+	.	+	+	+	.	1-3	.
Aplidium irregulare (Herdman, 1886)	+	.	.	.	.	.	.	1-3	.
Aplidium laevigatum Herdman, 1886	+	.	.	.	.	.	+	1	.
Aplidium leviventer Monniot and Gail, 1978	.	.	.	.	.	.	+	1	.
Aplidium longum F.Monniot, 1970	+	.	.	.	.	.	+	1	.
Aplidium loricatum (Harant and Vernières, 1938)	.	.	.	+	+	+	.	1-3	.
Aplidium magellanicum Sanamyan and Schories, 2003	+	.	.	.	.	.	.	1	
Aplidium meridianum, (Sluiter, 1906)	+	+	+	+	+	+	+	1-4	.
Aplidium millari Monniot and Monniot, 1994	.	.	.	.	+	+	.	1-2	.
Aplidium miripartum Monniot and Monniot, 1983	.	.	.	.	+	.	.	1-2	.
Aplidium nottii (Brewin, 1951)	.	.	.	.	.	.	+	1	2
Aplidium novaezealandiae Brewin, 1952	.	.	.	.	.	.	+	1	2
Aplidium ordinatum (Sluiter, 1906)	.	.	.	.	+	+	.	1-2	.
Aplidium ovum F. Monniot and Gaill, 1978	+	.	.	.	.	.	+	1-2	3
Aplidium paessleri (Michaelsen, 1907)	+	+	.	.	.	.	.	1	.
Aplidium pellucidum Kott, 1971	+	.	.	.	.	.	.	1	.
Aplidium pererratum (Sluiter, 1912)	.	.	+	+	+	+	.	1-2	.
Aplidium peresi F. Monniot, 1970	.	.	.	.	.	.	+	1	.
Aplidium quadriversum Millar, 1982	.	.	.	.	.	.	+	1	.
Aplidium radiatum (Sluiter, 1906)	.	.	.	.	+	.	.	1	.
Aplidium recumbens (Herdman, 1886)	+	.	+	+	+	.	.	1-2	.
Aplidium retiforme (Herdman, 1886)	.	.	.	.	.	.	+	1	.
Aplidium siderum Monniot and Monniot, 1983	.	.	.	.	+	.	.	1	.
Aplidium stanleyi Millar, 1960	+	+	.	.	+	.	.	1-2	.
Aplidium stewartense (Michaelsen, 1924)	+	+	.	.	.	.	+	1	2
Aplidium triplex (Sluiter, 1906)	+	.	.	.	+	.	.	1-2	.
Aplidium undulatum F. Monniot and Gaill, 1978	+	.	.	.	.	.	+	1	.
Aplidium vanhoffeni Hartmeyer, 1911	.	.	.	.	.	+	.	2	.
Aplidium variabile (Herdman, 1886)	+	+	.	.	.	.	+	1-2	2
Aplidium vastum (Sluiter, 1912)	.	.	.	.	+	.	.	1	.
Aplidium vexillum Monniot and Gail, 1974	.	.	.	.	.	.	+	1	.
Placentella translucida Kott, 1969	.	.	.	.	+	.	.	2	.
Polyclinum sluiteri Brewin, 1956	+	.	.	.	.	.	.	2,3	2
Ritterella mirifica Monniot and Monniot, 1983	.	.	.	.	+	+	.	2	.
Synoicum adareanum (Herdman, 1902)	.	+	+	+	+	+	+	1-3	.
Synoicum georgianum Sluiter, 1932	+	+	+	+	+	+	+	1-2	.
Synoicum giardi (Herdman, 1886)	+	+	.	.	.	.	+	1	.
Synoicum kerguelenense Hartmeyer, 1911	.	.	.	.	.	.	+	1	.
Synoicum ostentor Monniot and Monniot, 1983	.	.	+	.	+	+	.	1-2	.
Synoicum polygyna Monniot and Monniot, 1980	.	.	.	.	.	+	.	2	.
Synoicum ramulosum Kott, 1969	.	.	.	.	.	+	.	1	.
Synoicum salivum Monniot and Gail, 1978	.	.	.	.	.	.	+	1	.
Fam. Didemnidae Giard, 1872									.
Didemnum biglans (Sluiter, 1906)	.	+	+	+	+	+	.	1-4	.
Didemnum studeri Hartmeyer, 1911	+	+	.	+	.	.	+	1-4	2,3
Didemnum subflavum (Herdman, 1886)	.	.	.	.	.	.	+	1	.
Didemnum tenue (Herdman, 1886)	+	+	.	.	.	.	.	2-4	.
Diplosoma antarcticum Kott, 1969	.	.	.	.	+	+	.	1	.
Diplosoma longinquum (Sluiter, 1912)	.	+	.	.	+	.	.	1-2	.
Leptoclinides capensis (Michaelsen, 1934)	.	.	.	.	.	.	+	1	4
Leptoclinides kerguelenensis Kott, 1954	.	.	.	.	.	.	+	1	.
Polysyncraton trivolutum (Millar, 1960)	+	+	.	.	+	+	+	1-3	.
Trididemnum auriculatum (Michaelsen, 1934)	+	.	.	.	.	.	.	1	.
Trididemnum propinquum (Herdman, 1886)	+	.	.	.	.	.	.	2	.

TABLE 2 (CONT.). – Distribution of the Antarctic and Subantarctic ascidiofauna: (AC) Antarctic continent; (AP) Antarctic Peninsula; (MR) Magellan region; (SAI) Subantarctic islands (Gough, Bouvet, Prince Edward, Marion, Crozet, Kerguelen, Heard, McDonald, Macquarie); (SG) South Georgia Is.; (SO) South Orkney Is.; (SS) South Sandwich Is., (Dr) depth range: (1) 0-200 m; (2) 201-500 m; (3) 501-1000 m); (4) > 1000 m. (AZ) other zones: (1) Chile (<42ºS), Peru (>17ºS); (2) New Zealand sector (<50ºS); (3) Tasmania, Southern Australia; (4) South Africa, Namibia; (5) Cosmopolitan.

	MR	SG	SS	SO	AP	AC	SAI	Dr	AZ
Fam. Polycitoridae Michaelsen, 1904									.
Cystodites antarcticus Sluiter, 1912	.	.	.	.	+	.	.	1-2	.
Distaplia colligans Sluiter, 1932	+	+	.	+	+	.	.	1-2	.
Distaplia concreta (Herdman, 1886)	.	.	.	.	.	.	+	1	.
Distaplia cylindrica (Lesson, 1830)	+	+	+	+	+	+	+	1-3	.
Eudistoma australe F. Monniot, 1978	.	.	.	.	.	.	+	1	.
Polycitor magalhaensis (Michaelsen, 1907)	+	.	+	+	.	.	.	1	.
Sycozoa anomala Millar, 1960	.	.	.	.	+	.	.	1	2
Sycozoa gaimardi (Herdman, 1886)	+	+	.	.	+	+	.	1-2	.
Sycozoa georgiana (Michaelsen, 1907)	.	+	.	.	+	+	+	1-2	.
Sycozoa sigillinoides Lesson, 1830	+	+	+	.	+	+	+	1-3	2
Tetrazona glareosa (Sluiter, 1906)	.	.	+	.	+	.	.	1	.
Fam. Cionidae Lahille, 1890									.
Tylobranchion speciosum Herdman, 1886	+	+	+	+	+	+	+	1-2	.
Ciona antarctica Hartmeyer, 1911	.	.	.	.	+	+	.	1-2	.
?Ciona intestinalis (Linnaeus, 1767)	+	.	.	.	.	.	.	1-2	5
Fam. Corellidae Lahille 1890									.
Corella eumyota Traustedt, 1882	+	+	.	+	+	+	+	1-3	1,2,3,4
Corynascidia cubare Monniot and Monniot, 1994	.	.	.	.	.	+	.	2	.
Xenobranchion insigne Ärnbäck-Christie-Linde, 1950	+	.	.	.	.	.	.	1	.
Fam. Agneziidae Hunstsman. 1912									.
Adagnesia henriquei Monniot and Monniot, 1983	+	.	.	.	.	.	.	1	.
Adagnesia weddelli Monniot and Monniot, 1994	.	.	.	.	.	+	.	2-4	.
Agnezia antarctica Kott, 1969	.	.	.	.	.	.	+	1	.
Agnezia arnaudi (Monniot and Monniot, 1974)	.	.	+	.	.	+	+	1	.
Agnezia biscoei (Monniot and Monniot, 1983)	.	.	+	+	+	+	.	1	.
Agnezia glaciata (Michaelsen, 1898)	+	.	.	.	.	.	.	1	.
Agnezia tenue (Monniot and Monniot, 1983)	+	.	.	.	.	.	.	1	.
Caenagnesia bocki Ärnback, 1938	.	+	+	.	+	+	.	1-3	.
Caenagnesia schmitti Kott, 1969	.	.	.	.	+	+	.	1-4	.
Fam. Ascidiidae Adams, 1858									.
Ascidia challengeri Herdman, 1882	.	+	.	+	+	+	+	1-4	3,4?
Ascidia meridionalis Herdman, 1880	+	+	.	.	.	.	.	1-4	.
Ascidia translucida Herdman, 1880	.	+	.	.	.	.	+	1-2	3
Fam. Styelidae Sluiter, 1895									.
Alleocarpa bacca Ärnbäck, 1929	+	.	.	.	.	.	.	1	.
Alleocarpa bridgesi Michaelsen, 1900	+	.	.	.	.	.	.	1	.
Alleocarpa bigyna C. Monniot, 1978	.	.	.	.	.	.	+	1	.
Alleocarpa incrustans (Herdman, 1886)	+	+	.	.	.	.	.	1	.
Cnemidocarpa barbata Vinogradova, 1962	.	.	.	.	.	+	+	1	.
Cnemidocarpa drygalskii (Hartmeyer, 1911)	.	.	.	.	+	+	+	1-3	.
Cnemidocarpa effracta C. Monniot, 1978	.	.	.	.	.	.	+	1	.
Cnemidocarpa eposi Monniot and Monniot, 1994	.	.	.	.	.	+	.	2	.
Cnemidocarpa minuta (Herdman, 1881)	.	.	.	.	.	.	+	1	.
Cnemidocarpa nordenskjöldi (Michaelsen, 1898)	+	.	.	.	.	.	.	1	.
Cnemidocarpa ohlini (Michaelsen, 1898)	+	.	.	.	.	.	.	1-2	.
Cnemidocarpa pfefferi (Michaelsen, 1898)	.	+	.	+	+	+	.	1-3	.
Cnemidocarpa robinsoni Hartmeyer, 1926	+	.	.	.	.	.	.	1	1
Cnemidocarpa verrucosa (Lesson, 1830)	+	+	+	+	+	+	+	1-2	.
Cnemidocarpa victoriae Monniot and Monniot, 1983	+	.	.	.	.	.	.	1-2	.
Dextrocarpa misanthropos C. Monniot, 1978	.	.	.	.	.	.	+	1	.
Dicarpa cornicula (C. Monniot, 1978)	.	.	.	.	.	.	+	1	.
Dicarpa insinuosa (Sluiter, 1912)	.	+	.	.	+	+	.	1-2	.
Dicarpa tricostata (Millar, 1960)	.	+	.	.	.	+	.	1	.
Oligocarpa megalorchis Hartmeyer, 1911	.	.	.	.	.	.	+	1	.
Polyzoa minor C. Monniot, 1970	.	.	.	.	.	.	+	1	.
Polyzoa opuntia Lesson, 1830	+	+	+	.	.	.	+	1	.
Styela glans Herdman, 1881	+	.	.	.	+	+	.	1-4	.
Styela malgalhaensis Michaelsen, 1898	+	.	.	.	.	.	.	1-3	.
Styela mallei C. Monniot, 1978	.	.	.	.	.	.	+	1	.
Styela materna Monniot and Monniot, 1983	.	+	+	.	.	.	.	1-2	.
Styela paessleri Michaelsen, 1898	+	.	.	.	.	.	.	1	.
Styela schmitti f. simplex Millar, 1960	+	.	.	.	.	.	.	1	.
Styela squamosa Herdman, 1881	?	+	+	+	.	+	.	1-4	3
Styela talpina C. Monniot, 1978	.	.	.	.	.	.	+	1	.
Styela wandeli (Sluiter, 1911)	-	+	.	+	+	.	.	1	.

TABLE 2 (CONT.). – Distribution of the Antarctic and Subantarctic ascidiofauna: (AC) Antarctic continent; (AP) Antarctic Peninsula; (MR) Magellan region; (SAI) Subantarctic islands (Gough, Bouvet, Prince Edward, Marion, Crozet, Kerguelen, Heard, McDonald, Macquarie); (SG) South Georgia Is.; (SO) South Orkney Is.; (SS) South Sandwich Is.. (Dr) depth range: (1) 0-200 m; (2) 201-500 m; (3) 501-1000 m); (4) > 1000 m. (AZ) other zones: (1) Chile (<42°S), Peru (>17°S); (2) New Zealand sector (<50°S); (3) Tasmania, Southern Australia; (4) South Africa, Namibia; (5) Cosmopolitan.

	MR	SG	SS	SO	AP	AC	SAI	Dr	AZ
Fam. Pyuridae Hartmeyer, 1904									
Bathypera splendens Michaelsen, 1904	+	.	.	+	+	+	.	1-4	.
Pyura bouvetensis (Michaelsen, 1904)	.	+	.	+	+	+	+	1-3	.
Pyura chilensis Molina, 1782	+	.	.	.	.	.	.	1	1
Pyura discoveryi (Herdman, 1910)	.	+	.	+	+	+	.	1-4	.
Pyura georgiana (Michaelsen, 1898)	.	+	.	.	.	.	.	1-2	.
Pyura legumen (Lesson, 1830)	+	+	.	.	.	.	.	1	.
Pyura lycoperdon Monniot and Monniot, 1983	.	.	.	.	+	.	.	1,2	.
Pyura obesa Sluiter, 1912	.	.	.	+	+	.	.	1-2	.
Pyura paessleri (Michaelsen, 1900)	+	.	.	.	.	.	.	1,2	.
Piura pilosa Monniot and Monniot, 1974	.	.	.	.	.	.	+	1	.
Pyura setosa (Sluiter, 1905)	.	.	.	+	+	+	.	1-2	.
Pyura squamata Hartmeyer, 1909	.	+	.	+	+	+	+	2-4	.
Pyura stubenrauchi (Michaelsen, 1900)	+	.	.	.	.	.	.	1	.
Pyura tunica Kott, 1969	.	.	.	.	.	+	.	1	.
Fam. Molgulidae Lacaze-Duthiers, 1877									.
Eugyrioides guttula (Michaelsen, 1900)	+	.	.	.	.	.	.	1	.
Eugyrioides kerguelensis (Herdman, 1881	.	.	+	.	+	.	+	1	.
Eugyrioides polyducta Monniot and Monniot, 1983	.	+	+	.	+	+	.	1	.
Eugyrioides septum (C. Monniot, 1978)	.	.	.	.	.	.	+	1	.
Eugyrioides vannamei (C. Monniot, 1970)	+	.	.	.	.	.	.	1	.
Gamaster vallatum C. Monniot, 1978	.	.	.	.	.	.	+	1	.
Molgula arnbackae C. Monniot, 1978	.	+	+	.	.	.	+	1	.
Molgula enodis (Sluiter, 1912)	.	.	.	+	+	+	.	1	.
Molgula estadosi Monniot and Monniot, 1983	+	.	.	.	.	.	.	1	.
Molgula euplicata Herdman, 1923	.	+	+	+	+	+	.	1-3	.
Molgula georgiana Michaelsen, 1900	.	+	+	.	.	.	+	1	.
Molgula hodgsoni Herdman, 1910	.	+	.	+	+	+	.	1-2	.
Molgula macquariensis Kott, 1954	.	.	.	.	.	.	+	1	.
Molgula marioni Millar, 1960	+	+	.	.	.	.	+	1	.
Molgula mortenseni (Michaelsen, 1922)	+	+	.	.	.	.	.	1	2
Molgula pedunculata Herdman, 1881	.	+	+	+	+	+	+	1-3	.
Molgula pigafettae Monniot and Monniot, 1983	+	.	.	.	.	.	.	1-2	.
Molgula pulchra Michaelsen, 1900	+	+	+	.	.	.	+	1-2	.
Molgula pyriformis Herdman, 1881	+	+	.	.	.	.	.	1-4	.
Molgula robini Monniot and Monniot, 1983	.	+	.	.	+	+	.	1-4	.
Molgula setigera Ärnback-Christie-Linde, 1938	+	.	.	.	.	.	.	1	.
Molgula variazizi C. Monniot, 1978	.	.	.	.	.	.	+	1	.
Molguloides coronatum C. Monniot, 1978	.	.	.	.	.	+	+	2	.
Molguloides crinibus C. Monniot, 1978	.	.	.	.	.	.	+	2	.
Molguloides glans C. Monniot, 1978	.	.	.	.	.	.	+	2	.
Paraeugyrioides arnbackae (Millar, 1960)	.	.	+	.	+	+	.	1-4	.
Paraeugyrioides macquariensis Kott, 1954	.	.	.	.	.	.	+	1	.
Paramolgula gregaria (Lesson, 1830)	+	+	.	.	.	.	.	1-2	1
Paramolgula canioi Monniot and Monniot, 1983	+	.	.	.	.	.	.	1	.
Total spp.	70	55	28	34	63	58	73		

la eumyota, Ascidia challengeri, Cnemidocarpa drygalskii, Cnemidocarpa verrucosa, Pyura bouvetensis, P. squamata and *Molgula pedunculata*).

Zoogeographical affinities

The MDS analysis between zones (Fig. 2) for the 172 species listed in Table 2 shows the proximity between the Antarctic continent and the Antarctic Peninsula, and a clear separation from the Scotia Arc islands. The South Orkney Archipelago has a similar component to the Antarctic groups, and the ascidian fauna of the South Georgia and South Sandwich archipelagos is intermediate between that of the Antarctic, the Magellan region and the rest of the Subantarctic islands.

The comparison at species level of the main families (with percentages > 5%: Polyclinidae, Styelidae, Molgulidae, Pyuridae, Polycitoridae, Didemnidae, and Agneziidae; Table 3) confirms the differences between the archipelagos of the Scotia Arc. The South Orkney islands show similar percentages of Molgulidae (12%), Styelidae (12%), Polycitoridae (9%) and Didemnidae (6%) to the

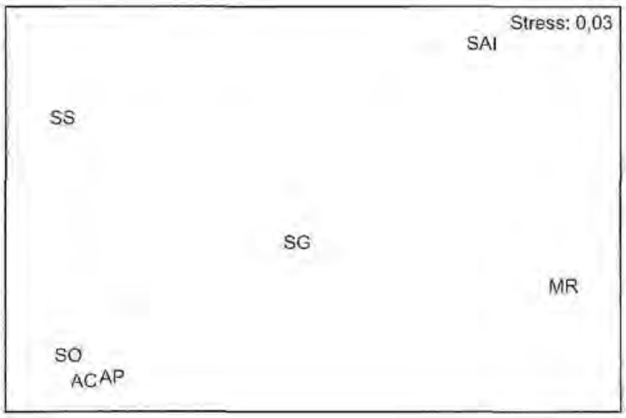

FIG. 2. – MDS analysis of the zones, based on the sampled ascidiofauna (distribution data completed with Monniot and Monniot, 1983). Legend: (AC) Antarctic Continent (without Antarctic Peninsula); (AP) Antarctic Peninsula (plus South Shetland Archipelago); (M) Magellan region; (SAI) Subantarctic Islands; (SG) South Georgia Archipelago; (SO) South Orkney Archipelago; (SS) South Sandwich Archipelago.

Antarctic region, and higher values than South Georgia and South Sandwich for Polyclinidae (32%) and Pyuridae (18%). The South Georgia and South Sandwich archipelagos have the lowest and the highest percentages of Polyclinidae (24-25%) and Molgulidae (22-29%) respectively among the Antarctic and Subantarctic zones; and Styelidae (14-16%) is intermediate between the Antarctic (12-13%) and Subantarctic (18-19%) regions. However, Pyuridae and Didemnidae are relatively important in South Georgia (9%), but scarce or never recorded (Pyuridae) in the South Sandwich Islands, whereas Agneziidae are well represented in the South Sandwich Islands (3 spp.), as in the Antarctic and Magellan regions (3-5 spp.). The lack or scarcity of the Pyuridae in the South Sandwich Islands is noteworthy, since this family presents big specimens and is easy to separate from the samples. Off the rest of the Subantarctic islands, Pyuridae are poorly represented (3 spp., with *Pyura bouvetensis* only reported from Bouvet island).

The biogeographical position of the ascidian fauna in the Scotia Arc is controversial. Reporting on this taxon, Kott (1969, 1969a) included the Antarctic Peninsula (with the Bellingshausen Sea) and the Scotia Arc in the South Georgia Province (or western Antarctic subregion, cf. Knox, 1994). However, Millar (1971) and Monniot and Monniot (1983) consider the South Georgia Archipelago to occupy an intermediate position between the Antarctic and Magellan regions, and to be a separate province, whereas the South Orkney and South Sandwich islands belong to the Antarctic region, in accordance with Ekman (1967) and Briggs (1974).

The present study supports the inclusion of the Antarctic Peninsula and adjacent islands in the Antarctic Province and the division of the Scotia Arc into two sectors: the South Orkney Archipelago, more related to the Antarctic Province, and the South Georgia Archipelago, a separate area, intermediate between the Antarctic Province and the Magellan region. The position of the South Sandwich islands is doubtful. It is related on the one hand to the South Georgia Archipelago and the Subantarctic islands, and on the other hand to the Antarctic Province. Nevertheless, the Scotia Arc has been poorly sampled, and much more sampling effort (as the LAMPOS cruise) must be carried out to elucidate its biogeographical relationships.

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TABLE 3. – Distribution by number of species (percentage in brackets) of the littoral ascidian families: (AR) Antarctic region; (MR) Magellan region; (SG) South Georgia; (SS) South Sandwich; (SO) South Orkney; (SAI) Subantarctic islands; (SAR) Subantarctic region (data from Table 2).

Families	MR	SAI	SG	SS	SO	AR	AR+SAR
Polyclinidae	23 (32.9)	27 (37.0)	13 (23.6)	7 (25.0)	11 (32.4)	29 (37.2)	57 (33.1)
Didemnidae	5 (7.1)	5 (6.8)	5 (9.1)	1 (3.6)	2 (5.9)	4 (5.1)	11 (6.4)
Polycitoridae	5 (7.1)	5 (6.8)	5 (9.1)	4 (14.3)	3 (8.8)	8 (10.3)	12 (7.0)
Cionidae	2 (2.9)	1 (1.4)	1 (1.8)	1 (3.6)	1 (2.9)	2 (2.6)	3 (1.7)
Corellidae	2 (2.9)	1 (1.4)	1 (1.8)	-	1 (2.9)	2 (2.6)	3 (1.7)
Agneziidae	3 (4.3)	2 (2.7)	1 (1.8)	3 (10.7)	1 (2.9)	5 (6.4)	9 (5.2)
Ascidiidae	1 (1.4)	2 (2.7)	3 (5.5)	-	1 (2.9)	1 (1.3)	3 (1.7)
Styelidae	13 (18.6)	13 (17.8)	9 (16.4)	4 (14.3)	4 (11.8)	10 (12.8)	31 (18.0)
Pyuridae	5 (7.1)	3 (4.1)	5 (9.1)	-	6 (17.6)	8 (10.3)	14 (8.2)
Molgulidae	11 (15.7)	14 (19.2)	12 (21.8)	8 (28.6)	4 (11.8)	9 (11.5)	29 (16.9)
Nº of species	70	73	55	28	34	78	172

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Soft-bottom macrobenthic faunal associations in the southern Chilean glacial fjord complex*

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SUMMARY: Macrobenthic associations were investigated at 29 sampling stations with a semi-quantitative Agassiz trawl, ranging from the South Patagonian Icefield to the Straits of Magellan in the South Chilean fjord system. A total of 1,895 individuals belonging to 131 species were collected. 19 species belong to colonial organisms, mainly Bryozoa (17 species) and Octocorallia (2 species). The phylum Echinodermata was the most diverse in species number (47 species), with asteroids (25 species) and ophiuroids (13 species) being the best represented within this taxon. Polychaeta was the second dominant group in terms of species richness (46 species). Multidimensional scaling ordination (MDS) separated two station groups, one related to fjords and channels off the South Patagonian Icefield and the second one to stations surrounding the Straits of Magellan. 45 species account for 90% of the dissimilarity between these two groups. These differences can mainly be explained by the influence of local environmental conditions determined by processes closely related to the presence/absence of glaciers. Abiotic parameters such as water depth, type of sediment and chemical features of the superficial sediment were not correlated with the numbers of individuals caught by the Agassiz trawl in each group of sampling stations.

Keywords: Magellan region, South Patagonian Icefield, Straits of Magellan, community structure, biodiversity.

RESUMEN: ASOCIACIONES FAUNÍSTICAS MACROBENTÓNICAS DE FONDOS BLANDOS EN EL COMPLEJO DE FIORDOS GLACIARES DE CHILE AUSTRAL. – Mediante el uso de una rastra Agassiz modificada se investigaron las asociaciones macrobentónicas presentes en 29 estaciones de muestreo, localizadas entre el Campo Patagónico de Hielo Sur y el Estrecho de Magallanes en el sistema de fiordos de Chile austral. Se colectó un total de 1.895 individuos pertenecientes a 131 especies, además de 19 especies de organismos coloniales, especialmente Bryozoa (17 especies) y Octocorallia (2 especies). El phylum Echinodermata fue el más diverso en términos de número de especies (47 especies), con una mejor representación de asteroideos (25 especies) y ofiuroideos (13 especies). El segundo grupo dominante en términos de riqueza de especies fue Polychaeta (46 especies). La técnica de "Escalamiento Multidimensional" (MDS) permitió separar dos grupos de estaciones: uno relacionado con los fiordos y canales del Campo Patagónico de Hielo Sur y el otro con las estaciones localizadas alrededor del Estrecho de Magallanes. Cuarenta y cinco especies explican el 90% de disimilitud entre estos dos grupos. Las diferencias se pueden explicar principalmente por la influencia de condiciones ambientales locales, determinadas por procesos estrechamente relacionados con la presencia/ausencia de glaciares. No hubo correlación entre parámetros abióticos tales como profundidad, tipo de sedimentos y características químicas del sedimento superficial y el número de individuos capturados por la rastra Agassiz en cada grupo de estaciones de muestreo.

Palabras clave: Región de Magallanes, Campo de Hielo Patagónico Sur, estrecho de Magallanes, estructura comunitaria, biodiversidad.

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INTRODUCTION

Much of the Magellan region at the southern tip of South America is still under the influence of a massive, elongated, narrow ice sheet, which continues to be active but reached its largest extension during the Last Glacial Maximum period (around 19,000-23,000 yr ago; Hulton *et al.*, 2002). At present, there is evidence of a wide and intensive retreat of several of the conforming fjordic glaciers which began 12,000 years ago (Moreno *et al.*, 1999). The resulting geomorphologic area is a large complex of fjords and channels whose linear extension is estimated at about 30,000 km of linear shoreline.

In contrast to northern hemisphere fjord environments (e.g. Pearson, 1980; Gulliksen *et al.*,1985; Holte and Gulliksen, 1998; Larsen, 1997; Kendall *et al.*, 2003; Wlodarska-Kowalczuk *et al.*,1998; Wlodarska-Kowalczuk and Pearson, 2004) and even in comparison with the Antarctic ecosystem (Dawber and Powell, 1997; Arntz *et al.*,1994; Jazdzewski *et al.*, 2001), there is a lack of biological information on the Magellan region. However, this region represents a corner-stone for elucidating several biogeographical and ecological questions related to latitudinal gradients in species diversity or biomass (Clarke, 1992; Gray, 2001a; b; Piepenburg *et al.*, 2002), origin and evolution of the (sub)Antarctic biota (Gallardo *et al.*, 1992; Arntz and Ríos, 1999) or the split of zoogeographical units along the western coast of South America (Brattström and Johanssen, 1983; Lancellotti and Vásquez, 2000; Camus, 2001; Montiel *et al.*, 2004).

The benthic sublittoral macrofauna inhabiting the Magellan region has been described mainly for the Straits of Magellan and related channels (e.g. Gutt *et al.*, 1999; Gerdes and Montiel, 1999; Thatje and Mutschke, 1999; Brey and Gerdes, 1999; Montiel *et al.*, 2001; Ríos *et al.*, 2003) and mostly after the 1994 "Victor Hensen" scientific cruise in the Magellan region (Arntz and Gorny, 1996). Nevertheless, there still is a lack of comparative studies for the Magellan region, including an update of the taxonomic knowledge of this Subantarctic area (Arntz, 1999). A study on the benthic macrofauna along the entire Magellan coastal zone by Gerdes *et al.* is still underway, focusing on the analysis of abundance and biomass of major taxa (e.g. Mollusca, Polychaeta, Crustacea and Echinodermata). The lowest values were obtained at the stations in the South Patagonian Icefield, with an increasing gradient of abundance and biomass towards the southernmost sampling areas.

The present study encompasses a geographically wide range of the Magellan region and is based on data from semi-quantitative benthic research in this heterogeneous marine ecosystem. The aim is to give a better insight into the structure of benthic macrofaunal communities for the area at species level. Additionally, we identify and compare benthic key species, which are representative of the fjord and channel ecosystem in this region. Finally, we evaluate the influence of some physical environmental variables on the obtained macrobenthic distribution patterns.

MATERIAL AND METHODS

Samples were taken during the CIMAR-Fiordo III (October 1995) and CIMAR-Fiordo VII (November 1997) campaigns organised by the Chilean Comisión Oceanográfica Nacional (CONA) from on board the R/V "Vidal Gormaz". A total of 29 localities were sampled using a modified Agassiz trawl (AGT) (3.15 m wide and 1.1 m high, with a mesh size of 10 mm) at depths of 24-732 m, ranging from the northern limit of the South Patagonian Icefield (SPI) to the eastern entrance of the Straits of Magellan (SM) (Fig. 1). Working time on the bottom for each haul averaged 12 min. Detailed sampling station data are summarised in Table 1.

Catch volumes of the AGT were relatively small at each station, in terms of both sediment and epibenthic fauna. Therefore, all the collected material was considered as a sample for later analysis and the number of caught specimens was used as representative of abundance for similarity analysis. The samples were immediately sorted onboard by separating all the collected fauna from the sediment using sieves with 1 mm mesh size. The sorted animals were preserved in a 5% formaldehyde seawater solution buffered with hexamethylentetramin.

The collected macrofauna was identified to the lowest possible taxonomic level, but for some taxa (e.g. Holothuroidea) identification was possible only to higher taxonomic levels. Organisms were identified based on standard publications (Retamal, 1974; Forcelli, 2000), experts who assisted in the identification of different taxa (see "Acknowledgement") and the identified benthic species at the "Edmundo Pisano Reference Collection" of the Instituto de la Patagonia, Universidad de Magallanes.

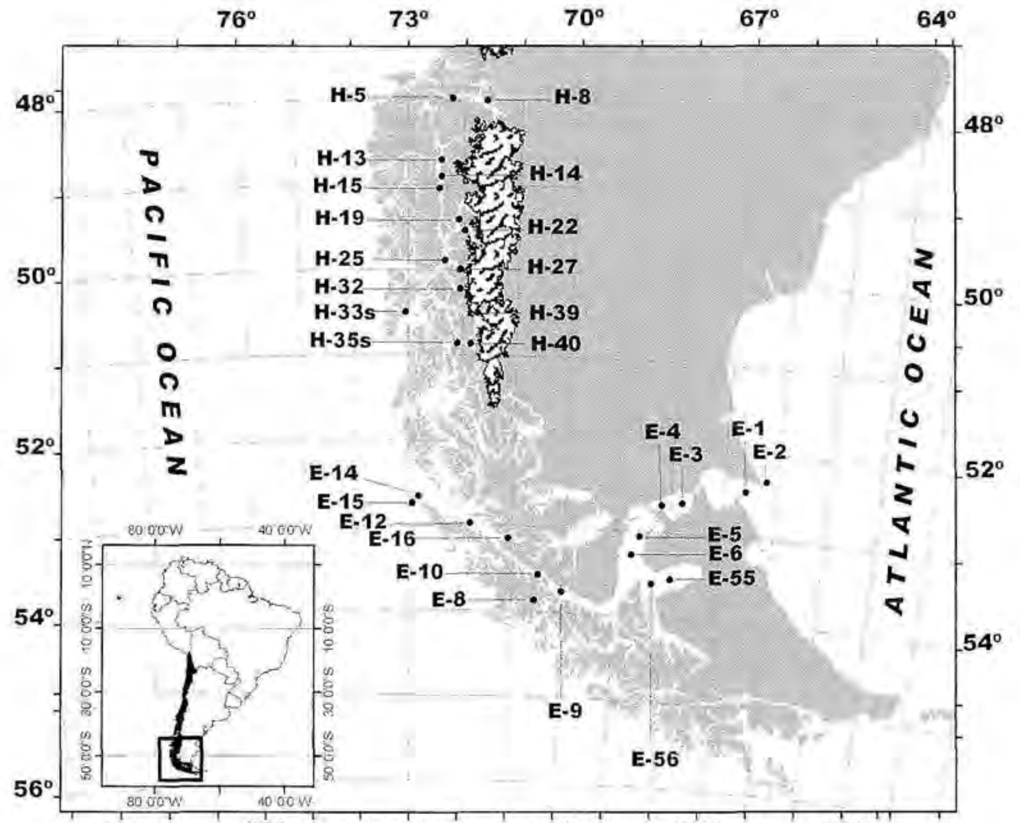

FIG. 1. – Map showing the Magellan region and the sampling sites in the South Patagonian Icefield (SPI) and Straits of Magellan (SM) areas.

TABLE 1. – List of stations sampled in the Magellan region. n.i. = no information.

Station N°	Locations	Depth (m)	Latitude S	Longitude W	Sampling date	Bottom type	C org (ug at/g)	N org (ug at/g)	P total (ug at/g)
H8	Canal Baker	723	47°58.6	74°13.2	22.08.95	Mud	540.7	86.5	14.4
H5	Canal Baker	382	48°00.3	73°36.7	22.08.95	Mud	403.5	72.2	11.7
H13	Canal Hammick	345	48°42.3	74°24.3	23.08.95	Sand	387.4	36.8	11.1
H14	Angustura Inglesa	385	46°53.9	74°24.2	23.08.95	Sand	540.7	89.3	12.3
H15	Paso del Indio	166	49°02.4	74°26.1	23.08.95	Sand	1024.9	187.8	16.2
H19	Fiordo Eyre	349	49°24.5	74°05.9	24.08.95	Mud	212.1	30.7	11.4
H22	Fiordo Falcon (sector Agüada)	122	49°32.1	73°59.1	24.08.95	Mud	355.1	58.8	9.4
H27	Fiordo Penguin	232	49°53.3	74°20.3	26.08.95	Mud	581.1	80.5	8.5
H25	Fiordo Penguin	298	49°59.6	74°03.7	26.08.95	Mud	322.8	48.1	11.8
H32	Fiordo Europa	66	50°13.5	74°03.1	27.08.95	Mud	226.0	34.5	11.1
H33S	Canal Oeste	75	50°29.6	75°02.5	28.08.95	Sand	n.i.	n.i.	n.i.
H35S	Fiordo Peel (Paso la Piedra)	117	50°51.7	74°05.9	29.08.95	Mud	355.1	53.2	18.5
H39	Fiordo Peel (Bahía Chubretovich)	110	50°30.3	73°44.3	29.08.95	Mud	266.3	23.0	10.7
H40	Fiordo Amalia (Interior)	148	50°52.3	73°50.8	29.08.95	Mud	500.4	71.5	13.5
E1	Boca Oriental E. de Magallanes	70	52°27.4	68°35.0	06.10.97	Sand gravel	n.i.	n.i.	n.i.
E2	Bahía Posesión	40	52°19.4	69°12.2	06.10.97	Mud	n.i.	n.i.	n.i.
E3	1° Angostura E. de Magallanes	24	52°38.6	69°46.48	07.10.97	Sand gravel	n.i.	n.i.	n.i.
E4	2° Angostura E. de Magallanes	41	52°41.1	70°10.2	07.10.97	Sand gravel	n.i.	n.i.	n.i.
E5	Paso Ancho	88	53°03.6	70°32.8	07.10.97	Sand gravel	n.i.	n.i.	n.i.
E6	Paso Ancho	177	53°16.5	70°41.2	07.10.97	Sand gravel	n.i.	n.i.	n.i.
E56	Bahía Inutil	270	53°32.6	69°54.7	08.10.97	Mud	n.i.	n.i.	n.i.
E55	Bahía Inutil	50	53°36.3	70°16.0	07.10.97	Mud	n.i.	n.i.	n.i.
E8	Bahía Snug	260	53°51.8	72°32.0	14.10.97	Mud	n.i.	n.i.	n.i.
E9	Isla Wood	313	53°45.1	71°59.9	15.10.97	Mud	n.i.	n.i.	n.i.
E10	Paso Tortuoso	404	53°33.7	72°28.6	15.10.97	Sand	n.i.	n.i.	n.i.
E15	Cabo Tamar	604	52°58.6	73°48.6	16.10.97	Sand gravel	n.i.	n.i.	n.i.
E14	Boca Occidental E. de Magallanes	66	52°39.5	74°48.5	16.10.97	Sand gravel	n.i.	n.i.	n.i.
E12	Boca Occidental E. de Magallanes	90	52°44.4	74°55.6	16.10.97	Sand	n.i.	n.i.	n.i.
E16	Golfo Xaltegua	411	53°8.65	73°4.70	16.10.97	Mud	n.i.	n.i.	n.i.

Data were analysed using the PRIMERv5 computer package (Clarke and Warwick, 1994). To analyse the spatial distribution of sampling sites over the study area, the MDS ("multidimensional scaling") program based on presence-absence matrix data was employed. This procedure also made it possible to consider colonial organisms (e.g. Gorgonaria and Bryozoa), which were collected at several sampling stations. Routine SIMPER ("similarity percentage") was used to discriminate species and their percentage of contribution to (dis) similarities within and between groups defined by the MDS. In this case, only solitary (counted) organisms were considered.

To determine whether the benthic distribution patterns showed relationships to environmental abiotic parameters, the BIO-ENV procedure from PRIMER was applied to data available for the study area. BIOENV (Clarke and Gorley, 2001) selects a combination of environmental factors best explaining a community pattern by maximising a Spearman rank correlation between the respective similarity matrices using all possible permutations of environmental factors. The similarity measure used was the Normalized Euclidean Distance. Environmental variables (water depth, substrate) and some sediment chemical features of the SPI (organic carbon and nitrogen, total phosphate) were obtained from Ahumada *et al.* (1996) and Silva and Prego (2002). Comparable information for the SM area is relatively scarce. The effects of water depth, bottom type, hydrodynamic regime and suspended particulate matter (Brambatti *et al.*, 1991; Fontolan and Panella, 1991) were also analysed.

RESULTS

Species composition and numerical dominance

The sampling stations showed relatively low numbers of specimens in the catches by the Agassiz trawl. A total of 1,895 individuals were caught belonging to 5 epi- and endobenthos major taxa, from which 131 species were identified (Table 2). Another 19 species belonged to colonial taxa, mainly Bryozoa (17 species) and Octocorallia (2 species).

The taxon Echinodermata was the most diverse in numbers of species (47 species), with 25 species belonging to asteroids, 13 species to ophiuroids, 6 species to holothuroids and 3 to echinoids. Polychaeta (46 species) were the second dominant taxon in terms of species richness. Mollusca (25 species) were the third important taxon, encompassing Bivalvia (13 species), Gastropoda (8 species), Polyplacophora and Scaphopoda (2 species each).

Echinodermata were the taxon with the highest number of individuals, representing 51% of the total catch. Ophiuroidea were the most abundant class, representing 20% of the total collected organisms.

The frequency of occurrence of species at the sampling stations was low, in accordance with the number of macrofauna caught. The echinoid *Pseudechinus magellanicus* was caught at 35% of the sampling sites, whereas *Ctenodiscus procurator* (Asteroidea), *Ophiuroglypha lymani* (Ophiuroidea) and *Euripodius latreillei* (Crustacea) were collected at 24% of the stations.

Comparison between sampling sites

Two major groups of stations can be discriminated in the two-dimensional MDS configuration of the 29 sampling sites, based on presence-absence data (Fig 2a). The stress value for the ordination (s = 0.13) corresponds to a good representation (Clarke and Warwick, 1994). One group includes all the stations associated with the South Patagonian Icefield and the second one comprises stations mostly situated in the Straits of Magellan area. The average dissimilarity of all pairwise coefficients in the SPI and SM group was 97.4. Of these, 10.5 were contributed by *Ctenodiscus procurator*, 7.3 by *Ophiuroglypha lymani* and 6.5 by *Magellania venosa*, accounting for 24.9% of the overall value of 97.4 (Table 3). These three species are representative of the SM station group. A total of 45 species account for 90% of the dissimilarity between these two groups. The stations in the Straits of Magellan show consistently higher catch levels than the stations off the SPI.

The ordination of sampling stations for the Straits of Magellan suggests a subordinate segregation of sampling sites, which was analysed in more detail considering only sample sites of this area (Fig 2b). In this case, distinct clusters of sites emerge, showing a relation to geographical positions across the Straits of Magellan. One group is related to the eastern entrance of the Straits (Boca Oriental, Primera Angostura, Segunda Angostura and Bahía Posesión), whereas stations from the Pacific entrance (e.g. Boca Occidental) form another separate subgroup. From sampling stations between the two Strait entrances (Atlantic and Pacific) there emerge two other subgroups. The sampling sites

TABLE 2. – A list of marine invertebrate species found in the areas of study. Number of individuals caught with the Agassiz trawl at each station is included (H = South Patagonian Icefield stations; E = Straits of Magellan stations). Colonial organisms are indicated by p=presence.

Species/stations number	H5	H8	H13	H14	H15	H19	H22	H25	H27	H32	H33s	H35s	H39	H40	E1	E2	E3	E4	E5	E6	E55	E56	E8	E9	E10	E12	E14	E15	E16
Anthozoa																													
Thouarella variabilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	p	0	0	0	p	0	0	0	0	0
Primnoella sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0
Polychaeta																													
Terebellidae INDET	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Polynoidea INDET	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	1	0	0	0	0	0	0	0	1	0
Opheliidae INDET	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ampharetidae INDET	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Sabellidae INDET	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Sabellariidae INDET	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Lumbrineridae INDET	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Eunereis patagonica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	2	0	0	0	0	0	0	0	0	0	0	0
Platynereis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Onuphis pseudoiridescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Chaetopterus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0
Maldane sarsi	0	1	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Melinna cristata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtys paradoxa	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cirratulus sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eunice pennata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphrodita magellanica	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Abyssoninoe abyssorum	0	0	0	0	1	0	0	0	1	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lumbrineris cingulata	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ninoe leptognatha	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asychis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nepthys sp.	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnonereis hartmannschroederae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicon maculata	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neanthes cf. abyssorum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neanthes kerguelensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Travisia kerguelensis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anaitides sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harmothoe cf. xanthena	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harmothoe campoglacialis	0	0	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hololepida sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyeunoa laevis	0	0	0	0	0	0	1	34	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypsicomus phaeotaenia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leanira quatrefagesi	0	0	0	0	6	3	0	1	2	0	3	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neoleanira magallanica	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laonice sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sternaspis scutata	0	0	0	0	13	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artacama valparaisiensis	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eteone sculpta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sthenolepis magellanica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Nothria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Lanice cf. flabellum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicolea chilensis	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pista cristata	0	0	7	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terebellides bisetosa	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terebellides sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Decapoda																													
Eurypodius latreillei	0	0	0	0	0	0	0	0	0	0	8	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	2	4	0
Halicarcinus planatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Stereomastis suhmi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pagurus comptus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Campylonotus semistriatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	8	0	0	0	0
Libidoclaea smithi	0	0	1	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Munida subrugosa	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Peltarion spinosulum	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Isopoda																													
Acanthoserolis schythei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	6	40	0
Cirolana chilensis	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aega sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thoracica																													
Austromegabalanus psittacus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	p	p	p	0	0	0	0	0	0	0	0	0	0	0
Polyplacophora																													
Stenoseurus exaratus	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callochiton puniceus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0

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Species/stations number	H5	H8	H13	H14	H15	H19	H22	H25	H27	H32	H33s	H35s	H39	H40	E1	E2	E3	E4	E5	E6	E55	E56	E8	E9	E10	E12	E14	E15	E16
Gastropoda																													
Crepidula dilatata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0
Trochita pileolus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Trochita pileus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adelomelon ancilla	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Berthella platei	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0	5	0	0	0	0	0	0	0	0	0	0
Trophon geversianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Pareuthria plumbea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
Photinula caerulescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0
Bivalvia																													
Aulacomya ater	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0
Lucinoma lamellata	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ennucula grayi	1	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0
Acesta patagonica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Camptonectus (P.) subhyalinus	0	0	0	0	0	0	0	191	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limopsis marionensis	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	72	0	0	5	0	0	0	0	0	0
Limopsis sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyclocardia velutina	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	14	0	0	0	0	0
Tindaria virens	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nucula sp.	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys patagonica	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0
Yoldia cf. *woodwardi*	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yoldia eightsii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scaphopoda																													
Dentalium majorinum	0	0	0	0	1	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	12	0	10	0	0	0	0	0	1
Dentalium cf. *perceptum*	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bryozoa																													
Reteporella magellensis	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nevianipora milneana	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hornera sp.	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microporella hyadesi	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhabdopleura normani	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adeonella sp.	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0
Orthoporidra petiolata	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aspidostoma giganteum	0	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	0	p	0	0	p	0	0
Catadysis pygmaeum	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carbacea ovoidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	p	p	p	p	p	p	p	0	0	0	0	0	0	0	0
Hippodinella adpressa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	p	0	0
Cellaria malvinensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	p	0	p	0	0	0	p	0	0	0	0	0
Heteporella chilensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	p	0	0	p	0	0
Smittina lebruni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	p	0	0	p	0	0
Ogivalia elegans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0
Arachnopusia monoceros	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fasciculipora meandrina	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Articulata																													
Terebratella dorsata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35	0	1	0	0	3	0	0	0	0	0	0	0	0	0
Magellania venosa	0	0	0	0	0	0	0	0	0	0	1	0	0	0	31	0	5	0	142	0	0	0	0	0	0	0	0	0	0
Asteroidea																													
Ctenodiscus procurator	0	0	0	0	50	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	12	29	10	0	0	6	0	0	22
Asterina fimbriata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Cheiraster (Luidiaster) planeta	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Solaster regularis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Poraniopsis mira	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lophaster stellans	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Doraster qawashqari	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cosmasterias lurida	0	0	0	0	0	0	0	0	0	0	16	0	0	0	2	8	0	0	0	0	0	0	0	0	0	0	0	0	0
Henricia obesa	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	4	0	0	0	0
Henricia studeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Labidiaster radiosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1
Calyptraster tenuissimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0
Odontaster penicillatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Odontaster meridionalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
Ceramaster patagonicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hippasterias sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Porania antarctica magellanica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5	0	0	0	3	0
Anasterias antarctica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anasterias sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0

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Asteroidea																													
Ganeria falklandica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	1	0	0	0	0	0	0	0	0	0	0
Bathybiaster loripes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	0	0	1	0	0	4
Poraniopsis echinaster	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cycethra verrucosa	0	0	0	0	18	0	0	0	0	0	0	0	0	0	2	0	1	10	0	0	0	0	0	0	4	0	0	0	0
Austrocidaris lorioli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Brisaster moseleyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Echinoidea																													
Tripylaster philippii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	2
Arbacia dufresnei	0	0	1	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pseudechinus magellanicus	0	0	0	0	0	0	2	0	0	0	8	4	24	0	0	6	1	0	11	20	0	0	0	5	9	0	0	0	0
Ophiuroidea																													
Ophiura INDET	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Ophiacantha cf. pentactis	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiactis sp.	0	0	0	0	0	0	0	0	0	0	111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiocten amitinum	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiacantha vivipara	0	0	0	0	0	0	2	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiuroglypha lymani	13	0	7	0	0	0	3	0	0	0	0	8	0	0	0	0	0	0	0	55	0	0	0	4	65	0	0	0	0
Gorgonocephalus chilensis	0	0	0	0	0	0	3	0	0	0	27	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiomyxa vivipara	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiactis asperula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	5	0	0	0	0	0	0	0	0	0	1	1
Astrotoma agassizii	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Homalophiura inornata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0
Ophioscolex nutrix	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Homalophiura sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holothuroidea																													
Hemoiedema spectabilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Psolus patagonicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	79	0	0	0	0	0
Pseudocnus leoninus dubiosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Holothuroidea sp 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Holothuroidea sp 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34	0	12	0	2	0	0	0
Holothuroidea sp 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	7	0	0	0	0	0

with the biggest catches were the two stations in Paso Ancho (stations C5 and C6; see Fig. 1), Isla Wood (C9), and Paso Tortuoso (C10). The most frequently occurring group of specimens in the entire SM area was Brachiopoda, with the articulate brachiopod *Magellania venosa* as the most prominent species. Another dominant group was the Asteroidea, mainly *Ctenodiscus procurator* and *Cycethra verrucosa*. The ophiuroids *Ophiuroglypha lymani* and *Ophiactis asperula*, and the holothurian *Psolus patagonicus* were also relatively abundant at some sampling stations.

Differences between the subgroups determined on the basis of samples from the Atlantic (eastern) and Pacific (western) entrance of the Strait of Magellan appear to be defined mainly by the occurrence of echinoderms and brachiopods. In the western area, the asteroids *Ctenodiscus procurator* and *Bathybiaster loripes* and the isopod *Acanthoserolis schythei* dominated the samples, whereas at the eastern entrance *Magellania venosa* and *Terebratella dorsata* (brachiopods), *Ophiactis asperula* (ophiuroid) and *Cycethra verrucosa* (asteroid) were the dominant species.

A similar analysis with the SPI sampling sites showed no clear-cut relation to geographical positions (Fig 2c). Agassiz trawl catches were larger at sampling sites situated in channels (e.g. Canal Oeste and Paso del Indio) and also at the entrance of the Penguin Fjord. The remaining stations, mainly those in the fjords, showed smaller catches as compared with the relatively big ones obtained at sites less influenced by glaciers. The bivalve *Camptonectus (P.) subhyalinus* was the most abundant species off the SPI, followed by the ophiuroids *Ophiactis* sp., *Ophiuroglypha lymani* and *Gorgonocephalus chilensis*. Other dominant species in this area were the polychaetes *Polyeunoa laevis* and *Harmothoe campoglacialis*, and the asteroids *Ctenodiscus procurator* and *Luidiaster planatus*.

According to the results from the BIOENV analysis, no relationship was found between the benthic distribution patterns observed and the abiotic parameters in the SPI area. A similar result was obtained for the SM area; however, a low level of correlation was obtained between the faunal composition, the hydrodynamic regime and suspended particulate matter (R = 0.040; p = 0.24).

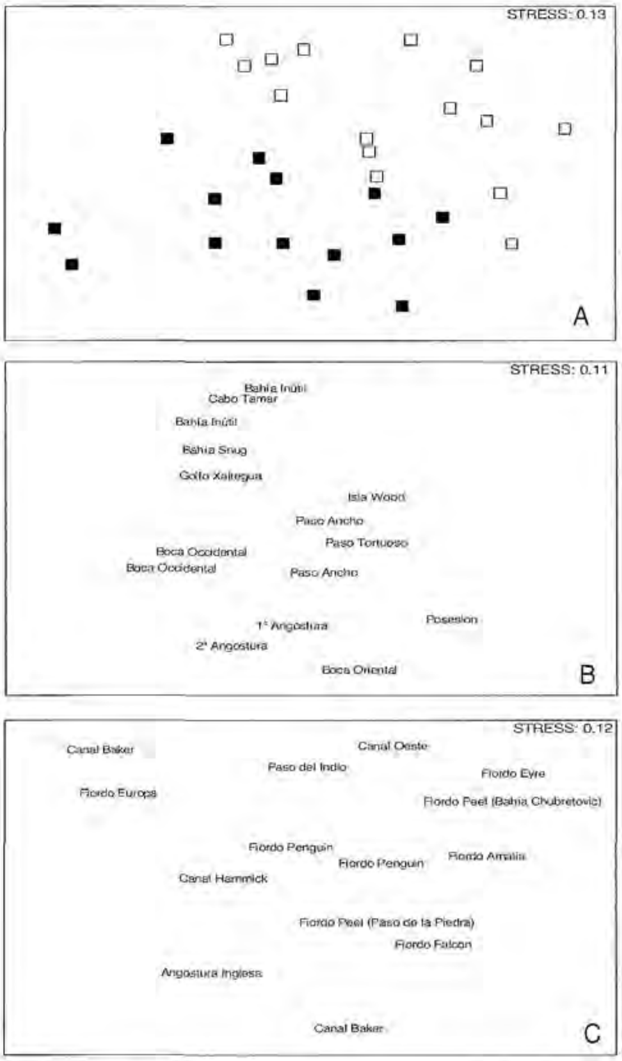

FIG. 2. – MDS plots of macrobenthic assemblages in the Magellan region (A; ❑ = SPI stations, ■ = EM stations), the Straits of Magellan (B) and the South Patagonian Icefield (C), based on the Bray-Curtis similarity index with presence/absence data.

DISCUSSION

This study is the first attempt to describe and compare macrobenthic associations on a species level in the south Chilean glacial fjords and channels. However, due to the sampling gear used (Agassiz trawl), some caution is needed for the interpretation of the resulting ecological patterns. The study of macrozoobenthic communities by trawls can be considered to give only a first insight into the distribution of epibenthic communities, as mentioned by Arnaud *et al.* (1998), but it represents a fairly good picture of the variety of benthic species living in an ecosystem. Further quantitative research on species composition, biotic and abiotic variables and their temporal and spatial variability is necessary for a more global understanding of community patterns and processes occurring in these fjords and channels.

A low number of specimens was an outstanding feature at all the sampling stations, especially at those stations located in the SPI area. Distribution patterns in the SM area were found to be more homogenous, as is obvious also from extensive quantitative analyses on a major taxon level. The lowest average abundance (625 ind/m^2) was observed at sampling stations in the South Patagonian Icefield, increasing significantly southwards to a maximum (3,972 ind/m^2) on the continental shelf off the eastern entrance of the Beagle Channel. The Straits of Magellan showed intermediate values (1,591 ind/m^2). These differences are attributed to certain environmental properties of the areas, mainly those related to the stability of the bottom sediments. Silva and Prego (2002) indicated that glaciers provide cold oligotrophic waters rich in silt to the inlets, features which may explain the scarcity of benthic abundance and biomass production, as was suggested for the phytoplankton scarcity found in several of the fjords considered in our study (Vera *et al.*, 1996).

However, lack of repeated study in this ecosystem, including seasonal and long-term fluctuations of abundance and environmental abiotic parameters, make a more comprehensive analysis and explanation of the observed trends rather difficult, especially for the SPI. For instance, melting of glaciers during the austral spring (September-early December) and summer (December-March) might cause a strong sedimentary input of inorganic matter to the bottom, producing additional disturbance in the benthic regime, and consequently a decrease in animal abundance. Sedimentation has been suggested as one of the important factors determining epifaunal distribution at Antarctic coastal glaciers (e.g. Dawber and Powell, 1997), and more specifically in Potter Cove (Kind George Island), where benthic colonisation (ascidians instead of sponges) is strongly influenced by inorganic siltation from the glacier (Klöser *et al.*, 1994; Kowalke and Abele 1998; Sahade *et al.* 1998; Tatián *et al.* 1998). Similar results have also been obtained in the Canadian Arctic and Alaskan fjords, where epifauna is restricted to areas with low sedimentation rates (Evans *et al.*, 1980; Carney *et al.*, 1999).

An important additional difference to sites located in the SPI area is the higher amount of inorganic carbon in surface sediments of the Straits of Magel-

TABLE 3. – Average dissimilarity (AvDiss) and ratio between AvDiss and its corresponding standard deviation (Diss/SD) between SPI (South Patagonian Icefield) and SM (Straits of Magellan) groups. Species are ranked in decreasing contribution (%) to dissimilarity values. Cum=cumulative percentage. Average dissimilarity = 97.35

Species	Group SPI AvAbund	Group SSM AvAbund	AvDiss	Diss/SD	Contrib%	Cum
Ctenodiscus procurator	3.64	5.40	10.45	0.65	10.71	10.71
Ophiuroglypha lymani	2.21	8.27	7.33	0.57	7.52	18.23
Magellania venosa	0.07	11.87	6.51	0.39	6.68	24.91
Pseudechinus magellanicus	2.71	3.47	5.02	0.52	5.15	30.05
Acanthoserolis schythei	0.00	3.93	4.94	0.36	5.07	35.12
Camptonectus(Pallioleum)subhyalinus	13.64	0.00	4.54	0.27	4.65	39.77
Dentalium majorinum	0.43	1.53	3.40	0.42	3.49	43.26
Limopsis marionensis	0.21	5.13	3.19	0.36	3.27	46.53
Psolus patagonicus	0.00	5.40	3.16	0.26	3.24	49.77
Holothuroidea sp 2	0.00	3.20	3.05	0.36	3.13	52.90
Cycethra verrucosa	1.29	1.13	2.91	0.36	2.99	55.88
Ophiactis sp.	7.93	0.00	2.36	0.27	2.42	58.30
Terebratella dorsata	0.00	2.60	2.35	0.28	2.41	60.71
Cheiraster (Luidiaster) planeta	2.14	0.07	2.31	0.26	2.37	63.07
Ophiactis asperula	0.00	0.80	1.73	0.37	1.77	64.85
Cosmasterias lurida	1.14	0.67	1.65	0.31	1.70	66.54
Leanira quatrefagesi	1.36	0.00	1.61	0.59	1.65	68.19
Bathybiaster loripes	0.00	0.67	1.36	0.49	1.40	69.59
Ennucula grayi	0.64	0.40	1.29	0.28	1.32	70.91
Eurypodius latreillei	0.64	0.73	1.19	0.42	1.22	72.13
Trypilaster philippi	0.00	1.07	1.10	0.31	1.13	73.26
Ophiocten namitinum	0.93	0.00	1.08	0.25	1.11	74.37
Gorgonocephalus chilensis	2.14	0.07	1.04	0.39	1.06	75.43
Polyeunoa laevis	2.57	0.00	1.03	0.35	1.06	76.49
Pista cristata	0.57	0.00	0.86	0.25	0.88	77.37
Maldane sarsi	0.43	0.00	0.85	0.42	0.88	78.25
Libidoclaea smithi	0.36	0.13	0.79	0.29	0.81	79.06
Crepidula dilatata	0.00	0.40	0.76	0.24	0.78	79.84
Ophiacantha cf. pentactis	0.64	0.00	0.75	0.25	0.77	80.61
Cyclocardia velutinus	0.14	1.20	0.75	0.35	0.77	81.37
Abyssoninoe abbyssorum	0.43	0.00	0.73	0.31	0.75	82.12
Sternaspis scutata	1.00	0.00	0.71	0.33	0.73	82.85
Porania antarctica magellanica	0.00	10.67	10.66	0.45	0.67	83.53
Laneria falklandica	0.00	0.33	0.64	0.24	0.66	84.18
Ophiacantha vivipara	1.29	0.00	0.62	0.37	0.63	84.81
Berthella platei	0.07	0.53	0.61	0.31	0.63	85.44
Aulacomya ater	0.00	0.40	0.60	0.34	0.61	86.06
Arbacia dufresnei	1.50	0.07	0.58	0.36	0.60	86.65
Munida subrugosa	0.21	0.13	0.55	0.41	0.57	87.22
Campylonotus semistriatus	0.00	0.87	0.52	0.34	0.54	87.75
Calyptraster tenuissimus	0.00	0.47	0.51	0.25	0.52	88.28
Halicarcinus planatus	0.00	0.27	0.51	0.24	0.52	88.80
Harmothoe campoglacialis	1.64	0.00	0.49	0.27	0.50	89.30
Chlamys patagonicus	1.21	0.27	0.46	0.34	0.48	89.77
Homalophiura inornata	0.00	0.60	0.41	0.25	0.42	90.20

lan (Silva and Prego, 2002), which according to Brambati *et al.* (1991) can be attributed to the presence of calcite in the remains of bivalves, gastropods, crustaceans and foraminiferans. Unfortunately, information on chemical and physical processes of pelagobenthic coupling (Cattaneo-Vietti *et al.*, 1999) and in the bottom sediments is scarce for the area of study, and this represents a limiting factor to explain the (dis)similarities we found between the study areas. More focused research on inter-annual variability of biotic parameters and their relationship with variability in sediments features are clearly needed for the Magellan region. Recently, Ríos *et al.* (2003) reported for the Straits of Magellan a significant seasonal abundance pattern, with variations in species richness and diversity in areas at the eastern SM entrance, and with maximum values observed in the austral summer period. Presently, this area is not affected by the direct influence of glacial processes. All these features suggest very intricate ecological dynamics in the benthic communities associated with the Chilean channel and fjord complex.

The most interesting result was the clear difference in species composition found between the South Patagonian Icefield and the Straits of Magellan. Recently, both areas have been separated into two different sectors according to carbon and nitrogen concentrations and distributions in the superficial sediment layers of the bottom (Silva and Prego, 2002). In addition, an east (glacially affected zone) and west (oceanically influenced zone) segregation in the SPI was identified. However, our biotic data do not indicate any clear relationship with the abiotic parameters determined by Silva and Prego (2002): the differences could be primarily explained by the occurrence of markedly different habitat conditions and gradients caused by the glaciers.

The discriminant invertebrate species determined for the SPI area are typical of the prevailing substrate (mud in the fjords and sand in the channels), but also for the presumably considerable disturbance produced by high sedimentation towards the bottom. These facts may explain the larger catches both in channels (*e.g.* Canal Oeste) and at the entrance of the fjords (e.g. Seno Pingüino). One of the discriminant genera in the SPI area, the ophiuroid *Ophiactis* sp. was collected at Canal Oeste sampling station, and has been frequently mentioned as being common in communities characterised by oligospecificity with dominance of suspension feeders, in which hydrodynamics represent both the most important limiting factor and the main carrier of organic matter (Giacobbe and Rinelli, 1991). Other species characterising this area were the carnivorous polynoids *Polyeunoa laevis* (dominant at the entrance of Seno Pingüino) and *Harmothoe campoglacialis* (Canal Oeste), and the ophiourid *Gorgonocephalus chilensis* (Canal Oeste). *P. laevis* has a circumpolar distribution, and is a dominant species in assemblages defined for deep water and hard bottoms off Subantarctic islands (Guillet, 1989). *H. campoglacialis* is a new, recently-identified species (Hilbig and Montiel, 2000) with a wide distribution range in the southern part of Chile, inhabiting mud and fine sand of fjords, channels and even microhabitats such as holdfasts of the kelp *Macrocystis pyrifera* (Montiel *et al*., 2004). Species of the genus *Gorgonocephalus* are considered as "fortuitous predatory suspension feeders" adapted to life in strong currents (Emson *et al*., 1991).

The SM represent a more diverse and probably less disturbed habitat for diverse benthic communities with higher organism densities. Furthermore, our data suggest the occurrence of separate subgroups of stations along the Straits with differences in community composition, e.g. at both entrances of SM. Such variability did not become evident in the comparison of mega-epibenthos distribution across the Straits by Gutt *et al*. (1999). In the SM area the most significant species regarding the discrimination from the SPI area (*Ctenodiscus procurator, Ophiuroglypha lymani* and *Magellania venosa*) have been previously reported as characteristic species of benthic communities in the Straits of Magellan (Dahm, 1999; Larraín *et al*., 1999; Gutt *et al*., 1999). The genus *Ctenodiscus* is considered to be a non-selective deposit feeder (Shick *et al*., 1981), whereas O. *lymani* is an omnivorous species and feeds mainly on crustaceans, the organic content of sediment and phytodetritus (Dahm, 1999). The brachiopod genus *Magellania* has been described as a dominant and characteristic filter feeder on deep soft substrates in the Subantarctic Prince Edward Islands (Branch *et al*., 1993) and on the continental shelf of the high Antarctic Lazarev Sea (Brey *et al*., 1995).

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

The Antarctic-Magellan connection: macrobenthos ecology on the shelf and upper slope, a progress report*

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SUMMARY: Ecological work carried out on the Antarctic and Magellan shelves since the first IBMANT conference held at the UMAG, Punta Arenas in 1997 is summarized to identify areas where progress has been made and others, where important gaps have remained in understanding past and present interaction between the Antarctic and the southern tip of South America. This information is complementary to a review on shallow-water work along the Scotia Arc (Barnes, 2005) and recent work done in the deep sea (Brandt and Hilbig, 2004). While principally referring to shipboard work in deeper water, above all during the recent international EASIZ and LAMPOS campaigns, relevant work from shore stations is also included. Six years after the first IBMANT symposium, significant progress has been made along the latitudinal gradient from the Magellan region to the high Antarctic in the fields of biodiversity, biogeography and community structure, life strategies and adaptations, the role of disturbance and its significance for biodiversity, and trophic coupling of the benthic realm with the water column and sea ice. A better understanding has developed of the role of evolutionary and ecological factors in shaping past and present-day environmental conditions, species composition and distribution, and ecosystem functioning. Furthermore, the science community engaged in unravelling Antarctic-Magellan interactions has advanced in methodological aspects such as new analytical approaches for comparing biodiversity derived from visual methods, growth and age determination, trophic modelling using stable isotope ratios, and molecular approaches for taxonomic and phylogenetic purposes. At the same time, much effort has been invested to complement the species inventory of the two adjacent regions. However, much work remains to be done to fill the numerous gaps. Some perspectives are outlined in this review, and suggestions are made where particular emphasis should be placed in future work, much of which will be developed in the frame of SCAR's EBA (Evolution and Biodiversity in the Antarctic) programme.

Keywords: macrobenthos, Antarctic, Magellan region, biodiversity, biogeography, ecology, evolution, disturbance.

RESUMEN: LA CONEXIÓN ANTÁRTICO-MAGALLÁNICA: ECOLOGÍA DEL MACROBENTOS EN LA PLATAFORMA Y TALUD SUPERIOR, UN INFORME SOBRE LA LABOR REALIZADA. – Las investigaciones ecológicas llevadas a cabo en la plataforma antártica y de Magallanes, desde la primera reunión del IBMANT en Punta Arenas en el año 1997, se resumen en este trabajo, con el fin de identificar las áreas en que se han realizado progresos considerables, así como aquellas en las que aún quedan muchos aspectos por cubrir para poder comprender tanto el pasado como el presente de las interacciones entre las áreas antárticas y el "Cono Sur" de Sudamérica. La información que aquí se ofrece complementa la revisión de los trabajos realizados en aguas someras a lo largo del Arco de Scotia (Barnes, 2005) así como los trabajos más recientes ejecutados en el mar profundo (Brandt and Hilbig, 2004). Si bien esta revisión que aquí presentamos se centra principalmente en trabajos realizados a bordo de buques oceanográficos y en aguas profundas, se presentan también las investigaciones más relevantes hechas en las bases de tierra. Seis años después del primer congreso IBMANT son numerosos los progresos realizados a lo largo del gradiente

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latitudinal desde la región de Magallanes hasta las zonas de la Alta Antártida en los campos de biodiversidad, biogeografía, estructura de comunidades, estrategias de vida y adaptaciones, papel de las perturbaciones y su significado para la biodiversidad así como en los aspectos referentes al acoplamiento trófico entre el sistema bentónico, la columna de agua y el hielo marino. Se ha perfeccionado nuestro conocimiento del papel de los factores evolutivos y ecológicos para las condiciones ambientales pasadas y presentes, así como para la composición y distribución de especies y funcionamiento del ecosistema. Además de los avances por parte de la comunidad científica en el conocimiento de las interacciones entre estas dos regiones geográficas, son numerosos los progresos que se han producido a nivel metodológico, como por ejemplo nuevas aproximaciones analíticas para comparar la diversidad entre zonas a partir de análisis de imágenes, determinación de crecimiento y edad, modelaje trófico empleando los valores de las proporciones de determinados isótopos estables, así como el trabajo con métodos moleculares con aplicaciones taxonómicas y filogenéticas. Paralelamente se ha realizado un gran esfuerzo en completar el inventario de especies de las dos regiones adyacentes. Sin embargo, queda todavía mucho trabajo por hacer para cubrir los vacíos aún existentes en el conocimiento de ambas regiones. En esta revisión se presentan algunas perspectivas, así como sugerencias, para el trabajo a realizar en el futuro, gran parte del cual se desarrollará en el marco del programa EBA (Evolution and Biodiversity in the Antarctic) del SCAR.

Palabras clave: macrobentos, Antártida, región magallánica, biodiversidad, biogeografía, ecología, evolución, perturbación.

INTRODUCTION

Macrobenthic research is just one major topic in the frame of the IBMANT (Biological Interactions between the Magellan Region and the Antarctic) approach, which encompasses the outcome of 40 Ma of evolution in these last fractions of the Gondwana continent (Crame, 1999). IBMANT deals with the consequences of tectonics and climate change, continental drift and glaciation, as well as with those environmental and biotic factors, which are presently structuring the biota on either side of the Drake Passage (Fig. 1). Macrobenthos is an important issue in this context, because it is a particularly rich compartment, which due to its relative site fidelity preserves many characters over longer time scales than the rapidly changing plankton. In our specific case, we are looking for the

FIG. 1. – Shallow waters exposed to the effects of storm and ice are a typical aspect at King George Island (above left) whereas in the polynya facing the ice shelf margin in the Weddell Sea (below left) "shallow" bottoms begin at about 150-200 m depth. While surface waters are usually fairly calm, the seafloor is disturbed by large icebergs (see Fig. 9). In the Straits of Magellan, open shores may be exposed to heavy storms but without ice effects (above right, off Punta Arenas) whereas glaciers produce cold, low salinity waters and heavy siltation in the fjords (below right). Photos AWI; W. Arntz.

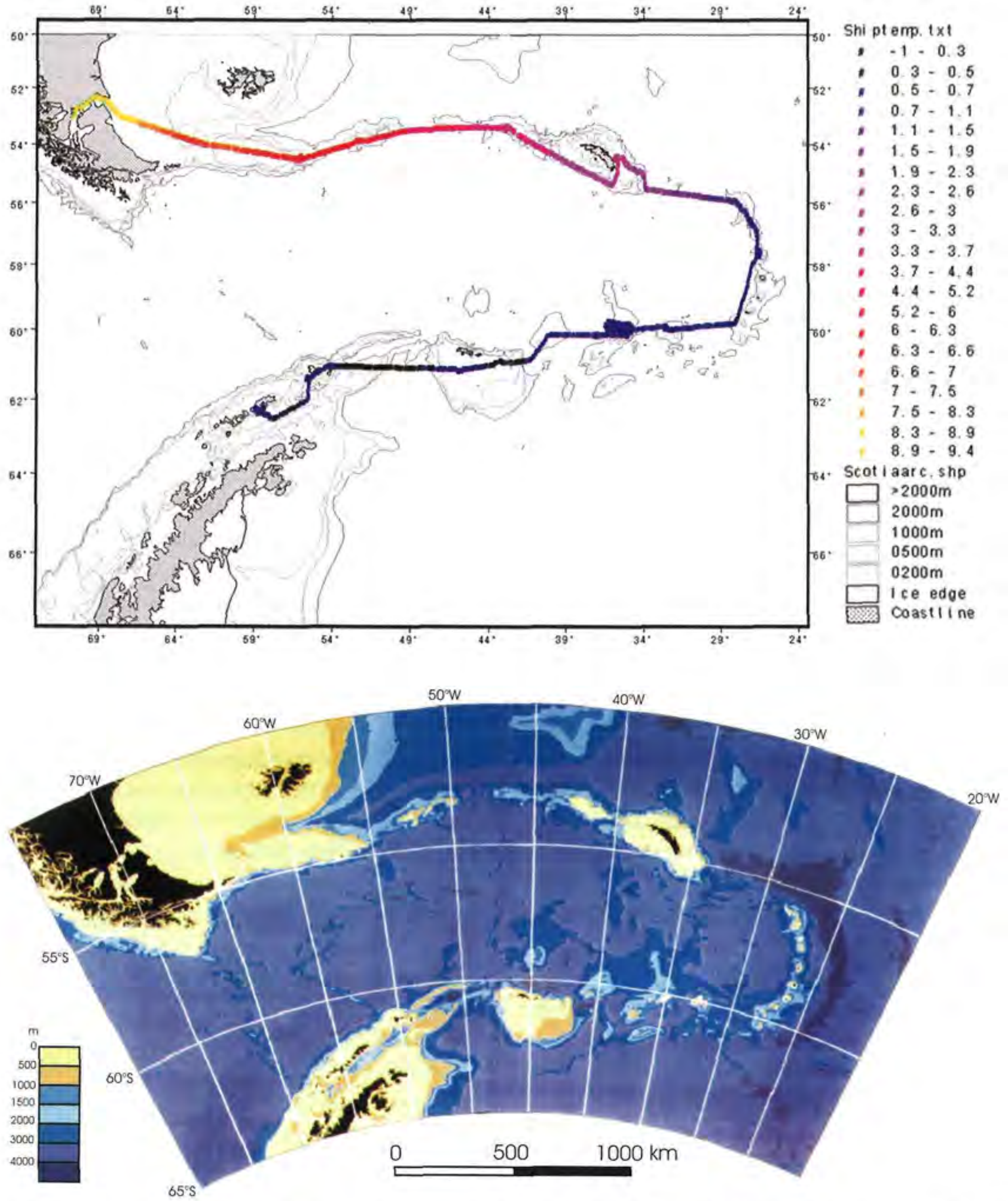

FIG. 2. – Sea surface temperatures (°C) along the Scotia Arc during the LAMPOS cruise (ANT XIX/5) of RV "Polarstern" (April 03 to May 05, 2002). Temperatures are shown from the start of the cruise in Punta Arenas to the South Shetland Islands, revealing that the Polar Front was south of South Georgia in April 2002. (From R. Knust, unpubl.; map courtesy M. Thomson).

common heritage of those parts of the great south continent, which drifted apart while major ocean gateways opened around Antarctica, giving rise to a vigorous circumpolar current system and the Antarctic Convergence (Polar Front). Unfortunately, the exact temporal sequence of those large-scale events in the past, particularly where the Drake Passage is concerned, is not yet as clearly understood as would be desirable for the purpose of linking environmental and evolutionary processes (see Thomson, 2005). It is very likely that major events, rather than gradual cooling over large periods, had marked effects, but we are still unable to establish a close connection between past physical events and biological processes.

A particularly interesting area for studying biogeographic and evolutionary links between the Magellan region and the Antarctic is the Scotia Arc, the only recent island and shallow-water bridge to the Antarctic, which was studied during the LAMPOS

"Polarstern" cruise (Arntz and Brey, 2003; for nearshore research see Barnes, 2005). Cross-transport of meroplanktonic larvae (Thatje and Fuentes, 2003) through frontal zones, e.g. by eddies (Glorioso *et al.*, 2005), might provide a connection between the northern and southern branches of the Scotia Arc, but this is more likely for deep than for surface waters (Fahrbach, pers. comm.). Clearly, W-E transport with the Westwind Drift/Antarctic Circumpolar Current (ACC), as can be seen from large amounts of drifting macroalgae (pers. obs.) and fauna rafted on algae or debris (Helmuth *et al.*, 1994; Barnes, 2002; Thiel and Gutow, 2004; Barnes, 2005) is more likely than the reverse, or than cross-transport in this area. The situation is complicated by temperature differences between the northern and southern branch (Fig. 2). For some molluscan taxa, extremely far travel with the ACC has been registered between Patagonia and New Zealand (16,000 km; Beu *et al.*, 1997), but even this may be easier than „island hopping" between the two branches of the Scotia Arc or movement against the main current direction.

This review compiles data from various cruises and some shore stations. Of course not all the information included here was created within the IBMANT frame, but the programme certainly stimulated interest in the Magellan-Antarctic connection, with a focus on work on the continental shelves. Deep-sea macrobenthos studies within the ANDEEP context, which were presented at the same Conference in Ushuaia, are published in another volume (Brandt and Hilbig, 2004). Taxonomic work is only marginally included in this review, because a full presentation would have gone far beyond its scope.

RECENT PROGRESS

Links to the past

Evolutionary and ecological factors shaping present-day environmental conditions and species composition

Much new information has been created in recent years on climate fluctuation and glaciation in Antarctica and the Southern Ocean in the past. Some of it is based on carbon and oxygen isotope records from fossil foraminifers in deep-sea sediments (Zachos *et al.*, 2001a,b). These and other data have led to conclusions about the origin of the present Antarctic ice sheet, formation of the Antarctic Circumpolar Current (ACC) and the gradual cooling of the ecosystem. There seems to be a consensus now that ice growth on East Antarctica began at least 40 Ma ago, and that the Tasman ocean gateway was essentially open by 34 Ma (Mackensen, 2004). However, while an improved scenario is developing on larger time scales, certain details of greatest interest to the biologists, such as the definite opening of the Drake Passage—a subduction zone—and the date of formation of a vigorous ACC, that seemed to be solved almost 30 years ago (Barker and Burrell, 1977) remain obscure, as has been reviewed in a recent paper (Barker and Thomas, 2004). Ocean gateways do not open overnight; the change from shallow seas connecting the former parts of Gondwana to the present deep-sea floor in the passage separating them must have been a gradual one. The Antarctic Circumpolar Current (ACC) is the mightiest current system on Earth, and to function the way it does it requires deep water without major obstacles (Barker and Thomas, 2004). Even nowadays, the relatively narrow opening of the Drake Passage creates numerous eddies as the West Wind Drift is forced through it (Glorioso *et al.*, 2005). A simultaneous definite opening of the two large gateways on either side of the Antarctic continent about 34 Ma ago, as is postulated by some geologists, seems unlikely from a biological point of view because of the much greater difference between the Australian and Antarctic marine fauna as compared to the relatively narrow faunistic relations between the Antarctic and South America (Arntz and Ríos, 1999). In fact, some molecular datings of major faunal changes (see below) might rather support a final separation of the Antarctic and South American continents by cold deep water at the time of mid-Miocene cooling (16-14 Ma) when the "tectonic reorganisation of the gateway regions may have altered poleward heat and moisture transport, resulting in Antarctic ice growth and global cooling" (Shevenell *et al.*, 2004). At any rate, notwithstanding the existence of intermittent continental ice sheets since the E/O transition, there is a marked $d^{18}O$ increase in middle Miocene cores that may have resulted from an increasing ice volume and deep-water cooling (Wright *et al.*, 1992), and which reflects one of the major steps in the process of Antarctic isolation.

In general, not one single event such as a meteorite impact seems to have shaped evolution in the Antarctic, but rather various tectonic, climatic, and oceanographic changes that influenced different taxa in different ways (Clarke and Johnston, 2003). Several Southern Ocean gastropod and bivalve genera can be traced back to at least the late Eocene (Crame, 1997). The origins of part of the present fauna are even with the coastal fauna of Gondwana prior to break-up, potentially going back to the Mesozoic or Palaeozoic (Aronson and Blake, 2001; Gili *et al.*, in prep.). Are the high Antarctic three-dimensional communities of sessile suspension feeders (sponges, bryozoans, anthozoans, ascidians) on high Antarctic soft bottoms a result of environmental conditions, which resemble those in Cretacean shallow epicontinental seas? For example, the lack of continental and riverine runoff from a frozen continent and the ensuing transparency of the water might favour sessile suspension feeders in a similar way. There are other similarities to palaeoconditions such as the lack of "skeleton-breaking" predators (Aronson and Blake, 2001). The fragmentation of Gondwana influenced the fauna particularly by the introduction of a Tethyan element through the Weddell Province (Clarke and Crame, 1989).

During evolution *in situ*, climate change and glaciation resulted in the extinction of some groups, and provided evolutionary opportunities for others. More recently, development of the fauna may have been triggered by exchange along the Scotia Arc, possibly assisted by eddies, and with the deep sea (for processes, ecological barriers and pathways involved in such exchange in the Arctic see Vermeij, 1991).

Present global warming may well provide once more a situation where exchange is enhanced. Conditions in the Potter Cove (South Shetland Is.), under heavy siltation from a melting glacier, show what the Weddell Sea shelf might look like under continued warming. However, conditions may have been less stable than supposed hitherto even during major glaciations, when the advancing ice cap pushed shelf sediments down the continental slope (Thatje *et al.*, 2005b). Presently there is a gradient of decreasing turbidity and increasing importance of sessile soft-bottom suspension feeders from Patagonia to the high Antarctic. Exceptions, such as the highly structured gorgonian assemblages on Burdwood Bank and in some Patagonian fjords, live on hard bottoms, as do most recent sessile suspension feeders worldwide.

For the Magellan region, recent work has concentrated mainly on the development after the last ice age. Glaciation in this region never quite reached the extremes occurring on the Antarctic continent, but there still was an extensive ice cap around the Late Glacial Maximum (LGM) about 21 ky BP (Clapperton, 1993b) and later (Clapperton *et al.*, 1995), the remainders of which are still recognizable in the South Patagonian Icefield. The fjords and channels of Patagonia and Tierra del Fuego were covered by a thick ice cap from 35 to 55°S during the LGM (Clapperton *et al.*, 1995; Benn and Clapperton, 2000). During this period the Southern Ocean suffered distinct cooling, accompanied by an expansion of Antarctic winter and summer sea ice (Gersonde *et al.*, 2003). Northward expansions and withdrawals of the ACC seemingly were also the main reasons for millennial-scale climate variations after the LGM and during Patagonian glacial retreat until about 12 ky BP (Lamy *et al.*, 2004). The LGM and the processes during gradual warming, which was interrupted by various glacier readvances (Clapperton, 1993a), probably shaped much of the biogeographic pattern that we find nowadays. The sea level was lower during glaciation than today, and the earliest seawater incursion into the Straits of Magellan after the retreat of the glaciers occurred only around 8 ky BP (McCulloch and Davies, 2001). Since then, the ice sheet has been retreating substantially (Lamy *et al.*, 2002), leaving as ultimate remains under global warming conditions the South Patagonian Icefield and a number of glaciers descending from the mountain chains of the Andes and the Cordillera Darwin.

During the Holocene, shifts of the latitudinal position of the Southern Westerlies became the principal climate factor in the "Cono Sur" (Lamy *et al.*, 1999, 2001, 2002). Temperature and salinity reached maximum values shortly after the "Holocene optimum" at about 6 ky BP and then started their decline to modern values (Lamy *et al.*, 2002). Reduced advection of cold, nutrient-rich Subantarctic water through the ACC, reduced precipitations, diminished advection of Chilean fjord water of low salinity and/or reduced supply of freshwater and micronutrients characterised the Chilean/Argentinean fjord region during the mid-Holocene. Continental rainfall increased again during the late Holocene, from about 4 ky BP, and decreasing temperatures point to another equatorward shift of both the ACC and the Westerlies in the period until present. Recently, Rignot *et al.* (2003) estimated the volume change of the largest 63 glaciers in Patagonia and found an acceleration of ice loss since 1995 as compared to the preceding period. Thinning of these glaciers is faster than can be explained from warmer air temperatures and decreased precipitation, and their contribution to sea level rise is relatively higher than that of Alaska glaciers (Rignot *et al.*, loc.cit.).

Recolonisation of the Beagle Channel and the Straits of Magellan, in comparison to the open oceans off Patagonia and Antarctic deep waters, occurred quite recently, as these areas became gradually ice-free only during glacial retreat after the LGM.

Recent ("ecological") factors shaping the benthos have been studied for quite some time, with emphasis on the Weddell and Ross seas in the high Antarctic, the Antarctic Peninsula, the Scotia Arc and the Straits of Magellan. Trends do not always go into the same direction: While the Peninsula is experiencing a period of rapid warming by about 0.5°C per decade, the Ross and Weddell seas appear to be undergoing a period of cooling (Vaughan *et al.*, 2003). Glacier retreat is reported from the western side of the Antarctic Peninsula and the Magellan region, and ice shelf retreat from the eastern side of the Antarctic Peninsula (Vaughan and Spouge, 2002). Inorganic silt of glacier origin increasingly impoverishes and alters benthic communities in such areas (Klöser *et al.*, 1996; Mutschke *et al.*, 1996; Thatje and Mutschke, 1999) and adds to the effect of storms, waves, ice scour by bergs and growlers, anchor ice and biotic interaction (Sahade *et al.*, 1998; Barnes, 2005).

The combination of evolutionary and ecological factors shapes the aspect of present-day assemblages in the Southern Ocean, presumably with a certain increase in importance of evolutionary, and a decrease in importance of ecological processes towards the pole. Presently, ecological factors may be gaining importance (Poulin *et al.*, 2002), making the Antarctic Peninsula less Antarctic and more similar to the Magellan region, but in the large-scale context of geological and climate history this represents just another oscillation.

We may have a long way to go until we can associate major extinctions, radiations etc. in the sea with specific tectonic, climatic, glaciological or oceanographic events. Hopefully, however, we may be able—in close cooperation with other disciplines—to identify some major events when several important groups were affected at the same time (see Thomson, 2005).

New molecular results on radiation and extinction in the Antarctic benthos

Some progress has been made in molecular and biochemical work on extinction and radiation of species. Antarctic decapods suffered major extinctions whereas pycnogonids, amphipods, and isopods underwent major radiations. Fish, not dealt with explicitly in this review, suffered broad extinction, and the teleost taxon Notothenioidei showed rapid active radiation within a few million years (Bargelloni *et al.*, 2000; Eastman, 2000; Pisano and Ozouf-Costaz, 2000). Chen *et al.* (1997) put the basal notothenioid radiation at about 15 Ma, which would coincide fairly well with the mid-Miocene cooling event and presumed significant growth of the East Antarctic ice sheet (Eastman and Clarke, 1998, Clarke, 2003a).

The isopod families Antarcturidae and Serolidae (Fig. 3) are among these latter taxa (Brandt, 1991, 2000; Brandt and Poore, 2003). Held (2000) did a molecular study on 16 species of serolid isopods from Antarctic waters, the deep sea, South America and Australia. This investigation has important consequences for understanding the biogeography of the Serolidae, indicating that all Antarctic species studied form a monophyletic group, which stems from species with closest extant relatives in South America. The 3 deep-sea species included in the study are closely related to species living on the Antarctic shelf, indicating parallel colonisation of the deep sea by way of polar submergence. The radiation of the shelf serolids probably occurred after the opening of the Drake Passage and increasing isolation of the Antarctic (Held, 2000).

Speciation rate of polar taxa does not seem to be slower than in warm water taxa (Held, 2001), a suggestion made also by Clarke and Crame (1997). "This suggests that the continuous evolutionary change (....) will not be mutation-limited" (Clarke, 2003a). This seems paradox in view of the long embryonic development, slow growth, late first maturity, reduced fecundity and retarded generation time of most Antarctic invertebrates (Arntz *et al.*, 1994).

Speciation seems to continue at a high pace nowadays. E.g., sequences from the mitochondrial 16S ribosomal RNA gene show that the serolid isopod *Ceratoserolis trilobitoides* consists of several species (Held, 2003), as had been suspected before by Wägele (1986) because of the polymorphism in this "species". At least four species seem to form the *Glyptonotus antarcticus* group (Held and Wägele, 2005). There may be many more cryptic species in the Antarctic benthos, raising considerable doubts as to the generally assumed "circumantarctic" distribution of the benthos.

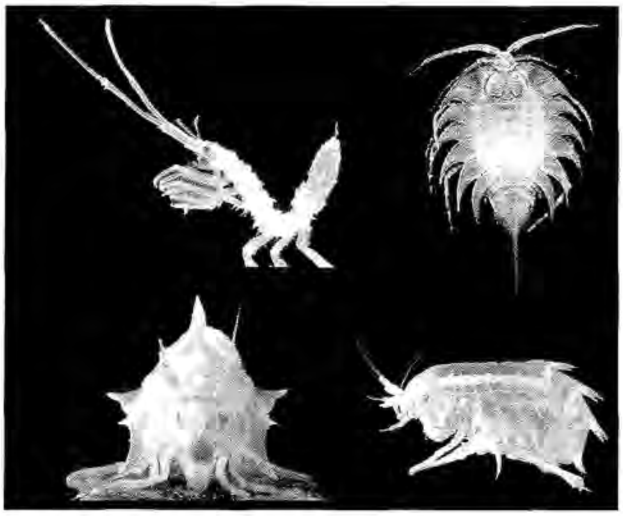

FIG. 3. – Among those peracarid crustaceans that radiated in the Miocene, Antarcturidae and Serolidae (above) are the most spectacular cases among the isopods while Epimeriidae and Iphimediidae (below) represent the amphipods. Due to their abundance and ubiquity, some species of these families are excellent candidates for checking circumantarctic distribution and cryptic speciation. (Photos: M. Klages, M. Rauschert).

Phylogenetic origins of Antarctic amphipod crustaceans are difficult to elucidate, because no fossil remains of this group have been found in the Antarctic. Lörz and Brandt (2004) studied phylogenetic relations of 14 species in the amphipod families Iphimediidae and Epimeriidae (cf. Fig. 3), both dominant taxa in the Antarctic benthos, which may result in a rearrangement, as e.g. the Eusiridae turned out to be closer to the Iphimediidae than thought hitherto. Ontogenetic characters were not helpful in revealing phylogenetic changes in two *Epimeria* species by Coleman (1990). So far no deep-sea material of the two amphipod families has been retrieved from the Antarctic, which might be helpful for the reconstruction of phylogenetic trees and the descendence of shallow-water forms in the high Antarctic Weddell Sea. Recent calculations arrive at a radiation date for Antarctic *Epimeria* species of 15.7 Ma (Lörz and Held, 2004, based on the cirripede rate of substitution). This would correspond better than previous datings with the proposed formation of the Antarctic Circumpolar Current isolating Antarctica (see above). High intraspecific variability suggests continuing speciation in the genus *Epimeria*.

Another molecular study dealing with the phylogeny of the common Antarctic sea urchin *Sterechinus neumayeri* (Lee *et al.*, 2004) revealed close relations to the South American urchin *Loxechinus albus*, concluding that the two species may have diverged from the lineage of a southernmost South American sea urchin by vicariance as Antarctica and South America separated. However, the temporal range given for this process, with 24-35 Ma ago, appears rather wide to relate it to specific environmental situations.

The phylogenetic relationship between the limid bivalves *Limatula ovalis*, living in the high Antarctic, and *L. pygmaea*, from the Subantarctic and the Magellan region were studied by Page and Linse (2002). Proposed divergence of these and a third species, *L. hodgsoni*, was between about 1.4-8.0, 6.8-19.1 and 0.2-2.9 Ma, depending on the molecular clock used, i.e. probably after the final opening of the Drake Passage and the formation of the Polar Front. This might be taken as a hint that the Polar Front is not as effective a barrier as usually thought.

Species distribution, zonation, biogeography and biodiversity

Completing the record

Enhanced research on the Magellan-Antarctic gradient has considerably increased data on biogeographic distribution and taxonomy of many taxa. Notable recent examples are Antarctic macroalgae (Wiencke and Clayton, 2002) and echinoids (David *et al.*, 2005), Magellanic shelled molluscs (Linse, 2002), opisthobranchs (Schrödl, 2003), and particularly, polychaetes (Parapar and San Martín, 1997; San Martín and Parapar, 1997; Cantone *et al.*, 2000; Gambi *et al.*, 2000; Montiel *et al.*, 2004, 2005). For a taxonomic update of all benthic groups see Clarke and Johnston (2003). Further information is being compiled on, e.g. Magellanic asteroids and Antarctic cnidarians. As this recent work adds to a large extant literature, the Southern Ocean shelves are now rather among the better studied parts of the world ocean. This does not hold, however, for the deep-sea areas surrounding Antarctica (Linse, 2004).

In some cases biogeographic patterns begin to emerge for recently studied taxa, which add to the data presented at IBMANT I (Arntz and Ríos, 1999). Macroalgae show a marked reduction from the Magellan region (Santelices, 1989, Cornejo, 1996) along the Antarctic Peninsula towards the high Antarctic, whose continental shelf exhibits a very sparse macroflora (Wiencke *et al.*, 1998; Wiencke and Clayton, 2002). There are, however, differences between the Ross Sea and the Weddell/Lazarev seas, where hitherto a single small piece of red alga has been found (Gambi, pers. comm.), which might be allochthonous. Polychaete similarity with the Magellan region is greater at the Antarctic Peninsula than in the Weddell Sea (Montiel *et al.*, 2005). The same is true for isopods and cumaceans (Brandt *et al.*, 1997, 1999). Like in other taxa, Antarctic endemism is currently reduced by new finds in adjacent areas. Tanaidaceans were subject of two recent studies in Admiralty Bay (Blazewicz and Jazdzewski, 1996) and the Beagle Channel (Schmidt and Brandt, 2001). Surprisingly, the Peninsula material showed a lower overlap (abt. 10%) with the Weddell Sea (Sieg, 1992) than the Magellan region (25%).

The IBMANT I compilations of decapod crustaceans in the Magellan region (Arntz *et al.*, 1999) and their Southern Ocean distribution (Gorny, 1999) have been complemented by recent finds of lithodids in the Amundsen and Ross seas (Arana and Retamal, 1999; Thatje and Lörz, 2005) and near Bouvet Island (Arntz and Brey, 2005; Spiridonov *et al.*, in press), of caridean shrimp along the Scotia Arc (Arntz and Brey, 2003; Romero *et al.*, 2003a), and of thalassinids in the Beagle Channel (Thatje, 2000; Thatje and Gerdes, 2000). The general picture is still valid; only caridean shrimps have been collected on the high Antarctic shelves, and except for king crabs (Anomura: Lithodidae), no anomurans and no brachyurans live in Antarctic waters as for these latter groups, the deep water of the Drake Passage and the Polar Front are a true faunal barrier (Thatje *et al.*, 2003, 2005a, but see Thatje and Fuentes, 2003). The Lithodidae have so far not been found on the high Antarctic shelves (Thatje and Arntz, 2004).

The "bell-shaped latitudinal curve", species richness and diversity

Latitude by itself is not an environmental factor, but it reflects to a certain degree some basic ecosystem properties such as day length, light, temperature and production. On the other hand, a comparison of the conditions along the Atlantic and Pacific coasts of America (Boschi, 2000; Gutt *et al.*, 2003) reveals that there are other factors, which make a differentiation necessary (see also Gallardo and Penchaszadeh, 2001; Valdovinos *et al.*, 2003). Therefore it is not surprising that the controversial issue of a bell-shaped curve (see Arntz and Gili, 2001), with decreasing species richness toward the pole, suggested by some authors for the terrestrial realm worldwide (see Gaston and Chown, 1999) and marine areas of the northern hemisphere (Roy *et al.*, 2000), seems to occur only in a few taxa in the southern hemisphere, whereas in many others even an increase from the Magellan region to the Antarctic can be observed.

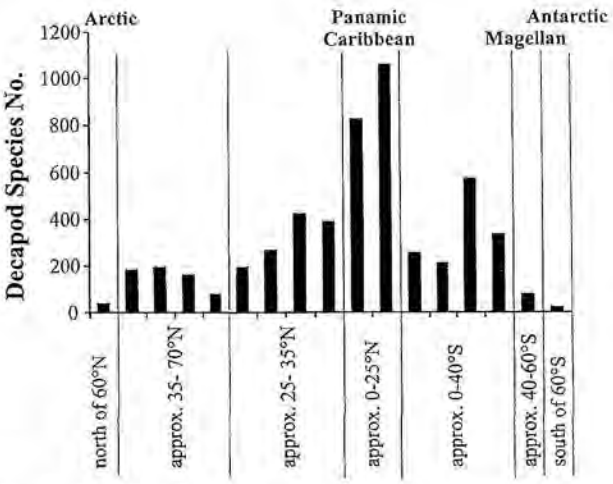

FIG. 4. – Numbers of decapod species from the Arctic to the Antarctic (data from Boschi, 2000). Note that the bars in the different latitudinal ranges do not represent consecutive latitudinal values but are from separate counts of species. This is one of the few cases where a "bell-shaped latitudinal curve" seems to exist, and in the case of decapods species numbers are indeed very low in the Antarctic.

A clear latitudinal cline is shown by macroalgae, whose distribution is highly dependent on water depth, light and temperature. In contrast to the (partly shallow) Ross Sea, in the southern Weddell Sea the non-existence of shallow bottoms excludes macroalgae (see above). Species richness in decapod crustaceans also seems to follow a bell-shaped curve (Boschi, 2000; Dworschak, 2000; Fig. 4); however, with marked differences in the subgroups (cf. above). A bell-shaped curve may apply to some extent also to fish, which are not dealt with here.

For gastropods and bivalve molluscs there is a clear decrease in species richness from the tropics to the Antarctic, but "local hotspots" deviate from a continuous decrease (Crame, 2000 a,b), and in the SE Pacific there is even a steep increase between 42°S and Cape Horn (55°S) (Valdovinos *et al.*, 2003). The number of polychaete species does not reveal a decreasing pattern along the Chilean Pacific coast (Hernández *et al.*, 2005) nor a Magellan-Peninsula-Weddell Sea gradient (Montiel, pers. comm.). Overall, latitudinal clines in species richness do not seem to be a general dominant pattern within the Antarctic due to a mostly non-meridional orientation of most of the shelves (except for the Peninsula) and the circumpolar currents (Clarke and Johnston, 2003). Obviously, the paradigm of a bell-shaped curve in general has to be abandoned for the southern hemisphere in favour of an asymmetric distribution of most taxa (Gray, 2001; Crame, 2000a).

Considerable progress has been made in the past decade in collecting and publishing quantitative data on zoogeographical patterns. To relate these data to ecosystem functioning along a latitudinal gradient, sampling has to be standardized in time and space, analytical methods have to be comparable, and many if not all species have to be determined. Even if these conditions are fulfilled, the innate complexity of biological systems and their dynamics may complicate comparisons. The ultimate step of relating Antarctic data to those of the Magellan region has not yet been taken, although the methodological prerequisites for such a comparison are now available.

From many scattered data we know that species richness in the Antarctic can range from very high to very low; overall the species richness was found to be higher than formerly expected (Arntz *et al.*, 1997; Clarke and Johnston, 2003), also in the deep sea (Brandt and Hilbig, 2004). In some taxa species richness has been increasing steeply in past years due to increased sampling, as has best been documented in amphipods (De Broyer *et al.*, 2003). The most speciose groups in the Antarctic are polychaetes, gastropods, amphipods and isopods. Macroalgae, decapods, bivalves (and teleost fish and selachians) are poorly represented if compared with these taxa at lower latitudes, even in the Magellan region, whereas pycnogonids and many suspension feeding taxa are particularly species rich. Echinoderms are well established on both sides of the Drake Passage. Decapods and fish were previously well represented in Antarctic waters, but impoverished in the course of Antarctic cooling (Thatje *et al.*, 2005a and lit. therein); other groups incl. pycnogonids, amphipods, isopods (and teleost fish) have undergone marked radiations (Lörz and Held, 2004). However, in all cases it is only some lines that have diversified (Clarke and Johnston, 2003). Poor groups can have a high share in the worldwide species (e.g., priapulids).

Species numbers per haul in bottom trawls (Table 1) or Agassiz trawls (not shown) are much higher than in temperate regions (own unpubl. data). Raw data of all species determined on EASIZ I with the help of many specialists arrived at a number of about 800 defined species. Gutt *et al.* (2004) made an extrapolation using species accumulation approaches (Ugland *et al.*, 2003) and calculation of the unknown number of species, which were not represented in the samples, as a function of the rare species (Colwell, 1997), arriving at an estimate for total macrozoobenthic species between 2100 and 10,000 for the Weddell Sea shelf and between 11,000 and 17,000 for the entire Antarctic shelf. Both estimates are likely too low, because the method is conservative; trawls were used, which are known to be selective; and the assumption is that there really is a circumantarctic fauna (cf. Held, 2003; Held and Wägele, 2005), i.e. all assemblages to be found in the future would resemble those that have been described to date.

This kind of species richness extrapolation cannot be used to compare diversity, which is a function of species numbers and their numerical share. However, assuming that the reduced species numbers in the samples are representative, the calculated „pseudodiversities" should also be representative of true diversities. Seabed photography and UW video fulfil this important criterium by focussing only on the mega-epifauna, as has been shown in a bipolar comparison (Gutt and Starmans, 2001).

The importance of considering scales in diversity studies was shown by Starmans and Gutt (2002), who used UW video to compare mega-epibenthic assemblages in the Weddell and Bellingshausen seas with Arctic assemblages (NE Greenland) in a depth range between 35 and 585 m. At regional scale (gamma diversity) taxa richness was greater in the Antarctic than in the Arctic, although shallow sites in the Arctic were slightly richer in species and species turnover (beta diversity), indicating also higher habitat diversity. At the local scale (alpha diversity) species numbers were higher in the Antarctic. As a next step, macrobenthic diversities derived from Antarctic photographs (Gutt and Starmans, 1998) might be compared with the material taken by Gutt *et al.* (1999) from the Magellan region.

Community structure

Numerous soft-bottom investigations on macrobenthic communities have recently been carried out in the southern hemisphere using both visual and invasive methods at different sites in Antarctica and covering in total a wide latitudinal range (for the period before IBMANT I, see Gerdes *et al.*, 1992 and citations therein): Saiz-Salinas *et al.*, 1997;

TABLE 1. – Number of invertebrate species per bottom trawl haul. A, in the Kapp Norvegia to Halley Bay area on cruise EASIZ I (ANT XIII/3). B, in the Kapp Norvegia - Austasen area on cruise EASIZ III (ANT XVII/3). Source: Sirenko *et al.* (1997, 2001); further details there. For exact positions, net characteristics, trawling duration, iceberg disturbance etc. see also Balguerias *et al.* in Arntz and Gutt (1997) and Knust *et al.* in Arntz and Brey (2001).

A: EASIZ I, No. station Mean depth	5 230	9 589	11 336	12 485	13 630	14 855	15 437	16 244	17 467
Porifera	27	6	17	22	20	28	15	20	34
Bryozoa	16	4	23	39	22	6	32	32	22
Polychaeta	14	12	22	18	15	8	26	18	1
Prosobranchia	15	4	16	5	8	3	9	6	8
Opisthobranchia	1	2	3	1	1	2	2	2	3
Bivalvia	11	9	7	4	2	1	8	2	5
Amphipoda	4	3	6	20	10	2	21	10	14
Holothuroidea	6	6	9	9	5	10	8	10	12
Asteroidea	8	5	10	7	12	7	12	12	16
Ophiuroidea	10	12	11	12	13	9	12	9	16
Ascidiacea	7	3	10	12	9	4	11	9	12
30 other taxa	48	33	43	47	45	27	46	33	54
Total	167	99	177	196	162	107	202	163	197
B: EASIZ III, No. station		65	85	102	109	119	124	135	136
Mean depth		648	318	312	311	237	269	251	260
Porifera		19	32	26	20	23	17	12	16
Bryozoa		26	30	35	31	27	28	16	19
Polychaeta		16	24	21	18	17	17	11	12
Prosobranchia		8	14	12	11	15	7	8	27
Opisthobranchia		1	3	3	5	3	2	1	4
Bivalvia		10	11	10	6	9	11	11	13
Amphipoda		5	15	33	23	36	12	13	30
Holothuroidea		16	14	17	10	15	12	9	10
Asteroidea		18	20	26	16	23	14	10	10
Ophiuroidea		15	20	16	16	14	10	8	10
Ascidiacea		11	22	25	11	13	9	11	9
30 other taxa		63	83	82	66	64	55	57	63
Total		208	288	306	233	259	194	167	223

Arnaud *et al.*, 1998; Starmans *et al.*, 1999; Gambi and Bussotti, 1999; Ramos, 1999; Cattaneo-Vietti *et al.*, 2000a; Gambi *et al.*, 2000; Piepenburg *et al.*, 2002; Cranmer *et al.*, 2003; Lovell and Trego, 2003). However, direct comparisons across latitudes remain rare.

Using a multibox corer Gerdes *et al.* (1992) had presented first abundance and biomass figures from the Weddell Sea shelf and slope and reviewed the data available at that time. Piepenburg *et al.* (2002) compared abundances and biomasses along two shelf/slope transects in the Drake Passage and Bransfield Strait. Table 2A summarizes the results of grab and corer based studies on the high Antarctic Weddell Sea shelf and in the Peninsula area. These studies showed the macrobenthos to occur often extremely patchy at the different sites, with minimum and maximum values of abundance and biomass (sieved over 500 μm) varying between 100 to more than 47,000 ind. m^{-2} , and 0.1 and 1673 g wet wt. m^{-2}, respectively. The Lovell and Trego (2003) epi- and infauna studies with grabs at Port Foster revealed even higher abundances but comparable biomass, because of sieving over 300 μm mesh size with groups such as foraminiferans, polychaetes, and nematodes being numerically dominant. Whereas a pronounced shelf-slope gradient in benthic abundances and biomasses was found everywhere in the Antarctic and the Magellan region, there did not seem to be any clear latitudinal trend in these parameters (Gerdes and Montiel, 1999; Piepenburg *et al.*, 2002). Macro- and megabenthic assemblages are most likely determined by food supply (which is depth-dependent), but apparently respond differently to secondary driving forces such as, e.g. seabed topography.

Locally biomasses can be extremely high, not only in the high Antarctic sponge dominated suspension feeder communities (Gili *et al.*, 2001; Gerdes *et al.*, 2003), but everywhere. The bivalve *Laternula elliptica* reaches biomasses of up to 5 kg wet wt. m^{-2} in the Potter Cove (Mercuri *et al.*, 1998), which is comparable to very productive upwelling beaches off Peru and Chile (Arntz *et al.*, 1987). Different species of scallops contribute to high benthic biomasses both in the Straits of Magellan and the

TABLE 2. – Macrobenthos community studies in the Atlantic sector of the Antarctic region (Drake Passage to Weddell Sea shelf) and in the Magellan region using invasive methods. For older data compare Gerdes *et al.*, 1992 and further citations therein.

Region	Method (No. of samples)	Water depth (m)	Bottom	Abundance Ind. m^{-2} Min.- Max.; (Mean)	Biomass g wet weight m^{-2} Min.-Max.; (Mean)	Annual production (g C m^{-2})	Dominant groups	Authors
A. Antarctic region								
Weddell Sea	multibox corer (233)	170-2037	soft bottom with mud, sand, gravel, boulders	131-12,846 (3806)	0.12-1673.0 (222.6)		sponges, holothurians, asteroids, polychaetes	Gerdes *et al.*, 1992
Weddell Sea shelf	multibox corer	132-548			12.0 (3.6 g C m^{-2} y^{-1})		sponges, echinoderms, polychaetes	Brey and Gerdes, 1999
Bransfield Strait	multibox corer (27)	200-800		7198-10,956	184.6-529.4			Piepenburg *et al*, 2002
Drake Passage	multibox corer (32)	100-2000		731-14,483	49.3-951.6			Piepenburg *et al*, 2002
South Shetland Islands	van Veen grab, box corer (130)	42-671		160-4380	23.3-5205.0 (1169.0)		ascidians, sponges, polychaetes,	Saiz-Salinas *et al.*, 1997
South Shetland Islands, Peninsula	Agassiz trawl	40 - 850	mud, sand, gravel	semiquantitative	semiquantitative		polychaetes, echinoderms, ascidians, crustaceans	Arnaud *et al*, 1998
Deception Island	grab samples (8)	155	poorly sorted mud, sand, rocks, cobbles, boulders	34,754-141,669	13-436 1)		forams, nematodes, polychaetes	Lovell and Trego, 2003
B: Magellan region								
Straits of Magellan	multibox corer (76)	8-459	high proportion of sand and gravel, partly with clay and mud	409-4727 (1591)	16.8-392.8 (96.8)		bivalves, polychaetes, crustaceans	Gerdes and Montiel, 1999
Beagle Channel	multibox corer (64)	38-348	high proportion of sand and gravel, partly with clay and mud	673-8782 (3643)	10.1-1466.3 (301.6)		bivalves, crustaceans, polychaetes, echinoids	Gerdes and Montiel, 1999
Continent. shelf off the eastern entrance of the Beagle Channel	multibox corer (67)	14-1162	high proportion of sand and gravel, partly with clay and mud	1049-7730 (3983)	1.3-662.8 (119.0)		holothurians, crustaceans, polychaetes, gastropods	Gerdes and Montiel, 1999
Straits of Magellan	multibox corer, Reineck box corer (94)	8 - 571		174-4972 (1857)	0.16-22.88 (2.7) 2	0.738		Thatje and Mutschke, 1999
Beagle Channel	multibox corer, Reineck box corer (119)	14-348		668-13,521 (4467)	0.54-16.99 (5.2) 2)	1.108		Thatje and Mutschke, 1999
Continent. shelf off the eastern entrance of the Beagle Channel	multibox corer (31)	102-1139		1136-4379 (2319)	0.05-14.51 (2.9) 2)	0.684		Thatje and Mutschke, 1999
South Patagonian Icefield	Reineck box corer (42)	20-711		30-1245 (627)	0.01-17.35 (2.1) 2)	0.393		Thatje and Mutschke, 1999
Magellan region	multibox corer	14-349			7.3 2)	5.1	molluscs, crustaceans, polychaetes, echinoderms	Brey and Gerdes, 1999

1) 0.3 mm mesh size; 2) g C m^{-2}

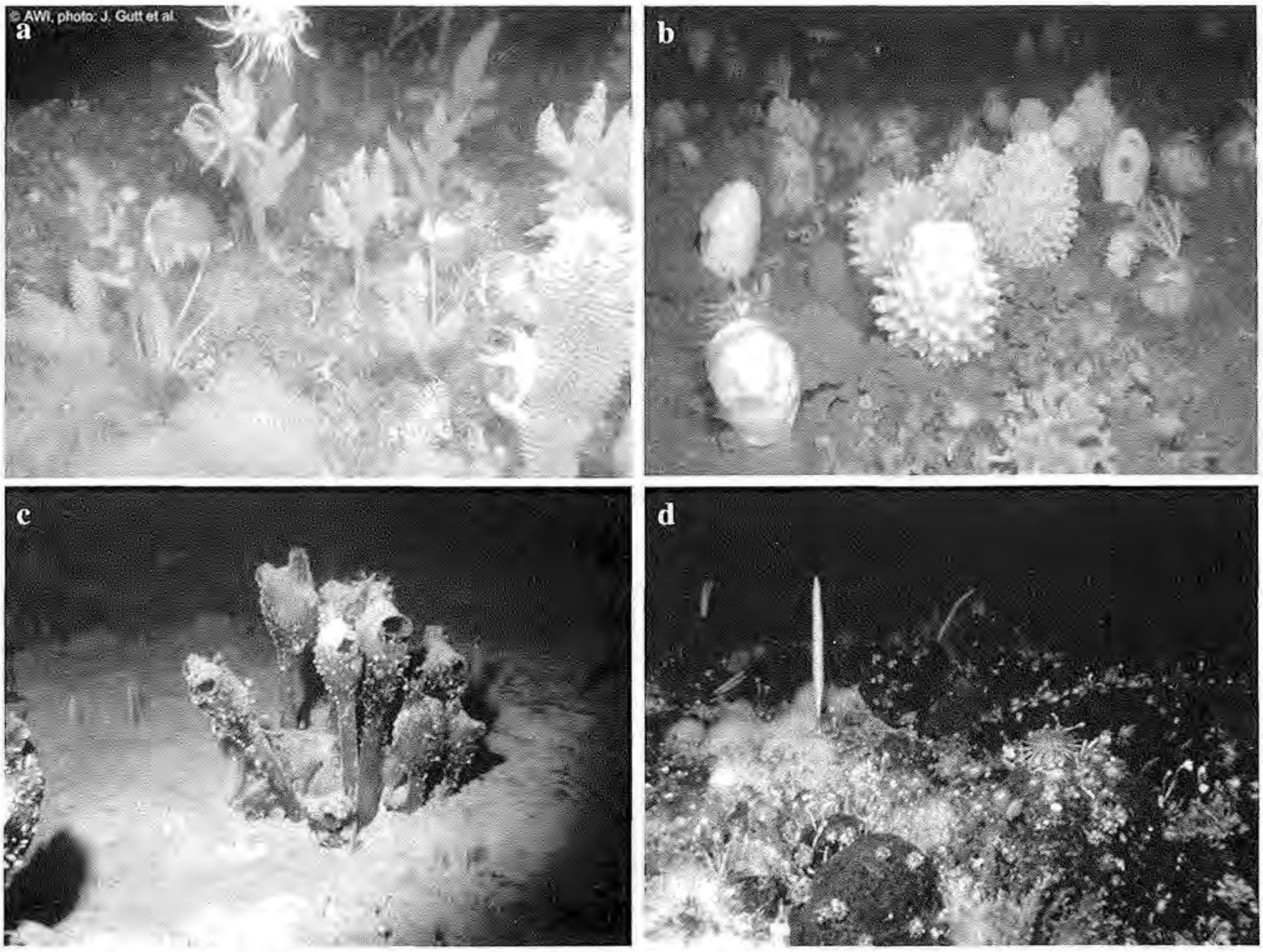

FIG. 5. – Typical aspects from Antarctic sessile suspension feeder communities. a) and b) gorgonian resp. sponge dominated (Weddell Sea shelf, 220 to 240 m; photos WG J. Gutt); c) ascidian and pennatularian dominated (Potter Cove, King George I., 30 m, under heavy siltation from glacier; photo S. Kühne); d) hydrozoan and stoloniferan dominated (hard bottom with boulders and cobbles on the isolated Four Seasons Bank, eastern Weddell Sea, 70 m; photo: WG J. Gutt).

Antarctic (Arntz and Gorny, 1996; Chiantore *et al.*, 2000; Heilmayer *et al.*, 2003).

In their comparison of mega-epibenthic communities by UW video between Antarctic areas and NE Greenland (cf. above), Starmans *et al.* (1999) detected distinct differences in community structure between all areas. Sessile suspension feeders dominated the assemblages in the Weddell Sea, probably due to favourable bottom currents, but were scarce in the other Antarctic areas (Fig. 5). Another community analysis of mega-epibenthos with a UW camera on the Weddell and Lazarev Sea (99 to 1243 m depth), where faunistic patterns were best explained by a combination of water depth and geographic gradient, was done by Gutt and Starmans (1998). There was a positive correlation between the abundance of large sponges and the number of all other taxa, and a gradient from rich, diverse suspension feeder assemblages to poorer assemblages with a higher share of deposit feeders.

Cranmer *et al.* (2003) recently sampled a megafaunal epifauna community at 150-160 m in Port Foster (Deception I.) using UW camera and bottom trawl. Compared to the high Antarctic this community was rather poor, maybe due to volcanic eruptions and their effects described already earlier by Gallardo and Castillo (1969), Gallardo (1987) and Arnaud *et al.* (1998). Principal dominants were the echinoderms *Ophionotus victoriae* and *Sterechinus neumayeri*, but even these with low abundances. Lower importance of epi- vs. infauna at the Peninsula was found as published before (cf. Arntz *et al.*, 1997). Faunal distribution turned out to be patchy similar to the high Antarctic (Starmans *et al.*, 1999). In Arnaud *et al.*'s (1998) semiquantitative trawl study at the tip of the Peninsula, shallow (40-130 m) stations differed from deeper stations, besides the Deception I. stations mentioned above.

Due to recent Italian studies, Terra Nova Bay is now a second well-known area in the Ross Sea beside McMurdo Sound. These benthic communities differ substantially from the McMurdo assemblages 650 km to the south, which does, however, not necessarily reflect a latitudinal cline. Benthos community structure in Terra Nova Bay was studied from the intertidal to 150 m depth by Cattaneo-Vietti *et al.* (2000a) and at three sites between 450 and 810 m depth by Gambi and Bussotti (1999). Abundances were low (between 430 and 1040 ind. m^{-2}, 0.5 mm mesh). Two sites showed more constant conditions and a high organic input from the water column, site 3 was highly disturbed. The benthos was predominantly small and the community likely to be immature.

Shallow hard bottoms to abt. 35 m in Terra Nova Bay were investigated by divers (Gambi *et al.*, 2000). Polychaetes were the most abundant and diverse taxon followed by molluscs and amphipods. The area was widely covered by the macroalgae *Iridaea cordata* and *Phyllophora antarctica*. This zone receives frequent disturbance by sea ice.

Benthic communities in the Magellan region were studied by several authors (Table 2B). Information on community structure was published by Gutt *et al.* (1999), and on the impoverished fauna in the glacier region (South Patagonian Icefield) by Mutschke *et al.* (1996) and Thatje and Mutschke (1999). The specific fauna of the intertidal cobble and boulder fields in the Magellan Straits was described by Mutschke *et al.* (1998) and Ríos and Mutschke (1999). The fauna in this highly heterogeneous environment was richer than previously mentioned, but was dominated by few polychaete and mollusc species. Some species in this community have a wide Subantarctic distribution. Comparisons can be made with the stony beaches at Arctowsky (Jazdzewski *et al.*, 2001) and King Sejong (Kim, 2001), both at King George Island. At Arctowsky, high abundance (50,000 ind m^{-2}) and biomass (600 g wet wt. m^{-2}) characterised the fauna. Biomasses in the Magellan community were similar (330 – 3300 g wet wt. m^{-2}), but abundances were two orders of magnitude lower.

Barnes and de Grave (2001) investigated the "encrusting fauna" along 25 degrees of latitude from Tierra del Fuego to the Ross Sea. The authors found distinct Patagonian, Falkland (!) and Antarctic groupings. The Antarctic grouping revealed a cline from more northerly and shallow to more southerly and deeper sites (details in Barnes, 2005).

As within the Antarctic, densities and biomasses in the Magellan assemblages appeared rather variable. No distinct latitudinal gradients between both regions were detected (cf. Piepenburg *et al.*, 2002), although the Magellanic fauna in general reveals higher production and productivity as pointed out by Brey and Gerdes (1999). Conversely, comparisons based on faunal composition allowed to distinguish different regions. Using trawl catches (Arntz *et al.*, unpubl. data) and multibox corer samples (Gerdes and Montiel, 1999), the various subregions are clearly discernible even on the level of higher taxa. The Scotia Arc with its intermediate position reveals closer association to the Magellan fauna on the northern branch, whereas the southern branch was faunally more closely associated to the Peninsula fauna. South Georgia occupied an intermediate position. Adding the Weddell Sea shelf and Bouvet Island to the picture, average similarity was greatest between the high Antarctic and Peninsula and lowest between the Magellan region and Bouvet Island. Winkler (1994) found clear differences between the Scotia Arc incl. South Georgia and the high Antarctic Weddell Sea. The Scotia Arc and the Magellan region were mostly separated on species and genus level.

Depth gradients

Improved data are now available also on zonation. A report on the zonation of macroalgae by Quartino *et al.* (1998) complements former work by Klöser *et al.* (1996) in the Potter Cove, South Shetland Is. In this Cove, shallow macrofaunal zonation was studied by Sahade *et al.* (1998), confirming former findings of Dayton (1990) that communities are poor in very shallow water due to the influence of ice, storms etc., and increase in richness toward deeper water below the major impact of growlers, anchor ice and other disturbants.

Due to the ice shelves, almost no free shallow sites exist on the Weddell/Lazarev shelves. An exception is the Four Seasons Bank close to Kapp Norvegia, with distinct zonation belts (Arntz and Brey, 2005). Part of the species normally occurring at these depths may live under the ice shelves; e.g. *Adamussium colbecki* (cf. above), which is common in the Ross Sea (Chiantore *et al.*, 2001).

A distinct allopatric depth distribution in the Weddell Sea was found in the serolids *Ceratoserolis trilobitoides* (shallow) and *C. meridionalis* (deep), and the aegids *Natatolana oculata* and *N. obtusata* (shallow) vs. *N. intermedia* (deep) (Summary Review in Arntz and Gutt, 1999).

Cattaneo-Vietti *et al.* (2000a) found a clear depth zonation from the intertidal to 150 m depth in Terra Nova Bay: a rocky shore with a poor upper zone at 2-3 m, algal belts to 70 m with a diverse vagile fauna, *Sterechinus* and *Odontaster;* below a complex community dominated by sponges and cnidarians with high biomass and species richness. Soft bottoms start at 20-30 m depth. These communities are characterized by the bivalves *Laternula elliptica, Adamussium colbecki, Yoldia eightsi* and polychaetes *(Tharyx cincinnatus* and others). On muddy sands at 150 m depth other polychaetes and brachiopods dominate. Similar diversity of epibenthic habitats in the Weddell Sea was described by De Broyer *et al.* (2001a,b).

Significant differences among polychaete taxa distributed in shallow and deep waters of the Paso Ancho (Straits of Magellan) were found by Montiel *et al.* (2001). A distinct zonation in this area has also been reported for other benthic groups (Ríos and Mutschke, 1999; Ríos *et al.*, 2003).

Latitudinal and longitudinal exchange

Environmental conditions change markedly on the latitudinal gradient but less on a longitudinal gradient, where exchange in the Southern Ocean is enhanced by the circular current systems and may occur over large distances (Beu *et al.*, 1997). There is a latitudinal cline in the severity of environmental conditions (mainly ice and wind disturbance, with gradients in opposite directions; Barnes and Arnold, 1991). Traffic, e.g. of algae in a N-S direction across the Polar Front is presumably difficult unless there is ship transport (see below). The role of eddies (Glorioso *et al.*, 2005) for latitudinal transport in the Scotia Arc has yet to be determined. Besides environmental factors, the dispersal abilities of larvae or drift stages also determine the success of exchange (Jablonski *et al.*, 2003).

In shallow water, sharp differences were recorded north and south of the Polar Frontal zone in rock fauna, both in the number of species and in individual species distributions (Barnes and Arnold, 1991). The shelf fauna in the Scotia Arc revealed a predominantly Magellanic faunal composition on the northern branch of the Arc and a predominantly Antarctic one on the southern branch, as one would expect (Arntz and Brey, 2003), but there were exceptions, which may be due to shifts in the position of the frontal zone (cf. Fig. 2). In the Drake Passage, the southern slope is clearly Antarctic, however with a better developed endofauna than in the high Antarctic whereas the typical high Antarctic epifauna is largely missing. Conversely, the northern slope is colonized by typical Magellan elements, which is best documented in the distinct southern limit of many decapod crustacean taxa (Arntz and Ríos, 1999; Arntz *et al.*, 1999; Gorny, 1999; Lovrich *et al.*, 2005).

Longitudinally, floating algae patches between the Argentinean coast and Burdwood Bank, >100 km offshore, and macroalgal communities at South Georgia demonstrate there is much eastward transport with the Circumpolar Current. However, the role of the South Sandwich Islands as a potential connecting agent for soft-bottom fauna seems to be low, similar to the shallows (Herdman and Discovery banks) due to their swept bottoms and strong currents (Arntz and Brey, 2003). Convey *et al.* (2002) have described the "extremely depauperate" conditions of the South Sandwich Islands with their remote position and lava or pumice bottoms, which were documented also in the LAMPOS cruise. Bouvet Island, lying even further east, was sampled during the BENDEX cruise; the first faunal analyses indicate Antarctic conditions and relations principally with the Antarctic Peninsula (Arntz and Brey, 2005; Arntz, in press). Theoretically, larvae or other dispersal stages arriving at Bouvet might travel with the Weddell gyre to the Lazarev or eastern Weddell Sea coasts, but so far there has been little faunal support for this hypothesis.

Circumantarctic transport is a prerequisite for the often cited "circumantarctic distribution" of many faunal elements, which is favoured by similar conditions around the entire continent and the (counter) clockwise current systems. A comparison of three Antarctic shallow-water sites (Atka Bay, Four Seasons Bank, Marguerite Bay) based on UW video transects distinguished the individuality of these sites; there was no greater similarity between the two former and the latter, despite very different distances for larval dispersal. The data also indicated that there is little exchange with adjacent deeper areas; otherwise the two former sites should also show greater similarity (Raguá-Gil *et al.*, 2004). This poses the question how the few shallow sites in the Weddell Sea maintain their typical aspect of Antarctic shallow water fauna. Circumantarctic shallow-water exchange should be seriously hampered by the existence of the large ice shelves in the Weddell Sea and extended areas of permanent sea ice on the eastern side of the Peninsula. However, the shallow-water bivalve *Laternula elliptica* was found at the isolated Hilltop site (Brandt *et al.* in Arntz and Gutt, 1999), together with many shallow-water hydroids (Gili, unpubl. data). Only 7 scallop (*Adamussium colbecki*) specimens have been found up to now in the entire Weddell Sea (Linse, pers. comm.). In summary, dispersal mechanisms of the shallow-water fauna are still far from clear.

Invasions

Due to its distinct environmental gradients, the Antarctic is an ideal natural laboratory under present global warming conditions. Recent arrivals of "alien" macroalgae at the Antarctic Peninsula were registered by Wiencke *et al.* (1998) in the Potter Cove, King George Island, comprising rare records such as *Durvillea antarctica* but also cosmopolitans (Wiencke and Clayton, 2002).

Recent literature mentions an increase of plastic debris as potential vehicles in the Circumantarctic Current (Convey *et al.*, 2002; Barnes, 2002, 2005). These debris are sometimes preferred to macroalgae, which are known to transport invaders, and may represent a greater danger because of their "longevity" (Barnes, 2005). On the other hand, Convey *et al.* (loc. cit.) did not detect any evidence of colonisation by biota.

Another interesting aspect is the present attempt of the Decapoda, one of the taxa poor in species in the Antarctic, to return to the cold (Aronson and Blake, 2001; Anger *et al.*, 2003; Thatje and Arntz, 2004; Thatje *et al.*, 2005a). There seems to be an increasing mismatch towards the pole between environmental variables (decreasing temperatures, seasonally limited food availability) and typical decapod properties (see below). This mismatch seems to have been the reason for the expulsion or extinction of Antarctic decapods in the Tertiary as well as for the failure of recolonisation in recent times, despite obvious pressure from the Magellan region (Arntz *et al.*, 1999; Thatje *et al.*, 2003). In the case of continued global warming, this pressure from other decapod taxa including the brachyurans is likely to increase. This suggestion is supported by recent detections at the Antarctic Peninsula of 9 "alien" specimens of meroplanktonic larvae belonging to Magellanic decapods (Thatje and Fuentes, 2003) and the find of the North Atlantic brachyuran *Hyas araneus* reported for 1986 by Tavares and Melo (2004; however, see also Thatje *et al.*, 2005a for discussion).

Specific Antarctic traits, strategies and adaptations

Reproductive strategies and population dynamics

Reproductive strategies change along latitudinal gradients, which is mainly due to differences in temperature, primary production cycles and food availability. Already before IBMANT II, there was a substantial literature describing special Antarctic characteristics, see e.g. Pearse *et al.*, 1991; Clarke, 1992; Arntz *et al.*, 1992, 1994 and refs. therein. Specific polar characteristics had been identified, but it was also clear that there were numerous exceptions, and that very different adaptations to polar conditions had been developed.

One of the traditionally controversial issues is "Thorson's rule" (for the background see Clarke, 1992; Pearse, 1994; Arntz and Gili, 2001). Stanwell-Smith *et al.* (1999) contributed a very important paper on the occurrence of pelagic marine invertebrate larvae in shallow water at Signy Island, where they registered a total of 181 pelagic larval types, many more than ever found in Antarctic waters. However, even this number is low in view of the high benthic species number in these waters (see above), and densities were extremely low in comparison with those in temperate regions. For most described morphotypes species identification remains unclear and the number of species with certain larval types may be biased by considering subsequent ontogenetic stages of the same species (Arntz and Gili, 2001). Another recent approach in Admiralty Bay (Freire *et al.*, 2005) yielded somewhat higher meroplanktonic larval numbers in shallow water, but still much less than at lower latitudes. In a first attempt to evaluate conditions in deeper, high Antarctic waters, a Dutch-German team found extremely low numbers of meroplanktonic larvae off Kapp Norvegia (Arntz and Brey, 2005; Lavaleye *et al.*, 2005), which principally supports Thorson's rule. Furthermore, many of the pelagic larvae found hitherto are lecithotrophic and occur year round, and some (such as the Caridea) have a high starvation resistance (cf. Thatje *et al.*, 2004, 2005c).

Why do some of the most abundant Antarctic shallow-water species deviate from the more frequently found patterns of non-planktotrophic development, and have become broadcasters (Poulin *et al.*, 2002)? These broadcasters include *A. colbecki*, *L. elliptica*, *O. validus*, *O. meridionalis*, *S. neumayeri*, *Porania antarctica*, and *Ophionotus victoriae* whereas the vast majority of other species are brooders or lecithotrophic. The authors explain the apparent ecological success of the first group by advantages in recolonisation e.g., after iceberg disturbance whereas the other species rather reflect an evolutionary success, permitting them to survive under conditions of glaciation. The question is, of course, whether demersal drift stages or lecithotrophic larvae would not serve the same purpose.

Contrary to the Antarctic, meroplanktonic larvae of benthic invertebrates are very common in the Straits of Magellan and the Beagle Channel, and many of them are planktotrophic with either extended or abbreviated development (Thatje *et al.*, 2003). The meroplankton community studied in November 1994 was dominated by decapod crustacean larvae, followed by polychaetes, echinoderms, cirripedes and molluscs.

Many individual studies have recently shed more light on reproductive strategies and population dynamics along the cold temperate Magellan to high Antarctic gradient. Growth of some endemic Antarctic macroalgae is restricted to very low temperature values (0-5°C, in some cases 10°C), much lower than for cold-temperate species (Wiencke and tom Dieck, 1989, 1990; Bischoff-Bäsmann and Wiencke, 1996; Gómez *et al.*, 1998). Light requirements for the completion of the life cycle of several Antarctic algal species are very low. Reproduction and growth of early stages takes place under dim light in winter (Wiencke, 1990a,b; 1996). The photosynthesis apparatus remains intact in some species (e.g., *Iridaea chordata)* during prolonged darkness but not in others such as *Palmaria decipiens* (Weykam *et al.*, 1997). Day length strongly governs the seasonal growth of many algal species (Wiencke, 1990a,b), and a minimal window of 10 days with 5 hours of light is required for formation of gametangia and gametes in large brown algae such as *Desmarestia anceps* (Wiencke *et al.* 1996), which explains the drop-out of many species on the latitudinal Ross Sea gradient towards McMurdo (Wiencke and Clayton, 2002). Similar studies in the Magellan region are necessary to extend the latitudinal aspect to the north.

Decapod reproductive biology has now been studied in the Antarctic and Magellan regions along a wide latitudinal range of 23 degrees of latitude (Arntz and Thatje, 2002; Thatje *et al.*, 2003, 2004). Growth was found to be slower, and mortality lower in Antarctic caridean shrimps than in related species living at lower latitudes. First maturity occurs at an advanced age and size, and longevity is very high (up to 10 yr or more) in the Weddell Sea (Gorny *et al.*, 1992). The caridean shrimps have adapted to the latitudinal gradient by reducing fecundity, better equipping their fewer eggs, and hatching as large, morphologically advanced larvae with a distinct starvation resistance (Gorny *et al.*, 1992, 1993; Romero *et al.*, 2003 a; Thatje and Lovrich, 2003, Thatje *et al.*, 2004). However, the step to complete lecithotrophy has not yet been undertaken by any caridean species except *Sclerocrangon boreas* in the Arctic, see Thatje *et al.* (2003), and seems to be a phylogenetic constraint in marine representatives of the taxon. Adaptation to increasing seasonality in this group has been achieved mainly by reducing the pelagic larval phase, e.g. in *Campylonotus vagans* (Magellan, Thatje and Lovrich, 2003) and *Chorismus antarcticus* (Antarctic, Bruns, 1992; Gorny *et al.*, 1992; Thatje *et al.*, 2003). Further characteristics are a decrease of moults and larval instars towards the pole, reduced energetic losses in very thin cast exuviae (Thatje *et al.*, 2003) and low Mg^{2+} concentrations in the haemolymph (Frederich *et al.*, 2000, 2001). The latter has, however, so far been confirmed only for adult stages. Adaptation of reptant decapod taxa to all these characteristics has been less efficient, and particularly the extended larval development and low starvation resistance may have caused evolution to select against Antarctic reptants (Thatje *et al.*, 2003, 2005a). An exception is the anomuran family of lithodid crabs, which besides the deep sea has conquered also high latitudes in both polar regions. Southern Ocean lithodids combine fully lecithotrophic larvae equipped with sufficient lipid reserves with strongly reduced demersal instars and a high tolerance against the cold (Lovrich and Vinuesa, 1996; Anger *et al.*, 2003, 2004). However, this tolerance may not yet be perfect, as lithodids have not been found on the very cold high Antarctic shelf with temperatures of less than -1.8°C (Fig.6) while the temperature threshold for successful larval development seems to be around 0 to 1°C (for temperature thresholds and discussion see Anger *et al.*, 2003, 2004; Thatje *et al.*, 2005a).

A number of interesting studies has been undertaken further north along the Chilean Pacific coast, which are related to the subject of decapod cold-water adaptation. These studies (Brante *et al.*, 2003; Fernández *et al.*, 2003) tried to integrate the cost of brooding in the reproductive effort to obtain a more

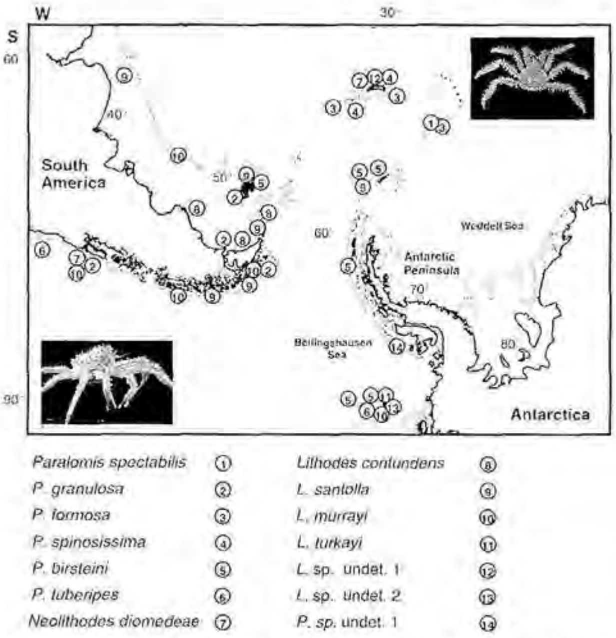

FIG. 6. – Distribution of lithodid crab species (Anomura) caught hitherto off southern South America, the Falkland Is. (Malvinas), along the Scotia Arc and the Antarctic Peninsula, and in the Bellingshausen Sea. Despite hundreds of hauls taken, not a single crab has ever been caught in the icy waters of the Antarctic continental shelf. (From Thatje and Arntz, 2004).

reliable estimate of reproductive investment, also along the latitudinal gradient. Temperature affects the period of embryo ventilation events, maternal abdominal flapping frequency, embryo losses during the brooding period, and the cost of embryo ventilation per unit of time. Crab females are able to adjust oxygen supplies to embryos according to their needs (Baeza and Fernández, 2002), but this may affect investment in reproduction, and might have important implications on larval survival and development.

While the quality of reproductive output changes with latitude towards a better outfit of less eggs and more lipid investment per embryo, the cost of embryo ventilation decreases with temperature, suggesting a trade-off between investment in eggs and the cost of providing oxygen to the embryos at different temperatures (latitudes). Should this not favour also the reptants, which are missing in cold water? Apparently the combination of very slow embryonic development with a mismatch between reduced metabolism and low food availability in the larval phase (Thatje *et al.*, 2003), combined with physiological constraints, counteract this advantage, as is the case also in the circumantarctic genus *Munida*, which has not conquered Antarctic waters despite an enormous dominance of up to 80% on the Magellan side (Tapella *et al.*, 2002; Arntz *et al.*, 1999).

At least some Antarctic suspension feeders have similar growth and reproduction rates to those of their temperate relatives (Orejas *et al.*, 2000) due to efficient food assimilation. Substantial progress has been made in elucidating reproductive strategies in this traditionally neglected group, which dominates the high Antarctic benthos over wide areas.

Antarctic ascidians are hermaphrodites and have lecitotrophic larvae. The genera *Cnemidocarpa*, *Molgula* and *Pyura* in Potter Cove exhibit strong seasonality in their reproduction. *M. pedunculata* and *C. verrucosa* reproduce in winter, *P. setosa* in summer. Paradoxically, the two winter-spawning species are the two most successful species in this ecosystem. Perhaps they are avoiding salp predation on the larvae, which is more intense in summer (Sahade *et al.*, 1998). Combining results from colonisation panels and respiration measurements, Kowalke *et al.* (2001) showed ascidians from Potter Cove to have high growth rates, favoured by a low basal metabolism and extended longevity. These properties, together with their ability to survive under intense sedimentation, make them effective competitors among benthic suspension feeders.

In gorgonians the number of eggs per mature polyp is in the same order of magnitude as in non-polar areas. During autumn in some female polyps larvae ready to be released were found together with oocytes in early stages of development, suggesting an extended development period from early spring to late austral summer. Thus these organisms might be in a continuous reproductive state, which would enable them to recruit successfully at any time, e.g. in areas disturbed by icebergs. This would explain, too, why *Primnoisis* sp. is among the first dwellers in iceberg scours. Their larvae are not pelagic but might function as drift stages (Orejas, own obs. EASIZ II).

Two size classes of oocytes in different developmental stages were found in *Ainigmaptilon* (Orejas *et al.*, 2002) in summer and autumn. The apical and medial parts of the colonies showed highest fecundity. The relative frequency of the largest size class decreased in the autumn samples. *Ainigmaptilon* is characterized by an extended oogenesis period (>1yr). Spawning seems to be delayed until the autumn-winter season, as was also observed in some *Thouarella* during EASIZ III. No larvae of this species were detected in summer and autumn. The absence of larval stages during autumn was surprising, considering that many octocoral species had larvae ready to be released, leaving the reproduction of *Ainigmaptilon* still as a mystery. The type of fertilization (external or internal) could not be determined. Our data do not allow us to state any special Antarctic features in the reproductive biology of *Ainigmaptilon*, although we think they exist.

Bryozoans have lecithotrophic larvae, which spend a very short time in the water column before settlement. The number of larvae produced daily is very small. The larvae of some species are incubated for up to 10 months before being released (Barnes and Clarke, 1998). Reproduction time in the Antarctic is summer and autumn (Zabala *et al.*, 1997; Barnes and Clarke, 1998; Bader, 2002).

Cellaria incula growth and age was analysed by stable carbon and oxygen isotope analysis (Brey *et al.*, 1999). The growth of one complete branch of this species takes one year; maximum age of a colony is likely to be more than 14 yr. P/B was 0.67, the highest value measured for any benthic invertebrate south of 62°S. Similar to another bryozoan, *Melicerita*, this fast-growing species is a pioneer in the recolonisation of iceberg scours (see below).

In a latitudinal comparison of pectinids, Heilmayer *et al.* (2003) studied the Antarctic scallop *Adamussium colbecki* in relation to (a.o.) the Magellan species *Zygochlamys patagonica*. Despite the fact that growth efficiency in pectinids was found to decrease at higher temperatures, the absolute growth of *A. colbecki* was found to be much slower than that of the Magellan species. *A. colbecki* attains a high age (Chiantore *et al.*, 2003, Heilmayer *et al.*, 2003 and references therein). Growth of the Antarctic shallow-water bivalve *Laternula elliptica* was studied by Voigt (2004) using material from King George Island. He reconstructed growth over 40 years (1961-2001), revealing interannual growth fluctuations correlated with changes in sea surface temperatures and ENSO indices. Very slow embryonic development of Antarctic molluscs had already been shown by Hain and Arnaud (1992) before IBMANT I.

The polychaete families Polynoidae and Sabellidae have a greater variability in reproductive features than assumed hitherto: *Harmothoe* spp. brood their eggs under the elytra, *Myxicola* cf. *sulcata* incubates its embryo within the tentacle crown (Gambi *et al.*, 2001).

Very slow embryonic development rates were found in the three echinoderms *O. validus*, *O. meridionalis* and *S. neumayeri*, 2-20 times slower than their temperate or tropical relatives (Stanwell-Smith and Peck, 1998). The authors proposed a window of optimal temperatures between +0.2°C and +1.7°C for *S. neumayeri* embryo development and viability. Embryos of further two species are released in winter, when water temperature is constantly below −1.6°C. Temperature, not larval food supply and predation during planktonic phases is the dominant ecological factor for these species.

Similar to most invertebrates, growth was found to be very slow and maximum age high in high Antarctic notothenioids (Morales-Nin *et al.*, 2000) and zoarcids from the Peninsula (Brodte, 2001).

Susceptibility of living resources (decapods, molluscs) to exploitation

The vulnerability of exploited or exploitable invertebrate stocks to fisheries is intimately related to the population dynamics of the respective target species. Three of the Antarctic caridean shrimp species *(C. antarcticus, N. antarcticus* and *N. lanceopes)* occur in appreciable quantities (see, e.g. Arntz and Gorny, 1991). However, their late maturity, low fecundity and slow growth (Gorny *et al.*, 1992) do not encourage a fishery, and the damage to be expected from a trawl fishery would be much greater than the potential benefit (Arntz *et al.*, 1994).

After heavy decimation of the spawning stock by the fishery, the population dynamics of lithodid crabs *(L. murrayi, P. granulosa)* have been studied in the Beagle Channel by various authors, mainly from Argentina (Lovrich and Vinuesa, 1996; Lovrich, 1997). Chilean landings of these two species in the XI and XII region have been oscillating between about 3000 and 9000 t annually between 1999 and 2004 (SERNAP, 2005). Notwithstanding their ability to adapt to (sub)polar conditions, this group is quite vulnerable to overfishing. It would be interesting to study the lithodids detected recently in the high Antarctic (Arana and Retamal, 1999) to check whether this taxon also reveals the kind of latitudinal reproductive gradients found in caridean decapods (Gorny *et al.*, 1992). An exploratory fishery on lithodids, mainly *P. spinosissima,* off South Georgia in 1994-96, with a precautionary TAC of 1600 t, yielded only about 500 t (CCAMLR, 1994, 1996; Collins *et al.*, 2002), but seems to have decimated the stock to a very low level. Exploitation has since been restricted to occasional bycatches in the roundfish fishery (Fanta, pers. comm.).

Another anomuran taxon, the squat lobster *Munida* spp., is distributed in the Magellan region incl. the northern branch of the Scotia Arc until South Georgia (Romero *et al.*, 2003a) but is missing in Antarctic waters, probably due to its reproductive characteristics which have recently been studied by Tapella *et al.* (2002) and Thatje *et al.* (2003). This very common genus is of potential use as a fisheries resource in Chile and Argentina.

The Antarctic scallop *(A. colbecki)* is one of the key species in the Ross Sea (Heilmayer *et al.*, 2003), whereas only few scattered individuals have so far been found in the Weddell Sea. Due to its consumption and production this active suspension feeder seems to play a significant role in the trophic web of the Ross Sea shelf. However, it would be very vulnerable to exploitation compared to other pectinids because of its very low overall growth performance and productivity.

Magellan bivalve resources include the scallops *Chlamys vitrea* and *Zygochlamys patagonica* and the mussel *Aulacomya ater*, all of them being exploited in Chile with 1999-2004 catches in the XI + XII region oscillating between about 100 and 2000 t (SERNAP, 2005), and several "almejas" (mostly Veneridae: *Venus antigua, Retrotapes exalbidus, Tawera gayi*) as potential resources. The gastropod *Adelomelon* sp. is gradually becoming exploited on the Atlantic side (Cledón, 2004); Volutidae *(Harpovoluta)* also occur in the Antarctic but are too rare to serve as a potential resource. Other gastropods, above all Muricidae and Buccinidae (*Trophon geversianus, Argobuccinum* spp.), do not play a great role commercially at this time but exploratory culture has been started for some species that might replace the reduced *Concholepas* stocks in Chile (C. Gallardo, pers. comm.).

Clearly the Magellan benthic ecosystem (Fig. 7) hosts many more potentially exploitable resources, at least for human consumption, than the Antarctic. Altogether there is increasing evidence, however, that all benthic crustacean and most mollusc species of potential commercial value in the Antarctic and along the southern border of the Magellan region deserve special care, with increasing tendency toward the high Antarctic, if exploitation is envisaged. The virtual destruction of most Antarctic fish stocks, which is presently culminating with the severe reduction of the last commercially important species *Dissostichus eleginoides* and *D. mawsoni* (Collins *et al.*, 2003; CCAMLR, 2005) should be taken as a warning indicating the vulnerability of cold water stocks to exploitation.

Tolerance limits and other adaptations

Much progress has been made in understanding physiological mechanisms of temperature adaptation; how did climate variability in the past influence biogeography and evolution of marine ectotherms? These questions are dealt with in the review by Pörtner *et al.* (2005) and recent work by Peck (2001) and Clarke (2003b).

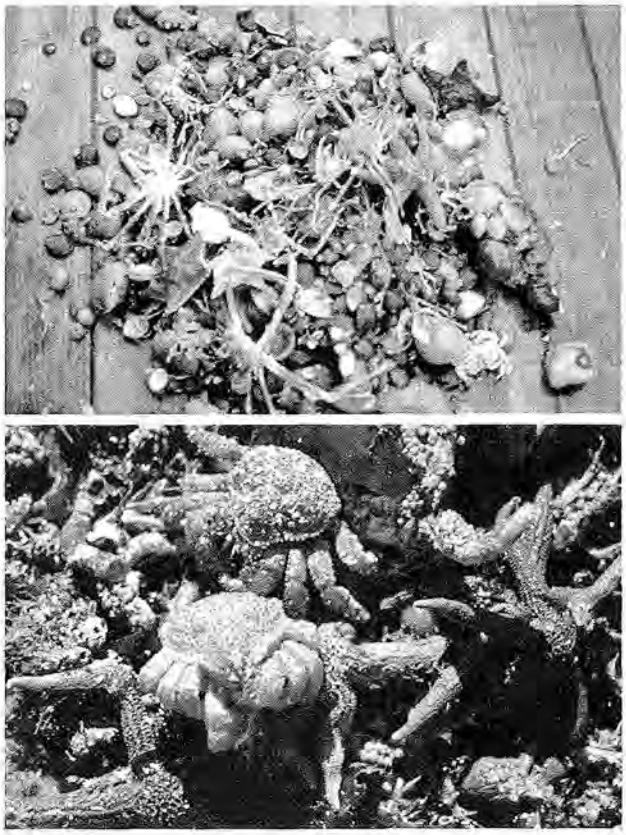

FIG. 7. – Trawl catches in the Magellan region are similar to high Antarctic catches in the dominance of echinoderms, but are quite different in the often striking appearance of large brachyuran and anomuran decapods and bivalves. Brachiopods are occasionally dominant in both areas. Canal Brecknock, 480 m (above) and I. Pícton, 63 m (below); photos W. Arntz.

Oxygen supply in the tissues may determine thermal tolerance and limit maximum size. A latitudinal cline in maximum size of amphipods due to better oxygenation and the architecture of the vascular system in cold water was detected by Chapelle and Peck (1999). Maximum sizes showed an inverse relationship to water temperature, which may explain the large size of many Antarctic amphipods. It should be noted, however, that the greater number of Antarctic amphipod species is rather small.

The benthic diatoms *Gyrosigma subsalinum* and *Odontella litigiosa* exhibited extremely low upper survival temperatures of 5-7°C in Potter Cove, and growth occurred only in the narrow range of 0-7°C. Optimal temperature for growth was 0°C, for photosynthesis 5°C. The northern limit of *G. subsalinum* is the 4°C summer isotherm, corresponding to the northern limit of the Antarctic, whereas *O. litigiosa* could also live in the Subantarctic up to the 7°C summer isotherm (Longhi *et al.*, 2003).

Surprisingly high values of lethal temperatures in Antarctic Peninsula molluscs (L_{t50} of *Laternula elliptica,* 14.9°C and *Nacella concinna,* 15.5°C), which are not likely to be reached by global warming in the near future, were found by Urban (1998). Reburial temperatures, however, were much lower (B_{t50} of *L. elliptica:* 3.6°C). Similar temperature threshold patterns have been suggested to be valid in lithodid crabs (Anger *et al.*, 2003, 2004); so L_{t50} may not be an adequate measure to indicate limits of survival (cf. Abele, below).

Distribution limits of macroalgae are not only set by ice abrasion and substrate, or biological factors such as competition (Klöser *et al.*, 1996) and herbivory (Iken, 1996; Iken *et al.*, 1998) but also by depth due to metabolic prerequisites. The upper distribution limit is determined by the capability for dynamic photoinhibition, a process by which excessively absorbed photosynthetically active radiation is dissipated as heat (Hanelt, 1996, Bischof *et al.*, 1998). For the lower distribution limit the low light requirements for photosynthesis and growth are of primary importance. Some algae are unable to inhabit depths greater than 30m. A critical daylight length during which algae are exposed to light saturated irradiances may be the key factor setting the lower distribution limits of these species (Gómez *et al.*, 1998).

The acclimatisation of Antarctic macroalgae to seasonal changes in light was investigated by Lüder (2001), using the photosynthetic apparatus of the alga *Palmaria decipiens* in culture experiments.

Light conditions also seem to play a major role for sponges in the Terra Nova ecosystem, between 70 and 120 m depth (Cattaneo-Vietti *et al.*, 2000b). They seem to survive oligotrophic conditions in winter by direct uptake of diatoms, which live for a long time in the sponge tissue. Spicules in the hexactinellid *Rossella racovitzae* conduct light as natural optical fibres and thus provide the diatoms with light.

Apart from specific Antarctic problems such as extremely low temperatures, seasonality of primary production and food shortage, stress caused by global warming and increased UV-B radiation has become an important issue in recent years. While the major part of the continent does not yet show signs of warming, the Antarctic Peninsula has experienced a distinct temperature increase by >1.5°C since the middle of the 20th century (Vaughan *et al.*, 2003), and the "ozone hole" continues to stress benthic life in shallow water. Both the effects of warming and of increased radiation are particularly interesting to study on the Magellan-Antarctic gradient.

Oxidative stress may be caused by hypoxia, hyperoxia, intoxication, high temperatures, but also by UV irradiation, liberating reactive oxygen species or leading to a dysfunction of the cellular antioxidant defense system (Abele *et al.*, 1998). Oxidative stress is critical for membrane integrity, may cause a disturbance of subcellular structures and eventually limit survival. In the Potter Cove (King George Is.) the effects of temperature increments causing oxidative damage in inter- and subtidal molluscs *(Yoldia eightsi, N. concinna)* were studied. "Critical temperatures" for survival, Tc of *L. elliptica* were 9°C, of *Y. eightsi* 4-5°C. No Tc was given for *N. concinna,* however oxidative stress occurred at 4°C, and mortality at 9°C, which seems very low for an intertidal animal. Paradoxically, intertidal animals seem to be more sensitive to warming than subtidal ones.

Under increased UV-B radiation, amphipods seek protection under algae. Unprotected in the laboratory they react with stress and higher mortality (Obermüller *et al.*, 2003). Hernando *et al.* (2001) identified repair and protective mechanisms that allow Antarctic algae to survive and reproduce under increased UVB radiation. Despite the existence of such mechanisms, the combination of rising temperatures and persistence of the ozone hole is a severe threat to Antarctic and Magellanic benthos, which may induce major changes in the near future.

Trophic strategies and coupling between subsystems

Trophic strategies on the Magellan-Antarctic gradient are mainly determined by a change from dominant endo- to dominant epifauna and shorter primary production cycles towards the pole. The energy flow through the Weddell Sea benthos was shown to be more diverse than in the Magellan region (Brey and Gerdes, 1999). While information on feeding strategies and food webs in the Antarctic has increased considerably in recent years, little new information has been created from the Magellan region (Schnack-Schiel and Isla, 2005).

The traditional view of Antarctic sessile suspension feeder communities feasting during the short period when fresh primary production is available from the algal blooms and "hibernating" without food uptake during the rest of the year became doubtful, when Barnes and Clarke (1995) demonstrated that certain Antarctic shallow-water suspension feeders are able to feed throughout the year with only short periods of starvation. They feed on pico- and nanoplankton (between 0.2 and 20 mm), which in these areas dominate the water column and the sediment most of the year (Clarke and Leakey, 1996; Cripps and Clarke, 1998) whereas phytoplankton (microplancton) is dominant only during short periods.

Similar finds by Orejas *et al.* (2001) on the deeper shelf of the high Antarctic Weddell Sea made it likely that the algal blooms rather play an indirect role through sedimentation, resuspension and advection (Gili *et al.*, 2001), and that trophic strategies under the pack ice are similar to those found in shallow water. In late summer (Feb/Mar), food input from the pelagial to the benthic system is rich as indicated by ROV pictures (Arntz and Gutt, 1997, Summary Review). However, food analyses of benthic suspension feeders in EASIZ I and II revealed that apart from some specific zooplankton feeders such as certain hydrozoans (Gili *et al.*, 1998) most benthic organisms made little use of these larger particles, despite their abundance. Instead, they ingested the food web based on bacteria, nano- and picoplankton, unicellular organisms and organic detritus contained in the seston (Orejas *et al.*, 2000; Gili *et al.*, 2001).

In the context of glaciation, pack ice cover must be considered an important evolutionary factor, as it may have prevented new production in the water column, and may have stimulated suspension feeders to rely more on resuspended and advected material (Arntz and Gili, 2001). This would indicate that benthic suspension feeders in these areas still maintain a feeding strategy, which served during glaciation, despite the fact that under present conditions fresh algal food is available during certain periods of the year. Towards the Magellan region, this fresh food window is open for most of the summer half.

The "new view" of less dependence on the short seasonal microalgal blooms in the Antarctic has now been supported by various studies. A wide range of diets was found in four cnidarian genera in the Antarctic, the hydrozoans *Oswaldella* and *Tubularia;* the stoloniferan *Clavularia*, and the anthozoan *Anthomastus,* indicating opportunistic behaviour by feeding on all available food sources and sizes (Orejas *et al.*, 2001). Main food of *Tubularia* and *Anthomastus* was zooplankton, *Oswaldella* fed on the fine fraction of seston, and *Clavularia* on resuspended material. In the two Antarctic octocorals *Primnoisis antarctica* and *Primnoella* sp., feeding experiments showed that components of seston, including the fine fraction of suspended organic matter, are an important part of the diet (Orejas *et al.*, 2003). In terms of the number of cells captured, the diatom *Fragillariopsis* was the most important food for *Primnoisis* whereas dinoflagellates dominated in *Primnoella.* Mesozooplankton was very scarce in the diet of these gorgonians but may have some importance because of its high carbon content. Despite their relatively small contribution to biomass, hydrozoans capture large amounts of zooplankton and seston, and play an important role in transferring energy from the pelagic to the benthic ecosystem (Gili *et al.*, 1998). Not all of them are carnivores although *Tubularia ralphii,* an exception in that it feeds on large particles, clearly is one: its predation rate was estimated at 1790 prey items $m^{-2}d^{-1}$, with a diet consisting entirely of planktonic copepods (Arntz and Gutt, 1999, Summary). Conversely, the Subantarctic hydrozoan *Silicularia rosea*—the other large particle feeder—feeds on benthic diatoms (Gili *et al.*, 1996). Another unusual trophic strategy was reported of the hydrozoan *Hydractinia angusta* living on *Adamussium* shells in Terra Nova Bay (Cerrano *et al.*, 2000): It ingests tube feet and pedicellariae of sea urchins *(Sterechinus)* grazing on the scallop shell, as well as masses of diatoms living in a kind of symbiosis in the hydrorhiza of the colony. There may be more examples for the trophic versatility of Antarctic suspension feeders.

The varied diet composition typical of opportunists, together with their feeding on the fine fraction of seston as indicated by experiments, reveals that passive suspension feeders in deeper waters, too, are likely to continue feeding under winter conditions in the high Antarctic.

In Terra Nova Bay carbon flux to the benthos is enhanced by katabathic winds, favouring the development of benthic detritus, and of large active suspension feeders such as *Laternula elliptica* (Povero *et al.*, 2001). This species is of great importance for benthopelagic coupling through biodeposition, as it enhances particle fluxes to and from the seabed, and has an important output of nutrients through excretion (Mercuri *et al.*, 1998).

Stable isotope ratios have turned out to be increasingly useful for trophic modelling attempts in the Antarctic. N isotopes serve as indicators of a consumer's trophic position relative to that of species occupying lower trophic positions. Wide ranges in $\delta^{15}N$ ratios in most benthic taxa of Antarctic food webs indicate feeding across a range of trophic levels. This is due to the high amount of omnivory, the ability of vertical niche expansion, the presence of multiple carbon sources, and the 3-dimensionality of the Antarctic benthos. The hypothesis that 3-dimensional habitats support longer food chains than 2-dimensional habitats has not been fully explored (Briand and Cohen, 1987; Pimm *et al.*, 1991), but it is consistent with recent findings that in Antarctic food webs the distance from phytoplankton to pelagic top predators is 2.5 trophic levels, whereas the distance to benthic top predators is about 3.5 trophic levels. At the Antarctic Peninsula seaweeds provide an important food source in the web, whereas krill *Euphausia superba* is important as food in the pelagic Weddell Sea food web (U. Jacob, unpubl. data).

A stable isotope approach to the eastern Weddell Sea food web, with a focus on 90 amphipod species, was made by Nyssen *et al.* (2002). In 8 amphipod species isotopic composition was compared with their previously described gut contents. Feeding strategies seem to remain stable over time. Amphipods do not belong to one trophic category but display a continuum of feeding modes from suspension feeders to scavengers.

Recent studies on the role of amphipods in the Antarctic food web, including aspects such as trophic guilds, were summarized by De Broyer *et al.* (2003). Other recent publications of the Belgian group include Dauby *et al.*, 2001a (trophic diversity of amphipods); Dauby *et al.*, 2001b (importance of amphipods as predators); and Dauby *et al.*, 2003 (amphipods as food for higher trophic levels). Many of the > 820 known species are of paramount importance as food to many invertebrate and vertebrate taxa. Annual consumption of amphipods was estimated at 60 million t (which would make them the second most important taxon after the krill (Dauby *et al.*, 2003)). Feeding of amphipods in the Potter Cove, King George Island was investigated by Momo *et al.* (1998). Most amphipods were detritivores and scavengers, herbivores were few despite large macroalgal stocks in the area.

Trophic relations between macroalgae and herbivores in the Potter Cove were studied by Iken *et al.* (1998). The herbivorous gastropod *Laevilacunaria antarctica* is not deterred by polyphenolic extracts of brown algae. Towards higher latitudes, where macroalgae are missing, herbivory gives way to specialized feeding strategies and increased necrophagy (Arnaud, 1970).

High Antarctic caridean shrimps, despite very different mandible shapes and stomachs, and despite living in different habitats, seem to make an exception (Storch *et al.*, 2001). They had ingested very similar food, and there did not seem to be a relation, either, to life style or habitat preferences; these shrimps were truly omnivorous. Shrimps in the Magellan region seem to be omnivorous, too, but detrital food there is derived from terrestrial sources (Romero *et al.*, 2003b). Comoglio and Amin (1999) studied the stomach contents of lithodid crabs in the Beagle Channel.

Schrödl's (2003) book on South American sea slugs contains notes on their biology. Similar monographs on other Magellanic and Antarctic taxa are urgently required.

Fish in the food web off the Antarctic Peninsula are important inshore benthos and zooplankton feeders, linking the upper and lower levels of the food web (Barrera-Oro and Casaux, 1998; Barrera-Oro, 2002). Olaso *et al.* (2000) studied the trophic ecology of the family Artedidraconidae in the eastern Weddell Sea, and Vacchi *et al.* (2000) investigated coastal fish predation (incl. its impact on the benthos) in the Ross Sea.

Few studies seem to exist on mutualisms. Sirenko (2002) makes an exception, describing the symbiosis between the gastropod *Dickdellia labioflecta* and pycnogonids.

The role of disturbance and its significance for biodiversity

Ice as a disturbant still plays a certain role in Magellan waters (cf. Fig. 1), but is decreasing in importance due to global warming and becomes increasingly more important towards the pole. In the Magellan region, local scouring effects of small icebergs or growlers may occur in the shallow water of some fjords, but such effects have not been reported. There are, however, distinct ice effects off the Patagonian ice fields caused by low salinity due to freshwater input (Dávila *et al.*, 2002) and increased siltation, resulting in an impoverishment in benthic species richness, abundance and biomass as mentioned above.

In a similar way, fine inorganic particles from glacier abrasion in Potter Cove (South Shetland Is., Antarctic Peninsula) favour ascidians, pennatulids, large *Laternula elliptica* and cumaceans and suppress sponges, small bivalves and polychaetes, whose filtering apparatus may be clogged (Kowalke *et al.*, 2001; Kowalke and Abele, 1998; Tatián *et al.*, 1998; Sahade *et al.*, 1998). On hard bottoms the foliage of macroalgae, particularly of large kelp *Himanthothallus*, may act as a disturbant in addition to ice effects; ascidians dominate here, too, due to their high competitive abilities (Sahade *et al.*, 1998).

The effects of large-scale disruption as occurred with the Larsen ice shelf (east coast of Antarctic Peninsula; Domack *et al.*, 2005) has not yet been studied in macrobenthic communities. However, a project has been developed (Gutt, unpubl.) and from all we know, remarkable changes have to be expected (Arntz, 1998).

Whereas information on ice disturbance is somewhat stagnant at lower latitudes, it has improved substantially in the high Antarctic. Gutt and Starmans (2001) analysed abt. 25 km^2 of video transects and UW photos on the Weddell Sea shelf and found signs of iceberg disturbance on 42-70 % of the bottoms. Fairly recent iceberg scours of different age cover about 7% of the Weddell Sea shelf, but in iceberg resting sites like Austasen the coverage is much higher, and only 20% are unaffected (Arntz and Gutt, 1999, Summary). Near Kapp Norvegia, icebergs cover a considerable part of the shelf between 200 and 400 m depth; iceberg resting sites can extend over areas between 40 and 170 km^2 (Knust *et al.*, 2003). Based on survey data and growth studies of the pioneer species *Cellaria incula* (Brey *et al.*, 1999), Gutt (2001) concluded that each square metre at depths <500 m on the Antarctic shelf is disturbed by icebergs every 340 yr on average.

Despite its immediate destructive effects, it is evident now that iceberg scouring enhances diversity whereas glaciers cause faunal impoverishment (Gutt, 2001). Iceberg disturbance destroys the fauna at small scale, but the large variety of successional patterns increases diversity at medium (regional) scales (Gutt *et al.*, 1998; Gutt, 2001; Gutt and Piepenburg, 2003; Fig. 8).

Cluster analysis of macrofauna clearly separated fresh scours, old scours and undisturbed areas (Knust *et al.*, 2003). Fresh scour marks were characterized by lowest total abundance and low biomass. Dominant taxa in fresh scours were polychaetes and crustaceans followed by juvenile brittle stars; tunicates and sponges were absent. In old scour marks a dominance of echinoderms, polychaetes, and brittle stars was found as well as of bryozoans and smaller sponges (both increasing), and in undisturbed areas a high dominace of sponges and echinoderms with bryozoans (however, the latter less dominant than in old scours).

A detailed taxonomic approach using polychaetes (Gerdes *et al.*, 2003) showed highest densi-

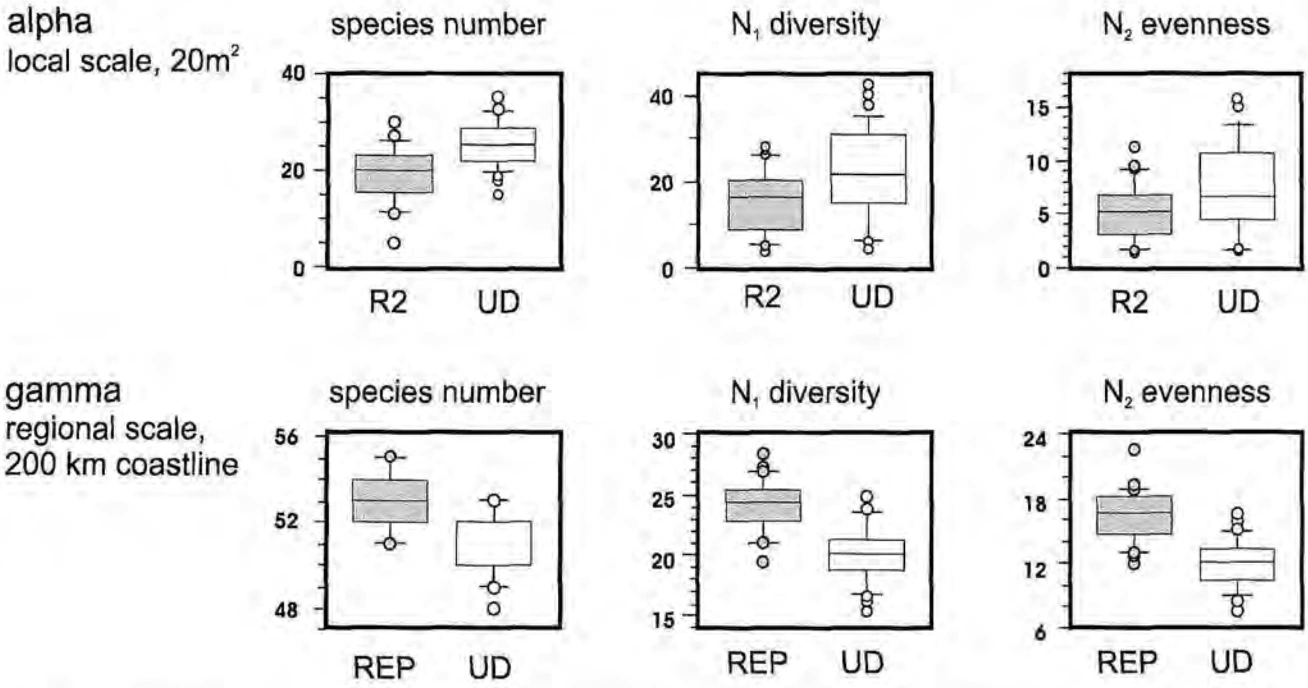

FIG. 8. – Dependence of Antarctic diversity and evenness on spatial scales. On larger scales values increase in areas subject to iceberg scour due to the simultaneous presence of different successional stages. REP, R2 are recolonisation stages, UD undisturbed areas. From Gutt and Piepenburg (2003), redrawn.

FIG. 9. – Hypothetical succession after iceberg impact, from the devastated stage via pioneer stages to a fully developed epibenthic assemblage (southeastern Weddell Sea). There are alternative successional stages, but the exact time scale for the process of recolonisation is still unknown. (Photos: WG J. Gutt)

ties and habitat species richness in undisturbed areas, followed by old and young scours. The polychaete fauna was found to be impoverished in iceberg scours also in terms of the variety of feeding types and life styles.

Various early colonisers were identified: colonial ascidians *(Synoicium),* bryozoans *(Cellaria, Cellarinella),* the stalked sponge *Stylocordyla,* the solitary ascidian *Molgula,* the gorgonians *Primnoisis, Ainigmaptilon* and the polychaete *Pista* (Gutt *et al.*, 1996; Arntz and Gutt, 1999, Summary Review; Bader, 2002). *Stylocordyla borealis* might be able to regenerate lost bodies if only the stem is left after a disturbance (Gatti, 2001). The stem contains only 20% of the total organic carbon of an individual. Other sponges produce buds under certain circumstances (Teixidó *et al.*, in press). Both may be mechanisms to speed up recolonisation.

Megafauna from UW camera and video transects produced data with a higher resolution and, consequently, better distinction between different successional stages (Fig. 9) in the Antarctic (e.g. Gutt and Starmans, 1998, 2001; Starmans *et al.*, 1999; Gutt and Piepenburg, 2003) and Magellan benthos (Gutt *et al.*, 1999). Teixidó *et al.* (2002, 2004) applied methods of landscape ecology to analyse quantitatively spatial patterns in Antarctic megabenthic communities. Using standardized UW camera photos and landscape indices, spatial patterns were studied in an undisturbed benthic assemblage and through successional stages after iceberg disturbance. The results describe a gradient from early stages of recovery with low coverage, low complexity of patch shape, small patch size, low diversity, and patches poorly interspersed to later stages with higher values of these indices. There was no fixed sequence of pioneer species during this process, but the pioneers occurred in high (sometimes almost monospecific) densities and were patchily distributed. Dominant taxa in this successional phase were demosponges, gorgonians, bryozoans, polychaetes and ascidians. Some species of these major taxa exhibit much faster growth than is normally found in Antarctic waters (e.g. Brey *et al.*, 1999; Kowalke *et al.*, 2001). In an advanced stage of succession it was mainly bryozoans that dominated. In this stage the highest values were encountered of cover area and density. The climax stage was characterized by large and presumably very old demosponges and siliceous sponges as well as (other) bryozoans, ascidians and gorgonians, whose cover area and density was, however, reduced as compared with the previous stage. Different growth forms dominated the various successional stages, and life strategies (presence of pelagic larvae or drift stages, brooding, budding) seemingly determined to a certain extent the course of succession. The most successful pioneers were characterized by tree-shaped growth form, relatively fast growth, and low to intermediate dispersal capacity of their larvae (Teixidó *et al.*, 2004).

In view of the inherent difficulties to collect material and data regularly in the Antarctic (less so in the Magellan region), consistent long-term data series are rare. In this case spatially explicit modelling of processes shaping diversity patterns may be a useful approach to answer questions on ecosystem functioning. A first attempt is presently being made to simulate benthic succession after iceberg scouring, emphasizing the role of biological characteristics such as dispersal, growth and recruitment, interactions between species inhabiting different successional stages and basic environmental parameters (Johst *et al.*, unpubl.; Potthoff, pers. comm.). The first results from this modelling suggest that former assumptions as to the extremely low pace of Antarctic community development may have to be reconsidered, and that the dispersal mode plays a very important role.

Hill's diversity concept (Hill, 1973) of a gradient with increasing weight of equitability and decreasing species numbers was used as a gradient of measures with increasing sensitivity to any kind of impact or environmental change, and applied to Antarctic benthos data to check the "intermediate disturbance hypothesis" (Gutt and Piepenburg, 2003). The authors did not find a decrease of diversity due to increasing competitive displacement at a late stage of succession following devastation of the community by grounding icebergs. However, adding to this concept landscape measures describing spatial patterns by computing areas covered by organisms and their circumference, an effect of competition seemed to occur (Teixidó *et al.*, 2002).

Other compartments in the high Antarctic benthal such as meiofauna and demersal fish are also affected by iceberg scouring (Lee *et al.*, 2001 a,b; Brenner *et al.*, 2001; Mintenbeck, 2001; Knust *et al.*, 2003). Through area fragmentation and continuous creation of free spaces, natural disturbance thus might be a process favouring speciation, and this process might be more active under present conditions in the Antarctic than in the Magellan region.

Anthropogenic disturbance affecting assemblages at the seafloor is another field, where comparisons on a latitudinal gradient would provide interesting results on benthic resilience.

Lenihan and Oliver (1995) investigated the structure of benthic communities around McMurdo station and the changes due to anthropogenic contamination as compared to two large-scale natural disturbances, anchor ice uplift and iceberg scour. The effects were similar; however contamination had a much more long lasting effect, and recovery from it was expected to be much slower. Human impact and the development of benthic communities responding to sewage, also at Mc Murdo, are studied by Conlan *et al.* (2003). A former sewage outlet, which ended at the shoreline, was replaced in 1991 by another outlet at 18 m depth, 56 m distant from shore; from 2003 the sewage has been treated. Presently a lot of contamination continues, also due to dumping of chemical waste in a nearby bay. Recovery velocity is followed under polar conditions after sewage abatement.

Human impact is also investigated in benthic communities at Casey (Stark and Riddle, 2003). Differences between impacted and reference stations around Casey Station are probably due to heavy metals and hydrocarbons. Field experiments have been conducted to demonstrate a causal relationship, showing that different assemblages developed at polluted and non-polluted sites.

Deficiencies and perspectives

Even though considerable progress has been made since the first IBMANT Conference in Punta Arenas, numerous gaps still remain in our knowledge, some of which were already identified during IBMANT I:

- Major tectonic, oceanographic and climatological events that supposedly shaped Antarctic biotic evolution should be identified and related to the molecular genetic results. Presently neither the former nor the latter approach provide a firm base to arrive at comprehensive conclusions across disciplines.
- Relations and interactions of the Antarctic with surrounding areas other than the Magellan region remain obscure; differences in similarity level with Antarctic biota between South America and Australia should be studied as an indirect measure of continental drift related evolutionary changes.
- Concerning almost all subjects dealt with in this review, research in the Magellan region must be strengthened. Presently the state of knowledge is much better for the Antarctic than for the "Cono Sur".
- More "circumantarctic" species should be studied using molecular techniques to detect cryptic species. For biodiversity purposes, traditional taxonomy remains important as most larger taxa (e.g., polychaetes) require identification to species level.

- Accessible fossil evidence is restricted to few sites in the Antarctic (Taviani *et al.*, 1998; Crame, 1999; Malumian and Olivero, 2005), and the record is only slowly improving.

- There is evidence for a convergent evolution of high Antarctic sessile suspension feeders to similar morphotypes as in the Cretaceous or earlier, however it requires further study of the responsible ecofactors.

- The Scotia Arc and Bouvet Island (see Arntz, in press) are clearly undersampled, considering their potential significance as transitory areas between the Magellan region, the tip of the Antarctic Peninsula and the high Antarctic.

- Further shallow areas should be studied in those high Antarctic regions where they are very scarce, to enable comparisons with shallow-water biota inside and outside the Antarctic and to elucidate the origin of their fauna.

- Areas under permanent pack ice cover and areas recently disclosed by ice shelf calving should be studied and compared with polynya areas to identify the consequences of extreme oligotrophy, and to follow recolonisation.

- Perturbation effects such as those from iceberg scour should be inflicted experimentally, and should include modelling approaches, to enable verification of successional processes and their duration, which will allow an improved judgement on ecosystem vulnerability and recoverability.

- Recolonisation experiments on soft and hard substrates, both short- and long term, should provide further data on the pace of succession and resilience under polar conditions.

- Influences from climate oscillations such as ENSO or the Antarctic Circumpolar Wave (White and Peterson, 1996) have been suspected by various authors but need more attention.

- More data on life cycles, reproductive strategies and physiological adaptations of benthic key species are badly needed.

- Meroplanktonic larvae, in particular, deserve an increased research input in deeper shelf areas.

- Close cooperation with physiologists should be enhanced, because it may lead to causal explanation of empirical ecological finds.

Similar to the EASIZ programme (Arntz and Clarke, 2002), which finished in 2004, the recently designed SCAR programme EBA (Evolution and Biodiversity in the Antarctic) provides an excellent thematic background for the continuation of IBMANT research on the interaction between the Antarctic and other remnants of Gondwana. Furthermore, cooperation with ANDEEP may enable us to check those potential links via the deep sea, which have emerged from research on the Antarctic and Magellan shelves.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
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Constraints and trade-offs in climate-dependent adaptation: energy budgets and growth in a latitudinal cline*

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SUMMARY: Characteristics of temperature-dependent metabolic adaptation as well as their implications for associated changes in energy budgets are analysed based on comparisons of fish and invertebrates from various latitudinal clines in northern and southern hemispheres and on integrated ecological and physiological approaches. To identify putative "bottlenecks" of adaptation and for a general cause and effect understanding, the temperature sensitivity of growth as a key energy budget component is investigated, considering underlying processes at population, whole animal and cellular levels. Available data support the hypothesis that natural selection favours individuals for energy efficiency and maximised growth, but is subject to constraints of limited energy availability and temperature. According to emerging relationships between energy turnover, temperature variability and thermal tolerance, the notion that selection should favour a certain metabolic rate according to mean temperature is too simplistic. Within the energy budget, savings in maintenance costs set free energy for growth, visible as growth increments at a low standard metabolic rate. Such energy savings are maximised at the permanently low temperature of the Antarctic. However, some variability persists as pelagic lifestyles in the Antarctic are fuelled by higher metabolic rates at the expense of reduced growth. Temperature variability in the cold, as in the Subarctic, causes a rise in maintenance costs at the expense of growth, but in favour of exercise and thus foraging capacity. Such transitions in energy cost between sub-polar and polar areas are not visible in the southern hemisphere, where there is less temperature variability. However, these patterns—as well as many of the underlying mechanisms—still remain incompletely investigated, especially with respect to the suggested hierarchy in energy allocation to energy budget components.

Keywords: Antarctic, energy efficiency, lifestyle, cold adaptation, growth performance, Magellan, temperature variability, eurythermy, stenothermy.

RESUMEN: RESTRICCIONES Y BALANCES EN LA ADAPTACIÓN DEPENDIENTE DEL CLIMA: PRESUPUESTOS ENERGÉTICOS Y CRECIMIENTO EN UN GRADIENTE LATITUDINAL. – Las características de la adaptación metabólica dependiente de la temperatura y sus implicancias en los cambios asociados a los presupuestos energéticos son analizadas sobre la base de: comparaciones de peces e invertebrados de varios gradientes latitudinales en los hemisferios septentrional y meridional, y de enfoques ecológicos y fisiológicos integrados. Para identificar los "cuellos de botella" putativos de la adaptación y para un entendimiento general de la causa-efecto, se investiga la sensibilidad del crecimiento a la temperatura como un componente clave del presupuesto energético, considerando los procesos subyacentes a niveles poblacional, individual (animal completo) y celular. Los datos disponibles sostienen la hipótesis que la selección natural favorece a los individuos con eficiencia energética y crecimiento maximizado, pero es sujeto de restricciones por la limitada disponibilidad energética y la temperatura. De acuerdo a las relaciones emergentes entre el intercambio energético, variabilidad de temperatura y tolerancia térmica, la noción acerca de que la selección debería favorecer ciertos niveles de tasas metabólicas de acuerdo con la temperatura promedio es demasiado simplista. Dentro del presupuesto energético, los ahorros en costos de mantenimiento liberan energía para crecimiento, visible como incrementos de crecimiento a tasas metabólicas estándar bajas. Tales ahorros energéticos son maximizados a las permanentes bajas temperaturas de la Antártida. No obstante, algo de variabilidad persiste en tanto estilos de vida pelágicos en la Antártida son sustentados por tasas metabólicas relativamente más altas a expensas de crecimiento reducido. La variabilidad de temperatura ambientes fríos, como en el boreal, causa un incremento en los costos de mantenimiento a expensas del crecimiento, pero a favor del movimiento y por tanto la capacidad de forrajeo. Tales transi-

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ciones en el costo energético entre áreas polares y subpolares no son detectables en el hemisferio sur, donde la variabilidad de temperatura es menor. Sin embargo, estos patrones como tantos otros mecanismos subyacentes todavía permanecen incompletamente investigados, especialmente con respecto a la jerarquía sugerida en la distribución energética y componentes de los presupuestos energéticos.

Palabras clave: Antártida, eficiencia energética, formas de vida, adaptaciones al frío, eficiencia del crecimiento, Magallanes, variabilidad de temperatura, euritermia, estenotermia.

INTRODUCTION

Animals, due to their inherently high levels of organisational complexity, specialise in environmental temperature much more than unicellular bacteria and algae (Pörtner, 2002a). Accordingly, thermal tolerance windows differ between ectothermal animal species (with body temperatures determined by ambient values)—and sometimes their populations—depending on latitude or seasonal temperature variation. They are therefore related to geographical distribution (e.g. Roy *et al.*, 1998; Pörtner, 2001, 2002a,b; Clarke, 2003). A consistent picture of how thermal tolerance windows develop between tropical and polar latitudes does not exist. There is, however, some evidence that towards colder regions/higher latitudes these patterns differ between northern and southern hemispheres; trends may follow the largely different patterns of temperature variability in the two hemispheres (Gaston and Chown, 1999; Pörtner, 2004). Trying to understand the limits and benefits of thermal specialisation, as well as their consequences for energy turnover, requires an understanding of the trade-offs and constraints in thermal adaptation. These become visible when temperature-dependent physiological characters are compared in ectotherms specialised in various temperature regimes. The marine realm, on a global scale, offers clearly defined thermal niches and, thus, an ideal basis for such comparisons. Marine animals of the high Antarctic—and possibly the deep sea—for example, rely on constant water temperatures. They include (possibly life's only) permanent stenotherms which are unable to sustain the complete set of life functions required for species survival and fitness at temperatures above 1 to 6°C (Pörtner *et al.*, 1999a; Peck, 2002).

In this context, the principle physiological factors that cause animals to undergo thermal specialisation on evolutionary time scales need to be identified. What are the benefits of specialising in a narrow window of thermal tolerance, especially in the cold or, alternatively, what has forced Antarctic ectotherms into stenothermy? Why would the levels of stenothermy or eurythermy correlate at least roughly with the ambient temperature regime? There is a need to address the way in which higher functions such as foraging activity, growth and reproduction, which mainly shape the lifestyle and survival of a species in its natural environment, are affected by temperature and temperature-dependent energy turnover. More specifically, how much energy out of its energy budget can the animal make available to each of these functions, and is this process of energy allocation subject to temperature-dependent constraints?

A key question is what are the ecological benefits that are primarily selected for depending on ambient temperature? The present study sets out to investigate to what extent the level of energy turnover (measured as standard metabolic rate, SMR) and the energy budget, i.e. energy allocation to growth, reproduction or foraging activity, are affected by environmental temperature as well as by the climate-dependent mode of life. In this case, we focus on growth rate (the absolute rate of new tissue production), considering aspects of growth efficiency (the fraction of energy converted to new tissue; Clarke, 1987). The integrated analysis of the ecological and physiological literature in fact illustrates how selection acts differently on the different components of the energy budget according to the climate regime. For data interpretation we consider recently established physiological principles of thermal tolerance windows and the key mechanisms of thermal adaptation and limitation. To identify putative "bottlenecks" and for a general cause and effect understanding, the thermal sensitivity of key energy budget components is addressed at population, whole animal and cellular levels. It should be noted that the rate of standard metabolism usually reported in the literature includes all physiological processes operative in the post-absorptive resting but non-dormant organism. These estimates usually also include processes associated with growth, although these may contribute to variable degrees, depending on the physiological status of the individual specimen.

The symposium theme is concerned with the separation and transition between Subantarctic and Antarctic realms. Since very little information is available for Subantarctic species, physiological answers for this special question can only be given once the general principles are known. The present study will therefore draw on examples from the Antarctic and temperate zones, as well as from the Subarctic where more detailed but still patchy knowledge is available. After describing some general principles it will then address the question of how these principles might apply to Subantarctic organisms and what specific research questions should be addressed in the future.

Antarctic lifestyles, energy turnover and thermal windows

The setting of thermal tolerance windows by the limited capacity of oxygen supply mechanisms emerges as a unifying principle across aquatic animal phyla (Pörtner, 2001, 2002a). For Antarctic species there is a need to consider why thermal windows differ between species (Pörtner *et al.*, 2000). Critical temperatures range between 2 and 3°C in the bivalve *Limopsis marionensis* and, more commonly, 6 to 10°C in other Antarctic bivalves, octopods or fish (Pörtner and Zielinski, 1998, Pörtner *et al.*, 1999a, 2000; Peck *et al.*, 2002; Peck, 2002). Even higher critical temperatures exist in the limpet *Nacella concinna*, enabling this species to enter the intertidal zone (Pörtner *et al.*, 1999a), and in the bivalve *Yoldia eightsi*, which carries out long digging excursions in the sediment to feed on deposits (Abele *et al.*, 2001).

A preliminary comparison of the lifestyles of these species suggests that exclusively sessile epifauna species like *Limopsis marionensis* (Pörtner *et al.*, 1999a) and *Liothyrella uva* (Peck *et al.*, 1987a,b) are characterised by lower critical temperatures than more mobile species. In general, a decrease in aerobic scope and thus functional capacity occurs as a first line of thermal sensitivity even before critical temperatures are reached (Pörtner, 2001, 2002a). This emphasises "heat" limitation at even lower temperatures and thus the level of extreme stenothermy in at least some Antarctic species, leading to an early loss of performance (Urban, 1998; Peck *et al.*, 2004). In addition, the capacity of oxygen provision by ventilation and circulation is likely to be higher in active fish or octopods than in mussels. This may explain the lower heat sensitivity in more mobile compared to sessile Antarctic species. In conclusion, the level of stenothermy among Antarctic species is probably co-defined by their level of agility and exercise capacity.

The historical concept of metabolic cold adaptation used to explain early findings of relatively high metabolic rates in Antarctic fish (Scholander *et al.*, 1953; Wohlschlag, 1964) has been disproved by more recent measurements of oxygen uptake in a number of Antarctic and Arctic invertebrates and fish under relatively stress-free conditions (Holeton, 1974; Ralph and Maxwell, 1977a,b; Peck *et al.*, 1987a; Chapelle and Peck, 1999; Whiteley *et al.*, 1996; Pörtner *et al.*, 1999a; van Dijk *et al.*, 1999; Clarke and Johnston, 1999; Marsh *et al.*, 2001; Heilmayer and Brey, 2003). It is now rather well established that the narrow thermal tolerance windows of Antarctic marine ectotherms go hand in hand with low resting or standard metabolic rates, and thus with lower costs of living than in warmer waters (Clarke and Johnston, 1999; Peck and Conway, 2000; Pörtner *et al.*, 2000). This statement is true especially for those benthic Antarctic invertebrates with the lowest activity levels and the narrowest windows of thermal tolerance.

Trade-offs in cold adaptation: stenotherms vs. eurytherms

Cold-induced hypometabolism in Antarctic stenotherms correlates, on average, with reduced net aerobic scopes for exercise and thereby reduces the flexibility to respond to ambient temperature fluctuations resulting in narrow windows of thermal tolerance (see Pörtner, 2002a, b, for review). The opposite is the case in cold-adapted eurytherms, as seen in animals from northern hemisphere temperate and Subarctic zones, which tolerate wider temperature fluctuations and are able to dynamically shift or change the widths of tolerance windows in accordance with seasonal temperature fluctuations. Adaptation to cold but unstable temperatures comes at a high cost during both seasonal and latitudinal cold (e.g. Pörtner *et al.*, 2000; Sokolova and Pörtner, 2003; Sommer and Pörtner, 2002, 2004; Sartoris *et al.*, 2003; Pörtner, 2004). High SMRs found in cold-adapted and cold-acclimated eurytherms extend to enhanced capacities of ventilation and circulation as a precondition for widened windows of thermal tolerance, and as a consequence they support cold-compensated metabolic scopes and activity levels, i.e. enhanced aerobic scopes for exercise in cold-adapted eurytherms (Pörtner, 2002b). A comparison of the contrasting trends of stenothermal versus eurythermal cold adaptation would already suggest that the capacity of aerobic exercise may not primarily be selected for but may rather follow passively the climate-dependent setting of aerobic energy turnover (cf. Pörtner, 2004).

MACRO-ECOLOGICAL AND MACRO-PHYSIOLOGICAL PATTERNS

According to the above, the level of energy turnover depends on climate-dependent temperature oscillations, especially in the cold, and plays an important role in the setting of thermal tolerance windows and fitness in ectothermal animals. Within these general constraints natural selection should favour those individuals which are energy efficient, grow fast and reproduce successfully. Natural selection should therefore operate at all (molecular to organismal) levels of animal energetics, finally including maintenance, growth and reproductive activity. The levels of these processes are interdependent as they all take a share in the organism's energy budget. Hence, the fitness of an organism (i.e. growth and reproductive success) depends on energy turnover and is largely influenced by temperature and its variability.

In various climates, depending on temperature variability the vast array of structural and physiological adjustments required for counteracting the reduction in chemical reaction rates at low temperature may only be possible in certain ways to ensure matching of energy production and consumption (cf. Pörtner *et al.*, 2005). These patterns will influence energy availability for growth and reproduction. Many of the underlying mechanisms still remain incompletely investigated (Zielinski and Pörtner, 1996; Guderley *et al.*, 1997; Pörtner *et al.*, 1998; Frederich and Pörtner, 2000; Peck *et al.*, 2002; Pörtner, 2002a, b; Sommer and Pörtner, 2002, 2004; Hochachka and Somero, 2002). As a contribution the present chapter attempts to identify large-scale patterns that may be shaped by these mechanisms. More specifically, it essentially focuses on how the relationship between metabolic costs and growth may change depending on latitude.

Growth patterns and energy turnover

In principle, there are two ways to enhance growth of an ectothermal organism depending on the temperature regime and on resource availability in its natural environment. Firstly, growth can be maximised by minimising energy expenditure for maintenance or activity, especially under conditions in which nutrient supply and assimilated energy are limited. This principle has been verified in various aquatic and terrestrial ectotherm species from different phyla, including marine molluscs (within species: Koehn and Shumway, 1982; Hawkins and Day, 1996), freshwater fish (within species: Wieser and Medgyesy, 1991), amphibians (within species: Mitton *et al.*, 1986) and reptiles (within species: Steyermark, 2002).

Alternatively, growth is maximised in high energy turnover life forms (e.g. among cephalopods or among endotherms in general) when selection for increased energy turnover and food conversion leaves excess energy for growth (cf. Pörtner, 2004). Such patterns may result from phylogenetic constraints in which, as among cephalopods, competition with vertebrates enforces a high energy turnover life associated with a high maintenance metabolism and growth (Pörtner *et al.*, 1995). Within species or phyla such evolutionary patterns may be supported by the selection for high energy turnover under the precondition of excess resource availability (Mueller and Diamond, 2001). Such selection is probably enforced by climate variability (Pörtner, 2004).

Climate variability and resource availability may also shape latitudinal patterns. In a system like the Antarctic, animal life may be food-limited and growth is periodic in those species relying on the extremely seasonal primary production (Arntz *et al.*, 1994, Clarke and Leakey, 1996; Brockington *et al.*, 2001; Clarke, 2003). Based on an extensive review of the existing literature, Brey (1999) showed that mean annual growth rates are low in high-latitude invertebrates. Under favourable circumstances, however, growth performance of some polar species can approach those of temperate or even tropical species of similar size and ecology. It is most likely that under such conditions energy is primarily allocated to the growth component of the energy budget, at the expense of energy savings in the maintenance metabolism. These savings may, however, affect the functional capacity of other processes like muscular activity, and are one reason why the activity component of metabolism is reduced in Antarctic stenotherms. In fact, the observations that net aerobic scopes are low and that there are no high-performance predators in the Antarctic would suggest such a common constraint on Antarctic lifestyles (cf. Clarke, 1998; Pörtner, 2002b). Long-term evolutionary adaptation to the very cold and stable environmental temperatures of the Antarctic may have supported the maximisation of energy efficiency, characterised by a low basal metabolism. This would contrast with the cold eurythermal, more cost-intensive form of cold tolerance found in Subarctic and Arctic species of the northern hemisphere (Pörtner, 2002b; Lannig *et al.*, 2003; Sartoris *et al.*, 2003).

Growth patterns in stenothermal and eurythermal fish

Previous work in eurythermal cod and eelpout, which are cold-acclimated or cold-adapted in a latitudinal cline of the northern hemisphere, suggested that the rising cost of maintenance in eurytherms occurs at the expense of a reduction in temperature-specific growth performance or in reproduction (Pörtner *et al.*, 2001). At the same time high levels of baseline energy turnover and of metabolic capacity associated with eurythermal cold adaptation are suitable to support enhanced exercise capacity (Pörtner, 2002b). Trade-offs result between exercise capacity and growth performance, which may be shifted to lower growth performance in Arctic compared to temperate eurytherms (see Fig. 1).

Similar trade-offs are probably operative within Antarctic notothenioid fish. A recent overview of age and growth in high Antarctic notothenioid fish revealed an overall increase in growth performance from pelagic to benthic lifestyles (La Mesa and Vacci, 2001). The common ecological index of "overall growth performance (OGP)" *P* (Pauly, 1979, for review Brey, 2001) is used to compare growth between populations or species. *P* is defined as the maximum rate of body mass increase during lifetime, i.e. the mass increment at the inflexion point of the Van Bertalanffy Growth Function which describes growth in body mass (for a detailed discussion see Vakily, 1992; Brey 2001). A comparison of *P* values with the levels of SMR in Figure 2 confirms that slow growth goes hand in hand with high SMR in high Antarctic Notothenioid fish.

Only a few nototheniids, such as *Pleurogramma antarcticum* and *Pagothenia borchgrevinki*, have successfully invaded the midwater (Clarke and Johnston, 1996; La Mesa and Vacci, 2001). Pelagic Antarctic fish species experience extreme seasonality of light and food availability, reflecting an additional challenge to ration energy intake during the short Antarctic summer in order to make a pelagic existence energetically feasible. These pelagic forms developed extensive energy saving strategies (neutral buoyancy through incorporation of lipids and extensive lipid deposits, reduced ion exchange activities, reduced calcification of the skeleton, reduction of bones, and morphometric parameters such as gill raker, fin and body sizes, De Vries and Eastman, 1981; Eastman and DeVries, 1982; Eastman, 1985; Andriashev, 1985; Ekau, 1988; Kunzmann and Zimmermann, 1992; Dorrien, 1993) to

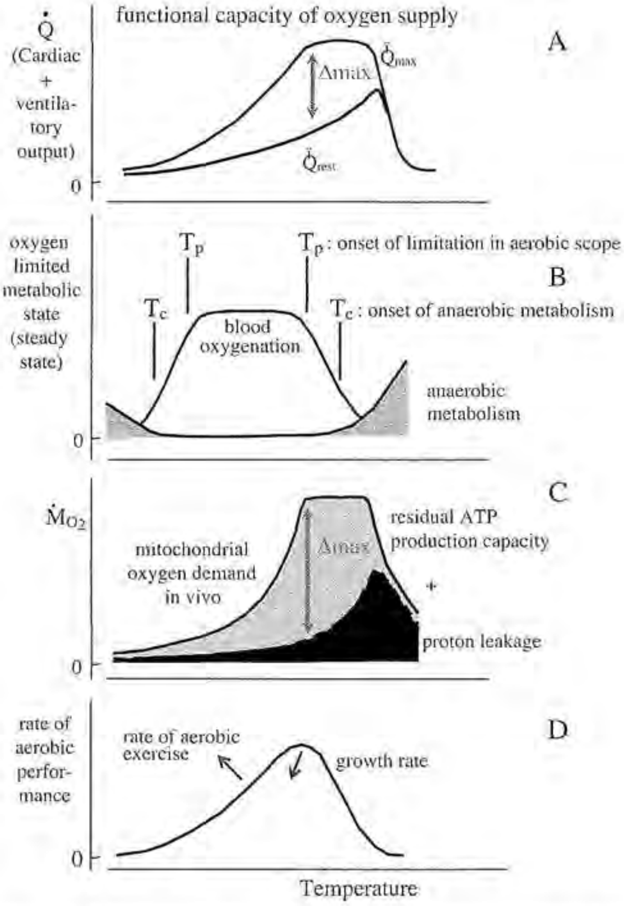

FIG. 1. – Schematic model of oxygen-limited thermal tolerance and performance capacity in fish and other metazoa, set by the capacity of oxygen supply mechanisms (adopted from Pörtner *et al.*, 2004). (A) Functional reserves in oxygen supply result as combined ventilatory and cardiac output (Q) and are maximum at the upper pejus temperature Tp, before aerobic scope becomes thermally limited (B). Maximum scope (Δmax) between resting and maximum output in oxygen supply is probably correlated with the one in mitochondrial ATP generation which is limited by oxygen supply in vivo (C). Low ATP formation capacity in the cold and high proton leakage in the warm contribute to insufficient oxygen supply (B). Maximum scope in ATP generation at the upper Tp supports an asymmetric performance curve of the whole organism (D). As a trade-off in eurythermal cold adaptation contrasting changes in exercise capacity versus those in growth rate are indicated by arrows in D (for further explanations see text).

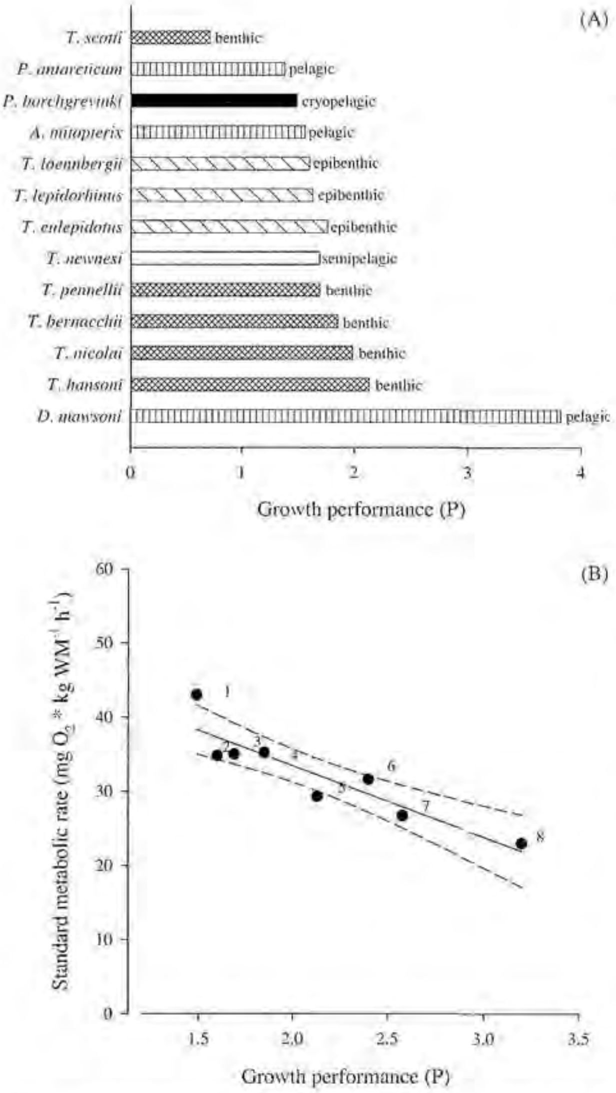

FIG. 2. – Overall growth performance (*P*) of notothenioid fish in relation to (A) their mode of life in the high Antarctic zone and (B) their standard metabolic rate (SMR) in the high Antarctic and lesser-Antarctic/Subantarctic zone. According to Pauly (1979) overall growth performance *P* (= log K + log M_∞) describes the growth rate at the point of inflection of the size (mass) growth curve (K, $year^{-1}$, is a measure of how fast fish attain their final size and M_∞ is the infinite mass of the fish, in g). (A) Graph redrawn using P values compiled by La Mesa and Vacchi (2001). (B) P values by La Mesa and Vacchi (2001) and Hubold (1991), SMR: Holeton (1970), Forster *et al*. (1987), Johnston *et al*. (1991); Johnston and Battram (1993); Macdonald *et al*. (1988); Wells (1987) in Montgomery and Wells (1993); Morris and North (1984) in Thurston and Gehrke (1993); Zimmermann and Hubold (1998); Steffensen (2002); SMR values correspond to resting or standard metabolic rates, all expressed as mg O_2 kg WM^{-1} h^{-1} (WM = wet mass) calculated for a 100 g fish at temperatures close to freezing. SMR values of one species from various citations were summarised to one mean. Linear regression: $y = -9.6\ x + 52.6$ ($r = 0.91$); dashed lines indicate the 95% confidence interval. High-Antarctic species are: 1 *Pagothenia borchgrevinki* (cryopelagic, active under sea ice), 2 *Trematomus loennbergii* (demersal), 3 *T. pennellii* (demersal), 4 *T. bernacchii* (demersal), 5 *T. hansoni* (demersal). Lower- to Subantarctic species: 6 *Notothenia neglecta* (benthopelagic), 7 *N. gibberifrons* (benthopelagic), 8 *N. rossii* (benthopelagic).

eliminate the higher costs associated with their lifestyle, achieve lower SMRs and thus higher growth rates. However, they are evidently not as successful in this strategy as demersal fish (Fig. 2, Priede, 1985; Dorrien, 1993; Zimmermann and Hubold, 1998).

High growth rates going hand in hand with low SMRs are in line with the above hypothesis of a trade-off leading to low growth performance at higher exercise capacities and vice-versa. Such trade-offs may also explain the different growth performance values between Antarctic and Arctic fish. Most stenothermal Antarctic notothenioids, with the exception of the very small (M_∞=37 g) *Trematomus scotti* (P=0.71) from the Weddell Sea and the exceptionally heavy (M_∞>100 kg) *Dissostichus mawsoni* from the Ross Sea (P=4.01), display *P* values of 1-3 (Kock and Everson, 1998; La Mesa and Vacchi, 2001). In contrast, Dorrien (1993) found low overall growth performance values of 0-1.5 in selected Arctic benthic fish species. This finding is in line with a higher level of eurythermy and thus baseline energy turnover in Arctic compared to Antarctic fish and agrees again with the suggested principle.

Latitudinal growth patterns in pectinid bivalves

The question arises whether similar trade-offs between growth rate and metabolic costs may prevail among invertebrates. A recent study by Heilmayer *et al.* (2004) investigated the overall growth performance of pectinid bivalves in a latitudinal cline.

With some exceptions, the general consensus in the literature is that bivalve molluscs from low latitudes grow more rapidly due to high ambient temperature, attain a smaller maximum size and have a shorter lifespan than do con-familial species from higher latitudes (Newell, 1964; Roy *et al.*, 2000; Heilmayer *et al.*, 2004). The relationship between scallop growth performance and latitude can be best described by a Gaussian model (Fig. 3, r^2= 0.39). Certainly, this relationship does not reflect a direct effect of geographic latitude, but of variables coupled to latitude and associated annual solar energy input such as water temperature affecting metabolism, and primary production, which affects food conditions.

Several studies in bivalves have emphasised that growth variations may be linked to various physiological components of growth, such as whole-animal metabolic rate (Widdows, 1978; Koehn and Shumway, 1982; Toro *et al.*, 1996), the intensity of protein turnover (Hawkins *et al.*, 1986; Hawkins and

Day, 1996; Storch and Pörtner, 2003) and the efficiency of protein synthesis and deposition (Bayne and Hawkins, 1997; Bayne *et al.*, 1999; Storch and Pörtner, 2003).

As found for other polar ectotherms (Brey and Clarke, 1993; Arntz *et al.*, 1994; Peck, 2002), the Antarctic scallop (*Adamussium colbecki*) displays slow annual growth (Fig. 3) compared with temperate and tropical counterspecies. Similar to the patterns found in fish, a reduced metabolic rate as shown by Heilmayer and Brey (2003) for *A. colbecki* might imply enhanced growth performance as less energy is "wasted" on the basal metabolism (Bayne and Newell, 1983; Clarke, 1987). Such a pattern would be in line with the trade-off in energy budget discussed above.

Recently, the ratio of *P*-to-mean SMR was investigated as a proxy for growth efficiency in pectinids across latitudes (Heilmayer *et al.*, 2004). This ratio reflects the fraction of metabolic energy channelled into somatic growth. In temperate bivalve molluscs, e.g. *Mytilus edulis*, individuals with low basal or standard metabolic requirements display comparatively higher growth rates (for details see Hawkins *et al.*, 1989; Wieser, 1994; Hawkins and Day, 1996) and thus high *P*-to-mean SMR ratios. This principle also appears to be operative between species across latitudes. In pectinids, the general decrease in growth efficiency with rising temperature across latitudes, as shown in Figure 4, gives evidence that metabolic rates increase faster with temperature than does overall growth performance, possibly as a consequence of enhanced energy availability, maintenance cost or cost of growth. The temperature coefficients (Q_{10}) computed from the corresponding Arrhenius models exemplify this difference: within the 0-25°C temperature range Q_{10} of scallop metabolic rate is 2.97, whereas overall growth performance changes more slowly with temperature (Q_{10}= 1.12, Heilmayer *et al.*, 2004). Accordingly, the between-species comparisons carried out for pectinids in a latitudinal cline support the hypothesis of a trade-off in energy budget in the permanent cold, with enhanced levels of energy efficiency and allocation to growth.

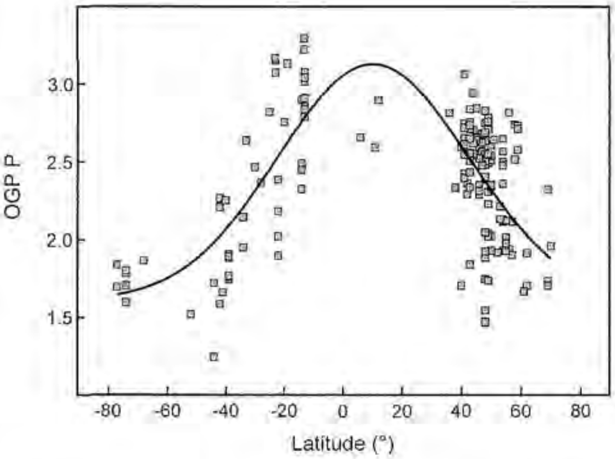

FIG. 3. – Relationship of overall growth performance (P = log K + log M_∞) and latitude of 198 populations of 26 scallop species (for references see Heilmayer 2003). Regression line:

$$OGP\ P = 1.6 + \frac{123.5}{64.72\sqrt{\frac{\Pi}{2}}} \bullet e^{\frac{-2\,(Lat-10.1)^2}{64.72^2}}\quad, (r^2 = 0.39;\ N=198)$$

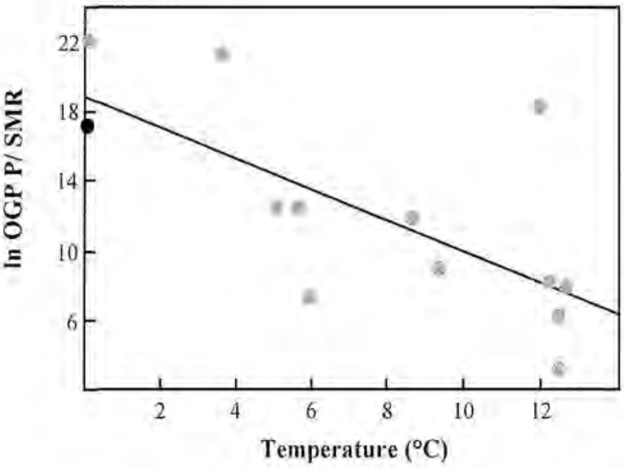

FIG. 4. – Relationship of the ratio of standard metabolic rate (mean *SMR*) over growth performance (*P*) to ambient temperature of 7 scallop species (grey dots: *A. opercularis*, *C. islandica*, *M. varia*, *M. yessoensis*, *P. magellanicus*, *Z. patagonica*; black dot: *A. colbecki*). Data presented are resting or standard metabolic rates at normal ambient temperatures. Where seasonal data were available the data were averaged for the whole year (for more details and references see Heilmayer *et al.*, 2004). Regression line: *OGP P*/mean SMR = 19.003 - 0.903 T (N= 13, r^2= 0.496, $p < 0.001$)

As a conclusion, trade-offs between growth, baseline energy turnover and the associated levels of agility or exercise capacity become apparent in macroscale comparisons between Arctic and temperate as well as Arctic and Antarctic fauna. They are also operative within Antarctic notothenioid fish (see above). For several groups, such as pectinids, it remains currently unclear to what extent this includes trade-offs in exercise capacity (Bailey *et al.*, 2003). The principle similarity of such trade-offs may reflect a unifying principle by which, among species with similar lifestyles, those with a lower level of SMR, and thus lower baseline costs associated with a quieter mode of life, benefit from higher growth rates.

Protein synthesis capacity

Growth and cellular functioning in tissues are closely related to protein synthesis and breakdown. Low rates of oxygen demand at low temperature therefore involve reduced protein turnover supported by reduced synthesis of highly complex protein systems like haemoglobin, ion pump systems, and possibly other protein complexes of basal metabolism (Clarke, 1991). The protein synthesis machinery will only be used for growth when excess energy in terms of food is available.

According to current understanding, annual growth of many polar species is low, but maximum growth rates in Antarctic stenotherms, invertebrates and fish can reach levels comparable to those found in the lower range for temperate species (Brey and Clarke, 1993; Arntz *et al.*, 1994; Kock and Everson, 1998; Brodte, 2001; Peck, 2002).

In the light of these findings and of the observed energy savings in the cold, the protein synthesis machinery should be at least as energy-efficient as at warmer temperatures. At the same time protein synthesis capacity should not become limiting when food availability is high in polar summers despite cold temperatures. A recent analysis of the ATP cost of protein synthesis in temperate and polar pectinids demonstrated that the cost of protein synthesis remains unchanged regardless of temperature (Storch and Pörtner, 2003). However, high tissue RNA levels (commonly used as a measure of "protein synthesis capacity") have been observed in cold stenothermal invertebrates leading to increased RNA/protein ratios, which might imply a higher energy cost due to the cost of RNA synthesis (Whiteley *et al.*, 1996; Robertson *et al.*, 2001; Marsh *et al.*, 2001; Fraser *et al.*, 2002a). These high RNA levels have been interpreted to compensate for a cold-induced reduction in RNA translational efficiency in vivo (i.e. the extent to which capacity is used to synthesise protein per quantum RNA in vivo).

Increased RNA contents as seen in cold-adapted invertebrates have to be confirmed for fish and may simply be the result of low RNA turnover rates at no high cost. In fact, no difference in RNA content could be found in gill and muscle collected from Antarctic and North Sea eelpouts at their ambient temperatures. However, upon long-term acclimation from 0 to 5°C, Antarctic eelpout showed a reduction in RNA levels, which would strengthen the hypothesis that RNA turnover rates influence the level of RNA, leading to a rise at low and a decrease at warm temperatures (Storch *et al.*, 2005). Independent of RNA levels, the finding of high translational capac-

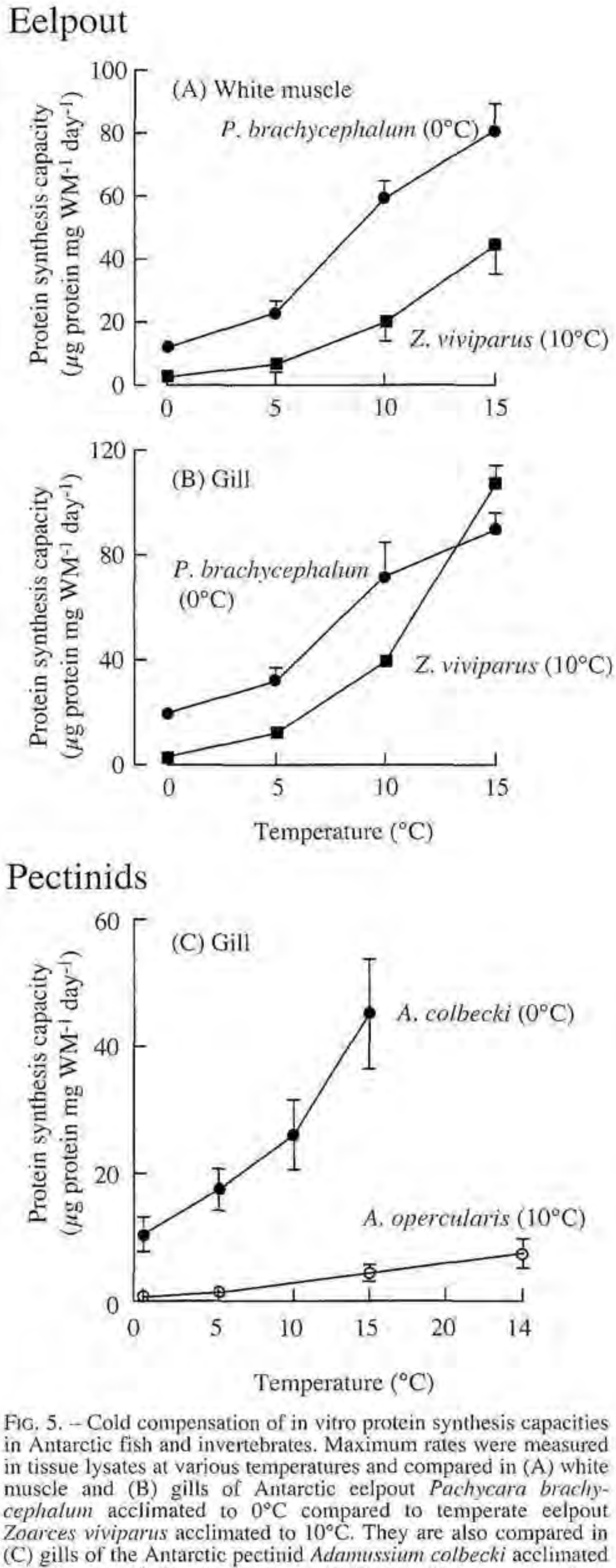

FIG. 5. – Cold compensation of in vitro protein synthesis capacities in Antarctic fish and invertebrates. Maximum rates were measured in tissue lysates at various temperatures and compared in (A) white muscle and (B) gills of Antarctic eelpout *Pachycara brachycephalum* acclimated to 0°C compared to temperate eelpout *Zoarces viviparus* acclimated to 10°C. They are also compared in (C) gills of the Antarctic pectinid *Adamussium colbecki* acclimated to 0°C and of the temperate pectinid *Aequipecten opercularis* acclimated to 10°C (data adopted from Storch *et al.*, 2003, 2005).

ities at low temperatures indicates that the RNA translation apparatus is cold-compensated in invertebrates as well as in fish (Storch *et al.*, 2003, 2005). All of these patterns would support enhanced functional capacities at maintained cost efficiency. Cold-compensated capacities of protein synthesis as found in white muscle and gills of Antarctic pectinids and eelpouts (Storch *et al.*, 2003, 2005) are in line with the suggested trend in polar ectotherms to maximise growth performance at low baseline metabolic costs (Fig. 5).

It thus appears that growth capacity is cold-compensated in Antarctic stenotherms but this capacity may only be exploited during the short Antarctic summer. A capacity for the thermal adjustment of this process is evident in the Antarctic eelpout, in which protein synthesis capacity decreases during long-term acclimation from 0 to 5°C (Storch *et al.*, 2005).

GROWTH WITHIN ENERGY BUDGETS: ARE THERE UNIFYING PRINCIPLES?

Growth is a complex process that is subject to controls and limitations at various levels. At first sight, an increase in SMR would indicate enhanced energy availability for growth. However, across phyla this may only be achieved at very high levels of energy turnover, as seen in cephalopods or mammals (cf. Pörtner, 2004). In the range of SMRs seen at low temperature or in hypometabolic fish and invertebrates, a high SMR apparently reflects high maintenance costs covered at the expense of growth. Studies within single invertebrate species led to the hypothesis that the primary physiological basis of an increase in production is reduced energy expenditure per unit of growth, indicating enhanced growth efficiency, rather than a straightforward increase in feeding and all other associated processes that are required for growth (Hawkins *et al.*, 1986, 1989; Hawkins and Day, 1996; Schultz *et al.*, 1996). According to the macroscale patterns discussed here, this principle is operative in ectotherms at high latitudes and probably reflects one major reason why Antarctic species are selected to minimize metabolic costs as much as lifestyle permits, at the expense of a high degree of stenothermy.

The trade-offs between energy turnover and growth in a latitudinal cline as depicted here were established in eastern Atlantic cod populations and for Antarctic fish as well as pectinids in a latitudinal cline. They also match observations of reduced growth capacities at increasing latitudes in anchoveta along the coast of Chile (Castro *et al.*, 2001). For limnic large-mouth bass, modelling of energy allocation strategies also revealed that smaller size-at-age occurs in the north than in the south, consistent with field patterns for this species (Garvey and Marschall, 2003). Further examples exist among fresh water fish.

However, as a note of caution, the trade-offs between growth rates and metabolic costs depicted here for cold-adapted low-activity fish and invertebrates may not easily explain all latitudinal growth patterns and energy allocation strategies observed. For example, growth capacity may not clearly differ between northwestern Atlantic cod populations in a latitudinal cline (Purchase and Brown, 2001), despite largely different temperatures. The growth patterns discussed and interpreted here also contrast higher growth capacities in northern than in southern populations of (North-American) silverside (*Menidia menidia*; Yamahira and Conover, 2002), which were suggested to compensate for the short growing season at high latitudes. This strategy is not apparently associated with different routine metabolic rates (Billerbeck *et al.*, 2000). For these studies it would be interesting to further analyze the metabolic and energetic background of these apparently contrasting strategies in relation to temperature variability of specific environments. Explanations of potential differences between species or population-specific strategies for overcoming thermal and seasonal constraints require consideration of temperature means and climate variability (Pörtner *et al.*, 2001) as well as the response to seasonal resource limitations (e.g. Hurst and Conover, 2003). The latter may also define seasonal changes in energy allocation (e.g. fattening strategies in autumn) and for cod, which were found to starve during winter in the Gulf of St. Laurence (Schwalme and Chouinard, 1999), may play a larger role on the western than the eastern side of the Atlantic.

Existing knowledge reviewed here leads to various lines of thought and testable hypotheses that might resolve these apparent discrepancies. It can be extrapolated from observations in Antarctic fish that cellular growth capacity can be fully compensated for the effect of low temperature. The level of standard metabolism will then decide whether such capacity can be fully exploited. For temperate species this pattern will depend on summer temperatures and low summer metabolic rates. This is in fact what is traditionally observed at temperate latitudes: summer temperatures support lower levels of temperature specific SMR than winter temperatures (e.g. van Dijk *et al.*, 1999). Even in Subarctic (Barents Sea) cod there is such a trend. At 4°C SMR increases above the level seen at 4°C in North Sea cod, while at 10°C SMR in the Barents Sea cod is reduced to almost the level seen in North Sea cod at 10°C (T. Fischer, R. Knust, H.O. Pörtner, unpubl.). This reduced "summer" SMR will then support high growth efficiency and maximised growth in Barents Sea cod, but still at rates below those of North Sea cod (Pörtner *et al.*, 2001).

According to these patterns, it appears that due to high summer temperatures species populations exist at high northern hemisphere latitudes which are able to use efficient summer metabolic rates for maximised growth. Enhanced metabolic efficiency may even support a shift of growth capacity to above the rates seen at lower latitudes. There is very little information in support of this hypothesis and future work will have to test the relationship between SMR and growth in those species with maximised summer growth.

Despite these apparent exceptions, the present findings lead to answers for numerous discussions in the literature which suggested three basic explanations for slow annual growth rates at high latitudes:

1. *The rate limiting effect of low temperature*: This argument can probably be dismissed for the cellular level as it was recently shown for some cold-adapted stenotherms that a rate-limiting role for the ribosomal machinery at low temperature is alleviated by a large degree of compensation (e.g. Storch *et al.*, 2003, 2005). Myogenic cell cycle duration also displays cold compensation (Brodeur *et al.*, 2003). Future studies are needed to quantify the degree of growth compensation capacity at whole organism levels.

2. *Seasonal activity*: This explanation invokes no effect of temperature and has been a focal point for numerous studies regarding growth and seasonality at high latitudes in recent years. Polar regions allow the ecological effects of food to be distinguished from those of temperature since a greatly reduced seasonal variation in temperature coincides with enhanced seasonality of food availability (Clarke and Leakey, 1996; Brockington and Clarke, 2001). However, it has been argued that the seasonality of growth in Antarctic ectotherms is mediated through seasonal variations in resource utilisation rather than seasonal resource availability or temperature-dependent effects on growth (Coggan, 1997). Depending on feeding habits during winter, there were variable factorial rises in oxygen consumption from winter to summer in the Antarctic limpet *Nacella concinna* (x 1.6; Fraser *et al.*, 2002b), the Arctic amphipod *Monoporeia affinis* (x 1.2; Lehtonen, 1996), the Antarctic infaunal bivalve *Laternula elliptica* (x 3; Brockington, 2001) and the Antarctic sea urchin *S. neumayeri* (x 2.5 to 3.1; Brockington and Peck, 2001). In *S. neumayeri* only 15-20% of the summer-induced increase in metabolism is explainable by the temperature increase, whereas 80-85% is caused by increased physiological activity associated with feeding, growth and spawning (Brockington and Clarke, 2001). While growth was found to fluctuate seasonally in Antarctic fish at South Georgia (North, 1998; North *et al.*, 1998) and at Signy Island (Ashford and White, 1995), the former authors concluded that seasonal food resource limitation had a major effect, whereas Ashford and White (1995) could not find conclusive evidence for growth limitation either by sea water temperature or by resource availability. As a correlate of enhanced growth, however, "appetite" was higher under summer conditions.

Possibly, it is energetically not worthwhile to grow all year round but to restrict growth to a short period at the peak of food availability. Therefore, overall annual growth is slow but once growth is actually underway, it may proceed rapidly. In the meanwhile, hibernation patterns have been identified, largely in invertebrates and fish, associated with low energy turnover, low protein synthesis capacities and suspended growth during the Antarctic winter (Ashford and White, 1995; Lehtonen, 1996; North, 1998; North *et al.*, 1998; Brockington, 2001; Brockington and Peck, 2001; Fraser *et al.*, 2002a; Storch *et al.*, 2003). The environmental triggers of hibernation are unclear, but some examples indicate that hibernation occurs with food available and may rather be due to a reduction of light and, to a minor extent, temperature. The use of hibernation strategies would thus explain the low average annual growth of Antarctic ectotherms. They may have been selected in response to low seasonal food availability and now support an energy saving stenothermal mode of life.

3. *A rising cost of maintenance at the expense of a reduction in growth and reproduction*: This argument considers the consequences of metabolic cold adaptation which may occur at the expense of growth (see above). In fact, metabolic cold compensation as seen in cold eurytherms would support enhanced levels of tissue energy turnover suitable

for supporting spontaneous activity and exercise capacity at the expense of reduced growth (Pörtner, 2002b). Conversely, the degree of metabolic cold adaptation is minimal in stenotherms, so this explanation does not hold to explain reduced annual growth. As outlined above, the reduction in aerobic capacity and SMR in Antarctic stenotherms includes a reduction in baseline metabolic costs such that metabolic energy becomes available for enhanced and energy-efficient growth and reproduction processes in the permanent cold. In the light of relatively high peak summer growth rates, this leaves the seasonality argument (2) as the key explanation for slow annual growth in the Antarctic.

In summary, the energy budget hypothesis developed here and the suggested trade-offs between lifestyle, exercise and growth performance most consistently explain the patterns observed in stenotherms and in eurytherms in a latitudinal cline. These observations suggest that there probably exist hierarchies of energy allocation which clearly need to be studied. This should include the investigation of regulatory mechanisms involved in setting the fraction of the energy budget allocated to growth and other components of SMR (cf. Wieser, 1994).

PERSPECTIVES: TRANSITIONS TO ANTARCTICA, PAST AND PRESENT

So far the analysis has compared Antarctic and Arctic (including Subarctic) as well as temperate zone ectotherms. It has also emphasised that cold-adapted eurytherms have largely been identified in the northern hemisphere, a phenomenon that may be linked to the more unstable temperatures at northern compared to southern latitudes. Considering the relatively stable temperatures at all latitudes of the southern hemisphere, the comparison of Subantarctic, Antarctic and Subarctic or Arctic species would make it possible to determine whether the evolution of marine Antarctic species occurred via a cold eurythermal intermediate form until the specialised cold stenothermal extant state was reached. Alternatively, the levels of energy turnover may be found lower at Subantarctic than at Subarctic latitudes, so a typical cold-adapted sub-polar eurytherm as found in the Subarctic may not exist in the south.

While studies of whole organism physiological patterns are underway in Magellan ectotherms (J. Calvo, personal communication) the patterns of mitochondrial metabolism depending on latitude

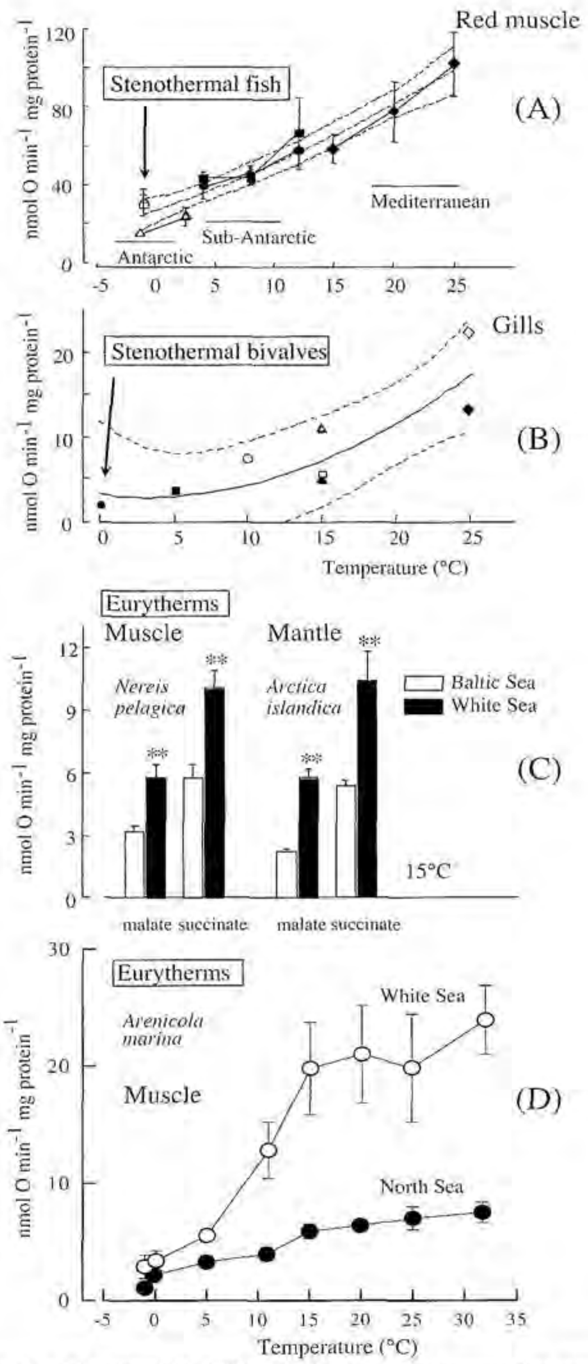

FIG. 6. – Mitochondrial ATP synthesis capacities (measured as state 3 respiration rates) in stenothermal and eurythermal ectotherms (adopted from Pörtner *et al.*, 2000; Pörtner, 2004). (A) State 3 respiration rates at various temperatures of isolated mitochondria from red musculature of Antarctic (open symbols), Subantarctic (South American, filled circles and squares) and Mediterranean fish species (filled diamon, redrawn from Johnston *et al.*, 1998). (B) State 3 respiration rates of mitochondria isolated from temperate and Antarctic bivalves and studied at various temperatures emphasize the down regulation of ATP synthesis capacities, similar to fish. (C) Elevated ATP synthesis capacities in mitochondria from White Sea compared to Baltic Sea populations of *Nereis pelagica* and *Arctica islandica* and from White Sea and North Sea populations of *Arenicola marina* (D) correlate with elevated proton leakage rates (Tschischka *et al.*, 2000; Sommer and Pörtner, 2004). Similar patterns were observed in a comparison of northeastern Arctic (Barents Sea) and North Sea cod (*Gadus morhua*) populations (T. Fischer, R. Knust, H.O. Pörtner, unpubl.).

may provide a hypothesis for the metabolic transition to life in Antarctica. One basic insight from recent studies of metabolic cold adaptation is that for two species with the same moderate performance levels, the one with the colder body temperature needs more mitochondria / more mitochondrial enzymes for the same aerobic and thus functional capacity. Compared to other vertebrates, aerobic design in terms of mitochondrial densities is maximised in (pelagic) Antarctic fish, but cellular space constraints limit mitochondrial densities (Lindstedt *et al.*, 1998). As a trade-off, mitochondrial proliferation is associated with a loss of contractile fibres and, thereby, maximum muscular force per unit muscular mass. The reduction in SMR is linked to minimised ATP synthesis capacities (determined as state 3 respiration) of mitochondria according to cold temperature (Fig. 6; Johnston *et al.*, 1998). Available data indicate that in parallel to minimised ATP synthesis capacities in Antarctic stenotherms, mitochondrial proton leakage rates were also minimised in the cold (Pörtner *et al.*, 1998, 1999b; Hardewig *et al.*, 1999). Low leakage rates and thus low SMR indicate that these animals escaped from the cost of cold tolerance associated with an uncompensated loss of performance levels in the permanent cold.

These principle considerations can also be applied to eurytherms. However, seasonal cold acclimatisation and eurythermal cold adaptation to high sub-polar (northern) latitudes are associated with a compensatory rise in mitochondrial ATP synthesis capacities (Fig. 6), and finally organismic oxygen demand (standard metabolic rate). Rises in mitochondrial ATP synthesis capacity and in proton leakage reflect eurythermal cold adaptation (e.g. Tschischka *et al.*, 2000; Sommer and Pörtner, 2002, 2004; T. Fischer, R. Knust, H.O. Pörtner, unpubl.). Cold tolerance at variable temperatures is therefore associated with enhanced costs of mitochondrial maintenance and associated high oxygen demand, as well as a high standard metabolic rate and high functional capacity.

As a generalised conclusion, eurytherms are exposed to the full cost associated with metabolic cold adaptation. This cost may be high because they need to make use of their mitochondria within the widest possible range of short-term ambient temperature fluctuations. As a precondition, the metabolic increase elicited by rising temperature must be kept small during short-term warming in order to maintain aerobic scope in the warm. In contrast to the situation in stenotherms, this minimises the degree to which temperature-dependent kinetic barriers like high activation enthalpies can be established in molecular, cellular and systemic processes (Pörtner *et al.*, 2000). Eurytherms may therefore choose to minimise mitochondrial densities and maximise ATP synthesis capacities instead (Fig. 6) in order to balance the cold-induced rise in baseline metabolic cost. The cost of cold adaptation is not only associated with proton leakage across the mitochondrial membrane, but also with ion movements (leakage) across the cellular membrane, which need to be compensated for by active ion exchange mechanisms (Pörtner *et al.*, 1998). Accordingly, the densities and modulation of ion transport proteins also shape the cost of cold adaptation.

These largely contrasting patterns of cold adaptation observed in Antarctic marine stenotherms versus more eurythermal northern hemisphere cold-adapted ectotherms emphasise that ambient temperature fluctuations play an important role in defining energy turnover. Accordingly, obligatory links very probably exist between the stability of (cold) climates and the level of energy demand. This principle insight can be applied to the mitochondrial data compiled by Johnston *et al.* (1998) for Mediterranean, Subantarctic and Antarctic fish (Fig. 6). Their data do not show any increase in mitochondrial capacities with falling temperatures, as would typify cold adapted eurytherms, but rather a progressive decrease occurs. The prediction results that the Subantarctic species, in terms of their mitochondrial capacities and in terms of their whole organism oxygen demand, fall onto a simple continuum between warm waters and the Antarctic. These patterns do not provide any evidence for a clearly eurythermal increase of mitochondrial capacity at Subantarctic latitudes. The patterns found rather mirror the more moderate temperature oscillations that characterise the sub-polar areas of the southern compared to those of the northern hemisphere.

On evolutionary time scales a similar conclusion arises in that moderate temperature oscillations during the long period of Antarctic cooling have not involved an obligatory transient expression of eurythermal, high-energy turnover life forms. Rather, notothenioid ancestors may have been pre-adapted to the extant notothenioid energy-saving mode of life, enabled and supported by moderate temperature oscillations and the resulting physiological features discussed here for stenotherms. These considerations demonstrate that the macro-scale comparisons of extant fauna from various latitudes, including comparisons between southern and northern hemispheres, appears to be an adequate tool for addressing and explaining the physiological bases of ecological patterns and, last not least, the pathways of climate-dependent animal evolution on earth.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Oxidative stress and antioxidant defences generated by solar UV in a Subantarctic marine phytoflagellate*

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SUMMARY: The reduction of the Antarctic stratospheric ozone resulted in significant increases in ultraviolet B radiation (UV-B, 280-320 nm) reaching the surface of the ocean. The main objective of this work was to study long-term (growth rate scale, days) stress responses (lipid oxidative damage, TBARS, and lipid soluble antioxidants) to UV-B and UV-A of a phytoflagellate species (*Asteromonas* sp.) isolated from a natural phytoplankton community of the Subantarctic Beagle Channel. The growth rate was inhibited by UV-B and UV-A radiation during the exponential phase. A marked increase in the TBARS content was observed on day 1 of the experiment, with significant differences between algae subjected to UV-B and UV-A treatments, thus suggesting high damage to the cell membrane. During the second day of the experiment TBARS in UV-A treatments were higher than under photosynthetically active radiation (PAR). The concentration of TBARS decreased to the level of the PAR control on day 3, remaining low until the end of the experiment. Lipid antioxidant concentrations (α-tocopherol and β-carotene) were delayed with respect to variations in TBARS, showing maximum values on day 3 of the experiment. This coincided with the minimum TBARS concentrations in all treatments. The content of both antioxidants increased significantly in cultures exposed to UV-B and UV-A on days 3 and 4. In Antarctic species (phytoflagellate *Asteromonas* sp., AP and diatom *Thalassiosira* sp., AT) α-tocopherol was more abundant than β-carotene. The phytoflagellate species showed a lag in reaching the maximum content of both antioxidants in relation to AT, which reached the maximum concentration within a short time scale (3 h) suggesting a more rapid response to oxidative stress. AT was more resistant to UVR stress than the phytoflagellate species. Overall, our results show that UVR damage/repair balance involves the combined action of several internal factors in the cell.

Keywords: TBARS, β-carotene, α-tocopherol, growth rate, ozone, UV radiation.

RESUMEN: ESTRÉS OXIDATIVO Y DEFENSAS ANTIOXIDANTES GENERADOS POR UV SOLAR EN UN FITOFLAGELADO MARINO SUBANTÁRTICO. – La reducción del ozono estratosférico antártico resulta en un incremento significativo de la radiación ultravioleta B (UV-B, 280-320 nm) en la superficie del océano. El principal objetivo de este trabajo fue un estudio de la respuesta a largo plazo al estrés producido por UV-B y radiación ultravioleta A (UV-A, 320-400 nm) en una especie de fitoflagelados (*Asteromonas* sp.). Dicha especie fue aislada de una comunidad subantártica natural del Canal Beagle y se analizó la tasa de crecimiento en escala diaria afectada por el daño oxidativo a lípidos, expresado como contenido de sustancias reactivas al ácido tiobarbitúrico (TBARS) y contenido de antioxidantes liposolubles. La tasa de crecimiento fue inhibida por la radiación UV-B y UV-A durante la fase exponencial. Se observó un incremento marcado en el contenido de TBARS el primer día del experimento, mostrando diferencias significativas entre algas sujetas a tratamientos de UV-B y UV-A, sugiriendo así un alto daño a la membrana celular. Durante el segundo día del experimento, los TBARS en el tratamiento de UV-A fueron mayores que aquellos en PAR (400-700 nm). La concentración de TBARS decreció al nivel del control PAR en el tercer día, permaneciendo baja hasta el final del experimento. Las concentraciones de antioxidantes lipídicos (α-tocopherol y β-carotene) estuvieron retrasadas con respecto a variaciones en TBARS, presentando valores máximos al tercer día de experimentación. Esto coincidió con las concentraciones mínimas de TBARS en todos los tratamientos. El contenido de ambos antioxidantes aumentó significativamente en cultivos expuestos a UV-B y UV-A durante los días 3 y 4. En especies antárticas (*Asteromonas* sp., AP y *Thalassiosira* sp., AT) α-tocopherol fue más abundante que β-carotene. Los flagelados

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mostraron un retraso en alcanzar el contenido máximo de ambos antioxidantes en relación con AT, las cuales presentaron la concentración máxima dentro de una escala de tiempo corta (3 h), sugiriendo una respuesta más rápida frente al estrés oxidativo. En conjunto, nuestro resultados muestran que el balance daño/reparación por UVR, involucra la acción combinada de varios factores internos en la célula.

Palabras clave: TBARS, β-caroteno, α-tocoferol, tasa de crecimiento, ozono, radiación UV.

INTRODUCTION

During the last few decades, spring-time stratospheric ozone depletion over the Antarctic and the Southern Ocean (Lubin *et al.*, 1989) has resulted in enhanced levels of ultraviolet-B (UV-B, 280-320 nm) radiation reaching the Earth's surface. UV-B can reduce survival, growth and production of phytoplankton (Skerratt *et al.*, 1998; Plante and Arts, 2000; Bischof *et al.*, 2000). Ultraviolet radiation (UV-R, 280-400) has been shown to be very effective in inducing lipid peroxidation of biological membranes (Takeuchi *et al.*, 1995; Hideg and Vass, 1996), polyunsaturated fatty acids (Yamashoji *et al.*, 1979) and phospholipid liposomes (Pelle *et al.*, 1990). Moreover, UV-B can destroy the natural lipid soluble antioxidants and promote the formation of lipid peroxidation products (Salmon *et al.*, 1990; Malanga and Puntarulo, 1995; Estevez *et al.*, 2001). In phytoplankton, there are four main defence mechanisms for avoiding the effects of ultraviolet radiation; namely, avoidance, screening, quenching and repair. The efficacy of each of these mechanisms is a function of the sensitivity of species, time exposure and climatic factors (Davidson, 1998). Several biological effects of UV-B involve endogenous photosensitising and formation of reactive oxygen species (Martin and Burch, 1990). There are a variety of sensitisers within cells which absorb UV-B. Interaction between excited sensitisers and triplet oxygen produces active oxygen intermediates (Ichiki *et al.*, 1994), consisting of singlet oxygen (^{1}O2), superoxide radical (O2$^-$), hydroxyl radical (·OH) and hydrogen peroxide (H_2O_2) (Ichiki *et al.*, 1994). One of the possible mechanisms that could counteract the damage generated by UV-B radiation induced oxidative stress is the synthesis of both enzymatic and non-enzymatic antioxidants (Davidson, 1998; Niyogi, 1999). The non-enzymatic antioxidants are generally small molecules, such as ascorbate and glutathione acting in the aqueous phase, whereas the lipophilic antioxidants (such as α-tocopherol and β-carotene) are active in the membrane environment. Especially α-tocopherol is known for its protective effect (Burton *et al.*, 1982) against lipid peroxidation of biological membranes via peroxyl and alkoxyl radical scavenging. By contrast, the main function of β-carotene is photoreceptive, because it acts as a pigment antenna in the photosynthesis process. Relatively low concentrations of β-carotene protect against oxidative damage initiated by singlet oxygen.

Growth and biomass accumulation will result from complex interactions between harmful direct and indirect effects of UV-R and a series of counteracting repair mechanisms (Lesser *et al.*, 1994). UV-R induced biological damage and the development of defence strategies has been studied in both Antarctic (Karentz *et al.*, 1991; Helbling *et al.*, 1996; Neale *et al.*, 2002) and Subantarctic organisms (Hernando *et al.*, 1998). However, no information is available about UV-induced oxidative stress for the phytoplankton from the Beagle Channel. The basis for this concern is that although the decrease in ozone concentration occurs mainly in the polar vortex above the Antarctic continent, the so-called "ozone hole" is a dynamic system which can be found in the south of the American continent (Orce *et al.*, 1995).

The main aim of this work was to study immediate effects on growth rate and oxidative stress parameters in response to UV-B and UV-A in phytoplankton from Subantarctic waters (phytoflagellate *Asteromonas sp.*) as a function of time and UV-R exposure under culture conditions.

MATERIALS AND METHODS

Culture conditions

The experiments were carried out in the Beagle Channel (CADIC, Ushuaia, 54°52'S, 68°18'W) (Fig. 1). Surface water samples were taken using a five-litre Niskin bottle and maintained in the laboratory at 8°C. Phytoflagellate (*Asteromonas sp.*) single cells were isolated with a micropipe using an inverted microscope, and inoculated into 200 ml flasks with filtered seawater plus F/2 culture medium (Guillard, 1975). Before the experiments, cultures

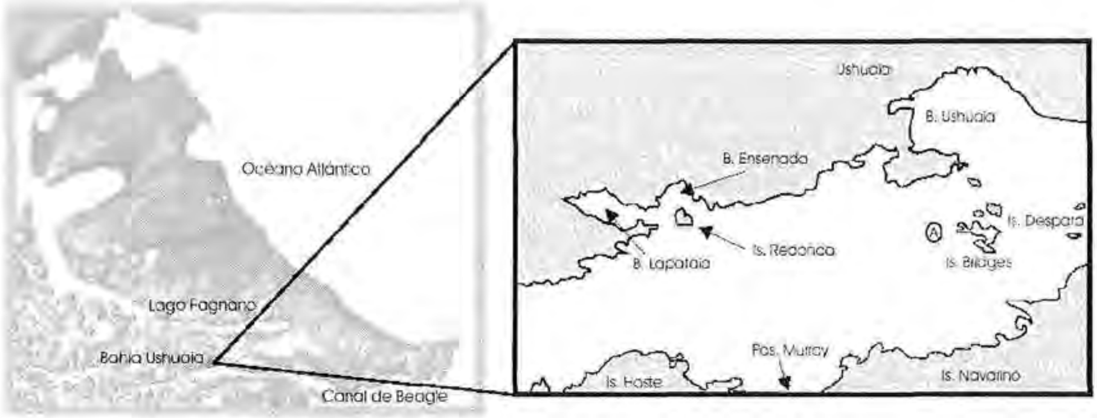

Fig. 1. - Map with sample location (A) in the Beagle Channel, Ushuaia, Argentina.

were grown at an irradiance of 210 uE.m^{-2}.s^{-1} photosynthetically active radiation (PAR), provided by 'cool-white' fluorescent bulbs on 12/12 h at 8°C. Once exponential growth was reached, aliquots of the mono-specific culture were inoculated into a series of 500 ml vessels and then exposed to solar radiation from February 24 to March 2, 1998. For chlorophyll-*a* analyses 20 ml water was filtered through Whatman fibreglass filters (GF/F, 25 mm), followed by the extraction of pigments in absolute methanol (Holm-Hansen and Riemann, 1978). Subsamples for cell counts were kept in dark bottles and fixed with formalin previously neutralised with sodium borate (final concentration 0.4% w/v). All the samples were counted with an inverted microscope using a Sedgwick-Rafter counting slide according to Villafañe and Reid (1995).

Experimental design

Cells were exposed in parallel to three irradiance treatments: PAR (control, 400-700 nm), UV-A (PAR + Ultraviolet-A radiation, 320-400 NM) and UV-B (PAR + UV-A + UV-B, 280-320). Cylindrical UV-transparent quartz flasks were used for exposure of phytoplankton. For the UV-A treatment, the bottles were covered with Mylar foil (DuPont country, which has 50% transmission at 323 nm) and PAR controls were performed with cylindrical Plexiglass flasks (UF3) (Röhm and Haas country) which cut off UV radiation (Hernando and San Román, 1999). Three replicate samples were used for each of the treatments and controls. Culture medium was added to the different treatments at the time 0 (to) of the experiments. The algae were exposed to natural sunlight in an outside tank, through which thermostated sea water could be pumped in order to maintain the temperature approximately constant (around 10°C). 80 ml samples were taken daily at 9 a.m. to determine the chlorophyll concentration, the cell number, the content of thiobarbituric acid reactive substances, the index of lipid peroxidation (TBARS) and the α-tocopherol and β-carotene content.

Irradiance measurements

Incident solar radiation was monitored continuously during the experiment using a spectroradiometer (model GUV 510, Biospherical Instruments, Inc.), which records irradiances at four wavelengths in the ultraviolet region (305, 320, 340 and 380 nm), and Photosynthetic Available Radiation (PAR, 400-700 nm). Data were recorded at a frequency of one per minute at a site close to the experimental setup. The equation from Orce *et al.* (1997) was used in order to calculate UV-B and UV-A doses in kJ.m^{-2}.

Growth measurements

Cell instantaneous growth rate was determined according to the following equation:

$$\mu = \ln (N_t/N_{n-1})$$

where μ is a specific rate constant (d-1), t_t is the time of measurement, and t_{n-1} is the time of the previous one, N_t is the cell concentration at time t_t, and N_{n-1} is the cell concentration at time t_{n-1}.

Lipid peroxidation

Fifteen ml cell suspensions were centrifuged for 10 min. at 12000 *g*. The pellet was suspended in 2 ml of 120 mM KCl in 50 mM potassium phosphate buffer (pH 7.0), sonicated and centrifuged for 10 min. at 600 *g*. A 0.8 ml volume aliquot of the supernatant was treated with 0.7 ml 30% (w/v) TCA and 50 mM potassium phosphate buffer (pH 7.0) and brought to a final volume of 2 ml before centrifugation. 0.2 ml of 3% (w/v) SDS and 0.05 ml of 4% (w/v) butylated hydroxytoluene (BHT) in ethanol were added to 1 ml of the supernatant. After mixing, 2 ml of 0.1 N HCl, 0.3 ml of 10% (w/v) phosphotungstic acid and 1 ml of 0.7% (w/v) 2-thiobarbituric acid were added. The mixture was heated at 95°C in a water bath for 45 min. and 5 ml of n-butanol was added, whereafter the samples were vortexed and centrifuged at 600 *g* for 10 min. The fluorescence of the organic layer (upper layer) was measured at 515 nm excitation and 555 nm emission. The values were expressed as nmol TBARS (malondialdehyde equivalents) per 10^4 cells. Malondialdehyde standards were prepared from 1,1,3,3-tetramethoxypropane (Fraga *et al.*, 1987).

Lipid soluble antioxidants

The content of α-tocopherol and β-carotene in the cell homogenates was quantified by filtering a 5 ml sample by reverse-phase HPLC with electrochemical detection using a Bioanalytical Systems LC-4C amperometric detector with a glassy carbon working electrode at an applied oxidation potential of 0.6 V (Desai, 1984). Extraction from the samples was performed with 1 ml of methanol and 4 ml of hexane. After centrifugation at 600 *g* for 10 min., the hexane phase was removed and evaporated to dryness under N_2. Extracts were dissolved in methanol:ethanol (1:1 v/v) and injected for HPLC analysis, HPLC conditions were:

isocratic reversed phase, column: Supelcosil LC-8; 3.3 cm x 4.6 mm x 3 μm.

mobile phase: 20 mM lithium perclorate in methanol/water 99/1 (v/v).

flow rate: 0.8 ml/min.

retention time: α-Tocopherol = 0.8 min and β-carotene = 1.6 min.

d, l-α-tocopherol from synthetic phytol (Sigma) and β-carotene were used as standards.

Statistical analyses

Parametric analysis of variance repeated measures were applied to test the significance of the differences observed between treatments. Data were checked prior to the analyses in order to verify the homoscedacity and normality requirements of the ANOVA. When such requirements were not satisfied, a standard transformation of data was applied (ln x on TBARS and 1/squar root x on α-tocopherol and β-carotene data). Days of exposure and treatments were used as factors. When the interaction was significant, the differences in treatment for each day were analysed.

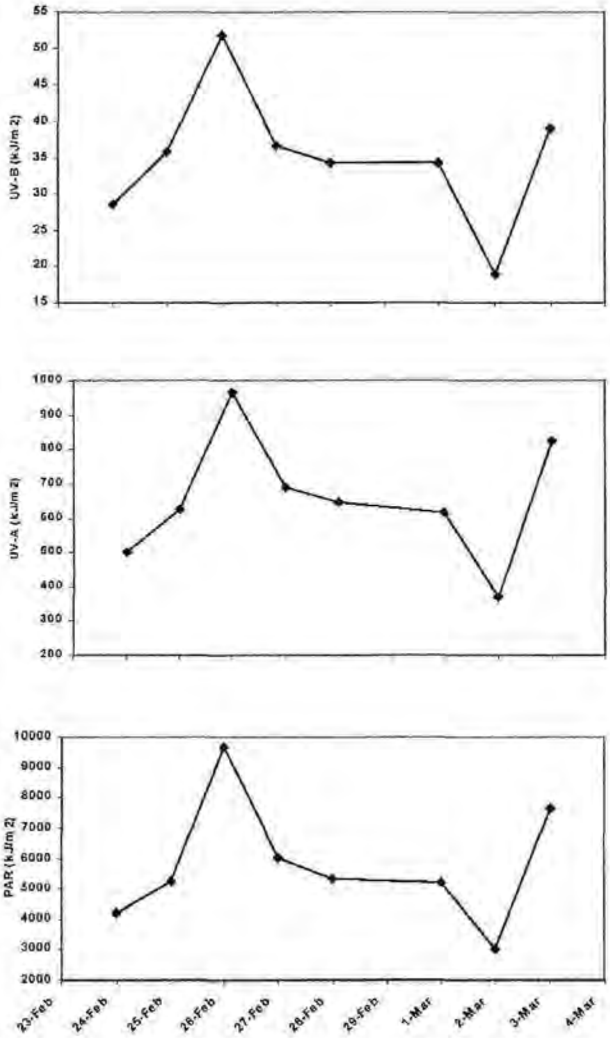

Fig. 2. - Variations in UVR doses at the Beagle Channel from February 24 to 28, 1998. (A) UVB doses (280-320 nm), in kJ/m²; (B) UVA doses (320-400 nm), in kJ/m²; (C) PAR (400-700 nm), in kJ/m². Each point represents the integrated value doses for each experimental day.

In all cases the exponential phase of the growth rate of PAR treatment was taken as control.

RESULTS

The data in Figure 2 show the variation of surface daily doses of UV-B, UV-A and PAR through-

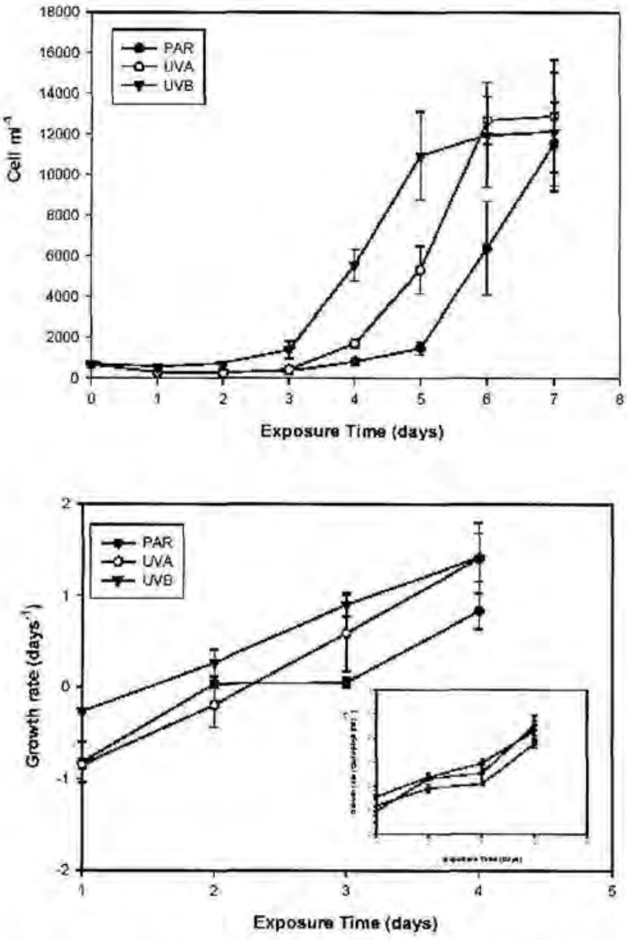

Fig. 3. – A, cell density during the complete experiment. B, exponential instantaneous growth rate of phytoflagellate · ml^{-1} using cell number when exposed to natural solar radiation for 4 days. Insert: instantaneous growth rate using chlorophyll-*a*. UV-B represents those algae exposed to UVB+UVA+PAR, UV-A those exposed to UVA+PAR, and PAR those exposed to PAR. Each point represents the mean +/- SD.

out the study period (Orce *et al.*, 1997). During the period of exponential growth rate, the average daily doses from 24 to 28 February 1998 were 37 kJ/m^2 for UV-B, 685 kJ/m^2 for UV-A and 6092 kJ/m^2 for PAR. At that time ozone concentration was often higher than 295 D.U., and the average was 285 D.U. The variability noted in the data was primarily due to changes in the degree of cloud cover, with a maximal dose recorded on day three of the experiment (February 26) (Fig. 2).

Figure 3a shows the temporal evolution of cell density during the experiment. The triggering of exponential growth was treatment-dependent, starting on days 3, 4 and 5 for PAR, UV-A and UV-B treatments respectively. Once exponential growth was reached, growth rate was identical for the three treatments. In order to understand in more detail cell changes in the different treatments before the period of exponential growth, instantaneous growth rates were calculated for the first 4 days of the experiment. Instantaneous growth rate was significantly inhibited in the UV-A and UV-B treatments respectively, in comparison with the PAR treatment (Table 1 A). Considering the days factor (Table 1 A), there was a significant increase between each day of exponential instantaneous growth rate. The growth rate evaluated using chlorophyll-*a* content showed the same profile (Fig. 3b inset). During the exponential growth phase, TBARS concentrations in algae exposed only to PAR did not show any significant difference between days ($P > 0.05$, Fig. 4). In contrast, UV-A and UV-B treatment showed a significant increase (Table 1 B, $P < 0.01$) on day one without showing differences between days ($P > 0.05$). On the following days TBARS concentrations decreased significantly, showing significant differences from the PAR treatment on day 2 in the UV-B ($P < 0.001$) and UV-A treatment ($P < 0.01$, Table 1B and Fig. 4). On day three and four no differences were found between any treatments (Table 1 B and Figure 4). The maximum TBARS content in both UV-R treatments was lagged by one day, with the higher values on days 1 and 2 for the UV-B and UV-A treatments respectively.

No significant differences were observed between days in the content of lipid soluble antioxidant (α-tocopherol and β-carotene) on phytoflagellates exposed to PAR ($P > 0.05$, Fig. 5a, b).

Except on day 1 for α-tocopherol in the UV-B treatment, no significant differences in the content of lipid soluble antioxidants were observed during the first two days of the experiment in algae exposed to UV-B and UV-A treatments, as compared to the PAR control ($P > 0.05$, Fig. 5 a, b).

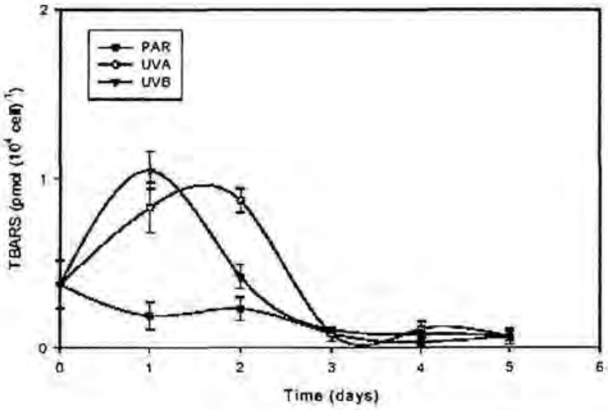

Fig. 4. - Effect of UV radiation on lipid peroxidation (TBARS content) in phytoflagellates as a function of exposure time. Each point represents the mean +/- SD.

TABLE 1. – Results of parametric analysis of variance repeated measures showing the significance of UV effects on the exponential instantaneous growth rate of a Subantarctic phytoflagellate (*Asteromonas sp.*). Note: The factors are Day (1, 2, 3 and 4) and Treatment (UV-B, UV-A and PAR), and the variable was μ (instantaneous growth rate). The same letter means no significant differences. For each factor, the differences were significant at $P < 0.01$ (*) or $P < 0.001$ (**) (Tuckey test).

A Factor	Growth rate F	Sign. Level	B Factor	TBARS F	Sign. Level
Day	68.02	< 0.0001	Day	23.44	< 0.01
Treatment	408.02	< 0.001	Treatment	65.97	< 0.001
Interaction	2.36	0.08	Interaction 3.97	<	0.01
Treatment	Means	Homog. Group	Day 1	Means	Homog. Group
UVB	0.02 a	(**)	UVB 0.043	a	
UVA	0.24 b	(**)	UVA -0.2	a	
PAR	0.53	c (**)	PAR	-1.72	b (**)
			Day 2		
Day			UVB -0.88	a	
1	-0.65	a (**)	UVA	-0.15	b (**)
2	0.018	b (**)	PAR	-1.49	c (*)
3	0.51	c (**)	Day 3		
4	1.17 d (**)		UVB -2.2	a	
			UVA -2.6	a	
			PAR -2.41	a	
			Day 4		
			UVB -2.72	a	
			UVA -2.26	a	
			PAR -3.44	a	
C Factor	α-tocopherol F	Sign. Level	**D** Factor	β-carotene F	Sign. Level
Day	32.02	< 0.01	Day	63.88	< 0.001
Treatment	166.19	< 0.01	Treatment 48.93	<	0.001
Interaction	112.58	< 0.01	Interaction	4.97	< 0.01
Day 1	Means	Homog. Group	Day 1	Means	Homog. Group
UVB	0.58	a	UVB 0.24	a	
UVA	0.17 b	(**)	UVA 0.26	a	
PAR	0.13 bc	(**)	PAR 0.32	a	
Day 2			Day 2		
UVB	0.16	a	UVB 0.22	a	
UVA	0.18	a	UVA 0.19	a	
PAR	0.13	a	PAR 0.22	a	
Day 3			Day 3		
UVB	0.049 a	(**)	UVB 0.04	a	
UVA	0.084 b	(**)	UVA 0.03	a	
PAR	0.099	c (**)	PAR	0.16	b (**)
Day 4			Day 4		
UVB	0.08	a	UVB 0.05	a	
UVA	0.11	a	UVA 0.12	a	
PAR	0.15	b (*)	PAR	0.26	b (**)

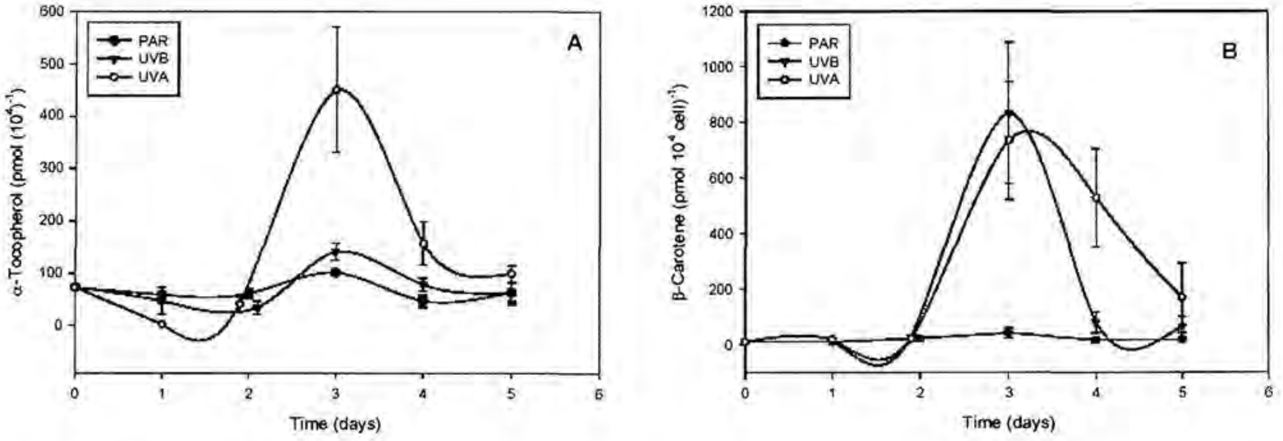

Fig. 5. - Effect of UV radiation on antioxidant lipid soluble in phytoflagellates as a function of exposure time. A, α-tocopherol content; B, β-carotene content. Each point represents the mean +/- SD.

The α-tocopherol content showed a significant decrease on the first day of the exposure for algae exposed to the UV-B treatment ($P < 0.01$, Table 1C), then increased sharply and reached maximum values of around 450 pmol 10^4 cell^{-1} on day three. Significant differences ($P < 0.01$) were found on that day with PAR. Afterwards, the content of α-tocopherol decreased again toward the end of the measurements, showing values that were not different from those observed for the PAR and UV-A treatments ($P> 0.05$). The same profile was observed for the α-tocopherol content in the UV-A treatment, but in this case the concentrations were lower than in the previous one (maximum concentration around 150 pmol 10^4 cell^{-1} on day three) (Fig. 5 a).

Like that of a-tocopherol, the b-carotene content increased steeply on day three of the experiment in the UV-B and UV-A treatments (around 800 pmol. 10^4 cell^{-1}) (Fig. 5b). Contrasting with the previous results (Fig. 5a), no significant differences were observed between the UV-A and UV-B treatments. A marked decrease was observed afterwards, being smoother in the UV-B than in the UV-A treatment. No significant differences were observed on day five between the three treatments ($P> 0.05$, Fig. 5b).

DISCUSSION

UV-B exposure has been demonstrated to stimulate the generation of ROS. The effects of UV-B on cell membranes are probably related to oxidation by free radicals (Predieri *et al.*, 1995). Therefore, the increase in the TBARS content is more precisely an indicator of a general UV-B-induced oxidative damage.

Significant differences in the TBARS content were observed in algae subjected to UV-B and UV-A at the beginning of the experiment, indicating that UV-B and UV-A radiation induced oxidative stress under our experimental conditions. This was accompanied by an inhibition of growth rate by UV-B and UV-A radiation during the exponential phase. In addition, chlorophyll levels decreased in both treatments (Fig. 3b inset), thus suggesting a reduction of photosynthetic capacity (Malanga *et al*, 1997). This is consistent with the idea that, under UV-B stress conditions, microalgae sacrifice their photosynthetic capacity of the chloroplast in order to protect the rest of the cell (Strid, 1993; Mackerness *et al.*, 1998). This led us to evaluate lipid soluble antioxidants, as the susceptibility to oxidative damage related to the balance between antioxidants and pro-oxidants. The decrease in TBARS levels in the UV-B and UV-A treatments on day three coincided with an increase in α-tocopherol and of β-carotene content. The subsequent decrease in tocopherol content suggests an active generation of active oxidant species during exposure of growing cultures, leading to the consumption of antioxidants. The connection between oxidative damage and antioxidant defence mechanisms has been postulated in both animal and plant cells (Kingston-Smith and Foyer, 2000).

β-carotene concentrations in the PAR controls were lower than those of α-tocopherol. β-carotene can directly quench singlet oxygen or can prevent the formation of a chlorophyll triplet excited state (Young *et al.*, 1997). Lipophilic molecules such as α-tocopherol are able to deactivate $^1O_2$, reduce O_2 and terminate lipid radical chain reactions (Polle and Rennenberg, 1994), and are regenerated by ascorbate. The β-carotene content increased significantly (Fig. 5b) in cultures exposed to UV-B and (contrasting with α-tocopherol results) UV-A on day three of incubation. These results could be explained by considering that in the UV-A treatment there was a significant increase in the TBARS content on day one and two of incubation. There was a significant decrease in β-carotene on day four and five in the UV-A treatment. Such results could indicate consumption or a decreased synthesis, suggesting a significant role of this antioxidant in protection against the damage produced by UV-A radiation. This could explain the tendency to decrease the inhibition in the UV-A treatment for the growth rate on days three and four (35% and 1% compared with the PAR treatment respectively; Fig. 3).

Jagtap and Bhargava (1995) postulated that the ability of plants to manipulate the antioxidant metabolism under stress conditions appears to be critical to stress tolerance. However, despite the fact that in the UV-A treatment the inhibition has a tendency to be lowest at the end of the exponential growth, in the UV-B treatment the inhibition remains high (95% and 42% for days three and four respectively, Fig. 3). Clearly, the damage (TBARS) was low on days 4 and 5, so protection was present somehow, but perhaps in the form of lipid antioxidants. Perhaps by that time the cells had found other ways to screen harmful UV.

These results could be explained considering that other stress conditions, such as DNA damage, could be involved in algae exposed to UV-B radiation (Karentz *et al.*, 1991). Our data clearly show that under our experimental design, TBARS production was independent of the doses received by the cultures (R^2=0.27, n=9) but dependent on the quality of the radiation. Maximum concentrations of cells were observed on day one and two of the experiment for the UV-B and UV-A treatments respectively, while the maximum doses were measured one day later (Fig. 2). Experimental observations in the Antarctic (Hernando, unpublished data) show that the same non-enzymatic antioxidants considered during this study are produced at lower concentrations. The maximum concentrations of α-tocopherol measured were around 150 and 30 pmol 10-4 cell-1 for a phytoflagellate and a diatom (*Thalassiosira sp.*) isolated from Antarctic coastal waters respectively. This is approximately 30% and 7% of the concentrations determined in the Beagle Channel. In addition, the Antarctic phytoflagellate and the diatom produced only 10% and 1.5% of β-carotene, as compared with the algae from Beagle Channel. This demonstrates more pronounced responses to UVR in the phytoflagellate from the Subantarctic environment. On the other hand, other defence mechanisms probably help the cells to cope with UVR damage, such as the synthesis of MAAs, which probably plays a significant role in photoprotection of Antarctic phytoplankton (Hernando *et al.*, 2002). Other mechanisms to be considered in further studies are carotenoids, the chlorophyll/carotenoid ratio and antioxidant enzymes, which will all confer an adaptive capacity.

A significant result emerging from this experiment is that UVR-induced oxidative stress, expressed here as membrane damage, affected the starting time of exponential growth, but not final biomass accumulation or growth during the exponential phase. This suggests that cells were able to cope with UV damage, and that the only significant effect was the delay in the timing of exponential growth. The consequences of these changes need to be considered in the framework of the natural environment, in order to understand the effects of UV-R on the timing and dynamics of phytoplankton blooms.

Overall, our results support the idea that UVR damage/repair balance involves the combined action of several internal factors in the cell. Taken as a whole, the data presented here strongly suggest that exposure to mild oxidative stress initiates a series of adaptive responses that provide increased protection against more severe stress.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Oxidative stress in gills of limpets from the Beagle Channel: comparison with limpets from the Antarctic*

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SUMMARY: The aim of this work was to study the oxidative profile of gills of two limpet species (*Nacella (Patinigera) magellanica* and *Nacella (Patinigera) deaurata*) (Gmelin, 1971) exposed to different environmental conditions. Due to the tidal characteristics of the Beagle Channel, *N. magellanica* are exposed to air twice daily for 3 to 5 hours each time, whereas *N. deaurata* are exposed to air for 3 hours only during spring tides. The different regime of exposure includes extreme temperatures under 0ºC during winter and more than 20°C in summer for *N. magellanica*, whereas *N. deaurata* are usually covered by more than 0.3 m of water at 4°C in winter and 11°C in summer. No significant differences were found between the two molluscs regarding the oxygen uptake, the content of α-tocopherol and β-carotene and the activities of the antioxidant enzymes catalase and superoxide dismutase. Lipid peroxidation in gills was estimated as the content of lipid radicals, assessed by electron paramagnetic resonance (EPR). Lipid radical content and total iron content were respectively 80.6 and 62% lower in *N. magellanica* than in *N. deaurata*. A typical EPR spectrum of ascorbyl radical in gills from both limpets was observed. Both the ascorbyl radical content and the ascorbyl radical content/ascorbate content ratio were significantly lower in *N. magellanica* than in *N. deaurata*. In the Antarctic *Nacella concinna* inhabits all levels of the littoral zone. Limpets at the highest level in the intertidal showed significantly increased activities of both catalase and superoxide dismutase as compared to their intertidal and subtidal relatives. Thus, it seems that Antarctic high intertidal conditions, involving regular exposure to air and presumably also thermal stress on sunny days during the Antarctic summer, cause a necessity for *N. concinna* to ward off higher oxygen radical species production by increasing its antioxidant defence. Taken as a whole, the data presented here indicate that coping with environmentally demanding conditions requires a complex adjustment of the physiological metabolic pathways to ensure survival by minimising intracellular damage.

Keywords: Antarctic region, antioxidant enzymes, ascorbyl radical, ascorbate, Subantarctic region

RESUMEN: ESTRÉS OXIDATIVO EN BRANQUIAS DE LAPAS DEL CANAL DEL BEAGLE: COMPARACIÓN CON LAPAS DE LA REGIÓN ANTÁRTICA.El objetivo del presente trabajo fue estudiar el perfil oxidativo en branquias de dos especies de lapas (*Nacella (Patinigera) magellanica* and *Nacella (Patinigera) deaurata*) (Gmelin, 1971) expuestas a diferentes condiciones ambientales. Debido a las características de las mareas en el Canal del Beagle, las lapas *N. magellanica* están expuestas diariamente al aire dos veces durante 3 a 5 h cada vez, pero las lapas *N. deaurata* están expuestas al aire durante 3 h, solamente en las mareas de primavera. El diferente régimen de exposición incluye temperaturas extremas debajo de 0°C durante el invierno y más de 20°C en verano para *N. magellanica*, mientras que las lapas *N. deaurata* están habitualmente cubiertas por más de 0.3 m de agua que alcanza una temperatura de 4°C en invierno y 11°C en verano. No se observaron cambios significativos en ambos moluscos con respecto al consumo de oxígeno, el contenido de α-tocoferol, β-caroteno y la actividad de las enzimas antioxidantes catalasa y superóxido dismutasa. La peroxidación lipídica fue estimada como el contenido de radicales lipídicos, determinados por resonancia paramagnética electrónica (EPR). El contenido de radicales lipídicos y de hierro total fue de 80,6 y 62% menor en *N. magellanica* en comparación con *N. deaurata*. Se observó un típico espectro de EPR del rad-

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ical ascorbilo en branquias de ambas lapas. Tanto el contenido de radical ascorbilo como el cociente contenido de radical ascorbilo/contenido de ascorbato fue significativamente menor en *N. magellanica* en comparación con *N. deaurata*. Estudios realizados en *Nacella concinna* (Antártida) indican que esta especie cuenta con mayor actividad de catalasa y superóxido dismutasa que sus congéneres de la región subantártica. Por lo tanto, condiciones de baja marea en la región antártica, con una exposición continua al aire y probablemente estrés térmico en días soleados durante el verano, podrían ser responsables de la necesidad de *N. concinna* de contar con una mayor protección antioxidante. Tomados en su conjunto, los datos presentados aquí indican que soportar condiciones ambientales demandantes requiere un complejo ajuste de las vías metabólicas fisiológicas para asegurar la supervivencia minimizando el daño intracelular.

Palabras clave: enzimas antioxidantes, radicales ascorbilos, ascorbato, región subantártica, región antártica.

INTRODUCTION

Since the discovery of the importance of radical reactions in normal biological processes, there has been an explosion of research into pro-oxidant and antioxidant processes, principally in mammalian systems (Halliwell and Gutteridge, 1984). The normal fate of most of the molecular oxygen consumed by animals is tetravalent reduction to water coupled with the oxidation of food and the production of energy. Partial reduction results in the formation of 'reactive oxygen species' (ROS), including superoxide anion radical (O_2^-), hydroxyl radical (${}^{\bullet}OH$), peroxyl radical ($ROO^{\bullet}$), alkoxyl radical ($RO^{\bullet}$), hydrogen peroxide (H_2O_2), singlet oxygen (${}^1O_2$) and peroxynitrite ($ONOO^-$). It has been estimated that about 1–3% of O_2 consumed in animal systems is converted to ROS (Halliwell and Gutteridge, 1984). Moreover, iron can catalyze the conversion of H_2O_2 into ${}^{\bullet}OH$, via Fenton or Haber-Weiss reactions. Of more recent interest has been ROS production and resulting oxidative damage as a mechanism of toxicity in aquatic organisms (Di Giulio *et al.*, 1989; Livingstone *et al.*, 1990; Livingstone, 1991; Winston and Di Giulio, 1991). Relatively little information is available on the mechanistic aspects of redox cycling in aquatic organisms, but measurements of oxygen consumption and ROS have demonstrated the production of O_2^-, the dismutation of O_2^- to H_2O_2, and the involvement of O_2^- and/or H_2O_2 in the production of ${}^{\bullet}OH$ (Di Giulio *et al.*, 1989; Livingstone, 1991; Estevez *et al.*, 2002). ROS produced in biological systems are detoxified by antioxidant defences, which are ubiquitous in aerobic species and vary in different tissue types. They are widely found in aquatic organisms and their presence, properties and other characteristics have been extensively reviewed (Di Giulio *et al.*, 1989; Livingstone, 1991; Viarengo *et al.*, 1998).

Limpets are very common archaeogastropod molluscs that inhabit intertidal rocky shores. *Nacella (Patinigera) magellanica* (Gmelin 1971) and *Nacella (Patinigera) deaurata* (Gmelin 1971) are the two most conspicuous limpet species in the Beagle Channel due to their abundance and their relatively large sizes. *Nacella magellanica* inhabits the middle and the upper intertidal zones, whereas *N. deaurata* lives in the lower intertidal and the subtidal zone (Morriconi and Calvo, 1993; Morriconi, 1999). Though they live in the same area, the difference in shore level location affects the animal's exposure to aerial or marine environmental conditions. Due to the tidal characteristics of the Beagle Channel, *N. magellanica* are exposed to air twice daily for 3 to 5 hours each time, and *N. deaurata* are exposed to air daily for 3 hours only during spring tides (Morriconi and Calvo, 1993; Morriconi, 1999). The different regime of exposure includes extreme temperatures below 0ºC in winter and above 20 ºC in summer for *N. magellanica*, whereas *N. deaurata* are usually covered by more than 0.3 m of water at 4ºC in winter and 11ºC in summer. Peculiarities of membrane lipids in marine organisms, particularly high contents of unsaturated fatty acids (Joseph, 1982), suggest a special susceptibility to lipid peroxidation. These organisms also showed a specific response of their antioxidant system that reflects their adaptation to the highly variable environment (Abele-Oeschger and Oeschger, 1995; Abele *et al.*, 1998 a, 1998b, 2002).

In molluscs, oxygen is mainly taken up through the gills, and gill tissue could be the main target for oxidative injury. Lipid radical content was assayed by EPR and antioxidant capacity was studied by assaying the activities of superoxide dismutase (SOD) and catalase. The content of non-enzymatic antioxidants (α-tocopherol, β-carotene, and ascorbate) and the ratio of ascorbyl radical/ascorbate content was studied in both animals. The aim of this work was to characterise the oxidative status of gills of two limpet species naturally exposed to different environmental conditions on an intertidal rocky shore in the Subantarctic Beagle Channel.

MATERIALS AND METHODS

Collection of animals

In July 2002, the limpets *N. magellanica* and *N. deaurata* were collected in the intertidal of Punta Occidental (54°50´S, 68°20´W) in the Beagle Channel, at the southern tip of South America. *N. deaurata* limpets were sampled at 0.3-0.5 m water depth in shallow subtidal areas. The animals had a mean shell length of 51 ± 1 and 51 ± 2 mm corresponding to a body fresh weight (free of shell) of 16 ± 1 and 12 ± 1 g for *N. magellanica* and *N. deaurata* respectively. No differentiation was made with respect to either sex or reproductive stage. Immediately after the collection of the animals, the gills were dissected and frozen at -40ºC for later analysis. A total of 6 samples were used for each independent assay, with 2 replicates in each experiment.

Intertidal and subtidal specimens of the limpet *Nacella concinna* were sampled at King George Island, Antarctica. Intertidal specimens were collected from a rocky shore area near Jubany Base (62°14´S, 58°38´W), which at low ebb tides is air-exposed for between 2 and 4 hours. Here, N. *concinna* colonises shallow intertidal pools, which have a maximum depth of 0.25 m and remain water-covered throughout the whole ebb tide. The intertidal limpets were air-exposed in moist rocky niches for several hours during low tides. Shell length varied from 25 to 40 mm. Live animals were kept for 2 days at most in aquaria at the Dallmann Laboratory, Jubany Base, with seawater from the cove. Enzyme activities were measured directly after sacrificing the animals, because liquid nitrogen was not available for freeze clamping and storing samples at the base.

Oxygen consumption measurements

The oxygen uptake under laboratory conditions (temperature 4ºC and salinity 3.12 PSU) was determined in the whole animal according to Peck and Veal (2001) using an Rank Brothers oxymeter (High Street, Bottisham, Cambridge CB5 9DA, England).

Ascorbyl radical content ($A^\bullet$)

The metabolism of ascorbate (AH^-) is an issue of particular importance since during its antioxidant action, AH^- undergoes two consecutive one-electron oxidations to dehydroascorbic acid (DHA) with intermediate formation of the ascorbyl radical (Hubel *et al.*, 1997). $A^\bullet$ has a relatively long lifetime compared to other free radicals and is easily detectable by EPR even at room temperature in aqueous solution (Buettner and Jurkiewicz, 1993). In contrast to $A^\bullet$, AH^- and DHA are EPR silent (Hubel *et al.*, 1997). Thus, there is an increasing interest in the use of $A^\bullet$ content in biological tissues as an informative, non-invasive and natural indicator of oxidative stress (Roginsky and Stegmann, 1994), and as an indicator of the phagocytic immune response (Halliwell and Gutteridge, 1984).

A Bruker ECS 106 spectrometer was used for $A^\bullet$ measurements. The homogenates were prepared in dimethylsulfoxide (DMSO) and the spectra were scanned under the following conditions: field modulation 50 kHz, room temperature, microwave power 20 mW, modulation amplitude 1 G, time constant 655 ms, receiver gain 1×10^5, microwave frequency 9.81 GHz, and scan rate 0.18 G/s (Giulivi and Cadenas, 1993). Quantification was performed according to Kotake *et al.* (1996).

Ascorbate content (AH^-)

Ascorbate content was measured according to Foyer *et al.* (1983). The acid extracts were neutralised with 1.25 M K_2CO_3 and the amounts of ascorbate were determined by addition of 5 U/ml ascorbate oxidase. Ascorbate was used as standard.

Content of lipid radical by electron paramagnetic resonance (EPR) spin trapping

The homogenates were prepared in 50 mM α-(4-pyridyl 1-oxide)-N-t-butyl nitrone (POBN). EPR spectra were obtained at room temperature using an ECS 106 Bruker spectrometer operating at 9.81 GHz with a 50 kHz modulation frequency. EPR instrument settings for the spin trapping experiments were: microwave power 20 mW, modulation amplitude 1,194 G, time constant 81.92 ms, and receiver gain 2×10^4 (Jurkiewicz and Buettner, 1994). Quantification was performed according to Kotake *et al.* (1996).

Content of thiobarbituric acid reactive substances (TBARS)

The content of thiobarbituric acid reactive substances (TBARS) was measured according to Uchiyama and Mihara (1978) as an index of lipid peroxidation.

Iron content

Isolated gills were digested with an HNO_3 solution. After heating to dryness, the digests were dissolved in 2 ml 5% (v/v) HCl (Lawrie *et al.*, 1991). Concentrations of iron in the extracts were measured spectrophotometrically after reduction with thioglycolic acid followed by the addition of bathophenanthroline (Brumby and Massey, 1967).

Enzyme assays

Total SOD activity (EC 1.15.1.1) was determined according to Misra and Fridovich (1972). Catalase activity (EC 1.11.1.6) was assayed spectrophotometrically by the decomposition of H_2O_2 at 240 nm in a reaction mixture consisting of 50 mM potassium phosphate buffer (pH 7.0) containing 1% Triton-X100, 1:9 (w/v) and 12.5 mM H_2O_2 (Aebi, 1984). Protein measurements were performed according to Lowry *et al.* (1951).

Content of lipid soluble antioxidants

The content of α-tocopherol and β-carotene in the gill homogenates supplemented with 100mM SDS was quantified by reverse-phase HPLC with electrochemical detection using a Bioanalytical Systems LC-4C amperometric detector with a glassy carbon working electrode at an applied oxidation potential of 0.6 V (Desai, 1984). Samples were extracted with methanol:hexane (1:4). After centrifugation at 600 *g* for 10 min, the hexane phase was removed and evaporated to dryness under N_2. Extracts were dissolved in methanol/ethanol (1:1) and injected for isocratic HPLC analysis (Desai, 1984). D,L-α-Tocopherol (Sigma) and β-carotene were used as standards.

Statistical analyses

Data are expressed as means ± SEM of 6 independent samples, with 2 replicates in each experiment. Statistical tests were carried out using Statview for Windows, ANOVA, SAS Institute Inc. version 5.0.

RESULTS

Tidal level, and thus air exposure, differ substantially for *N. deaurata* and *N. magellanica*. However, gills isolated from *N. deaurata* and *N. magellanica* showed no statistically significant difference with respect to the oxygen uptake or activity of the antioxidant enzymes catalase and superoxide dismutase (Table 1). Moreover, no significant differences were determined between the gills of the two molluscs regarding the content of α-tocopherol and β-carotene (Table 1).

TABLE 1. – Oxygen uptake and antioxidant capacity in *N. deaurata* and *N. magellanica*. Data are expressed as means SEM of 6 independent samples.

	N. deaurata	*N. magellanica*
Oxygen uptake (10^{-2}) (μmol/h/g FW)	8 ± 1	10 ± 2
Catalase (U/mg prot)	4 ± 1	3 ± 1
SOD (U/mg prot)	3 ± 1	4 ± 1
α-Tocopherol (10^{-1}) (nmol/mg prot)	7 ± 2	6 ± 1
β-carotene (10^{-1}) (nmol/mg prot)	14 ± 4	9 ± 2

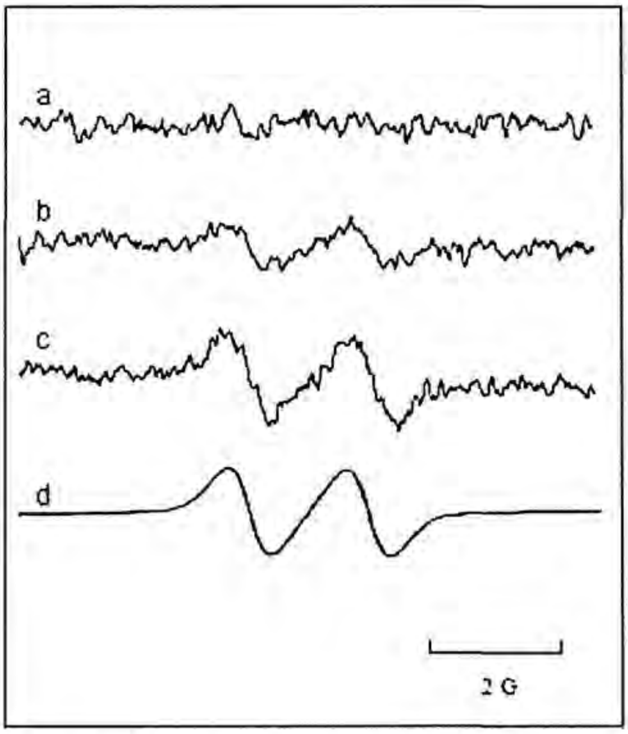

FIG. 1. – EPR detection of ascorbyl radicals. (a) EPR spectra of DMSO, (b) Typical EPR spectra of *Nacella magellanica* gills, (c) Typical EPR spectra of *Nacella deaurata* gills, and (d) computer simulated-spectra.

A typical EPR spectrum of ascorbyl radical ($A^•$) was recorded in gills from both limpets. The EPR spectrum showed the characteristic two lines at $g = 2.005$ and $a_H = 1.8$ G (Fig. 1 b, c), in accordance with computer spectral simulated signals obtained using the parameters given in the Material and Methods section (Fig. 1 d). DMSO was examined and no DMSO spin adduct was observed (Fig. 1 a). $A^•$ con-

TABLE 2. – Ascorbyl radical content/ascorbate content ratio in *N. deaurata* and *N. magellanica*. Data are expressed as means SEM of 6 independent samples.

	N. deaurata	*N. magellanica*
$A^\bullet$ (10^{-1}) (pmol/mg FW)	60 ± 20	36 ± 2*
Ascorbate (nmol/mg FW)	14 ± 2	17 ± 2
$A^\bullet$/AH (10^{-5})	49 ± 6	25 ± 7*

* significantly different at $P < 0.05$.

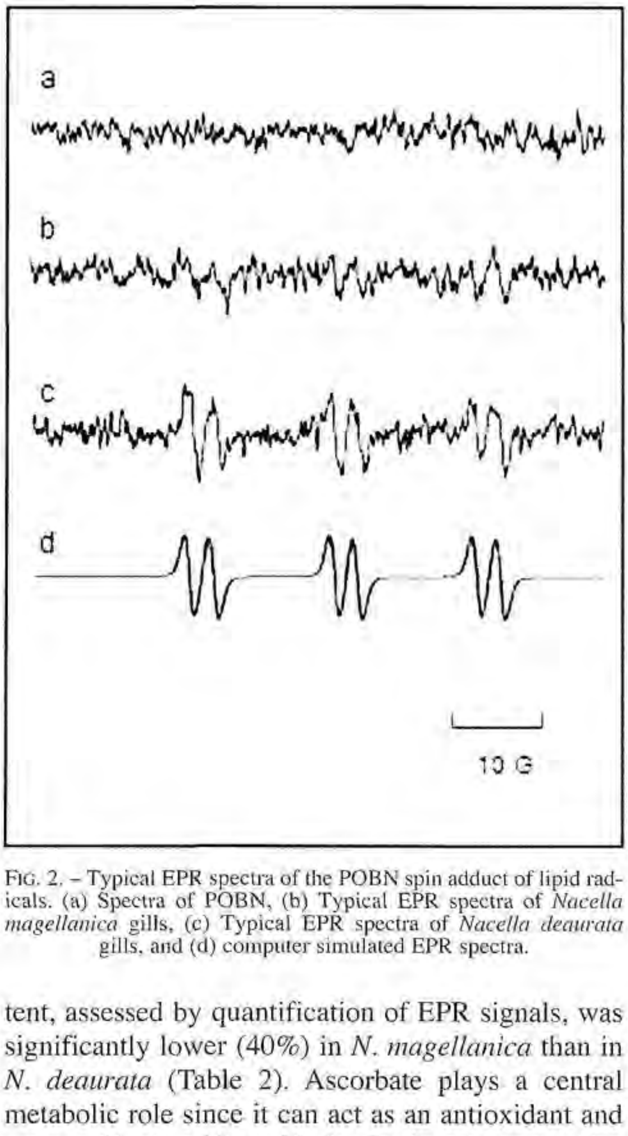

FIG. 2. – Typical EPR spectra of the POBN spin adduct of lipid radicals. (a) Spectra of POBN, (b) Typical EPR spectra of *Nacella magellanica* gills, (c) Typical EPR spectra of *Nacella deaurata* gills, and (d) computer simulated EPR spectra.

TABLE 3. – Lipid peroxidation, and iron content in gills from *N. deaurata* and *N. magellanica*. Data are expressed as means SEM of 6 independent samples.

	N. deaurata	*N. magellanica*
Lipid radicals (pmol/mg FW)	412 ± 98	80 ± 36*
Iron content (pmol/mg FW)	4453 ± 154	1930 ± 414*

* significantly different at $P < 0.05$.

tent, assessed by quantification of EPR signals, was significantly lower (40%) in *N. magellanica* than in *N. deaurata* (Table 2). Ascorbate plays a central metabolic role since it can act as an antioxidant and a pro-oxidant and its oxidation leads to $A^\bullet$ generation (Sadrzadeh and Eaton, 1988; Arrigoni, 1994). Ascorbate pro-oxidant activity is a result of its ability to reduce transition metals (especially iron) causing them to react with oxygen and initiators of lipid radical reactions (Wills, 1966). Ascorbate antioxidant activity consists in the ability to reduce various types of radicals, including peroxyl radicals that propagate lipid peroxidation, and to regenerate the antioxidant α-tocopherol from the oxidised form (Doba *et al.*, 1985). The $A^\bullet/AH^-$ ratio, which serves as an appropriate and accurate indicator of oxidative stress (Galleano *et al.*, 2002), was significantly lower in the gills of the intertidal *N. magellanica* than in the subtidal *N. deaurata* (Table 2). The exposure of high intertidal *N. magellanica* to variable environmental conditions did not cause an increased oxidative status at the hydrophilic cellular level, as compared to subtidal *N. deaurata*. The $A^\bullet/AH^-$ ratio indicates that tissue oxidation might be decreased by 49% in the gills of the intertidal *N. magellanica* as compared to the subtidal *N. deaurata*.

The lipid peroxidation in both organisms was estimated as the content of lipid radicals assessed by EPR. The lipid radicals combined with the spin trap POBN resulted in adducts that gave a characteristic EPR spectrum with hyperfine coupling constants of a_N= 15.56 G and a_H= 2.79 G (Fig. 2 b, c), in accordance with computer spectral simulated signals obtained using the overall mentioned parameters (Fig. 2 d). POBN was examined and no POBN spin adduct was observed (Fig. 2 a). Even though these constants could be assigned to lipid radicals, spin trapping studies cannot distinguish between peroxyl ($ROO^\bullet$), alcohoxyl ($RO^\bullet$) and alkyl ($R^\bullet$) adducts, owing to the similarity of the corresponding coupling constants (Jurkiewicz and Buettner, 1994). Bulk lipid radical content was significantly lower (80.6%) in the high intertidal *N. magellanica* than in the subtidal *N. deaurata* (Table 3). As no differences of tissue oxygen consumption and antioxidant enzyme activities were found, the higher levels of lipid peroxide formation may result, among other factors, from an elevated accumulation of transition metals in the tissues of the subtidal animals. To study the possible role of iron in the catalysis of lipid peroxidation, the gills iron content in both molluscs was examined. The overall iron content was found to be 62% lower in *N. magellanica* than in subtidal *N. deaurata* (Table 3).

The activity of catalase in the gills of the Antarctic mollusc *N. concinna* was 44 ± 22 U/mg prot in animals from the subtidal areas, 140 ± 40 U/mg prot in animals from the intertidal areas, and 213 ± 57 U/mg prot in animals temporarily air-exposed on intertidal rocks. Superoxide dismutase activity was 4 ± 2 U/mg prot in subtidal limpets, 4 ± 3 U/mg prot in intertidal limpets, and 13 ± 2 U/mg prot in the high intertidal limpets. TBARS concentrations were 42 ± 7 nmol g fresh weight in subtidal limpets and 33 ± 9 in intertidal limpet gills, but were not measured in the high intertidal limpets.

DISCUSSION

A number of biochemical alterations have been described and, in turn, proposed as a basis for the injury that may follow exposure of cells to partially reduced oxygen species generated under stressful environmental conditions. The data reported in the present work compare the gill oxidative status of three limpet species from Subantarctic and Antarctic environments exposed to different abiotic conditions in their natural habitats. Limpets from the high intertidal, such as *N. magellanica* and *N. concinna* from King George Island, could both undergo transient metabolic depression during low tides, a behaviour common to intertidal molluscs during air exposure (Pannunzio and Storey, 1998). This shell closure strategy prevents desiccation and predation during low tides and triggers a hypoxic response in the enclosed animal, consisting in metabolic reduction and a switch of anaerobic metabolism (Ortmann and Grieshaber, 2003). Thus, adaptation to high shore environments involves extended periods of metabolic reduction which may reduce the overall rate of metabolically produced oxygen radicals compared to subtidal limpet species. Moreover, oxidative stress may be enhanced by a frequent shift between low oxygen and normoxic conditions, comparable to ischemia-reperfusion insult.

The $A^{\bullet}/AH^{-}$ ratio reflects the actual state of the oxidative defence system mainly in the hydrophilic phase and provides an early and simple means of diagnosing oxidative stress (Kozak *et al.*, 1997; Estevez *et al.*, 2001; Galleano *et al.*, 2002). In the case of the two species from the Beagle Channel, a lower $A^{\bullet}/AH^{-}$ ratio is indicative of lower oxidative stress levels in the gills of the intertidal species *N. magellanica* as compared to the subtidal *N. deaurata*. The same tendency is found in the lipophilic cellular phase. A significantly lower lipid radical content was detected by EPR in the high intertidal *N. magellanica* as compared to the subtidal *N. deaurata* (Table 3). Besides playing a key role in the functioning of important metabolic enzymes and redox compounds, iron is a strict requirement for growth, but also in its reduced Fe^{2+} form it is an effective catalyst for lipid peroxidation (Puntarulo and Cederbaum, 1988). The initiation reaction of lipid peroxidation is indicated by reaction 1, in which one proton is abstracted.

$$\text{Lipid} \xrightarrow[-\,H^{+}]{Fe^{2+}} \text{Lipid radical } (LR^{\bullet}) \qquad (1)$$

The role of iron and superoxide anion in the initiation step of lipid peroxidation has been extensively discussed (Aust *et al.*, 1985; Puntarulo and Cederbaum, 1988; Ursini *et al.*, 1989). Lower levels of lipid peroxidation in *N. magellanica* as compared to *N. deaurata* correlate with a lower iron content. This agrees with previous observations in which we found a correlation of lipid peroxidation rates and iron content in digestive gland material of the mud clams *Laternula elliptica* and *Mya arenaria* (Estevez *et al.*, 2002). Additionally, the lower lipid radical formation in *N. magellanica* as compared to *N. deaurata* could be ascribed to the lower conversion rate of bound to bio-available forms of iron in *N. magellanica*. In this regard, gastropods are known to accumulate iron also in non-bioactive forms, while there are no reported data that these species possess regulatory mechanisms for iron uptake. The higher lipid radical formation in *N. deaurata* compared to *N. magellanica* could be mainly ascribed to the higher concentration of catalytically active iron in *N. deaurata* or to a higher conversion rate of bound to bioavailable iron. In an aerobic environment, iron is only available in the form of insoluble ferric iron (Fe^{3+}). Mechanisms of iron mobilisation are still unclear. However, recent data suggest that reduction of bound iron might be the key primary event (Fontecave and Pierre, 1993). Fe^{3+} is reduced to Fe^{2+} to be incorporated into ferritin, where it is stored as Fe^{3+} (*inert* form). However, by redox reaction with other cellular components (i.e. superoxide anion), Fe^{3+} from ferritin could be reduced to Fe^{2+}, be released to the cytoplasm and become a catalyst in Fenton-type reactions. Future studies are required to assess the amount of the catalytically active iron in gills from both organisms and to explain what intrinsic (ctenidial intracellular haemoglobins, Terwilliger and

TABLE 4. – Ratio of lipid radical content to α-tocopherol content in Subantarctic molluscs.

	N. deaurata	*N. magellanica*
Gills (10^{-2})	6 ± 2*, **	5 ± 1*, **
Digestive glands (10^{-1})	13 ± 1**	14 ± 4**

* significantly different from digestive gland values at $P< 0.05$.
** Taken from Malanga *et al.* (2004).

Terwilliger, 1985) or extrinsic factors cause the higher iron content of the subtidal limpets. Moreover, different food algae might cause differences of lipid content and lipid saturation levels, which may be the basis of the disparate rates of lipid peroxidation in the two limpet species.

The content of the antioxidants α-tocopherol and β-carotene in the gills of *N. magellanica* was not significantly different from that in *N. deaurata*. Hence, we hypothesise that the basic defence strategy in these animals is aimed at preventing the formation of the active species by controlling the iron uptake.

Lipid radical content could be understood as an indicator of radical-dependent damage to lipids, and α-tocopherol content as the most efficient antioxidant protection in the lipid compartment. The ratio of lipid radical content to α-tocopherol content (damage/protection) can be considered as an index of oxidative stress levels in the lipid phase (Galleano *et al.*, 2002). Significantly lower ratios in gills than in digestive glands were measured in both species (Malanga *et al.*, 2004). Table 4 shows non-significant differences of this ratio in gills or digestive glands between the two limpets. Under physiological control conditions, pro-oxidant and antioxidant processes seem well balanced in the digestive glands and gills of molluscs, but this balance is not perfect and some low-level oxidative damage to key molecules such as DNA, protein and lipid occurs physiologically over the life span.

Oxidative damage associated with an imbalance of pro- and antioxidant functions occurs when cellular or whole animal metabolic functions are severely disturbed under severe physiological stress. The intertidal *N. magellanica* may have developed a particular evolutionary strategy to cope with the extreme fluctuations in its high shore habitat, for example by controlling the tissue iron content to minimise oxidative tissue damage and thus render the animals less susceptible to environmental stress.

Catalase and superoxide dismutase activity in gill tissues from the Subantarctic limpets can be compared to data from the Antarctic congener *N. concinna*. While SOD activities of sub- and intertidal specimens were in the same range in Subantarctic (Beagle Channel) and Antarctic animals, catalase activities were tremendously higher in the Antarctic species. This agrees with a general view that Antarctic species may be especially prone to suffering oxidative stress in their low-temperature, high-oxygen environment, and many species therefore acquire higher antioxidant levels (for a review see Abele and Puntarulo, 2004). However, as the data were obtained with slightly different protocols, caution must be taken in comparing the absolute values of catalase activity, until further confirmation is obtained. With respect to a "stress gradient" between high and low shore levels, our Antarctic data show that high intertidal limpets clearly up-stage their intertidal and subtidal relatives with respect to activities of both antioxidant enzymes analysed. Thus, without knowing the iron levels in *N. concinna* specimens, we conjecture that Antarctic high shore conditions, involving regular exposure to air and presumably also thermal stress on sunny days during the Antarctic summer season, lead to the necessity for *N. concinna* to ward off higher oxygen radical species production by increasing its antioxidant defence. However, these data provide only an initial hint and open up the field for more comprehensive comparative investigations.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Somatic energy content and histological analysis of the gonads in Antarctic fish from the Scotia Arc*

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SUMMARY: Histological characteristics of the gonads and the energy contents of axial muscle, liver and gonads of Antarctic notothenioid fish collected during the LAMPOS (Latin American Polarstern Study) survey in April 2002 were analysed. Ovaries and testes were staged following histological maturity criteria. Oocyte diameters frequency were established and fecundity values were estimated. The energetic values (kJ/g) of different organs were determined using a microcalorimetric bomb. Ovaries of *Chaenocephalus aceratus* showed a generalised atretic process. The gonadal histology of *Champsocephalus gunnari, Pseudochaenichthys georgianus* and *Chionodracus rastrospinosus* suggests that their spawnings take place in autumn. *Gobionotothen gibberifrons* and *Lepidonotothen larseni* females were in the process of maturation, with the ovaries of the former containing yolked and atretic oocytes together. Ovaries of *Lepidonotothen kempi* showed old postovulatory follicles, which provided evidence of previous spawning. Gonads from both sexes of *Dissostichus eleginoides* were immature. Absolute and relative fecundity were lower in Channichthyidae than in Nototheniidae. The energy contents of the different organs analysed were: liver > gonads > axial muscle. The highest energy density value (kJ/g wet body mass) was found in *Dissostichus eleginoides*.

Keywords: energy content, reproduction, gonadal histology, ovary, testis, Antarctic fish, notothenioids.

RESUMEN: CONTENIDO ENERGÉTICO SOMÁTICO Y ANÁLISIS HISTOLÓGICO GONADAL DE PECES ANTÁRTICOS DEL ARCO DE SCOTIA. – Se analizaron las características histológicas de las gónadas y los contenidos energéticos del músculo axial, hígado y gónadas de peces provenientes del crucero LAMPOS (Latin American Polarstern Study) realizado durante abril 2002. Los ovarios y testículos fueron clasificados en diferentes estadios de maduración siguiendo criterios histológicos, se establecieron las distribuciones de frecuencias de diámetros oocitarios y se estimaron los valores de fecundidad de los especímenes en avanzado estado de madurez. El contenido energético (kJ/g) fue determinado utilizando una microbomba calorimétrica. Los ovarios de *Chaenocephalus aceratus* presentaron un generalizado proceso de atresia oocitaria. La histología gonadal de *Champsocephalus gunnari, Pseudochaenichthys georgianus* y *Chionodracus rastrospinosus* sugiere que se produjo un desove al inicio del otoño antártico. *Gobionotothen gibberifrons* y *Lepidonotothen larseni* se encontraron en proceso de maduración, ovarios de la primera especie contuvieron oocitos vitelados y atrésicos simultáneamente. Los ovarios de *Lepidonotothen kempi* mostraron folículos postovulatorios viejos que evidencian un desove previo. Las gónadas de ambos sexos en *Dissostichus eleginoides* fueron inmaduras. Tanto la fecundidad absoluta como la relativa calculadas fueron menores en las especies de Channichthyidae que en las de Nototheniidae. En las diferentes especies estudiadas el contenido energético (kJ/g de peso seco libre de cenizas) del hígado alcanzó los valores más altos seguido por las gónadas y el músculo axial. *Dissostichus eleginoides* presentó los valores de densidad energética (kJ/g peso húmedo del cuerpo) más elevados.

Palabras clave: contenido energético, reproducción, histología gonadal, ovario, testículo, peces antárticos, nototénidos.

INTRODUCTION

In terms of species abundance and biomass, the sub-order Notothenioidei constitute the dominant fish group in the Southern Ocean (Eastman and Mc Cune, 2000). The suborder is thought to have evolved before the formation of the Antarctic Polar Front (APF), around 20 million years ago (Clarke and Johnston, 1996). Almost a hundred notothenioid species have an exclusively Antarctic distribution,

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whereas there are 26 non-Antarctic species (Eastman and Eakin, 2000; Montgomery and Clements, 2000). Evidence from molecular phylogenetic analysis suggests that some families, namely Bovichtidae, Pseudaphritidae and Eleginopidae, spread out of Antarctic waters before the establishment of the APF (Stankovic *et al.*, 2002). Similar analyses suggest that the barrier of APF was permeated in some opportunities allowing a successful migration from the Antarctic and colonisation of Subantarctic waters (Bargelloni *et al.*, 2000). The largely non-Antarctic genus Patagonotothen resulted especially successful, giving rise to 14 species (Eastman, 1995).

Information about reproductive features such as maturation and spawning schedule, fecundity or reproductive effort of Subantarctic species of notothenioids is available only for a few species. Therefore, comparative analyses between species with Antarctic and Subantarctic distributions are hampered.

The energetic demands for reproduction and growth are conditioned by food intake and the physiological reproductive strategies (Calow, 1985). Low temperatures and highly seasonal productivity of the Antarctic marine environment modulate the energy budget of Antarctic fish and the seasonality of spawning. Some species of Antarctic Notothenioidei, like *Notothenia rossii, N. coriiceps* and a great number of channichthyids, spawn a few thousand large yolky oocytes (more than 3 mm in diameter), usually during autumn, while other species of Nototheniidae spawn a greater number of small oocytes at any time of the year (Ekau, 1991; Kock and Wilhelms, 2003). *Pseudochaenichthys georgianus* and *Champsocephalus gunnari* require about one year to complete the yolk deposition, while *Chaenocephalus aceratus and N. coriiceps* need a longer time (Everson *et al.*, 1996; Everson, 1994; Kock and Everson, 1997; Kock and Kellermann, 1991). To understand the gonadal cycle and yolk deposition process, a more intense sampling schedule throughout the year would be necessary.

The reproductive characteristics of fish from the Southern Ocean were studied in many species, in some of which histological gonadal descriptions were made (Eastman and DeVries, 2000; Everson *et al.*, 1991; La Mesa *et al.*, 2003; Macchi and Barrera-Oro, 1995; Russo *et al.*, 2000; Shandikov and Faleeva, 1992; Van der Molen and Matallanas, 2003; see Kock and Kellerman, 1991 and references therein). Most studies on reproduction were carried out only in summer–autumn (Kock and Kellermann, 1991; Duhamel *et al.*, 1993; Kock *et al.*, 2000; Kock and Wilhelms, 2003) because that is the season when most of the Antarctic scientific cruises take place.

Different attempts to determine the energy budget of fish species of the Southern Ocean have been made in recent years. Food intake requirements and feeding energetics were analysed by Kock (1992) in several species of notothenioids, by Johnston and Battram (1993) in *Notothenia neglecta* and by Chekunova and Naumov (1982) in *Notothenia rossi marmorata*. The proximal biochemical compositions of *N. r. marmorata* and *Lepidonotothen (=Notothenia) gibberifrons* were studied by Kozlov (1981; 1982). The lipid compositions of high Antarctic nototheniod fish were studied by Friederich and Hagen (1994), Hagen *et al.* (2000) and Kamler *et al.* (2001).

In the present study we analysed the reproductive characteristics of Antarctic Notothenioidei species, comparing fish samples from the northern and southern branches of the Scotia Arc. In addition, we analysed the energetic content in gonads, liver and muscle of Antarctic nototheniods for the first time.

MATERIAL AND METHODS

Fishes were collected during the LAMPOS survey in April 2002 (Fig. 1) and detailed cruise information has been published by Arntz and Brey (2003) for the total number of fishes caught during the cruise and the number considered for the various investigations in this paper (see Tables 1 and 2). Shipboard sampling involved taxonomic identification, labelling and measurement of total length (TL) and standard length (SL) to the nearest cm below. Total weight (TW), sex, and weight of liver, stomach and gonads were determined to the nearest 0.1 g below. Gonado-somatic index (GSI) was calculated as the percentage of gonadal weight per total body weight.

Gonad samples for histological studies were preserved in Bouin fixative, dehydrated and included in Paraplast. Histological sections (5 to 7 μm thick) were stained with haematoxylin-eosin and Periodic Acid-Schiff-haematoxylin (PAS-H).

Absolute fecundity was estimated by extrapolating the number of oocytes of 3 weighed subsamples to the weight of the entire ovary. The number of oocytes produced per gram of total weight (relative fecundity) was also determined. A portion of ovary

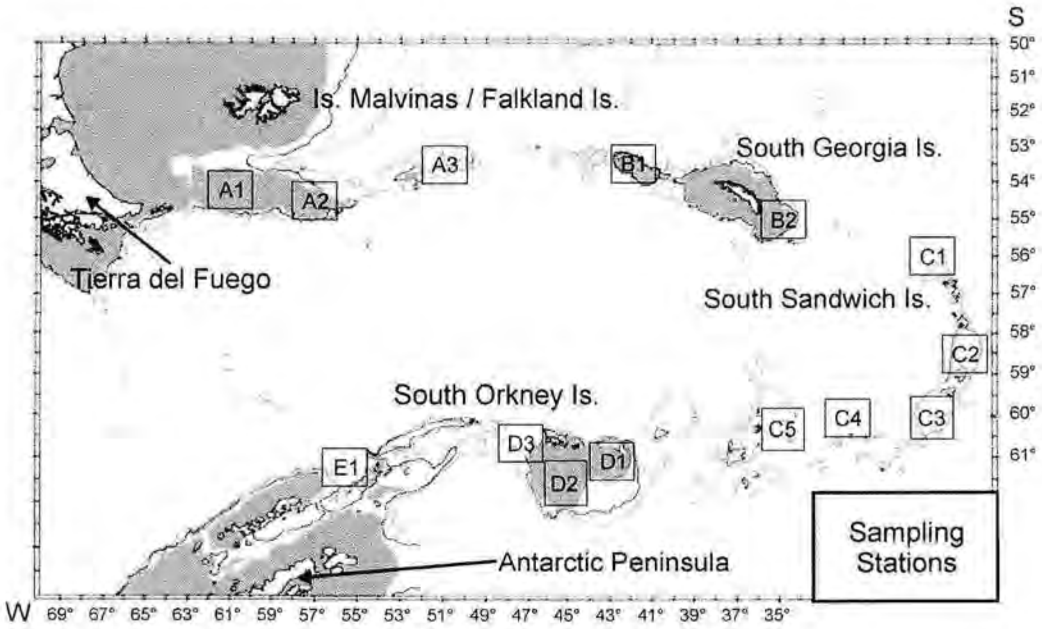

FIG. 1. – Sampling stations of the Latin American "Polarstern" Study

TABLE 1. – Oocyte diameter, absolute and relative (Oocytes/ TW) fecundity in Antarctic Notothenioidei (*no ripe oocytes).

Species	n	Oocyte diameter (μm)	Oocyte wet weight (mg)	Oocyte dry weight (mg)	Absolute fecundity	Relative fecundity
N. rossii	1	2150 - 3150	8.06	2.67	89793	27
C. gunnari	4	1800 - 3100	6.52	2.33	3933	14
C. rastrospinosus	1	3900 - 4600	30.24	8.41	4073	10
G. gibberifrons	4	500 - 1200*	0.51	0.13	84067	103
P. georgianus	2	3800 - 4700	26.92	7.54	7317	9
L. kempi	1	700 - 1200*	0.62	0.19	116420	175

TABLE 2. – Relationship between total body weight (TW) / total body length (TL) and total energy content (TEC) / TL. Mean percentage water content (MWC %). TEC for standardised fish at 40 cm TL (TEC $_{40}$). Mean energy density (ED ± SD) for each species analysed. n_1= total number of specimens caught in the LAMPOS survey; n_2 = number of specimens used for energetic determination.

Species	n_1	TW = a $\cdot$TL^b	r^2	n_2	TEC = a $\cdot$TL^b	r^2	MWC %	TEC $_{40}$	Mean ED (SD)kJ g^{-1} wet mass
C. aceratus	78	$0.0010\cdot LT^{3.44}$	0.96	8	$0.0043\cdot TL^{3.53}$	0.99	78.8	1944	5.38 (0.45)
C. gunnari	76	$0.0005\cdot LT^{3.76}$	0.95	5	$0.4933\cdot TL^{2.28}$	0.47	76.8	2217	5.21 (0.50)
P. georgianus	49	$0.0008\cdot LT^{3.64}$	0.97	11	$0.0003\cdot TL^{4.29}$	0.89	80.0	2238	4.55 (0.41)
C. rastrospinosus	13	$0.0040\cdot LT^{3.63}$	0.97	10	$0.0040\cdot TL^{3.63}$	0.93	78.8	2615	4.99 (0.24)
G. gibberifrons	92	$0.0015\cdot LT^{3.52}$	0.97	14	$0.0028\cdot TL^{3.78}$	0.98	76.9	3183	4.89 (0.17)
D. eleginoides	38	$0.0249\cdot LT^{2.71}$	0.95	5	$0.2216\cdot TL^{2.70}$	0.88	68.7	4689	7.80 (1.27)
L. kempi	158	$0.0042\cdot LT^{3.42}$	0.99	8	$0.0279\cdot TL^{3.38}$	0.97	75.5	7253	5.40 (0.48)

was preserved in 10% formaldehyde to determine the frequency distribution of the oocyte diameters.

Samples of axial somatic muscle, liver and gonads were kept frozen (-20°C) for energy studies. Wet mass of each sample was measured, and the material was dried at 60°C to constant weight and ground in a pestle mortar. Pellets (75-200 mg) were burned in a Parr 1425 micro-bomb calorimeter (Lucas, 1996). The values, corrected by ash and acid contents, were expressed as kJ$\cdot$g^{-1} ash free dry weight (AFDW).

Total energy content was calculated as the sum of the energy content of gonads, liver, and muscle. Wet and dry weight values were used to calculate wet weight/dry weight conversions for energy determinations. The Friedman test was performed to compare the energy content between organs of each species (STATISTICA software).

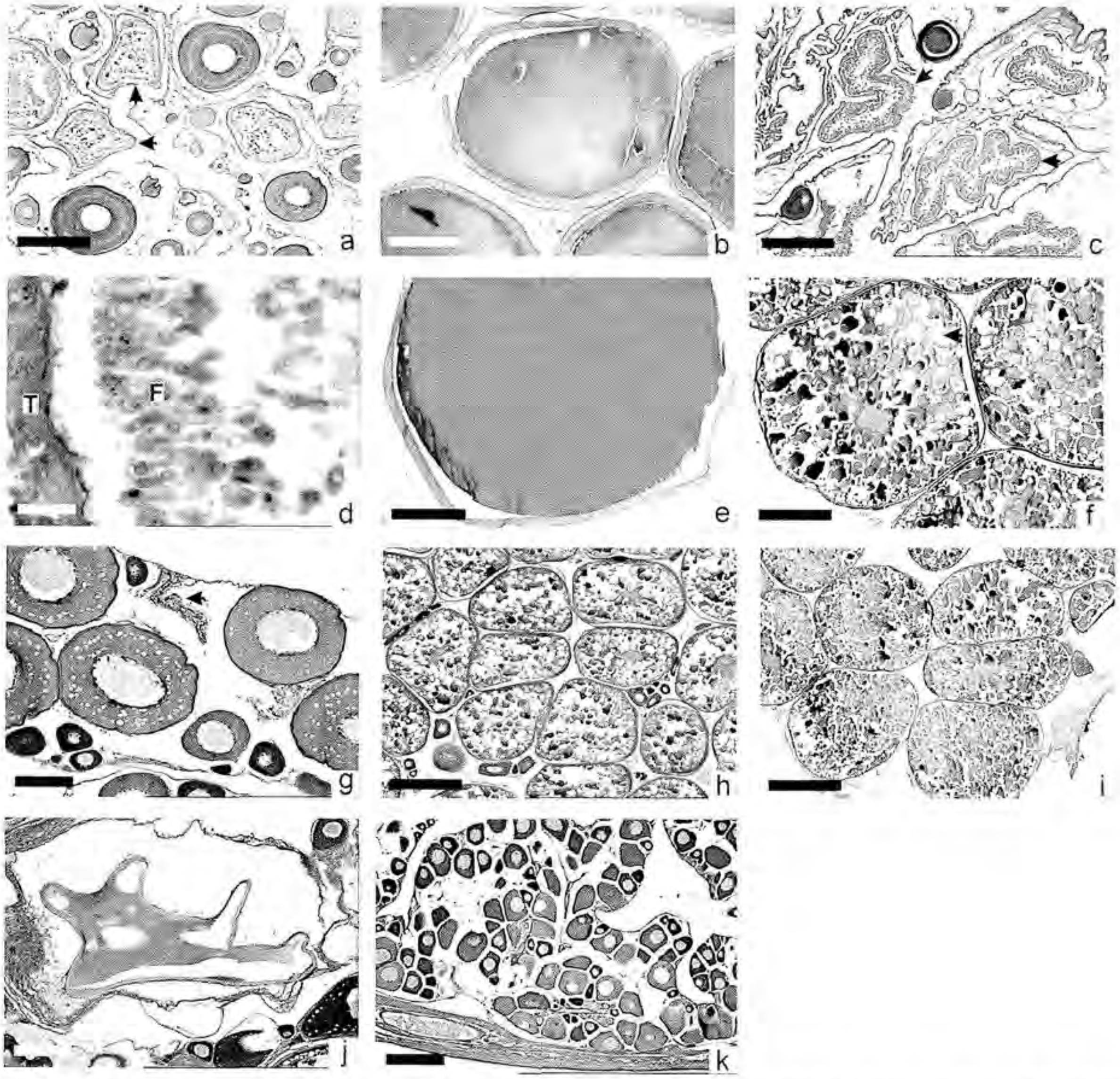

FIG. 2. – a: *Chaenocephalus aceratus*. Atretic oocytes (Arrows); b: *Champsocephalus gunnari*. Mature hyaline oocyte; c: *Chionodraco rastrospinosus*. Recent POF (Arrows); d: *Chionodraco rastrospinosus*. Recent POF. F: follicular cells. T: theca; e: *Chionodraco rastrospinosus*. Mature hyaline oocytes; f: *Lepidonotothen larseni*. Maturing oocytes with yolk globules starting the coalescence (Arrow); g: *Lepidonotothen kempi*. Previtellogenic oocytes and old POF (Arrow); h: *Lepidonotothen kempi*. Maturing oocytes with yolk globules; i: *Gobionotothen gibberifrons*. Maturing yolky oocytes; j: *Gobionotothen gibberifrons*. Residual mature oocyte; k: *Dissostichus eleginoides*. Basophilic oocytes. Scale bar represents: 500 μm (a, b, c, g, h); 200 μm (e, i, j); 100 μm (f); 20 μm (d). PAS – Haematoxylin.

RESULTS

Gonad maturation

Chaenocephalus aceratus

In the ovaries of *Chaenocephalus aceratus* (off South Georgia and South Orkney Islands) the vitellogenic oocytes showed different degrees of atresia (Fig. 2a). Some oocytes were starting the atretic process, with a fragmented chorion and hypertrophy of granulose cells. Other oocytes were already in an advanced stage of resorption, with a reduced cytoplasm invaded by phagocytic cells distributed between yolk globules.

Champsocephalus gunnari

All the ovaries of *Champsocephalus gunnari* showed a bimodal oocyte diameter distribution (Fig. 3). The smaller oocytes (< 600 μm) had basophilic cytoplasm and primary yolk vesicles. The bigger oocytes (1600 to 3200 μm) were in an advanced stage of maturation, with homogeneous yolk stained heavily by PAS and eosin (Fig. 2b; GSI = 8). Males had testes with wide central tubules full of sperm and the more external tubules containing isolated spermatogoniae placed against the tubule wall (Fig. 4a, GSI = 2.5).

Pseudochaenichthys georgianus

Samples of *Pseudochaenichthys georgianus* were composed of both juvenile and sexually mature adult individuals. Ovaries of the former contained only basophilic or previtellogenic oocytes, while the latter had ovaries with mature oocytes (3800 to 4800 μm, Fig. 3; GSI = 18). Sampled males were all mature. Their testes had tubules with numerous spermatogonia and a small amount of cysts containing spermatocytes (Fig. 4b; GSI = 2.02). Abundant spermatozoa, both in cysts and free, were observed in the central ducts. The irregular arrangement of spermatozoa and the phagocytic cells found between them suggested a previous evacuation.

Chionodraco rastrospinosus

Two types of ovaries were distinguished in this species. One type had scanty oocytes, with few yolk globules and recent post-ovulatory follicles (POF, Fig. 2c; GSI= 2.54). The POF were large, with a wide central lumen, and consisted of hypertrophied follicular cells arranged in an irregular convoluted structure (Fig. 2d). A monolayer theca with abundant small blood vessels and connective fibres surrounded the POF. The other type contained mature oocytes with homogeneous yolk (Fig. 2e; GSI= 22.49) and a batch of previtellogenic oocytes. This second type of ovary showed a bimodal distribution of oocyte diameters with a batch larger then 700 μm and a batch of mature oocytes between 3900 and 4600 μm (Fig. 3). In all sampled males the central testis tubules contained free spermatozoa while the peripheral tubules contained a small number of residual spermatozoa (Fig. 4c; GSI = 1.33). Occasionally, phagocytic cells were present among the residual spermatozoa. Isolated spermatogoniae (about 12 μm) were distributed along the tubule walls and groups of them were close to the blind end of the tubules. The general histology of the testes suggested a recent evacuation of sperm.

Lepidonotothen larseni

The ovaries had oocytes with numerous secondary yolk globules. Some of them were starting the process of yolk coalescence (Fig. 2f; GSI = 5.15).

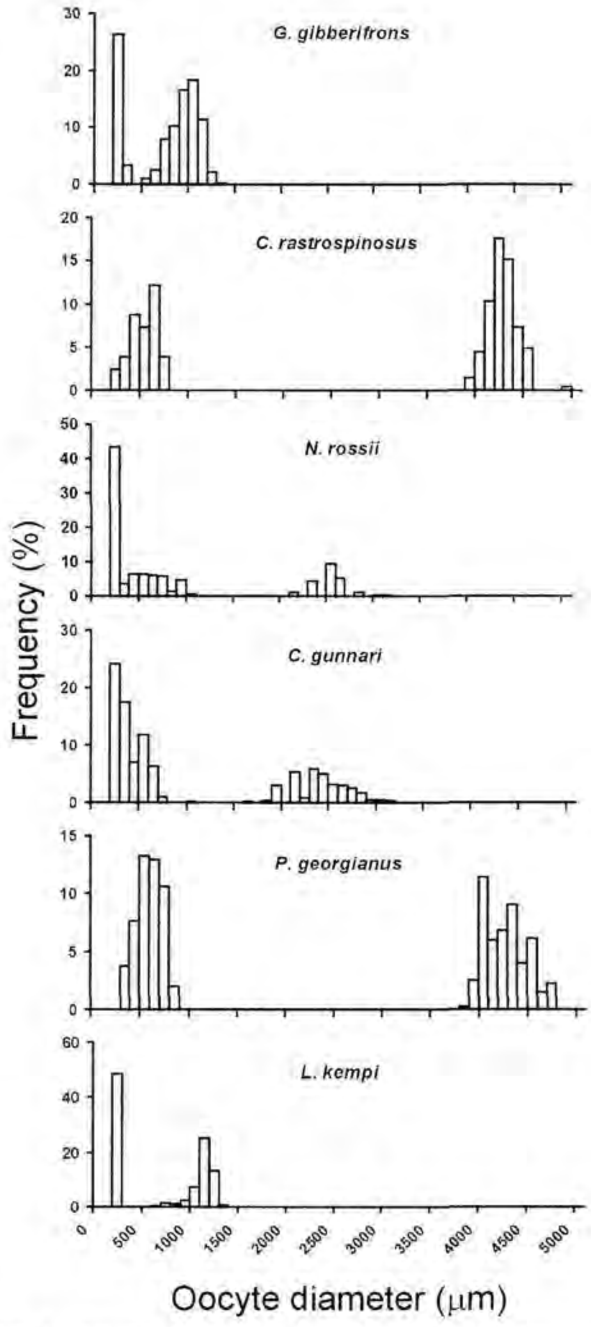

FIG. 3. – Size-frequency distribution of oocytes in each species: a) *Gobionotothen gibberifrons* (n= 1774); b) *Chionodraco rastrospinosus* (n= 205); c) *Notothenia rossii* (n= 1165); d) *Champsocephalus gunnari* (n= 2075); e) *Pseudochaenichthys georgianus* (n= 607); f) *Lepidonotothen kempi* (n= 705).

Lepidonotothen kempi

Two ovary categories were found in the samples of this species. One type (fish captured especially at station C2, near the South Sandwich Islands), with GSI lower than 2, contained advanced (old) POF, oocytes in primary vitellogenesis and some residual oocytes in the process of resorption (Fig. 2g; GSI = 1.7).

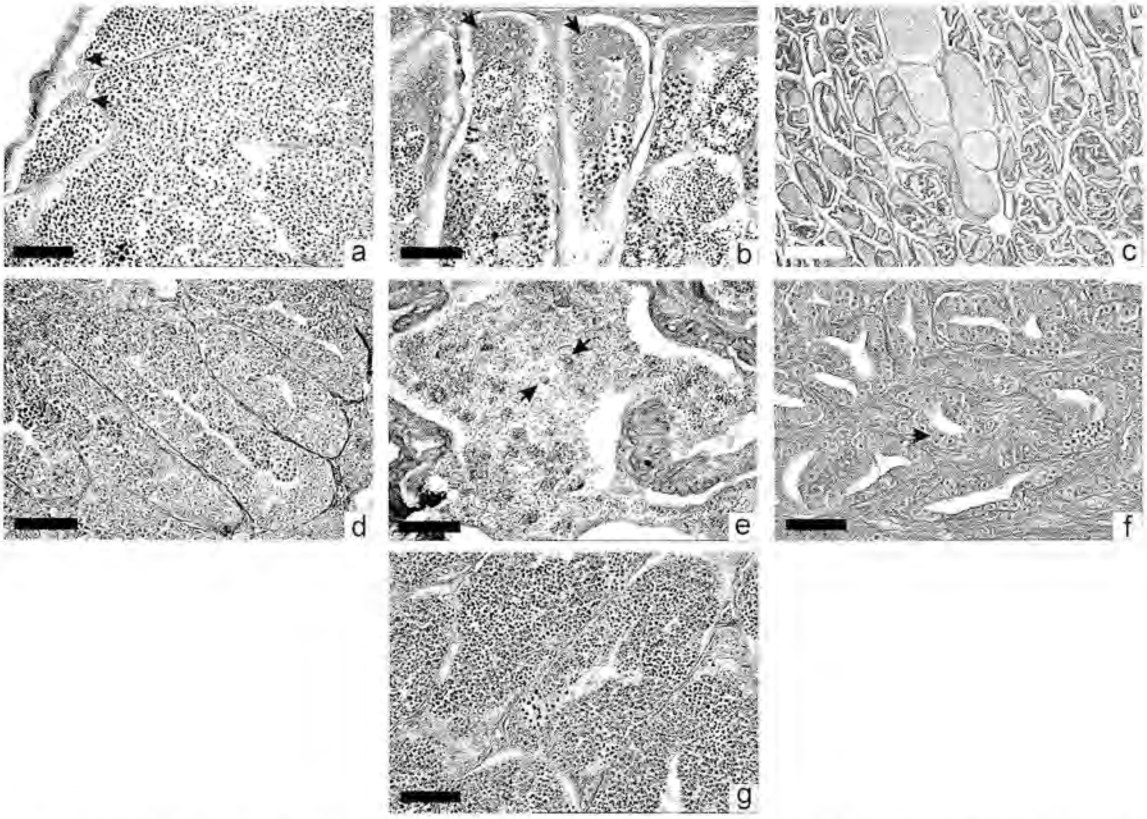

FIG. 4. – a: *Champsocephalus gunnari*. Isolated spermatogoniae (arrows). Abundant spermatozoa in the tubules; b: *Pseudochaenichthys georgianus*. Blind end of tubules with spermatogoniae (arrows), cysts of spermatocytes; c: *Chionodraco rastrospinosus*. Central ducts with free spermatozoa and shrunken peripherical tubules with residual sperm; d: *Lepidonotothen kempi*. Peripherical tubules with spermatogonia in cysts or isolated (arrow) and spermatocytes; e: *Lepidonotothen kempi*. Spermatozoa free in the lumina of the ducts with phagocytes (Arrow) between them; f: *Dissostichus eleginoides*. Tubules with spermatogoniae. A mitotic division is shown (arrow); g: *Dissostichus eleginoides*. Cysts with spermatogoniae and spermatocytes. Scale bar represents: 50 μm (a, b, d, e, f, g); 200 μm (c). PAS – Haematoxylin.

The other group of ovaries (most of the fish captured at station C5) showed GSI between 3 and 10, and contained a batch of oocytes in secondary vitellogenesis (Fig. 2h; GSI = 7.2). The diameter distribution of oocytes in smears showed a bimodal distribution with 50% of basophilic oocytes (300 μm) and 50% of maturing oocytes (500 – 1300 μm, Fig. 3).

Two different degrees of maturation were found in males of *Lepidonotothen kempi*. One group showed testes with active spermatogenesis, containing a large number of cysts of spermatogonia and spermatocytes arranged close to the tubule walls (Fig. 4d). A second group had scarce spermatogoniae, spermatozoa free in the lumina of the ducts and phagocytes between the spermatozoa (Fig. 4e), suggesting a previous sperm evacuation.

Gobionotothen gibberifrons

Ovaries of this species contained basophilic, previtellogenic and yolky oocytes (Fig. 2i). The ovaries from the fish sampled off South Georgia (B2 Station, Fig. 1) showed a lower degree of maturation (GSI=1.4) than the ovaries from the fish sampled off Elephant Island (E1 Station, Fig. 1; GSI =5.9). In histological sections the oocytes from fish sampled off South Georgia had a diameter of about 700 μm, while in the ones from off Elephant Island the diameter was around 880 μm.

In smears, a bimodal distribution of oocytes was found, with previtellogenic ones of less than 500 μm diameter and yolky ones between 500 and 1300 μm in diameter (Fig. 3).

Residual mature oocytes, which appeared to be a remainder from a previous spawning, were found in ovaries from fish sampled off Elephant Island (Fig 2j). Testes were in the process of maturation, containing cysts of spermatocytes.

Dissostichus eleginoides

The total length of the specimens (53 to 93 cm) was smaller than or close to the first maturation size (Everson and Murray 1999). Ovaries had basophilic

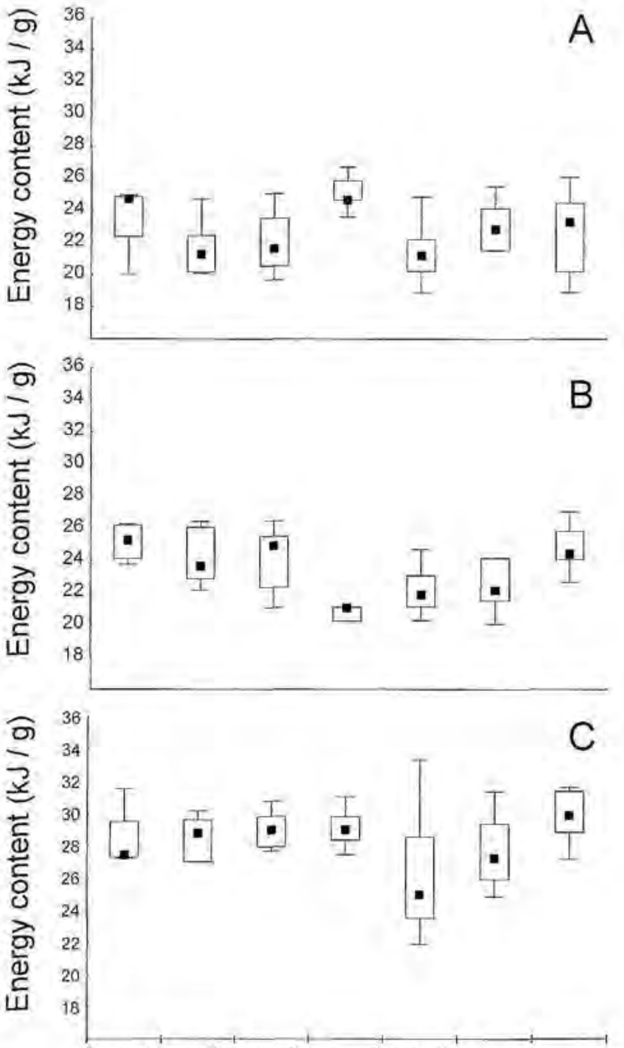

FIG. 5. – Energy content of different organs and tissues (kJ/g; ash free dry weight). ■ Median. Box: 25-75%. Whiskers: min-max. A: axial muscle; B: gonad; C: liver.

and previtellogenic oocytes filling the ovigerous lamellae (Fig. 2k). Two types of testes were found, one of them containing exclusively spermatogoniae covering the tubule wall (Fig. 4f, GSI = 0.02) and the other one containing cysts with spermatogonia and spermatocytes (Fig. 4g, GSI= 3.2). There was a lumen in the centre of each tubule. Spermatozoa were not found in cysts or in tubules.

Notothenia rossii

Only one female specimen was captured, with its ovary in maturation. In smears almost 45% of the oocytes were previtellogenic opaque oocytes (300 μm diameter), while small diameter oocytes (400 to 1000 μm.) containing globular yolk reached about 35%. The larger translucent yolky eggs had diameters between 2100 and 3200 μm (Fig. 3).

Fecundity

The number of oocytes contained in the ovary was estimated in three species of Channichthyidae and in three species of Nototheniidae (Table 1). The only species with ovaries containing fully mature oocytes were *N. rossii, C. rastrospinosus* and *C. gunnari*. In the other species used for the estimation, the larger oocytes were in an advanced stage of vitellogenesis. Absolute and relative fecundity were lower in the Channichthyidae than in the Nototheniidae.

Energy content

Due to the small number of specimens studied in each species, the energy content (kJ/g) of both sexes was analysed together. The energy content of muscle and gonads only showed significant differences in *D. eleginoides* and *C. rastrospinosus* (Fig. 5A and B). The former had higher energy content in the muscle than in the gonads. Conversely, the latter had higher energy content in the gonads than in the muscle. The energy content of the liver was higher than the energy content of the gonads in all species ($p<0.001$), except in *C. gunnari*.

The energy content of the liver of *G. gibberifrons* (Fig. 6) was significantly higher in individuals sampled off South Georgia than in individuals sampled off Elephant Island (stations B2 and E1 respectively; Fig. 1).

The total energy content, size and mass for each species are shown in Table 2. Total energy content

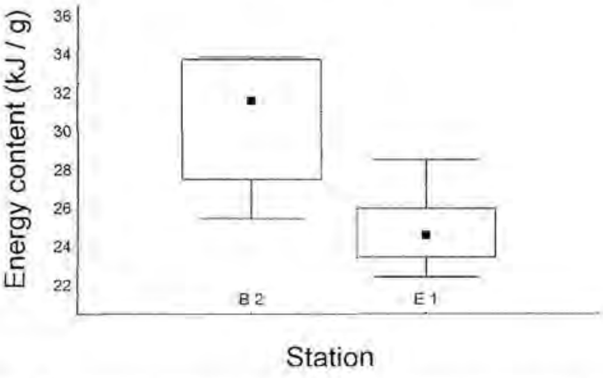

FIG. 6. – Energy content in liver of *G. gibberifrons* captured on opposite sides of the Polar Front (kJ/g; ash free dry weight). ■ Median. Box: 25-75%. Whiskers: min-max.

calculated for a standard specimen (40 cm TL) was lower in channichthyids than nototheniids. The highest value was measured in *L. kempi*. Minimum and maximum values of energy density (ED kJ/g wet mass) were found in *C. aceratus* and *D. eleginoides* respectively.

DISCUSSION

The scarcity of material sampled from different species at the stations covered does not allow for generalisations about reproductive patterns and energetic characteristics of notothenioids along the Scotia Arc. However, the data are sufficient to perform an analysis in nine fish species caught mainly off South Georgia and in the southern branch of the Scotia Arc.

Biogeographically, our sampling sites are located in the ichthyofaunistic subregion of the Seasonal Pack Ice Zone and northern islands in which the Scotia Arc is included (sensu Kock, 1992). This is dominated by notothenioids of the genera *Notothenia* and *Lepidonotothen*, harpagiferids and channichthyids. Six of the species analysed in this study (Tables 1 and 2) were described as inhabiting exclusively this subregion The other three species studied show a wider distribution. *Chionodraco rastrospinosus* inhabits both low and high Antarctic zones (Kock and Stransky, 2000); *Lepidonotothen kempi* (=*L. macrophtalma* + *L. squamifroms*, Schneppenheim *et al.*, 1994, Eastman and Eakin, 2000) occurs in the low Antarctic zone and on the Patagonian shelf (Kock and Stransky, 2000); and *Dissostichus eleginoides* has a wide latitudinal distribution related to Subantarctic deep waters (as far as 35°S, off southern Peru in the Pacific Ocean, and off Uruguay in the Atlantic Ocean; De Witt *et al.*, 1990).

Christiansen *et al.* (1998) found differences in the reproductive timing between low and high Antarctic species, and considered that they were caused by both geographical gradients and different modes of spawning. In the present study, two principal reproductive groups were recognised in agreement with Christiansen *et al.* (1998): substrate spawning fish, with low fecundity, demersal oocytes of great diameter with a high energetic content (most of channichthyids), and pelagic spawners with numerous small-diameter oocytes (notothenioids and *C. gunnari*).

The values of relative and absolute fecundity found in this study (Table 1) are in agreement with the range of the values found in previous studies (Christiansen *et al.*, 1998; Kock, 1989; Kock and Kellermann, 1991; Kock and Everson, 1997; Permitin, 1973). Although the mature females were few in number, our results help to understand the reproductive patterns of Antarctic notothenioids. They are characterised by delayed gonadal maturation, prolonged gametogenesis, usually one unique spawning per year and moderately high fecundity (North and White, 1987; Kock, 1992). Accordingly, most of the species analysed in the present study showed synchronous oocyte growth, with only one generation of maturing oocytes indicating that spawning occurred only once in each spawning season.

In all specimens of *C. aceratus* captured near both the South Orkney and South Georgia islands (Stations B2 and D2 respectively, Fig. 1), yolky oocytes of up to 1500 μm diameter were found in atretic condition (Fig. 2a). The presence of atretic oocytes and the small size of healthy oocytes (1 mm) suggest that these fish neither had spawned recently nor were prepared to spawn given the proximity of the spawning season (March – May, c.f. Permitin 1973; Kock, 1989). This generalised atretic phenomenon is considered as a failure in the attainment of final oocyte maturation that could be caused by the poor physical condition of the females, probably due to food shortage (Hunter and Macewicz, 1985; Yoneda *et al.*, 2002). In the case of this species, food should be available all year round because adult specimens are considered opportunistic predators (Everson *et al.*, 2000). The main cause of massive ovarian atresia in all sampled female specimens is not clear. Nevertheless, skipping spawning, when environmental conditions are unsuitable, could be a way to maintain somatic viability (McEvoy and McEvoy, 1992). When one species shows massive ovarian atresia and the reproductive cycle is studied using only macroscopic staging of ovaries without histological support, the risk of confusion between pre-reproductive atresia and the normal maturation process is high because the atretic oocytes can be misidentified as maturing ones (La Mesa *et al.*, 2003).

Ovaries of *C. gunnari* captured off the South Orkneys (Station D2) contained mature oocytes with homogeneous yolk, with a diameter of about 3.2 mm. The advanced stage of maturation of the ovaries and the testes full of mature sperm ready to evacuate found in the present study suggest the proximity of the spawning season in March–May, in agreement with Kock (1989). The ovaries analysed were healthy and showed no signs of an atretic process. Pre-reproductive regression was described in different opportunities for *C. gunnari* off South Georgia (Everson *et al.*, 1991; Macchi and Barrera-Oro, 1995). These authors established a relation between the failure in ovarian maturation and the interannual variation in krill availability, the main food source for this species. Kock and Kellermann (1991) postulated that part of the population of *C. gunnari* in the Atlantic sector of the Southern Ocean does not spawn every year. The annual variability of individuals participating in spawning emphasises the importance of checking the actual percentage of spawning individuals every year in species under exploitation.

The coexistence of mature males and females of *P. georgianus* with oocytes around 4500 μm in the South Georgia samples indicates the occurrence of spawning during April in agreement with Kock's and Kellermann's (1991) findings.

In *C. rastrospinosus* ovaries with either mature oocytes or recent POF (Fig. 2c-e) were found off South Georgia (Station B2). The histology of the testes showed sperm evacuation. These data are in agreement with the data of Kock (1989) and Kock and Kellermann (1991), who described the spawning of this species taking place in April around Elephant Island. These results suggest that spawning occurs simultaneously in an extensive area at both sides of the Antarctic Polar Front.

Female *L. larseni* (off Elephant Island, Station E1) had ovaries containing oocytes with numerous secondary yolk globules beginning the yolk coalescence process (Fig. 2f). This ovarian histology suggests that this species probably spawns in early winter, in agreement with the results of Kock (1989).

In *L. kempi*, the presence of two kinds of ovaries and testes (spent and maturing) indicates that spawning had occurred previously near the South Sandwich Islands (Fig. 1, Station C2, 254-262 m deep) since a maturing process with heavier ovaries containing yolked oocytes took place in deeper waters (Fig. 1, Station C5, 380-390 m deep). Our samples containing yolky oocytes in April suggest a protracted maturation during winter and spring. The presence of old POF in April (Fig. 2g) indicates either that the POF remained in the ovary as long as four months, or that the spawning off the South Sandwich Island occurred near the end of summer. If this was the case, spawning could occur later than November-December, as was described by Kock and Kellermann (1991) off the South Orkney Islands.

In April ovaries of *G. gibberifrons* were in the process of maturation. The yolky oocytes had not yet reached their maximum diameter (Fig. 3), which Kock (1989) determined at 2.5 mm. The presence of mature residual oocytes in the ovaries collected in April (Fig. 2j) could indicate the occurrence of a slow process of resorption, since the anterior spawning period should have been in the previous winter, according to Kock (1989) for the population at Elephant Island. Testes in our samples contained only spermatocytes and not spermatozoa, suggesting that males were in the early process of maturation as well.

Female *D. eleginoides* were immature, probably because they had not reached the size of first maturity yet (98.2 cm for females, Everson and Murray, 1999). One group of males was smaller than the size of first maturity (78.5 cm, Everson and Murray, 1999), and accordingly the testes were immature. A second group, composed of bigger males, was in the process of maturation (Fig. 4g), suggesting that these specimens could be ready to evacuate during the next spawning season, which Kock and Kellerman (1991) established as July-September.

Comparisons of reproductive features between the Antarctic and Subantarctic notothenioids are difficult because available data concerning the latter group are restricted to a few species, usually inhabiting shallow waters and without closely related species in the Antarctic zone. There are two exceptions: the genera *Harpagifer* and *Champsocephalus*. The first comprises several species in coastal waters of different peri-Antarctic islands (*H. bispinis, H. georgianus georgianus, H. georgianus palliolatus, H. kerguelenensis, H. spinosus*) and one Antarctic species (*H. antarcticus*) (Fischer and Hureau, 1985). Reproductive characteristics were studied only in *H. antarcticus* (Daniels, 1978; White and Burren, 1992). The genus *Champsocephalus* has the non-Antarctic species *C. esox*, confined to the Magellan Province, whose reproductive biology was studied in a population inhabiting the Beagle Channel (Calvo *et al.*, 1999). Sexually mature males are found from January to September, and females containing 3300 to 8600 mature oocytes or POF are found from February to November.

Individuals of the non-Antarctic species *Patagonotothen tesellata* spawn twice a year, in winter and at the end of summer. Each male guards egg masses spawned by several females in nests under flat rocks in lower levels of the intertidal zone of the Beagle Channel. Female *P. tessellata* spawn

7600–62,000 oocytes with a diameter of 1000 to 1500 μm (Rae and Calvo, 1995; 1996). *P. cornucola* has not specifically been studied but preliminary observations indicate a similar timing of spawning (unpubl. observ.).

The non-Antarctic notothenioids show the only verified protandric hermaphroditic species that inhabits the Magellan region, *Eleginops maclovinus* (Calvo *et al.*, 1992). This species spawns partially in June in central to southern Chile (Panozo, 1996), and shows a protracted spawning season between September and December around the Islas Malvinas/Falkland Islands in waters of 30-100 metres depth. Each batch comprises between 1.1 and 7.3 million oocytes with a diameter of 1 to 1.2 mm (Brickle *et al.*, 2005). Hence, taking into account the extended spawning period and the possible repetitive spawning of the non-Antarctic notothenioids vs. the usual single spawning of Antarctic notothenioids, Subantarctic waters obviously impose less severe constraints on the reproductive effort than Antarctic waters.

The axial swimming muscles of fish represent more than 60% of their total body mass (Johnston, 2001; Sanger and Stoiber, 2001), and their energy content affects the total energy content value of the body. In all the species analysed in this study the energy content (kJ/g) of the axial muscle had similar values except for *D. eleginoides*, which reached a significantly higher value (Fig. 5A). Gonads of *D. eleginoides* had the lowest energetic content but differences from other species were not significant. It is noticeable that the average values of the energy content (kJ/g) of gonads (Fig. 5B) were not different between the species studied in spite of the diverse degree of sexual maturation.

Energetic values of liver in *G. gibberifrons* showed a great dispersion (Fig. 5C) that could probably be explained by the different origin of fishes. *G. gibberifrons* caught off Elephant Island (Station E1, Fig. 6) had significantly lower values of liver energy content and higher GSI and bigger yolky oocytes than the females caught off South Georgia (Station B2).

These results support the function of liver as an energy reservoir before the gonadal maturation starts, because the energy content of the liver is higher than 30 kJ/g, suggesting a high percentage of lipid content (Lucas, 1996). A similar variation in relation with the reproductive cycle was found in the liver of other notothenioid fish (*N. coriiceps* and *L. nudifrons*, Kamler *et al.*, 2001).

D. eleginoides showed the highest values of energy density (7.8 kJ/g wet mass, Table 2), probably due to the high lipid content of this species (Eastman, 1993). The rest of the species studied varied between 4.55 and 5.40 kJ/g.

The energy density (ED) of notothenioids (Table 2) is higher than the values reported for *Pleuronectes asper* (3.5 to 4.5 kJ/g wet mass; Paul, 1997) but equivalent to or slightly lower than the energy values of sexually mature *Clupea pallasii* (8-10 kJ/g; Paul *et al.*, 1998). These results stress the important role played by notothenioids in energy transfer in Southern Ocean food webs.

The highest total energy content (TEC) found in this study (Table 2) for a standardised fish of 40 cm TL corresponds to *L. kempi* (7253 kJ), although the ED (5.4 kJ/g) of this species was not the highest. This high TEC could be explained by the higher TW/TL relationship that *L. kempi* has in comparison with the other notothenioids, which have TEC values of 2000 to 4600 kJ (Table 2). These values are similar to the values reported for *Gadus morhua* of 45 cm TL (2400 to 4100 kJ; Lambert and Dutil, 1997).

The estimations of total energy density in the species studied (expressed in relation to TL or TW; Table 2) could be useful to quantify the energy transfer in piscivorous predators such as seabirds or marine mammals (Anthony *et al.*, 2000; Cherel y Ridoux, 1992).

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Influence of temperature, habitat and body mass on routine metabolic rates of Subantarctic teleosts*

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SUMMARY: Subantarctic notothenioids are exposed to wider variations in temperature than those encountered in the Antarctic Ocean, the ancestral environment of the group. In this study the influence of temperature on the routine metabolic rate of Subantarctic teleosts was described and the results were compared with routine metabolic rates of species with different geographical distributions, exploring the concept of Metabolic Cold Adaptation (MCA). Oxygen consumption (VO_{2R}) was determined as an estimate of the routine metabolic rate for the following Subantarctic notothenioids: *Paranotothenia magellanica*, *Patagonotothen sima*, *Eleginops maclovinus*, *Harpagifer bispinis* and the eelpout *Austrolycus depressiceps*. In all studied species and tested temperatures, body mass and VO_{2R} showed a positive correlation. A drop in the temperature from 10 to 2°C produced a significant reduction of VO_{2R} values with a $Q_{10\,(10\text{-}2)}$ varying between 4.69 and 9.54. VO_{2R} values were related to species habitat: pelagic species reached the highest values of VO_{2R}, while sluggish species had the lowest ones. We can conclude that the metabolic rates of these species of Subantarctic fish do not show MCA at the investigated temperatures.

Keywords: metabolic cold adaptation, Subantarctic fish, notothenioids, respirometry, temperature.

RESUMEN: INFLUENCIA DE LA TEMPERATURA, HÁBITAT Y MASA CORPORAL EN LA TASA METABÓLICA DE RUTINA DE TELEÓSTEOS SUBANTÁRTICOS. – Los nototénidos subantárticos se encuentran expuestos a mayores variaciones de temperatura que las del Océano Antártico, el ambiente ancestral del grupo. En este estudio, se describe la influencia de la temperatura en la tasa metabólica de rutina de teleósteos subantárticos. Los resultados fueron comparados con tasas metabólicas de rutina de especies con diferente distribución geográfica, explorando el concepto de Adaptación Metabólica al Frío (AMF). Se determinó el consumo de oxígeno (VO_{2R}) como una estimación de la tasa metabólica de rutina para las siguientes especies de nototénidos subantárticos: *Paranotothenia magellanica*, *Patagonotothen sima*, *Eleginops maclovinus*, *Harpagifer bispinis* y el Zoarcidae *Austrolycus depressiceps*. La masa del cuerpo y la VO_{2R} mostraron una correlación positiva en todas las especies estudiadas y temperaturas experimentales. Una disminución de la temperatura de 10 a 2°C produjo una reducción significativa de los valores de VO_{2R}, con un $Q_{10\,(10\text{-}2)}$ que varió entre 4,69 y 9,54. Los valores de VO_{2R} estuvieron correlacionados con el hábitat particular de cada especie. Las especies pelágicas alcanzaron los valores más altos, mientras que las especies poco activas tuvieron los más bajos. Podemos concluir que la tasa metabólica de estos peces subantárticos no presenta AMF a las temperaturas ensayadas.

Palabras clave: adaptación metabólica al frío, peces subantárticos, nototenioideos, respirometría, temperatura.

INTRODUCTION

The hypothesis of Metabolic Cold Adaptation (MCA) predicts a higher metabolic rate than that expected by extrapolation of data from warmer water species. Since this was started by Krogh (1916), followed by Scholander (1953) and Wohlschlag (1960), the Metabolic Cold Adaptation (MCA) theory has gained support among some authors (Torres and Somero, 1988a, b; Crockett and Sidell, 1990; Pörtner *et al.*, 2000; Pörtner, 2002), and generated disagreement among others (Holeton,

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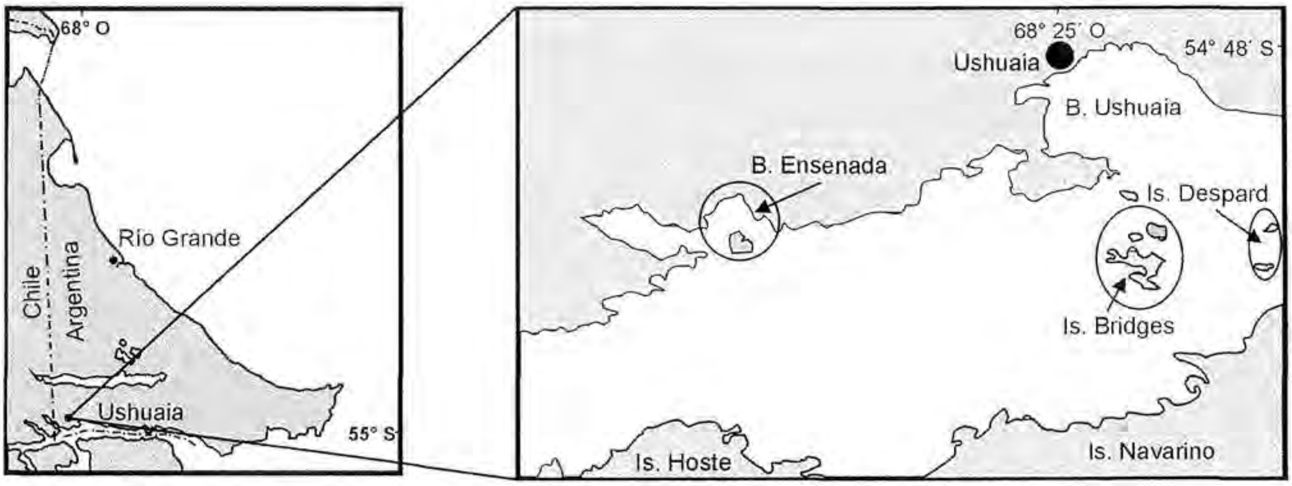

FIG. 1. – Geographical reference of the sampling area (in dark grey). Ushuaia Bay, Despard Is, Bridges Is. and Ensenada Bay.

1974; Steffensen *et al.*, 1994; Steffensen, 2002). As a valid method, Somero (1991) suggested a comparison between species belonging to the same genus or family. Clarke and Johnston (1999) emphasised the value of comparisons between Antarctic notothenioids and perciforms of warmer waters. Remarkably, Clarke (1991) proposed initially an approach at cellular level to contribute to the discussion on MCA and temperature compensation.

Metabolism of Antarctic and Arctic poikilotherms has been under review, in the search for a deeper understanding of the influence of body size, life style and temperature on metabolic activity. These aspects vary according to the evolutionary history of each species and the individual thermal record (Peck, 2002; Sidell, 2000).

Scaling is the structural and functional consequence of changes in body size or scale among otherwise similar organisms (Schmidt-Nielsen, 1984). For fishes, this correlation has been fairly well demonstrated (Clarke and Johnston, 1999; Willmer *et al.*, 2000).

Oxygen consumption rate was found to be correlated with the habitat for Arctic and Antarctic fishes (Morris and North,1984; Zimmermann, 1997).

Subantarctic notothenioids are exposed to a wider variation in temperature than those encountered in the Southern Ocean, making this group well suited to perform comparative analyses. However, only few data are available on their metabolic aspects (Johnston et *al.*, 1998).

The aims of this study are to investigate the influence of temperature, habitat and body mass on the routine metabolic rate of Subantarctic teleosts, and to compare the results with routine metabolic rates of species with different geographical distributions, exploring the concept of Metabolic Cold Adaptation (MCA).

MATERIAL AND METHODS

Samples

The adults or juvenile fish used in this study were captured by hand, trammel nets or seine around the area of Bahía Ushuaia (Tierra del Fuego, Argentina) and its vicinity in summer, from 1999 to 2003 (Fig. 1). Water temperature ranged from 4 to 10°C in winter and summer respectively.

The following species were used in this study: Nototheniidae: *Paranotothenia magellanica* (Hutton, 1875; capture technique, trammel net; depth, 10 m); *Patagonotothen sima* (Richardson, 1845; Capture technique, trap; depth, 0-5 m). Eleginopidae: *Eleginops maclovinus* (Valenciennes, 1830; Capture technique, seine; depth, 0-1 m), Harpagiferidae: *Harpagifer bispinis* (Schneider, 1801; capture technique, hand; depth, intertidal zone), Zoarcidae: *Austrolycus depressiceps* (Regan, 1913; capture technique, hand; depth, intertidal zone). The standard

TABLE 1. – Habitat and physical characteristics of species which were studied in the present work. ± = standard deviation.

Species	Habitat	Standard Length (LS mm)	Body Mass (M g)
P. magellanica	Pelagic	202 ± 32	126.87 ± 64.63
P. sima	Benthopelagic	117 ± 11	27.35 ± 7.14
E. maclovinus	Benthopelagic	97 ± 36	14.29 ± 14.15
H. bispinis	Benthic	74 ± 5	6.26 ± 1.15
A. depressiceps	Benthic	111 ± 58	10.55 ± 20.27

length (SL), body mass (M) and habitat of each species under study were different (Table 1).

The experiments were carried out with a photoperiod of 12 hours dark/12 hours light and the fish were not fed for at least 15 days before VO_{2R} measurements were obtained. Each specimen was acclimatised to 10°C (± 1) for 15 days inside individual stop flow respirometric chambers immersed in a tank of air-saturated seawater. The acclimatisation time was according to Shrode *et al.* (1982). After this period, the chamber was closed for 1-6 hours. The time that the camera remained closed was adjusted to make sure that the O_2 saturation never descended below 80%. Samples of 10 ml of water were taken through a rubber cup with a syringe. The flexible material of the walls of the chamber allowed the volume compensation. Oxygen concentration was measured using a Clark-type polarographic electrode. Oxygen consumption data were taken 1-2 times a day until O_2 consumption reached a stable routine level. The last 5 days of routine O_2 consumption were used to calculate VO_{2R} by a mean.

Respirometric chambers were made of translucent plastic material, which prevented visual stimulation from external sources. Three types of respirometric chamber were used, according to the fish size. The biggest one, used with only one specimen of *E. maclovinus*, had a volume of 11 l, about 10 times the fish. The second chamber type had a volume of 3.17 l, about 12 times the volume of the biggest *P. magellanica* used in this kind of chamber. The third type of chamber had a volume of 316 ml, about 30 times the volume of the biggest *A. depressiceps* used in this kind of chamber. In all cases, the volume of the chamber was found to be sufficient to allow spontaneous fish movements. The first and second types of chamber were furnished with transparent observation windows, regularly closed with a translucent lid during the experiments.

After VO_{2R} at 10°C was measured, the temperature was lowered by 1°C per day until a temperature of 4°C was reached. This temperature was maintained for ten days before VO_{2R} was determined. The same procedure was followed for the determination at 2°C.

E. maclovinus did not tolerate prolonged confinement, so two groups of fish were used. One group of fishes was used in the experiment at 10°C and another at 4°C and 2°C.

In order to compare species and VO_{2R} at different temperatures, the allometric scaling equations ($\mathrm{Ln}\ VO_{2R} = a\ \mathrm{Ln}\ M + b$) were obtained for each temperature and species. To perform a more general comparison, three inter-specific power equations were calculated for each temperature. For one of them, data from all species were used. For the other two, data obtained from benthic and pelagic and benthopelagic species were separated. The rate of O_2 consumption was calculated for a standard fish of 50 g body mass and expressed by kilogram using the allometric equations mentioned above.

Q_{10} values were calculated from the variation in oxygen consumption of a standard fish of 50 g body mass and expressed by kilogram. The formula used was:

$$Q_{10} = (VO2_{R2} / VO2_{R1})^{10/(t2-t1)}$$ (Jobling, 1994).

Statistics

To test dependence between body mass and VO_{2R}, an ANCOVA analysis was performed. Differences between slopes and elevations of regression lines were analysed to test the influence of temperature on VO_{2R} (Zar, 1984).

RESULTS

The results of oxygen consumption in the different species studied are synthesised in Figure 2. Oxygen consumption increased with both fish body mass and water temperature. Regression analysis showed that the VO_{2R} increased significantly with fish body mass (M) ($p<0.05$) for all temperatures and for all species. The same statistically significant relationship was found for all species considered together and for the active and sluggish groups (Table 2; Fig. 2).

A specific response was obtained when temperature was reduced from 4 to 2°C (Table 2): the decrease in VO_{2R} was small in the most active species (*E. maclovinus* and *P. magellanica*), whereas in the other—more sedentary—species the decrease was more pronounced.

A decrease in temperature from 10 to 4 °C caused significant differences ($p<0.05$) in the elevation of all regressions that describe VO_{2R} response, except for *P. sima*. Reduction of temperature from 4 to 2°C produced significant differences in VO_{2R} only in *P. sima* and *H. bispinis*, while in the other species it produced a non-significant reduction. Differences between elevations of the 10 and 2°C curves were significant in all species.

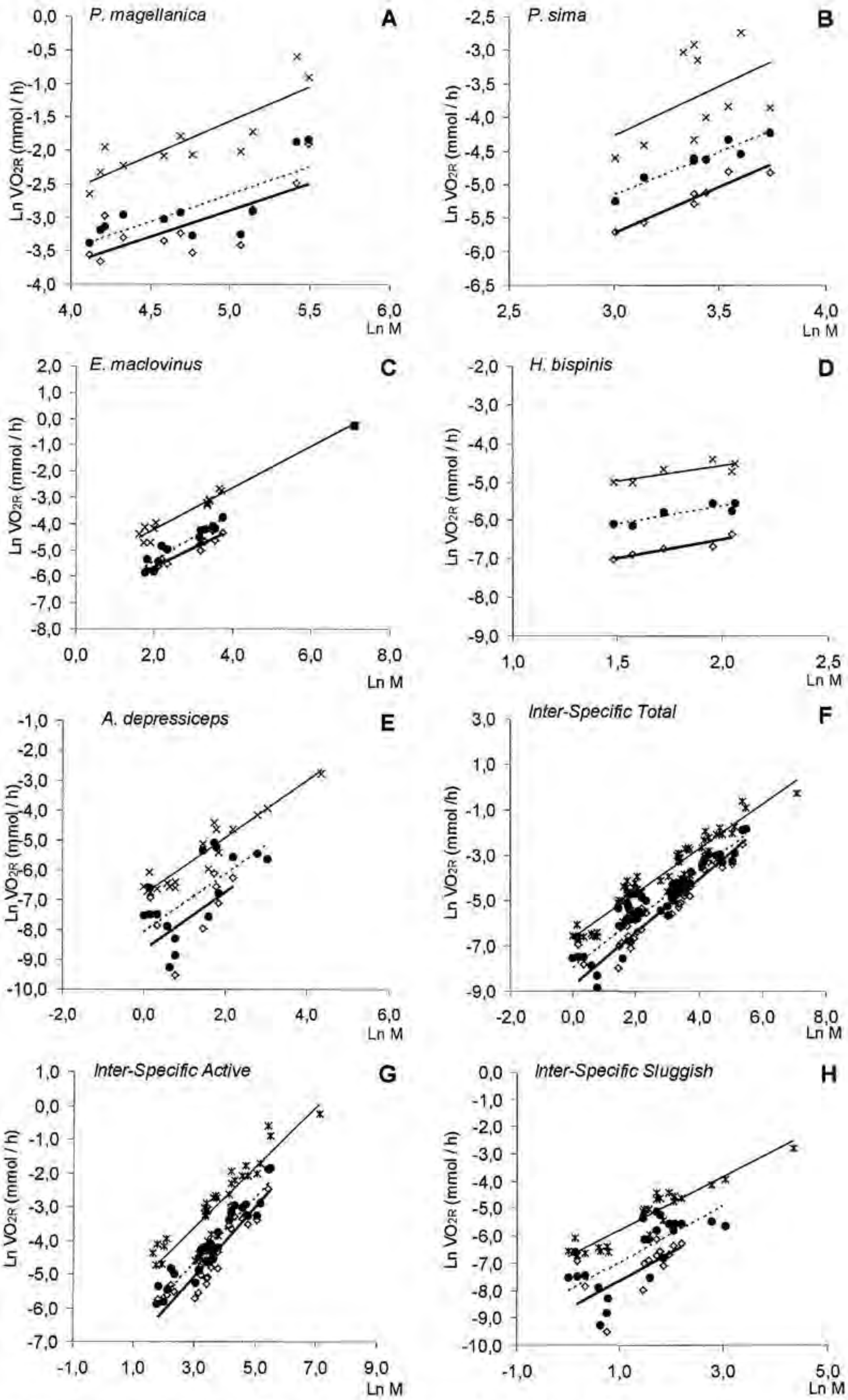

FIG. 2. – Relationship between the logarithm of body mass in g (Ln M) and the logarithm of the routine metabolic rate in mmol O_2 / h, (Ln VO_{2R}) at different experimental temperatures (× = 10ºC; ● = 4ºC; ◊ = 2ºC). A – E) Subantarctic teleosts used in present work (■ in *E. maclovinus* out of ANCOVA analysis). F) Interspecific total. G) Inter-specific active. H) Inter-specific sluggish.

TABLE 2. – Allometric scaling equation for species and temperature. Differences between elevation of regression lines are exposed in the Elev column. Routine Oxygen Consumptions (VO_{2R}) for a standard 50 g fish (mmol O_2/h/kg). Values of R^2 are shown.

Species	T (°C)	n	Scaling Equation Ln VO_{2R} =	Elev	VO_{2R} mmol/h/kg	R^2
P. magellanica	10	11	1.029 Ln M - 6.7163	a	1.36	0.73
	4	11	0.8135 Ln M - 6.737	b	0.57	0.57
	2	11	0.7913 Ln M - 6.8565	b	0.47	0.55
P. sima	10	10	1.4684 Ln M - 8.6727	a	1.08	0.21
	4	8	1.2814 Ln M - 9.0024	b	0.37	0.91
	2	7	1.3547 Ln M - 9.7871	c	0.23	0.92
E. maclovinus	10	13	0.7862 Ln M - 5.7888	a	1.33	0.97
	4	12	0.9132 Ln M - 7.2614	b	0.50	0.91
	2	10	0.7272 Ln M - 7.1057	b	0.28	0.92
H. bispinis	10	6	0.8056 Ln M - 6.1847	a	0.96	0.68
	4	6	0.8922 Ln M - 7.436	b	0.39	0.80
	2	5	0.964 Ln M - 8.4283	c	0.19	0.88
A. depressiceps	10	14	0.9504 Ln M - 6.8193	a	0.90	0.89
	4	13	0.9569 Ln M - 8.0607	b	0.27	0.45
	2	7	0.9605 Ln M - 8.6686	b	0.15	0.33
Inter-Specific Total	10		0.9843 Ln M - 6.6778		1.18	0.92
	4		1.06 Ln M - 7.9919		0.43	0.86
	2		1.1662 Ln M - 8.735		0.31	0.89
Inter-Specific Active	10		0.8901 Ln M - 6.2661		1.28	0.83
	4		0.9545 Ln M - 7.5172		0.46	0.90
	2		1.0256 Ln M - 8.1422		0.32	0.86
Inter-Specific Sluggish	10		0.9755 Ln M -6.7603		1.05	0.88
	4		1.0381 Ln M - 8.0354		0.38	0.50
	2		1.0378 Ln M - 8.6893		0.20	0.42
Intra-Specific b mean			0.99			

TABLE 3. – Q_{10} values obtained of changes in temperature 2-10°C and 4-10°C. Q_{10} were calculated using oxygen consumption for a 50 g standard fish by kg.

Thermic range (°C)	*P. magellanica*	*P. sima*	*E. maclovinus*	*H. bispinis*	*A. depressiceps*
2-10	3.81	7.04	6.91	7.60	9.63
4-10	4.22	6.00	5.08	4.56	7.61

In the analyses of the scaling equations, separately for each species or after pooling data according to the habitat, the active species (*E. maclovinus*, *P. sima*, *P. magellanica*) showed a consistent tendency to reach higher values than the sluggish species (*A. depressiceps*, *H. bispinis*) for each temperature (Fig. 2, Table 2). Except for *P. magellanica*, in all the studied species the Q_{10} values for the 2-10ºC interval were higher than for 4-10ºC (Table 3). The highest values of Q_{10} were reached by the non-notothenioid sluggish *A. depressiceps*.

DISCUSSION

The experimental temperatures applied in this study (10-2ºC) with Subantarctic notothenioids fills the discontinuity between metabolic responses of Antarctic nototheniods and temperate percifoms (Fig. 3). This gap constitutes a problem mentioned by Clarke and Johnston (1999), and originates in the inability of polar fish to live at temperatures higher than 6ºC and the lethal effect of temperatures close to 0°C for temperate perciform fishes. The highest experimental temperature used in this study (10ºC) represents the maximum to which some Subantarctic species are exposed during a "regular summer". Oxygen consumption at this temperature showed a noticeable increase, reaching values two or three times greater than the "regular winter" (4ºC) conditions (Fig. 3 and Table 2).

Oxygen consumption rate, like many other metabolic processes, is largely related to body mass, following the general power equation $VO_{2R} = a\ M^b$,

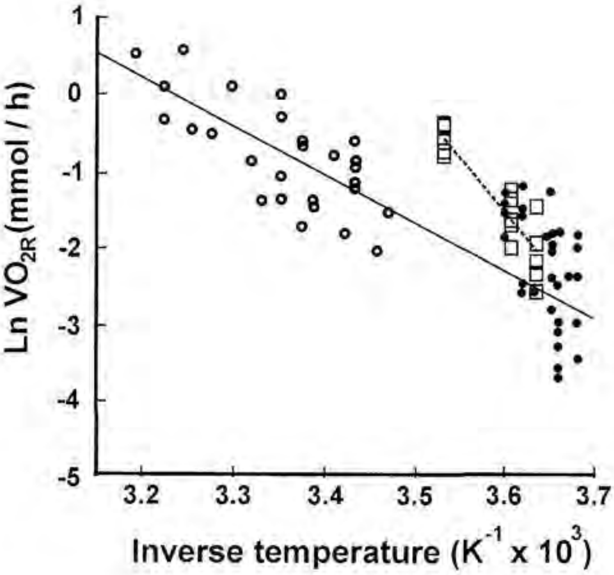

FIG. 3. – Arrhenius plot of VO_{2R} of Subantarctic perciforms (❏; present work), Antarctic notothenioids (●) and warmer water perciforms (○ non notothenioids). Oxygen consumption values standardised for a 50 g fish. Regression line (—) fitted to warmer water perciforms. Regression line (---) fitted to Subantarctic perciforms (present work). Adapted from Clarke and Johnston (1999)

(Jobling, 1993; West *et al.*, 1997). Clarke and Johnston (1999) reviewed this subject, analysing the results of 138 publications on relationships between temperature, body size and routine oxygen consumption in 69 species of fishes. The slope (b) of specific equations varied between 0.3 and 1.2, with a mean value of 0.79. In our study values of b for active, sluggish or all the species together at each experimental temperature (Table 2) were higher than the mean obtained by Clarke and Johnston (1999) but within the range of distribution of their data.

VO_{2R} values of Subantarctic species of this study were correlated with habitat (Table 2). *Paranotothenia magellanica* has the highest oxygen consumption rates at all experimental temperatures. This species was reported as highly mobile (Moreno and Jara, 1984) and shows swimming movements in aquaria more frequently than the other Subantarctic species studied in our laboratory (pers. obs.).

VO_{2R} values of *E. maclovinus* are similar to *P. magellanica* values at 10 and 4 °C but drop to a level similar to that observed in the less active species at 2°C (Table 2). An explanation of this phenomenon could be that *P. magellanica*, more active than *E. maclovinus*, could maintain a higher O_2 consumption at low temperatures. On the other hand, the authors saw that many specimens of *E. maclovinus* showed signs of low tolerance to the confinement in respirometric chambers, which can cause a high VO_2, especially at summer temperatures. However, O_2 consumption in this species remained stable once routine values were reached, after the initial stress period. Although oxygen consumption of *H. bispinis* and *A. depressiceps* was virtually identical at 10°C, a higher VO_{2R} was calculated for the Harpagiferidae at 4 and 2°C. This species is more active than *A. depressiceps* in both aquaria and the rocky intertidal zone, its natural environment (pers. obs.). This correlation between habitat and VO_{2R} was also reported for other notothenioids by Morris and North (1984) and Zimmermann (1997), but a correspondence between temperature or habitat is not observed for the specific mass exponent b (Table 2).

At both temperature ranges, 2-10 and 4-10°C, Q_{10} values of *P. magellanica* were the lowest, while *A. depressiceps* reached the highest values (Table 3). A Q_{10} with a similar value, around 9, has been calculated for the Antarctic eelpout *Pachycara brachycephalum* at 3-9°C (Hardewig *et al.*, 1998). It is therefore possible to assume a greater effect of temperature limiting the oxygen consumption for the sluggish Subantarctic eelpout in this thermal range. This difference in reactions to changes in temperature would be predictable if a strong influence of habitat in VO_2 consumption were present. However, high values of Q_{10} were observed in the other species used in this study. Another explanation is that in this work the fish did not show compensation responses during the acclimation time. When VO_2 became stable, it persisted for longer than 15-20 days. However, if this time was too short to allow the expression of compensation processes, an overreaction could be expected in the Q_{10} values.

The VO_{2R} values of Subantarctic teleosts obtained in this study (Fig. 3) are higher than the general regression line drawn up by Clarke and Johnston (1999) with non-notothenioid warm water fish. Although data used by Clarke and Johnston were obtained under resting conditions, the difference is negligible at 4 and 2°C. This small difference from the resting data at winter temperatures could show an effective acclimation process to winter temperatures in the time that the animals had available to carry out this process.

The present values obtained at 10°C are considerably higher than the regression line obtained by Clarke and Johnston (1999) for temperate perciforms. A possible explanation for Subantarctic notothenioid species could be the hypothesis of Pörtner *et al.* (2000) and Pörtner (2002). These authors relate the reduction in energy demand and high activation energies of mitochondrial enzymes involved in the oxygen demand with the low metabolic rates in stenothermal fish adapted to cold. In the case of Subantarctic notothenioids, kinematic barriers could be established by the environmental temperatures, producing an extremely high value of VO_{2R} at 10ºC (Fig. 3). Another reason for this overreaction at 10°C could be an increase in the corporal movement caused by high temperature. Again, an appropriate quantification of activity could be necessary to determine resting O_2 consumption.

Our results are not conclusive, but the wide range of responses obtained suggests an evolutionary adjustment to the variable Subantarctic environment and an increase in width of the tolerance window over the ancestral thermal range. We can conclude that the metabolic rates of the studied species of Subantarctic notothenioids do not show MCA in the Krogh (1916) definition *sensu stricto*. However, an overreaction in the metabolic responses of notothenioids at Subantarctic summer temperatures could be the expression of the metabolic adjustment of the more stenothermal Antarctic ancestors to cold temperatures.

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Muscle growth in Antarctic and Subantarctic notothenioid fishes*

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SUMMARY: The suborder Notothenioidei comprises 122 species divided into 8 families, with members of 6 of the families living outside Antarctic waters. The Antarctic species underwent an extensive radiation from a small demersal ancestor to occupy different ecological niches and levels in the water column. The axial muscle of Antarctic and some Subantarctic notothenioids is unusual in containing very large diameter muscle fibres and a low muscle fibre number. Maximum fibre diameters are greater than 500 μm in many species. There is no indication of systematic differences in fibre number, fibre type composition, ATPase activity, time of cessation of fibre recruitment (hyperplasia) and swimming performance between Antarctic and Subantarctic species. Instead, fibre number is significantly decreased in species belonging to the most derived families relative to the more basal families (a trend that also correlates with an increase in the diameter of the fibres). The length of the cell cycle of the muscle fibres shows cold compensation in the Antarctic species *H. antarcticus* relative to the closely related Subantarctic one (*H. bispinis*). Feeding after a starvation period results in a strong stimulation of the proliferation of muscle fiber progenitors in *H. bispinis*. Similar studies have not yet been performed on any Antarctic species.

Keywords: Antarctic notothenioids, Subantarctic notothenioids, muscle development, muscle growth, temperature, hypertrophy, hyperplasia.

RESUMEN: CRECIMIENTO MUSCULAR EN NOTOTÉNIDOS ANTÁRTICOS Y SUBANTÁRTICOS. – El suborden Notothenioidei comprende 122 especies divididas en 8 familias, incluyendo miembros de 6 de las familias que viven en aguas subantárticas. Las especies antárticas sufrieron una impresionante radiación a partir de un ancestro pequeño y demersal que les permitió ocupar diferentes nichos ecológicos y niveles en la columna de agua. El número total de fibras de la musculatura axial de nototénidos antárticos y algunos subantárticos es escaso y las fibras presentan un tamaño inusualmente grande, alcanzando diámetros máximos mayores a 500 μm en muchas de las especies estudiadas. No existen diferencias sistemáticas entre la musculatura axial de nototénidos antárticos y subantárticos en el número de fibras musculares, los tipos de fibras musculares, la actividad ATPasa, el momento de cese de incorporación de fibras musculares (hiperplasia), ni en la capacidad (performance) natatoria a diferentes temperaturas. De hecho, el número de fibras musculares es significativamente menor en las especies pertenecientes a las familias más derivadas en comparación con especies de las familias más basales (una tendencia que también se correlaciona con un incremento en el diámetro de las fibras). La duración del ciclo celular muestra una compensación al frío en la especie antártica *H. antarcticus* en comparación con la especie subantártica más relacionada (*H. bispinis*). La alimentación luego de un período de ayuno produce una fuerte estimulación en la proliferación de progenitores de las fibras musculares en *H. bispinis*. No se han realizado aún estudios similares en especies antárticas.

Palabras clave: nototénidos antárticos, nototénidos subantárticos, desarrollo muscular, crecimiento muscular, temperatura, hipertrofia, hiperplasia.

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THE SOUTHERN OCEAN

Antarctica is certainly the most isolated and extreme continent in terms of the environmental conditions to which terrestrial and marine organisms are exposed. The Antarctic continent is surrounded by the Southern Ocean, one of the deepest and coldest seas in the world. The Southern Ocean is fairly stable in terms of water temperature, with the continental shelf waters typically at or below the freezing point of seawater (Eastman, 1993) and with warming episodes during summer time (Hunt *et al.*, 2003). Up to half of the Southern Ocean is covered with pack ice during the maximum coverage period in the region south of the Antarctic Polar Front (APF). The isolation of Antarctica is a very interesting and long process that took place over more than a hundred million years and culminated after the establishment of the APF, initiating a long period of climatic cooling that persists up to the present (Eastman, 1993). The understanding of the geological evolution of the Antarctic continent is very important in order to understand the natural history of the extant fauna.

By the end of the Cretaceous (75-65 Ma) the Antarctic continent was still connected to Australia and South-America. Geological and geophysical evidence indicates that the link to Australia, the South Tasman Rise, may have been submerged by as early as 64 Ma and fully separated from Antarctica by deep water around 50 Ma. The separation from South America, the opening of the Drake Passage, occurred later, but the exact time of occurrence is still uncertain. Seafloor spreading produced magnetic anomalies in the Drake Passage region by at least 28 Ma. Moreover, palaeoceanographic evidence suggests the existence of a significant marine opening, probably shallow waters, as early as 36 Ma (reviewed in Crame, 1999).

Changes in the palaeotemperature of the globe have been inferred from the ratio of the oxygen isotopes in the calcium carbonate of microfossil foraminiferal shells (Clarke and Johnston, 1996, Zachos *et al.*, 2001) (Fig. 1). Major cooling of marine temperatures occurred after the Eocene Climatic Optimum, with much of the change occurring over the early-middle (50 to 48 Ma) and late Eocene (40 to 36 Ma), the early Oligocene (35 to 34 Ma), and the middle-late Miocene (14 to 10 Ma).

The southernmost part of South America is the closest landmass to Antarctica. Under present-day conditions the interchange of fauna between them is restricted by deep water, but that was not the case for a long period of time prior to the establishment of the APF.

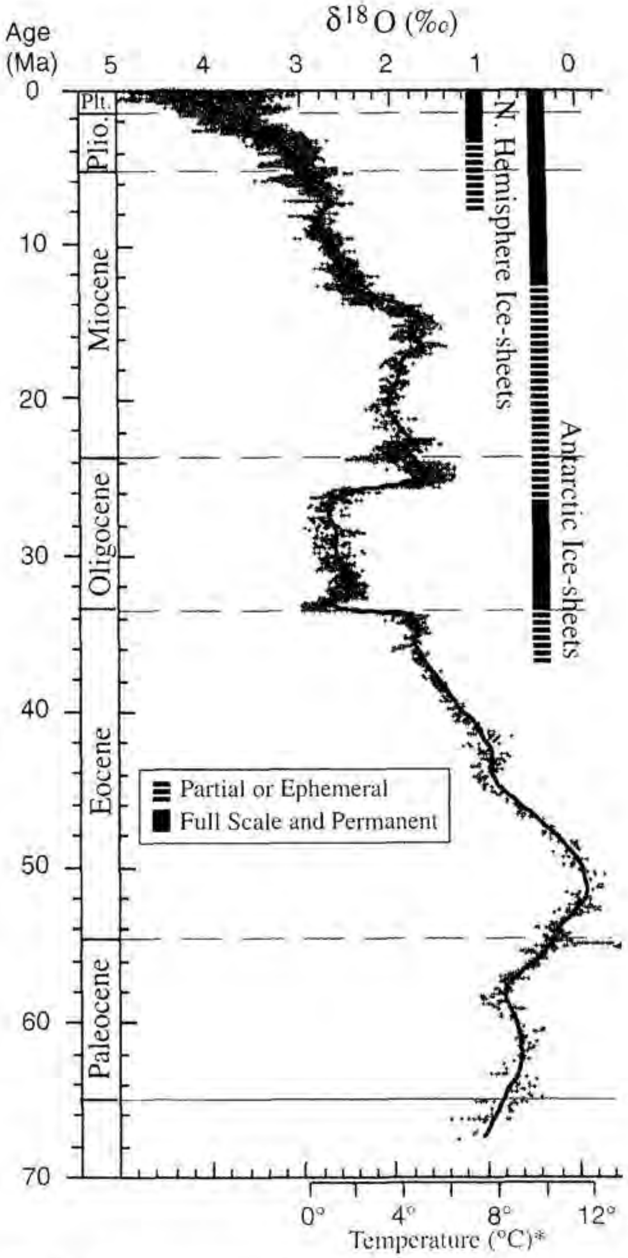

FIG. 1. – Schematic representation of the variation of the deep-sea water temperatures inferred from palaeoclimate data. Modified from Zachos *et al.* (2001).

THE SUBORDER NOTOTHENIOIDEI

The highly endemic adaptive radiation of the suborder Notothenioidei (Perciformes) is the best example of extensive radiation in a marine fish group (Eastman and Eakin, 2000) and can be considered as a species flock similar to the cottoid species flock in Lake Baikal (Eastman and McCune, 2000). The Notothenioidei dominate the fish fauna of the continental shelf of the Southern Ocean. The suborder comprises 8 families, 43 genera and 122 species, with 26 species belonging to 6 of the families living outside Antarctic waters (Eastman and Eakin, 2000).

The ancestral form of the notothenioids is generally considered to have been a small temperate bottom-living species without a swimbladder. Despite the lack of swimbladder they have undergone an extensive ecological diversification, currently occupying a variety of niches in the water column. Moreover, they show a large diversification in terms of body size, body colour, buoyancy, etc. (Eastman, 1993). The key physiological feature that allowed the Notothenioidei to diversify and become dominant in the fish fauna of the Southern Ocean was almost certainly the development of antifreeze glycoproteins (AFGPs) (Cheng and DeVries, 1991; Eastman, 1993). There are many other important features that are associated unequivocally with the AFGPs, or more widely with living at very low water temperatures: higher blood osmolarity, aglomerular kidneys, low haematocrit counts, etc. The key ecological feature that permitted the diversification of the suborder was probably the weak competition Notothenioids experienced due to the extinction events related to the cooling conditions and the isolation of Antarctica (Eastman, 1993).

Phylogeny of notothenioids

Morphological and molecular-based phylogenies have been constructed in order to understand the radiation that the suborder accomplished. Morphological based phylogenies have been built since the eighties (Eakin, 1981; Balushkin, 1990, 1992, 2000; Eakin *et al.*, 2001), including cladistic analysis (Andersen, 1984; Iwami, 1985). In the absence of a unique osteological character, the suborder was diagnosed by a combination of morphological characters. It was not possible to identify a sister group, with blennioids and zoarcioids as likely candidates. Therefore, characters have often been polarised relative to the Bovichtidae (functional outgroup).

The molecular approach only started about a decade ago, making use of DNA sequence data from mitochondrial and nuclear genes. It mostly supported the analysis based on morphological data. Nevertheless, it contradicts the morphological studies in some instances, for example proposing that Bovichtidae (*Bovichtus* and *Cottoperca*) is the basal family of the suborder (Lecointre *et al.*, 1997) instead of the family Pseudaphritidae (Balushkin, 2000). However, the more basal families (Bovichtidae, Pseudaphritidae and Eleginopsidae) are well established at the base of the tree and except for a single species of bovichtid are represented exclusively by non-Antarctic species (Fig. 2).

Divergence times have been calculated by different authors and methods, and at present there is a

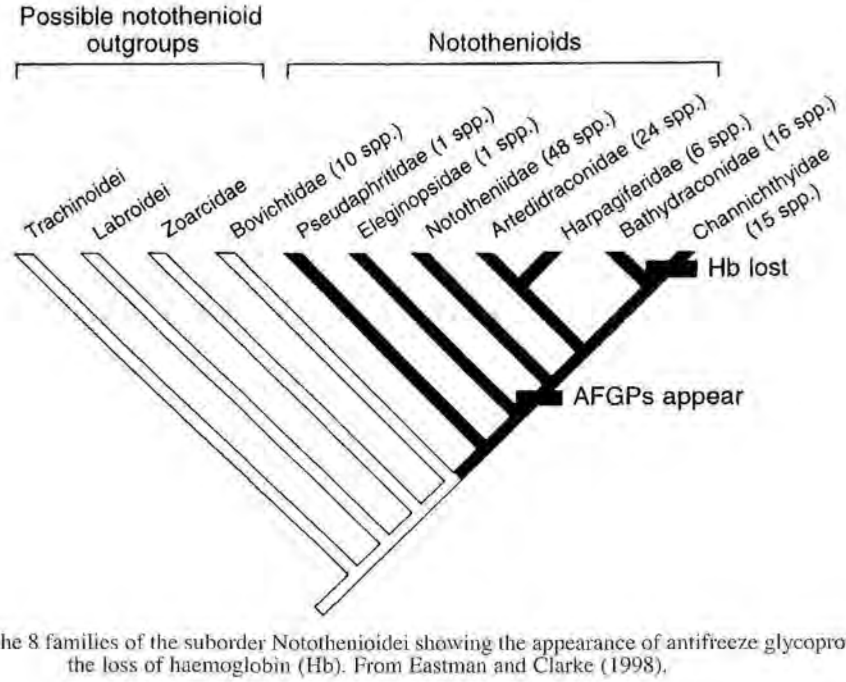

FIG. 2. – Phylogenetic tree of the 8 families of the suborder Notothenioidei showing the appearance of antifreeze glycoproteins (AFGPs) and the loss of haemoglobin (Hb). From Eastman and Clarke (1998).

lack of consensus about the time of occurrence of some important events. For example, the radiation of the AFGP-bearing Antarctic notothenioids took place only about 7-15 Ma (Bargelloni *et al.*, 1994) or 24 Ma ago (Near, 2004) depending on the calibration of the molecular clock. The appearance of the AFGPs was mapped in the tree of the suborder and evidence was found that they evolved only once in the group, after the divergence of the Eleginopsidae (Eastman and Clarke, 1998) that occurred 27 Ma (Bargelloni *et al.*, 1994) or 40 Ma ago (Near, 2004) (Fig. 2). Independently of the divergence times, the number of species in the families derived after the appearance of AFGPs is much higher than that in the basal families (109 versus 12, calculated from Fig. 2), stressing the fact that the acquisition of AFGP was the main characteristic that allowed diversification.

MUSCLE DEVELOPMENT AND GROWTH IN FISH

Four main phases of muscle growth have been described in teleosts, one corresponding to embryonic growth and the other three to post-embryonic growth (reviewed in Rowlerson and Veggetti, 2001). Postembryonic growth can be divided, according to the predominant process that is taking place at a given time of muscle growth, as stratified hyperplasia, mosaic hyperplasia and hypertrophy. Not all phases are present in all fish species, with some species lacking mosaic and/or stratified hyperplasia. The final size of a given species is strongly regulated by the duration of the hyperplastic phases, since that is the period of time when the final number of muscle fibers is established. The final number of fibres restrains the final size of the species because the maximum size of a given fibre has physiological constraints, probably due to limitations in diffusion rates. Only one teleost group, the notothenioids, have shown evidence of an increase in the maximum size of the muscle fibres, probably representing a relaxation of diffusional constraints in a very cold and stable environment.

Embryonic growth

In vertebrates, including fish, the skeletal muscles of the trunk and limb are derived from the somites. The somites are formed from the paraxial mesoderm in a rostral to caudal sequence and their number varies greatly in teleost fish, from 26 in the platy fish to more than 200 in some eels (Richardson *et al.*, 1998). The basic helix-loop-helix family of transcription factors (bHLH), *MyoD*, *Myf5*, *myogenin* and *MRF4* play a major regulatory role in myogenesis (Megeney and Rudnicki, 1995; Ordahl and Williams, 1998). *MyoD* and *Myf5* are somehow redundant but necessary for myogenic determination, and the loss of both in double mutant mouse results in myoblasts failing to form skeletal muscle (Rudnicki *et al.*, 1993). Myogenin and MRF4 act afterwards in myogenic differentiation (Tajbakhsh and Buckingham, 2000).

The patterning of the embryonic muscle is regulated by interplay of midline signals, including at least three different families of proteins: Hedgehog (Hh), bone morphogenic protein (BMP) and Wnt. These signals play an important role in the regulatory network that controls *Myf5* and *MyoD* activation in muscle progenitors (Pownall *et al.*, 2002). Devoto *et al.* (1996) demonstrated that sonic hedgehog induces slow muscle fate in zebrafish. More recently, it has been shown that sonic hedgehog behaves as a morphogen, inducing four different cell types in a concentration-dependent manner. The induction is not restricted to the slow muscle lineage, with a subset of fast muscle fibres also depending on sonic hedgehog expression (Wolff *et al.*, 2003).

The patterning of the paraxial mesoderm has been extensively studied in zebrafish. Two populations of muscle precursors are present in the embryo: the adaxial and the lateral presomitic cells. The adaxial cells are medial cuboidal cells adjacent to the notochord that express *MyoD* and slow myosin isoforms early in the embryo development, prior to their morphological change and migration to the surface of the myotome to form the monolayer of slow muscle fibres (Devoto *et al.*, 1996). The migration of the adaxial cells to form the monolayer of slow muscle fibres has also been described for other teleost such as pearlfish (*Rutilus frisii meidingeri*) (Stoiber *et al.*, 1998), rainbow trout (*Oncorhynchus mykiss*) (Rescan *et al.*, 2001), Atlantic herring (*Clupea harengus*) (Temple *et al.*, 2001), and sea bream (*Sparus aurata*) (Tan and Du, 2002). A subset of the adaxial cells, the muscle pioneers, expresses *Engrailed* proteins and remains attached to the notochord, extending from the notochord to the surface of the somite. The lateral presomitic cells are smaller, have an irregular shape and are separated from the notochord by the adaxial cells. They only express *MyoD* after somite formation and will form in the embryo the bulk of fast muscle fibres (Devoto *et al.*, 1996).

Post-embryonic growth

Two processes occur during postembryonic growth: the addition of new fibres (hyperplasia) and the growth in size of the existing ones (hypertrophy). The proliferation of a population of myogenic progenitors is the source of nuclei for fibre recruitment and hypertrophy (Koumans and Akster, 1995). These progenitors correspond to the cells that had first been identified as "satellite cells" in frog by Mauro (1961) and afterwards in avian and mammalian muscle (reviewed in Bischoff, 1994). Muscle is a postmitotic tissue and all growth that occurs after the embryo formation, as well as regeneration after injury episodes, is due to the activation of the satellite cell population. The progeny of these cells either fuse to each other forming a new muscle fibre (hyperplasia) or fuse to the surface of existing fibres to increase their size (hypertrophy). Several quiescent and satellite cell markers, including *MNF, c-met, Pax-7, M-cadherin* for the former and desmin, *MyoD and Myf5* for the latter, have been identified in recent years (reviewed in Hawke and Garry, 2001). Hyperplasia is without doubt the most important process for determination of the final size of a given species. New fibres can be added in a specific area (stratified hyperplasia) or all over the myotome (mosaic hyperplasia). The process of stratified hyperplasia presupposes the existence of germinal zones that have been described in the myotome of several marine teleost larvae, including anchovy (*Engraulis mordax*) (O'Connel, 1981); Atlantic herring (*Clupea harengus*) (Johnston, 1993); cod (*Gadus morhua*) (Galloway *et al.*, 1999a); halibut (*Hyppoglossus hyppoglossus*) (Galloway *et al.*, 1999b); plaice (*Pleuronectres platessa*) (Brooks and Johnston, 1993); sea bass (*Dicentrarchus labrax*) (Veggetti *et al.*, 1990); sea bream (*Sparus aurata*) (Rowlerson *et al.*, 1995); turbot (*Scophthalmus maximus*) (Gibson and Johnston, 1995); and zebrafish (*Danio rerio*) (Waterman, 1969). There are two main models proposed for stratified growth: A) In zebrafish new slow and fast muscle fibres are first added at the end of the segmentation period from growth zones near the dorsal and ventral extremes of the myotome and close to the horizontal septum. This mode of muscle growth has been proven to continue into larval life, by traditional fibre size measurement, BruU labeling and *in situ* hybridisation (Barresi *et al.*, 2001; Fernández, unpublished results, Fig. 3). This mechanism of growth is the one described for most teleost fishes. B) Rowlerson and Vegetti (2001) proposed another model based especially on sea bream and sea bass (Sparidae). This model postulates the existence of a proliferation zone underneath the monolayer of slow muscle

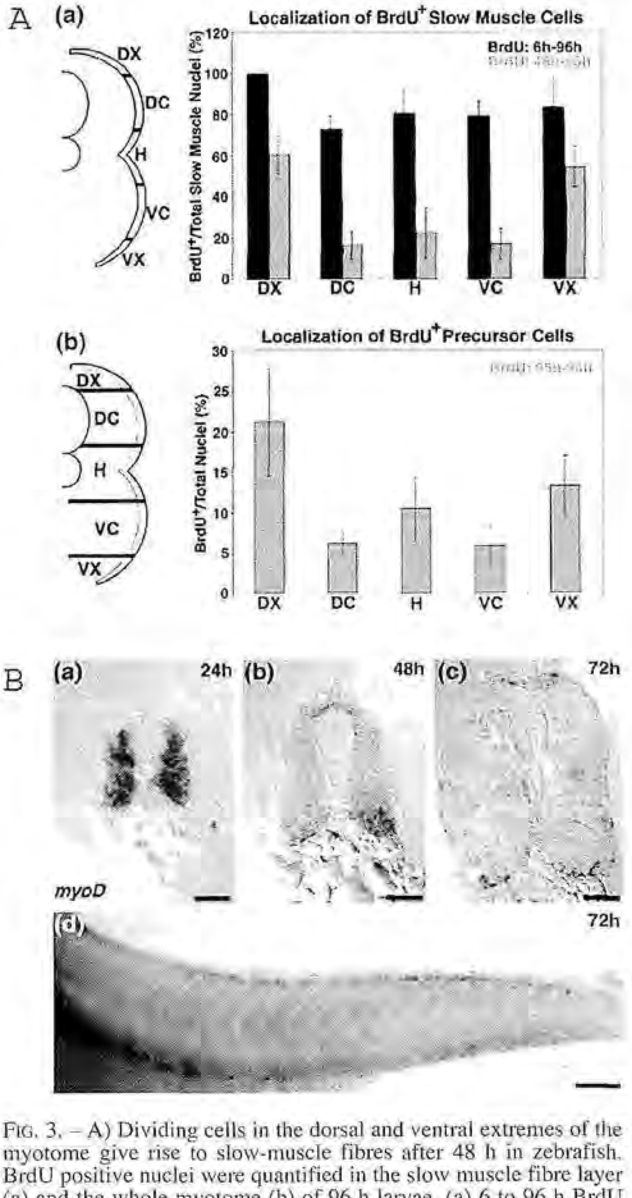

FIG. 3. – A) Dividing cells in the dorsal and ventral extremes of the myotome give rise to slow-muscle fibres after 48 h in zebrafish. BrdU positive nuclei were quantified in the slow muscle fibre layer (a) and the whole myotome (b) of 96 h larvae. (a) 6 to 96 h BrdU incubation showed an even distribution of BrdU-positive nuclei throughout the slow-muscle monolayer (dark bars). However, 48h to 96 h BrdU incubation showed a higher percentage of BrdU nuclei at the dorsal and ventral extremes of the monolayer (light bars). (b) The percentage of BrdU nuclei was higher at the dorsal and ventral extremes of the myotome in larvae incubated in BrdU for one hour (95 to 96 h). B) (a,b,c) Dorsal and ventral growth zones after 48 h in zebrafish. Transverse sections of embryos probed for *MyoD* expression at 24, 48, and 72 h of development show that while *MyoD* is expressed in the whole myotome at 24 h, it is restricted to the dorsal and ventral extreme of the myotome at 48 and 72 h. (d) Lateral view of whole-mount showing *MyoD* expression in every somite of a 72 h embryo. Modified from Barresi *et al.* (2001).

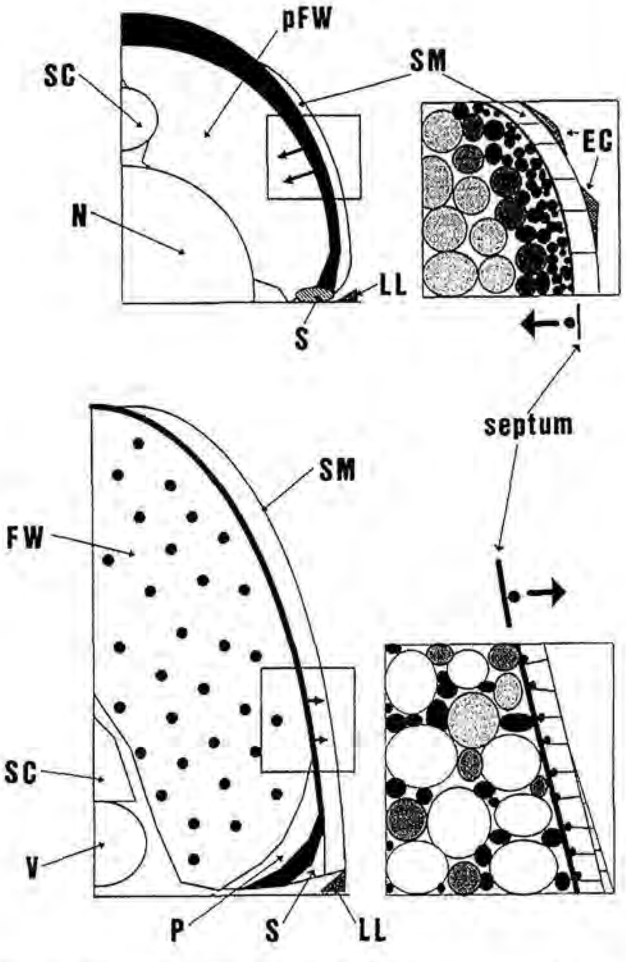

FIG. 4. – Schematic representation of post-embryonic growth in an epaxial quadrant of lateral muscle. Above: in the mosaic hyperplastic phase new fast muscle fibres are generated throughout the myotome generating the characteristic mosaic pattern of fibre diameters in cross-sections. The previous proliferation zone persists for a while but giving rise now to slow muscle fibres and probably to intermediate fibres (also called pink fibres) in the region close to the lateral line. SC= spinal cord, N= notochord, FW= fast muscle layer, pFW= presumptive FW muscle layer, P= pink fibres, V= vertebral column. Below: Stratified hyperplasia occurs in a restricted region of the myotome indicated in black, producing mainly new fibres that contribute to the fast muscle population (see arrows). At the surface of the monolayer of slow muscle fibres (SM), external cells (EC) may be present and may contribute to an additional layer of slow muscle fibres. Phenotypically slow muscle fibres (S) start to appear close to the lateral line (LL). From Rowlerson and Veggetti (2001).

fibres that gives rise to the new fast fibres. At the same time, the new slow fibres could be generated from external cells, appearing mainly close to the horizontal septum (Fig. 4). Other authors have also described external cells but considered that they were not myogenic due to their transient appearance (Johnston, 1993) or to their ultrastructure (Stoiber and Sanger, 1996); their exact role is still uncertain.

The last phase of post-embryonic growth is the one due exclusively to hypertrophy, probably in the same way that muscle growth occurs in mammals after birth. Muscle fibres increase in diameter due to the absorption of additional nuclei, maintaining the nuclei:cytoplasmic ratio between certain limits (Koumans *et al.*, 1993). As stated above, it is likely that a pluripotent stem cell population gives rise to the precursor myogenic cells involved in hyperplasia, hypertrophy and muscle repair, though the embryological origin of these populations remains to be determined.

NOTOTHENIOIDEI MUSCLE

Muscle development in notothenioids

Little is known about muscle development of notothenioid fishes. Embryological development has not been studied yet, while larvae have shown the usual one or two fibre thick superficial layer of slow muscle fibres and a bulk of fast muscle fibres (Dunn *et al.*, 1989, Calvo *et al*, 1995). Muscle development in notothenioids using molecular tools has only started to be studied recently. Partial sequences of M*yoD* were cloned in some species of Antarctic and Subantarctic notothenioids (Fernández *et al.*, unpublished data, GenBank accession nos. AF 396675-80; Johnston *et al.*, 2002) and they showed a very high similarity to the zebrafish sequence (Fig. 5).

Fibre type distribution in the myotome and pectoral fin muscle

At least four different fibre types have been characterised in the axial muscles of Subantarctic notothenioids by means of histochemical techniques for myosin ATPase, succinic dehydrogenase (SDHase), glycogen and lipid: slow, tonic, intermediate and fast (Fernández *et al.*, 2000). Slow and fast muscle fibres show respectively high and low activities of SDHase, reflecting their different mitochondrial contents. The myosin ATPase of slow and fast muscle fibres shows a different susceptibility to inactivation by low (pH 4.3) or high pH (10.4). Preincubation at different pHs prior to staining for myosin ATPase can be used to characterise different fibre types when performed at room temperature in Subantarctic notothenioids (Fernández *et al.*, 2000), but fibres are not well differentiated at 4-6°C (Fernández *et al.*, unpublished data). Similar results were previously reported for Antarctic notothenioids (Davison and MacDonald, 1985; Harrison *et*

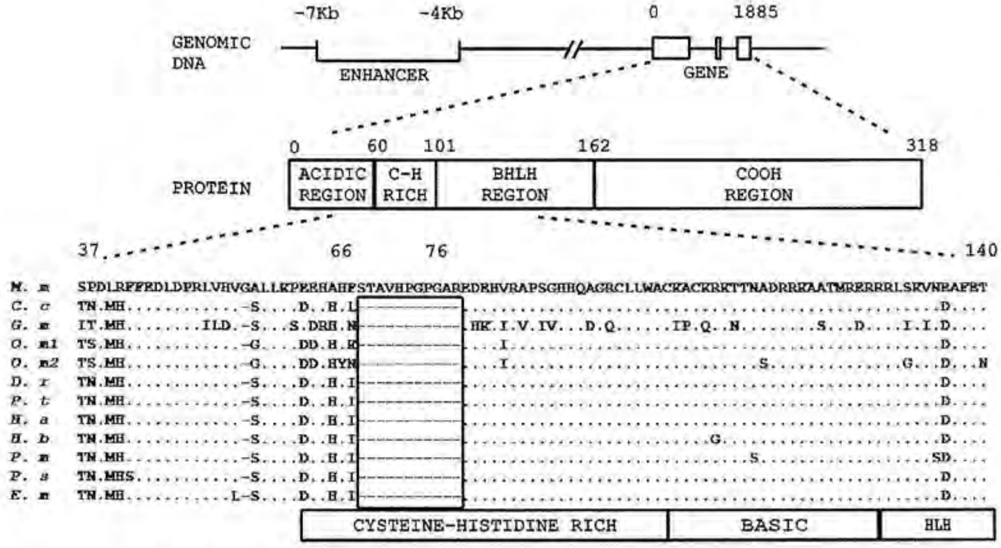

FIG. 5. – Schematic representation of mouse MyoD genomic DNA and protein structure aligned with ten teleost fish species. All fish proteins show an eleven amino acid deletion in the cysteine-histidine (C-H) rich region. *M.m, Mus musculus; C.c, Cyprinus carpio; G.m, Gadus morhua; O.m1, Om2, Oncorhynchus mykiss; D.r Danio rerio; P.t, Patagonotothen tessellata; H.a, Harpagifer antarcticus; H.b, Harpagifer bispinis; P.m, Paranotothenia magellanica; P.s, Patagonotothen sima; E.m, Eleginops maclovinus.* From Johnston *et al.* (2002).

al., 1987; Dunn *et al.*, 1989). The order of inactivation of the different fibre types with alkaline pre-incubation in notothenioids was fast > intermediate > slow (Fig. 6), different to the order found for temperate species which is slow > fast > intermediate (Johnston *et al.*, 1974). Therefore, in general the pH-sensitivity of the ATPase activity of fast muscle fibres in Antarctic and Subantarctic notothenioids was similar to that for slow muscle fibres in temperate or tropical species. However, Johnston (1987) measured the shortening speeds of live fibre bundles and demonstrated that the SDH^{+ve} and SDH^{-ve} muscle fibres in the notothenioid *Chaenocephalus aceratus* corresponded to slow and fast twitch muscle fibres respectively, as in other teleosts. The ATPase results could indicate the existence of different myosin isoforms in notothenioids compared to other teleosts. Interestingly, comparing the sequence and the structure of ATPase sites in myosins, Gauvry *et al.* (2000) found that there was a high similarity between the fast myosin of tropical species and the slow myosin of Antarctic species.

The different fibre types are relatively segregated in the myotome of notothenioids, with a superficial layer of tonic, slow and intermediate fibres surrounding a core of fast fibres. The same kind of segregation has been described for many other teleost species (Johnston *et al.*, 1974; Smialowska and Kilarsky, 1981) and is strongly related to the needs for swimming. The different fibre types are specialised for working at different swimming speeds (Bone *et al.*, 1978; Johnston and Altringham, 1991).

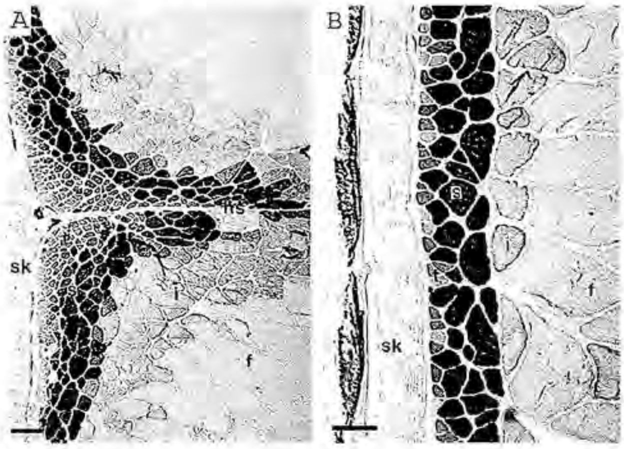

FIG. 6. – Myosin ATPase staining of myotomal muscles in the Subantarctic notothenioid *Patagonotothen tessellata* (13 cm) following pre-incubation at pH 10·6 for 30 s. Slow fibres (s) stain darkly, presumptive tonic fibres (t) and intermediate (i) have a residual activity and fast fibres (f) are completely inactivated. (A) Section at the level of the main horizontal septum; (B) section of the superficial muscle fibres. hs, major horizontal septum; sk, skin. Scale bars: (A) 100 μm, (B) 50 μm. From Fernández *et al.* (2000).

Electromyographic studies on common carp (*Cyprinus carpio*) established that the fibres are sequentially recruited, first slow, then intermediate and finally fast with increasing swimming speed (Johnston *et al.*, 1977). Temperature affects fibre recruitment for swimming; for example, at lower temperatures the carp starts recruiting the fast fibres at lower swimming speeds (Rome *et al.*, 1984). Maximum length specific velocity and acceleration as well as inertial power output during fast-starts varied significantly with temperature in the Subantarctic notothenioid *E. maclovinus* acclimated and tested at

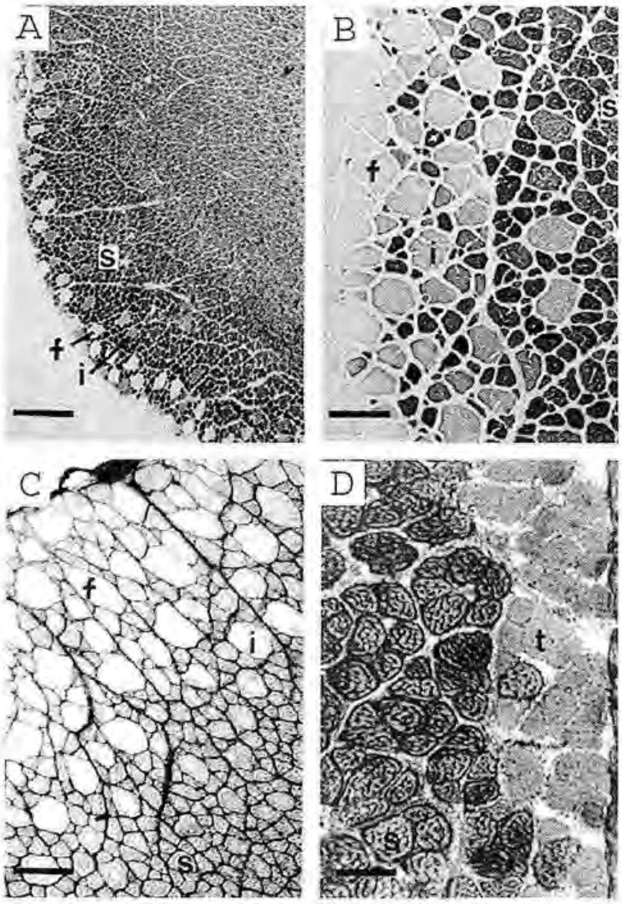

FIG. 7. – Histochemistry of pectoral fin adductor muscle in (A,B) *Eleginops maclovinus* (10 cm *LT*) and (C,D) *Patagonotothen tessellata* (14 cm *LT*). (A) Section stained for myosin ATPase following 30 s pre-incubation at pH 10·4. (B) Section stained for myosin ATPase following 90 s pre-incubation at pH 10·4. (C) Section stained for glycogen. (D) Section stained for succinic dehydrogenase. f, Fast muscle fibres; i, intermediate muscle fibres; s, slow muscle fibres; t, presumptive tonic muscle fibres. Scale bars: (A) 250 µm, (B) 100 µm, (C) 100 µm, (D) 50 µm. From Fernández *et al.* (2000).

2 to 10°C, being maximum at 8°C (Fernández *et al.*, 2002). Burst swimming velocity also varied significantly with temperature for the Antarctic species *Trematomus bernachii* and *T. centronotus* tested between -1°C and 10°C, being maximum at 6°C (Wilson *et al.*, 2001). The analysis of burst swimming after a 4-week acclimation period at -1°C and 4°C showed no significant difference for *Pagothenia borchgrevinki* (Wilson *et al.*, 2001).

The same four fibre types have been described for the pectoral fin muscles (Fernández *et al.*, 2000). The fibre type distribution in the *abductor profundis* muscle of all the species described was similar, comprising four different zones. The tonic fibres were found close to the pectoral girdle bones, followed by a core of slow muscle fibres, a zone of slow muscle fibres intermingled with fast ones, and finally a zone of fast fibres occupying the surface of the muscle (Fig. 7). Even though the distribution of the fibre types was conserved in all the species, there was a consistent variation in the proportion of the different zones from the proximal to the distal ends of the muscle (Fernández *et al.*, 2000).

Special characteristics of notothenioid muscle

The axial muscle of the notothenioids is unusual in containing very large diameter muscle fibres in comparison to other teleosts (Smialowska and Kilarsky, 1981; Dunn *et al.*, 1989; Battram and Johnston, 1991; Fernández *et al.*, 2000; Johnston *et al.*, 2003) and low muscle fibre numbers (Battram and Johnston, 1991). The maximum fibre diameters increase linearly with standard length (SL), reaching 500 µm in many of the species studied (Johnston *et al.*, 2003) (Fig. 8). With regard to the fibre number, for example, *E. maclovinus*, a notothenioid with an unusually large number of fibres, has only 164,000 fibres as against 1,200,000 fibres in an Atlantic salmon (*Salmo salar*) of a similar size (Johnston *et al.*, 2003). Phylogenetic Independent Contrast Analysis showed that fibre number differs significantly between species that belong to the most basal and the most derived families, suggesting a decreasing trend in fibre numbers during the evolution of the suborder (Fig. 9). Moreover, the decrease in the

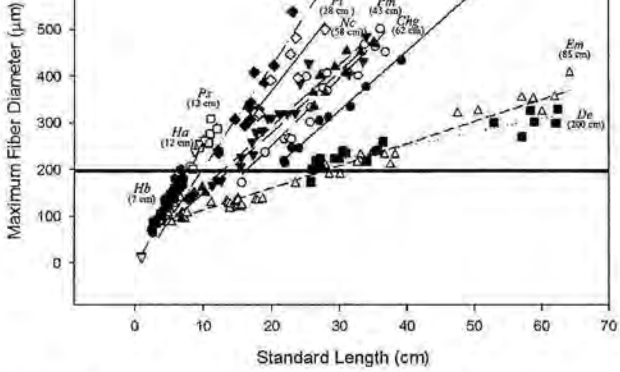

FIG. 8. – Relationship between the estimated maximum fast muscle fibre diameter and standard length in 11 species of notothenioid fishes from the Antarctic Ocean and Patagonian shelf. The slope of the regression line for each species correlates inversely to the final length of the species (in brackets close to the name of each species). *Notothenia coriiceps, Nc*; *Dissostichus eleginoides, De*; *Eleginops maclovinus, Em*; *Patagonotothen tessellata, Pt*; *P. longipes* sp., *Pl*; *P.sima, Ps*; *Chaenocephalus aceratus, Cha*; *Champsocephalus gunnari, Chg*; *Paranotothenia magellanica, Pm*; *Harpagifer antarcticus, Ha* and *Harpagifer bispinis, Hb*. The line drawn at 200 µm represents the common maximum fibre diameter for temperate and tropical teleosts. Modified from Johnston *et al.* (2003).

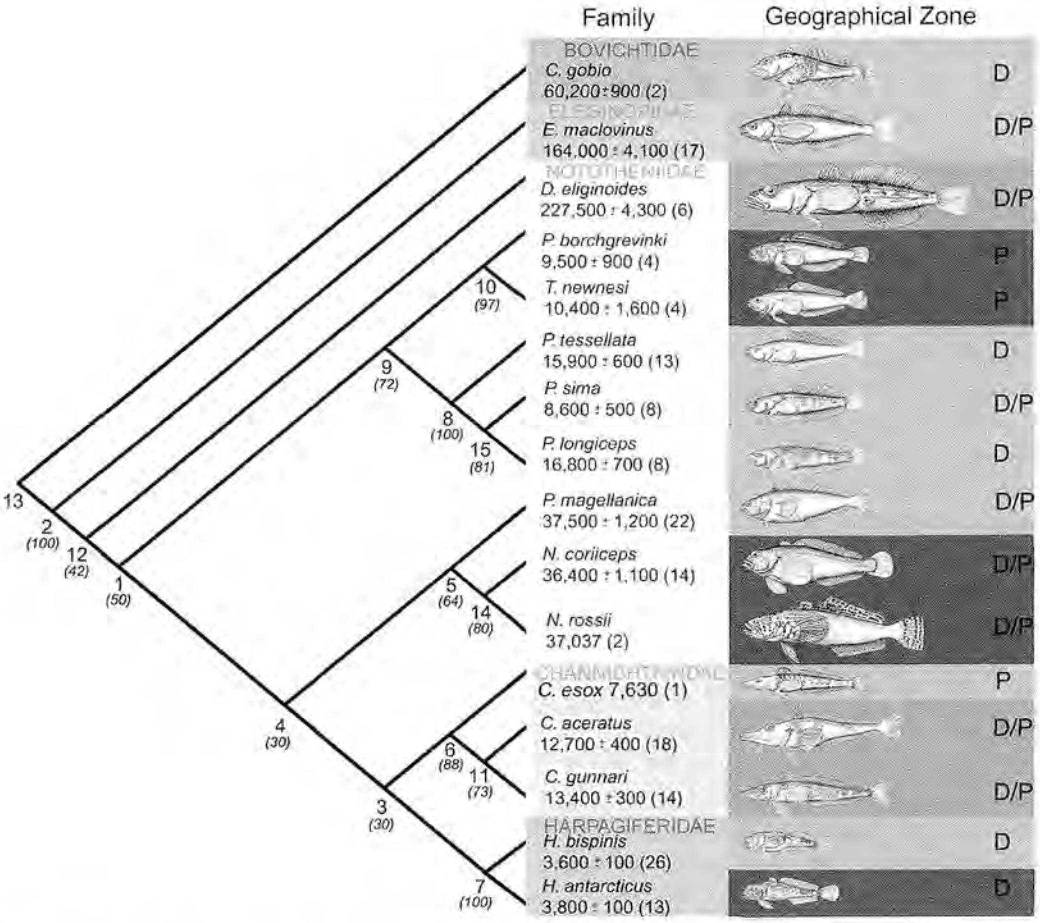

FIG. 9. – Maximum likelihood phylogenetic tree estimated from 12S mitochondrial rRNA sequences and the trait values for the final number of fast muscle fibres (FN_{max}) for the notothenioid fishes studied using Phylip. Values are means ± S.E.M. (number of individuals). The bootstrap support values obtained from the Phylip analysis are shown italicised in parentheses by the nodes. The fish are not drawn to scale. The locomotory habit of each species is also shown: D, demersal; D/P, demerso-pelagic and P, pelagic. The shading on the right-hand side shows the geographical zones of capture for each species: Beagle Channel (light grey), Shag Rocks, South Georgia (grey) and Antarctic Peninsula (dark grey). The shading on the left-hand side indicates the current taxonomic families, some of which are not monophyletic. Modified from Johnston *et al.* (2003).

number of fibres correlates with an increase in the diameter of the fibres (Johnston *et al.*, 2003). On the other hand, there is no evident relationship between the geographical zone (Antarctic and Subantarctic) and the maximum fibre diameter of the species. Therefore, a major conclusion from this work is that the special traits (low fibre number and giant fibre size) of the muscle of notothenioids have an important phylogenetical component, apart from the well-established relationship between low temperature and large fibre diameter.

Since muscle growth in teleosts involves the recruitment of new fibres (hyperplasia) and the increase in size of existing ones (hypertrophy), and the two processes are regulated through the activity of myosatellite cells, these two traits in the evolution of the suborder could be regulated through a single mechanism. The main phases in post-embryonic muscle growth are stratified and mosaic hyperplasia. The latter is absent in all the species of the more derived families that have already been studied (Harpagiferidae and Channichthyidae), giving a clue about how muscle fibre number has been adjusted during the evolution of this suborder (Johnston *et al.*, 2003).

The main process involved in muscle growth of notothenioids, hypertrophy, has been studied in adult *Harpagifer antarcticus* (Antarctic) and *Harpagifer bispinis* (Subantarctic) acclimated to summer and winter temperatures (Brodeur *et al.*, 2003a; Brodeur *et al.*, 2003b). These species are very good models for studying hypertrophy since hyperplasia no longer exists in adult fishes. Cell cycle times were estimated for *H. bispinis* at 10ºC (81.3 h) and 5ºC (150 h) and *H. antarcticus* at 0ºC (111 h). The longer duration of the cell cycle at 5ºC in *H. bispinis* than at 0 ºC in *H. antarcticus* indicates the existence of a cold compensation in the cell cycle time of the Antarctic species, allowing them a substantial reduction in the cell cycle progression rate at low temperatures. It would be interesting to investigate whether this is a common feature for all Antarctic species.

Brodeur *et al.*, (2003b) found evidence of a direct stimulation of myogenic cell proliferation by feeding at two different temperatures (about a two-fold increase in the c-met positive cells) in *H. bispinis*. The number of myogenic cells generated in response to feeding did not appear to be directly related to temperature. The main difference between the responses to feeding of fish acclimatised to simulated winter and summer conditions resided in the expression of myogenin, which was much less pronounced in summer. Interestingly, the delay between the ingestion of the meal and the activation of the myogenic progenitors (c-met positive cells) in *H. bispinis* was shorter than the cell cycle duration estimated for both summer and winter temperatures (150 and 81 h respectively). This result could indicate either that the cell cycle progression rate is accelerated by feeding or that a proportion of the activated cells were stopped at a checkpoint in the cell cycle and could therefore divide faster after activation since they had already progressed through part of the cell cycle (Walworth, 2000). The latter is in agreement with previous results on *Notothenia coriiceps* suggesting that myogenic cells activated by feeding were cells stopped at G1/S checkpoint of the cell cycle (Brodeur *et al.*, 2002).

Eurythermal fish respond to cold-acclimation with almost a two-fold increase in the abundance of muscle mitochondria. Diverse adaptive explanations have been proposed to explain this fact, including the hypothesis that increases in mitochondrial volume density partially compensate for the reduced catalytic capacity at low temperatures (Johnston, 1982; Egginton and Sidell, 1989) or otherwise compensate the reduced diffusion coefficients of cytosolic metabolites (Tyler and Sidell, 1984; Sidell and Hazel, 1987). Antarctic and Subantarctic notothenioids, living regularly at very low temperature, also have abundant mitochondria in the slow muscle fibres (Johnston, 1987; Londraville and Sidell, 1990). For example, reported mitochondrial volume density values of slow muscle fibres were 0.56 for *Pleuragramma antarcticum* and 0.51 for *Champsocephalus esox*, amongst the highest recorded for vertebrates (Johnston *et al.*, 1988; Johnston *et al.*, 1998). Nevertheless, there seems to be variability in the mitochondrial volume density values due to species habits (Johnston *et al.*, 1998). The same adaptive explanations proposed for cold-acclimation may apply for fishes living at low temperature like notothenioids, with increased volume and surface density of mitochondrial clusters as the main mechanism for enhancing the aerobic capacity of muscle in cold-water species (Johnston *et al.*, 1998).

CONCLUSIONS

The comparison of the muscles of Antarctic and Subantarctic notothenioids have shown no differences in fibre type composition, ATPase activity, cessation of fibre recruitment (hyperplasia) and swimming performance at different temperatures. The length of the cell cycle of the muscle fibres shows cold compensation in the Antarctic species *H. antarcticus* relative to the closely related Subantarctic species (*H. bispinis*). Feeding after a starvation period resulted in an increased proliferation of muscle fibre progenitors in *H. bispinis*, but no such study has been performed yet in any Antarctic species.

The finding that the diversification of notothenioids was associated with a size-specific reduction in fibre numbers with a subsequent increase in fibre diameter gives us a great opportunity to study the variation of basic mechanisms of muscle growth in relation to temperature in an evolutionary context. Multiple scenarios are open to consideration. Is the stem cell population that gives rise to myogenic progenitors reduced at lower temperatures? Is the proliferation capacity of this population reduced? Is the interplay between midline signalling pathways affected by developmental temperature, setting in this form the special characteristics of the muscle of notothenioids?

The new field of Developmental Ecology has been growing intensively in the last twenty years. Notothenioids offer a unique opportunity to study the mechanisms of muscle development and growth in a particularly interesting group of diverse fishes exposed to extreme environmental conditions for at least the last 25 Ma.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Quaternary molluscan faunas from the island of Tierra del Fuego after the Last Glacial Maximum*

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SUMMARY: Palaeontological studies on postglacial molluscan faunas from marine deposits located along the northern coast of the Beagle Channel (lat. 54°55'S, long. 68°34'-67°11'W) showed differences of various molluscan assemblages during a period of climatic stability after deglaciation. Oceanographic changes, different local environmental conditions and/or episodes of minor climatic fluctuations are pointed out as causes for the variations in faunal composition. Comparison with Quaternary molluscs from Antarctica showed that these palaeofaunas overlap slightly at the species level, but have a considerable number of genera (23%) and families (50%) in common. These affinities and relationships are better explained on the basis of more recent migrating taxa than by ancient connections when the two regions formed part of the Weddellian Province.

Keywords: mollusc assemblages, Tierra del Fuego, Beagle Channel, palaeoenvironments, Quaternary.

RESUMEN: FAUNAS CUATERNARIAS DE MOLUSCOS DE LA ISLA DE TIERRA DEL FUEGO DESPUÉS DEL ÚLTIMO MÁXIMO GLACIAL. – Estudios paleontológicos en faunas de moluscos postglaciales hallados en depósitos marinos sobre la costa norte del Canal Beagle (lat. 54°55'S; long. 68°34'-67°11'O) demostraron que las diferencias en varias asociaciones de moluscos ocurridas en un período de estabilidad climática después de la última deglaciación se deben a variaciones en la composición faunística que siguen a los cambios oceanográficos, a situaciones ambientales localmente diferentes y/o episodios con fluctuaciones climáticas menores. La comparación con moluscos cuaternarios de Antártica muestra que estas faunas tienen un ligero solapamiento a nivel especie, pero un considerable número de géneros (23%) y familias en común (50%). Estas afinidades y relaciones se explican mejor en base a migraciones recientes de taxones, que en base a antiguas conexiones cuando las dos regiones formaban parte de la Provincia Weddelliana.

Palabras clave: asociaciones de moluscos, Tierra del Fuego, Canal Beagle, paleoambientes, Cuaternario.

INTRODUCTION

Quaternary shallow molluscs are by far the most common taxa recovered and described in raised marine deposits along the eastern and southern coasts of the Isla Grande de Tierra del Fuego (Gordillo, 1992). These faunas are of considerable interest to life and earth scientists studying faunal change in these latitudes because Tierra del Fuego (Fig. 1) lies between the Atlantic and the Pacific oceans and had a common past with Antarctica as part of the Gondwana continent (Crame, 1993; 1996; 1999).

In addition, Quaternary climatic changes during the last 10,000 years (i.e. the Holocene) did not equally affect terrestrial and benthic marine ecosystems.

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FIG. 1. – Map of Tierra del Fuego showing sites (A. labelled dots; B. black and white dots) with Quaternary molluscan faunas used for comparison with the Antarctic. Black dots (B) indicate sites considered to evaluate changes in faunal composition after deglaciation: Lago Roca, Río Ovando, Bahía Golondrina and Río Varela. References: 1. San Pablo; 2. Río Chico; 3. La Sara (unpublished data)

Expansion and recession of terrestrial vegetation from the Beagle Channel area reflect changes from warm and dry in the Early Holocene to cool and wet in the Middle to Late Holocene (Heusser, 1998). In opposition, marine molluscs from the same area reveal a period of climatic stability during the past 8 ka BP (Gordillo, 1999). Thus, episodes of minor climatic fluctuations that have slightly affected these associations composed of wide ecological amplitude taxa cannot be ruled out (Gordillo *et al.*, 1992). These examples show that cross-disciplinary research provides frameworks for evaluating ecosystem responses to climate variations during Holocene times.

Taphonomic analysis to evaluate the fidelity of fossil assemblages, and whenever possible the reconstruction of palaeocommunities and their palaeotrophic structure, have been carried out previously (Gordillo, 1999). The available palaeoenvironmental information, including previous and new data, will be analysed together in this work. It deals with postglacial faunal changes and migration patterns that probably affected these faunas in the recent past.

Following a review of some different geological and physical factors capable of affecting faunal distributions in the region, a synthesis of the major events after the Last Glacial Maximum associated with the environmental evolution of an area located on the northern Beagle Channel coast will be given. Finally, a comparison with Quaternary molluscan faunas from Antarctica will be made.

MATERIAL AND METHODS

Palaeontological work in this paper is concentrated on four localities (Fig. 1B, black dots) located on the northern coast of the Beagle Channel: Lago Roca (lat. 54°49´S, long. 68°34´W); Río Ovando (lat. 54°51´S, long. 68°35´W); Bahía Golondrina (lat. 54°50´S, long. 68°19´W) and Río Varela (lat. 54°12´S, long. 67°11´W). These sites are considered as suitable for the preservation of small, thin shells.

The new records, especially small taxa and juvenile specimens, were collected in December 2002. In the field, small specimens were recovered from the marine deposits using a bulk sampler operated by hand. In the laboratory, the total volume of sediment was sieved on a 0.5 mm mesh size, and the material retained was sorted manually under a binocular microscope. Specimens were deposited in the Quaternary mollusc collection from Tierra del Fuego (TDF-Q) at the Centro de Investigaciones Paleobiológicas (CIPAL), Universidad Nacional de Córdoba (Córdoba, Argentina).

The systematics is based on previous identification carried out by Gordillo (1992), but recent taxonomic revisions on living mollusca by Linse (1999a), Ponder and Worsfold (1994) and Reid and Osorio (2000), among others, are also taken into account. The comparison with Quaternary mollusca from the Antarctic was made on the basis of all

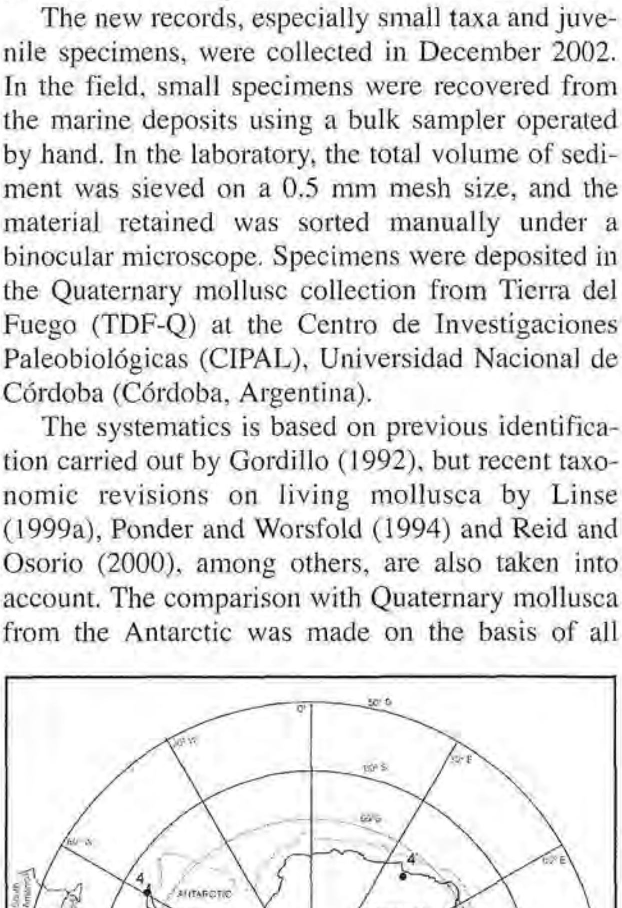

FIG. 2. – Map of Antarctica showing the location of sites with Quaternary Mollusca: raised beaches are pointed out with black dots and drillcores with black squares. References: 1. Zhang *et al.*, 1983; 2. Pickard (1985); 3. Baroni and Orombelli (1991); 4. Berkman (1992); 5. Taviani *et al.* (1998).

available fossil records from Tierra del Fuego (Fig. 1A, three numbered dots and Fig. 1B, black and white dots; Gordillo 1992, 1999; unpublished data). Records from different localities around Antarctica (Fig. 2)—including raised beaches and drillcore data—were taken from Baroni and Orombelli (1991), Clapperton and Sugden (1982), Orombelli *et al.* (1991), Pickard (1985), Pickard *et al.* (1983, 1986), Taviani *et al.* (1998, 2000) and Zhang *et al.* (1983). Information on mollusca from Quaternary deposits in the Buenos Aires province (Argentina; Aguirre, 1990), on the northern Atlantic Argentine coast, was used for a broader scale comparison.

GEOLOGICAL AND PHYSICAL FACTORS AFFECTING FAUNAL DISTRIBUTIONS IN SOUTHERN SOUTH AMERICA

Plate tectonics, glaciations and Antarctic Convergence as barriers and/or dispersal routes

Mesozoic/Earliest Cenozoic. It is known that in the geological past the Magellan region—as the southern part of South America—was linked to other parts of Gondwana, such as Antarctica, New Zealand and Australia, with a final phase of fragmentation occurring during the latest Mesozoic and earliest Cenozoic (Briggs, 1995). During the beginning of this phase these continents were separated by shallow seas. This region extended from West Antarctica into both southern South America and eastern Australia. Because of the overall uniformity of the faunas, it is considered to represent a single broad biogeographic province, designated by Zinsmeister (1979) as the Weddellian Province. It appears that this high latitude region acted as a centre of origin and dispersal for a broad spectrum of taxa, including molluscs (Zinsmeister and Feldmann, 1984; Crame, 1992).

Late Cenozoic. In the marine realm, it seems that climatic deterioration during Plio-Pleistocene glaciations produced environmental changes that normally resulted in regional or local extinctions followed by a repopulation by migrants from other areas (hypothesis of "ecological opportunity"; Vermeij, 1991). In the Southern Ocean, Pickard *et al.* (1983) suspected that during Quaternary glaciations the fauna either survived and dispersed from ice-free refugia or immigrated from nearby South America or Antarctica. Crame (1997) too considered that during most glacial advances in the Antarctic region, the marine fauna would have had to retreat into some form of refugia; an unglaciated part of the shelf, or the deeper waters of the outermost shelf (or top of the slope), or one of the Subantarctic islands. This strategy could explain the considerable degree of evolutionary stability within Antarctic molluscan faunas over the last 40 Ma.

Some similarities between faunas from different regions in the southern seas could also be explained by considering the West Wind Drift circulation in more recent times. It is possible that the opening of the Drake Passage (25-22 Ma.) and the completion of circum-Antarctic deep water circulation may have promoted various forms of both vicariance and dispersal (Crame, 1999). For example, Beu *et al.* (1999) recognised three phases of dispersal between South America and New Zealand via the West Wind Drift; the last one, the Pleistocene phase, involved at least several mollusc taxa (*Mytilus*, *Protothaca* and *Tawera*, among others). Moyano (1999) pointed out that a real path for migrating bryozoans is the chain of archipelagos stretching between the southernmost tip of South America and the northernmost tip of the Antarctic Peninsula. In this regard, it is important to note that the Antarctic Convergence, as the main physical barrier between Antarctica and the Magellan region, appears to be crossed by several taxa (Antezana, 1999b; Moyano, 1999).

It has not yet been determined whether Antarctic taxa inhabiting Tierra del Fuego migrated via the Scotia Ridge and/or inversely Antarctic derived taxa migrated to the Fuegian region.

Glaciations and faunal exclusion in the Beagle Channel

The Beagle Channel is a 200 km long drowned glacial valley formerly occupied by the "Beagle Glacier", a large outlet glacier which flowed from the Cordillera Darwin (lat. 55°S; long 69°W; Fig. 1). This valley was repeatedly glaciated, at least in two major episodes, and the ice occupied the entire channel basin as far east as Bahía Sloggett during the "Lennox Glaciation" (Oxygen Isotopic Stage -OIS- 6) and Punta Moat during the "Moat Glaciation" (OIS 2, 24 cal.; Rabassa *et al.*, 1990; 1992; 1996; 2000).

It is suspected that during glaciations the ice excluded much of the benthic marine fauna inhabiting the marine environment, as was the case in the Arctic region with the Laurentide ice during the last Wisconsinan glaciation (Lubinsky, 1980). In the study region, a few poorly preserved specimens included in compact lodgement tills in Bahía Golondrina (Rabassa *et al.*, 1986) and Isla Gable (Gordillo, 1990) respectively were probably deposited either when a glacier advanced over pre-existing marine deposits, perhaps of Mid-Wisconsian or Sangamonan age, or when the advancing glacier was in contact with the sea level. Anyway, these records indicate that the Beagle Channel had been occupied by sea water at least once before the late Wisconsinan maximum. During glaciations, as indicated previously by Crame (1996), species were able to persist by moving into deeper water or moving into warmer regions, or perhaps survived in unglaciated pockets on continental shelves.

Other physical factors affecting taxa distribution in the Beagle Channel: sills, tides, currents and depth.

A water mass characterisation of the Beagle Channel system has been proposed by Antezana (1999a). Despite major connections to the Pacific Ocean at the mouth of the Beagle Channel, the presence of shallow sills is likely to constrain water exchange to the upper 30-40 m. In particular, the shallow depth of the eastern end of the Beagle Channel apparently restricts the inflow of subsurface ocean water. As water exchange with the Pacific Ocean is limited and it apparently takes place through narrow and shallow openings, most of the water filling the Fuegian basin must be semi-isolated or trapped seasonally. The currents and tides and the depth are probably important factors determining basin to basin linkages.

The Beagle Channel has been described as an estuary by Isla *et al.* (1999), since thermal stratification and water mixing at 12 m depth was observed near the western Isla Gable cliffs (Fig. 1). It was assumed that this island acts as a sill in the estuarine dynamics generating the joining of tidal waves and the consequent sediment accumulation, and forms an obstruction to the wind-streams which promotes high wave erosion on the western side of the island. Sediment capture and decantation occur in the western waters of Isla Gable, whereas to the east greater depth allows the accumulation of weathered bedrock clays and silts, and sand and gravel in the rare shallow waters (Isla *et al.*, 1999).

Physical characteristics that are locally different, as mentioned above, probably influence the species composition of plankton between nearby inlets and may cause complex patterns of retention, dispersal and exchange of plankton species between fjords (Antezana, 1999b).

Links to the Antarctic and other Subantarctic regions can also be explained by examining bathymetry and hydrography. For example, Antezana (1999b) has noted that the Polar Front—while meandering across the Pacific Ocean near South America—may form cold rings which transport endemic Antarctic plankton communities into warmer regions as they fade away in the course of

TABLE 1. – Physical and palaeontological characterisation of four sites on the Beagle Channel.

Characterisation	Lago Roca	Río Varela	Río Ovando	Bahía Golondrina
Assemblage type	Parauthochthonous assemblage; Epifaunal community	Allochthonous assemblage	Authochthonous assemblage; Semi-infaunal community	Authochthonous assemblage; Infaunal community
Elevation (a.s.l.)	3.0 m	3.0 m	2.5 m	2.0 m
Sediment	Massive grayish clays (> 1.00 m)	Massive grayish clays (> 1.70 m)	Coarse sand with pebbles of varied lithology	Fine sandy clays
Uncorrected radiocarbon age and C^{14} laboratory sample code	7518 +/- 58 yr BP (NZ-7730; Gordillo *et al.*, 1993)	6240 +/- 70 yr BP (Pta 7581; Coronato *et al.*, 1999)	4160 +/- 45 yr BP (Pta 7573; Coronato *et al.* 1999)	Not dated; 1400 +/- 300 yr BP (+2.7 m a.s.l.; Urien, 1968)
Distance from the Beagle Channel	2500 m	500 m	1000 m	30 m
Palaeoenvironmental considerations	Early Holocene conditions (phase 2)	Middle Holocene climatic deterioration (phase 3)	Middle Holocene climatic amelioration (phase 4)	Late Holocene neoglacial events (phase 5)
Regional climate conditions	Deglaciation	Maximum Neoglacial (I – II)	Warmer conditions	Neoglacial events (III – VII)
Range of time	10 – 6.5 ka	6.5 – 4.5 ka	4.5 – 4.0 ka	3.5 ka - present

Ka=1000 years

several months. After passing the shallow sills at the mouth of inland passages, these organisms are probably trapped within the system, and become expatriates or vagrants, as must be the case for Subantarctic and Atlantic species in the Fuegian fjords.

ENVIRONMENTAL EVOLUTION AFTER THE LAST GLACIAL MAXIMUM

Based on multiple kinds of data such as geomorphological, stratigraphical and palaeontological studies, neontology, radiocarbon dates and isotopic analyses, the environmental evolution of the northern coast of the Beagle Channel microbasin can be interpreted.

The physical and palaeontological characterisation of the four sites is summarised in Table 1.

The assemblages are mostly composed of small taxa and juvenile specimens of gastropods and bivalves (Table 2). Each taxon is presently extant within the Beagle Channel (Linse, 1999a) and most of them are eurybathic, occurring in shallow and deeper waters. Other preserved groups include chitons, brachiopods, cirripedes, ostracods, foraminifers, echinoid remains and small fish vertebrae.

Previous analysis of these units (Gordillo, 1992; Gordillo *et al.*, 1993; Gordillo, 1999), which considered post mortem mechanical processes (i.e. disarticulation, fragmentation, orientation, abrasion, bioerosion, overgrowth) affecting fossil remains, and their palaeontological attributes (i.e. taxa composition, abundance, size frequency, mode of life), showed that—despite the bias in preservation due to taphonomic processes—these assemblages retain useful information pertaining to life habit and habitats of the marine benthos from which they are derived.

The chronology and deglaciation history of this area has been summarised in previous works (Gordillo *et al*, 1993, Grill *et al.*, 2002, Heusser, 1989a,b, Heusser and Rabassa, 1987; Rabassa *et al.* 1986, 1990, 1996, 2000). The radiocarbon dates used in this work are conventional ^{14}C age; they are uncorrected and not calibrated.

Thus, following the major events during postglacial times different phases can be distinguished:

Phase 1: Deglaciation after the Last Glacial Maximum

Evidence suggests that the Last Glacial Maximum in the Beagle Channel area and in the surrounding mountains took place *ca.* 20 ka BP (Rabassa *et al.*, 1990). By 12 ka BP the ice had probably disappeared from the southern coast at Puerto Williams (lat. 54°56´S, long 67°38´W; Heusser, 1989a) and from the northern coast at Ushuaia (lat. 54°47´S, long 68°20´W; Heusser, 1998). Large volumes of meltwater were discharged into the Beagle valley not only from the main receding glacier, but also from the meltwater streams coming from the valley glaciers located along both coasts.

No fossil marine benthic records were found for this period. This lack is probably related to the presence of unstable substrates not suitable for this kind of fauna, since the incoming freshwater and the consequent influx of continental organic matter must have restricted marine circulation and nutrient regeneration, creating food-limited benthic habitats, especially for suspension feeders.

Phase 2: Early Holocene conditions

Since 10 ka BP meltwater influx into the Beagle Channel has decreased sharply. Mean sea temperature has been estimated as 3-6° C lower than at present (Heusser, 1989a, b). The maximum transgressive episode occurred between 9 and 7 ka BP (Isla, 1989). Around 8 ka BP the present Beagle Channel, as one of the inland passages in the complex network of channels, inlets and islands of the Fuegian Archipelago, was occupied by marine waters that flooded progressively via constricted waterways connected to the open ocean. This episode might correlate with the oldest sea level identified at Bahía Lapataia (8240 +/- 60 yr BP; Rabassa *et al.*, 1986) and with the highest sea level at Lago Roca (7518 +/- 58 yr BP; Gordillo *et al.*, 1993).

This area was a valley-glacier system during the Last Glacial Maximum, but after the deglaciation it was flooded by sea waters from the Beagle Channel and converted into a complex marine inlet. Around 8 ka. BP, the Lago Roca-Lapataia area was a low energy, freshwater estuarine environment, but around 7.5 ka BP, during the Holocene marine transgression, the whole area turned into a fjord (Gordillo *et al.*, 1993), and Lago Roca and Río Ovando (located in its vicinity) became a shallow marine environment.

Fossil record. Although not described here, it is mentioned that earlier migrants after deglaciation (around 8 ka BP) are represented by mytilids and cirripeds, collected from the oldest postglacial raised beach at Bahía Lapataia (Gordillo, 1992).

TABLE 2. – Preliminary list of molluscs recorded from the four sites.

	Lago Roca	Río Varela	Río Ovando	Bahía Golondrina
GASTROPODA				
Patellidae				
"Nacella" spp.	X		X	
Fissurellidae				
Fissurella spp.		X	X	
Scissurellidae				
Scissurella timora? Melvill and Standen, 1912			X	
Trochidae				
Calliostoma cf. *nudum* (Philippi, 1845)			X	
Margarella violacea (King and Broderip, 1831)	X	X	X	X
Orbitestellidae				
Microdiscula? sp.			X	
Cyclotrematidae				
Cirsonella sp.			X	
Cerithiopsidae				
Eumetula pulla (Philippi, 1845)	X	X	X	
Eumetula michaelseni (Strebel, 1906)	X			
Turritelidae				
Mathilda aff. *malvinarum* (Melvil and Standen, 1907)	X			
Colpospirella algida (Melvil and Standen, 1912)		X		
Omalogyridae				
Omalogyra antarctica Egorova, 1991			X	
Littorinidae				
Laevilitorina caliginosa Gould, 1848		X	X	X
Eatoniellidae				
Eatoniella spp.	X		X	X
Rissoidae				
Onoba spp.	X	X	X	X
Calyptraeidae				
Trochita pileolus (Orbigny, 1845)	X		X	
Trochita pileus (Born, 1778)		X		X
Capulidae				
Capulus? sp.				X
Buccinulidae				
Metheutria martensi (Strebel, 1905)	X	X	X	
Pareuthria spp.	X	X	X	
Savatieria frigida Rochebrune and Mabille, 1885	X		X	
Muricidae				
Xymenopsis muriciformis (King and Broderip, 1832)	X	X		
Xymenopsis buccinea Lamarck, 1816			X	
Trophon geversianus (Pallas, 1769)		X		
Fuegotrophon pallidus Broderip and Sowerby, 1833		X	X	
Pyramidellidae				
Turbonilla smithi (Strebel, 1905)			X	
Sum of families	**9**	**9**	**15**	**6**
Sum of taxa	**12**	**12**	**19**	**6**
BIVALVIA				
Nuculidae				
Linnucula pisum (Sowerby, 1832)	X		X	
Nucula spp.		X	X	X
Malletidae				
Tyndariopsis sulcata (Couthouy, 1852)	X		X	
Philobryidae				
Philobrya sublaevis? Pelseneer, 1903	X		X	
Lissarca miliaris (Philippi, 1845)			X	
Mytilidae				X
Aulacomya atra atra (Molina, 1782)			X	
Mytilus sp.			X	
Pectinidae				
Zygochlamys patagonica (King and Broderip, 1832)	X			
Limidae				
Limatula pygmaea (Philippi, 1845)			X	
Leptonidae				
Neolepton sp.	X	X	X	X
Erycinidae				
Lasaea spp.	X	X	X	
Montacutidae				
Mysella aff. *miniuscula* (Martens and Pfeffer, 1908)	X	X		
Cyamiidae				
Cyamium spp.	X	X	X	X
Carditidae				
Carditella naviformis (Reeve, 1843)			X	
Carditopsis flabellum (Reeve, 1843)			X	
Cyclocardia compressa (Reeve, 1843)			X	
Solenidae				
Ensis macha (Molina, 1782)				X
Veneridae				
Protothaca antiqua (King, 1831)		X		X
Retrotapes exalbidus (Dillwyn, 1817)		X	X	
Tawera gayi (Hupé, 1854)			X	
Hiatellidae				
Hiatella solida (Sowerby, 1834)	X	X	X	X
Sum of families	**9**	**7**	**11**	**7**
Sum of taxa	**9**	**8**	**17**	**7**

These taxa are epibenthic and tolerate estuarine conditions. The other bed, the Lago Roca deposit, was previously considered in Gordillo *et al.* (1993) and Gordillo (1999). The presence and dominance of suspension feeders in the epifaunal *Zygochlamys patagonica* palaeocommunity (Gordillo, 1999) showed that marine conditions were fully established around 7.5 ka BP. The predominance of epifauna is most probably associated with the prevalence of firmground substrates more suitable to these groups.

Phase 3: Middle Holocene climatic deterioration

Several palaeoclimatic records have demonstrated that cold climatic conditions occurred *ca.* 6 ka BP along the Beagle Channel. At the Río Varela site marine waters flooded the present mouth area at *ca.* 6.2 ka BP (6240 +/- 70 yr BP; Coronato *et al.*, 1999), developing a shallow, low-energy, nearshore environment, strongly fluvially influenced and seasonally ice-covered (Grill *et al.*, 2002). Apparently, a phase of climatic deterioration in the region took place between 6.5 and 5 ka BP (Obelic *et al.*, 1998; Grill *et al.*, 2002), but its origin remains unclear.

Fossil record. The sequence at Río Varela site is a succession of marine sediments and organic horizons which underlie fluvial sediments (Grill *et al.*, 2002). From base to top, several stratigraphic units were identified. The basal unit consists of massive greyish clays containing shells. This assemblage is composed of a mixing of epifauna and infauna. Taphonomic analysis indicates that it corresponds to an allochthonous, transported assemblage. However, the presence of venerids and other infaunal taxa showed that around 6 ka BP in the Beagle Channel physical conditions were suitable to the development of organisms associated with soft substrata. Considering that both kinds of organisms (epifauna and infauna) are able to live at present in the Beagle Channel, the absence of Pectinidae may be more related to taphonomic biases or the distinctly patchy distribution of epifaunal communities in the Magellan region (Linse, 1999b) than to a regional or local absence due to a retraction of this group associated with minor climatic changes.

Phase 4: Middle Holocene climatic amelioration

Palynological records taken from the surrounding peat-bogs in the area indicate cool conditions with significant forest expansion between 4 and 2 ka. BP (Heusser, 1998). However, this cooler and more humid period was probably preceded by a short period of warmer conditions between 4.5 and 4 ka BP, as pointed out by Obelic *et al.* (1998) in the marine realm.

Palaeotemperatures presented by these authors, calculated from oxygen isotopic composition in shells from archaeological sites along the Beagle Channel, indicate higher temperature values for the period 4.5-4 ka BP. Our own data support the view that around 4.5 ka BP the marine conditions persisted well-developed within the Lago Roca-Lapataia area, forming a true marine archipelago (Rabassa *et al.*, 1986; Gordillo *et al.*, 1993). Then, the sea level continued its relative regression until it reached the present conditions as a freshwater archipelago.

Fossil record. A well-developed raised marine terrace at the head of the Río Ovando was described by Rabassa *et al.* (1986). This unit consists of coarse sands and pebbles of varied lithology and marine shells, lying on greenish clays with mytilid fragments. Extensive beds of Veneridae (*Tawera gayi*, *Protothaca antiqua*, *Retrotapes exalbidus*) and other molluscs in growth position (*Hiatella solida*) characterise the area. Considering palaeotemperatures and the diversification of this fauna (e.g. the appearance of the Carditidae in these beds, which is the most notable addition), it appears that the Río Ovando associations (4.4-4.1 ka BP) correspond to warmer waters. Finally, another characteristic of these assemblages is the incidence of drilling (approximately 25% of the shells are bored). Thus, predation by boring gastropods is apparently more effective in lower-warmer latitudes (Vermeij, 1978; 1995).

All this information is interpreted here in the way that during this phase a major expansion of the fauna with further diversification of taxa took place, indicating an evolution towards modern conditions.

Phase 5: Late Holocene neoglacial events

Neoglaciation of terrestrial ecosystems is represented in this phase by several ice readvances or glacial episodes which took place in the glacial *cirques* and summits of the surrounding mountains above 900 m (Rabassa *et al.*, 1992; Planas *et al.*, 2002). No absolute dates are available for the Fuegian Andes, although many correlations with neoglacial episodes occurring after 3.5 ka BP in Darwin Cordillera, Subantarctic Islands and Antarctica have been suggested (Clapperton and Sudgen, 1988; Kuylenstierna *et al.*, 1996; Strelin *et al.*, 2002). In the marine realm, measurements of palaeotemperatures from the Beagle Channel show a fall in values at about 3.5-3 ka BP (Obelic *et al.*, 1998).

Fossil record. Deposits from this area were previously studied by Auer (1959), Urien (1968) and Gordillo (1992, 1999). This section (> 1 m), composed of fine, greyish sandy sediments was considered in Gordillo (1999). The lack of sedimentary structures and macrofossils in life position (*Ensis macha, Protothaca antiqua*) was interpreted as being due to rapid accumulation processes, probably caused by regional storms in the region.

No radiocarbon dating has been performed for this level, but considering its proximity and their similar elevation, it could be correlated with the lowest level of 1400 +/-300 yr BP described by Urien (1968) at 5 m above sea level.

An impoverishment in this association with respect to the others is recognised. Buccinulidae, Muricidae, Cerithiopsidae and Malletidae are all missing. Although not rejected, these differences do not necessarily reflect advances or retractions of taxa associated with minor climatic fluctuations. It is plausible that this absence is related to taphonomic biases (noise) and/or to the nature of the substratum that creates patchy distributions of benthic communities along the Beagle Channel.

COMPARISON WITH QUATERNARY MOLLUSCA FROM ANTARCTICA

Age and altitude. Our data showed that the oldest postglacial raised beaches occurring in Tierra del Fuego (Bahía Lapataia: 8240 +/- 60 yr BP; Rabassa *et al.*, 1986; 7770+/- 130 yr B.P., Borromei and Quattrochio, 2001) are comparable in age (ca. 8-7 ka BP) with those in West Antarctica (Victoria Land: 7505+/-230 yr BP; Orombelli *et al.*, 1991) and East Antarctica (Vestfold Hills: 7590+/-80 yr BP; Pickard, 1985). However, Holocene uplifted deposits in Antarctica containing shells *in situ* reach altitudes that usually exceed 10 m (Orombelli *et al.*, 1991; Ingólfsson *et al.*, 2003), while their equivalents from Tierra del Fuego do not exceed 10 m above the present sea level.

Distribution and dominance. Berkman (1992) showed that Holocene marine molluscs from Antarctica have a circumpolar distribution, and they represent the most consistent circumpolar fossil record. This consistency and dominance is also evident from our data in Tierra del Fuego (Gordillo, 1992).

Climatic conditions. In taxa composition and molluscan assemblages the postglacial molluscs from the Beagle Channel correspond to the fauna living in the region today. Thus, climatic conditions remained stable enough to allow the survival of the same marine faunistic associations, which have a wide ecological range equivalent to taxa living today (Gordillo, 1999). This wide ecological range is also evidenced in the Antarctic Holocene (Pickard, 1985). Living Antarctic forms also have very extensive depth ranges (Dell, 1990), and it is not possible to set any meaningful depth limit for analytical purposes; thus, a simple division into shallow and deep water faunas is impractical in the Antarctic region (Crame, 2000). With local variations, a climatic optimum starting after 4.2 ka BP is recognised for different regions in the Antarctic (Ingólfsson *et al.*, 1998; 2003). Warmer conditions between 4.5-4 ka BP (phase 4 in this work) are also evidenced in the Beagle Channel waters from isotopic analysis by Obelic *et al.* (1998).

Taxonomic composition. Zoogeographic studies on living molluscs from the Magellan region have shown that this region shares taxa with the Antarctic. Brandt *et al.* (1999) obtained the highest percentage of shared species within bivalves (29%), and Linse (2002) found that the regions around the Antarctic continent share species with percentages

TABLE 3. – Number of shelled fossil and living taxa from Tierra del Fuego and the Antarctic.

Region	Gastropoda No. of species	Gastropoda No. of genera	Gastropoda No. of families	Bivalvia No. of species	Bivalvia No. of genera	Bivalvia No. of families
Fossil taxa						
Tierra del Fuego	47	33	23	32	31	19
Antarctic	33	24	19	19	16	13
Living taxa (1)						
Tierra del Fuego	195	87	31	131	75	36
Antarctic	207	90	37	68	32	21

(1) Source of data on living mollusca: Tierra del Fuego (Linse, 1999a; Nudibranchia excluded). Antarctic (Dell, 1990).

TABLE 4. – Taxonomic diversity.

Region	Gastropoda DSG	Gastropoda DSF	Gastropoda DGF	Bivalvia DSG	Bivalvia DSF	Bivalvia DGF
Tierra del Fuego	0.979	0.950	0.963	0.997	0.954	0.952
Antarctic	0.976	0.905	0.962	0.983	0.966	0.967
Buenos Aires	0.984	0.939	0.983	0.912	0.972	0.981

DSG: Species/genus diversity; DSF: Species/family diversity, DGF: Genus/family diversity.

TABLE 5. – Percentage of species, genera and families shared with the Antarctic and northern Argentina based on the Quaternary fossil record.

Region compared with the Magellan region	Gastropoda Species	Gastropoda Genera	Gastropoda Families	Bivalvia Species	Bivalvia Genera	Bivalvia Families
Antarctic	3 (n=2)	23 (n=11)	50 (n=14)	6 (n=3)	23 (n=9)	52 (n=11)
Buenos Aires	4 (n=3)	12 (n=6)	31 (n=10)	0	6 (n=3)	20 (n=6)

of between 9.2 and 0.9%, with decreased values towards the Scotia Arc islands.

In this work the taxonomic composition of Magellan molluscs focuses on shelled gastropods and bivalves from Tierra del Fuego. Tables 3 and 4 show taxonomic distribution and taxonomic diversity indices for fossil and living taxa respectively. Furthermore, shared taxa with the Antarctic and a portion of the northern Argentine coast (in the Buenos Aires province) are compared (Table 5). At species level there are no strong similarities, with values of less than 10% of species in common. When one considers the degree of overlap between Buenos Aires and Tierra del Fuego, there are still differences at genus and family levels, with overlaps of 6-12 and 20-30%, respectively, but the Antarctic and Tierra del Fuego overlap to a higher degree, with 23% of genera and 50% of families in common.

Figure 3 compares the taxonomic distribution of Quaternary gastropods and bivalves from Tierra del Fuego with their equivalents from the Antarctic.

The bivalve families Veneridae, Mactridae and Mytilidae, which are well-represented in Tierra del Fuego, are absent in the Quaternary of the Antarctic. However, they were prominent in Palaeogene strata of this region (La Meseta Formation; Zinsmeister, 1984), and thereafter they diminished and disappeared. The costate pectinids (the *Chlamys* group) also appear to have become extinct in the Antarctic before the initiation of the Quaternary. These changes in faunal composition are perhaps not always associated with physiological limitations of these taxa under climatic deterioration or cooling, but could rather be linked to substrate changes (e.g. physical destruction of fine-grained substrates; Crame, 1996) associated with glaciations.

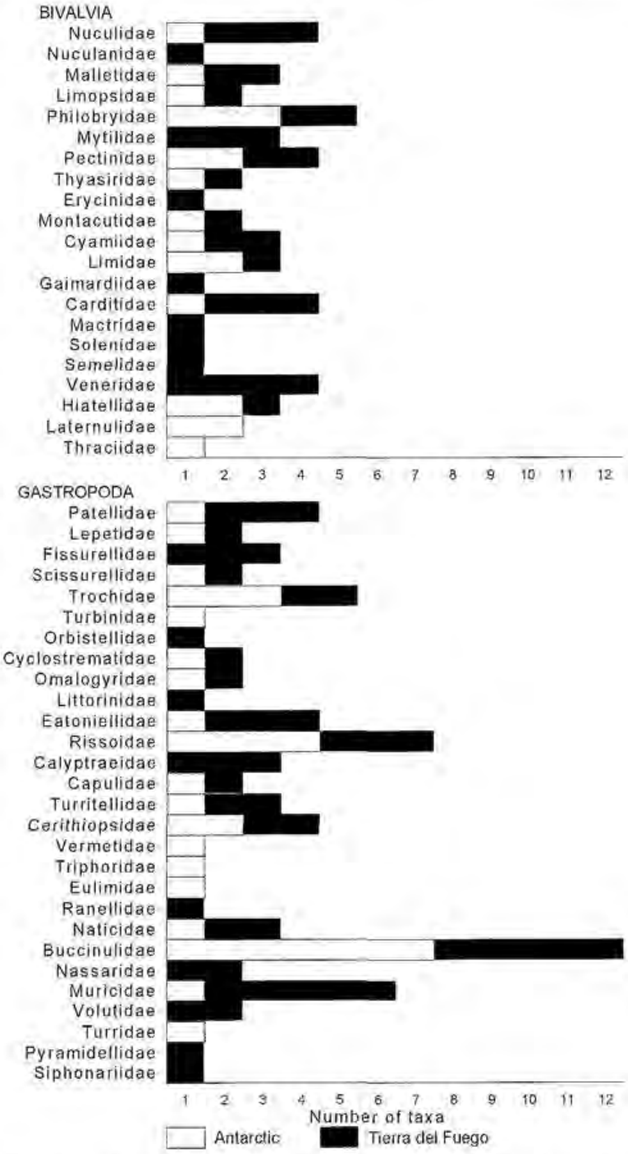

FIG. 3. – Number of gastropods and bivalves per family in the Quaternary of Antarctica and Tierra del Fuego.

It would appear most likely that most of these affinities and relationships (Fig. 3) are the product of high-latitude radiations in Quaternary times, since they do not reflect ancient similarities (pointed out by Zinsmeister and Feldmann, 1984; and Crame, 1996) during the Palaeogene when the two regions formed part of the Weddellian Province.

SUMMARY AND CONCLUSIONS

Lindberg and Lipps (1996) refer to the Quaternary period as: "an ideal venue for this cross-training of palaeontologists and neontologists". In this sense cross-disciplinary research that incorporates geological, geomorphological and oceanographic information is also necessary in order to interpret changes in faunal composition during the Quaternary.

In Tierra del Fuego, it is probable that after the glaciers fully receded (*ca.* 10 ka BP), the vacant areas were occupied by new communities formed by immigration of species living in any location with geographic access to these new habitats. Our data support the hypothesis that during the interval 5-4 ka BP (under relatively warmer conditions) a major expansion of the fauna took place, and further diversification of mollusc assemblages was characterised by the dominance of Veneridae and the appearance of other families or groups, indicating an evolution towards modern conditions. Most of these species, if not all of them, were able to sustain life in the area, even during Neoglacial climatic deterioration. Local absences of specific groups are best interpreted on the basis of local environmental conditions that create a diversified space, with habitat islands or discontinuities within the continuous seascape. Thus, faunal differences during this period of climatic stability in the marine realm are explained on the basis of different factors which affected these associations: changes in faunal composition following oceanographic episodes after deglaciation; different local environments; and/or episodes of minor climatic fluctuations.

When our data are compared with those from the Antarctic, our evidence supports similarities comprising the oldest ages of Holocene uplifted deposits, climatic conditions and the fact that the oldest postglacial beaches from both regions were developed at about 7-8 ka BP. In both regions, the mollusc group represents the most consistent fossil record, and all the recovered taxa are extant species, with a wide ecological range within their respective surrounding waters. These palaeofaunas overlap only slightly in composition at the species level, but have a considerable number of genera (23%) and families (50%) in common. These affinities and relationships are best explained on the basis of more recent migrating taxa rather than ancient connections when the two regions formed part of the Weddellian Province.

To conclude, the evidence summarised here shows that, despite major physical changes that produced introductions or exclusions of some elements, the Quaternary mollusc assemblages of Tierra del Fuego and the Antarctic have remained intact during this period. It appears that modern and Quaternary fossil taxa from these regions are "plastic" or broadly tolerant to environmental changes, which allows the fauna to be ecologically and evolutionarily persistent.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Shallow-water late middle Eocene crinoids from Tierra del Fuego: a new southern record of a retrograde community structure*

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SUMMARY: One of the very few crinoid records in Patagonia is that of the abundant columnals of the genus *Isselicrinus* found in several localities in shallow marine, glauconitic sandstones of the Leticia Formation (upper middle Eocene of Tierra del Fuego Island). Some of them, up to 10 cm long, are preserved in a position almost perpendicular to the stratification, which is attributed to episodes of high sedimentation rate. The *Isselicrinus* remains occur either almost alone or associated with solitary corals, gastropods, bivalves, rare nautilids, shark teeth, penguin bones and well-preserved specimens of *Ophiura elegantoides*. The associated microfossils, mainly Foraminifera, are characterised by the anomalous abundance and dominance of large Nodosariacea. These records reflect a peculiar success of a retrograde, dense, suspension-feeding crinoid population as a regional extension of previously described distribution in the Antarctic upper Eocene.

Keywords: Tierra del Fuego, Eocene, Leticia Formation, shallow-marine, crinoids, *Isselicrinus*, Nodosariacea, retrograde community structure.

RESUMEN: CRINOIDEOS DE AMBIENTES SOMEROS EN EL EOCENO MEDIO TARDÍO DE TIERRA DEL FUEGO: NUEVO REGISTRO AUSTRAL DE UNA COMUNIDAD CON ESTRUCTURA RETRÓGRADA. – Uno de los pocos registros de crinoideos en Patagonia está representado por abundantes columnas del género *Isselicrinus*, en areniscas glauconíticas someras de la Formación Leticia (Eoceno Medio superior de Tierra del Fuego). Algunas columnas, de hasta 10 cm de largo, están preservadas en forma casi perpendicular a la estratificación, posición que se atribuye a episodios de alta tasa de sedimentación. Los restos de *Isselicrinus* se presentan en forma aislada o están asociados a corales solitarios, gastrópodos, bivalvos, escasos nautiloideos, dientes de tiburones, huesos de pingüinos, y ejemplares bien preservados de *Ophiura elegantoides*. Los microfósiles asociados, principalmente foraminíferos, se caracterizan por la dominancia y abundancia anómala de grandes conchillas de Nodosariacea. Estos registros reflejan un peculiar éxito de poblaciones suspensívoras, retrógradas y densas, de crinoideos y demuestran una extensión regional de poblaciones similares descriptas para el Eoceno superior de Antártida.

Palabras clave: Tierra del Fuego, Eoceno, Formación Leticia, ambientes someros, crinoideos, *Isselicrinus*, Nodosariacea, comunidades de estructura retrógrada.

INTRODUCTION

The Mesozoic marine biotic revolution is thought to have caused irreversible changes in the life habits of many invertebrates. This is exemplified by the stalked isocrinid crinoids, which today are only known in deep-water environments. When they appeared in the Triassic, isocrinids were mostly restricted to shallow waters but, with few exceptions, during the Late Cretaceous they migrated to deep-water settings (Bottjer and Jablonski, 1988). Crinoids from Tierra del Fuego have been known

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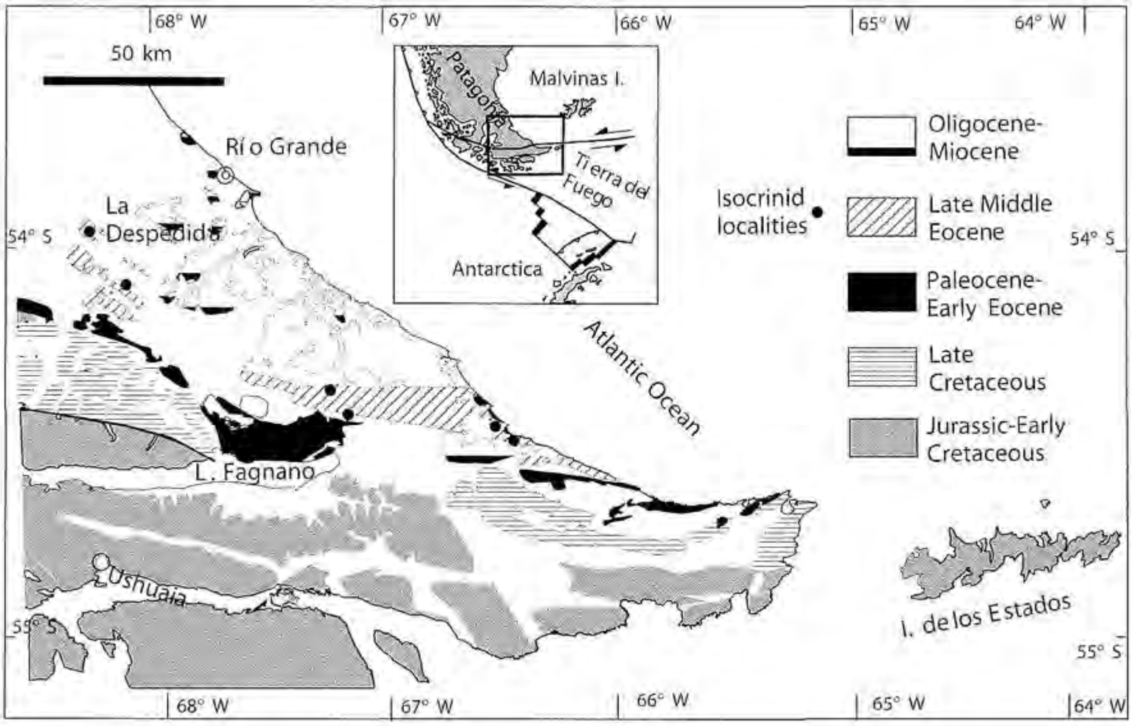

FIG. 1. – Schematic geology of Tierra del Fuego, distribution of upper middle Eocene rocks, and localities with the fossil isocrinid *Isselicrinus* sp.

since the beginning (Doello-Jurado, 1922) and middle of the last century (Furque and Camacho, 1949) in the La Despedida and Leticia beds, originally dated as Cretaceous-Early Cenozoic and Late Cretaceous respectively. However, Codignotto and Malumián (1981) and Olivero and Malumián (1999, and unpublished results) indicate that fossil crinoids from the Argentinean portion of the Tierra del Fuego Island are all isocrinids restricted to the shallow-water Leticia Formation of late middle Eocene age (Fig. 1). The palaeoecologic and stratigraphic implications of these anomalous, shallow-marine isocrinids are addressed and compared with similar records, mainly from Antarctica.

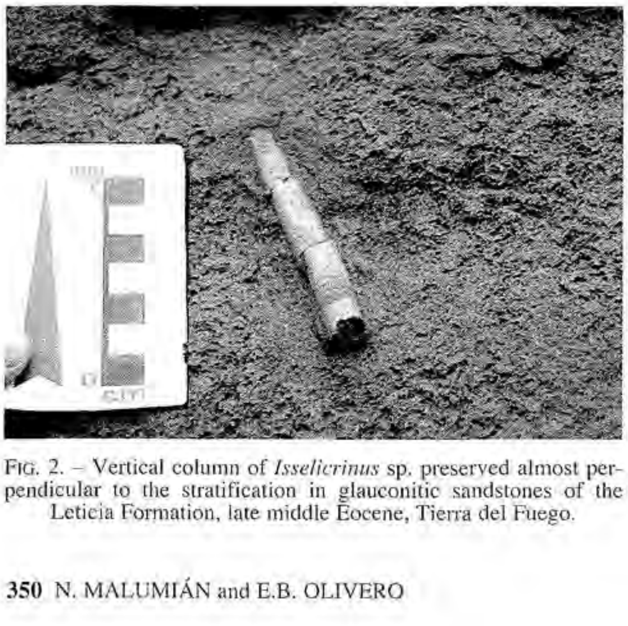

FIG. 2. – Vertical column of *Isselicrinus* sp. preserved almost perpendicular to the stratification in glauconitic sandstones of the Leticia Formation, late middle Eocene, Tierra del Fuego.

DISTRIBUTION AND RECORD OF ISOCRINID CRINOIDS IN TIERRA DEL FUEGO

Short segments of the column of stalked crinoids, sometimes preserved almost perpendicular to the stratification (Fig. 2), are common to abundant in certain fine, glauconitic, sandstone beds of the Leticia Formation in different localities of the central and coastal parts of Tierra del Fuego Island (Fig. 1). Segments of the column, occasionally up to 10 cm long, are the only preserved parts; isolated cups or partial broken arms were not recorded. The section of the column is pentagonal or less frequently cylindrical and the nodals bear three small, subcircular cirrus sockets (Fig. 3). Based on these features the material is assigned to *Isselicrinus* sp.

In the coastal localities, *Isselicrinus* sp. is associated with an abundant megafauna, which comprises solitary corals, gastropods, bivalves, rare nautilids, shark teeth (Olivero and Malumián, 1999), penguin bones (Clarke *et al.*, 2003), and in particular well-preserved specimens of *Ophiura elegantoides*

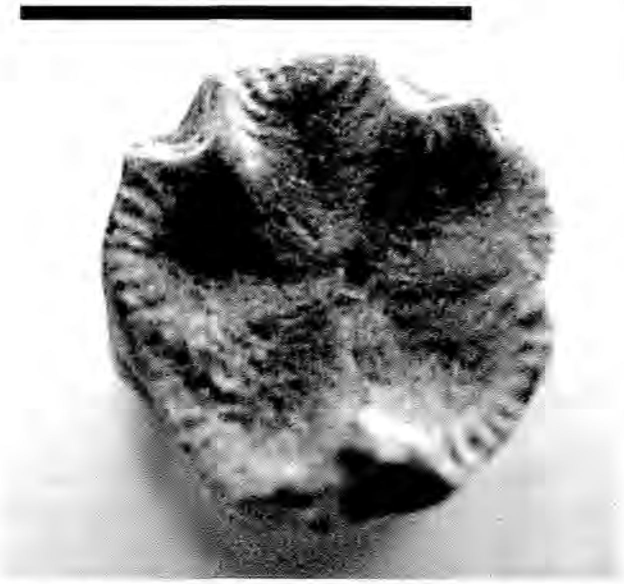

FIG. 3. – Vertical view of a nodal of *Isselicrinus* sp. with three cirrus sockets. Late middle Eocene, La Despedida Section, Tierra del Fuego. Scale bar 1 cm.

(Furque and Camacho, 1949). In the central localities, the megafauna is poorly represented, but the associated Foraminifera are characterised by the great abundance of large Nodosariacea, which commonly reach up to 4 mm in length and are the largest calcareous Foraminifera found in Argentina (Malumián, 1990). The sedimentology, ichnology, and foraminiferal assemblages all indicate shallow marine to marginal marine settings, including estuarine and subtidal channel environments, for the crinoid-bearing Leticia Formation (Olivero and Malumián, 1999). The record of the first appearance datum of the planktonic foraminiferan *Globigerinatheka index* (Finlay), just below the crinoid horizons, indicates a late middle Eocene age for the Leticia Formation (not older than 42.9 Ma, *cf.* Berggren *et al.*, 1995).

Recent studies in Tierra del Fuego recognised a rather complete Upper Cretaceous-Middle Miocene stratigraphic column. The Upper Cretaceous, part of the Palaeocene, and the Lower Eocene are relatively deep-marine deposits; the Oligocene-Lower Miocene are deep-marine deposits; and parts of the Palaeocene and Eocene, and the Middle Miocene are shallow-marine deposits (Olivero *et al.*, 2002, 2003). Isocrinid crinoids and ophiuroids are only known from the Leticia Formation and are apparently absent from the rest of the stratigraphic column in Tierra del Fuego. With the only exception of some scarce columnals records from the Danian (Fig. 4) that do not belong to the genus *Isselicrinus*, crinoids are also apparently absent in the rest of the shallow marine Patagonian Cenozoic deposits. In the Chilean portion of the Austral Basin, there is only a mention of *Balanocrinus*, in the Chorrillo Chico Formation (Charrier and Lahsen, 1969), recently assigned to a post-Danian Palaeocene age (Quattrocchio and Sarjeant, 2003).

DISCUSSION

Post-late Cretaceous, shallow-water records of fossil isocrinids are exceedingly rare and they are only known in the Southern Hemisphere. A few specimens of isocrinids were recorded in shallow-water deposits from New Zealand (*Metacrinus* sp. in

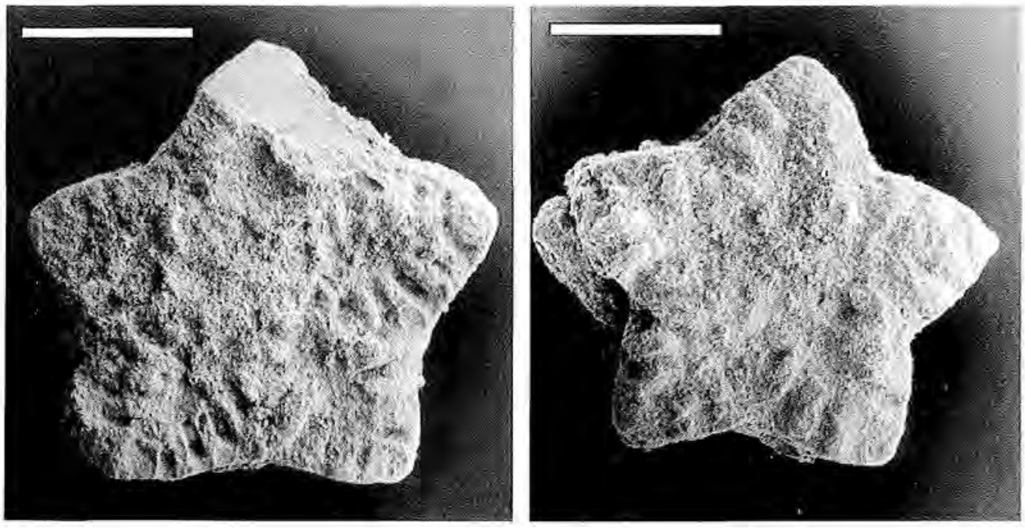

FIG. 4. – SEM photographs of isolated columnals of crinoids from the Salamanca Formation, Danian, Patagonia. Scale bar 1 mm.

Palaeocene conglomerates and indeterminate isocrinids in Oligocene limestones; Stilwell *et. al.*, 1994) and Australia (*Nielsenicrinus* sp. in late Paleocene limestones; Oji, 1996). On the other hand, abundant specimens of *Metacrinus fossilis* Rasmussen, *Eometacrinus australis* Baumiller and Gazdzicki, and ophiuroids are known from the late Eocene subtidal deposits of the La Meseta Formation in Seymour Island, Antarctica (Rasmussen, 1979; Meyer and Oji, 1993; Baumiller and Gazdzicki, 1996). The abundance of *M. fossilis* in the late Eocene shallow-water, tidally influenced deposits of Antarctica is particularly significant as the only reliable known fossil species of a modern isocrinid genus widespread in deep-water settings in the Indo-Pacific region. Species of the genus *Isselicrinus* are also mostly restricted to deep-water settings in the Cenozoic. In parallel with *M. fossilis* from Antarctica, the record of *Isselicrinus* sp. in the late middle Eocene of Tierra del Fuego demonstrated the shallow water occurrence of taxa that were prevalent in deep-water settings during the Cenozoic.

Only the cups and the proximal columnals are preserved in *M. fossilis* from Seymour Island, and this was interpreted as a secondary stalkless condition following autotomy of juvenile stalks during ontogeny (Meyer and Oji, 1993). On the other hand, only part of the stalk is preserved in *Isselicrinus* sp. from Tierra del Fuego. Isocrinids never have a radix and they are attached to the bottom by distal cirri. However, they sometimes lose the basal hold and drift away until the cirri grasp a new surface again; during this process, part of the distal column may break off and it could remain buried if followed by a sudden, high-rate sedimentation event. Moreover, given the recent finding that stalk fragments detached and isolated from a living crinoid in aquaria can survive more than one year (Oji and Amemiya, 1998), the burial chances of parts of the remaining column could be very high. This is probably the best taphonomic explanation for the isolated, almost perpendicular-to-bedding preservation of part of the column of *Isselicrinus* sp. in the Leticia Formation.

Shallow-water, suspension feeder benthic communities with abundant stalked crinoids were dominant in the Paleozoic and their success was correlated with the lack of an intensive predation pressure. The success of bivalves and gastropods with defensive structures as the dominant benthic, shallow-water communities in the Cenozoic was related to the Mesozoic marine revolution, characterised by the increasing dominance of durophagous predators since the Jurassic, including sharks, teleostean fishes and crustacean decapods. The abundant record of isocrinids and ophiuroids in localised horizons in the late Eocene from Antarctica was considered as an anomaly and explained as a retrograde community reminiscent of Paleozoic marine and modern deep-sea communities (Aronson *et al.*, 1997, Aronson and Blake, 2001). Low-predation levels for the late Eocene as in the Paleozoic were interpreted as driven by global cooling and changes in productivity associated with increased upwelling in Antarctica (Aronson and Blake, 1997).

The finding that the isocrinid crinoids from Tierra del Fuego are stratigraphically restricted to the late middle Eocene has significant palaeoecologic implications, as it clearly indicates a regional extension of anomalous, suspension-feeding communities with abundant stalked crinoids in the late middle and late Eocene of the southern ocean. The anomalous success of retrograde, dense, suspension-feeding echinoid populations in the late Eocene of Antarctica has been explained by the joint combination of three critical conditions: low predation pressure; low rates of sediment resuspension; and a high flux of particulate organic mater. The accelerated cooling trend during the late Eocene was linked to the disappearance or marked diminution of durophagous predators and to the high productivity of particulate organic matter promoted by increased upwelling (Aronson and Blake, 1997, 2001).

Similar outstanding associated characteristics are inferred for the late middle Eocene of Tierra del Fuego. Abundant crinoid columns are recorded in glauconite-rich intervals, suggesting localised periods of low sedimentation rates. Recent observations demonstrate that the phosphatic concretions, so common in different late Eocene-Miocene conglomerates in Tierra del Fuego (*cf.* Leanza and Hugo, 1992), have been reworked from late middle Eocene sediments, suggesting the existence of nutrient-rich oceanic waters during this time. The excellent preservation of the Foraminifera associated with isocrinids at La Despedida section is linked to disaerobic bottom conditions suggestive of a high flux of particulate organic matter. In addition, a striking feature is the absolute dominance and diversity of Nodosariacea in certain horizons. Absolute dominance of this superfamily is typical of the Jurassic and early Cretaceous, with a declining relative dominance in the Palaeocene, and thus the dominance of Nodosariacea in the late middle Eocene can also be considered as a retrograde feature.

Extant isocrinids are stenothermal, living generally within a short range of temperatures and in the deep sea, where their bathymetric distribution is controlled by temperature (Oji, 1996). Fossil isocrinids were probably also stenothermal. Thus, it seems reasonable to assume that the late middle to late Eocene declining temperature of the seawater led to a decline in predation pressure and favoured the preferred range of temperature for different isocrinid groups at slightly different times, allowing the bloom of shallow-water, isocrinid populations in the Southern Ocean.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Thoughts on controls on evolution and dispersal of benthos in the Magellan-Scotia Sea region: a workshop proposal*

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SUMMARY: The Scotia Arc and the Scotia Sea comprise a geologically young feature of the Earth's surface that evolved over the last 40 million years (Ma) or so, between the southern tip of South America and the northern tip of the Antarctic Peninsula. With the notable exception of the much younger South Sandwich Islands, the islands, banks and seamounts of the arc represent dispersed fragments of a previous continental link between southern South America (Magellan region) and the Antarctic Peninsula. The benthic marine shelf faunas of the region are the focus of the IBMANT (Investigación Biológica Marina en Magallanes relacionada con la Antártida) programme, and those of the surrounding oceanic deeps are the focus of ANDEEP (Antarctic Benthic Deep-Sea Biodiversity). Elucidating the potential relationships between the faunas of the region and the profound geographical, oceanographic and climatic changes undergone by the region in later Cenozoic time is hampered by significant unknowns in the geological history, the expense of further geoscientific exploration to fill these, and a general lack of communication between the biological and geological science communities. It is suggested that the time is opportune for a truly multidisciplinary workshop at which all the involved science communities have much to gain from the others.

Keywords: Antarctic, evolution, invertebrates, faunistic exchange, interdisciplinary perspectives.

RESUMEN: REFLEXIONES SOBRE LOS CONTROLES DE LA EVOLUCIÓN Y DISPERSIÓN DE ORGANISMOS BENTÓNICOS EN LA REGIÓN MAGALLÁNICA Y DE SCOTIA: UNA PROPUESTA DE TRABAJO. – El Arco de Scotia y el Mar de Scotia tienen características geológicas jóvenes, que evolucionaron en los últimos 40 millones de años (Ma), a partir de los actuales Cono Sur de América del Sur y extremo septentrional de la Península Antártica. Con la notable excepción de las mucho más jóvenes Islas Sándwich del Sur, las islas, bancos y montes sumergidos del arco representan fragmentos dispersos de una conexión continental previa entre la parte austral de Sudamérica (región magallánica) y la Península Antártica. La fauna marina bentónica de plataforma de la región ha sido el objetivo del programa IBMANT (**I**nvestigación **B**iológica Marina en la Región **Ma**gallánica relacionada con la **Ant**ártida) y la concerniente con las profundidades oceánicas circundantes son el eje de estudio del ANDEEP (**An**tarctic Benthic **Deep**-Sea Biodiversity). La dilucidación de las relaciones potenciales entre las faunas de la región y los profundos cambios geográficos, oceanográficos y climáticos que sucedieron durante el Cenozoico tardío está dificultada por significativos desconocimientos en la historia geológica, los costos de exploraciones científicas adicionales para resolverlos, y una falta general de comunicación entre las comunidades científicas biológicas y geológicas. Se sugiere que es tiempo oportuno para un verdadero trabajo multidisciplinario en el cual las comunidades científicas involucradas tienen mucho por ganar unas de otras.

Palabras clave: Antártida, evolución, invertebrados, intercambio faunístico, perspectivas interdisciplinarias.

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GEOLOGICAL AND BIOLOGICAL CHANGE IN THE MAGELLAN-SCOTIA ARC REGION

The Scotia arc and the Scotia Sea comprise a geologically young feature of the Earth's surface that evolved over the last 40 million years (Ma) or so. Lying between the southern tip of South America and the northern tip of the Antarctic Peninsula, the region is composed geologically of a number of islands, submarine banks or seamounts and ocean deeps. With the notable exception of the much younger South Sandwich Islands, the islands, banks and seamounts represent dispersed fragments of a previous continental link between southern South America and the Antarctic Peninsula. At some time prior to 40 Ma ago, there would have been a terrestrial link between the two continents, enabling the dispersal of land animals and plants (Reguero *et al.*, 2002). There would also have been flanking continental shelves providing a habitat for marine benthos and related fish, the implication being that in the geological past there should have been close similarities between the benthic faunas of what now constitute the Magellan and Antarctic Peninsula regions. This scenario raises some major questions. How might the marine faunas have evolved in response to the tectonic break-up of the continental link, the dispersal of the fragments, oceanographic changes, and the major climatic deterioration across the entire region? These issues are a focus of the IBMANT (**I**nvestigación **B**iolólogica Marina en **M**agallanes relacionada con la **Ant**ártida) programme (Arntz and Ríos, 1999).

In a recent paper (Thomson, 2004), the author reviewed the literature on the geological evolution of the Scotia Sea from the point of view of an interested observer. A more detailed review addressing many of the issues raised here was published independently by Mackensen (2004). The region is infamous for its stormy seas and it is a testament to the ships' crews and scientists who have persevered over the years to map its sea bed, to chart its currents, and to unravel its geological history. Much has been written, but not all the interpretations agree and that is because there remain some critical unknowns or uncertainties, notably:

- the relative timing of events,
- the precise movement history of the continental blocks within and around the Scotia Sea, and
- the detailed palaeogeographic configuration of the region through time.

Of these, timing is arguably the most critical because, whilst many of the models put forward are ever more sophisticated, an error of one or two million years in the timing of an event (easily possible depending on the dating methods used) could turn an argument on its head. In particular, there is a substantial body of evidence suggesting that the opening of Drake Passage, the separation of the south Tasman Rise from northern Victoria Land, the onset of the Circum-Polar Current (ACC) and the development of the first Antarctic ice sheets occurred between 32.5 and 34 Ma ago (e.g. Barrett, 2001; Lawver and Gahagan, 1998). There are several chickens and eggs here and knowing the true relative order is crucial to any view on whether or not the inception of the ACC may have had a causal (or even any) effect on Antarctic glaciation (Barker and Thomas, 2004; Thomson, 2004;). Furthermore, although there is a distinct movement away (Livermore *et al.*, 2004; Thomson, 2004) from the Barker and Burrell (1977) model, with a sliver of continental crust blocking Drake Passage until about 23.5 Ma ago, Maldonado *et al.* (2003) argued that, whilst Drake Passage was open to the Pacific, a deep-water passage through the east Scotia Sea was effectively blocked by an arc of continental fragments to the east and that there was a deep-water gyre within it until 20.7 Ma ago. It would seem that the ultimate effect would have been the same—no ACC until about 20 Ma ago. Even today the ACC, the "strongest current in the world's ocean" (Barker and Thomas 2004), is constrained within the 1000 km wide opening of Drake Passage and further obstructed by islands and continental shallows of the Scotia arc. Given the uncertainties over the evolution of these obstacles, it is a moot point as to just when it became possible for the ACC to develop into its present vigorous state.

With the use of computer models, it is now possible to attempt some rather detailed histories of block movements and the development of oceanic basins within the Scotia Sea (Lawver and Gahagan, 2003; Eagles, 2000). However, there are still some important areas of ocean floor whose ages are poorly constrained or essentially unknown (Barker, 2001), and there are two interpretations of the movement history of South Georgia: one where it moves from an original position near the southern tip of South America, eastward along the northern margin of the Scotia Sea (Barker and Burrell, 1977; Lawver *et al.*, 1992; Eagles, 2000), and a second where it breaks off initially with Discovery Bank (Lawver and Gahagan, 2003) and moves to the southern side of the Scotia Sea before moving subsequently northeast to its present position at the eastern end of the North Scotia Ridge. These two possibilities have potentially different consequences for the environmental pressures on and the evolutionary history of the faunas of the South Georgia continental shelf, and they need to be resolved.

Palaeogeography means different things to different people. In the case of the Scotia Sea, for some it can be little more than mapping the relative disposition of continental fragments within the region, but others would wish to know more about the physical structure of those fragments. For example, was there any land, how much was covered by sea and to what approximate depth, and would any significant transport of water have been possible across or between the blocks? Apart from those continental fragments where there are limited areas of land that can be visited by geologists (South Georgia, South Sandwich Islands, South Orkney Islands), we know frustratingly little about the geology of the continental blocks and even less of their continental shelves (Thomson, 2004) . Only the continental shelf of the South Orkney Islands has been sampled by drilling (Barker, Kennett *et al.*, 1988) but then only at its margin and with poor core recovery of a partial sequence.

Whilst remote geophysical methods, such as magnetic or multi-channel seismic systems, are invaluable for providing information on a region's gross geological structure, they cannot provide hard information on whether or not any sedimentary rocks are marine or terrestrial, and offer only inferential information about age. In order to obtain precise palaeoenvironmental, stratigraphical and age information, which comes from sediment types, fossils and datable (mainly magmatic) rocks, there is no other recourse than to collect a sample. But deep-sea drilling is expensive, the Scotia Sea is stormy, and it is likely to be many years before further sampling is undertaken. Furthermore, given that geological investigations in Antarctica seem to be somewhat out of fashion at present and that the focus is more and more on short-term climate change, further progress in the collection of geological data from the Scotia Sea region may seem somewhat remote, however desirable it is.

TOWARDS A SOLUTION

Despite this somewhat gloomy prospect outlined above, there is a yet untried and novel approach that might help us to squeeze out the last drops of information from existing studies and perhaps to place some apparently unaccountable pieces of data into some meaningful context—a workshop of marine biologists, geologists and geophysicists, and palaeo-oceanographers. It is suggested that interaction between such disparate groups of scientists who, nonetheless have all been working on the same region, might produce some surprising advances.

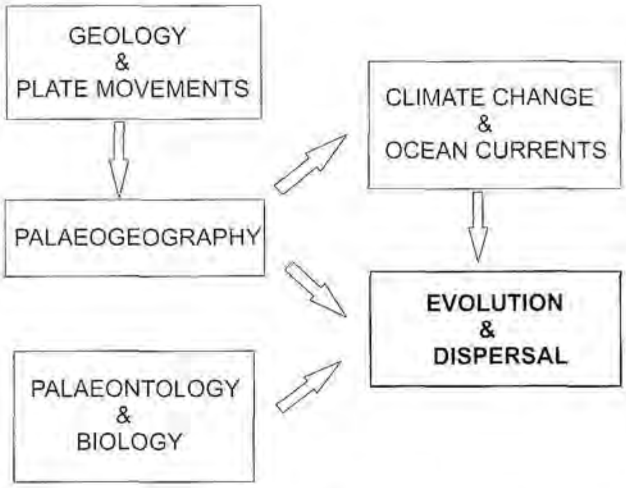

FIG. 1. – Diagram to show the interaction between key factors affecting the evolution and dispersal of benthic marine organisms in the Magellan-Scotia Sea region.

Figure 1 is a simple representation of the controls on the evolution and dispersal histories of marine faunas in the Magellan–Scotia Sea region and their possible interactions. It could provide a model for structuring the workshop. Geological, landscape, and plate-movement histories control the palaeogeography which, in turn, has a profound effect on oceanic currents and climate change. Palaeogeography, palaeontology and biology, and climate change and ocean current configurations all provide data for, or act as direct controls on, the understanding of the evolution and dispersal of taxa. There are many critical questions to be posed and no doubt everyone will have their own favourites. Here are some suggestions:

- What is the best present model for the break-up history of the palaeocontinental link between South America and the Antarctic Peninsula and formation of the Scotia Arc?

- How good is the geological dating and what assumptions constrain the data and the numbers? Be honest.

- What is the best geological estimate for the onset of the ACC and is there any supporting evidence from the palaeobiological record?

- What are the most significant controls on the distribution of benthic taxa in the region? How important was climate deterioration and ice-sheet extension?

- Are there any disparate biological distributions that might be explained by tectonic movements?

- How important is the ACC to biological distribution and evolution? It appears that it was not causal in the deterioration of the Antarctic climate, and the presence of associated eddies suggests that larvae might be able to cross it (Thatje and Fuentes, 2003; Glorioso and Leben, 2005; Thomson, 2004).

It is suggested that such a workshop, with close interaction between discipline groups that rarely have contact with each other, would lead to:

- a general clarification of the critical issues, and a better understanding of the region's geological and biological history based on a comprehensive view of available data,
- the solution of some problems or at least a new perspective on issues previously confined within a single disciplinary area, and
- identification of critical problems for further investigation.

But, most important of all, it should encourage the development of integrated cross-disciplinary studies, including multi-disciplinary cruises, in pursuit of a common goal.

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Although these few words contain many of my personal prejudices, for which I must take the responsibility, I nevertheless extend sincerest thanks to many who have inspired and encouraged me to contribute to the debate and causes of the IBMANT programme. In particular I wish to thank Professor W. Arntz (Alfred-Wegener-Insitut) for including me as a geologist in his biological community, and also Professor Angelika Brandt (Universität Hamburg) for welcoming me also into the ANDEEP community and making me write the review on which this note is based.

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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

The Magellan-Antarctic connection: links and frontiers at southern high latitudes. Summary review

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Eight years of research in the Magellan region and Antarctic marine ecosystems have passed since the first IBMANT Symposium held in Punta Arenas in 1997 (Arntz and Ríos, 1999). Considerable biogeographic and biodiversity work, supported by physiological and molecular genetic approaches, has been published during this time, especially in the Antarctic, much of it in the framework of SCAR's EASIZ and EVOLANTA programmes (Di Prisco *et al.*, 1998; Davison *et al.*, 2000; Arntz and Clarke, 2002; Huiskes *et al.*, 2003; Clarke *et al.*, subm.), and recently by research extending into the deep sea (Brandt and Hilbig, 2004). Marine science in the Magellan region, which had received important stimuli from the "Victor Hensen" and "Vidal Gormaz" campaigns in the previous period (Arntz and Gorny, 1996; CONA, 1999 a, b), was advanced rather by individual approaches such as the decapod and fish work carried out by the CADIC and colleagues from Ushuaia (e.g. Lovrich *et al.*, 2003; Fernández *et al.*, 2000) but also received further input from CIMAR Fiordo cruises nos. 3, 4, and 7 between 1997 and 2001, and the "LAMPOS" cruise of RV "Polarstern" along the Scotia Arc (CONA, 1999 a, b; Arntz and Brey, 2003).

Despite all these efforts, and a wealth of information presented and discussed during the Ushuaia IBMANT II Symposium, it is obvious that important gaps remain and a number of basic questions may not be solved in the immediate future (see Editorial to this volume). Among these are issues to be solved by geologists, palaeontologists and oceanographers, such as the exact timing of the final ocean gateway opening and the onset of a vigorous circum-Antarctic current system (Barker and Burrell, 1977; Barker and Thomas, 2004; Mackensen, 2004; Thomson*). Furthermore, the use of molecular approaches for the timing of biogeographic, radiation and extinction events has by no means been further advanced: depending on the method applied the results may differ by several million years (Hillis *et al.*, 1996). Thus, while it is hard to imagine how we can reach, at least in the short term, the intended close correlation between revolutionary changes in the polar environment and important biological processes, the only possible way out is close cooperation between disciplines, as is intended for the upcoming International Polar Year.

In the following an attempt is made to briefly summarise some of the results presented in this second IBMANT volume. They contribute to, and to some extent complement, the major issues and questions presented in the Foreword, and may therefore be seen as an updating of knowledge on biological interactions between the Magellan region and the Antarctic.

A traditional view is to see the Antarctic as an ecosystem that is almost perfectly isolated by deep sea, circular currents and powerful fronts between water bodies of different properties. But how hermetic are these fronts? Mesoscale eddies are a dominant feature of circulation and play a fundamental role in the transport of water along and across the Antarctic Circumpolar Current (ACC; **Glorioso *et al.***). Cross-frontal eddy transport and meandering have been encountered in particular along the Subantarctic Front and the southern ACC Front. These results are of utmost importance in the present situation of a warming planet, in which small increases in Southern Ocean water temperature may result in increased settling success of alien meroplanktonic larvae south of the Polar Front (Thatje and Fuentes, 2003), where the benthic biota may not have developed defence mechanisms.

Diversity and distribution of zooplankton, compared to the benthos, are much less affected by the Polar Front, although the cold-water convergence of the Polar Front is more important than the front between the tropics and subtropics. Worldwide, species richness of benthos is several degrees of magnitude higher than that of plankton, whose ecological relevance is not paralleled by its diversity. However, zooplankton species in the Atlantic sector of the Southern Ocean contribute an important share to the world-wide inventory of this group, which is almost twice as high as that of benthos. On the other hand, benthic endemism in these cold waters is much higher than that of plankton. Detachment from the bottom apparently results in wider geographic ranges and lower degrees of endemism (**Boltovskoy *et al.***).

A first study of mesozooplankton was carried out in the northern Beagle Channel near Ushuaia (**Fernández and Hoffmeyer**). Copepods were the dominant taxon. Most of the species found are typical of the Subantarctic, but some common species are present in high numbers also at Antarctic coastal sites, confirming that the Polar Front is probably not a major geographic barrier for the distribution of pelagic species.

Pelagobenthic coupling has been well studied in the Antarctic but sadly little is known from the Magellan region. The marked spring-summer peak of particle fluxes in the Antarctic water column and at shallower depths is concealed at the deeper seabeds due to suspension and lateral advection. Faecal pellets of various origins are the main constituents of the biogenic matter flux, but the role of distinct taxa requires further study. Aggregation of particles favours the transfer of high-quality organic matter to the benthos. Both faecal pellets and aggregates reduce the residence time of biogenic matter in the water column and favour the accumulation of highly nutritive material on the seafloor. The suspected poor species number and abundance of meroplanktonic larvae needs further confirmation (**Schnack-Schiel and Isla**).

The Patagonia-high Weddell Sea gradient is not the only latitudinal gradient presently under study. Marine research is also being undertaken along Victoria Land (Ross Sea) between 72 and 86°S by a consortium of Italian, New Zealand and U.S. scientists (**Berkman *et al.***). The preliminary results show that this area will yield highly interesting comparisons with results obtained in the Weddell Sea, including an extension to even higher latitudes. As only part of the Victoria Land gradient has an ice shelf coast, one important research issue might be to find out to what extent ice shelves influence the composition of the "circum-Antarctic" fauna and flora; e.g. missing macroalgae and rare occurrence of scallops in the Weddell Sea vs. abundant populations in the Ross Sea.

The Scotia Arc is the only shallow-water and island bridge linking the Antarctic nowadays with the surrounding continents. It has now amongst the fastest rates of environmental change measured. Shallow-water benthos was studied by **Barnes** in the context of this change. Due to the long dark winter, benthic life is mostly in the slow lane. During summer, shallow communities are intensely disturbed by ice scour and wave action, resulting in a lack of shore zonation and low species richness contrary to the conditions in the subtidal. As in deeper water (see Arntz *et al.*) there is no consistent latitudinal cline in species richness, rather a dependency on the degree of isolation of various sites, and some taxa are much more speciose than in southern hemisphere temperate waters. The islands of the Arc might serve as stepping stones for those faunal and floral elements which have dispersal capabilities to bridge short deep-sea distances. Eastward transport with the ACC is much more likely than the return in westerly direction, but the Weddell Sea Eddy, the East Wind Drift, and transport across the Polar Front by eddies originating from the valve effect of the Drake Passage (Glorioso *et al.*) might also contribute to exchange processes, which under the present fast rates of climate change might result in successful colonisation by "aliens".

Another shallow-water study (to 40 m depth) deals with the distribution of actinians along the

Chilean coast (**Häussermann and Försterra**). A total of 32 species of Actiniaria and Corallimorpharia were found, 23 of which occurred in the well-structured southern fjord system. A comparison based on extensive literature is made with data from Argentina (18 overlapping spp. of a total of 70) and the Antarctic (13 overlapping species). Many literature records need revision or confirmation.

Studying the 78 bryozoan species collected during the LAMPOS cruise, **Moyano** distinguished the island groups east and south of Shag Rocks as Antarctic, whereas Burdwood Bank clustered with Tierra del Fuego. Considering all records hitherto (214 spp.), the Antarctic Peninsula clustered with the Scotia Arc, whereas a second cluster comprised the Magellan region and the Falklands. Using bryozoan material (genera) from Australia and New Zealand, these areas join the Magellan region.

From bivalve material (74 spp.) sampled during the same expedition along the Scotia Arc, **Zelaya** noticed a higher similarity with the Weddell Sea (50-85% overlap) than with Patagonia and the Falkland (Malvinas) Islands (12-29%). The high Antarctic Weddell Sea and Patagonia/Falklands only shared 10% of their species. Bivalves from South Georgia were predominantly Antarctic. Bivalve distribution supports the placement of the Scotia Arc islands within the Antarctic region.

The species number of polychaetes in the south Chilean channel system from material collected in the last 124 yr amounts to 431 (**Montiel *et al.***). Based on this material the authors divided the Magellan region into an Atlantic and a Pacific subregion, both with <10% endemics. The great majority of the Magellan polychaete species show wide distribution ranges and an obvious affinity both with Subantarctic and Antarctic areas. For the actual distribution pattern of polychaetes in the Cono Sur, the West Wind Drift plays an important role.

Harpacticoid copepods from sublittoral and bathyal depths in the "Cono Sur" still hold a great potential for future study. The large material encountered during two expeditions only allowed for species determination in six (out of 25) major taxa, which yielded 122 species, >80% of which were new to science (George). The author emphasises the need for studies at species level, because species often show a much more restricted distribution than higher taxa. A second harpacticoid study was carried out in the Potter Cove (South Shetlands) (**Veit-Köhler**), with particular emphasis on the two species *Pseudotachidius jubanyensis* and *Scottopsyllus praecipuus*. Besides presenting numbers, the biovolume of the meiobenthic copepods was measured, the latter being related rather to total organic matter than to the C-N ratio, chloroplastic equivalents, grain size or depth. However, neither of the two specifically studied species showed a relation to total organic matter.

A molecular survey of within-species genetic diversity on the Antarctic isopod *Glyptonotus antarcticus*, hitherto considered a single species, revealed high variability in the mitochondrial LSU (16S) gene (**Held and Wägele**). From a total of eleven unique mitochondrial haplotypes four groups were differentiated, which may represent cryptic species at the Antarctic Peninsula, in the Ross Sea and in the SE Weddell Sea (2).

The species inventories of two malacostracan crustacean taxa were updated in the south of the Magellan region. Shallow-water Asellota (isopods) from the Beagle Channel now amount to 23 species (**Doti *et al.***). Faunistic affinities were high (65%) with the Straits of Magellan; the entire Magellan region showed 30% overlap with the Scotia Arc and 26% with the Antarctic Peninsula. Species richness and faunal affinities of gammaridean and corophiidean amphipods in southern Tierra del Fuego were studied by **Chiesa *et al.*** The authors identified 61—mostly small—species, most of which belong to the Phoxocephalidae, Stenothoidae and Lysianassidae. Of these 39% were endemic to the Magellan region.

Decapod distribution on the northern and southern branch of the Scotia Arc reveals a clear separation of Magellan and Antarctic elements respectively (**Lovrich *et al.***), with an occurrence of both reptant and caridean species on the northern, and an impoverished caridean fauna on the southern branch. However, South Georgia holds a transitional position in combining these elements, which might be explained by occasional changes in the position of the Polar Front, as suggested in the review by Arntz *et al.* Differences were detected in the reproductive cycle of *Notocrangon antarcticus* and in the oocyte number of *Munida subrugosa* from different localities. A new index measuring the energy invested in reproduction revealed that this investment is species-specific, larger in caridean shrimps than in galatheid crabs, and independent of the sampling site. The decapod faunas from southern Chile and southern Argentina combined in the Magellanic Biogeographic Province are closely related, but show little association with the circum-Antarctic decapod fauna (**Boschi and Gavio**), confirming work published by e.g., Gorny (1999) and Thatje *et al.* (2005).

A Belgian interactive data base on Antarctic echinoids (south of the Polar Front) now comprises 81 species (**David** *et al.*), summarising taxonomic, ecological, morphological and distributional data and the sources of information. The CD-Rom is distributed with this volume.

A similar distribution as in the decapods (northern branch of the Scotia Arc: Magellan, southern branch: Antarctic) was found in 42 ascidian species collected during three Spanish expeditions (**Ramos-Esplá** *et al.*). South Georgia again holds a transitional position, with an intermediate ascidian fauna between the Antarctic Province and the Magellan region. Another ascidian study from the LAMPOS cruise, yielding 25 species or morphospecies, also states a transitional role of South Georgia, as it represents the northern limit for Antarctic species and the southern limit for Magellanic species (**Tatián** *et al.*). The lower depth limits of the two studies (600 m) were identical, but the latter upper range (250 m) was much deeper than the former (10 m), which may explain the different species numbers.

Mega- and macrobenthic associations were sampled in the south Chilean fjord system by **Ríos** *et al.* using an Agassiz trawl. A total of 131 species were collected, with echinoderms (47 spp.) and polychaetes (46 spp.) as dominant taxa. Marked differences were found between the impoverished benthic fauna in the fjords and channels off the South Patagonian Icefields, revealing strong glacier impact, and the richer fauna in the Straits of Magellan.

Progress in macrobenthic studies on the Antarctic and Magellan shelves and upper slopes since the first IBMANT Symposium is reported by **Arntz** *et al.*, placing the emphasis on shipboard sampling. Considerable progress is visible in biodiversity and biogeography on the Magellan-Antarctic latitudinal gradient, the influence of disturbance on biodiversity, and the general role of evolutionary and ecological factors in shaping past and present-day environmental conditions, species composition and distribution, and ecosystem functioning. Benthic life strategies and physiological adaptations (see Pörtner *et al.*) have also received due attention. Methods have been improved substantially, and modern approaches play an increasing role. On the other hand, much remains to be done. Research in the Magellan region, which has not advanced with the pace experienced in the Antarctic, must be enhanced. The same is true for other undersampled areas, such as most of the East Antarctic, Bouvet Island or the Bellingshausen Sea, or the rare shallow sites in the Weddell Sea. Areas recently freed from ice shelves such as the Larsen ice shelf should be studied intensely. Much more interdisciplinary work is necessary to tackle the numerous open questions about the relations between environmental change and organismic evolution in the Subantarctic and Antarctic. Molecular methods need to be improved, and validation with the help of palaeontologists increased in order to reach more concise datings of evolutionary processes.

Based on comparisons of fish and invertebrate metabolism along latitudinal gradients in both hemispheres, **Pörtner** *et al.* analyse characteristics of temperature dependent metabolic adaptation and their consequences for changes in energy budgets. Temperature sensitivity of growth is considered a key component for energy budgets. Apparently, natural selection helps individuals to reach high energy efficiency and maximized growth, but is constrained by limited energy availability and temperature. However, the assumption that levels of metabolic rates could be estimated just from mean temperatures is too simple, and there are distinct differences between the permanently low temperature ecosystems of the Antarctic as compared to the Subarctic and Arctic, where temperature variability is greater. This variability causes a rise in maintenance costs at the expense of growth but in favour of agility and foraging capacity, whereas savings in maintenance costs, setting free energy for growth, are maximised under the permanently low temperatures of the Antarctic. The authors emphasise that their energy budget hypothesis and the suggested trade-offs between life style, agility and growth performance explain most of the patterns observed in stenotherms and eurytherms on a latitudinal gradient.

Ultraviolet B radiation reaching the surface of the Southern Ocean has significantly increased due to the reduction of the stratospheric ozone. Based on the investigation of a phytoflagellate and a diatom, **Hernando** *et al.* conclude that the balance between damage and repair after UV radiation involves the combined action of several internal factors in the cell, suggesting that exposure to mild oxidative stress initiates adaptive responses that provide increased protection against more severe stress. In another study, **Malanga** *et al.* investigated the effect of air exposure and temperature fluctuations at different tidal levels on oxidative stress parameters in gills of Magellan and Antarctic limpets *(Nacella* spp.). In the Beagle Channel, *N. magellanica* lives in the intertidal and suffers high environmental variability, whereas *N. deaurata* is usually covered by shallow water and experiences comparatively constant conditions. The Antarctic *N. concinna* is found both at inter- and subtidal levels. Antarctic Peninsula specimens from the upper intertidal showed significantly increased activities of catalase and superoxide dismutase as compared to their relatives at lower levels. No pronounced difference in oxidative stress parameters or in oxygen uptake was detected between the two limpets from the Beagle Channel. The proposed mechanism that controls oxidative stress in the intertidal *N. magellanica* could, according to these authors, be the way in which the limpets control the content of catalytically active iron II (including reduction rates of iron III) in their tissues. The conclusion from the two contributions is that coping with a demanding environment requires complex metabolic adjustments to minimise intracellular damage.

Antarctic fish (Notothenioidei) deserve special attention because unlike most other fish taxa, this group adapted successfully to cold conditions. The reproductive development of notothenioid fish caught in the Scotia Arc during the LAMPOS cruise differed substantially among the different species. Fecundity in channichthyids was lower than in nototheniids. Spawning revealed the same characteristics as in the high Antarctic, with delayed maturity, moderate fecundity, a single spawning per year and prolonged gametogenesis (**Vanella *et al.***). **Vanella and Calvo** studied the influence of temperature on the routine metabolic rate of Subantarctic teleosts and compared the results with the rates of species with different geographical distributions. In the 5 studied species and all tested temperatures, body mass and oxygen consumption showed a positive correlation. A massive drop in temperature caused a significant reduction in oxygen consumption. Pelagic species had a higher O_2 consumption than sluggish demersal species. The authors conclude that similar to fish in the Antarctic proper, Subantarctic fish have not developed metabolic cold adaptation.

The axial muscle of Antarctic and some Subantarctic notothenioids contains exceptionally large muscle fibres and a low fibre number. Species from both regions showed no differences in the number and type composition of fibres, or in ATPase activity, fibre recruitment and swimming performance. However, fibre number and fibre diameter decrease in the more derived families, and the duration of the cell cycle showed cold compensation in the Antarctic *Harpagifer* species in comparison with its Subantarctic relative. Apparently, the diversification of Antarctic notothenioids was associated with a size-specific reduction in fibre numbers and an increase in fibre diameter. This finding presents a great opportunity to study the temperature-related mechanisms of muscle growth in an evolutionary context (**Fernández *et al.***).

Stalked crinoids were a conspicuous member of shallow marine benthic communities throughout much of the Palaeozoic, before they were outcompeted by the Mesozoic increase of durophagous predators (Aronson and Blake, 2001) and gave way to the mobile forms that prevail in the benthos today, with the exception of some refuges such as the deep sea. While post-late Cretaceous shallow water records of isocrinids are generally very rare, these forms were still abundant in Antarctic shallow water of the La Meseta Formation of Seymour Island in the late Eocene. **Malumián and Olivero** report the existence of another retrograde, dense *Isselicrinus* population, which successfully extended its distribution into the Leticia Formation of Tierra del Fuego. These occurrences in shallow water are in contrast with the depth distribution of stalked crinoids by that time, which was almost entirely a deep-water distribution.

The Late Glacial Maximum (LGM) in the Beagle area probably occurred ca. 20,000 yr BP (Rabassa *et al.*, 1990). By 12,000 yr BP the ice seems to have disappeared from the coasts at Pto. Williams and Ushuaia, and large amounts of meltwater were filling the Beagle Channel (Heusser, 1989, 1998). Fossil marine records were first showing up around 8000 yr BP (**Gordillo *et al.***). A diversification and expansion of molluscan assemblages occurred during the interval 5000-4000 yr BP, when an evolution towards modern conditions took place. Most species once established also survived later climatic deterioration. Both in Tierra del Fuego and in the Antarctic, molluscs are the most consistent fossil record, and all recovered taxa are extant species. Overlap of these palaeofaunas at the species level is low, as for recent species where it is <10%, but on genus and family level it is high. From the study of the fossil molluscan assemblages the authors conclude that most of the affinities and relationships between the Magellan and Antarctic molluscan faunas are a product of high-latitude radiation in the Quaternary rather than reflecting ancient connections during the Weddellian Province in the Palaeogene.

The opening of the channel system of the "Cono Sur" after the LGM may have also created pathways for the exchange of Magellan polychaetes (Montiel *et al.*).

An outlook based on the presentations and discussions during the meeting is given by **Thomson**, who concludes that in the face of all the uncertainties about the late Cenozoic geological history, the doubts about major oceanographic processes and many unknown patterns in palaeontology and evolution, the time is opportune for a truly multidisciplinary international workshop. Both IBMANT and ANDEEP, under the roof of SCAR, might provide a framework for convoking the biological community, but efforts are also necessary from the other disciplines. After all, as Thomson says, the involved science communities have much to gain from each other.

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