

MARINE BENTHIC COMMUNITIES OF THE MAGELLAN REGION,  
SOUTHERN CHILE: CONTRIBUTIONS OF DIFFERENT HABITATS TO  
THE OVERALL BIODIVERSITY

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2007

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BUNDESREPUBLIK DEUTSCHLAND – FEDERAL REPUBLIK OF GERMANY

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Vorgelegt an der Universität Bremen (Fachbereich 2 – Biologie/Chemie)  
Als Dissertation zur Erlangung des akademischen Grades  
Doktors der Naturwissenschaften (Dr. rer. nat.)  
Bremen 2007

## SUMMARY

The Magellan region is located at the southern tip of South America, ranging from about 42°S (South Patagonian Icefield) to 56°S (Cape Horn Archipelago). The marine realm in this area is formed by a complex net of fjords, channels and internal seas created by glacier processes that occurred after the Last Glacial Maximum ca. 12,000 years BP.

The aim of this thesis was to obtain more detailed information about the characteristics of typical macrozoobenthic communities in relation to the marine environmental variability in the Magellan region. In order to achieve this goal, the community structure in three of the most characteristic types of habitats characterizing the heterogeneous geomorphological conditions of the Magellan waters was studied. Structural parameters such as abundance, biomass, species richness and composition, dominance, diversity and evenness were considered in the investigation. Two of the habitats - intertidal boulder and cobble terraces and sublittoral soft-bottom areas - derive directly from the glacier processes affecting the region as a whole. The third one is a specific biogenic habitat provided by the holdfasts of the kelp *Macrocystis pyrifera*. The obtained information served as a base to evaluate the importance of these habitats with their specific communities for the overall biodiversity of the Magellan region and to check some specific hypotheses.

The intertidal boulder and cobble terraces are a particularly harsh environment. Principal factors structuring this habitat are the size of boulders and cobbles, the type of rock, the degree of compactness of the soft sediment below and between the rocks, together with tidal waves, local hydrodynamics, burial by sand, and exposure to air during low tide. This distinct habitat heterogeneity determined a great amount of biotic variability, i.e. a high species turnover among replicates within and between sites. The intertidal habitat was characterized by the numerical and weight dominance of a few species and reduced species richness. A total of 66 macrofaunal species and higher taxa was sampled, representing the benthic community with the lowest species number, density and biomass among the three types of assemblages considered for this thesis.

The sublittoral soft bottoms were studied considering quantitative samplings in the eastern Straits of Magellan and qualitative samplings in a transect from the central and western Straits and off the South Patagonian Icefield (SPI). The main environmental factor disturbing the sublittoral communities in the eastern Straits were semidiurnal spring tidal currents, whereas the benthic communities off the SPI suffered the effects of high

sedimentation rates, freshwater input and stratification of the water column. A total of 301 macrobenthic species and higher taxa were obtained from six periods of quantitative sampling in the Segunda Angostura. Again low sample species richness, relatively low abundances and strong dominance of few species were found. Pooling all samples over the study period, relatively high species richness and diversity resulted. Species richness and the abundances of single species populations varied considerably. Analyses based on species presence/absence data obtained from the qualitative transect reveal differences between the stations in front of the SPI and those in the rest of the Straits. Species richness was about the same in the two discriminated areas, but the abundances in the channels were consistently higher than in the SPI area influenced by glaciers. All catches were dominated by few species.

The kelp (*Macrocystis pyrifera*) forests provide another characteristic habitat in the Magellan region. Strong wind and resulting currents are the most important abiotic factors in this community, causing destruction and stranding of the individual plants including their holdfast. Only the holdfast associated organisms from two kelp forests in the Straits of Magellan were considered in this thesis, with a total of 114 species and higher taxa identified. The results showed a distinct dominance of few species and a high species turnover within and between sites. The two studied communities were found to be comparably rich in species as compared to others further south toward Cape Horn. The mismatch between the low longevity of kelp as a habitat and the much longer life-spans of the inhabiting benthic species suggests that the holdfast communities have to be regarded as immature communities.

Local densities, species composition and species richness differed greatly within and among study habitats. Patterns in community structure were found, especially changes with depth in species richness, abundance and biomass, however without any latitudinal trend along the Magellan region although the composition of species did change with latitude. For all the studied habitats the species richness at sample scale was found to be rather low (low  $\alpha$  diversity) and with a high turnover of species, resulting in an increased regional diversity. However, more detailed analyses of the communities' species composition and richness, combining different types of gear and with a long-term basis is obviously necessary, especially considering that almost 1,400 benthic invertebrate species have been reported hitherto for the Magellan region.

Particularly impoverished conditions in abundance and biomass, but not in species richness, were found in the fjords influenced by the SPI. Similar effects were caused by winds and waves in intertidal, and by winds and currents in *Macrocystis* holdfast communities.

It is difficult to define a “typical Magellan benthos” for the region, which seems to be rather a heterogeneous transition area for the fauna of the surrounding oceans.

A comparison with the northern hemisphere benthic systems of the southern North and Baltic seas, which are also post-glacial areas and of the same young age as the Magellan region, reveals that young ecosystems as such are not necessarily poor in species. The Magellan region was found to be considerably richer than the northern hemisphere seas, most likely due to lower disturbance by anthropogenic factors.

## ZUSAMMENFASSUNG

Die Magellanregion an der Südspitze Südamerikas erstreckt sich von etwa 42°S (Südpatagonisches Eisfeld) bis 56°S (Kap Horn-Archipel). Dieses Meeresgebiet besteht aus einem komplexen Netz von Fjorden, Kanälen und Binnenseen, die nach dem Maximum der letzten Vereisung, vor ca. 12.000 Jahren, durch Gletschereinwirkung entstanden sind.

Das Ziel der vorliegenden Dissertation war, mehr detaillierte Information über die Charakteristika typischer Makrozoobenthosgemeinschaften im Magellangebiet in Abhängigkeit von der Variabilität der marinen Umwelt zu schaffen. Zu diesem Zweck wurde die Gemeinschaftsstruktur in drei Biotopen untersucht, welche die heterogenen geomorphologischen Bedingungen der Magellanregion in besonders charakteristischer Weise widerspiegeln. Abundanz, Biomasse, Artenreichtum, Artenzusammensetzung, Dominanz, Diversität und Äquität wurden dabei als Strukturparameter berücksichtigt. Zwei der untersuchten Biotope – Steinpflaster im Gezeitenbereich und sublitorale Weichböden – gehen direkt auf die Gletscherprozesse zurück, welche die Region insgesamt beeinflussen. Der dritte ist ein spezieller biogener Lebensraum, der von dem „Wurzelgeflecht“ des Tangs *Macrocystis pyrifera* gebildet wird. Die gewonnene Information diente als Grundlage für eine Einschätzung der Bedeutung dieser Lebensräume mit ihren spezifischen Gemeinschaften für die marine Biodiversität der Magellanregion insgesamt und zur Überprüfung einiger spezifischer Hypothesen.

Die eulitoralsten Steinpflaster sind ein besonders schwieriger Lebensraum. Die wichtigsten Faktoren, die diesen Biotop strukturieren, sind die Größe der Steine, die Art des Gesteins, die Kompaktierung des Weichbodens unter und zwischen den Steinen sowie Gezeitenwellen, lokale Hydrodynamik, Übersichtung mit Sand und Exposition an der Luft während Niedrigwasser. Die ausgeprägte Heterogenität dieses Lebensraums bewirkte eine hohe Variabilität in der Besiedlung, d.h. große Verschiedenartigkeit in der Artenzusammensetzung von Unterproben an einer Station und zwischen Stationen. Der Gezeitenbereich zeichnete sich durch numerische und Gewichts-Dominanz weniger Arten und reduzierten Artenreichtum aus. Insgesamt wurden hier 66 Makrofauna-Arten und höhere Taxa gefunden. Damit war die Steinpflaster-Assoziation die Gemeinschaft mit der niedrigsten Artenzahl, Dichte und Biomasse unter den drei Gemeinschaftstypen, die in dieser Arbeit untersucht wurden.

Für die Bearbeitung der sublitoralen Weichböden wurden quantitative Aufsammlungen in der östlichen Magellanstraße und qualitative Proben aus einem Transekt berücksichtigt, der von der mittleren Magellanstraße bis vor das Südpatagonische Eisfeld (SPI) verlief. Der wichtigste Umwelt-Störfaktor im Osten der Magellanstraße waren halbtägige Gezeitenströme im Frühjahr, während die Gemeinschaft vor dem SPI hohen Sedimentationsraten, Süßwasser-Zufluss und Schichtung der Wassersäule ausgesetzt war. Insgesamt wurden 301 Makrobenthosarten und höhere Taxa aus den sechs quantitativen Aufsammlungen in der Segunda Angostura bestimmt. Auch hier wurden niedriger Artenreichtum pro Probe, relativ niedrige Abundanzen und starke Dominanz weniger Arten verzeichnet. Aus der Gesamtheit der Proben über den Sammelzeitraum ergaben sich jedoch relativ hohe Werte für Artenreichtum und Diversität. Sowohl der Artenreichtum als auch die Abundanzen der einzelnen Populationen unterlagen großen Schwankungen. Analysen aus dem qualitativen Transekt auf der Basis von Präsenz/Absenz trennten die Stationen vor dem SPI und den Rest. Der Artenreichtum in den beiden unterschiedenen Gebieten war etwa gleich hoch, aber die Abundanzen in den Kanälen waren durchweg höher als im SPI-Gebiet, das von Gletschern beeinflusst wird. Alle Fänge wurden von wenigen Arten dominiert.

Die *Macrocystis pyrifera*-Tangwälder sind ein weiterer charakteristischer Biotop in der Magellanregion. Starkwind und – als Folge davon – starke Strömungen sind die wichtigsten abiotischen Faktoren in dieser Gemeinschaft und führen zu Zerstörung und Strandung der Tange einschließlich ihres „Wurzelgeflechts“. Nur die Organismen aus diesen Geflechten wurden aus zwei Tangwäldern in der Magellanstraße berücksichtigt und ergaben 114 Arten und höhere Taxa. Auch hier zeigten sich starke Dominanz weniger Arten und große Verschiedenartigkeit in der Artenzusammensetzung innerhalb von und zwischen Stationen. Die beiden untersuchten Gemeinschaften erwiesen sich als relativ artenreich im Vergleich zu anderen *Macrocystis*wäldern weiter südlich bei Kap Horn. Das Missverhältnis zwischen der geringen Lebensdauer der Tange als Biotop und der viel längeren Lebensspanne der Benthosarten, die das Geflecht bewohnen, deutet darauf hin, dass die „Wurzelgeflecht-Gemeinschaften“ keine reifen Gemeinschaften sind.

Lokale Dichten, Artenzusammensetzungen und Artenreichtum unterschieden sich stark in und zwischen den untersuchten Biotopen. Obwohl sich bestimmte Muster abzeichneten, z.B. Veränderungen von Artenreichtum, Abundanzen und Biomasse mit der Wassertiefe, zeigte sich kein latitudinaler Trend in der Magellanregion; lediglich die

Artenzusammensetzung veränderte sich mit der Breite. In allen untersuchten Biotopen war der Artenreichtum pro Probe ziemlich niedrig (geringe  $\alpha$ -Diversität) und der Artenumsatz hoch (erhöhte regionale Diversität). Genauere Analysen der Artenzusammensetzung und des Artenreichtums in den magellanischen Gemeinschaften, mit Kombination verschiedener Probennahmegeräte und auf Langzeitbasis, sind jedoch offensichtlich notwendig, insbesondere angesichts der Tatsache, dass bislang fast 1400 benthische Evertibratenarten aus diesem Gebiet verzeichnet wurden.

Besonders arme Bedingungen hinsichtlich Abundanz und Biomasse, aber nicht bezüglich des Artenreichtums wurden in den Fjorden gefunden, die vom SPI beeinflusst werden. Ähnliche Auswirkungen haben Wind und Wellen im Eulitoral sowie Wind und Strömungen in den Tangwäldern.

Aus biogeographischer Sicht ist es schwierig, ein "typisches magellanisches Benthos" für die Region abzugrenzen; sie ist eher ein heterogenes Übergangsgebiet für die Fauna aus den angrenzenden Ozeanen.

Ein Vergleich mit den benthischen Ökosystemen der südlichen Nordsee und der Ostsee auf der Nordhemisphäre, die ebenfalls postglaziale Gebiete sind und das gleiche geringe Alter aufweisen wie die Magellanregion, zeigt, dass junge Ökosysteme an sich nicht notwendigerweise artenarm sein müssen. Das Magellangebiet ist wesentlich artenreicher als die beiden Meere auf der Nordhemisphäre, vermutlich aufgrund geringerer Störung durch anthropogene Einflüsse.



**RESUMEN**

La región de Magallanes está ubicada en el extremo austral de América del Sur, aproximadamente entre los 42°S (Campo de Hielo Sur) y los 56°S (Archipiélago del Cabo de Hornos). El dominio marino de la región está conformado por una compleja red de fiordos, canales y mares interiores, formada por procesos glaciares ocurridos después del Último Máximo Glacial hace aproximadamente 12 mil años AP.

Esta tesis tuvo como propósito el obtener información lo más detallada posible acerca de las características de comunidades macrozoobentónicas características de Magallanes y su relación con la variabilidad ambiental de la región. Para tal efecto, se estudió la estructura de la comunidad considerando tres tipos de hábitats que reflejan la heterogénea condición geomorfológica del ambiente marino de Magallanes. Se consideraron parámetros estructurales tales como abundancia, biomasa, riqueza y composición de especies, dominancia, diversidad y uniformidad. Dos de los hábitats estudiados (terrazas intermareales de bloques y cantos y zonas sublitorales de fondos blandos) son producto directo de la pasada acción glacial que afectó a toda la región. El tercer hábitat es de tipo biogénico y está constituido por los grampones de la macroalga *Macrocystis pyrifera*. La información obtenida servirá de base para evaluar la importancia que tienen estos hábitats y sus comunidades específicas en relación con la biodiversidad global de la región de Magallanes y para analizar algunas hipótesis específicas.

Las terrazas intermareales de bloques y cantos constituyen un ambiente severo particular. Los principales factores que estructuran el hábitat son el tamaño de los bloques y cantos, el tipo de roca, el grado de compactación del sedimento blando subyacente a las rocas, en conjunto con las mareas, la hidrodinámica local, la cobertura con arenas y la exposición al aire durante las bajamares. Esta característica heterogeneidad abiótica determina una gran variabilidad biótica, i.e. un alto reemplazo de especies entre réplicas tanto dentro como entre sitios. El hábitat fue caracterizado por la dominancia numérica y en biomasa por parte de pocas especies y una reducida riqueza específica. Se recolectó un total de 66 especies y taxa superiores de la macrofauna, constituyéndose en la comunidad bentónica con el menor número de especies, densidad y biomasa de las tres comunidades estudiadas en esta tesis.

El sublitoral de fondos blandos fue estudiado considerando muestres cuantitativos en el sector oriental del Estrecho de Magallanes y muestres cualitativos realizados en un transecto que comprendió desde la zona central y oeste del Estrecho hasta el Campo de

Hielo Sur (SPI). Los principales factores que generan disturbios en las comunidades sublitorales de la parte oriental del Estrecho son las fuertes corrientes semi-diurnas, mientras que en el SPI las comunidades están bajo el efecto de las elevadas tasas de sedimentación, ingreso de aguas no salinas y la estratificación de la columna de agua. A partir del muestreo cuantitativo realizado en seis períodos en el sector de la Segunda Angostura, se obtuvo un total de 301 especies y taxa macrobentónicos superiores. Una vez más, se encontró una baja riqueza de especies en las muestras, una abundancia relativamente baja y una fuerte dominancia por parte de pocas especies. Reuniendo toda la información de los seis períodos, se obtuvo una riqueza de especies y una diversidad relativamente altas. La riqueza de especies y las abundancias de cada especie particular variaron considerablemente. Análisis basados en datos de presencia/ausencia de especies obtenidos a partir de los muestreos cualitativos revelaron diferencias entre estaciones localizadas en el SPI y aquellas muestreadas en el Estrecho de Magallanes. La riqueza de especies fue similar en las dos áreas discriminadas, aunque la abundancia en la zona de canales fue consistentemente superior que la obtenida en las zonas del SPI influenciadas por los glaciares. Todas las capturas fueron dominadas por pocas especies.

Los huirales de *Macrocystis pyrifera* constituyen otro hábitat característico de la región de Magallanes. Los factores más importantes y que causan la destrucción y el desprendimiento de las plantas incluyendo los grampones y posterior enredo de unas con otras, son los fuertes vientos y las corrientes. En esta tesis se consideraron sólo los organismos asociados a los grampones en dos huirales localizados en el Estrecho de Magallanes, habiéndose identificado un total de 114 especies y taxa superiores. Los resultados muestran una dominancia por parte de pocas especies y un alto reemplazo de especies dentro y entre sitios. Las dos comunidades estudiadas tuvieron una riqueza de especies comparable con las obtenidas para otros huirales ubicados hacia el Cabo de Hornos. La no sincronía entre la baja longevidad del huiral como hábitat y la mayor duración de la vida de muchas de las especies que habitan ese espacio, sugiere que las comunidades de los grampones pueden ser consideradas como unas comunidades inmaduras.

Las densidades locales y la composición y riqueza de especies difiere marcadamente dentro y entre los tipos de hábitats estudiados. Se encontraron patrones en la estructura de la comunidad, especialmente relacionados con cambios en la riqueza de especies, abundancia y biomasa en relación con la profundidad. Sin embargo, no se observaron

tendencias latitudinales aunque la composición de especies cambió con la latitud a lo largo de la región. La riqueza de especies a una escala local (diversidad alfa) fue más bien baja, con un alto reemplazo de especies, lo cual resultó en una mayor diversidad a escala regional. Sin embargo, es obviamente necesario un análisis más detallado y a largo plazo sobre la composición y riqueza de especies en las comunidades combinando diferentes tipos de equipos de muestreo, especialmente considerando que hasta el momento se han reportado alrededor de 1.400 especies de invertebrados bentónicos para la región de Magallanes.

En los fiordos influenciados por el SPI se encontraron valores de abundancia y biomasa especialmente bajos, aunque no en riqueza de especies. Efectos similares fueron causados por el viento y las mareas en la zona intermareal y por los vientos y corrientes en el caso de las comunidades asociadas a los grampones de *M. pyrifera*.

Es difícil definir un “bentos típicamente Magallánico” para la región, la cual parece ser más bien un área heterogénea de transición para la fauna de los océanos circundantes.

Una comparación con los sistemas bentónicos del mar Báltico y los del sector sur del Mar del Norte en el hemisferio norte, los cuales también son áreas post-glaciares y tan jóvenes como la región de Magallanes, indica que los ecosistemas jóvenes no necesariamente son pobres en especies. Se encontró que la región de Magallanes es considerablemente más rica que los mares del hemisferio norte, muy probablemente debido a los pocos factores antropogénicos que podrían causar disturbios.

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## 1. INTRODUCTION

Benthic biodiversity and biogeography research in and around Antarctica has experienced great interest in recent years (Battaglia et al. 1997; Arntz & Clarke, 2002; Huiskes et al. 2003), especially after the multinational BIOMASS program, which was restricted to research in the pelagial and based on a regional approach, focussing on the ecology of the Antarctic krill and its predators (El-Sayed 1996; Clarke & Arntz 2006). The importance of ecosystem studies in Antarctic waters, emphasized previously by Hempel (1985) and others, has been stressed after an initial series of exploratory studies, after which more sophisticated and integrated programs designed to study the Antarctic marine ecosystem as a whole followed. The historical development of Antarctic marine research has been summarized, among others, by El-Sayed (1996) and Hempel (2007). A post-BIOMASS phase is recognized with the initiation of several multidisciplinary scientific programs oriented towards the study of biological phenomena in relation to environmental factors, and gradually turning towards processes of global significance. In the context of global change research, the polar areas are studied as part of the Earth's biosphere, in which Antarctica and its surrounding seas play a key role.

The understanding of key ecological, biogeographical and evolutionary processes operating in the coastal and open polar systems, as well as the monitoring of natural changes and man-made (anthropogenic) effects on high and Subantarctic communities and their abiotic environments have been of increasing importance in several international biological research programs and expeditions dedicated to the ecology of Antarctic waters and the surrounding oceans. These multidisciplinary scientific efforts have been undertaken with the aim to study, e.g. diversity and structure of pelagic and benthic communities, the biological effects of ice on communities, the cryo-pelagic, pelago-benthic and benthic-pelagic coupling, the ecophysiology of polar marine organisms, and the molecular bases for evolutionary biology. They were endorsed by numerous national scientific initiatives, which also included multidisciplinary investigations on the structure of, and processes within benthic ecosystems (e.g. Faranda & Guglielmo 1993; CONA 1995, 1997; 1999; Arntz & Gorny 1996; Faranda et al. 1996; Fahrback & Gerdes 1997; Ramos & Moya 2003; Fütterer et al. 2003; Arntz & Brey 2003, 2005; Ramorino 2004). Much effort has been invested in the high Antarctic Weddell Sea (cf. review in Arntz & Clarke 2002), in comparison with the research activities performed in other areas such as the Ross Sea (e.g. Dayton et al. 1974; Gambi et al. 1997; Cattaneo-Vietti et al. 2000;

Rehm et al. 2006), the Bellingshausen Sea (e.g. Shreeve & Peck 1995; Garcia-Raso et al. 2005) and the Antarctic Peninsula (e.g. Gallardo 1987; Mincks & Smith 2007).

• **EPOS, EASIZ: collaborative research in the Antarctic**

Among the various international programs and expeditions which have attempted to integrate the different components of the Antarctic ecosystem, EPOS (the European “Polastern” Study) was the first to address this issue in broad international cooperation, using the German icebreaker “Polarstern” as a platform (Hempel 1993). The third leg of the EPOS cruise was dedicated principally to benthic and ichthyological research in the high Antarctic, mainly on an exploratory basis. The 10 years program Ecology of the Antarctic Sea-Ice Zone – EASIZ (Arntz & Clarke 2002; Clarke & Arntz 2006), performed mainly in the high Antarctic Weddell Sea region and around the Antarctic Peninsula, provided new insights into a number of key ecological processes operating in the coastal and shelf Antarctic ecosystem. This program integrated processes occurring in the pack ice, the water column and the benthos, thus stressing by cryo-pelago-benthic coupling studies the “whole ecosystem” aspect. In particular, this program has led to the reassessment of the history, diversity, history and ecology of the Antarctic benthos, the coupling of this system to ice and water-column processes, and a review of physiological adaptation to low temperature in polar marine organisms (Arntz & Clarke 2002; Clarke & Arntz 2006). In the context of marine benthic diversity, EASIZ data yielded results on species composition and distribution of most macroinvertebrate taxa, fish and macroalgal groups, on the characterisation of typical Antarctic species assemblages in the benthos and plankton, the structure and life of the different forms of sea ice and the ice biota. The biodiversity information suggests an asymmetric latitudinal distribution of taxonomic richness in the two hemispheres, questioning that the marine latitudinal gradient documented for the northern hemisphere also exists in the southern hemisphere forming the so-called ‘bell-shaped curve’ (i.e. high diversity in the tropics and depauperate faunas towards the poles). The species-rich Southern Ocean around Antarctica (Arntz et al. 1997; Clarke & Johnston 2003) is central to this topic. The outcome of climatic, glacial and evolutionary processes through the Cenozoic in the Antarctic marine realm has been a generally rich and diverse marine fauna, with some particularly speciose taxa (Clarke & Johnston 2003). Based on data from the Weddell Sea, the total number of macrozoobenthic species for the entire Antarctic shelf was estimated between 11,000 and

17,000 (Gutt et al. 2004). Considering vast areas not studied to date, this may rather be an underestimation. For some invertebrate groups, the species richness may also be underestimated in view of recent molecular evidence for cryptic speciation in the Antarctic benthos (e.g. crustaceans: De Broyer et al. 2003; Held 2003). In general, the species richness in the Antarctic marine ecosystem has been found to be higher than formerly expected (Arntz et al. 1997). For more comprehensive reviews of this subject see Battaglia et al. (1997), Arntz & Clarke (2002), Clarke & Johnston (2003) and Huiskes et al. (2003). In future studies the importance of scales, i.e. the role of local versus regional species richness must be included (Gray 2001; Arntz & Clarke 2002; Gutt & Piepenburg 2003).

The effect of ice disturbance on benthic assemblages was another main topic within the EASIZ program. Due to the mechanical damage by ice and swell (Barnes 2005), the polar and subpolar benthic intertidal assemblages are relatively poor in terms of number of species, abundance, and diversity. Presumably environmental stability increases with increasing depth, but the benthic assemblages experience physical disturbance by iceberg scouring, creating a very patchy pattern of benthic organisms on the seafloor. Iceberg impact is common and widely distributed in Antarctic waters, enhancing overall diversity due to the co-existence of different successional stages (Gutt 2001; Gutt & Piepenburg 2003). Ice impact has also been important in the origin of the present-day benthic invertebrate assemblages. Especially the sessile suspension feeders represent a retrograde community type typical of palaeozoic communities (Gili et al. 2006). Investigations on the interactions between the pelagic and the benthic ecosystems demonstrate that many benthic suspension feeders in the Southern Ocean continue feeding in winter and can make use of the food web based around bacteria, nano- and picoplankton, unicellular organisms and organic detritus contained in the seston (Gili et al. 2001). This contrasts with the ancient hypothesis that in Antarctic communities there is a prolonged period of minimal activity during the austral winter. Despite low primary production and a short productive period, the Southern Ocean thus does not appear to be a food-limited system for benthic suspension feeders. The feeding strategies of Antarctic suspension feeders do not differ from those of tropical and temperate ecosystems (Gili et al. 2001). The principal role of Antarctic benthic suspension feeders seems to be related to the efficient recycling of the water column production, which is only partly assimilated by the highly seasonal zooplankton and other secondary consumers during particle sinking through the water column (Orejas et al. 2000).

The activities summarized for EASIZ were partly integrated with other national and international research programs carried out from shipboard and shore stations, for instance the US Palmer Long Term Ecological Research (Palmer-LTER) program (Smith et al. 1995) the Southern Ocean Global Ocean Ecosystem Dynamics (SO-GLOBEC) in the western Antarctic Peninsula and Marguerite Bay areas (Fogarty & Powell 2002) a range of Italian biological oceanographic studies undertaken in the Ross Sea, e.g. the Ross Sea Marginal Ice Zone Ecology – ROSMIZE – project (Faranda et al. 2000), the Spanish BENTART program (Ramos & Moya 2005), the Polish activities in Admiralty Bay (Rakusa-Suszczewski 1993) and various other activities from shore stations, mostly around the Antarctic Peninsula.

All these multidisciplinary and collaborative research programs performed from the 1990s onward have substantially increased insights into the different ecosystem components (from species to community levels) and have led to a conceptual frame of the diversity, history and evolution of the Antarctic benthos.

- **IPY, CoML/CAML: polar research in a global context**

The study of benthic biodiversity and biogeography is an important issue also involved in some recent global initiatives. Under this frame the *International Council for Science* (ICSU) and the *World Meteorological Organisation* (WMO) sponsored the **International Polar Year (IPY)**, a large international collaborative program focused on the Arctic and Antarctic regions. The IPY is an intense internationally coordinated research campaign involving a wide range of research disciplines, including social science but with clear emphasis on natural sciences. Another relevant initiative is the global network of researchers engaged in the **Census of Marine Life (CoML)** which aims to assess and explain the changing diversity, distribution, and abundance of marine species from the past to the present, and to predict future ocean life. This information is expected to become an important tool for monitoring and managing future ocean ecosystems (Yarincik & O'Dor 2005). The Antarctic initiative within this program is **CAML (Census of Antarctic Marine Life)**.

- **The Magellan region**

The landscape of the Magellan region was shaped by glacial and post-glacial processes for about 85-90% of the last 800,000 years (McCulloch et al. 1997). During much of this



time, the region was covered by a thick ice cap similar to that of the Antarctic today (Bujalesky et al. 2004; McCulloch et al. 1997). Repeated glacier advances and retreats created the water-filled basins and major rivers and channels that exist nowadays. The sea level was lower during glaciations than it is now, and the earliest seawater transgression to the western Straits of Magellan occurred between about 14,500 and 13,500 years BP (Kilian et al. 2007). Atlantic water has been unable to penetrate over the shallow threshold of the eastern entrance to the Straits before approximately 9000 years BP (McCulloch et al. 1997). Since then, the ice sheet retreated substantially (Lamy et al. 2002), leaving as its ultimate remains the South Patagonian Icefield and the Cordillera Darwin Icefield located in southwestern Tierra del Fuego. The physiographical and ecological environmental features of the marine Magellan realm probably influenced considerably the biogeographical and ecological patterns observed nowadays. It is suggested that biotic recolonisation of the Beagle Channel and the Straits of Magellan occurred quite recently, as the areas became gradually ice-free during glacial retreat after the LGM (Gordillo 1999; Montiel et al. 2005b; Kilian et al. 2007; Gordillo et al. 2005), i.e. the benthic communities of these waters have to be considered as relatively young ones.

• **Environmental conditions in the Magellan region**

Along the roughly 32,000 km long coastline of the Magellan region (Guzmán 1992) a number of disturbance factors can be identified among which the glacial regime is the most important disturbant on regional and local scales. The typical geomorphology and predominant types of sediments in the Magellan marine realm such as sublittoral soft-bottoms with varying mud to coarse sand fractions, biogenic debris, boulders and cobbles derive even today from climate and glacier dynamics, which have affected this region since the last Pleistocene glaciation (cf. Clapperton et al. 1995; McCulloch et al. 1997; Rignot et al. 2003; Lamy et al. 2004; Kilian et al. 2007 for a review of features and consequences of this active glaciological process). After the retreat of the ice sheet the highly complex Magellan region came under the influence of southern marine current systems driven by the broad eastward flowing West Wind Drift. This current diverges into the northward directed Humboldt Current and a southern branch called the Cape Horn Current. As remnants of the last glaciation period the North and South Patagonian Icefields are the largest temperate ice masses in the southern hemisphere. These almost 18,000 km<sup>2</sup> large icefields discharge at their western edge via rapidly flowing glaciers ice

and meltwater to the marine realm. The waters in front of the South Patagonian Icefield are part of a system of channels and fjords, in which the peculiar topography affects the thermal and saline structure (Pinochet & Salinas 1996). The bottom relief is extremely irregular with maximum water depths down to 1400 m. The sediments in the deeper parts consist of mud and silt, in the shallower parts they also contain variable proportions of clay being transported by the glaciers. At present the glaciers introduce considerable amounts of clay that are distributed in the fjord system by superficial wind-induced currents. The sedimentation processes are strongly influenced by the settling velocities of clay minerals and flocculation processes, which in turn depend on salinity and water temperature. The whole area is affected by heavy continental runoff due to extreme rainfalls all over the year making the water column strongly stratified (surface water: 14 ‰ S, 4 °C, deeper 50 m: 33 ‰ S, 11°C). East-west gradients exist in salinity and temperature with low values near the glaciers increasing towards the open Pacific shelf (Pinochet & Salinas 1996), whereas sediment loads of 30 to 40 mg l<sup>-1</sup> were measured in front of the glaciers decreasing rapidly towards the western parts of the fjords (Kilian et al. 2007). The inshore fjord and channel waters have to be regarded as low in nutrients, these are transported to inshore zones by oceanic Subantarctic water (Acha et al. 2004). Extremely high terrestrial runoff and precipitation in this area create in the interior sea a basically two-layer structure. The runoff (carrying large amounts of Fe) is mixed with the nutrient rich oceanic water building up rich phytoplankton blooms with Chla concentrations (Pizarro et al. 2000) up to 18 mg m<sup>-3</sup> and extending 200 to 300 km offshore (Longhurst 1998). In deeper parts of the inshore inlets and fjords these enormous blooms may cause low oxygen saturation near the bottom, as reported by Silva & Prego (2002). Mixing of oceanic water with freshwater from precipitation, river runoff and glacier meltwater, produces a positive estuarine circulation, with low and cold salinity water leaving the inshore areas at the surface and warmer, saltier and nutrient rich oceanic water entering the system at the bottom (Antezana 1999). This general pattern in combination with shallower sills may hamper the exchange between marine and freshwater. Kilian et al. (2007), e.g. have recently found in the Seno Skyring ca. 2000 year old marine water. How does this water mass affect sedimentation rate and thus sediment stability, inorganic particle concentration and amount of organic matter in the sediments? All these parameters are suggested as important factors determining distribution and abundance patterns of fauna and flora in such areas. Unfortunately to date no benthos studies have

been performed in this interesting environment that could give us more detailed information on the composition of an “old benthic fauna” having survived under these ancient local conditions.

### • Marine biological research in the Magellan region

Recently, the Chilean National Oceanographic Committee (CONA, Silva & Palma 2006) published a compendium summarizing all studies performed in southern Chilean coastal areas, including the South Patagonian Icefield. In the Appendix I publications performed so far on the benthos in the Magellan region are included. It is evident that the bulk of the early studies focussed on individual taxa rather than on ecological questions on community level such as community structure, composition, taxonomy/biodiversity or productivity. Work on biogeographical relationships of the Magellan region with other ancient parts of Gondwana was also lacking.

Due to all international and multidisciplinary scientific efforts mentioned above, the Antarctic waters with their fauna are much better studied than the Magellan region, where only a handful of scientific expeditions (excluding the early naturalist expeditions between 1800-1900) has been carried out so far (Table 1).

Table 1. Scientific cruises carried out in the Magellan region after the early naturalist expeditions between 1800-1900. n.i. = no information

Cruise	Vessel	Studied area	Date	Benthic studies	Source
Lund University-Chile	n.i.	Pto. Montt-Laguna San Rafael	September 1948 - July 1949	yes	Brattström & Dahl 1951
Expedition HERO 72-4	R/V “Hero”	Golfo de Penas-Straits of Magellan	September 1972	no	n.i.
Italian Cruise	R/V “Explora”	Magellan region	October/November 1989	yes	Brambati 1991
Italian Oceanographic Cruise	B/I “Cariboo”	Straits of Magellan	February/March 1991	yes	Faranda & Guglielmo 1991
US Cruise	R/V “Polar Duke”	Straits of Magellan	July-August 1993	no	Rojas 1993
Joint Chilean-German-Italian Magellan Campaign	R/V “Victor Hensen”	Magellan region	October/November 1994	yes	Arntz & Gorny 1996
Italian Cruise	R/V “Italica”	Magellan region	Summer 1995	yes	Faranda et al. 1996
Expedition ANTARKTIS XIII/4	R/V “Polarstern”	Continental slope south of Tierra del Fuego	May 1996	yes	Fahrbach & Gerdes 1997
Investigación Científica Marina en los Fiordos y Canales adyacentes a Campos de Hielo Sur	R/V “Vidal Gormaz”	South Patagonian IceField	August-September 1995	yes	CONA 1995
CIMAR 2 FIORDOS	R/V “Vidal Gormaz”	Magellan region	October/November 1996	yes	CONA 1997
CIMAR 3 FIORDOS	R/V “Vidal Gormaz”	Magellan region	October 1997	yes	CONA 1999

In addition, some specific studies as part of more local projects in certain locations of the Magellan region were performed contributing to a better knowledge of the marine Magellan ecosystem (e.g. Dayton 1985; Santelices 1992).

The biogeographical position of the Magellan region is an open question even today, which is controversially discussed in the scientific community mainly related with the criteria used to define the number of specific biogeographical units (Camus 2001). This holds true although first attempts to define the zoogeographic position of the Magellan region date back over 200 years ago (e.g. Forbes 1854). Hedgpeth (1969) considered the southern tip of South America to differ as a Subantarctic Region from the Antarctic Region. He included into the Subantarctic Region areas south of the Subtropical Convergence and the shallow waters at the tip of South America. Within this Subantarctic Region Hedgpeth defined the Magellan Subregion or Province without, however, a precise definition of its borders. From his Fig. 10 it become obvious that he, as already did Knox almost a decade ago (1960), included the Falkland Islands in the Magellan Province.

Camus (2001) resumed 27 biogeographic classifications published so far for the entire Chilean coastline resulting from the distributional breaks and classifications based mainly on the analysis of one or few selected benthos groups. Most studies have proposed two main biogeographical provinces (or regions) along Chile, the northern warm-temperate Peruvian Province and the southern cold-water Magellanic Province (e.g. Brattström & Johanssen 1983). A border at about 42°S between these two provinces has been suggested, which coincides with changes in topography, climate and hydrography (see Ahumada et al. 2000). However, Camus (2001) assumes this concept to be unsatisfactory to define borders, and he therefore established a new concept integrating one or several marine communities with borders defined also by climatic and physiographic parameters. This classification identifies two major spatial units: a southern area derived from an ancient austral biota (Magellan Province) and a northern area with warm-temperate biota (Peruvian Province) with a “non transitional, intermediate area” in between formed by Subantarctic and Subtropical components. Camus (2001) considered the Magellan Province to show affinities to the central and northern Chilean biotas and, consequently, not to be considered as a biogeographic region on its own. In this context, an important question is related to the extension of this province into the Atlantic (until the La Plata river) as has been suggested among others by Balech (1954), Stuardo (1964) and Moyano (1991).

Recently, Montiel et al. (2005a) contributed to the discussion of the biogeographical position of Magellan waters based on distribution patterns of the polychaete fauna in this and adjacent areas. He concluded that the traditionally defined Magellan Province sensu Hedgpeth (1969) has to be divided into three different districts (entities sensu Montiel 2005a): i) the Cape Horn District on the western continental shelf of the Magellan region; ii) the Falkland District on the southeastern Atlantic shelf; and iii) the Humboldt District on the Pacific shelf north of 42°S.

I define my study areas covering from the South Patagonian Icefield in the north to the Cape Horn Archipelago in the south to belong to the Cape Horn District sensu Montiel et al. (2005a).

• **IBMANT (LAMPOS): the Magellan region related to the Antarctic**

In the middle of the 1990's the southern tip of South America came into the focus of comparative ecological research, with emphasis on the investigation of the marine ecosystem structure and organization and its biological relationships with the adjacent Antarctic ecosystem. The southernmost tip of South America is of special interest for ecological and biogeographical studies because of the common past of the two regions as part of the ancient Gondwana continent and their close vicinity today after their separation about 20 million years ago. In fact, the opening of the Drake Passage may have occurred slowly over a long period between about 35 Ma BP (opening of the Tasman ocean gateway) and 15 Ma BP, when the process was obviously finished (for a discussion see Arntz et al. 2005). Distances between Antarctica and other surrounding continents are much wider (Crame 1999). Present day marine assemblages on either side of the Drake Passage "reflect the regional development in the past, including periods of isolation and interchange, extinction and radiation; they represent a unique case study of ecosystem change and evolution within a worldwide perspective" (Arntz & Ríos 1999). As a consequence, German biologists in close cooperation with several European and South American institutes initiated the 'Marine Biological Investigations in the Magellan Region related to the Antarctic – IBMANT' program to improve the understanding of the ecological, biogeographical and evolutionary relations between the Magellan and Antarctic regions (see Arntz & Ríos 1999; Arntz et al. 2005). Because exchange of faunal elements may have lasted longer and may have been more intense with this near-by South American system than with any other landmass surrounding Antarctica, the overall

scientific aim of this program was to assess and explain marine biodiversity on either side of the Drake Passage, to show what present-day marine fauna and flora on either side look like and how exchange is reflected in the specific communities, their structures and compositions. The program was based on several scientific cruises both in Antarctic waters and in the Magellan region (Arntz & Gorny 1996; CONA 1995, 1997, 1999; Arntz & Brey 2003). The 1994 'Victor Hensen' cruise (Arntz & Gorny 1996) obviously initiated a new period in Magellan marine studies resulting in a large amount of published information on the marine ecosystem around the southern tip of South America and its relationships to other adjacent systems. Since this cruise, the Magellan region, in particular its benthos inventory, has been incorporated into a more global context of ecology, biogeography and evolution. Some of the results obtained for a variety of taxa suggest links of the Magellan benthos both to the Peruvian and Panamanian Biogeographic Provinces and to the Antarctic Province (e.g. Montiel et al. 2005b; Pansini & Sarà 1999). Latitudinal clines in species richness may exist in one or the other direction, as is suggested for example by some groups such as decapods, stomatopods and cirripedes, which decrease towards the Antarctic, and sponges, amphipods, isopods and most echinoderms, which increase (Clarke & Johnston 2003; Arntz et al. 2005). Species taxonomy and richness data are also available for molluscs, hydroids, polychaetes, and other peracarid crustaceans. Community studies suggest for the megabenthic epifaunal assemblages a distinctly patchy distribution, which seems to be determined by medium-scale environmental conditions rather than by large-scale regional differences (Gutt et al. 1999).

The **L**atin **A**merican '**P**olarstern' Study (LAMPOS) was planned as a successor of EPOS (the **E**uropean '**P**olarstern' Study) in order to study biogeographical and evolutionary links between the Magellan region and the Antarctic. Work during this cruise focussed on the benthic fauna in the Scotia Arc region. Its main objective was to study the influence of faunal dispersal in the northern and southern chain of the islands and shallows within the Arc, and thus explore potential pathways of recolonisation of the Antarctic waters from the Magellan region or vice versa after climate-induced extinctions (Arntz & Brey 2003). There is still a high degree of similarity between the Magellan and Antarctic faunas, e.g. in the polychaetes and various echinoderm taxa, but this is not true for all groups; e.g. the decapods show the opposite. Under the present climate conditions, the Drake Passage with the Polar Front is a highly effective barrier. The northern slope of Drake Passage is clearly

Magellanic, becoming only gradually more Antarctic towards deep water, and the same is true for the northern branch of the Scotia Arc until South Georgia, which represents a mixture of Antarctic and Magellan faunal elements. The southern slope of Drake Passage is totally Antarctic, as is also the southern branch of the Scotia Arc, whose faunal composition is most similar to the Antarctic Peninsula and has overlaps also with the southeastern Weddell Sea. The most likely mechanisms of dispersal and interchange are W-E transport with the Antarctic Circumpolar Current and N-S transport with the eddies generated by the narrowing of the Drake Passage, however with a limited survival rate south of the Polar Front under present conditions. “Jumping from island to island” occurs probably only using these vehicles or – in the case of eurybathic species – via the deep sea (Arntz & Gutt in press, who also present many more details).

Many important studies contributing to the structure and function of the Magellan marine benthic realm have resulted from the IBMANT scientific program. The results have been presented on two international scientific workshops and have been published in two special issues of “*Scientia Marina*” (Arntz & Ríos 1999; Arntz et al. 2005).

- **Gaps and perspectives**

Despite the increasing research activities in the Magellan marine ecosystem during the last thirteen years, the marine benthic communities south and north of the Magellan region can be considered as being much more intensely studied than those of the Magellan region. This was also concluded in recent reviews of Fernández et al. (2000), Escribano et al. (2003) and Valdovinos et al. (2003), who addressed the scarce information about latitudinal trends in species richness and diversity of benthic communities along the South Chilean coastline. Consequently research in the Magellan region has to be enhanced to fill the various gaps still existing.

Several key questions remain and others have emerged new (cf. Arntz 1999; Arntz et al. 1997, 2005) within the frame of interactions between Antarctica and other remnants of Gondwana. One of these questions was ‘How do Antarctic communities compare with those in other parts of the world ocean?’ This topic is closely related with important ecological, biogeographical and evolutionary paradigms - for instance, the existence of latitudinal clines and depth gradients in species richness, the origin of the Antarctic shallow- and deep-water fauna, predictions of future changes in benthic communities due to natural and/or human-induced environmental changes, etc.

A basic gap is still the lack of taxonomic knowledge, which is a prerequisite for ecological research, for many benthic taxa. Although some progress has been made, e.g. in polychaete (Montiel et al. 2002; Montiel & Hilbig 2004; Montiel et al. 2004; Montiel et al. 2005a, 2005b) and echinoderm taxonomy (Larraín et al. 1999; Mutschke & Ríos 2006), this basic tool has to gain importance urgently for proper descriptions of benthic communities, their structure and composition and for the comparison of species richness and diversity along latitudes. In addition the effort of sampling campaigns has to be increased in order to complete the Magellan species inventories, the knowledge of which is a prerequisite for the evaluation of the Magellan Province as a zoogeographical entity and to allow comparisons with other provinces. Until now, it is very difficult to argue for significant differences or similarities in species richness and diversity, both at local and regional scales. How many species can be expected in the entire Magellan region? How does this species inventory compare with those of other provinces? How varying, patchily distributed and locally diverse are benthic communities in this topographically diverse region? These questions remain an important challenge for the next years, activities which need to be analyzed in the context of climatic changes in benthic communities, the effects of natural and man-made disturbance, and habitat variability.

All these gaps pose difficulties to evaluate, interpret and predict important aspects related with biogeographical patterns along the South Pacific and Atlantic coastlines and towards the Antarctic. Ecological patterns in biodiversity and the urgently needed data for sustainable use of the ecological and economically important Chilean coastal marine natural resources are only partly available at the moment. This holds true especially for the Magellan region.

- **Aims of this thesis**

This work is based on community studies performed in three marine environments which are characteristic of the Magellan region. It also intends to summarize recent investigations on benthic communities in the Magellan region, paying special attention to those communities which have hardly been considered up to now.

In my own studies, special emphasis is laid on the spatial structure and temporal dynamics, the species inventories, patterns in organism densities and the diversity of benthic communities living in:

- ◆ intertidal boulder and cobble fields



- ◆ *Macrocystis pyrifera* holdfasts
- ◆ sublittoral bottoms of the south Chilean glacial fjord complex.

The benthic communities studied in these habitats are described in the following papers and manuscripts:

**Publ. I**

Ríos C & E Mutschke (1999) Community structure of intertidal boulder-cobble fields in the Straits of Magellan, Chile. *Scientia Marina*, 63 (Suppl. 1): 193-20

**Publ. II Data Report**

Community structure of intertidal boulder and cobbles fields in the Magellan region (unpublished data). To get more detailed insights into the dynamics of such boulder and cobble communities, also over a wider latitudinal gradient, unpublished data from 8 localities between the Segunda Angostura (Straits of Magellan) and the Cape Horn Archipelago are included into this thesis.

**Publ. III**

Ríos C, E Mutschke & E Morrison (2003) Biodiversidad bentónica sublitoral en el Estrecho de Magallanes, Chile. *Revista de Biología Marina y Oceanografía*, 38(1): 1-12

**Publ. IV**

Ríos C, E Mutschke, A Montiel, D Gerdes & W E Arntz (2005) Soft-bottom macrobenthic faunal associations in the southern Chilean glacial fjord complex. *Scientia Marina*, 69 (Suppl. 2): 225-236

**Publ. V**

Ríos C, W E Arntz, D Gerdes, E Mutschke & A Montiel (2007) Spatial and temporal variability of the benthic assemblages associated to the holdfasts of the kelp *Macrocystis pyrifera* in the Straits of Magellan, Chile. *Polar Biology*. DOI 10.1007/s00300-007-4

The main objective of this thesis is to describe the spatial structure and temporal dynamics of benthic communities living in each of the three habitat types and to evaluate the importance of the different structured habitats with their specific communities for the overall biodiversity of the Magellan region as a zoogeographic province. In a next step these Magellan benthic communities can be compared with those from adjacent

zoogeographic provinces in order to arrive at conclusions about specific characteristics of Magellan (Subantarctic) communities in comparison to benthic communities of other climatic zones.

Furthermore, various hypotheses have to be checked which are derived from work in similar (Subarctic) and other (Antarctic, Arctic, temperate) ecosystems:

- 1) The heterogeneity of Magellan habitats is reflected in a pronounced heterogeneity also in benthic communities.
- 2) Due to strongly varying environmental factors in shallow waters and more “stable” conditions in deeper waters, the benthos in shallow waters should be more heterogeneous/patchily distributed than that in deep waters. I expect different relationships between sample species richness (alpha diversity) and regional species richness (beta diversity). Here I include also temporal data to the analysis to test if the expected trend is also observed through time.
- 3) As habitat complexity enhances diversity, the richly structured habitats of *Macrocystis pyrifera* holdfasts should show high benthic holdfast diversity.
- 4) In view of increasing environmental harshness in poleward direction I would expect latitudinal gradients in major biological parameters such as abundance, biomass, species richness and diversity.
- 5) Beside physical disturbance by means of wind and high current velocities glaciers are expected to have a strong impact on sublittoral and shallow water benthic faunal communities due to iceberg scouring, inorganic siltation and terrestrial freshwater runoff, as shown e.g. by Klöser et al. (1994) in the Potter Cove, King George Island, Antarctica. I therefore expect benthic communities in glaciated areas or those exposed to wind and currents to be poorer in species richness, diversity and evenness.
- 6) Despite all heterogeneity in Magellan benthic communities I hypothesize that the Magellan region is a unit ecosystem and has the rank of an autonomous biogeographic province between the Antarctic Province and the Peruvian Province.
- 7) As is typical for comparatively young ecosystems, local benthic communities in the Magellan region should exhibit low species numbers, high dominance of a few species, low diversity and low evenness similar to other young areas (e.g. Baltic, North Sea).

## 2. MATERIAL AND METHODS

This thesis covers very different habitats and benthic assemblages in the Magellan region, from the intertidal zone to sublittoral soft bottoms in >700 m water depth. As I had to base much of my thesis on material, the procurement of which depended largely on the availability of ship time and the weather conditions, the approach is sometimes all but ideal. This adds to the difficulty of studying a very heterogeneous area, which requires the use of quite different types of gear. For these reasons, not all my results can be compared directly with each other or with the literature.

As a consequence, I tried to put more emphasis on determining within-site tendencies with the aim of deducing general patterns and differences between sites. Most likely, temporal series at each site would have been useful to define more precisely the variability of the investigated parameters and to facilitate the comparison of means and tendencies, but this was not possible. So I am trying to combine those data, which were available, and to arrive at conclusions considering the available literature.

In this chapter I summarize shortly the applied methods and refer the reader for more detailed information to the respective papers of this cumulative thesis.

### 2.1 Field Work

#### 1) Studies in intertidal boulder and cobble fields

Benthic organisms were collected directly from the shoreline along transects perpendicular to the beach contour. In each transect samples were taken at specific sampling points determined by the beach profile between high and low tide level according to Emery's method (1961). In each sampling level 3 random samples were collected using squares of 50 x 50 cm in upper sandy fringes (if existing) down to 15 cm sediment depth or 20 cm in the boulder and cobble terrace samples. All samples were sieved over 1 mm mesh size and the organisms were stored until further analysis in the lab in 5 % formalin-seawater solution.

#### 2) Studies in sublittoral soft bottoms

Sublittoral studies on benthic communities were performed with different gear:

- a) qualitative and semi-quantitative sampling was performed with a modified Agassiz trawl of 3.15 m width and 1.1 m height; the mesh size of the codend was 10 mm.

Deployment time on the bottom for each standard haul averaged 12 min. All organisms in the catches were sorted on board and considered for further analyses.

- b) quantitative benthos studies were performed using a McIntyre grab of 0.1 m<sup>2</sup> sampling area. The samples were carefully sieved onboard over 0.5 mm mesh size and stored until further analysis in the lab in 5 % formalin-seawater solution.

### 3. Studies on *Macrocystis pyrifera* holdfast associated fauna

Divers performed the collections. The stipeses of each plant were cut before the holdfasts were detached from the substrate by means of a mechanical lever. Each holdfast was immediately placed in a labelled plastic bag and kept frozen in the laboratory at -20°C before later analysis. The holdfast volume (cm<sup>3</sup>) was estimated and all invertebrates inside the holdfasts were sorted by dissecting the holdfasts and separating all sediment and macro-specimens. After sieving all organisms using a sieve with 1 mm mesh size, the sorted material was analysed under a binocular microscope to separate all the macro-organisms present in each sample.

## 2.2 Laboratory work

In the laboratory all organisms were sorted to the highest taxonomic level possible using standard publications (e.g. Norman 1937; Menzies 1962; Retamal 1974; Bernasconi & D'Agostino 1977; Castellanos 1998-93; Rozbaczylo 1985). Further help of experts who assisted in the identification of different taxa is gratefully acknowledged. In addition, the "Edmundo Pisano Reference Collection" of the Instituto de la Patagonia, Universidad de Magallanes, served as a tool for species identification. In a next step densities and biomass (wet weights) of the quantitative samples were adjusted to 1 m<sup>2</sup> basis in order to allow comparisons between samples and regions. In case of the holdfast associated fauna standardization was done to 1,500 ml holdfast volume. The qualitative samples were standardized to presence/absence.

## 2.3 Statistical analyses

Abundance data of all macrobenthic replicates obtained for each type of habitat were analysed by means of univariate methods and distributional techniques using the PRIMER v5 software (Clarke & Gorley 2001). Diversity indices (Shannon-Wiener diversity  $H'$ -log<sub>2</sub>) and evenness index  $J$  were calculated from species abundance data. The spatial distribution of each sampling site was analysed by means of nonmetric multidimensional

scaling (n-MDS) and by an agglomerative hierarchical clustering. The matrix of similarities was based on the Bray-Curtis similarity index (Bray & Curtis 1957). Prior to the analysis, a double square-root or a presence/absence transformations was applied. Differences between groups of samples were addresses using the ANOSIM (“analysis of similarities”) test and routine SIMPER (“similarity percentage”) was used to discriminate species and their percentage contribution to similarities within and dissimilarities between the groups defined by the cluster and MDS analyses. ANOVA and post-hoc tests were performed using the software StatView®.

### 3. PUBLICATIONS

In the following section the publications that constitute this thesis are included and my contribution thereof is explained.

As a first author of all the articles, I have the responsibility for the main ideas and concepts of each of the publications included in this thesis. I wrote all the initial manuscripts and the final version was a joint work with all co-authors. I participated in all field campaigns and contribute to take the samples considered for the investigations. Under my responsibility the campaigns were organized and sampling strategies were planned

**Publ. I**, the second author (E. Mutschke) contributed to the sampling in the field and in the taxonomical work in the laboratory. The sampling and analytical procedures and statistical analyses were carried out by both authors. I wrote the manuscript together with the co-author.

**Publ. II Data Report**, the initial idea originates from myself. I was responsible (and still I'm) for all statistics analysis and guided taxonomic work.

**Publ. III**, the second author (E. Mutschke) contributed to elaborate the conceptual approach of the project to be presented to the Chilean Oceanographic Committee (CONA). She participated in the field campaign to the South Patagonian Icefield and to the Straits of Magellan and in the sorting and analysis of the samples. The third author (A. Montiel) helped to sort the samples and he participated in the taxonomical work. The last two authors (D. Gerdes and W. Arntz) contributed to the analysis of data and helped to improve the final version of the manuscript.

**Publ. IV**, both co-authors participated in the sampling procedures on board, in the sorting of the biological material, in the taxonomical work and contributed to the analysis of the data.

**Publ. V**, the first co-author (W. Arntz) contributed to define the scope the work. The conceptual approach, objectives and the analytical procedures were defined with the second co-author (D. Gerdes), who in addition improve the final version of the manuscript. The third co-author (E. Mutschke) participated in the design of the sampling procedures, in the field campaigns an in the taxonomical work. A. Montiel contributes in the sampling campaigns and with the taxonomical work.

**PUBLICATION I**

**COMMUNITY STRUCTURE OF INTERTIDAL BOULDER-COBBLE  
FIELDS IN THE STRAITS OF MAGELLAN, CHILE**

**Carlos Ríos & Erika Mutschke**

**SCIENTIA MARINA**



## Community structure of intertidal boulder-cobble fields in the Straits of Magellan, Chile\*

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**SUMMARY:** Based on quantitative samples taken along 4 transects in mobile hard-bottom intertidal areas of the Canal Whiteside, Magellan region, biotic composition, abundance and distribution patterns are described. The intertidal substrates, mainly formed by boulders and cobbles, represent highly heterogenous habitats from the structural point of view, and demonstrated a species richness higher than previously mentioned in some preliminary reports. Community structure parameters (abundance, species richness, diversity, and evenness) were not homogenous in the study areas, suggesting local dynamics. Differences in the vertical distribution of organisms were also found, suggesting changes of the zonation pattern along the beach profile. The macrofaunal assemblages were dominated by few species, with different specific compositions between transects. In general, representatives of Mollusca (*Mytilus chilensis*, *Perumytilus purpuratus*), Polychaeta (*Hemipodus simplex*), and Amphipoda (*Paramoera fissicauda*, *P. brachyura*, *Transorchestia chilensis*) were the numerically dominant groups. In terms of biomass, molluscs were highly dominant, mainly *M. chilensis* and *P. purpuratus*. Among the macroalgae, rhodophytes were the group with the highest presence, but *Ulva lactuca* (Chlorophyta) was the dominant species. In the upper sandy terrace, no macroorganisms were found. Several species found at Canal Whiteside have a wide circumpolar distribution in Sub-Antarctic regions.

**Key words:** Magellan region, diversity, intertidal zone, boulder-cobble beach, benthos.

**RESUMEN:** ESTRUCTURA DE LA COMUNIDAD EN CAMPOS INTERMAREALES DE BLOQUES Y CANTOS DEL ESTRECHO DE MAGALLANES, CHILE. – A partir de muestras cuantitativas tomadas en cuatro transectos paralelos a la línea de costa, se describe la composición biótica y los patrones de distribución y abundancia de una comunidad intermareal presente en ambientes de fondos duros móviles en el Canal Whiteside, Región de Magallanes. El sustrato intermareal, formado principalmente por bloques y cantos, representa un hábitat altamente heterogéneo y mantiene una riqueza de especies mayor que la mencionada en algunos informes preliminares. Algunos parámetros de la estructura comunitaria (abundancia, riqueza de especies, diversidad y equitabilidad) mostraron diferencias en el área estudiada, sugiriendo dinámicas locales. Se encontraron diferencias en la distribución vertical de los organismos, sugiriendo cambios en el patrón de zonación a lo largo de la playa. La comunidad estuvo dominada por unas pocas especies, aunque la composición específica variara entre transectos. Los grupos numéricamente dominantes fueron Mollusca (*Mytilus chilensis*, *Perumytilus purpuratus*), Polychaeta (*Hemipodus simplex*) y Amphipoda (*Paramoera fissicauda*, *P. brachyura*, *Transorchestia chilensis*). En biomasa, los moluscos, principalmente *M. chilensis* y *P. purpuratus* fueron altamente dominantes. Entre las macroalgas, el grupo de las Rhodophyta fue el más representativo aunque *Ulva lactuca* (Chlorophyta) fue la especie dominante. En la parte superior arenosa de la playa no se encontraron macroorganismos. Varias especies encontradas en el Canal Whiteside muestran una amplia distribución en la zona subantártica.

**Palabras clave:** Región de Magallanes, diversidad, zona intermareal, playas de bloques y cantos, bentos.

\*Accepted March 9, 1999.

## INTRODUCTION

Along the shoreline of the Magellan region, a typical and representative mobile hard-bottom substrate is formed by boulder-cobble intertidal fields, originated by glacial processes about 12,000 years ago (Clapperton *et al.*, 1995). From a structural point of view, this type of physical habitat can be considered as an intermediate situation between soft substrate (*e.g.* sandy beaches) and typical hard-bottom substrate (*i.e.* rocky shores).

Initial studies in this intertidal habitat started after the 1974 "Metula" oil spill in the Straits of Magellan (see Guzmán and Campodónico, 1981). More recently, some community characteristics have been preliminarily described in areas located at the Cape Horn Archipelago (Ríos and Guzmán, 1982; Guzmán and Ríos, 1986) and at several sites in the Strait of Magellan (Ríos and Gerdes, 1997; Ríos and Mutschke, 1995; Mazzella and Gambi, 1993). A low species richness and diversity has been reported especially for some sites in the Straits of Magellan (Benedetti-Cecchi, 1996). Recently, Benedetti-Cecchi and Cinelli (1997) have shown inconsistency in patterns of vertical distribution (*i.e.* no general pattern of zonation) of macroalgae and invertebrates in rocky intertidal sites in the Straits of Magellan.

Specific studies have been developed on individual growth, reproductive biology, and distribution and abundance of some dominant boulder-cobble intertidal species (Guzmán and Ríos, 1987; Ríos *et al.*, 1987; Santana, 1997; Guzmán, 1978; Langley *et al.*, 1980; Miranda and Acuña, 1979).

The aim of this paper is to provide, in a broad sense, a description of the macrofaunal and floral assemblages and their distribution and density patterns, based on surveys carried out in a boulder-cobble intertidal system located in a secondary branch of the Straits of Magellan. Analysis of vertical distribution patterns of species in this intertidal habitat was done in order to define zonation patterns, which are known from other intertidal boulder-cobble fields (*e.g.* Ríos and Guzmán, 1982; Guzmán and Ríos, 1986) in the Magellan region. Finally, our results are compared with information reported from other Subantarctic areas.

## MATERIAL AND METHODS

Data used in this paper were collected during November 1994 in Canal Whiteside, located in the eastern part of Isla Tierra del Fuego (Fig. 1). Canal Whiteside is considered as one of the two secondary basins, which branch off from the basin of Punta Arenas. It is about 90 km long and 10-15 km wide (Brambati *et al.*, 1991). No information is available in relation to hydrography or biological features of this area.

In the sampling area, the intertidal zone consisted physically of an upper sandy-gravel beach and a terrace of boulder-cobble substrate, originated from deglaciation processes, which occurred in the Magellan region *ca.* 12,000 years ago (Uribe, 1982). In this area, boulders and cobbles rest on a sandy-sediment matrix (Fig. 2). Types of sediments are classi-

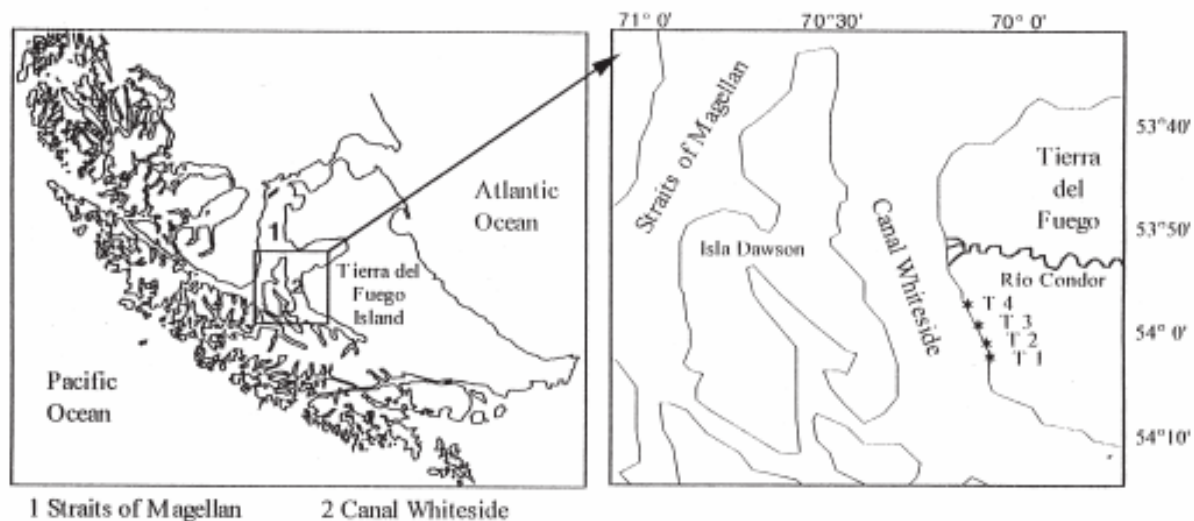


FIG. 1. - Map of the southern tip of South America showing the Magellan Region and the sampling area of this study.

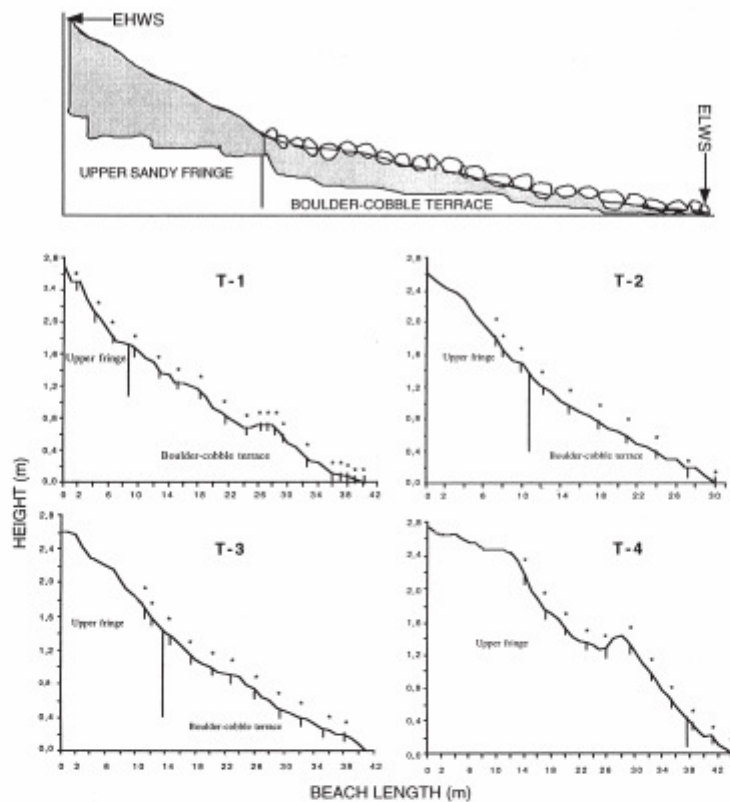


FIG. 2. - Scheme of a typical boulder-cobble intertidal zone in Canal Whiteside (a) and of the beach profiles in the four sampled transects (T1-T4) (b). EHWS = extreme high tide level for spring tide; ELWS = extreme low tide level for spring tide. (\*specific sampling points).

fied according to the Wentworth grade classification (Buchanan, 1984).

Four transects of the beach separated by 1 km each and differing in the length of the upper sandy fringe and boulder-cobble terrace were selected to describe distribution and abundance patterns of macroalgae and macrofauna. In each transect, samples were taken in lines 4 m wide each, running perpendicular to the shoreline from the top of the intertidal zone to about mean low tide level. Transect profiles (Fig. 2) were done according to Emery's (1961) method.

Specific sampling points along the transect profiles (see positions in Fig. 2) were determined by the beach width during low tide. In the upper sandy fringe, three random samples of sediment were collected in each sampling point using squares of 50 x

50 cm and 15 cm (sandy sediments) or 20 cm depth (boulder-cobble area). They were sieved *in situ* over 1 mm mesh size to retain the macrofauna. In the boulder-cobble terrace a mixture of sampling procedures was employed, but always three random samples were taken at each sampling point. First, all the macroorganisms attached or found on the undersurface, sides or below the boulders or cobbles, present on a surface of 0.25 m<sup>2</sup> were manually collected. In a second step, each boulder or cobble inside the 0.25 m<sup>2</sup> surface was lifted onto its side or overturned and all the sediment below was collected and sieved *in situ* over 1 mm mesh size to sort the macroinfauna fraction. All sorted biological material was fixed in 5 % buffered formalin for later analysis.

Distribution and abundance of macroalgae and cirripedes along each transect were evaluated by

TABLE 1. – Mean abundance of macroalgae (% of coverage including Cirripedia) and total number (N) and biomass (B; g) of animal species or major taxa (presented as N/B) collected in the four transects (T1–T4) of Canal Whiteside.

Transects/Taxa	T - 1	T - 2	T - 3	T - 4
<b>Macroalgae</b>				
<b>Chlorophyta</b>				
<i>Urospora penicilliformis</i> (Roth) Areschoug	2	8	-	-
<i>Ulva lactuca</i> Linnaeus	12	-	1	23
<i>Aorisiphonia pacifica</i> (Montagne) J. Agardh	-	1	-	-
<i>Enteromorpha</i> sp.	-	-	1	-
<b>Rhodophyta</b>				
<i>Porphyra columbina</i> (Montagne)	5	12	1	-
<i>Iridaea tuberculosa</i> (Hooker & Harvey) Leister	1	1	1	-
<i>Dasyptilon harveyi</i> (J.D. Hooker) Papenfuss	1	-	7	-
<i>Ceramium dozei</i> Hariot	-	-	1	-
<i>Ptilonia magellanica</i> (Montagne) J. Agardh	-	-	7	-
<i>Stictosiphonia hookeri</i> Hooker	1	-	-	-
<i>Delesseria lanifolia</i> (Hooker & Harvey) J. Agardh	-	-	-	2
<i>Polysiphonia anisigona</i> J.D. Hooker & Harvey	-	-	-	4
<b>Phaeophyta</b>				
<i>Caecidium antarcticum</i> J. Agardh	1	-	-	-
<i>Pilayella littoralis</i> (L.) Kjellmann	-	2	-	-
<i>Seytosiphon lomentaria</i> (Lyngbye) J. Agardh	-	1	1	-
<i>Adenocystis utricularis</i> (Bory)	-	1	1	-
<i>Sphaecelaria bornetti</i> Hariot	-	-	4	-
<b>Macrofauna</b>				
<b>Anthozoa</b>	24/6.1	1/0.3	-	93/15
<b>Turbellaria</b>	121/0.7	99/0.3	21/0.13	7/0.012
<b>Nematoda</b>	20/0.09	17/0.02	-	3/0.0001
<b>Nemertini</b>	48/8.4	50/5.4	3/0.35	81/6.7
<b>Oligochaeta</b>	5/0.07	-	-	-
<b>Polychaeta</b>				
<i>Neoleprea</i> sp.	11/1.4	-	-	-
<i>Thelepus setosus</i> (Quatrefages, 1866)	41/5.3	-	5/1.3	17/3.9
<i>Platynereis australis</i> (Schmarda, 1861)	21/4.1	-	1/0.02	17/3.1
<i>Hemipodus simplex</i> (Grube, 1857)	63/6.6	-	4/0.8	15/1.6
<i>Eunoe</i> sp.	24/0.4	-	-	1/0.1
<i>Harmothoe</i> sp.	5/0.2	-	-	4/0.5
<i>Perinereis falklandica</i> (Ramsay, 1914)	-	-	-	1/0.07
<i>Eteone sculpta</i> Ehler, 1897	1/0.1	-	-	-
<i>Nicolea chilensis</i> (Schmarda, 1861)	-	-	-	3/0.4
<i>Nereis callaona</i> (Grube, 1857)	-	-	-	5/0.3
<i>Nereis eugeniae</i> (Kinberg, 1866)	3/1.5	-	-	3/0.1
<b>Bivalvia</b>				
<i>Aulacomya ater</i> (Molina) 1782	11/41.1	-	-	-
<i>Mytilus chilensis</i> (HupE, 1840)	353/4423	2580/1447	1555/2437	4464/9654
<i>Peramytillus purpuratus</i> Lamarck, 1819	330/1379	2687/932	924/724	88/68.1
<i>Clausinella gayi</i> (HupE) 1854	15/23.4	-	-	-
<b>Gastropoda</b>				
<i>Collisella</i> sp.	3/0.4	-	9/1.5	-
<i>Naoella deaurata</i> (Gmelin, 1791)	109/305.1	-	10/28.6	11/6.3
<i>Naoella magellanica</i> (Gmelin, 1791)	111/494.6	-	30/191.7	11/71.1
<i>Naoella flammea</i> (Gmelin, 1791)	13/18.8	-	-	3/1.9
<i>Naoella</i> sp.	7/24.4	-	-	-
<i>Fissurella picta</i> (Gmelin, 1791)	9/73.9	-	-	-
<i>Fissurella</i> sp.	-	-	-	1/5.1
<i>Ximenopsis murioformis</i> (King & Broderip, 1831)	1/1.9	-	-	-
<i>Plaxiphora aurata</i> (Spalowsky, 1795)	1/0.9	1/0.3	-	-
<i>Chiton</i> sp.	1/0.3	-	-	-
<i>Siphonaria lessona</i> (Blainville, 1824)	3/0.7	3/3.2	28/11.5	-
<i>Acanthina monodon</i> (Solander, 1786)	-	-	-	7/29.7
<i>Trochophora geversianus</i> (Pallas, 1769)	-	-	-	3/5.3
<b>Isopoda</b>				
<i>Exosphaeroma gigas</i> (Leach, 1814)	1/0.01	1/0.01	60/0.86	13/0.2
<i>Serolis</i> sp.	1/0.03	-	-	-
<b>Amphipoda</b>				
<i>Transirohestia ohiliensis</i> (Milne-Edwards, 1840)	216/5.3	36/0.9	-	-
<i>Paramoera fissicauda</i> (Dana, 1852)	524/9.3	15/0.2	553/13.79	-
<i>Paramoera brachyura</i> Schellenberg, 1931	121/0.8	-	228/0.5	-
<i>Paramoera pfeferi</i> Schellenberg, 1931	-	-	-	17/0.2
<i>Hyale hirtipalma</i> (Dana, 1852)	-	-	5/0.08	113/1.2
<b>Decapoda</b>				
<i>Acanthocyclus albatrossis</i> Rathbun, 1898	13/10.8	-	9/2.53	19/4.6
<i>Haliacarcinus planatus</i> (Fabricius) 1793	1/0.3	-	-	1/0.07
<i>Pagurus</i> sp.	10/0.13	-	1/0.0003	-
<i>Peltarion spinosulum</i> (White)	3/1.2	-	-	-
<b>Cirripedia</b>				
<i>Chthamalus scabrosus</i> Darwin, 1854	5	-	4	23
<b>Asteroida</b>				
<i>Anasterias antarctica</i> (L. tkam, 1886)	29/30.9	-	8/11.6	25/4.3
<b>Echinoidea</b>				
<i>Pseudoechinus magellanicus</i> (Phillipi, 1857)	-	-	-	3/17.3
<b>Holothuroidea</b>				
<i>Harpagifer bispinis</i> (Schneider)	1/6.9	-	-	3/0.2



cover estimations using an optically-sighted point-frame of 0,25 m<sup>2</sup>, with 100 points defined by superimposed pairs of cross wires. At each sampling point, three of the four squares were evaluated.

All collected animals of each species or major taxon were counted and their wet weight was determined after blotting on filter paper until dry. Mean abundance and biomass data of each species or of major taxa (on m<sup>2</sup> basis) were calculated for each sampling point.

Numerical procedures employed for the analysis of the biological data were performed using the Plymouth Routine In Multivariate Ecological Research (PRIMER) computer package (Clarke and Warwick, 1994). Using logarithms to base "e" indices of species richness (Margalef's d), Shannon-Wiener diversity (H') and evenness (Pielou's J) were calculated and the significance of the differences between transects was tested by one way ANOVA. Comparisons among values were done with the unplanned multiple comparison test LSD (Least Significant Difference; Sokal and Rohlf, 1995). Hierarchical clustering technique (PRIMER routine CLUSTER) was used to discriminate groups of samples and to show faunistic zonation patterns along the beach profiles of transects 1, 2, and 3. Transect 4 was not considered in the analysis due to the physical features of the beach which allowed samples to be taken at only three sampling points (see Fig. 2). Similarity was estimated by the Bray and Curtis (1957) similarity coefficient measure for double square-root transformed species abundance data.

## RESULTS

An important feature of all transects was the total absence of macrofauna (animals >1mm) and macroalgae species in the upper sandy fringe. Consequently, all further descriptive analyses are valid for the terrace of boulders and cobbles as the main site for the establishment of intertidal macrobenthic communities.

A total of 6 taxonomic groups and 60 species were collected from the four transects. Macroalgae were present with 17 species, polychaetes with 11, crustaceans with 12, molluscs with 17, echinoderms with 2, and one fish species was found. All species of actinians, turbellarians, nematodes, nemerteans, oligochaetes and holothurians were considered as one taxon each (Table 1).

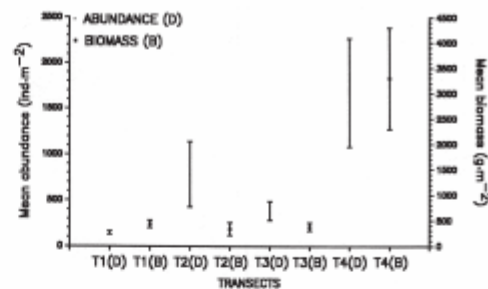


FIG. 3. - Mean biomass (wet weight) and density of macrobenthos in the four transects in Canal Whiteside

Average abundance in terms of number of individuals m<sup>-2</sup> varied between 144.7 (transect 1) and 1677.3 in transect 4 (Fig. 3). The highest biomass values were obtained in transect 4 (3300.8 g/m<sup>2</sup>) and the lowest (336.2 g/m<sup>2</sup>) in transect 2 (Fig. 3). Differences in mean abundance and biomass for the four transects were statistically significant (ANOVA;  $p < 0.001$ ). The unplanned multiple comparison test LSD applied to the mean number of individuals indicated that values of transect 4 differ significantly from the other three transects ( $p < 0.05$ ), whereas no significant differences occurred between transect 1 and 3 ( $p = 0.286$ ) and transect 2 and 3 ( $p = 0.143$ ). The same test applied to biomass values showed that transect 4 differed significantly from the other three transects ( $p < 0.0001$ ), and the differences between transects 1, 2 and 3 were not significant ( $p > 0.05$ ).

The composition of species and major taxa also was highly heterogenous between the transects. High dominance of few species or major taxa and high numbers of taxa comprising less than 2 % of the total number of individuals were characteristic of all four transects (Table 2). A high number of species ( $n = 40$ ) was collected in transect 1, but the dominance of 29 species and major taxa was less than 2 %. In this transect the amphipod *Paramoera fissicauda* was the dominant species (23 %) followed by the bivalves *Mytilus chilensis* (15 %) and *Perumytilus purpuratus* (14 %). A total of 11 species and taxonomic groups were collected in transect 2, and *P. purpuratus* (49 %) and *M. chilensis* (47 %) were the numerically dominant species. Both bivalve species were also dominant in transect 3 and 4, and in the later transect, *M. chilensis* represented 89 % of the total number of individuals (Table 2). Both bivalve species seem to develop a single-layer bed. In terms of biomass, a clear dominance of bivalve molluscs was found in all four

TABLE 2. - Percent dominance in number (N) and biomass (B) of taxa in the four transects (T-1 / T-4) of Canal Whiteside, Tierra del Fuego. Category "Others" includes all animals with dominance  $\leq 2\%$ . \* indicates presence but  $\leq 2\%$  dominance of the corresponding taxa.

Transects Taxa	T-1		T-2		T-3		T-4	
	N	B	N	B	N	B	N	B
<i>Paramoera fissicauda</i>	22.6	-	-	-	16	-	-	-
<i>Mytilus chilensis</i>	15.3	64.2	47.0	60.6	44.9	71.1	88.7	97.4
<i>Perumytilus purpuratus</i>	14.3	20.0	48.9	39.0	26.7	21.1	-	-
<i>Transorchestia ohiliensis</i>	9.3	-	-	-	-	-	-	-
<i>Paramoera braehytara</i>	5.2	-	-	-	6.6	-	-	-
<i>Hyalae hirtipalma</i>	-	-	-	-	-	-	2.3	-
<i>Nacella magellanica</i>	4.8	7.2	-	-	-	5.6	-	-
<i>Nacella deaurata</i>	4.7	4.4	-	-	-	-	-	-
<i>Hemipodus simplex</i>	2.7	-	-	-	-	-	-	-
Turbellaria	5.2	-	-	-	-	-	-	-
Nemertini	2.1	-	-	-	-	-	-	-
Holothuroidea	2.5	-	-	-	-	-	-	-
Others	11.9	4.2	4.1	0.4	5.6	2.1	10.0	2.6
Total number and biomass (g)	2324	6892	5490	2389	3454	3427	5032	9901
Total number of taxa	40		11		19		30	

transects, with *M. chilensis* being the dominant species, representing between 61 % (transect 2) and 97 % (transect 4) of the total biomass.

A total of 17 macroalgae species were determined for the studied area (see Table 1), however, with high variability in abundance between the four transects. Species number ranged between 3 (transect 4) and 10 (transect 3). On average, *Ulva lactuca* was the most abundant species in this area.

Species richness and diversity were not homogeneous (Fig. 4). According to ANOVA applied to each index used, richness ( $F=5.558$ ;  $p=0.004$ ), diversity ( $F=6.03$ ;  $p=0.002$ ) and evenness ( $F=5.858$ ;  $p=0.003$ ) were significantly different between transects. The unplanned multiple comparison test with LSD suggests possibilities to cluster the transects into different categories according to the utilized index. Richness in transects 2 and 3 was significantly different from values obtained in transects 1 and

4. For  $H'$  it is possible to group transects 2, 3, and 4 which differed significantly from transect 1. Evenness obtained for transect 4 differed significantly from those calculated for transect 1, 2, and 3.

Measurements of similarity of species abundance between samples by means of cluster descriptive analysis are shown in the dendrograms of Figure 5. High heterogeneity was obtained at stations 1 and 2 in all transects, and relatively high homogeneity at stations 3-4, 5-6 in transect 2 and stations 11-16 in transect 1. Station 7 from transect 3 (with only three species and low abundance each) also has a great dissimilarity compared to all the other sampling stations of the transect. Independent of the similarity level chosen for grouping, stations in all transects can be ordered according to their position on the beach profiles, i.e. no samples from the upper part of the beach are grouped with samples taken down on the shore. At an arbitrary similarity level of 50%,

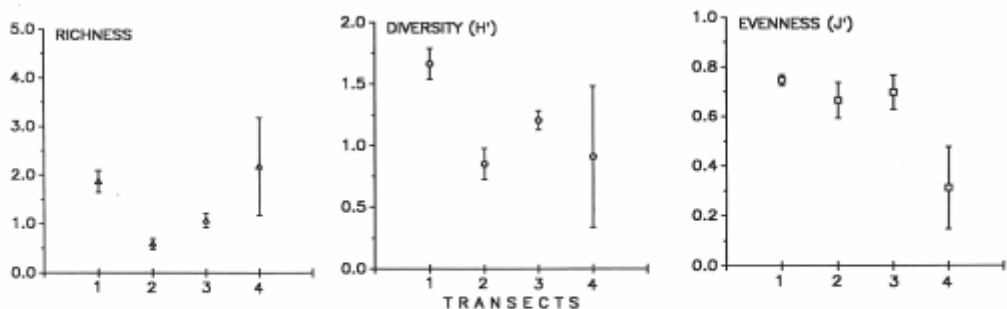


FIG. 4. - Species richness, diversity ( $H'$ ) and evenness ( $J'$ ) based on animal species abundance data along the four studied transects in Canal Whiteside.

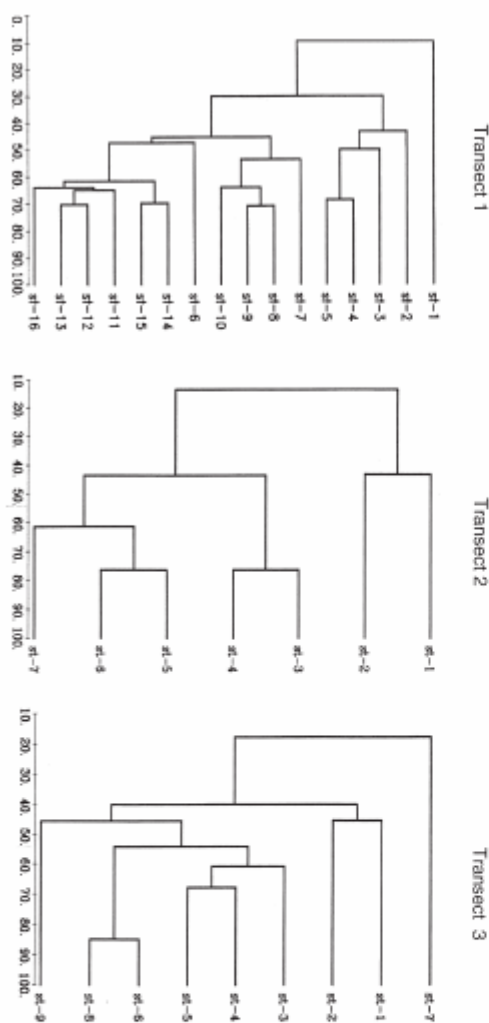


FIG. 5. — Dendrogram of three studied transects, using group similarities -average clustering from Bray-Curtis on double square-root transformed animal species abundances. (ST= sampling station).

samples are divided into 6 groups in transect 1, and 4 in transect 2 and 3. These groups can be associated with different beach height.

## DISCUSSION

Data on structure and organization of marine intertidal communities are scarce for the Magellan region, although some effort has been made to

describe the main features of the assemblages inhabiting the intertidal boulder-cobble system of the region (e.g. Guzmán and Campodónico, 1981; Ríos and Guzmán, 1982; Guzmán and Ríos, 1986; Cornejo, 1996; Ríos and Gerdes, 1997; Benedetti-Cecchi and Cinelli, 1997).

One important feature of this type of intertidal zone is the relatively high level of species richness found with more intensive surveys at some localities. In our study we recognized at least 17 macroalgae species and 44 macrofauna species, even though we excluded from the analysis taxa such as actinians, turbellarians, nematodes, nemertean, oligochaetes and holothurians due to restricted taxonomic knowledge. In Bahía Laredo, which presents a similar type of physical habitat, Ríos and Gerdes (1997) recognized at least 26 invertebrate species inhabiting the top surface of boulders and cobbles, and the molluscs *Mytilus chilensis*, *Laevittorina caliginosa*, *Kerguelenella lateralis*, *Pareuthria plumbea*, *Nacella deaurata*, *Acanthina monodon* and *Trophon geversianus* were most abundant. Cornejo (1996) determined at least 56 macroalgae species in the same area. According to Mutschke *et al.* (in press) at least 110 benthic species including macroalgae and macrofauna occur in the boulder-cobble intertidal zone in the Straits of Magellan inhabiting the top surface of rocks, the interstitial area and fine sediment below the boulders and cobbles. These results are in contrast with those published by Benedetti-Cecchi (1996) and Mazzella and Gambi (1993), who reported both low species richness and diversity for some intertidal zones in the Magellan areas, but based on more restricted and isolated sampling effort.

As has been reported for Subantarctic and Antarctic areas (e.g. Arnaud, 1992) and for the Straits of Magellan (e.g. Ríos and Gerdes, 1997), the biotic assemblages of intertidal boulders and cobbles at Canal Whiteside were highly dominated by one or two species, whereas the others were rare or very rare. In this sense, the studied community can be considered as a *Mytilus chilensis*-dominated community, with mussels forming a single-layer bed. Interestingly, the microhabitats formed by *M. chilensis* do not enhance species richness by the establishment of specific assemblages of different sessile and mobile organisms, as has been suggested as typical for mussel beds (e.g. Alvarado and Castilla, 1996). Transect 1, with its lower *M. chilensis* dominance as compared to the other three transects showed the highest species richness.



Dominance of mussels in abundance and biomass (mainly *Mytilus chilensis* and *Perumytilus purpuratus*) seems to be characteristic of communities in boulder-cobble covered areas in the Magellan Region. Other typical epifauna species of this habitat are the herbivorous limpets of the genus *Nacella*, which have a wide circumpolar distribution (e.g. South Georgia: Davenport, 1997; Heard Island: Smith and Simpson, 1985; Macquarie Island: Simpson, 1976a). In Antarctic areas, *N. concinna* is the dominant limpet in some intertidal areas (e.g. Camus, 1995; Knox, 1994; Castilla and Rozbaczylo, 1985). In the Magellan Region, *N. magellanica* and *N. deaurata* are the dominant species of this genus (e.g. Ríos and Gerdes, 1997; Ríos and Guzmán, 1982). Circumpolar distribution occurs also in other faunal and floral elements of the studied intertidal area. Macroalgae such as *Enteromorpha*, *Porphyra*, *Adenocystis*, *Urospora*, and *Iridaea* have been reported for the intertidal zone of Robert Island in the Antarctic Peninsula (Castilla and Rozbaczylo, 1985), and *Porphyra* and *Enteromorpha* are common in the solid-rock intertidal zone at Macquarie Island (Simpson, 1976b) and Heard Island (Smith and Simpson, 1985). Benthic species like the isopod *Exosphaeroma gigas*, the chiton *Plaxiphora aurata*, and also the genus *Anasterias* (sea star) are present in solid rocky-shore substrates at Macquarie Island, but those types of habitat are largely dominated by macroalgae (Simpson, 1976b). Arnaud (1974) found, in an extensive study of Antarctic and Sub-Antarctic marine benthos at Kerguelen Island, several animal species, which also occurred at Canal Whiteside, like the brachyuran *Halicarcinus planatus* and the gammarids *Paramoera fissicauda* and *Hyale hirtipalma*. These results are consistent with the biogeographical regions mentioned by Knox (1994) for the benthos of the Southern Ocean, which include the Magellanic sub-region as a Sub-Antarctic District as well as areas located in the eastern part of the Pacific like Heard Island, Macquarie Island and Kerguelen island. Recently, it turned out that the decapod fauna of the southern tip of South America includes species with Antarctic distribution (Arntz *et al.*, 1999).

Although the grouping provided by the cluster analysis must be regarded with a certain degree of caution, our results suggest a clear zonation pattern of species along the transects of a boulder-cobble shore, in contrast to results of Benedetti-Cecchi and Cinelli (1997), who concluded from a small data base the non-existence of a general pattern of zonation

in the rocky intertidal of the Straits of Magellan. Bahía Laredo, one of the areas studied by Benedetti-Cecchi and Cinelli (1997) and erroneously considered as a (sic) "site with continuous rocky shore", represents a typical boulder and cobble intertidal zone similar to the shore of Canal Whiteside studied by us. For that area, Ríos and Gerdes (1997) reported differences in the vertical distribution of epifaunal species, a pattern also found in Canal Whiteside.

#### ACKNOWLEDGEMENTS

This study was partially supported by funds from the Universidad de Magallanes under Grant F3-02B-96, and from the Forestal Trillium Ltda. and Bayside Ltda., USA, under Grant N° 94-03 supervised by the Scientific Commission for the Rio Condor Project. Most importantly, we are grateful to Prof. Dr. Wolf Arntz and Dr. Dieter Gerdes, from the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany, for their intensive and insistent input in order to get information regarding the intertidal systems of this impressive region of the world. We must also acknowledge the helpful comments and suggestions on an earlier version of this paper of Drs. Matthias Gorny (Instituto de la Patagonia, Universidad de Magallanes) and Julian Gutt (Alfred Wegener Institute, Bremerhaven).

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**PUBLICATION II**

**COMMUNITY STRUCTURE OF INTERTIDAL BOULDER-COBBLE  
FIELDS IN THE MAGELLAN REGION**

**DATA REPORT**

**Publ. II: INTERTIDAL COMMUNITY STRUCTURE (UNPUBLISHED DATA)**

Glacier advances and retreats make different types of boulder and cobble intertidal terraces a characteristic feature along the entire Magellan shoreline up to almost 10 m depth or even more. In addition to the results reported in Paper N° 1 for Canal Whiteside in the western part of the Straits of Magellan, further unpublished data from different localities between the Straits of Magellan and the Cape Horn Archipelago indicate significant differences among and within macrozoobenthos communities determined by environmental differences of the habitats. These differences become obvious in species abundances and biomasses as well as in diversity, evenness and species richness.

Table 1. Abundance ( $\text{ind m}^{-2} \pm \text{SD}$ ), biomass ( $\text{g m}^{-2} \pm \text{SD}$ ), Shannon-Wiener index ( $H'$ ), evenness ( $J$ ) and total species numbers ( $S$ ) per study site from the macrobenthic assemblages of boulder and cobble intertidal zones of the Magellan region.  $n$ =number of sampling stations, each sampled with 3 replicates. Bold: austral summer sampling

Locations	n	Sampling date	Abundance ( $\pm$ SD)	Biomass ( $\pm$ SD)	$H'$	$J$	$S$
<b>Caleta Toledo</b>	<b>15</b>	<b>November 1993</b>	<b>4,081.7 <math>\pm</math> 3,994.02 (163 to 13,701)</b>	<b>927.8 <math>\pm</math> 284.22 (73.4 to 304.1)</b>	<b>1,87</b>	<b>0,54</b>	<b>29</b>
<b>Caleta Lientur</b>	<b>16</b>	<b>November 1993</b>	<b>1,618.1 <math>\pm</math> 1,615.84 (9 to 4,574)</b>	<b>269.7 <math>\pm</math> 66.34 (0.5 to 1,353.3)</b>	<b>1,51</b>	<b>0,51</b>	<b>19</b>
<b>Seno Canoa</b>	<b>9</b>	<b>January 1994</b>	<b>847.1 <math>\pm</math> 687.31 (28 to 1,596)</b>	<b>2,792.6 <math>\pm</math> 2,610.23 (0.6 to 6,157.5)</b>	<b>1,93</b>	<b>0,66</b>	<b>17</b>
<b>Seno Indio</b>	<b>9</b>	<b>January 1994</b>	<b>664.4 <math>\pm</math> 410.40 (16 to 1,204)</b>	<b>1,484.3 <math>\pm</math> 1,396.49 (0,6 to 3,983.3)</b>	<b>1,71</b>	<b>0,62</b>	<b>15</b>
<b>Canal Whiteside*</b>	<b>35</b>	<b>November 1994</b>	<b>465.8 <math>\pm</math> 781.44 (14 to 3,337)</b>	<b>645.9 <math>\pm</math> 158.18 (0.23 to 5,939.79)</b>	<b>1,32</b>	<b>0,68</b>	<b>50</b>
<b>Cabo Negro</b>	<b>11</b>	<b>November 1995</b>	<b>1,621.2 <math>\pm</math> 1,369.35 (39 to 4,689)</b>	<b>1,648.3 <math>\pm</math> 941.89 (1.68 to 6,403.6)</b>	<b>1,16</b>	<b>0,36</b>	<b>28</b>
<b>Seno Otway</b>	<b>30</b>	<b>November 1995</b>	<b>1,470.4 <math>\pm</math> 1,413.00 (111 to 5,333)</b>	<b>960.5 <math>\pm</math> 353.84 (1.2 to 1,839.0)</b>	<b>0,76</b>	<b>0,33</b>	<b>10</b>
Cabo Negro	12	June 1995	262.9 $\pm$ 256.07 (37 to 952)	394.7 $\pm$ 480.54 (60.6 to 1,557.9)	1,08	0,37	22
Seno Otway	25	June 1995	311.6 $\pm$ 224.89 (11 to 822)	391.3 $\pm$ 165.83 (1.0 to 618.0)	1,55	0,61	11
Bahía Posesión	14	July 1996	208.1 $\pm$ 373.29 (4 to 1,429)	155.0 $\pm$ 278,00 (3.0 to 1,064.4)	1,27	0,50	13
Terminal Clarencia	12	July 1996	330.0 $\pm$ 244.30 (37 to 893)	472.9 $\pm$ 278.06 (59.1 to 1,425.7)	1,96	0,63	24

\*data from Ríos & Mutschke (1999)

A total of 66 macrofauna species plus seven major taxa such as nemerteans, anthozoans, turbellarians, oligochaetes, priapulida, ascidians and nematodes were identified in the boulder and cobble intertidal assemblages (Appendix I). Caleta Toledo and Caleta Lientur as unprotected exposed habitats with higher disturbance probability (instable substrates/wave action etc.) in the Cape Horn Archipelago are dominated by motile tiny

crustaceans such as e.g. *Exosphaeroma gigas* and *Paramoera fissicauda*. The fauna at these southernmost sites appeared rather diverse and rich in species as compared to the sites in the Straits of Magellan. At these more protected and stable intertidal areas Seno Indio, Seno Canoa and Canal Whiteside in the western part of the Straits sessile organisms such as the bivalves *Mytilus chilensis* and *Perumytilus purpuratus* dominated the fauna. All sites studied in the Straits of Magellan appeared less diverse as compared to the Cape Horn sites. Seno Otway in the central part of the Magellan Straits showed lowest species numbers with high dominance of the bivalves *Perumytilus purpuratus* and *Mytilus chilensis*. The composition of the Cabo Negro community composition resembles more the western sites in the Straits. The study sites in the Cape Horn Archipelago differ from those of the Straits of Magellan by the absence of an 'upper sandy fringe' which normally connects this habitat directly with the terrestrial system. Consequently more terrestrial invertebrates such as terrestrial worms, spiders and isopods were present.

No clear latitudinal trend in abundance among the sites in the Cape Horn Archipelago and the Straits of Magellan became obvious. The mean abundance at Caleta Toledo was outstanding high (4,081 ind m<sup>-2</sup>), areas like Cabo Negro, Seno Otway, Caleta Lientur, Seno Indio and Seno Canoa showed intermediate densities (Fig. 1A) and Canal Whiteside was the area with the lowest mean density (466 ind m<sup>-2</sup>).

According to an ANOVA test the differences among sites were significant ( $P < 0.0001$ ). Pairwise post-hoc test (Fisher's PLSD) showed the higher value from Caleta Toledo to differ significantly from all other values ( $P < 0.0001$ ); the lowest Canal Whiteside mean abundance furtheron differed significantly from the values of Seno Otway and Caleta Lientur.

As did the abundance values the biomass average values, too, varied considerably between a maximum (2792.7 g wet weight m<sup>-2</sup>) at Seno Canoa in the western part of the Straits and a minimum value of 269.7 g m<sup>-2</sup> at Caleta Lientur in the south. Contrasting, however, biomass values seem to increase from south to north (Fig. 1B). ANOVA test ( $P < 0.0001$ ) evidenced also for biomass significant differences among sites. According to the Fisher's PLSD post-hoc test, only the high biomass at Seno Canoa differed significantly from all other values, whereas the lowest value obtained at Caleta Lientur differed significantly from Seno Indio, Cabo Negro and Seno Canoa.

Mean biomass values, too, evidence a patchy distribution, however, without any latitudinal trends. Instead the data show sites with high abundances to be low in biomass

and vice versa suggesting a change in the benthic communities from tiny motile forms in the south to few but big grown sessile forms in the study sites along the Straits of Magellan (Fig. 2).

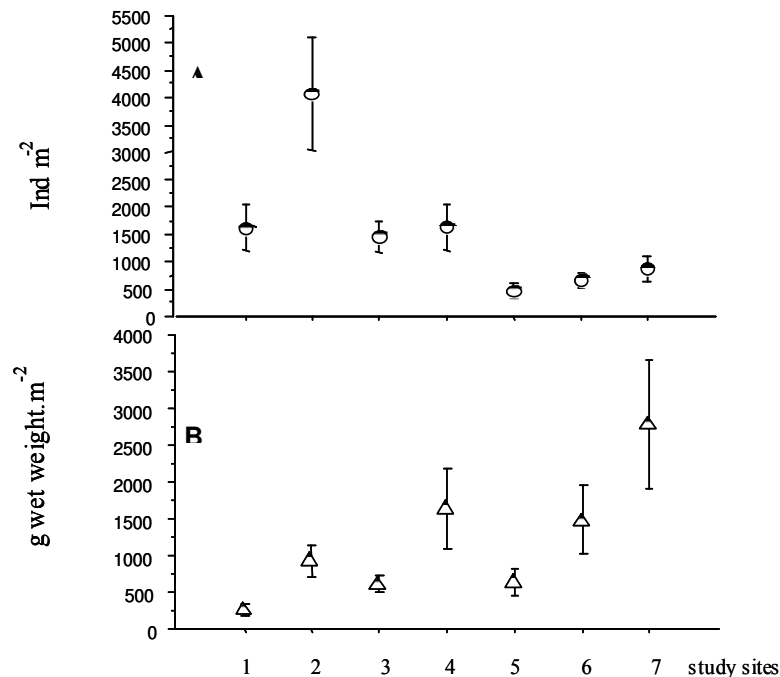
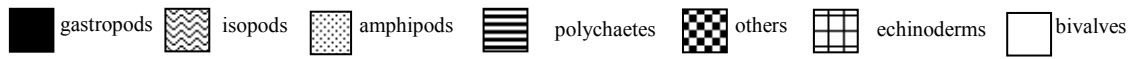


Fig. 1: Mean abundance (A) and biomass (B) values ( $\pm$  SD) of macrozoobenthos samples from boulder and cobble intertidal zones of different regions in the Magellan region.

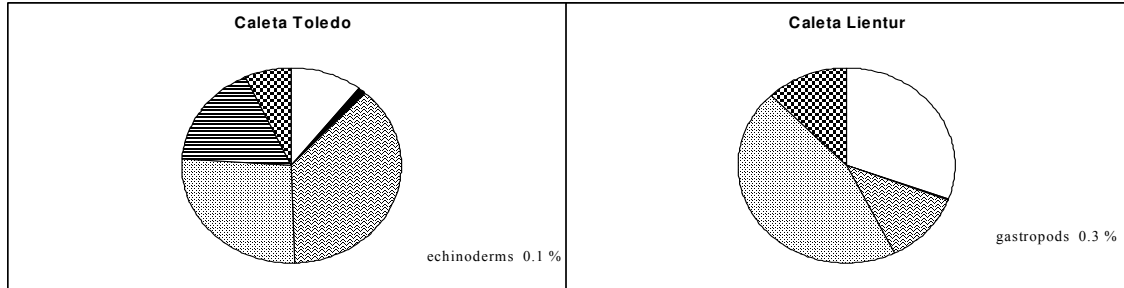
Cape Horn region:                    1 = Caleta Lientur                    2 = Caleta Toledo  
 central Straits of Magellan:        3 = Seno Otway                        4 = Cabo Negro  
 western Straits of Magellan:       5 = Canal Whiteside                6 = Seno Indio                        7 = Seno Canoa

In the Cape Horn area (Caleta Lientur and Caleta Toledo) the most important species are peracarid motile little crustaceans such as *Exosphaeroma gigas* and *Paramoera fissicauda*, whereas sessile species, especially the bivalves *Mytilus chilensis* and *Perumytilus purpuratus* dominate the sites in the Straits of Magellan.

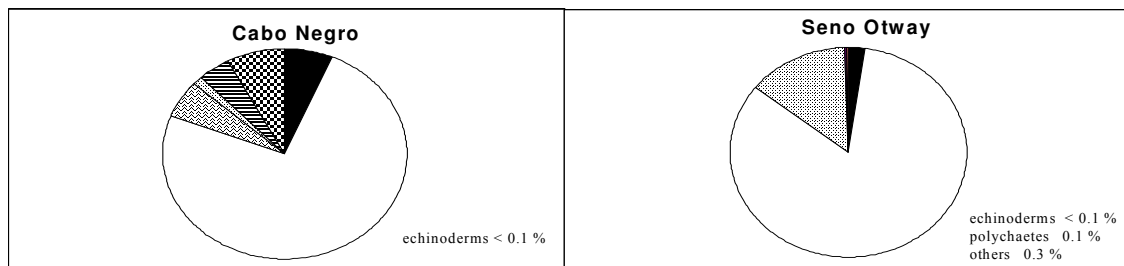
A heterogeneous spatial and temporal variability of the intertidal assemblages was clear in all the sites, reflecting a patchy occupancy of the habitat, both along the intertidal profiles (zonation) and also between spaced profiles, related with very local abiotic and biotic factors. Probably, the crossed effects of size of sediments, the degree of compactness of the finer soft-sediment matrix below the boulders and cobbles, the presence/absence of an upper intertidal related sandy fringe, and the degree of exposure to waves are among the most important factors in determine abundance and biomass, types of organisms, species richness and diversity in this type of intertidal habitat.



**Cape Horn Area**



**Central Straits of Magellan**



**Western Straits of Magellan**

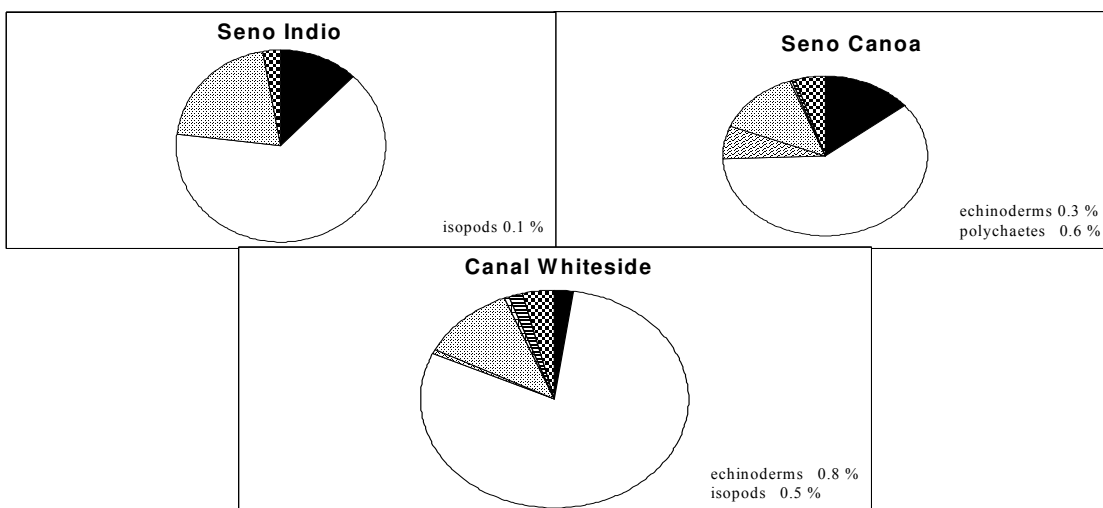


Fig.2: Composition of the macrozoobenthos communities in intertidal boulder and cobble terraces of different regions in the Magellan region based on abundance values.

As obvious in the abundance and biomass patterns distinct differences also were evident in diversity, evenness and species numbers among sites. The mean species numbers per sample in the different study sites ranged from 3 species  $m^{-2}$  in Seno Otway to 12  $m^{-2}$  in Cabo Negro (Fig.3A). Concerning species numbers Seno Otway with lowest and Cabo Negro, Caleta Toledo and Canal Whiteside with highest species numbers are outstanding; significant differences, however, only existed between Cabo Negro and C. Whiteside and Caleta Toledo and Whiteside. Beside the lowest average species number Seno Otway was special by differing significantly in diversity from all other sites (Fig.3 B), whereas the mean evenness significantly differed from Canal Whiteside, Caleta Lientur and Seno Indio (Fig.3 C).

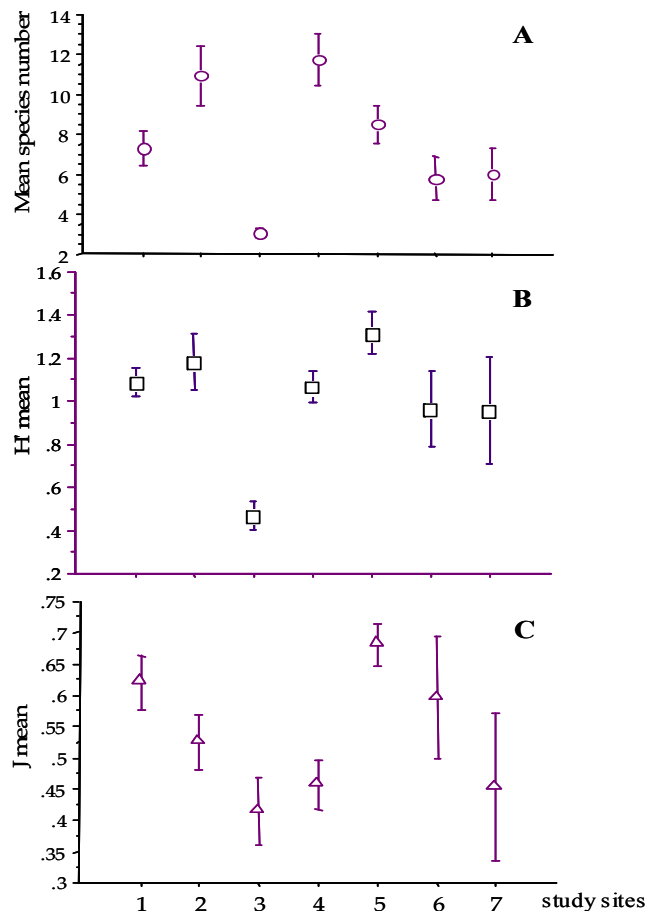


Fig.3: Species numbers (A), diversity (B) and evenness (C) for intertidal boulder and cobble sites in the Magellan region; values represent means per sample

Cape Horn region:	1 = Caleta Lientur	2 = Caleta Toledo
central Straits of Magellan:	3 = Seno Otway	4 = Cabo Negro
western Straits of Magellan:	5 = Canal Whiteside	6 = Seno Indio
		7 = Seno Canoa

It is interesting to mention that beside this significant differences in the mean diversity only existed between C. Whiteside and the two other sites Seno Canoa and Seno Indio in the western part of the Straits of Magellan.

Altogether these community parameters evidenced a patchy distribution in the different Magellan sites, but they did not evidence any significant patterns related to latitudes, they rather seem to be ruled by the specific environments of the study sites.

Community structure also was compared considering temporal variability in two sites in the Straits of Magellan (Fig. 4). At both study sites ANOVA reveals significant differences between summer and winter in all parameters ( $P < 0.0001$ ,  $P = 0.0001$  and  $P = 0.0027$  for species number, diversity and evenness, respectively). Seno Otway again appeared special with species numbers being almost the same in both periods, whereas  $H'$  and  $J$  were significantly different (Fisher's test  $P = 0.009$  and  $0.0003$ , respectively) with higher values in winter time. Contrasting in Cabo Negro the mean species numbers differed significantly between the periods ( $P < 0.0001$ ) with summer values being almost three times higher than in winter, whereas neither  $H'$  nor  $J$  differed significantly at this site (Fisher's test  $P = 0.570$  and  $0.394$ , respectively).

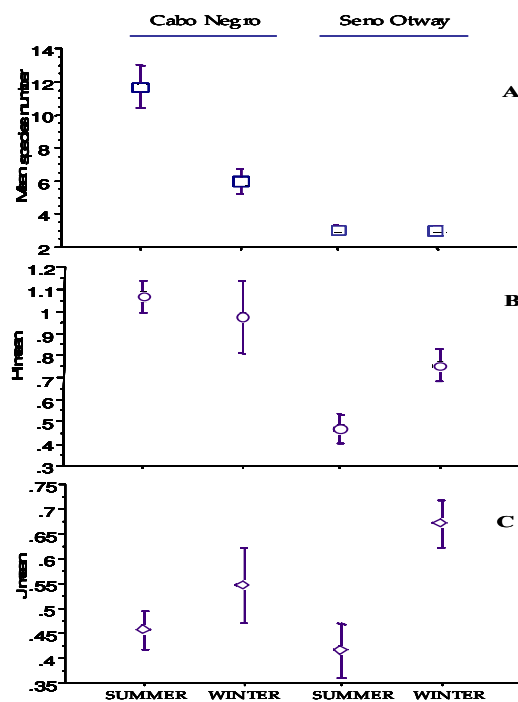


Fig.4: Species number (A), diversity (B) and evenness (C) in intertidal boulder and cobble assemblages of two study sites in the central Straits of Magellan, sampled in Austral summer and winter; values represent means per sample.



## **APPENDIX I**

MEAN ABUNDANCE (ind m<sup>-2</sup>) AND BIOMASS (g m<sup>-2</sup>) OF MACROBENTHIC  
ORGANISMS SAMPLED IN DIFFERENT BOULDER AND COBBLE  
INTERTIDAL TERRACES IN THE MAGELLAN REGION

SENO CANOA	Sampling stations									TOTAL
	st1	st2	st3	st4	st5	st6	st7	st8	st9	
ABUNDANCE										
Amphipoda Indet.	0	0	0	212	120	680	0	0	0	1012
Polychaeta Indet	0	0	0	8	0	0	0	0	40	48
Oligochaeta Indet	28	32	36	0	16	32	0	0	100	244
Aranae Indet	3	2	0	0	0	0	0	0	0	5
<i>Exosphaeroma gigas</i>	0	0	0	0	0	40	24	4	440	508
<i>Halicarcinus planatus</i>	0	0	0	32	20	0	24	0	32	108
<i>Acanthocyclus albatrossis</i>	0	0	0	0	0	0	0	0	4	4
<i>Mytilus chilensis</i>	0	0	0	872	892	580	60	132	220	2756
<i>Aulacomya ater</i>	0	0	0	0	0	0	224	280	232	736
<i>Perumytilus purpuratus</i>	0	0	0	344	208	124	208	112	104	1100
<i>Nacella deaurata</i>	0	0	0	0	0	0	0	16	0	16
<i>Nacella magellanica</i>	0	0	0	20	32	16	0	0	0	68
<i>Pareuthria plumbea</i>	0	0	0	0	0	4	0	4	0	8
<i>Laevilittorina caliginosa</i>	0	0	0	36	0	60	0	0	0	96
<i>Siphonaria lessoni</i>	0	0	0	68	40	24	156	256	344	888
<i>Chaetopleura peruviana</i>	0	0	0	0	0	0	0	4	0	4
<i>Harpagifer bispinis</i>	0	0	0	4	4	0	0	0	0	8
<i>Anasterias antarctica</i>	0	0	0	0	0	0	0	12	8	20
									<b>TOTAL</b>	<b>7629</b>
BIOMASS										
Amphipoda Indet.	0	0	0	1.31	0.45	3.35	0	0	0	5.11
Polychaeta Indet	0	0	0	0.004	0	0	0	0	0.09	0.094
Oligochaeta Indet	0.9	0.6	1.6	0	0.05	0.05	0	0	0.06	3.26
Aranae Indet	0.22	0.19	0	0	0	0	0	0	0	0.41
<i>Exosphaeroma gigas</i>	0	0	0	0	0	0.12	4.24	0.48	3.82	8.66
<i>Halicarcinus planatus</i>	0	0	0	3.48	0.83	0	3.31	0	2.19	9.81
<i>Acanthocyclus albatrossis</i>	0	0	0	0	0	0	0	0	0.27	0.27
<i>Mytilus chilensis</i>	0	0	0	1666.4	2090	1383.2	1459	2829	3666.8	13094
<i>Aulacomya ater</i>	0	0	0	0	0	0	3982	2802	1844.4	8628.2
<i>Perumytilus purpuratus</i>	0	0	0	903.6	518.4	366.9	101.2	460.4	524.4	2874.9
<i>Nacella deaurata</i>	0	0	0	0	0	0	0	28.9	0	28.9
<i>Nacella magellanica</i>	0	0	0	69.1	145.2	65.6	0	0	0	279.9
<i>Pareuthria plumbea</i>	0	0	0	0	0	0.1	0	1.4	0	1.5
<i>Laevilittorina caliginosa</i>	0	0	0	0.95	0	1.58	0	0	0	2.53
<i>Siphonaria lessoni</i>	0	0	0	19.5	9.3	8.7	30.5	26.7	80.7	175.4
<i>Chaetopleura peruviana</i>	0	0	0	0	0	0	0	3.2	0	3.2
<i>Harpagifer bispinis</i>	0	0	0	9.9	1.7	0	0	0	0	11.6
<i>Anasterias antarctica</i>	0	0	0	0	0	0	0	5.5	0.9	6.4
									<b>TOTAL</b>	<b>25134</b>

SENO INDIO

SENO INDIO	Sampling stations									TOTAL
	st1	st2	st3	st4	st5	st6	st7	st8	st9	
ABUNDANCE										
Turbellaria Indet.	0	0	0	0	16	0	0	0	0	16
Oligochaeta Indet.	8	0	24	0	0	0	4	0	0	36
Aranae indet.	8	2	1	0	0	0	0	0	0	11
Amphipoda Indet.	8	752	4	52	328	60	0	0	0	1204
<i>Exosphaeroma gigas</i>	0	0	0	0	0	0	0	0	4	4
<i>Halicarcinus planatus</i>	0	0	0	24	12	44	20	0	12	112
<i>Mytilus chilensis</i>	0	0	0	676	628	704	284	104	108	2504
<i>Aulacomya ater</i>	0	0	0	0	0	24	160	224	372	780
<i>Perumytilus purpuratus</i>	0	0	0	32	68	240	0	140	108	588
<i>Nacella deaurata</i>	0	0	0	0	0	4	16	48	60	128
<i>Nacella magellanica</i>	0	0	0	12	20	76	8	0	8	124

II. DATA REPORT

<i>Laevilittorina caliginosa</i>	0	0	0	0	8	0	0	0	0	8
<i>Siphonaria lessoni</i>	0	0	0	24	8	48	208	84	84	456
<i>Trophon geversianus</i>	0	0	0	0	0	0	0	0	4	4
<i>Chaetopleura peruviana</i>	0	0	0	0	4	0	4	0	0	8
<i>Harpagifer bispinis</i>	0	0	0	4	0	4	0	0	0	8
									<b>TOTAL</b>	<b>5991</b>

BIOMASS	st1	st2	st3	st4	st5	st6	st7	st8	st9	
<i>Turbellaria</i> Indet.	0	0	0	0	0.07	0	0	0	0	0.07
<i>Oligochaeta</i> Indet.	0.39	0	0.48	0	0	0	0.15	0	0	1.02
<i>Aranae</i> Indet	0.15	0.41	0.04	0	0	0	0	0	0	0.6
<i>Amphipoda</i> Indet.	0.16	5.71	0.1	0.21	1.14	0.34	0	0	0	7.66
<i>Exosphaeroma gigas</i>	0	0	0	0	0	0	0	0	0.39	0.39
<i>Halicarcinus planatus</i>	0	0	0	2.24	1.84	4.5	0.52	0	1.19	10.29
<i>Mytilus chilensis</i>	0	0	0	1645.2	1294	25.7	1465.4	1205.6	1286.8	6922.7
<i>Aulacomya ater</i>	0	0	0	0	0	69.12	460.93	1216.4	1649.2	3395.7
<i>Perumytilus purpuratus</i>	0	0	0	109.09	133.2	766.8	0	510.4	923.2	2442.7
<i>Nacella deaurata</i>	0	0	0	0	0	2.55	13.44	30.57	42.44	89
<i>Nacella magellanica</i>	0	0	0	62.81	125.35	154.8	2.61	0	63.16	408.73
<i>Laevilittorina caliginosa</i>	0	0	0	0	0.21	0	0	0	0	0.21
<i>Siphonaria lessoni</i>	0	0	0	6.35	2.49	10.27	23.31	5.22	11.78	59.42
<i>Trophon geversianus</i>	0	0	0	0	0	0	0	0	5.16	5.16
<i>Chaetopleura peruviana</i>	0	0	0	0	2.36	0	4.88	0	0	7.24
<i>Harpagifer bispinis</i>	0	0	0	6.49	0	1.73	0	0	0	8.22
									<b>TOTAL</b>	<b>13359</b>

SENO OTWAY SUMMER ABUNDANCE	Sampling stations												
	st7	st8	st9	st10	st11	st12	st13	st14	st15	st16	st17	st18	st19
<i>Polychaeta</i> Indet.	0	0	0	16.5	0	0	0	0	5.5	0	0	0	0
<i>Amphipoda</i> Indet.	22	0	44.5	689	11	0	66.5	0	0	0	1366.5	239	272.5
<i>Mytilus chilensis</i>	111	155.5	206	83.5	150	16.5	72	333	50	127.5	22	144.5	33.5
<i>Perumytilus purpuratus</i>	1139	2050	1672	1116.5	877.5	872	539	2422	3155.5	983.5	694	727.5	289
<i>Nacella deaurata</i>	0	0	0	0	0	0	0	0	5.5	0	0	0	0
<i>Nacella magellanica</i>	0	0	0	0	0	0	0	0	11	11	0	0	0
<i>Pareuthria plumbea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Siphonaria lessoni</i>	11	0	0	5.5	5.5	5.5	28	33.5	5.5	11	27.5	16.5	44.5
<i>Acanthocyclus albatrossis</i>	5.5	0	0	0	0	0	0	0	0	5.5	0	0	0
<i>Anasterias antarctica</i>	0	0	0	0	0	0	0	0	0	28.5	0	0	0

ABUNDANCE	st20	st21	st22	st23	st24	st25	st26	st27	st28	st29	st30	st31	TOTAL
<i>Polychaeta</i> Indet.	0	0	0	0	5.5	0	0	0	0	0	0	0	27.5
<i>Amphipoda</i> Indet.	0	155.5	139	0	44.5	0	0	183.5	805.5	494.5	0	0	4533.5
<i>Mytilus chilensis</i>	583	166.5	0	61	5.5	22	61	5.5	0	0	16.5	61	2487
<i>Perumytilus purpuratus</i>	2722	289	39	750	1272	550	1755.5	828	361	5.5	1350	883.5	27343
<i>Nacella deaurata</i>	0	0	0	0	5.5	0	33.5	0	0	0	0	0	44.5
<i>Nacella magellanica</i>	0	0	11	0	0	0	22	5.5	0	0	5.5	0	66
<i>Pareuthria plumbea</i>	0	0	0	0	0	0	0	0	0	0	0	5.5	5.5
<i>Siphonaria lessoni</i>	16.5	78	33.5	33.5	22	28	55.5	16.5	39	0	11	22	549.5
<i>Acanthocyclus albatrossis</i>	0	5.5	5.5	11	0	11	22	11	0	0	0	0	77
<i>Anasterias antarctica</i>	0	0	0	0	0	0	5.5	0	0	0	0	5.5	39.5
												<b>TOTAL</b>	<b>35173</b>

BIOMASS	st7	st8	st9	st10	st11	st12	st13	st14	st15	st16	st17	st18	st19
<i>Polychaeta</i> Indet.	0	0	0	0	0	0	0	0	0.75	0	0	0	0

II. DATA REPORT

Amphipoda Indet.	0.015	0	0.18	0	0.01	0	0.48	0	0	0	1.25	0.55	0.56
<i>Mytilus chilensis</i>	176.45	407.05	159	189.85	216.7	118	254.2	245.8	26.75	134.5	82.4	108.85	53
<i>Perumytilus purpuratus</i>	663.2	1223.2	729	1162.1	758	1093	586.4	1173.3	1056.2	572	362	357.85	818
<i>Nacella deaurata</i>	0.175	0	0	0	0	0	0	0	6.9	0	0	0	0
<i>Nacella magellanica</i>	0	0	0	0	0	0	0	0	3.66	94.95	0	0	0
<i>Pareuthria plumbea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Siphonaria lessoni</i>	1.3	0	0	0.125	0.58	0.01	9.195	1.575	0.45	4.25	7.8	1.73	11.7
<i>Acanthocyclus albatrossis</i>	1.1	0	0	0	0	0	0	0	0	46.7	0	0	0
<i>Anasterias antarctica</i>	0	0	0	0	0	0	0	0	0	10	0	0	0
<b>BIOMASS</b>	<b>st20</b>	<b>st21</b>	<b>st22</b>	<b>st23</b>	<b>st24</b>	<b>st25</b>	<b>st26</b>	<b>st27</b>	<b>st28</b>	<b>st29</b>	<b>st30</b>	<b>st31</b>	<b>TOTAL</b>
Polychaeta Indet.	0	0	0	0	1.4	0	0	0	0	0	0	0	2.15
Amphipoda Indet.	0	0.35	0.3	0	0.17	0	0	0.5	0.69	0.61	0	0	5.665
<i>Mytilus chilensis</i>	293	11.15	0	36.65	8.8	38.1	134.8	13.4	0	0	47.3	11.65	2767.4
<i>Perumytilus purpuratus</i>	1176.6	298.6	18.8	397.7	1141	930	1604.9	729	568.9	2.65	1602	876.1	19900.5
<i>Nacella deaurata</i>	0	0	0	0	24.3	0	77.05	0	0	0	0	0	108.425
<i>Nacella magellanica</i>	0	0	182.9	0	0	0	9.93	84.6	0	0	13.4	0	389.44
<i>Pareuthria plumbea</i>	0	0	0	0	0	0	0	0	6.05	0	0	4.8	10.85
<i>Siphonaria lessoni</i>	6.95	22.8	9.7	12.35	3.55	9.9	11.2	1.05	0	0	0.85	4.55	121.615
<i>Acanthocyclus albatrossis</i>	0	0.4	3.35	3.65	0	4.91	16.45	12.8	0	0	0	0	89.36
<i>Anasterias antarctica</i>	0	0	0	0	0	0	1.38	0	0	0	0	2.15	13.53
												<b>TOTAL</b>	<b>23408.9</b>

SENO OTWAY WINTER

ABUNDANCE	Sampling stations													
	st9	st10	st11	st12	st13	st14	st15	st16	st17	st18	st19	st20	st21	st22
Polychaeta errantia Indet.	44.5	0	0	0	0	0	0	0	0	0	5.5	5.5	5.5	0
Polychaeta sedentaria Indet.	0	0	0	5.5	161	0	5.5	39	0	5.5	11	5.5	0	0
<i>Mytilus chilensis</i>	33.5	133.5	33.5	72	133.5	61	100	66.5	55.5	50	16.5	39	22	161
<i>Perumytilus purpuratus</i>	367	300	261	300	255.5	178	355.5	505.5	178	105.5	205.5	222.5	11	250
<i>Nacella magellanica</i>	5.5	0	0	28	0	5.5	0	0	0	0	16.5	16.5	11	0
<i>Nacella deaurata</i>	0	0	0	33.5	0	0	0	0	0	0	0	0	0	0
<i>Siphonaria lessoni</i>	50	16.5	83.5	0	27.5	55.5	116.5	61	0	0	22	33	50	0
<i>Pareuthria plumbea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda Indet.	0	0	0	0	0	0	0	0	0	0	50	0	16.5	33.5
<i>Acanthocyclus albatrossis</i>	0	0	0	0	0	0	0	0	0	0	0	5.5	5.5	0
<i>Anasterias antarctica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiura Indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nothotenidae Indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0

ABUNDANCE	st23	st24	st25	st26	st27	st28	st29	st30	st31	st32	st33	st34	TOTAL	
Polychaeta errantia Indet.	0	0	0	0	0	16.5	0	11	0	5.5	5.5	0	99.5	
Polychaeta sedentaria Indet.	5.5	22	0	28	77.5	22	39	22	67	105.5	33.5	5.5	660.5	
<i>Mytilus chilensis</i>	5.5	127.5	5.5	27.5	0	0	0	5.5	5.5	0	0	0	1154.5	
<i>Perumytilus purpuratus</i>	205.5	16.5	16.5	55.5	5.5	5.5	0	0	0	0	0	0	3800	
<i>Nacella magellanica</i>	0	0	0	0	0	11	11	22	0	0	0	11	138	
<i>Nacella deaurata</i>	0	0	0	0	0	11	0	0	0	11	5.5	0	61	
<i>Siphonaria lessoni</i>	39	44.5	28	33.5	0	0	0	0	0	0	0	5.5	666	
<i>Pareuthria plumbea</i>	0	0	5.5	0	0	0	0	0	0	0	0	0	5.5	
Amphipoda Indet.	0	50	0	11	122	22	155.5	61	0	0	188.5	178	888	
<i>Acanthocyclus albatrossis</i>	11	0	16.5	0	0	11	0	0	0	0	0	5.5	55	
<i>Anasterias antarctica</i>	0	0	0	0	11	0	0	5.5	0	0	5.5	0	22	
Ophiura Indet.	0	0	5.5	0	0	0	0	0	5.5	0	0	0	11	
Nothotenidae Indet	5.5	0	0	0	0	0	0	0	0	0	0	0	5.5	
													<b>TOTAL</b>	<b>7566.5</b>

II. DATA REPORT

BIOMASS	st9	st10	st11	st12	st13	st14	st15	st16	st17	st18	st19	st20	st21	st22
Polychaeta errantia Indet.	0.9	0	0	0	0	0	0	0	0	0	0.7	0.2	0.2	0
Polychaeta sedentaria Indet.	0	0	0	0.15	4.8	0	0.04	5.8	0	0.6	0.35	1.2	0	0
<i>Mytilus chilensis</i>	69.05	146.35	74.65	65.05	132.7	35.6	13.05	68.7	103.8	17.9	25.2	33.6	1.1	9.65
<i>Perumytilus purpuratus</i>	316.35	232.55	174.7	242	89.85	74	110.8	267.7	113	54.35	216.2	293.9	19.05	632.9
<i>Nacella magellanica</i>	6.85	0	0	224.7	0	3.6	0	0	0	0	13.55	23.8	92.3	0
<i>Nacella deaurata</i>	0	0	0	0	0	7.45	0	0	0	0	0	0	0	0
<i>Siphonaria lessoni</i>	68.85	4.7	18.45	7.65	25.5	0	36.35	16.3	0	0.6	5.75	152.6	9.35	0
<i>Pareuthria plumbea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda Indet.	0	0	0	0	0	0	0	0	0	0	5.75	0	0.5	0.2
<i>Acanthocyclus albatrossis</i>	0	0	0	0	0	0	0	0	0	0	0	0	4.55	0
<i>Anasterias antarctica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiura Indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nothotenidae Indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BIOMASA	st23	st24	st25	st26	st27	st28	st29	st30	st31	st32	st33	st34	TOTAL	
Polychaeta errantia Indet.	0	0	0	0	0	3.3	0	1.9	0	0.41	0.79	0	8.4	
Polychaeta sedentaria Indet.	0.55	0.95	0	7.1	6.5	0.5	0.86	3.3	10.1	0.6	2.5	1.25	47.15	
<i>Mytilus chilensis</i>	46.95	95.95	1.25	57.3	0	0	0	0.25	0.25	1.1	1.25	0	1000.7	
<i>Perumytilus purpuratus</i>	394.3	18.15	6.15	73.6	13.05	0.2	0	0	0	0	0	0	3342.8	
<i>Nacella magellanica</i>	0	0	0	0	0	130.8	28.45	51.25	0	0	0	144.4	719.7	
<i>Nacella deaurata</i>	0	0	0	0	0	16.4	0	0	0	13.4	23.8	0	61.05	
<i>Siphonaria lessoni</i>	8.2	3.95	4.2	4.15	0	0	0	0	0	0	0	1.45	368.05	
<i>Pareuthria plumbea</i>	0	0	4.55	0	0	0	0	0	0	0	0	0	4.55	
Amphipoda Indet.	0	0.55	0	0.03	0.8	0.06	0.06	1.15	0	0	1	5.55	15.65	
<i>Acanthocyclus albatrossis</i>	5.55	0	76.05	0	0	17.3	0	0	0	0	0	34.65	138.1	
<i>Anasterias antarctica</i>	0	0	0	0	3.2	0	0	1.95	0	0	2.6	0	7.75	
Ophiura Indet.	0	0	0	0	0	0	0	0	0.85	0	0	0	0.85	
Nothotenidae Indet	24.5	0	37.75	0	0	0	0	0	0	0	0	0	62.25	
<b>TOTAL</b>													<b>5777</b>	

CALETA TOLEDO

ABUNDANCE	Sampling stations															TOTAL
	st1	st2	st3	st4	st5	st6	st7	st8	st9	st10	st11	st12	st13	st14	st15	
Oligochaeta Indet.	24	30.7	105.3	1.3	0	0	0	0	0	0	0	0	0	0	0	161.3
Turbellaria Indet.	0	0	0	0	0	5.3	265.3	682.7	585.3	596	568	362.7	274.7	168	36	3544
Nemertini Indet.	0	0	0	0	0	0	0	0	0	1.3	22.7	38.7	9.3	2.7	2.7	77.4
Nematoda Indet.	0	0	0	0	0	0	0	25.3	16	0	0	0	0	0	0	41.3
<i>Rubrius antarctica</i>	166.7	76	4	0	0	0	0	0	0	0	0	0	0	0	0	246.7
<i>Erigone antarctica</i>	17.3	32	0	0	0	0	0	0	0	0	0	0	0	0	0	49.3
<i>Lycosa</i> sp.	1.3	0	5.3	0	0	0	0	0	0	0	0	0	0	0	0	6.6
Polychaeta Indet. 1	0	0	4	58.7	6.7	750.7	1761	1517	472	777.3	206.7	692	804	309.3	101.3	7460.7
Polychaeta Indet. 2	0	0	0	0	0	0	0	0	0	0	1.3	0	4	0	0	5.3
Polychaeta Indet. 3	0	0	0	0	0	0	0	0	0	0	0	0	2.7	0	2.7	5.4
Polychaeta Indet. 4	17.3	21.3	44	531	1044	1080	60	44	1.3	0	2.7	2.7	0	2.7	5.3	2856.3
<i>Exosphaeroma gigas</i>	0	0	0	0	1.3	0	9.3	6624	6541	3801.3	960	1156	2533.3	380	1260	23266.2
<i>Orchestia scutigerula</i>	0	2.7	245.3	257	20	1.3	0	0	0	0	0	0	0	2.7	0	529
<i>Paramoera fissicauda</i>	0	0	1.3	0	1.3	454.7	5727	4803	2468	200	165.3	168	52	5.3	10.7	14056.6
<i>Paramoera</i> sp.	0	0	0	0	0	0	0	0	6.7	25.3	38.7	444	436	245.3	482.7	1678.7
<i>Halicarcinus planatus</i>	0	0	0	0	0	0	0	0	1.3	0	1.3	0	17.3	48	33.3	101.2
<i>Mytilus chilensis</i>	0	0	0	0	0	0	0	1.3	0	6.7	33.3	50.7	38.7	45.3	26.7	202.7
<i>Perumytilus purpuratus</i>	0	0	0	0	0	0	0	0	0	2.7	4	14.7	13.3	20	14.7	69.4
<i>Alacomya ater</i>	0	0	0	0	0	0	0	0	0	1.3	8	9.3	12	49.3	25.3	105.2
<i>Gaimardia</i> sp.	0	0	0	0	0	0	2.7	22.7	58.7	633.3	834.7	1405.3	93.3	3050.7	6101.4	
<i>Lassaea militaris</i>	0	0	0	0	0	0	0	0	0	1.3	1.3	4	2.7	4	0	13.3
<i>Glypteuthria</i> sp.	0	0	0	0	0	0	0	0	0	0	1.3	0	0	2.7	4	
<i>Laevilittorina caliginosa</i>	0	0	0	0	0	2.7	4	0	4	9.3	32	28	4	5.3	0	89.3
<i>Nacella deaurata</i>	0	0	0	0	0	0	0	0	1.3	14.7	46.7	61.3	61.3	152	49.3	386.6
<i>Nacella magellanica</i>	0	0	0	0	0	0	1.3	4	26.7	38.7	25.3	13.3	9.3	0	118.6	
<i>Pareuthria plumbea</i>	0	0	0	0	0	0	0	0	0	0	0	1.3	0	2.7	4	
<i>Plaxiphora</i> sp.	0	0	0	0	0	0	0	0	0	1.3	0	0	0	0	1.3	
<i>Anasterias antarctica</i>	0	0	0	0	0	0	0	0	0	0	1.3	2.7	21.3	16	41.3	

II. DATA REPORT

<i>Harpagifer bispinis</i>	0	0	0	0	0	0	0	0	0	1.3	0	0	0	0	1.3	0	2.6
<b>TOTAL 61225.7</b>																	

BIOMASS	st1	st2	st3	st4	st5	st6	st7	st8	st9	st10	st11	st12	st13	st14	st15	TOTAL
<i>Oligochaeta</i> Indet.	39.64	65.39	241.7	3.187	0	0	0	0	0	0	0	0	0	0	0	349.89
<i>Turbellaria</i> Indet.	0	0	0	0	0	0.392	17.67	43.02	32.81	42.037	39.71	22.67	15.807	8.481	2.132	224.73
<i>Nemertini</i> Indet.	0	0	0	0	0	0	0	0	0	0.147	5.868	5.998	3.521	1.951	0.791	18.28
<i>Nematoda</i> Indet.	0	0	0	0	0	0	0	0.035	0.04	0	0	0	0	0	0	0.075
<i>Rubrius antarctica</i>	68.41	67.94	3.248	0	0	0	0	0	0	0	0	0	0	0	0	139.60
<i>Erigone antarctica</i>	0.254	2.195	0	0	0	0	0	0	0	0	0	0	0	0	0	2.449
<i>Lycosa</i> sp.	0.469	0	5.811	0	0	0	0	0	0	0	0	0	0	0	0	6.28
<i>Polychaeta</i> Indet. 1	0	0	0.085	1.487	1.427	14.49	40.87	26.68	8.591	9.253	4.739	12.96	6.885	3.441	0.808	131.72
<i>Polychaeta</i> Indet. 2	0	0	0	0	0	0	0	0	0	0	0.129	0	0.771	51.17	4.019	56.09
<i>Polychaeta</i> Indet. 3	0	0	0	0	0	0	0	0	0	0	0	0	0.097	0	0.957	1.054
<i>Polychaeta</i> Indet. 4	1.677	1.364	4.894	59.48	98.78	77.86	4.524	1.643	0.135	0	0.065	0.087	0	9.965	25.436	285.9
<i>Exosphaeroma gigas</i>	0	0	0	0	0.04	0	0.265	283.6	361.4	261.17	89.91	106.6	399.23	61.4	136.76	1700.4
<i>Orchestia scutigerula</i>	0.803	295.1	140.1	9.257	1.505	0	0	0	0	0	0	0	0.187	0	0	447.04
<i>Paramoera fissicauda</i>	0	0	0.129	0	0.02	32.35	512.5	394.2	265.7	18.883	16.1	11.64	4.813	0.417	0.556	1257.3
<i>Paramoera</i> sp.	0	0	0	0	0	0	0	0	0.209	0.617	1.037	12.55	11.171	5.112	15.111	45.804
<i>Halicarcinus planatus</i>	0	0	0	0	0	0	0	0	0.329	0	0.502	0	31.213	76.13	53.791	161.97
<i>Mytilus chilensis</i>	0	0	0	0	0	0	0	33.68	0	152.99	591.4	437.1	210.17	349.6	168.721	1943.7
<i>Perumytilus purpuratus</i>	0	0	0	0	0	0	0	0	0	73.172	61.83	151.5	198.42	523.9	310.374	1319.2
<i>Alacomya ater</i>	0	0	0	0	0	0	0	0	0	1.653	130.9	151.2	58.191	427.2	170.788	939.9
<i>Gaimardia</i> sp.	0	0	0	0	0	0	0	0	0.242	2.168	8.013	88.35	76.933	95.4	3.347	274.5
<i>Lassaea miliaris</i>	0	0	0	0	0	0	0	0	0	0.04	0.065	0.04	0.027	0.075	0	0.247
<i>Glypteuthria</i> sp.	0	0	0	0	0	0	0	0	0	0	0	6.93	0	0	1.415	8.345
<i>Laevilitorina caliginosa</i>	0	0	0	0	0	0.407	0.53	0	0.234	1.329	3.08	3.164	0.259	0.676	0	9.679
<i>Nacella deaurata</i>	0	0	0	0	0	0	0	0	5.165	88.081	153.5	450.5	298.66	1079	444.751	2519.4
<i>Nacella magellanica</i>	0	0	0	0	0	0	0	2.791	65.24	431.25	434.5	391.6	165.29	53.64	0	1544.3
<i>Pareuthria plumbea</i>	0	0	0	0	0	0	0	0	0	0	0	0	13.515	0	41.964	55.479
<i>Plaxiphora</i> sp.	0	0	0	0	0	0	0	0	0	0	14.42	0	0	0	0	14.423
<i>Anasterias antarctica</i>	0	0	0	0	0	0	0	0	0	0	0	5.504	71.813	179	81.841	338.13
<i>Harpagifer bispinis</i>	0	0	0	0	0	0	0	0	3.767	0	0	0	0	116.5	0	120.3
<b>TOTAL 13916.1</b>																

CALETA LIENTUR	Sampling stations																
	st1	st2	st3	st4	st5	st6	st7	st8	st9	st10	st11	st12	st13	st14	st15	st16	TOTAL
<i>Oligochaeta</i> Indet.	6.7	26.7	25.3	38.7	8	4	1.3	0	0	0	0	0	0	0	0	0	110.7
<i>Polychaeta</i> Indet.	0	0	0	0	0	38.7	241.3	201.3	70.7	80	130.7	104	33.3	21.3	30.7	18.7	970.7
<i>Turbellaria</i> Indet.	0	0	0	0	0	1.3	10.7	146.7	137	290.7	180	205.3	168	76	136	146.7	1498.4
<i>Nemertini</i> Indet.	0	0	0	0	28	0	0	0	9.3	33.3	36	46.7	69.3	49.3	61.3	72	405.2
<i>Rubrius antarcticus</i>	2.6	16	16	10.7	1.3	0	0	0	0	0	0	0	0	0	0	0	46.6
<i>Erigone antarctica</i>	0	12	8	0	1.3	0	0	0	0	0	0	0	0	0	0	0	21.3
<i>Lycosa</i> sp.	0	1.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.3
<i>Exosphaeroma gigas</i>	0	0	0	0	0	0	0	26.7	1257	1032	129.3	76	12	312	41.3	192	3078.3
<i>Orchestia scutigerula</i>	0	0	1.3	41.3	133.3	52	14.7	4	5.3	44	65.3	196	81.3	61.3	24	5.3	729.1
<i>Paramoera fissicauda</i>	0	0	0	0	28	48	33.3	809.3	2791	1267	844	745.3	490.7	685.3	1133.3	2087.7	10962.6
<i>Halicarcinus planatus</i>	0	0	0	0	0	0	0	0	0	0	10.6	13	2.7	5.3	10.6	12	54.2
<i>Mytilus chilensis</i>	0	0	0	0	0	0	0	0	0	0	1.3	1.3	1.3	1.3	2.7	0	7.9
<i>Laevilitorina caliginosa</i>	0	0	0	0	0	0	1.3	4	13.3	42.7	133.3	428	1477.3	1786.7	2026.7	2012	7925.3
<i>Nacella magellanica</i>	0	0	0	0	0	0	0	0	0	0	0	0	1.3	0	0	1.3	2.6
<i>Nacella mytilina</i>	0	0	0	0	0	0	0	0	0	0	0	0	2.7	0	1.3	0	4
<i>Nacella deaurata</i>	0	0	0	0	0	0	0	0	0	0	0	0	4	16	18.7	16	54.7
<i>Tonicia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	2.7	1.3	1.3	1.3	5.3
<i>Austrolycus depressiceps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.3	6.7	8
<i>Harpagifer bispinis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.7	2.7
<b>TOTAL 25888.9</b>																	

BIOMASS	st1	st2	st3	st4	st5	st6	st7	st8	st9	st10	st11	st12	st13	st14	st15	st16	TOTAL
<i>Oligochaeta</i> Indet.	0.2	34.4	31.5	70.2	6.6	2.9	2.2	0	0	0	0	0	0	0	0	0	148
<i>Polychaeta</i> Indet.	0	0	0	0	0	4.1	22.9	12.9	1.2	1.2	1.7	1.4	0.3	0.1	0.1	0.09	45.99
<i>Turbellaria</i> Indet.	0	0	0	0	0	0.04	0.4	5	14.7	20.4	5.5	5.9	3.5	1.9	5.8	7.7	70.84
<i>Nemertini</i> Indet.	0	0	0	0	31	0	0	0	2.2	7.3	6.5	11.6	13.2	12.4	12.5	17.1	113.8
<i>Rubrius antarcticus</i>	0.3	50.1	19.2	12.1	7	2.7	0	0	0	0	0	0	0	0	0	0	91.4
<i>Erigone antarctica</i>	0	1.5	1.1	0	0.1	0	0	0	0	0	0	0	0	0	0	0	2.7
<i>Lycosa</i> sp.	0	0.09	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.09
<i>Exosphaeroma gigas</i>	0	0	0	0	0	0	0	0.6	35.2	26.5	1.9	1.5	0.3	6.3	0.9	2.8	76
<i>Orchestia scutigerula</i>	0	0	2.7	65.3	179	59.4	13.4	3.3	4.3	34.6	74.1	152.7	62.7	46	20.2	4.9	722.6
<i>Paramoera fissicauda</i>	0	0	0	0	4	6.5	3.5	83.5	67.8	160.8	69.3	53.6	57.5	78.6	137.5	308.3	1030.9

II. DATA REPORT

<i>Halicarcinus planatus</i>	0	0	0	0	0	0	0	0	0	0.51	0.71	0.11	0.24	0.55	0.68	2.8
<i>Mytilus chilensis</i>	0	0	0	0	0	0	0	0	0	1.8	9.8	3.6	19.1	0.1	0	34.4
<i>Laevilittorina caliginosa</i>	0	0	0	0	0	0.1	0.2	0.5	1.2	6.1	15.7	52.2	63.7	74.9	74.8	289.4
<i>Nacella magellanica</i>	0	0	0	0	0	0	0	0	0	0	0	40.5	0	0	86.9	127.4
<i>Nacella mytilina</i>	0	0	0	0	0	0	0	0	0	0	0	3.3	0	0.4	0	3.7
<i>Nacella deaurata</i>	0	0	0	0	0	0	0	0	0	0	0	62.1	271.1	225.6	366.2	925
<i>Tonicia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	60.6	6.6	3.1	70.3
<i>Austrolycus deppressiceps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	78.6	390.8	469.4
<i>Harpagifer bispinis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	89.9	89.9
<b>TOTAL</b>																<b>4314.62</b>

CABO NEGRO SUMMER

ABUNDANCE	Sampling stations												TOTAL
	st-6	st-8	st-10	st-12	st-14	st-15	st-16	st-18	st-20	st-22	st-24		
Amphipoda Indet.	2.8	2.2	12.9	3.7	7.4	0	13.3	7.4	7.4	0	188.9	246	
Nematoda Indet.	0	4.4	0	20.4	70.4	738.9	73.3	0	14.8	66.7	255.6	1244.5	
Ascidia Indet.	0	0	0	0	0	0	4.4	0	0	0	11.1	15.5	
Actiniaria Indet.	0	0	0	0	9.3	33.4	0	0	3.7	38.9	0	85.3	
Nemertini Indet.	0	0	0	0	0	0	4.4	3.7	0	0	0	8.1	
Oligochaeta Indet.	0	0	0	0	0	0	0	3.7	0	0	0	3.7	
Polychaeta errantia Indet.	8.4	2.2	101.9	12.9	79.6	16.7	28.9	25.9	25.9	5.6	11.1	319.1	
Polychaeta sedentaria Indet.	0	37.8	11.1	5.6	31.5	133.4	66.7	11.1	0	83.4	55.6	436.2	
<i>Priapulus</i> sp.	0	2.2	1.9	0	0	0	2.2	0	0	0	0	6.3	
<i>Halicarcinus planatus</i>	0	2.2	0	9.3	1.9	0	8.9	0	0	0	0	22.3	
<i>Edotea magellanica</i>	2.8	40	44.4	14.8	148.2	44.4	26.7	59.2	288.9	238.9	0	908.3	
<i>Exosphaeroma gigas</i>	22.2	6.7	1.9	51.9	1.9	5.6	2.2	0	0	0	0	92.4	
<i>Aulacomya ater</i>	0	2.2	0	0	7.4	0	0	3.7	0	0	0	13.3	
<i>Mytilus chilensis</i>	0	573.3	483.4	494.4	2050	300	615.4	566.5	2348.2	1716.7	3955.6	13103.5	
<i>Perumytilus purpuratus</i>	0	0	9.3	7.4	59.3	0	44.5	48.1	14.8	0	0	183.4	
<i>Trophon geversianus</i>	0	0	1.9	0	1.9	0	0	0	0	0	0	3.8	
<i>Fissurella picta</i>	0	0	0	0	0	0	2.2	0	0	0	0	2.2	
<i>Pareuthria plumbea</i>	0	0	0	0	1.9	11.1	2.2	14.8	0	0	0	30	
<i>Kerguelenella Lateralis</i>	0	55.6	22.2	18.5	11.1	0	160	59.2	88.9	27.8	0	443.3	
<i>Laevilittorina caliginosa</i>	2.8	0	3.7	3.7	18.5	0	0	7.4	240.7	111.1	188.9	576.8	
<i>Margarella violacea</i>	0	0	0	1.9	0	0	0	0	0	0	0	1.9	
<i>Nacella deaurata</i>	0	2.2	14.8	9.3	5.6	0	0	0	0	0	0	31.9	
<i>Nacella magellanica</i>	0	2.2	0	0	1.9	5.6	2.2	0	0	0	22.2	34.1	
<i>Siphonaria lessoni</i>	0	0	0	0	0	0	4.4	0	0	0	0	4.4	
<i>Anasterias antarctica</i>	0	0	0	1.9	1.9	0	0	0	0	0	0	3.8	
<b>TOTAL</b>												<b>17820.1</b>	

BIOMASS	Sampling stations												TOTAL
	st-6	st-8	st-10	st-12	st-14	st-15	st-16	st-18	st-20	st-22	st-24		
Amphipoda Indet.	0.12	0.004	0.33	0.05	0.02	0	0.13	0.05	0.03	0	5.2	5.934	
Nematoda Indet.	0	0.02	0	0.03	0.09	0.8	0.09	0	0.23	0.06	0.3	1.62	
Ascidia Indet.	0	0	0	0	0	0	1.85	0	0	0	0	1.85	
Actiniaria Indet.	0	0	0	0	3.46	12.92	0	0	6.82	26.38	0	49.58	
Nemertini Indet.	0	0	0	0	0	0	0.11	0.002	0	0	0	0.112	
Oligochaeta Indet.	0	0	0	0	0	0	0	0.52	0	0	0	0.52	
Polychaeta errantia Indet.	1.3	0.21	1.24	0.69	1.25	2.8	5.42	1.38	1.88	0.29	1.13	17.59	
Polychaeta sedentaria Indet.	0	0.32	0.75	0.13	7.64	8.17	6.59	11.49	0	12.72	62.17	109.98	
<i>Priapulus</i> sp.	0	15.48	1.35	0	0	0	16.73	0	0	0	0	33.56	
<i>Halicarcinus planatus</i>	0	0.15	0	0.64	0.05	0	1.95	0	0	0	0	2.79	
<i>Edotea magellanica</i>	0.04	1.3	1.1	1.36	6.43	0.94	1.58	4.33	15.13	8.52	0	40.73	
<i>Exosphaeroma gigas</i>	0.16	0.79	0.08	9.84	0.02	0.2	0.62	0	0	0	0	11.71	
<i>Aulacomya ater</i>	0	1.28	0	0	10.5	0	0	2.68	0	0	0	14.46	
<i>Mytilus chilensis</i>	0	302.35	381.24	575.92	1832.4	248.34	1084.9	1405.4	2784.08	1901.73	5845.6	16362	
<i>Perumytilus purpuratus</i>	0	0	17.14	11.6	18.94	11.1	105.14	151.83	34.97	0	0	350.72	
<i>Trophon geversianus</i>	0	0	3.68	0	3.25	0	0	0	0	0	0	6.93	
<i>Fissurella picta</i>	0	0	0	0	0	0	6.58	0	0	0	0	6.58	
<i>Pareuthria plumbea</i>	0	0	0	0	0.08	11.1	0.78	5.06	0	0	0	17.02	
<i>Kerguelenella Lateralis</i>	0	11.75	9.46	3.42	0.49	0	34.33	15.5	13.88	2.54	0	91.37	
<i>Laevilittorina caliginosa</i>	0.06	0	0.03	0.04	0.12	0	0	1.4	1.46	0.57	1.09	4.77	
<i>Margarella violacea</i>	0	0	0	0.09	0	0	0	0	0	0	0	0.09	

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<i>Nacella deaurata</i>	0	5.28	35.06	98.69	96.78	0	0	0	0	0	0	235.81
<i>Nacella magellanica</i>	0	60.96	0	0	84.5	96.1	8.85	0	0	0	488.11	738.52
<i>Siphonaria lessoni</i>	0	0	0	0	0	0	10.35	0	0	0	0	10.35
<i>Anasterias antarctica</i>	0	0	0	1.7	9.86	0	0	0	0	0	0	11.56
<b>TOTAL</b>												<b>18126.1</b>

CABO NEGRO WINTER

ABUNDANCE	Sampling stations												TOTAL
	St1	St2	St3	St4	St5	St6	St7	St8	St9	St10	St11	St12	
Amphipoda Indet.	0	0	7.4	0	3.7	0	3.7	0	0	0	3.7	0	18.5
Polychaeta errantia Indet.	0	11.1	3.7	3.7	0	0	22.2	3.7	0	14.8	0	3.7	62.9
Polichaeta sedentaria Indet.	0	0	3.7	0	0	0	7.4	0	0	0	0	0	11.1
Oligochaeta Indet.	0	14.8	0	7.4	0	0	14.8	0	3.7	0	14.8	0	55.5
Nematoda Indet.	0	0	7.4	0	0	0	18.5	0	0	11.1	0	0	37
Anthozoa Indet.	0	0	0	0	0	0	0	0	0	3.7	0	0	3.7
<i>Halicarcinus planatus</i>	11.7	7.4	7.4	7.4	0	3.7	22.2	0	14.8	29.6	0	7.4	111.6
<i>Edotea magellanica</i>	0	0	0	18.5	14.8	3.7	0	7.4	0	3.7	3.7	29.6	81.4
<i>Exosphaeroma gigas</i>	0	0	0	3.7	11.1	0	0	0	0	133.3	0	3.7	151.8
<i>Mytilus chilensis</i>	404	0	59.2	225.9	896.3	133.3	66.7	22.2	29.6	118.5	151.8	318.5	2425.7
<i>Perumytilus purpuratus</i>	0	0	0	0	0	3.7	0	0	0	0	0	0	3.7
<i>Margarella violacea</i>	0	3.7	0	0	0	0	3.7	0	0	0	0	0	7.4
<i>Laevilittorina caliginosa</i>	0	0	0	0	22.2	0	0	0	0	0	0	0	22.2
<i>Nacella magellanica</i>	0	3.7	0	3.7	0	0	0	0	0	3.7	55.6	18.5	85.2
<i>Siphonaria lessoni</i>	0	0	0	0	3.7	0	0	0	0	7.4	0	0	11.1
<i>Pareuthria plumbea</i>	0	0	0	0	0	0	0	0	0	33.3	0	0	33.3
<i>Trophon geversianus</i>	0	0	0	0	0	0	0	0	0	7.4	0	0	7.4
<i>Kerguelenella lateralis</i>	0	0	0	0	0	0	0	3.7	0	0	0	0	3.7
<i>Anasterias antarctica</i>	0	0	0	0	0	0	0	0	3.7	7.4	0	0	11.1
<b>TOTAL</b>													<b>3144.3</b>

BAHIA POSESION WINTER

ABUNDANCE	Sampling stations														TOTAL
	st-8	st-9	st-10	st-11	st-12	st-13	st-14	st-15	st-16	st-17	st-18	st-19	st-20	st-21	
Amphipoda Indet.	0	0	0	0	0	4	4	0	0	4	0	4	4	4	24
<i>Edotea magellanica</i>	0	0	0	0	4	0	0	0	0	0	0	0	0	0	4
Polychaeta Indet.	0	0	0	7	7	7	26	0	0	11	0	4	19	974	1055
Oligochaeta Indet.	4	4	0	0	7	15	7	0	4	0	0	4	30	0	75
Nematoda Indet.	0	0	0	0	0	0	0	0	4	0	0	0	0	244	248
Actiniaria Indet.	0	0	0	0	4	0	0	0	4	0	4	0	0	0	12
<i>Mytilus chilensis</i>	0	0	0	159	141	178	11	0	0	104	122	459	4	207	1385
<i>Pareuthria plumbea</i>	0	4	0	0	0	0	0	0	0	0	0	0	0	0	4
<i>Nacella magellanica</i>	0	0	0	0	4	4	0	0	0	0	0	0	0	0	8
<i>Kerguelenella lateralis</i>	0	0	4	0	11	4	0	4	11	0	4	0	11	0	49
<i>Siphonaria lessoni</i>	0	0	11	0	4	0	0	11	4	0	4	4	4	0	42
<i>Trophon geversianus</i>	0	0	0	0	0	0	0	0	0	0	4	4	0	0	4
<i>Tonicia atrata</i>	0	4	0	0	0	0	0	0	0	0	0	0	0	0	4
<b>TOTAL</b>															<b>2914</b>



## TERMINAL CLARENCIA WINTER

ABUNDANCE	Sampling stations											TOTAL	
	st7	st8	st9	st10	st11	st12	st13	st14	st15	st16	st17		st18
Amphipoda Indet.	4	0	0	0	4	19	0	0	0	0	0	4	31
<i>Edotea magellanica</i>	0	4	0	0	4	0	0	0	0	0	0	0	8
<i>Exosphaeroma gigas</i>	0	0	0	0	11	4	0	0	0	0	4	0	19
<i>Halicarcinus planatus</i>	0	7	0	4	11	26	0	0	0	0	0	0	48
Polychaeta errantia Indet.	26	0	4	0	11	48	26	7	22	0	74	11	229
Polychaeta sedentaria Indet.	4	0	0	0	0	0	0	0	0	0	0	0	4
Oligochaeta Indet.	0	4	4	4	0	0	0	0	11	0	0	0	23
Nematoda Indet.	15	19	22	37	15	0	0	0	41	0	85	122	356
<i>Mytilus chilensis</i>	7	0	93	0	237	0	93	7	15	0	89	370	911
<i>Perumytilus purpuratus</i>	256	0	259	0	30	159	422	59	44	0	59	274	1562
<i>Gaimardia trapezina</i>	0	0	0	0	0	0	0	0	0	0	0	4	4
<i>Margarella violacea</i>	0	0	0	11	0	0	0	0	7	37	0	74	129
<i>Pareuthria plumbea</i>	0	0	0	4	11	0	0	0	0	0	0	0	15
<i>Pareuthria</i> sp.	4	0	0	0	7	7	0	4	0	0	4	7	33
<i>Trophon geversianus</i>	0	0	0	0	0	0	0	0	52	0	0	0	52
<i>Nacella deaurata</i>	0	0	0	26	22	0	0	0	0	0	0	0	48
<i>Nacella magellanica</i>	0	0	0	0	0	0	0	4	0	0	4	0	8
<i>Kerguelenella lateralis</i>	4	0	0	0	0	0	0	0	0	0	0	4	8
<i>Siphonaria lessoni</i>	133	0	100	0	0	0	0	19	0	0	0	0	252
<i>Photinula caerulea</i>	0	0	0	0	0	0	0	0	0	0	26	0	26
<i>Ischnochiton</i> sp.	0	100	0	0	0	0	0	0	0	0	0	0	100
Actiniaria Indet.	0	0	0	7	19	22	0	0	4	0	11	19	82
<i>Anasterias antarctica</i>	0	0	0	0	0	0	0	0	0	0	4	4	8
												<b>TOTAL</b>	<b>3956</b>

**PUBLICATION III**

**SOFT-BOTTOM MACROBENTHIC FAUNAL ASSOCIATIONS IN THE  
SOUTHERN CHILEAN GLACIAL FJORD COMPLEX**

**Carlos Ríos, Erika Mutschke, Américo Montiel, Dieter Gerdes & Wolf E. Arntz**

**SCIENTIA MARINA**

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 asteróideos (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.

\*Received April 26, 2004. Accepted July 11, 2005.

## 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; Włodarska-Kowalczyk *et al.*, 1998; Włodarska-Kowalczyk 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 Johansson, 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 gradi-

ent 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 hexamethylenetetramin.

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.

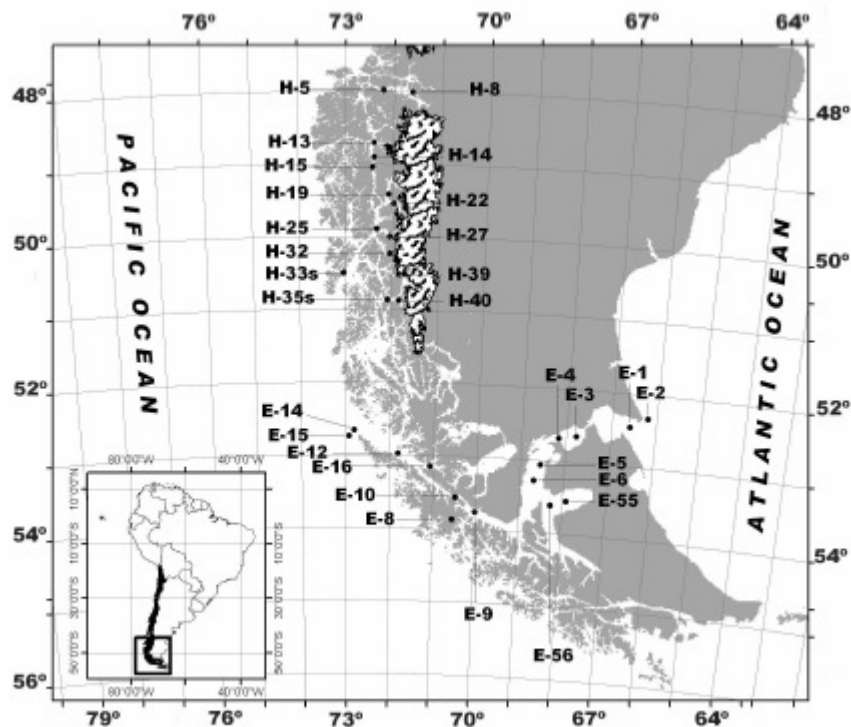


FIG. 1. – Map showing the Magellan region and the sampling sites in the South Patagonian Icefield (SPI) and Straits of Magellan (SM) areas.

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 (µg at/g)	N org (µg at/g)	P total (µg 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	Angostura 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 Xaltega	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 Panela, 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 (Cont.). – 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	H13H14	H15	H19	H22	H25	H27	H30H33	H35s	H39	H40	E1	E2	E3	E4	E5	E6	E5SE56	E8	E9	E10	E12	E14	E15E16	
<b>Gastropoda</b>																										
<i>Crepidula dilatata</i>	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
<i>Trochita pileolus</i>	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
<i>Trochita pileus</i>	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
<i>Adelomelon ancilla</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Berthella platei</i>	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
<i>Trophon geversianus</i>	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
<i>Pareuthria plumbea</i>	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
<i>Photinula caerulea</i>	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
<b>Bivalvia</b>																										
<i>Aulacomya ater</i>	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	3
<i>Lucinoma lamellata</i>	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
<i>Emucula grayi</i>	1	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
<i>Acesta patagonica</i>	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
<i>Camptonectus (P.) subhyalinus</i>	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
<i>Limopsis marionensis</i>	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	72	0	0	5	0	0	0	0	0
<i>Limopsis sp.</i>	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
<i>Cyclocardia velutina</i>	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	14	0	0	0	0
<i>Tindaria virens</i>	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
<i>Nucula sp.</i>	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
<i>Chlamys patagonica</i>	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0
<i>Yoldia cf. woodwardi</i>	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
<i>Yoldia eightsi</i>	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
<b>Scaphopoda</b>																										
<i>Dentalium majorinum</i>	0	0	0	0	1	0	0	0	5	0	0	0	0	0	0	0	0	0	12	0	10	0	0	0	0	1
<i>Dentalium cf. perceptum</i>	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
<b>Bryozoa</b>																										
<i>Reteporella magellensis</i>	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
<i>Nevanipora milneana</i>	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
<i>Hornera sp.</i>	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
<i>Microporella hyadesi</i>	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
<i>Rhabdopleura normani</i>	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
<i>Adeonella sp.</i>	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0
<i>Orthoporida petiolata</i>	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
<i>Aspidostoma giganteum</i>	0	0	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0	0	0	p	0	0	p	0	0
<i>Catadysis pygmaeum</i>	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
<i>Carbacea ovoidea</i>	0	0	0	0	0	0	0	0	0	0	0	0	p	p	p	p	p	p	p	p	p	p	p	p	p	p
<i>Hippodina adpressa</i>	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
<i>Cellaria mahinensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	p	p	0	0	p	0	0	0	0	0
<i>Heteroporella chilensis</i>	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
<i>Smittina lebruni</i>	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
<i>Ogivalia elegans</i>	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
<i>Arachnopusia monoceros</i>	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
<i>Fasciculipora meandrina</i>	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
<b>Articulata</b>																										
<i>Terebratella dorsata</i>	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
<i>Magellania venosa</i>	0	0	0	0	0	0	0	0	0	1	0	0	31	0	5	0	142	0	0	0	0	0	0	0	0	0
<b>Asteroida</b>																										
<i>Ctenodiscus procurator</i>	0	0	0	0	50	0	1	0	0	0	0	0	0	0	0	0	0	2	12	29	10	0	0	6	0	22
<i>Asterina fimbriata</i>	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
<i>Cheiraster (Luidia) planeta</i>	30	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
<i>Solaster regularis</i>	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
<i>Poraniopsis mira</i>	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
<i>Lophaster stellans</i>	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Doraster gawashgari</i>	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
<i>Cosmasterias lurida</i>	0	0	0	0	0	0	0	0	0	16	0	0	0	0	2	8	0	0	0	0	0	0	0	0	0	0
<i>Henricia obesa</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	4	0	0	0
<i>Henricia studeri</i>	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	
<i>Labidiaster radiosus</i>	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	
<i>Calyptaster tenuissimus</i>	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	
<i>Odontaster penicillatus</i>	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	
<i>Odontaster meridionalis</i>	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	
<i>Ceramaster patagonicus</i>	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	
<i>Hippasterias sp.</i>	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	
<i>Porania antarctica magellanica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5	0	0	3	
<i>Anasterias antarctica</i>	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	
<i>Anasterias sp.</i>	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	



TABLE 2 (Cont.). – 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	H13H14	H15	H19	H22	H25	H27	H32H33	H35	H39	H40	E1	E2	E3	E4	E5	E6	E55E56	E8	E9	E10	E12	E14	E15E16			
<b>Asteroidea</b>																												
<i>Gamaria falklandica</i>	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		
<i>Bathybiaster loripes</i>	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
<i>Poraniopsis echinaster</i>	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	
<i>Cycethra verrucosa</i>	0	0	0	0	18	0	0	0	0	0	0	0	0	2	0	1	10	0	0	0	0	0	0	4	0	0	0	
<i>Austrocidaris lorioli</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	
<i>Brisaster moseleyi</i>	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	
<b>Echinoidea</b>																												
<i>Tripylaster philippii</i>	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	
<i>Arbacia dufrénei</i>	0	0	1	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
<i>Pseudechinus magellanicus</i>	0	0	0	0	0	2	0	0	0	8	4	24	0	0	6	1	0	11	20	0	0	5	9	0	0	0	0	
<b>Ophiuroidea</b>																												
<i>Ophiura</i> INDET	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	
<i>Ophiacantha cf. pentactis</i>	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	
<i>Ophiactis</i> sp.	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	
<i>Ophiocten amitinum</i>	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	
<i>Ophiacantha vivipara</i>	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	
<i>Ophiuroglypha lymani</i>	13	0	7	0	0	3	0	0	0	8	0	0	0	0	0	0	0	55	0	0	4	65	0	0	0	0	0	
<i>Gorgonocephalus chilensis</i>	0	0	0	0	0	3	0	0	0	27	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Ophiomyxa vivipara</i>	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	
<i>Ophiactis asperula</i>	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	
<i>Astrotoma agassizii</i>	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	
<i>Homalophiura inornata</i>	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	0	
<i>Ophioscolex nutrix</i>	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	
<i>Homalophiura</i> 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	
<b>Holothuroidea</b>																												
<i>Hemotodema spectabilis</i>	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	
<i>Psolus patagonicus</i>	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	
<i>Pseudocnus leoninus</i>																												
<i>dubiosus</i>	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	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	34	0	12	0	2	0	0	0	0	
Holothuroidea sp 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	7	0	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 ( $R = 0.040$ ;  $p = 0.24$ ).



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
<i>Ctenodiscus procurator</i>	3.64	5.40	10.45	0.65	10.71	10.71
<i>Ophiurogrypha lymani</i>	2.21	8.27	7.33	0.57	7.52	18.23
<i>Magellania venosa</i>	0.07	11.87	6.51	0.39	6.68	24.91
<i>Pseudechinus magellanicus</i>	2.71	3.47	5.02	0.52	5.15	30.05
<i>Acanthoserolis schythei</i>	0.00	3.93	4.94	0.36	5.07	35.12
<i>Camptonectus (Pallioleum) subhyalinus</i>	13.64	0.00	4.54	0.27	4.65	39.77
<i>Dentalium majorinum</i>	0.43	1.53	3.40	0.42	3.49	43.26
<i>Limopsis marionensis</i>	0.21	5.13	3.19	0.36	3.27	46.53
<i>Psolus patagonicus</i>	0.00	5.40	3.16	0.26	3.24	49.77
<i>Holothuroidea sp 2</i>	0.00	3.20	3.05	0.36	3.13	52.90
<i>Cycethra verrucosa</i>	1.29	1.13	2.91	0.36	2.99	55.88
<i>Ophiactis sp.</i>	7.93	0.00	2.36	0.27	2.42	58.30
<i>Terebratella dorsata</i>	0.00	2.60	2.35	0.28	2.41	60.71
<i>Cheiraster (Luidiaster) planeta</i>	2.14	0.07	2.31	0.26	2.37	63.07
<i>Ophiactis asperula</i>	0.00	0.80	1.73	0.37	1.77	64.85
<i>Cosmasterias lurida</i>	1.14	0.67	1.65	0.31	1.70	66.54
<i>Leanira quarefagesi</i>	1.36	0.00	1.61	0.59	1.65	68.19
<i>Bathybaster loripes</i>	0.00	0.67	1.36	0.49	1.40	69.59
<i>Emmucula grayi</i>	0.64	0.40	1.29	0.28	1.32	70.91
<i>Eurypodius latreillei</i>	0.64	0.73	1.19	0.42	1.22	72.13
<i>Trypilaster philippi</i>	0.00	1.07	1.10	0.31	1.13	73.26
<i>Ophiocten namatinum</i>	0.93	0.00	1.08	0.25	1.11	74.37
<i>Gorgonocephalus chilensis</i>	2.14	0.07	1.04	0.39	1.06	75.43
<i>Polyeunoa laevis</i>	2.57	0.00	1.03	0.35	1.06	76.49
<i>Pista cristata</i>	0.57	0.00	0.86	0.25	0.88	77.37
<i>Maldane sarsi</i>	0.43	0.00	0.85	0.42	0.88	78.25
<i>Libidoclaea smithi</i>	0.36	0.13	0.79	0.29	0.81	79.06
<i>Crepidula dilatata</i>	0.00	0.40	0.76	0.24	0.78	79.84
<i>Ophiacantha cf. pentactis</i>	0.64	0.00	0.75	0.25	0.77	80.61
<i>Cyclocardia velutinus</i>	0.14	1.20	0.75	0.35	0.77	81.37
<i>Abyssoninoe abyssorum</i>	0.43	0.00	0.73	0.31	0.75	82.12
<i>Sternaspis scutata</i>	1.00	0.00	0.71	0.33	0.73	82.85
<i>Porania antarctica magellanica</i>	0.00	10.67	10.66	0.45	0.67	83.53
<i>Laneria falklandica</i>	0.00	0.33	0.64	0.24	0.66	84.18
<i>Ophiacantha vivipara</i>	1.29	0.00	0.62	0.37	0.63	84.81
<i>Berthella platei</i>	0.07	0.53	0.61	0.31	0.63	85.44
<i>Aulacomya ater</i>	0.00	0.40	0.60	0.34	0.61	86.06
<i>Arbacia dufresnei</i>	1.50	0.07	0.58	0.36	0.60	86.65
<i>Munida subrugosa</i>	0.21	0.13	0.55	0.41	0.57	87.22
<i>Campylonotus semistriatus</i>	0.00	0.87	0.52	0.34	0.54	87.75
<i>Calyptraster tenuissimus</i>	0.00	0.47	0.51	0.25	0.52	88.28
<i>Halicarcinus planatus</i>	0.00	0.27	0.51	0.24	0.52	88.80
<i>Harmothoe campoglacialis</i>	1.64	0.00	0.49	0.27	0.50	89.30
<i>Chlamys patagonicus</i>	1.21	0.27	0.46	0.34	0.48	89.77
<i>Homalophiura inornata</i>	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 pat-

tern, 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).

#### ACKNOWLEDGEMENTS

The following experts assisted in the identification of different taxa: Boris Sirenko (polyplacophora), Igor Smirnov (ophiuroids), Hugo Moyano (bryozoa), Christoph Held (isopods), Erika Mutschke (echinoderms) and Américo Montiel (polychaetes). The scientific cruises to obtain the benthic data analysed in this article (CIMAR-FIORDO III and VII) were organised and developed by the Comité Científico Nacional (CONA) on board the R/V "Vidal Gormaz". The support of the R/V "Vidal Gormaz" crew is greatly appreciated. Jorge Ramírez V. (Laboratorio de Hidrobiología, Instituto de la Patagonia, Universidad de Magallanes) was an important help during all the fieldwork and also in the laboratory, and we extend our gratitude for his effort. We thank the Universidad de Magallanes (Punta Arenas, Chile) and CONA for partial financial support.

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**PUBLICATION IV**

**BIODIVERSIDAD BENTÓNICA SUBLITORAL EN EL  
ESTRECHO DE MAGALLANES**

**Carlos Ríos, Erika Mutschke & Evelyn Morrison**

**REVISTA DE BIOLOGÍA MARINA Y OCEANOGRAFÍA**



## Biodiversidad bentónica sublitoral en el estrecho de Magallanes, Chile

Benthic sublitoral biodiversity in the Strait of Magellan, Chile

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**Resumen.** Se analiza la diversidad de especies de invertebrados bentónicos marinos, recolectados mediante draga McIntyre (muestreo cuantitativo), en seis periodos, en el sector sublitoral comprendido entre la Primera y Segunda Angostura del estrecho de Magallanes. Se identificaron 301 especies y categorías taxonómicas superiores. Los grupos dominantes en términos de riqueza de especies fueron Polychaeta, Crustacea y Gastropoda. Las especies numéricamente dominantes fueron *Astarte longirostris*, *Eurhomalea exalbida* y *Cyamocardium denticulatum* (bivalvos), *Trochita pileolus* (gastropodo), *Themiste* sp. (sipuncúlido), *Hemipodus simplex* y *Notocirrus lorum* (poliquetos), *Magellania venosa* (braquiópodo) y *Euvallentia darwini* (isópodo). Estas especies presentan una distribución geográfica presumiblemente restringida al cono sur de Sudamérica, extendiéndose tanto hacia sectores del océano Pacífico como del océano Atlántico. No han sido mencionadas para ningún sector al sur de los 55°S y son prácticamente inexistentes al norte de los 46°S. Los parámetros univariados que permiten analizar la biodiversidad presente en el área muestran una dominancia (*J*) intermedia por parte de pocas especies, con altos valores de diversidad según Shannon-Wiener. En el tiempo, estos valores muestran una clara tendencia a la fluctuación permitiendo definir un patrón preliminar de biodiversidad, con una clara separación de al menos tres grupos de valores. Estos resultados sugieren que la necesaria valoración cuantitativa de la diversidad debe contar no sólo con un referente espacial (e.g. área/superficie cubierta para su determinación) sino también con una escala temporal que permita definir rangos de valores probables de diversidad (i.e. muestreos en diferentes periodos).

Palabras clave: Bentos, Magallanes, subantártica, conservación

**Abstract.** Marine benthic invertebrates species diversity is analyzed. Samples were obtained using a McIntyre dredge (quantitative sampling), deployed during six periods in a sublitoral zone of the Strait of Magellan, between its First and Second Narrow. Three hundred and one species and major taxonomic categories were identified. Polychaeta, Crustacea and Gastropoda were the dominant groups in terms of species richness. *Astarte longirostris*, *Eurhomalea exalbida* and *Cyamocardium denticulatum* (bivalves), *Trochita pileolus* (gastropod), *Themiste* sp. (sipunculid), *Hemipodus simplex* and *Notocirrus lorum* (polychaetes), *Magellania venosa* (brachiopod) and *Euvallentia darwini* (isopod) were the numerical dominant species. All these species have a geographical distribution apparently restricted to the tip of Southern South America, with a distribution in both the Atlantic and Pacific Ocean. The species have not been reported south of the 55°S and north of the 46°S. Univariate parameters used to analyze the biodiversity of sampling sites, indicate an intermediate evenness (*J*) from few species, with high values of Shannon-Wiener diversity. Indices show a clear fluctuation trend through time, with a preliminary biodiversity pattern conformed by three value groups. The results suggest the necessity to obtain quantitative values of diversity not only considering spatial references (e.g., area considered for estimations), but also a temporal scale to define range of probable values of diversity (e.g. different sampling periods).

Key words: Benthos, Magallanes, Sub-Antarctic, conservation

### Introducción

La investigación sobre biodiversidad en ecosistemas marinos australes se ha visto incrementada notablemente en las décadas recientes, aunque los esfuerzos de investigación en los diferentes sectores australes no han sido uniformes (Arntz 1997; Arntz & Ríos 1999). La Antártica ha recibido una significativa

dedicación científica, la cual incluye investigación sobre aspectos biogeográficos, evolutivos (e.g. Hedgpeth 1969; Dayton 1990; Clarke 1990; Wägele 1991; Crame 1994; Arntz *et al.* 1997), sistemáticos, taxonómicos (e.g. Cairns 1982; Brandt 1991; Sieg 1992; López-González & Gili 2000, 2001) y ecológicos (e.g. Gutt & Starmans 1998; Gili *et al.* 1999; Lörz 2000; Gray 2001a). En la



región de Magallanes ha habido un incremento importante de la investigación a partir del crucero científico del RV "Victor Hensen", desarrollado en 1994 (Arntz & Gorny 1996; Mazzocchi *et al.* 1995; Arntz & Ríos 1999; Thajje & Mutschke 1999; Ríos & Mutschke 1999; Montiel *et al.* 2002) y, más recientemente, el Campo Patagónico de Hielo Sur ha sido incorporado a esta línea de investigación (Mutschke *et al.* 1996; Hromic 2001). En estas dos últimas áreas aún existen notorias faltas de conocimientos básicos, entre los cuales se incluyen estudios taxonómicos principalmente de invertebrados marinos (Mutschke *et al.* 1998).

Dentro de la región austral del cono sur de Sudamérica, el estrecho de Magallanes tiene la particularidad de estar constituido por masas de agua provenientes de tres océanos: el Pacífico, el Atlántico y el Mar del Sur (Panella *et al.* 1991; Antezana 1999). Por tal razón, éste ofrece singularidades interesantes para el estudio de la biodiversidad, en cualquiera de las escalas de riqueza de especies comúnmente utilizadas (*e.g.* Gray 2001b). La generación de esta información básica es fundamental para definir aspectos relacionados con la conservación de la naturaleza (Simonetti 1995; Gray 1997; Lancellotti & Vásquez 2000), para contribuir a los análisis biogeográficos y ecológicos (Gray 2000, 2001a; Fernández *et al.* 2000), o como elemento para determinar cuán negativa puede ser la eventual pérdida de biodiversidad para el funcionamiento del ecosistema (Purvis & Hector 2000).

El objetivo general de este trabajo es presentar la primera evaluación cuantitativa de la diversidad (riqueza de especies o diversidad, de un cierto número de unidades de muestreo tomadas desde un área definida, *sensu* Gray 2001a) para un sector sublitoral del estrecho de Magallanes localizado hacia su entrada oriental (*i.e.* atlántica). Las características oceanográficas, particularmente aquellas relacionadas con las corrientes oceánicas y sistemas de mareas predominantes en el área, generan un ambiente abiótico de alta inestabilidad, con una permanente modificación en la estructura de los sedimentos. En consecuencia, en estos sectores sublitorales, es esperable una baja diversidad biológica, producto de un número relativamente reducido de especies y cuyas abundancias también se esperan deprimidas. Adicionalmente, se esperan fluctuaciones poblacionales, en número y en biomasa, dentro de rangos más bien estrechos y que podrían reflejar una cierta constancia a lo largo del tiempo en términos de distribución y abundancia. Los objetivos específicos del estudio fueron: a) definir la

macrofauna bentónica característica del área en términos de parámetros univariados asociados a la diversidad, b) analizar la variabilidad temporal de los parámetros cuantitativos utilizados como indicadores de biodiversidad, y c) contribuir al entendimiento de las interacciones bióticas dentro de la región de Magallanes y entre ésta y sectores del Atlántico, Pacífico y Antártica, como parte de posibles gradientes latitudinales. El trabajo es parte de un programa más amplio que considera el análisis de la distribución y abundancia de grupos selectos de invertebrados marinos en el área subantártica del cono sur de Sudamérica.

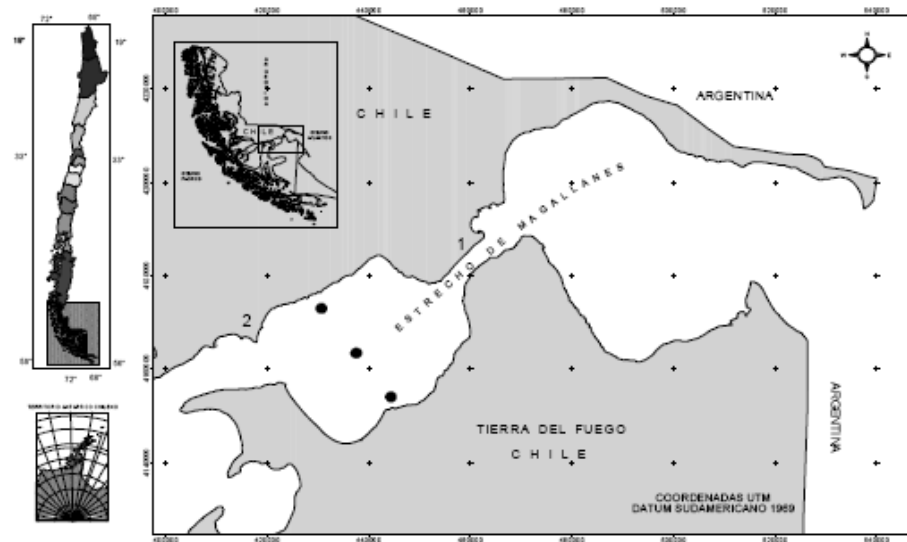
## Materiales y Métodos

### Área de estudio

Según Guglielmo & Ianora (1995), el área de estudio se encuentra localizada en el sector denominado Entrada Somera Oriental del estrecho de Magallanes, la cual se extiende desde Punta Pelicano hasta Punta Dungeness (Fig. 1). El área de estudio presenta profundidades que varían entre 30-50 m. Las aguas del sector parecen originarse a partir de la mezcla de la capa superficial de las aguas intermedias del Atlántico provenientes del sur, con aguas más diluidas en términos de salinidad y de origen continental. Estas son verticalmente homogéneas como resultado de la mezcla significativa originada por las fuertes corrientes mareales presentes en el área. Durante el período de estudio la salinidad superficial varió entre 30,6 - 31,1 ppm, mientras que la temperatura superficial del agua de mar varió entre 6°C - 7°C.

La característica hidrodinámica más relevante del área son las fuertes corrientes mareales que se originan a partir de las olas de mareas semi-diurnas del océano Atlántico. El régimen mareal del estrecho es macromareal, derivado de la amplificación de olas a lo largo de la amplia plataforma continental del Atlántico, con rangos de mareas promedio y de primavera que varían entre 7,8 - 9,5 m y entre 1,2 - 1,8 m en la Primera y Segunda Angostura, respectivamente. La velocidad de la corriente superficial varía entre 4,5 m/s en la Primera Angostura y 3 m/s en la Segunda, con una reducción a menos de la mitad de estos valores en las velocidades de la corriente de fondo debido a la fricción (Medeiros & Kierfve 1988).

Las fuertes corrientes, en conjunto con las profundidades someras existentes, resultan en niveles energéticos medios y altos con transporte de gravas y arenas, zonas de erosión y un sustrato con predominancia de gravas, gravas arenosas y arenas gravosas (Brambati *et al.* 1991).



**Figura 1**

Localización de las áreas de estudio en el sector oriental del estrecho de Magallanes, Chile. 1 y 2 representan las posiciones de la Primera y Segunda Angostura, respectivamente. Los círculos indican las ubicaciones de las tres estaciones de muestreo  
 Location of the studied stations in the eastern sector of the Strait of Magellan, Chile. 1 and 2 correspond to the Primera and Segunda Angostura, respectively. Dots show locations of the three sampling areas

### Metodología de trabajo

Los muestreos fueron realizados entre mayo de 1999 y febrero de 2001, completándose seis periodos de muestreo.

En el área de estudio se determinaron 3 sectores de muestreo, representativos de la parte central del área entre las dos angosturas del estrecho, otro hacia el borde de Tierra del Fuego y un tercero asociado al margen continental (Fig. 1). Esta división arbitraria del sector se basa en: a) el interés por determinar y analizar la biodiversidad de un área particular más que de una comunidad biológica determinada y b) por restricciones logísticas impuestas por la naturaleza del sector a estudiar. Dentro de cada uno de estos sectores se recolectaron al azar 15 muestras, para totalizar 45 muestras por período de muestreo para el área en su

conjunto. Las muestras de sedimentos fueron tomadas con una draga McIntyre de mordida = 0,1 m<sup>2</sup>, lanzada desde una embarcación con propulsión propia. Los sedimentos obtenidos fueron utilizados en su totalidad para la separación de la fracción macrofaunística presente en cada muestra. Esta se realizó en el Laboratorio de Hidrobiología del Instituto de la Patagonia, tamizando cada una de las muestra a través de un tamiz con abertura de malla de 0,5 mm. Cada muestra tamizada fue separada y analizada manualmente bajo una lupa binocular de amplificación 10X, para posteriormente realizar el proceso de identificación hasta el nivel taxonómico más bajo posible, además de la contabilización y determinación del peso de los ejemplares de cada especie o taxon superior identificado. Para las identificaciones taxonómicas principales se utilizaron como referencia los siguientes trabajos: para equinodermos, Bemasconi

(1969), Bernasconi & D'Agostino (1971, 1977); para moluscos, Castellanos (1988-93); para poliquetos, Rozbaczylo (1985); para crustáceos, Menzies (1962), Retamal (1974), para peces, Norman (1937).

### Análisis de las muestras

La determinación de la biodiversidad ha generado una importante diversidad de criterios tanto conceptuales como metodológicos (véase Gray 2000 para una discusión del tema) y, de acuerdo con el propósito del presente trabajo, se ha considerado la valoración de la riqueza de especies o diversidad de un cierto número de unidades de muestreo tomadas desde un área definida, *sensu* Gray (2001a), equivalente a la "diversidad alfa" planteada por Whittaker (1972).

Para la determinación de índices ecológicos univariados sólo se consideraron aquellos taxa sobre los cuales se tenía una importante presunción de estar representando un sólo tipo de especie. Esto es válido desde la categoría de especie hasta otras categorías superiores (e.g. Actiniaria INDET 1, Amphipoda INDET 1; Ascidiacea INDET 1). En consecuencia, no fueron considerados en los análisis aquellas unidades que pudiesen estar representando más de una especie después de un análisis taxonómico más detallado (e.g. Sipunculidea INDET). El conjunto matricial de datos así establecido (filas o especies  $n = 295$ ; fechas de muestreo o columnas  $n = 6$ ) fue analizado siguiendo las rutinas del programa computacional PRIMER (Clarke & Warwick 1994; Clarke & Gorley 2001). Se realizó además, un procedimiento de cálculo considerando la sumatoria de todas las abundancias por período de muestreo en conjunto con la inclusión de todas las especies, categoría que en los resultados se han considerado como representativa del total para el área.

En particular, se efectuaron los siguientes cálculos utilizándose el menú DIVERSE de PRIMER:

- Índice de diversidad según Shannon-Wiener:  $H' = -\sum p_i (\log p_i)$ , en donde  $p_i$  es la proporción del número total de individuos que aparece representada en la especie  $i$ . Para los cálculos correspondientes se utilizó logaritmo en base 2. El índice permite obtener un indicador ( $H'$ ) de la relación entre el número de especies en cada período de muestreo y sus respectivas abundancias numéricas, reflejando el grado de incerteza (en términos de información) dentro de la comunidad (Magurran 1991).
- Índice de Margalef para la riqueza de especies:  $d = (S-1)/\log N$ , en donde  $N$  es el número total de individuos y  $S$  el número de especies. El índice representa la riqueza de especies en un sentido

clásico pero en función del número total de individuos por período de muestreo.

- Equitabilidad según el índice de uniformidad de Pielou:  $J = H'_{(observado)}/H'_{(máx)}$  en donde  $H'_{(máx)}$  es la diversidad máxima posible que se podría obtener si todas las especies fueran igualmente abundantes. El índice representa la uniformidad (equitabilidad) en la distribución numérica entre las diferentes especies del conjunto estudiado en cada período de muestreo.

Finalmente, los parámetros univariados fueron representados de manera multivariada o bi-dimensional utilizando el criterio de ordenación de muestras (en este caso, períodos de muestreo) según el método de escalamiento multidimensional (MDS) (Field *et al.* 1982). Esta ordenación se basó en una transformación previa de los datos de abundancia por especies o taxa superiores (raíz cuarta) y cálculo de una matriz de similitud utilizando el índice de Bray-Curtis (1957)

## Resultados

### Características generales del ensamble bentónico

En total se identificaron 301 especies y taxa superiores las cuales se distribuyeron en un total de 6.611 individuos recolectados para los seis períodos de muestreo, los cuales presentaron importantes variaciones entre un muestreo y otro en función de su presencia/ausencia (Tabla 1).

En términos de riqueza de especies, la mayoría de los taxa recolectados tuvieron una representación inferior al 5% respecto del número total de taxa identificados durante todo el período de muestreo.

El grupo taxonómico más diverso correspondió a Polychaeta (119 especies), representando prácticamente más del tercio de todas las especies o taxa superiores recolectados en el área de estudio a través del tiempo (Fig. 2). Particularmente importante fue la familia Polynoidea (16 especies). Los poliquetos fueron dominantes en términos de número de especies en prácticamente todos los muestreos, exceptuando el correspondiente a junio de 1999.

Otros grupos relevantes fueron Crustacea (68 especies), particularmente el grupo de los anfípodos con 30 especies y Gastropoda (44 especies), con las familias Trochidae y Buccinidae como dominantes, ambas con 8 especies. Un grupo ocasionalmente dominante fue Bivalvia, no superando el 7% respecto del total de taxa identificados. La familia más diversa fue Philobryidae, aunque con bajas abundancias.

Tabla 1

Lista de los taxa macrofaunísticos bentónicos y sus correspondientes abundancias numéricas, recolectados entre la Primera y Segunda Angostura del estrecho de Magallanes, Chile, en seis periodos de muestreo (A-F). T = Total. Los grupos coloniales fueron considerados como Presentes (Pte.). A=01/05/99; B=01-06/06/99; C=23-26/10/99; D=27-30/03/00; E= 08/07/00; F= 21/02/01

Taxonomic list and abundance of macrobenthic organisms sampled between the First and Second Narrow, Strait of Magellan, Chile, in six sampling periods (A-F). T= total. Colonial taxa were considered as Present (Pte.). A=01/05/99; B=01-06/06/99; C=23-26/10/99; D=27-30/03/00; E=08/07/00; F= 21/02/01

Taxa	Fechas de muestreo							Taxa	Fechas de muestreo							
	A	B	C	D	E	F	T		A	B	C	D	E	F	T	
<b>FORIFERA</b>																
INDET	Pte.	Pte.	Pte.	Pte.	Pte.	Pte.	Pte.	<i>Ecoglossus</i> INDET								
								<i>Longicollis</i> sp.				4	1	4		
<b>Cnidaria</b>								<i>Trypanocylla</i> sp.				59	6	65		
INDET	1						1	<i>Typoclype</i> sp.	1	1		3	16	21		
								<i>Nereididae</i> INDET	11	1		10		22		
<b>HYDROZOA</b>								<i>Eusertis patagonica</i>	(Molnosh) 1885			39	8	47		
INDET	Pte.	Pte.	Pte.	Pte.	Pte.	Pte.	Pte.	<i>Gyrocampa karimatachoudhri</i>	Petitot, 1970			3		3		
								<i>Nereis bergselenzi</i>	(Molnosh) 1885	1	9	7	14	2	33	
<b>ANTHOZOA</b>								<i>Nereis pelagicus</i>	Ehlers, 1901				11	1	5	
Acinaria INDET 1				1			1	<i>Nereis argentea</i>	(Kirberg) 1866	11	29	25	21	86		
Acinaria INDET 2				3			3	<i>Nereis pelagicus foveolata</i>	Linnæus, 1758			3		3		
Acinaria INDET 3				2			2	<i>Nereis</i> sp.			3			3		
Acinaria INDET	5	4		3	2		14	<i>Nereis</i> sp.				1		1		
Octocornis INDET	Pte.							<i>Platynereis aculeata</i>	(Schmarda) 1861				1	1	2	
INDET		3					3	<i>Nephtys</i> INDET			1			1		
								<i>Aglyptophanes</i> of <i>virgata</i>		2	1			1	4	
<b>PLATHYELMINTHES</b>								<i>Aglyptophanes macronus</i>	(Schmarda) 1861	10	3	33	15	16	77	
<b>TURBELLARIA</b>								<i>Aglyptophanes</i> sp.		14	12	17		4	1	48
INDET				2	1		3	<i>Nephtys</i> sp.		1	3	1			5	
								<i>Spisaeodonta</i> sp.				1			1	
<b>NEMERTINI</b>								<i>Glycera capitata</i>	Cersted, 1843	6	2		25	7	40	
INDET 1				49			49	<i>Glycera</i> sp.						10	10	
INDET 2				2			2	<i>Hemipodius simplex</i>	(Grube) 1857	1	7	105	23	17	153	
INDET 3				2			2	<i>Hemipodius</i> of <i>simplex</i>				5	1	6		
INDET	2	2	7		25	4	40	<i>Hemipodius</i> sp.			7	2		9		
								<i>Glycide armata</i>	F. Müller, 1858	4	4	2			11	
<b>NEMATODA</b>								<i>Goniada fulvicornis</i>	Frost, 1901	3	1		4		8	
INDET		3	19	11	1		34	<i>Goniada</i> of <i>fulvicornis</i>				2		2		
								<i>Ophiolepta eresia</i>	(Ehlers) 1900	5	6	6	9	1	4	31
<b>SPUNCULA</b>								<i>Omphalodes</i> INDET			1				2	
<b>SPUNCULIDEA</b>								<i>Kirbergophanes dorsalis</i>	(Ehlers) 1897	9	4	9	1		23	
<i>Thalassia</i> sp.	26	66	60	148	99		451	<i>Nelusetta</i> sp.					5	5		
INDET	6	1	2		1		10	<i>Lumbrineris</i> of <i>magallanensis</i>				1		1		
								<i>Lumbrineris</i> of <i>tetraxera</i>		1				1		
<b>ECHINURA</b>								<i>Lumbrineris</i> sp.			1	2		1	4	
<b>ECHINURIDEA</b>								<i>Arabella</i> INDET			2		1		3	
INDET				1			1	<i>Arabella tricolor caerulea</i>	(Schmarda) 1861			38	41	6	85	
<b>FRUAPULIDA</b>								<i>Arabella</i> sp.							1	
INDET	1			3			4	<i>Nitocirrus lanus</i>	Ehlers, 1897	79	44	87	18		228	
								<i>Doevillidae</i> INDET					2	2		
<b>ANNELIDA</b>								<i>Nannosyllis dendritica chilensis</i>	Carrasco, 1977	7		26	6	6	45	
<b>POLYCHAETA</b>								<i>Phylo fide heterostoma</i>	Hartmann-Schubler, 1965			1		1	2	
<i>Polynoides</i> INDET			1	12	1		14	<i>Aricidea</i> sp.					7	7		
<i>Halosydna</i> sp.	1						1	<i>Spioptanes</i> of <i>hombyx</i>	(Claperede) 1870			5	1	6		
<i>Harmothoe</i> of <i>crassifera</i>				1			1	<i>Spioptanes</i> sp.						1	1	
<i>Harmothoe</i> of <i>optona</i>	Kirberg, 1855			12	63		75	<i>Polydora</i> sp.				5	1	6		
<i>Harmothoe</i> of <i>spinosa</i>				1	2		1	<i>Chaetopteriidae</i> INDET			1			2		
<i>Harmothoe</i> sp.		1					1	<i>Cirratulidae</i> INDET						1	1	
<i>Harmothoe</i> sp. 1				55	21		77	<i>Caulerillia alata</i>	(Southern) 1914			2		2		
<i>Harmothoe</i> sp. 2				1	3		5	<i>Caulerillia</i> of <i>alata</i>						3	3	
<i>Harmothoe</i> sp. 3							1	<i>Caulerillia</i> sp.						6	6	
<i>Harmothoidea</i> INDET 1				69			69	<i>Cirryformis</i> sp.				2		2		
<i>Harmothoidea</i> INDET 2				2			2	<i>Tharyx</i> sp.				9	3	1	13	
<i>Harmothoidea</i> INDET 3				7			7	<i>Cocconeis</i> sp.						1	1	
<i>Harmothoidea</i> INDET		15	3	1			22	<i>Flabelligeridae</i> INDET			14	1			16	
<i>Hermadion magallanense</i>	Kirberg, 1855				11		11	<i>Braida</i> sp.				3		3		
<i>Hermadion</i> sp.					1		1	<i>Flabelligera</i> of <i>indata</i>	Ehlers, 1897				4	6	10	
<i>Phaloe</i> sp.				4			4	<i>Pharus</i> sp.				1		1		
<i>Phyllodoce</i> INDET				6	2		8	<i>Scalibergemutidae</i> INDET				1		1		
<i>Anatidea</i> sp.							1	<i>Ophelidae</i> INDET				1		1		
<i>Eteone sculpta</i>	Ehlers, 1897	3	1	1	31		20	<i>Eteone</i> ( <i>Thoracophelia</i> ) <i>furcyferus</i>	Ehlers, 1897				1		1	
<i>Eteone</i> sp.				1			1	<i>Ophelina delapitana</i>	(Kirberg) 1866			1		1		
<i>Eteone</i> of <i>magallanensis</i>				2			2	<i>Ophelina</i> sp.				1		1		
<i>Hesione</i> INDET				45	25		70	<i>Ophelina</i> of <i>pyrogopyge</i>	(Ehlers) 1901			3	6	9		
<i>Dalmanella</i> sp.		1					1	<i>Travisis bergselenzi</i>	Molnosh, 1885					1	1	
<i>Filicidae</i> INDET					1		1	<i>Travisis</i> sp.			2	3	2	2	9	
<i>Syllidae</i> INDET				2	2		6	<i>Capitellidae</i> INDET				3	1		4	
<i>Eteone</i> sp.					1		1	<i>Mediomastus</i> sp.						1	1	
<i>Exogone</i> sp.				8			8	<i>Notomastus lateralis</i>	Sous, 1851			7	6	1	14	

Taxa		Fechas de muestreo						
		A	B	C	D	E	F	T
Maldanidae INDET		8	3	21	15	5	52	
Eudymene grossa	(Beard) 1871	4	2				6	
Idanthyrax armatus	Kinberg, 1867	2	2	6	11	4	25	
Lygdaea sp.						1	1	
Phragmatopoma moerchi	Kinberg, 1867					1	1	
Phragmatopoma virgini	Kinberg, 1867					2	2	
Phragmatopoma sp.					8		8	
Ampharetidae INDET		29	5	2		4	25	65
Ampharetidae INDET 1					3			3
Ampharetidae INDET 2					2			2
Amphicteis sp.			11					11
Melita cf. cristata					1			1
Seseridae glaudiverte	Hartmann-Schröder, 1965				28			28
Seseridae sp.					61	8		69
Terobellidae INDET		1	4	1	11	5		22
Amphitrite kerguelensis	McIntosh, 1876	2						2
Pista sp.			17					18
Polycirrus sp.			1		4			5
Thalopus sp.		3						3
Sabellidae INDET		5	2		2			9
Perkiniana sp.					65	22	2	89

## MOLLUSCA

## POLYPLACOPHORA

Leptoplaxa callerati	Reichena, 1899				1		1	
Leptochiton kerguelensis	(Heriksen, 1886)			72				72
Leptochiton medusae	(Pilsbry, 1899)	1		12	50	1		64
Calliochiton botwelli	(Thiele, 1906)					2		2
Calliochiton punctatus	(Gould, 1846)			5	3			8
Calliochiton stevensi	(Pfeffer, 1886)				1			1
Platychiton aurata aurata	(Spalowsky, 1795)			1				1
Tonnicia atrata	(Sowerby, 1840)				1			1
Tonnicia chilensis	(Framley, 1828)				1			1
Tonnicia lebruni	(Reichena, 1884)				4			4

## GASTROPODA

Nacella (Pattinsonia) deaurata deaurata	(Gmelin, 1791)			2				2
Isithia coppingeri	(Smith, 1881)		2	20	8	8		38
Pantodonella sp.				1				1
Calliostoma rostratum	Strobel, 1905	1						1
Calliostoma madam	(Philippi, 1845)			3				3
Margarita violacea	(King & Broderip, 1831)		2	12	9	3		26
Margarita sp.				1				1
Phormisula taeniata	(Wood, 1825)	2				5		8
Phormisula caerulea	(King & Broderip, 1831)	1	1		3	3	4	12
Phormisula rosulifera	Smith, 1905	5	2	1	2			10
Homalopus caespitosus	(Smith, 1881)	2	17	4	4			27
Azascorbicium pulchrum	(Philippi, 1845)	5						5
Trochus (Fragmatrochus) pallidus	(Broderip, 1832)	5	1	5	3	4		18
Eatonella argenteonere	Castell & Fernández, 1972			1				1
Eatonella sp.					1			1
Trochita pilosus	(Orbigny, 1845)			18	62	28	21	129
Trochita pilosus	(Lamarck, 1822)	7	35	6	6	9	9	72
Balanus carolinensis	Dall, 1900			2			1	3
Natica fallaxoides	Freston, 1913			1				1
Natica imperata	Philippi, 1845		1	6	2			9
Natica tuberculata	D'Orbigny, 1840		2	2				4
Aforia sp.		1					1	2
Agladilla foveolata	(Smith, 1888)			7				7
Cerodilla eliana	(Dall, 1919)						1	1
Mangrovea michaelis	(Strobel, 1905)	1	3					4
Luvellia sp.			1	2				3
Anomacme smithi	(Strobel, 1905)			1				1
Saxidomus aerolatus	Strobel, 1905			1				1
Trombia sp.1						1		1
Pareuthria juncei	Strobel, 1905	2	1					2
Pareuthria michaelis	(Strobel, 1905)		1		5	2		8
Pareuthria powelli	Cernohorsky, 1977	14	1					15
Pareuthria ringei	(Strobel, 1905)	7	1	9	7	3	11	38
Adelostoma anella	(Lightfoot, 1786)		1					1
Admete magellanica	Strobel, 1905	3	1	2	6			12
Tarbovella serrata	Castellana, 1982			1				1
Tarbovella smithi	Pfeffer, 1906			1				1
Acteon cf. hylaeus					1			1

## BIVALVIA

Pholobrya brachytroni	Soot-Ryen, 1959					1		1
Pholobrya crispata	Lima, 2000					2		2

Taxa		Fechas de muestreo						
		A	B	C	D	E	F	T
Pholobrya mblarevi	Pelamzer, 1908				1			1
Pholobrya sp.						5		5
Atalapha ater ater	(Molina, 1782)	1			1	1		3
Mytilus chilensis	Lamarck, 1819				4			4
Brachiodonta (Homomya) Navicularis	(Melville & Stauden, 1914)					1		1
Limacina pygmaea	(Philippi, 1845)		1			4		5
Chlamys patagonica	(King & Broderip, 1831)		3	3	1	1		8
Kella magellanica	Smith, 1881					1		1
Pseudokella cardiformis	(Smith, 1885)		1					1
Mytilus sp.						2		2
Cyathocardium denticalatum	E.A. Smith, 1907	6		9				204
Antaris longirostris	D'Orbigny, 1846	24	18	47	118	35	16	258
Neslepton concentricum	Dall, 1964					2		2
Mytilus edulis	(King & Broderip, 1832)		8					8
Eurhombula exaltata	(Chemnitz, 1795)	1	4	726	197			928
Hiatella solida	(Sowerby, 1834)			2				2
Entoloma elongata	Soot-Ryen, 1957			1				1
Parafora patagonica	Dall, 1886					2		2
Crepidula patagonica	(E.A. Smith, 1885)				1			1

## ARTHROPODA

## CRUSTACEA

Taxa		Fechas de muestreo			
		Pta	Pta	Pta	Pta
Cirripedia INDET					
Notochthamalus subrostratus	(Darwin, 1854)				
Ampeliscidae INDET		3			
Desmoiniidae INDET 1			10	3	2
Desmoiniidae INDET 2			1	3	
Desmoiniidae INDET 3			6		
Elasmopus sp.		1	10	2	3
Janus sp.			3		
Lysianassidae INDET		9	6	5	10
Phococopeidae INDET		1	3	15	8
Platyscoloplos INDET		1	1	38	16
Eudaeopopop gracilipes	(Schellenberg, 1931)			6	6
Hyperidae INDET				3	
Edwardsia sp.		1			
Amphipoda INDET 1		2	5	1	34
Amphipoda INDET 2			1	5	5
Amphipoda INDET 3		3	27	40	2
Amphipoda INDET 4		1	23	1	26
Amphipoda INDET 5		1	15	32	3
Amphipoda INDET 6		3	102	2	4
Amphipoda INDET 7		4	1	13	6
Amphipoda INDET 8		1	37	9	4
Amphipoda INDET 9		2	8	2	1
Amphipoda INDET 10		11	1	53	4
Amphipoda INDET 11		1	1	3	1
Amphipoda INDET 12		1	6	7	14
Amphipoda INDET 13			1	3	4
Amphipoda INDET 14			14	7	21
Amphipoda INDET 15			14	4	18
Amphipoda INDET 16			12	11	23
Amphipoda INDET 17			7	1	8
Amphipoda INDET 18			19		19
Amphipoda INDET 19			1		1
Aega magnifica	Dana, 1852		1		
Aega sp.				1	
Cyrtolana albivittata	Vanhöffen, 1914	2	1		
Cyrtolana chilensis	Menzies, 1942				1
Squilla (Squilla) paradosa	Fabricius, 1933			1	1
Squilla cf. gaudichaudi				1	1
Squilla sp.		2	1	5	1
Jaegeropsis cf. halesi				3	3
Jaegeropsis chilensis	(Bovallius, 1886)		1	15	12
Jaegeropsis sp.				1	1
Jaegeropsis acuticauda	Menzies, 1948			1	1
Jaegeropsis laevis	Menzies, 1942			17	5
Jaegeropsis sp.			1	2	
Antarctiana americana	Balch, 1886	1	2	2	2
Antarctiana sp.				2	2
Neastacilla magellanica	(China) 1901		1	16	9
Neastacilla sp.				2	4
Edotea dalii	Menzies, 1942		1	1	1
Edotea cf. shufi			1		1
Edotea cf. tuberculata			2		2
Edotea magellanica	Cummingham, 1871	1	1	1	3
Edotea sp.				1	1
Edotea transversa	Menzies, 1942			1	1
Macrochirodites stebbingi	China, 1901	1		1	2

Taxa	Fecha de muestreo	Fechas de muestreo						T	Taxa	Fecha de muestreo	Fechas de muestreo						T			
		A	B	C	D	E	F				A	B	C	D	E	F				
<i>Eoropharona lanceolata</i>	(White, 1847)	1			2	2	5													
<i>Eoropharona stahleri</i>	(Van Hoffe, 1914)				1	3	4													
<i>Dynamenella acutirostris</i>	Menzies, 1942				6		6													
<i>Dynamenella eatoni</i>	(Miers, 1875)	1	1	5			7													
<i>Euvallentula darwini</i>	(Cunningham, 1871)	3	9	13	51	24	119													
<i>Paniphaea acutifrons</i>	Bate, 1888				2		2													
<i>Paniphaea granulosa</i>	(Jacquinot, 1847)				1		1	2												
<i>Pagurus ocellatus</i>	White, 1847	1	14	10	2	2	5	34												
<i>Morida subrugosa</i>	Henderson, 1847				6		6													
<i>Haliscarcinus planatus</i>	(Fabricius, 1775)	3	1	4	8	7	23													
<i>Peltarion spinulosum</i>	(White, 1843)	5	3	8	4	3	8	31												
Cumacea INDET			9		63	3	1	76												
Tanaidacea INDET					16	2	18													
<b>HYCNOGONIDA</b>																				
INDET					1	1	2	4												
<b>ECHINODERMATA</b>																				
<b>ASTEROIDEA</b>																				
<i>Comasterias larida</i>	(Philippi, 1858)	2		2	3		1	8												
<i>Odontaster penicillatus</i>	(Philippi, 1870)					1	1													
<i>Porianopsis echinaster</i>	Ferrier, 1891	3	1			3	7													
<i>Anasterias antarctica</i>	(Latham, 1856)				2		2													
<b>OPHEUROIDEA</b>																				
<i>Gorgonocephalus chilensis</i>	(Philippi, 1858)					1	1													
<i>Ophiocystis asperula</i>	(Philippi, 1858)	13	48	24	8	4	97													
<i>Ophioglypta vivipara</i>	Studer, 1876				2		2													
<b>ECHINOIDEA</b>																				
<i>Pandolites magellanicus</i>	(Philippi, 1857)				4	1	4	4	2	15										
<i>Trypanaster philippi</i>	(Ormy, 1851)	1	1				2													
<b>HOLOTHUROIDEA</b>																				
<i>Psolus patagonicus</i>	Eckman, 1925					3	3													
<i>Athyridium chilensis</i>	(Semper, 1860)	25	7	19	21	11	8	91												
<i>Pandolites dubionis leonatus</i>	(Semper, 1868)	25	8	15	5	2	1	56												
<b>HEMICHORDATA</b>																				
<b>ASCIDIACEA</b>																				
<i>Molgula pyroformis</i>	Hertmann, 1881					1	1													
INDET 1						1	2	2	5											
INDET 2						4	1	5												
INDET		6	4					2	12											
<b>BRACHIOPODA</b>																				
<b>ARTICULATA</b>																				
<i>Terebratulid dorsata</i>	(Ormelin, 1791)			1	2		1	4												
<i>Magellanella venosa</i>	(Solander, 1786)	3	3	18	175	15	11	225												
<b>BRUZOZA</b>																				
INDET		Pta.	Pta.	Pta.	Pta.	Pta.	Pta.													
<b>CHORDATA</b>																				
<b>OSTEICHTHYES</b>																				
<i>Congostipia peruviana</i>	Ouvier & Valenciennes, 1829							1	1											
<i>Nototremis elegans</i>	Günther, 1860							2	2											
<b>TOTAL</b>			465	546	585	3129	1300	586	6611											

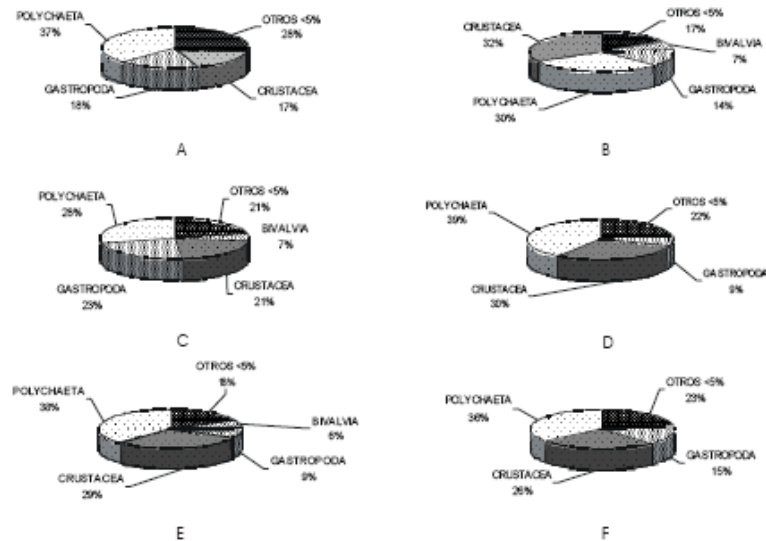


Figura 2

Representación porcentual del número de especies por categorías taxonómicas superiores. La categoría "otros" incluye a todos los grupos cuyas representaciones en función del total de especies identificadas fueron inferior al 5%. A-F=periodos de muestreo

Species number percentage by superior taxonomical categories. "Others" category includes all the groups which representation, with respect to the total of the identified species, was less than 5%. A-F = sampling periods

Tabla 2

Indices univariados de la estructura comunitaria bentónica para los ensambles faunísticos presentes en el sublitoral del área comprendida entre las dos angosturas del estrecho de Magallanes, para diferentes periodos de muestreo. S=Número de especies. N=Número de individuos. d=Riqueza de especies. J=Uniformidad y H'=Diversidad. En todos los casos n=45. Total se refiere al cálculo de los diferentes índices utilizando el conjunto de la información como un todo.

Univariate indices of benthic community structure obtained for faunal assemblages from the sublitoral zone in the Strait of Magellan, in different sampling periods. S= species number. N= individual number. d= species richness. J= evenness index. H'= diversity. In all cases n=45. Total refers to the values obtained for the indices using pooled information.

Fecha de muestreo	S	N	d	J	H'
01/05/1999	69	465	11,12	0,83	3,51
01-06/06/1999	95	546	14,96	0,82	3,72
23-26/10/1999	77	585	12,07	0,79	3,47
27-30/03/2000	172	3.129	21,37	0,72	3,75
08/07/2000	139	1.300	19,29	0,79	3,89
21/02/2000	76	586	11,82	0,69	3,00
Total	295	6.611	33,57	0,75	4,31

### Medidas univariadas de la biodiversidad

Los valores de diversidad y parámetros asociados obtenidos para cada periodo de muestreo se entregan en la Tabla 2. Considerando un mismo esfuerzo realizado, tanto de muestreo (en todos los casos n = 45) como de resolución taxonómica, se aprecia un incremento importante en el número de especies (S) desde el primer periodo de muestreo (S = 69) hasta el cuarto (S = 172)

para, posteriormente, descender nuevamente a niveles similares el primer muestreo (S = 76). Esta tendencia también se observa en relación con el número total de individuos recolectados en cada periodo y, claramente, ambas tendencias se reflejan en los valores que toma el índice de riqueza de especies según Margalef. En el cuarto periodo de muestreo se notan los mayores valores en todos estos parámetros.

En relación con la equitabilidad en la distribución de las abundancias numéricas por cada categoría taxonómica, en todos los casos J superó el valor de 0,5. Esto indica una dominancia por parte de unas pocas especies en todos los periodos de muestreo. Los casos extremos se aprecian en el primer muestreo (J = 0,83) y en el último realizado (J = 0,69).

Los valores del índice de diversidad de Shannon-Wiener (H') fluctúan entre 3,00 (muestreo de marzo de 2000) y 3,89 (muestreo de julio de 2000). En la mayoría de los casos que se analizan, el valor de H' está alrededor de 3,50.

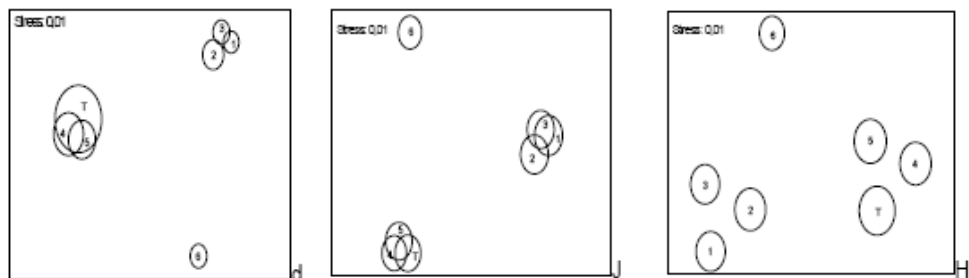
Con estos valores se estimaron los índices de los parámetros univariados considerados en el trabajo y que pueden ser tomados como valores teóricamente posibles. En tal caso, la equitabilidad fue de J= 0,75 reflejando una situación de dominancia intermedia entre los valores calculados para cada periodo de estudio. Por su parte, H' resultó ser considerablemente mayor que todos los valores obtenidos por periodo (H' = 4,31).

En la Fig. 3 se presenta la ordenación bi-dimensional de acuerdo al método del MDS para los seis periodos de muestreo, incluyendo los valores calculados para la sumatoria de los datos de número de especies y abundancia numérica.

Figura 3

Ordenación MDS de los seis periodos de muestreo (1 - 6) en función de los valores calculados de riqueza de especies (d), uniformidad (J) y diversidad (H'). T representa los valores obtenidos con las sumatorias de S y N de todos los muestreos. Los datos fueron transformados a la raíz cuarta previo al cálculo de la matriz de similitud según Bray-Curtis

MDS ordination of the six sampling periods (1 - 6) related with the values of species richness (d), evenness (J) and diversity (H'). T represents values calculated with the sum of S and N for all sampling periods. Data were transformed to fourth root before Bray-Curtis matrix similarities calculations



En la figura se han sobrepuesto en la ordenación de los periodos de muestreo, los valores obtenidos para la riqueza de especies ( $d$ ), uniformidad ( $J$ ) y diversidad ( $H'$ ). Tres agrupaciones distintivas aparecen para cada configuración de los parámetros univariados. Los valores más bajos determinados para los seis periodos de muestreo se ordenan claramente como una configuración diferente a la que constituyen los valores relativamente intermedios y, finalmente, se ordena el sexto periodo de muestreo en forma relativamente independiente a las dos configuraciones anteriores. Los valores obtenidos al considerar las sumatorias de  $S$  y  $N$  se ordenan asociadas al grupo que, en cada caso, corresponde con los valores más altos obtenidos a partir de los datos por periodo de muestreo. Los valores de estrés (estrés = 0,01) indican que el gráfico bidimensional resultante es una representación precisa de las interacciones existentes entre periodos de muestreo, al menos desde la perspectiva de los índices univariados utilizados.

## Discusión

El sistema marino de la región de Magallanes representa un ambiente de alto interés biogeográfico por sus posibles interacciones bióticas con la región antártica (Arntz & Ríos 1999) y con áreas contempladas dentro de la denominada Provincia Peruviana (Brattström & Johansson 1987). Sin embargo, la falta de información sobre biodiversidad a escala de país (Simonetti *et al.* 1995), y sobre antecedentes de distribución y abundancia de especies involucradas en comunidades a nivel local, representa un serio obstáculo para el análisis detallado de los patrones en gradientes latitudinales en los ecosistemas marinos australes y sus posibles causas (Gray 2001, Lancellotti & Vásquez 2000). Esta situación es causa fundamental de la no inclusión de la porción austral del cono sur de Sudamérica en trabajos que pretenden, por ejemplo, establecer normas para la conservación de los recursos marinos (e.g. Fernández *et al.* 2000). No obstante ello, datos recientes (Arntz & Ríos 1999) han mostrado que, para un cierto número de taxa, el número de especies incrementa desde el área de Magallanes hacia el continente antártico.

Los taxa dominantes en el sector estudiado del estrecho de Magallanes corresponden, en general, con los grupos mejores representados a lo largo de la costa chilena (*i.e.* Mollusca, Polychaeta y Crustacea) y que parecen determinar un patrón general de biodiversidad (Lancellotti & Vásquez 2000). Polychaeta también resultó ser el grupo dominante en la microcuenca sublitoral denominada Paso Ancho, en el mismo estrecho de Magallanes (Montiel *et al.* 2001). Los mismos grupos contribuyen con más del 90% de la

producción bentónica del estrecho de Magallanes (Brey & Gerdes 1999).

Para el área comprendida entre la Primera y Segunda Angostura del estrecho de Magallanes se determinaron al menos 119 especies de poliquetos, cifra importante en relación con las 160 especies señaladas por Lancellotti & Vásquez (2000) para el estrecho de Magallanes, quienes, sin embargo, no indican áreas específicas de localización. En contraste con lo señalado por estos autores para el grupo de los poliquetos, en la zona comprendida entre ambas angosturas la riqueza de especies estuvo concentrada en el orden Polynoidae y no en Phyllocidae. Los polinoides estuvieron representados por especies que tuvieron una abundancia numérica relativamente baja y con una distribución temporal, en términos de presencia/ausencia de especies, muy heterogénea. Esto último podría ser relevante si se consideran los resultados obtenidos por ejemplo para mayo de 1999, en donde sólo se registraron dos especies dentro del grupo, o en el muestreo de octubre del mismo año, en donde se recolectó una sola especie. En contraste, marzo de 2000 fue el periodo con una mayor riqueza de poliquetos polinoides.

En términos generales, los taxa identificados corresponden con aquellos que han permitido segregar una unidad zoogeográfica distintiva en la región de Magallanes y el cabo de Hornos, con bajas conexiones con la fauna de sectores más al norte de los 48°S. Sin embargo, además del deficiente grado de conocimiento taxonómico de la fauna invertebrada, los muestreos cuantitativos que permitan valorar aspectos como la biodiversidad son también escasos. Esto dificulta la realización de valoraciones más precisas acerca de las tendencias en biodiversidad hacia las zonas más australes del Sudamérica. Así, por ejemplo, Lancellotti & Vásquez (2000) sugieren evidencias de suaves gradientes de disminución de biodiversidad de moluscos en un sentido norte-sur, señalando la existencia de 611 especies a lo largo de la costa chilena. Sin embargo, Linse (1999) indica para la región de Magallanes la existencia de 397 especies de moluscos (10 de aplacóforos, 250 de gasterópodos, 6 de escafópodos y 131 de bivalvos), mientras que Forcelli (2000) describe 627 especies de moluscos para la región faunística de Magallanes incluyendo las zonas del Pacífico y Atlántico (3 de aplacóforos, 423 de gasterópodos, 1 de escafópodos, 136 de bivalvos, 26 de cefalópodos y 38 de poliplacóforos). Para el área de estudio se reconocieron al menos 69 especies de Mollusca. Por otro lado, Brandt (1991) indica para Magallanes la presencia de al menos 180 especies de isópodos y De Broyer & Rauschert (1999) obtuvieron 137 especies de



anfipodos, de las cuales un 20% resultaron ser especies nuevas para la ciencia.

Los valores obtenidos para los índices de diversidad y parámetros asociados han resultado ser altos en comparación con información previa obtenida para otros sectores sublitorales del estrecho de Magallanes (e.g. Gutt *et al.* 1999). Ello, en parte, es el reflejo de un mayor conocimiento taxonómico alcanzado hasta la fecha, aunque se reconoce la falta de una revisión más exhaustiva para muchos grupos taxonómicos que tienen sus descripciones iniciales, principalmente de distribución espacial puntual, en expediciones de mediados y fines del siglo antepasado (e.g. Discovery, Romanche, entre otras fundamentalmente europeas). Adicionalmente, se ha logrado agregar en la última década un mayor esfuerzo de muestreo, mayoritariamente de tipo cuantitativo (e.g. Montiel *et al.* 2001; Thatje & Mutschke 1999; Morrison 1999).

Los valores que toman los índices univariados en relación con el tiempo, aunque se trata sólo de seis períodos de muestreo, permiten sugerir la existencia de interesantes patrones asociados a la variable temporal. Para el presente caso de estudio se han definido al menos tres secuencias, una de las cuales estaría reflejando condiciones de biodiversidad reducida y, en el otro extremo, una condición relacionada con valores superiores. Una tercera fase parece indicar situaciones intermedias. Normalmente, los valores indicadores de biodiversidad consideran, en una gran medida, la variable espacial como referente para lograr aceptables estimaciones e indicadores. ¿Son realistas las estimaciones basadas en un sólo esfuerzo de muestreo, por más exhaustivo que éste sea? Para el caso del segmento estudiado en el estrecho de Magallanes, resulta evidente que una sola valoración no sería suficiente. Dependiente del período de muestreo es razonable esperar modificaciones importantes en las abundancias numéricas de las especies para un sector determinado, lo cual puede ser relevante sobretodo para las denominadas especies raras. En consecuencia, la valoración de la biodiversidad, aunque sea para situaciones locales, debe basarse más que en extensas listas de presencia/ausencia de especies, en estimaciones con una gran componente cuantitativa (Gray 2001a). Esta característica permitirá la determinación de rangos de diversidad esperables según las componentes espaciales y temporales y bajo las condiciones bióticas y abióticas del hábitat bajo estudio. Esto puede ser significativo considerando que, por ejemplo, ciertas estrategias para la definición de prioridades para la conservación de la biodiversidad marina se basan solamente en la consideración de hábitats con alta diversidad (Gray 1997).

## Agradecimientos

A los Sres. Rodolfo Vera y Victor Araniz y su Grupo de Trabajo Submarino (ENAP-Magallanes), por el apoyo entregado para el desarrollo del trabajo. Especialmente a nuestros compañeros de trabajo Jorge Ramírez, Jacqueline Parada, Bladimiro (BIL) López, Yanko Cariceo-Yutronic y Cristian Muñoz, todos miembros del GEA-UMAG, Instituto de la Patagonia, Laboratorio de Hidrobiología. Al colega Juan I. Cañete (Facultad de Ciencias, Universidad de Magallanes) por su colaboración en la identificación del grupo Polychaeta. Los revisores anónimos de la Revista obligaron a una mejor definición del objetivo del trabajo, por lo que agradecemos sus valiosas críticas y sugerencias. Artículo financiado parcialmente por el proyecto IFS N°A/2503-1.

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**PUBLICATION V**

**SPATIAL AND TEMPORAL VARIABILITY OF THE BENTHIC  
ASSEMBLAGES ASSOCIATED TO THE HOLDFAST OF THE KELP  
*Macrocystis pyrifera* IN THE STRAITS OF MAGELLAN**

**Carlos Ríos, Wolf E. Arntz, Dieter Gerdes, Erika Mutschke & Américo Montiel**

**POLAR BIOLOGY**

## Spatial and temporal variability of the benthic assemblages associated to the holdfasts of the kelp *Macrocystis pyrifera* in the Straits of Magellan, Chile

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Received: 2 October 2006 / Revised: 29 June 2007 / Accepted: 2 July 2007  
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**Abstract** *Macrocystis pyrifera* (L.) C. Agardh is a characteristic macroalga in the Magellan region covering almost 30% of the shallow coastal waters. The focus of this study was to analyse the spatial and seasonal patterns in macrofauna communities associated to the holdfasts of *Macrocystis pyrifera* at two study sites in the Straits of Magellan, South Chile. In total, 114 species from 10 major taxa were isolated from the holdfasts. MDS clearly separated the holdfast fauna collected in different seasons, with autumn and winter collections being richer in terms of species richness and abundance as compared to the spring and summer situation. MDS also clearly separated the holdfast associated faunas of the two study sites, Bahía Laredo and Fuerte Bulnes. The community structure and species composition of the associated macro-invertebrates and vertebrates appeared rather heterogeneous, probably due to the extremely heterogeneous environmental conditions along the entire coastline of the Subantarctic Magellan region.

**Keywords** Macrofauna · Kelp holdfasts · Straits of Magellan · Chile · Biodiversity

### Introduction

The brown macroalga *Macrocystis pyrifera* (L.) C. Agardh forms kelp forests along rocky coastlines in a mid-latitude belt (roughly 40–60°) of both hemispheres (Steneck et al. 2002). *Macrocystis pyrifera* kelp forests are very abundant also in shallow waters around the southernmost tip of South America, where they offer food and refuge for many invertebrate and vertebrate species (e.g. Ojeda and Santelices 1984; Castilla 1985; Vásquez 1993; Vanella et al. 2007; Viddi and Lescauwae 2005). Kelp species along the whole Chilean coast, including the genus *Macrocystis*, have been considered as an outstanding biodiversity reservoir (Vásquez and Buschmann 1997; Vásquez et al. 2001).

*Macrocystis pyrifera* like other kelp plants consists of three different body parts, the holdfast, the stipe and the blade, all of which offer different kinds of habitats for various invertebrate and vertebrate species. Drifting rafts of *Macrocystis pyrifera* have the potential to disperse fauna among isolated kelp areas (Hobday 2000). Species richness and abundance are particularly high in the kelp holdfast (hapteron) microhabitats (e.g. Ojeda and Santelices 1984; Castilla 1985; Vásquez 1993; Smith 2000; Cariceo et al. 2002), but also the fronds host a rich and diverse fauna, characterized especially by filter-feeding species such as the small bivalve *Gaimardia trapesina* and bryozoans or browsers like the amphipod *Paramphitoe femorata* (Adami and Gordillo 1999).

Some preliminary studies on macro-invertebrate assemblages inhabiting the holdfasts of *Macrocystis pyrifera* populations in southern South America show biodiversity values to be rather similar as compared to those reported for kelp holdfasts in the northern parts of Chile and also in the northern hemisphere (Vásquez et al. 2001; Ghelardi 1971). However, the great heterogeneity of environmental conditions

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along the entire Subantarctic Magellan region (see Arntz 1999) suggests also a great heterogeneity in macro-invertebrate holdfast community structures and dynamics. This aspect has not been studied in detail for the kelp forests of the Magellan fjord and channel complex, but the little data available so far seem to confirm these suggestions (Ojeda and Santelices 1984; Adami and Gordillo 1999).

The present study describes spatial and temporal patterns of macro-invertebrate and fish assemblage structures associated to the holdfasts of *Macrocystis pyrifera* populations. Important community parameters such as organism densities, species composition/richness and resulting diversity values are analysed in order to evaluate the contribution of biodiversity in this specific habitat to the overall biodiversity in the Straits of Magellan.

## Materials and methods

### Study areas

Samples of *Macrocystis pyrifera* holdfasts were collected from sublittoral kelp forests in Bahía Laredo (52°56.5'S; 70°50'W) and Fuerte Bulnes (53°38'S; 70°55'W) in the Straits of Magellan (Fig. 1). According to Antezana (1999), the two sampling areas are situated at the boundaries of the sub-basin Paso Ancho of the Straits of Magellan. In this part of the Straits, the cold and brackish water masses are mostly vertically homogeneous as a result of the mixing by tidal currents. Temperature and salinity are low as the water mixes with inner waters of the Straits. In addition, water from the southern hydrological system of Tierra del Fuego

also influences this area. Towards the Pacific side of the Straits, salinity and temperature increase slightly related to the inflow of warmer and saltier Pacific water.

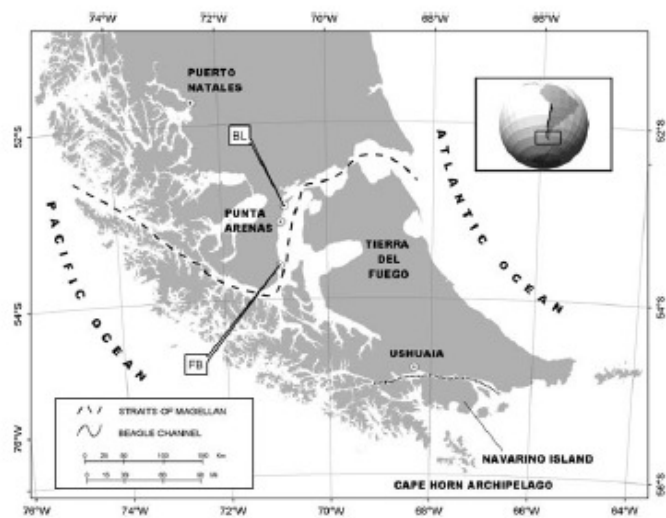
At Bahía Laredo, the bottom substrate occupied by the *Macrocystis pyrifera* kelp is characterized by inserted patches of sand, very coarse sand, granules and cobbles (Mutschke et al. 1998). This feature of the biotope is considered as indicative of unstable or transitional environment derived from a highly or moderately energetic environment (Brambati et al. 1991; Prieto 1992). The kelp forest at this site is situated in about 8 m water depth and covers an area of about 5.1 ha with an average of 0.16 holdfast  $m^{-2}$ . Surface temperatures fluctuate between 1.5°C (June) and 14.0°C (January), and salinity ranges between 30 and 33 ppt. The *Macrocystis pyrifera* holdfasts were collected between September 1999 (austral spring season) and January 2001 (austral summer season).

At Fuerte Bulnes, the area occupied by the *Macrocystis pyrifera* kelp is formed by cobbles and rocky substrates (Prieto 1992). The kelp is growing, as is the case in Bahía Laredo, at 8 m water depth and covers an area of about 2.1 ha with an average of 0.25 holdfast  $m^{-2}$  at this site. Surface water temperatures ranged from 1.0 (June) to 12.0°C (January) during the sampling periods, and the salinity varied between 32 and 34 ppt.

### Field work

*Macrocystis pyrifera* attaches to hard substrates by a holdfast and fronds initiated at a basal meristem grow vertically towards the surface, buoyed up by gas filled bladders. Each holdfast anchors by means of multiple rope-like stipes and

**Fig. 1** Position of the two study sites Bahía Laredo (BL) and Fuerte Bulnes (FB) in the Straits of Magellan





comprises intertwined haptera forming a structurally complex lattice.

The sampling schedule for the holdfasts is summarized in Table 1. Two divers performed the collections. In order not to disturb the kelp forest too much, we restricted our collections to 10–18 holdfasts per sampling period. The stipes of each plant was cut before the holdfasts were detached from the substrate by means of a mechanical lever. Each holdfast was immediately placed in a labelled plastic bag and kept frozen in the laboratory at  $-20^{\circ}\text{C}$  till later analysis. The holdfast volume ( $\text{cm}^3$ ) was estimated by placing all holdfast pieces in a graduate beaker and measuring the volume of displaced water. All invertebrates inside the holdfasts were sorted by dissecting the holdfasts and separating all sediment and macro-specimens. After sieving all organisms using a sieve with 0.1 cm mesh size, the sorted material was analysed under a binocular microscope to separate all the macroorganisms present in each sample. The collected macrofauna was identified to the lowest possible taxonomical level, counted and measured with a calliper to 0.1 mm accuracy. However, for some taxa, identification was possible only to higher taxonomic levels. Organisms were identified based on standard publications (e.g. Norman 1937; Menzies 1962; Retamal 1974; Bemasoni and D'Agostino 1977; Castellanos 1988–1993; Rozbaczylo 1985). Further experts who assisted in the identification of different taxa are mentioned in the acknowledgements. In addition, the “Edmundo Pisano Reference Collection” of the Instituto de la Patagonia, Universidad de Magallanes served as a tool for species identification.

Abundances and numbers of species were standardized on the basis of a  $1,500\text{ cm}^{-3}$  holdfast in order to allow comparisons between study sites and sampling periods.

#### Statistical analyses

Statistical analyses were performed on fourthroot transformed abundances of macro-invertebrates collected from all individual holdfasts, standardized on the basis of a holdfast

volume of  $1,500\text{ cm}^{-3}$ . MDS plots from PRIMER 5 (Clarke and Warwick 2001) were constructed from samples collected from April 2000 to January 2001 to analyse the relations between holdfast associated fauna and seasons both at Fuerte Bulnes and Bahía Laredo. ANOSYM analysis of PRIMER was used for each sampling site to test the effect of the factor ‘season’ on abundance of the holdfast associated fauna.

Spatial differences between both sampling sites were analysed by the same approach. The significance of differences in the community parameters abundance, evenness, diversity and number of species per holdfast between both study sites were evaluated by an unpaired *t*-test using the software StatView. The relative contribution of different species to patterns of similarity within each sampling site and dissimilarities between the sites were calculated using the SIMPER (“similarity percentages”) routine of PRIMER. This method was applied for the seasonal and the spatial aspects.

## Results

### Holdfast data and general remarks on associated fauna

Considering all sampling periods at both sampling sites, the individual holdfast volumes ranged between 100 and  $3,500\text{ cm}^3$ . However, mean holdfast volumes did not differ significantly, neither between study sites ( $t=1.634$ ;  $df=134$ ;  $P=0.105$ ) nor between sampling periods (ANOVA Fuerte Bulnes:  $F_{(4,53)}=2.151$ ;  $P=0.087$ ; Bahía Laredo:  $F_{(5,62)}=1.698$ ;  $P=0.148$ ). Because of the considerable size variability, all abundance data were standardized on the basis of a  $1,500\text{ cm}^3$  holdfast to allow comparison of the abundances for spatial and temporal variability in the data.

In total, we documented 114 faunal species from 10 major taxa (Table 2). Most dominant were polychaetes with 43 species/genera, followed by arthropods (21 crustacean and 1 pantopod species/genera), molluscs (19 species/genera),

**Table 1** Sampling schedule and environmental data for the two study areas in the Straits of Magellan, Bahía Laredo and Fuerte Bulnes. Bold letters mark samples considered for seasonal aspects at both study sites

Sampling	Season	Fuerte Bulnes			Bahía Laredo		
		No. of holdfasts collected	So/co	T°C	No. of holdfasts collected	So/co	T°C
Sep 1999	Spring	–			12	34	5.6
Jan 2000	Summer	–			18	34	10.0
<b>Apr 2000</b>	<b>Autumn</b>	12	33	8.5	12	33	9.0
<b>Jul 2000</b>	<b>Winter</b>	10	34	6.0	12	34	6.2
Sep 2000	Spring	12	32	7.0	12	34	5.0
Jan 2001	Summer	12	32	10.0	12	34	10.0
Jul 2001	Winter	12	32	5.0	–		

**Table 2** List of macro-invertebrates associated to standardized holdfasts (1,500 cm<sup>-2</sup>) of *Macrocystis pyrifera* and mean abundances per sampling period, Straits of Magellan

	Bahía Laredo						Fuerte Bulnes				
	Sep-99	Jan-00	Apr-00	Jul-00	Sep-00	Jan-01	Apr-00	Jul-00	Sept-00	Jan-01	Jul-01
<b>Cnidarians</b>											
<i>Anthothoe</i> cf. <i>chilensis</i>	0.9	1.2	0.0	0.6	2.2	0.0	0.0	0.0	0.0	0.0	0.6
<i>Anthothoe</i> cf. <i>alicemartinae</i>	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.2	0.0
<i>Anthothoe</i> sp.	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.1	0.0
<i>Antholoba</i> sp.	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.2	0.0
<b>Nemerteans</b>											
<i>Parborlasia</i> cf. <i>corrugatus</i>	0.0	0.0	0.0	0.0	0.4	0.6	0.0	0.0	0.0	0.2	0.5
<b>Molluscs</b>											
Polyplacophora indet.	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
<i>Tonicia atrata</i>	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.0	0.0	0.1	0.0
<i>Plaxiphora aurata</i>	0.0	0.0	0.0	0.0	0.0	0.6	0.6	0.0	0.0	0.0	0.0
<i>Callochiton puniceus</i>	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0
Bivalvia indet.	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mytilus edulis chilensis</i>	0.0	1.4	9.0	4.6	17.0	0.1	0.0	0.3	0.3	0.0	0.0
<i>Aalacomya ater</i>	0.0	0.2	6.4	4.6	1.6	0.9	2.5	0.9	0.2	0.2	0.3
<i>Chlamys patagonicus</i>	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Hiatella solida</i>	13.5	1.6	4.3	1.6	1.7	2.8	1.2	0.1	0.0	0.0	0.5
Gastropoda indet.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
<i>Nacella mytilina</i>	0.4	0.0	0.0	0.1	0.6	0.0	0.0	0.0	0.0	0.0	0.0
<i>Fissurella</i> sp.	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.1	0.0
<i>Fissurella picta</i>	0.1	0.0	0.0	0.0	0.0	0.0	1.6	1.6	0.1	0.1	0.0
<i>Fissurella oriens</i>	0.1	0.0	0.0	0.0	0.0	0.0	1.8	0.4	0.0	0.0	0.0
<i>Crepidatella dilatata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
<i>Margarella violacea</i>	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.2	0.9	0.0	0.0
<i>Ximenesopsis muriciformis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.2	0.0
<i>Pareuthria plumbea</i>	0.0	0.0	0.0	0.2	0.1	0.0	0.2	0.9	0.0	0.2	0.9
Cephalopoda indet.	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0
<b>Arthropods</b>											
Amphipoda indet. 1	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Amphipoda indet. 2	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Amphipoda indet. 3	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Amphipoda indet. 4	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Amphipoda indet. 5	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
<i>Nebalia</i> sp.	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isopoda indet.	0.3	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Iathrippa chilensis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.2	0.9
<i>Janthopsis laevis</i>	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.4
<i>Idothea</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.2	0.0
<i>Exosphaeroma studeri</i>	0.0	0.0	2.6	0.9	0.9	1.3	10.4	24.2	1.1	3.4	14.6
<i>Exosphaeroma</i> sp.	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Exosphaeroma lanceolata</i>	0.0	0.0	3.8	0.4	2.2	0.5	13.2	13.9	3.9	11.3	7.3
<i>Dynamenella eatoni</i>	0.0	0.0	3.5	7.6	10.5	1.4	81.8	51.3	3.1	18.4	90.7
<i>Cassinopsis emarginata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9
<i>Pagurus comptus</i>	0.0	0.0	0.0	1.0	0.0	0.5	0.1	1.4	0.0	0.1	1.5
<i>Lithodes santolla</i>	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Eurypodius latreillei</i>	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0



Table 2 continued

	Bahía Laredo						Fuerte Bulnes				
	Sep-99	Jan-00	Apr-00	Jul-00	Sep-00	Jan-01	Apr-00	Jul-00	Sept-00	Jan-01	Jul-01
<i>Halicarcinus planatus</i>	7.7	13.0	12.3	18.9	28.4	7.4	0.5	2.7	0.7	1.5	1.6
<i>Campylonotus semistriatus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
<i>Peltarium spinosulum</i>	1.4	0.0	0.0	0.2	0.0	0.0	0.0	0.5	0.0	0.0	0.0
<i>Pycnogonida</i> indet.	0.0	0.4	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sipunculids											
<i>Themiste</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
Echinoderms											
<i>Ceramaster patagonicus</i>	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
<i>Anasterias antarctica</i>	9.2	9.2	3.2	3.0	0.3	1.2	7.1	10.2	8.1	0.8	1.6
<i>Cosmasterias lurida</i>	0.0	0.0	0.0	7.1	5.4	1.9	0.0	3.8	2.9	1.2	2.6
<i>Asterina fimbriata</i>	1.8	6.2	0.2	1.8	0.7	1.1	0.0	6.2	0.2	0.0	0.5
<i>Cyathra verrucosa</i>	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
<i>Odontaster validus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
<i>Ophiactis asperula</i>	85.8	97.5	65.5	56.7	25.0	4.4	44.2	17.4	45.2	44.9	26.0
<i>Ophiactis kroyeri</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
<i>Psolus patagonicus</i>	0.0	2.1	0.2	0.0	0.0	0.0	0.5	0.0	2.1	0.2	0.1
<i>Pseudocnus dubiosus leoninus</i>	12.6	21.6	36.8	11.9	14.4	13.0	2.6	3.1	0.3	5.2	4.3
<i>Pseudechinus magellanicus</i>	61.0	14.9	15.2	14.6	4.8	5.8	1.9	6.4	4.6	0.1	4.5
<i>Loxechinus albus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Brachiopods											
<i>Magellania venosa</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Ascidians											
<i>Ascidia</i> indet.	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Fish											
<i>Crossostomus sobrali</i>	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.3	0.0	0.0	0.0
<i>Pogonochus marinae</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.7	0.3	0.5
<i>Leptholychus macrophthalmus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
<i>Maynea microphthalmus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
<i>Notothenia cornucola</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
<i>Notothenia macrophthalma</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
<i>Nototheniidae</i> indet.	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Agonopsis chilensis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
<i>Phucocoetes latitans</i>	1.2	0.3	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0
<i>Patagonotothen cornucola</i>	0.0	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes											
<i>Autolytus</i> sp.	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Aglaothamus macroura</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
<i>Augeneria tentaculata</i>	0.0	0.0	0.6	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
<i>Amphiteis</i> sp.	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Chaetopterus variopeatus</i>	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Cirratulus cirratus</i>	2.5	10.6	0.4	2.1	0.2	1.4	2.1	0.1	0.0	0.0	0.0
<i>Cirratulus</i> sp.	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Chymenella minor</i>	0.0	0.0	0.0	0.6	0.0	0.0	0.7	0.0	0.0	0.0	0.0
<i>Eteone sculpta</i>	0.0	0.8	0.1	0.5	0.3	0.6	0.3	0.5	0.0	0.0	0.5
<i>Hermadion rhizoicola</i>	2.0	0.0	6.2	7.3	9.3	0.6	6.4	1.7	0.0	0.0	0.0
<i>Eanereis patagonica</i>	0.0	0.2	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Glycera capitata</i>	0.0	0.2	0.3	0.8	0.2	0.0	2.7	0.0	0.0	0.0	0.0

Table 2 continued

	Bahía Laredo						Fuerte Bulnes				
	Sep-99	Jan-00	Apr-00	Jul-00	Sep-00	Jan-01	Apr-00	Jul-00	Sept-00	Jan-01	Jul-01
<i>Halosydna patagonica</i>	0.0	0.0	0.0	0.0	0.0	1.2	0.0	1.6	0.2	0.0	3.9
<i>Hamothoe</i> sp.2	2.3	2.5	2.8	2.2	1.0	0.8	2.6	0.0	0.0	0.0	0.0
<i>Hamothoe</i> sp.3	0.1	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
<i>Hemipodus</i> sp.	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Hermadion magalhaensis</i>	21.4	17.3	4.2	6.8	2.7	0.9	5.8	0.8	0.7	1.3	0.0
<i>Idanthyrsus armatus</i>	0.0	3.2	0.6	1.0	1.0	0.0	0.5	0.0	0.0	0.0	0.0
<i>Kimbergonuphis dorsalis</i>	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Leitoscoloplos kerguelensis</i>	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lumbrineris magalhaensis</i>	0.0	0.4	0.7	1.2	2.3	0.0	1.2	2.5	0.6	0.7	0.0
<i>Lumbrineris cingulata</i>	1.2	0.6	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
<i>Neanthes kerguelensis</i>	0.4	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Nereis eugeniae</i>	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Nereis pelagica</i>	0.0	0.0	2.0	0.5	2.5	0.6	9.2	0.7	0.4	1.8	0.5
<i>Melinna cristata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
<i>Nicolea chilensis</i>	0.6	0.4	0.9	2.8	1.6	0.0	0.6	1.5	5.6	0.4	0.0
<i>Notalia</i> sp.	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Notomastus latericeus</i>	0.0	0.4	0.0	1.1	2.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ophioglycera eximia</i>	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0
<i>Ophioglycera</i> sp.	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
<i>Perkinsiana antarctica</i>	1.5	0.0	0.1	4.3	0.6	1.5	0.0	0.0	0.0	0.0	0.0
<i>Perkinsiana</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Phragmatopoma virgini</i>	0.0	0.9	0.2	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Pista cristata</i>	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.2
<i>Platynereis australis</i>	58.9	55.0	37.7	104.4	0.0	31.7	57.5	43.2	20.4	8.2	16.2
<i>Polycirrus</i> sp.	4.8	25.6	0.3	0.4	0.4	0.6	4.3	0.0	0.0	0.0	0.0
<i>Steggoa magalhaensis</i>	0.0	0.8	0.3	0.6	0.5	0.0	0.6	0.3	0.1	0.2	0.7
<i>Sthenelais blanchardi</i>	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0
<i>Scalibregma</i> sp.	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Thelepus plagiostoma</i>	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Thelepus setosus</i>	0.3	3.9	0.9	3.7	1.1	5.1	4.9	0.0	0.0	0.0	0.5
<i>Trypanosyllis gigantea</i>	0.0	0.2	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Not considered are colonial bryozoans and sponges

echinoderms (12 species/genera), 10 fish species, 4 cnidarian species/genera, nemerteans, sipunculids, brachiopods and ascidians, all recorded with only 1 species. High dominance of polychaete species was observed at both sampling sites (Fig. 2), followed by crustaceans, molluscs and echinoderms.

#### Seasonal aspects in holdfast fauna abundance and composition

Table 3 summarizes important community parameters such as abundance, species richness, evenness and diversity for both study sites and seasonal sampling periods at each site. Overall, the number of species collected in the sampling periods ranged from 29 in winter to 42 in autumn at Fuerte

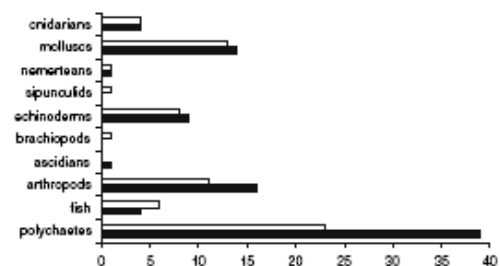


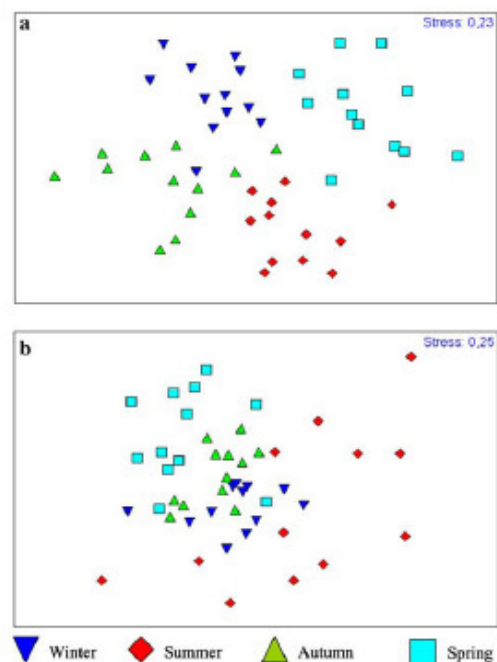
Fig. 2 Species numbers of the holdfast associated fauna at Bahía Laredo (black bars) and Fuerte Bulnes (white bars), Straits of Magellan

**Table 3** Summarized data on species numbers, abundances, evenness and Shannon-Wiener index of holdfast associated macro-invertebrates collected in different seasons and areas (Bahía Laredo and Fuerte Bulnes, Straits of Magellan)

	Bahía Laredo	Fuerte Bulnes
<i>Species number</i>		
Minimum per holdfast	6	7
Maximum per holdfast	23	26
Mean per area	38 ± 6	34 ± 6
Means per Spt/Sum/Aut/Win	14/11/14/18	11/10/16/16
<i>Abundances</i>		
Minimum per holdfast	11	32
Maximum per holdfast	1,100	795
Mean per area	228 ± 213	173 ± 133
Means per Spt/Sum/Aut/Win	146/94/222/278	104/102/278/200
<i>Evenness</i>		
Means per Spt/Sum/Aut/Win	0.771/0.703/0.849/0.842	0.765/0.777/0.706/0.728
Mean per area	0.784 ± 0.07	0.736 ± 0.06
<i>Shannon—Wiener diversity</i>		
Means per Spt/Sum/Aut/Win	1.991/1.997/2.222/2.012	2.089/2.125/1.706/1.654
Mean per area	2.029 ± 0.25	1.882 ± 0.31

Bulnes and from 29 in spring to 45 in winter in Bahía Laredo. Mean abundances of associated fauna per sampling period varied between 102–278 and 94–278 for Fuerte Bulnes and Bahía Laredo, respectively. At a first glance, species numbers as well as abundance values look rather similar at both sampling sites, whereas seasonal differences in these parameters seem to be more pronounced. The highest species numbers and abundance values occur in austral autumn and winter, whereas the spring and summer values are lower. Contrasting at both sites appear evenness and diversity values: whereas in Bahía Laredo evenness and diversity are higher in spring and summer as compared to the autumn and winter values, the opposite holds true at Fuerte Bulnes.

In the MDS ordinations at both sampling sites, the seasonal sampling events were clearly separated (Fig. 3). The relatively high stress levels of the plots at both sites indicate that the true relationships between the seasonal communities might be poorly represented. However, at both sites, the holdfast communities in the different seasons differed significantly in all combinations (Global  $R = 0.695$ , significance level 0.1% and  $R = 0.372$ , significance level 0.1% for Fuerte Bulnes and Bahía Laredo, respectively). At both sites, the average within seasonal holdfast associated community similarity was highest in winter and autumn as compared to spring and summer (cf. Table 4). Discriminating species contributing most to the seasonal dissimilarities differ among seasons and also between the two sampling sites; the exceptions are *Cosmasterias lurida*, *Pseudocnus dubiosus leoninus* and *Dynamenella eatoni*, which several times were reasonable discriminator species between different seasons at both sites.



**Fig. 3** Non-metric multidimensional scaling of abundance data of macro-invertebrate assemblages associated to *Macrocystis pyrifera* holdfasts collected in different seasons at Fuerte Bulnes (a) and Bahía Laredo (b), Straits of Magellan, Chile. Bray-Curtis similarity indices were computed with double square-root transformed species abundances

**Table 4** Average similarities within and dissimilarities between seasons in Bahía Laredo and Fuerte Bulnes including the most important discriminating species

Autumn (59.28%)		Winter (56.70%)		Spring (46.08%)		Summer (34.30%)	
<b>Bahía Laredo (average within season similarity)</b>							
Ophiactis asperula	17.71%	Platynereis australis	18.59%	Ophiactis asperula	19.42%	Platynereis australis	24.20%
Platynereis australis	15.66%	Ophiactis asperula	15.24%	Halicarcinus planatus	17.90%	Pseudocnus dubiosus	15.78%
Halicarcinus planatus	11.75%	Halicarcinus planatus	7.97%	Pseudocnus dubiosus	13.94%	Hiatella solida	7.65%
Mytilus chilensis	11.04%	P. magellanicus	7.25%	Mytilus chilensis	7.48%	Ophiactis asperula	7.57%
Autumn (61.34%)		Winter (63.17%)		Spring (55.82%)		Summer (61.31%)	
<b>Fuerte Bulnes (average within season similarity)</b>							
Dynamenella eatoni	16.03%	Dynamenella eatoni	14.87%	Ophiactis asperula	24.67%	Ophiactis asperula	25.66%
Platynereis australis	14.58%	Platynereis australis	14.72%	Platynereis australis	14.54%	Dynamenella eatoni	20.58%
Ophiactis asperula	14.00%	Exosphaeroma studeri	11.70%	E. lanceolata	13.11%	Platynereis australis	16.59%
E. lanceolata	10.47%	E. lanceolata	10.96%				
Autumn		Winter		Spring		Summer	
<b>Bahía Laredo (average dissimilarity between seasons)</b>							
Winter	48.6%						
	Cosmasterias lurida	5.75%					
	Pseudocnus dubiosus	5.61%					
	Pseudechinus magellanicus	4.89%					
	Hermadion rhizoicola	4.62%					
	Mytilus chilensis	4.13%					
	Dynamenella eatoni	3.92%					
Spring	54.8%		56.8%				
	Platynereis australis	9.92%	Platynereis australis	11.28%			
	Pseudechinus magellanicus	4.73%	Pseudocnus dubiosus	4.27%			
	Pseudocnus dubiosus	4.66%	Pseudechinus magellanicus	4.11%			
	Hermadion rhizoicola	4.53%	Mytilus chilensis	3.82%			
	Dynamenella eatoni	3.83%	Dynamenella eatoni	3.59%			
	Cosmasterias lurida	3.81%	Hermadion magalhaensis	3.32%			
Summer	63.2%		63.8%			70.6%	
	Ophiactis asperula	7.11%	Ophiactis asperula	6.24%	Platynereis australis	7.24%	
	Mytilus chilensis	6.47%	Platynereis australis	4.55%	Mytilus chilensis	4.72%	
	Pseudocnus dubiosus	5.00%	Pseudocnus dubiosus	4.17%	Ophiactis asperula	4.67%	
	Aulacomya ater	5.00%	Halicarcinus planatus	4.09%	Halicarcinus planatus	4.66%	
	Pseudechinus magellanicus	4.63%	Hermadion rhizoicola	4.08%	Hermadion rhizoicola	3.98%	
	Halicarcinus planatus	4.38%	Dynamenella eatoni	4.05%	Pseudechinus magellanicus	3.62%	
Autumn		Winter		Spring		Summer	
<b>Fuerte Bulnes (average dissimilarity between seasons)</b>							
Winter	48.0%						
	Thelepus setosus	4.85%					
	Nereis pelagica	4.48%					
	Cosmasterias lurida	4.45%					
	Asterina fimbriata	4.39%					
	Ophiactis asperula	3.94%					
	Hermadion magalhaensis	3.90%					

Table 4 continued

	Autumn	Winter	Spring	Summer		
Spring	55.7%	52.9%				
	Dynamenella eatoni	8.71%	Dynamenella eatoni	8.24%		
	Nereis pelagica	5.02%	Exosphaeroma studeri	7.03%		
	Thelepus setosus	4.99%	Nicolea chilensis	4.86%		
	Exosphaeroma studeri	4.73%	Ophiactis asperula	4.74%		
	Nicolea chilensis	4.44%	Asterina fimbriata	4.73%		
	Hermadion magalhaensis	4.07%	Pseudocnus dubiosus	3.85%		
Summer	51.4%	50.1%	52.0%			
	Thelepus setosus	5.59%	Exosphaeroma studeri	7.25%	Dynamenella eatoni	7.88%
	Exosphaeroma studeri	5.32%	Anasterias antarctica	5.79%	Pseudocnus dubiosus	7.23%
	Pseudocnus dubiosus	5.12%	Pseudechinus magellanicus	5.78%	Anasterias antarctica	6.65%
	Nereis pelagica	4.91%	Asterina fimbriata	5.54%	Nicolea chilensis	6.40%
	Anasterias antarctica	4.86%	Ophiactis asperula	5.18%	Pseudechinus magellanicus	5.65%
	Hermadion rhizoicola	4.45%	Cosmasterias lurida	4.50%	Cosmasterias lurida	4.85%

Spatial differences in the holdfast fauna of two different locations in the Straits of Magellan

The MDS also clearly separated the holdfast associated faunas from Fuerte Bulnes and Bahía Laredo (Fig. 4). This differentiation is confirmed by ANOSIM (Global  $R = 0.498$ ,  $P = 0.1\%$ ). The within site similarity was lower in Bahía Laredo (42.78%) as compared to Fuerte Bulnes (51.35%). The brittlestar *Ophiactis asperula* and the polychaete *Platynereis australis* contributed at both sites most to these similarities (cf. Table 5). The dissimilarity between both sites was high (64.38%) and *Dynamenella eatoni*, *Exosphaeroma lanceolata*, *Halicarcinus planatus*, *Pseudocnus dubiosus leoninus* and *Exosphaeroma studeri* contributed most to this dissimilarity.

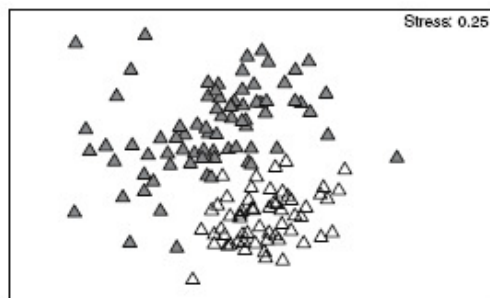


Fig. 4 Non-metric multidimensional scaling for data from *Macrocystis pyrifera* holdfast faunal assemblages collected from Fuerte Bulnes (open triangle) and Bahía Laredo (gray filled triangle) within the Straits of Magellan. Bray-Curtis similarity indices were computed with double square-root transformed species abundance

Significant differences between sites also became obvious in the community parameters evenness  $J'$  ( $P < 0.0001$ ) and diversity  $H'$  ( $P = 0.0026$ ), whereas abundances ( $P = 0.875$ ) and species numbers ( $P = 0.4602$ ) did not differ significantly.

## Discussion

*Macrocystis pyrifera* is a characteristic floral element of the Magellan region. Even some decades ago, Darwin (1909) made first observations in the Magellan region of a great variety of *Macrocystis pyrifera* associated holdfast organisms.

The distribution of *Macrocystis pyrifera* appears to be restricted to protected environments with rocky substrate and with the boulder and cobble substrates typical of this region. The algae are distributed at 8–10 m depth producing kelp forests of almost 30–40 m width (Santelices 1989). Considering just the Subantarctic Fuegian channels and fjords south of the Straits of Magellan down to the Cape Horn Archipelago, including the Beagle Channel and surrounding areas, *Macrocystis pyrifera* kelp forests can be estimated to cover almost 30% of the ca. 11,000 km long coastline of this area. This means that this “structuring” or “ecosystem engineering species” sensu Jones et al. (1994) produces strong modifications in the architecture of the sublittoral habitats in this region. The anatomic structure of the macroalgae, mainly the architecture of the holdfasts, contributes to an increased ‘alpha’ or local diversity by creating an additional habitat for various invertebrates and vertebrates. Peale’s dolphins are documented to live frequently in kelp beds of *Macrocystis pyrifera* of the protected channels and fjords, especially during feeding periods (Viddi



**Table 5** Average within site similarities and average dissimilarities between Bahía Laredo and Fuerte Bulnes (Straits of Magellan) and discriminating species

Bahía Laredo		Fuerte Bulnes	
Average within site similarity (42.8%)		Average within site similarity (51.4%)	
<i>Ophiactis asperula</i>	19.28%	<i>Ophiactis asperula</i>	19.16%
<i>Platynereis australis</i>	15.17%	<i>Platynereis australis</i>	16.54%
<i>Halimacrinus planatus</i>	10.82%	<i>Dynamenella eatoni</i>	15.48%
<i>Pseudocnus dubiosus</i>	10.01%		
Average dissimilarity between sites (64.4%)			
<i>Dynamenella eatoni</i>	6.64%		
<i>Exosphaeroma lanceolata</i>	5.21%		
<i>Halimacrinus planatus</i>	4.35%		
<i>Pseudocnus dubiosus</i>	4.29%		
<i>Exosphaeroma studeri</i>	4.19%		
<i>Pseudechinus magellanicus</i>	4.16%		

and Lescauwat 2005). Different stages of fish (larvae, juveniles and adults) have been associated with different parts of the macroalgae (Nelson 2001).

In our study, the examination of 136 holdfasts from just two distinct localities in the Magellan region resulted in the identification of 114 associated species from 10 major taxa. The polychaetes as the dominant taxon in the holdfast were present with 43 different species, which is quite a large number as compared to 199 species identified recently by Montiel et al. (2005a, b) for the whole Magellan region from the South Patagonian Icefield in the north down to the Beagle Channel and the continental shelf and slope off the eastern Beagle entrance. Comparing the 43 polychaete species found in the holdfasts with the inventories of adjacent shallow stations (VH 807, 14 m; VH 916, 26 m; VH 961, 38 m after Montiel et al. 2005b), only *Aglaophamus macroura*, *Glycera capitata*, *Lumbrineris cingulata*, *L. magalhensis* and *Perkinsiana antarctica* are common in both habitats, whereas the other 38 species, mostly motile suspension feeders, were found exclusively in the holdfasts. A less pronounced but similar trend is obvious in the echinoderms. Recently, Mutschke and Ríos (2006) reported for the Straits of Magellan 37 echinoderm species. According to this study, the holdfasts off Fuerte Bulnes and Laredo Bay hosted 12 species; 9 of these species occurred in both habitats, the distribution of *Odontaster validus*, *Ophiactis kroyeri* and *Loxechinus albus* was restricted to the holdfasts. Lancellotti and Vásquez (2000) reported for the whole region (48–54°S) a total of 52 species. For the *Macrocystis* kelp forests in the southern Beagle Channel, Ojeda and Santelices (1984) reported nine echinoderm species, and Adami and Gordillo (1999) reported seven species for the kelp forests from the northern Beagle Channel; the overall number of species and abundances in these studies were lower as compared to our figures. Species richness at our study sites may be even higher because several taxa were not identified to species level (e.g. amphipods and

ascidians) and colonial bryozoans and sponges were not considered in our analysis. The poor resolution in taxonomy could explain the differences in species richness documented for holdfast associated fauna in several regions in the southern hemisphere. A study of the *Ecklonia radiata* (C. Agardh) holdfast fauna along the northeastern coast of New Zealand recorded, e.g. >385 species from 152 families and 10 phyla, not including species of compound ascidians, hydroids or bryozoans, while other groups such as platyhelminthes, sipunculids and nemerteans were assessed only as a count for the phylum (Smith et al. 1996).

There is no doubt that *Macrocystis pyrifera* forests contribute considerably to the habitat heterogeneity in the Magellan region. The heterogeneous environmental conditions along the entire Subantarctic Magellan region suggest the possibility also of a great heterogeneity in community structure and population dynamics of associated macro-invertebrates and vertebrates, both on temporal and spatial scales. *Macrocystis pyrifera* forests in this region are highly dynamic structures, which according to Santelices and Ojeda (1984) and Barrales and Lobban (1975) are totally destroyed by heavy storms every 3–4 years. We assume this lifespan of the kelp to be much shorter than the lifespans of many associated invertebrates, some of which may live up to 50 years. According to Davenport et al. (1984), the mussels *Mytilus chilensis* and *Aulacomya ater* can reach ages up to 30 years; Dahm (1999) determined ages of up to 33 years for the brittlestars *Ophionotus victoriae*, *Ophiurolepis brevirima* and *Ophiurolepis gelida*. The maximum age estimates for *Loxechinus albus* are 11 years (Gebauer and Moreno 1995). These associated invertebrate communities probably never reach a climax phase; they are rather controlled by frequent disturbance events and oscillate between different stages of maturity, all of which, however, exhibit intermediate species richness and organism densities. As Williamson (1987) questioned, 'are such communities ever stable?' This resembles in some way the situation on high

Antarctic shelves, where grounding icebergs impact benthic communities and cause a patchwork of different recolonization stages, all of which increase considerably the overall ( $\beta$ ) diversity of the benthic shelf fauna (Gutt 2001; Gerdes et al. 2003; Knust et al. 2003).

Local environmental conditions such as water temperature, turbidity and especially wind induced currents and wave action seem to govern the existence and longevity of kelp forests in the South American waters and their associated fauna. van Tussenbroek (1993) already mentioned the 'more stable Falkland Islands *Macrocystis* population' because of the absence of winter storms in the Falkland region as compared to other high latitude kelp forests in South America. The heterogeneous morphology of the marine Patagonian system with fjords and channels, open coastlines, sheltered bays and exposed beaches creates locally very different environments for kelp forests.

Lowest species numbers and abundance values in austral spring and summer sampling periods can be related with the disturbance produced by the strong wind and related factors, which are predominant in these areas during these periods. For instance, Santana et al. (2001) reported for Bahía Laredo average wind strength of 6.2 m/s in January (austral summer); in July (austral winter), the average value was 2.4 m/s. This disturbing factor can determine small-scale temporal and spatial variability in both recruitment and mortality patterns of *Macrocystis pyrifera* and, consequently, affect the microhabitat provision for the associated vertebrate and invertebrate species.

The multivariate analyses of data show significant differences in species composition, diversity and evenness both within and between sites in addition to significant differences in the temporal trend of community parameters inside each site. Variations among locations have been reported for the fauna inhabiting kelp holdfasts in north-eastern New Zealand at several spatial scales; they were due primarily to differences in the composition and richness of specific taxa such as bryozoans and molluscs (Anderson et al. 2005). In our case, high variability was observed both between areas and sampling periods, with few species maintaining similarity within sites and a greater number of species contributing to dissimilarity between sites. Our results can be related to the sporadic events of regional or local recruitment of a number of rare species of low abundance.

Due to the local differences in abiotic and biotic features, homogeneous recruitment patterns between sites are highly unlikely. Natural variations, both in space and time, of communities associated to the *Macrocystis pyrifera* holdfasts are a specific theme of interest in order to determine, for instance, human-induced effects (Smith 2000) or generality of biogeographic and historical causes determining the distribution of this species (e.g. Ojeda and Santelices 1984).

Within the Magellan region, a gradient of increasing community structure similarity to the Antarctic is found from north to south, with a gradual rather than an abrupt transition (Amtz 1999). Abundance and biomass, however, vary considerably within both regions (Gerdes and Montiel 1999). These authors suggest that the *Macrocystis* kelp forests in the shallow part of the Magellan region may provide structuring features for the communities, similar to the rich, three-dimensional suspension feeding communities based on sponges, hydrozoans and bryozoans, causing local peaks in benthic abundance or biomass.

More detailed research on species distribution and abundance patterns, including spatial and temporal variability within and between these habitats is urgently required to understand how these biological communities are structured, what factors are responsible for their structure and how the natural community should function (Dayton et al. 1998).

**Acknowledgements** Our warmest thanks to the following experts who assisted in the identification of different taxa: Igor Smirnov (Ophiuroidea), Boris Sirenko (Polyplacophora), Christoph Held (Isopoda) and Evelyn Morrison (Pisces). Funding was provided partially by the Universidad de Magallanes (Grant PR-F3-01B-98). Jorge Ramirez, Pamela Soto and Christian Muñoz kindly assisted with the field and laboratory work.

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## 5. SYNTHESIS

This thesis is dealing with three typical benthic habitats in the Straits of Magellan, which so far have received little attention: boulder and cobble fields in the intertidal, kelp forests in the upper subtidal, and level soft bottoms in the lower subtidal (Fig.1).

In summary, the principal characteristics of these habitats and their communities were found to be as follows:

- The 9 intertidal boulder and cobble terraces studied along the Straits are a particularly harsh environment. Principal factors structuring this habitat are the size of boulders and cobbles, the type of rock, and the degree of compactness of the soft-sediment matrix below and between the rocks, together with tidal waves, the related hydrodynamic flow and burial by sand, and exposure to air during low tide. Sediments between and under the stones consisted of gravel, sand or clay; an upper intertidal sandy fringe may also exist. This distinct habitat heterogeneity determined a great amount of biotic variability, i.e. a high species turnover among replicates within and between sites. Boulder and cobble fields were characterized by the numerical and weight dominance of a few species and locally reduced species richness. From these habitats, a total of 66 macrofaunal species and higher taxa was sampled; they hosted the benthic community with the lowest species number, density and biomass among the three types of assemblages considered for this thesis.
- The kelp (*Macrocystis pyrifera*) forests, two of which were considered off Fuerte Bulnes and Bahía Laredo in the Straits of Magellan, provide another characteristic habitat in the Magellan region, which due to its dense structure and high biomass from the surface to about 18 m depth is of great importance for all marine life. Strong winds and resulting currents are the most important abiotic factors in the Magellan region, causing considerable destruction and stranding of the plants including their holdfasts (cf. Fig. 3). For this thesis, only the holdfast community was studied. A total of 114 species and higher taxa were identified in these root-like structures, again with a distinct dominance of few species and a high turnover within and between sites. Despite reduced sample species richness, overall species richness and diversity in this community were high. However, seasonal sampling yielded highest values for abundance and species numbers at the two sites in autumn and winter whereas the seasonal development of evenness and diversity took a contrasting course in both areas. In Bahía Laredo evenness and diversity were higher in spring and summer than the autumn and winter values, whereas the oppo

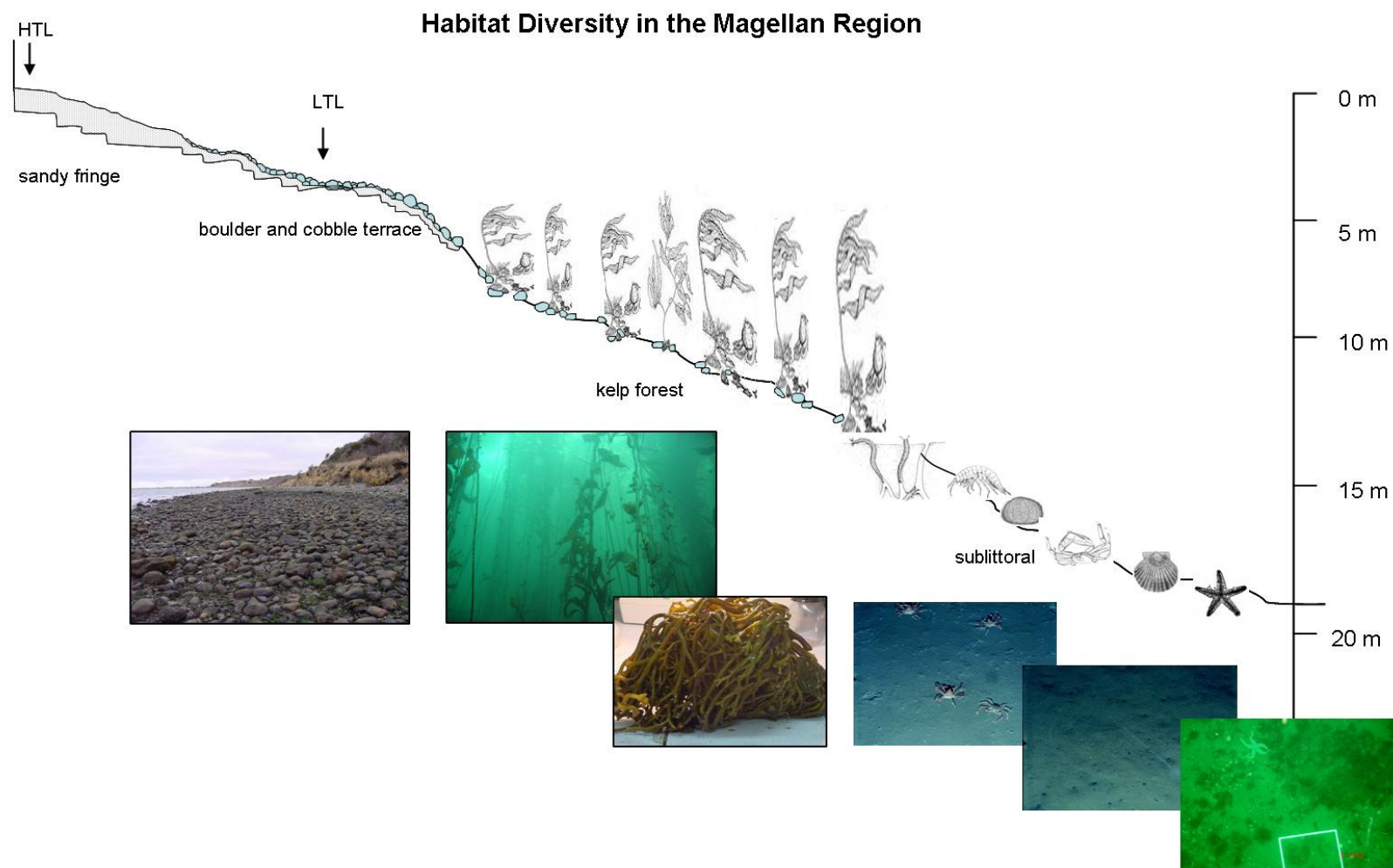


Fig. 1: Characteristic types of marine habitats in the Magellan region. Sublittoral represented just to m20m.

site hold true at Fuerte Bulnes. The two holdfast communities studied in the Straits were found to be comparably rich in species as compared to others further south towards Cape Horn, because they develop in more sheltered sites. However, even these communities do not seem to be climax communities because they are subject to frequent disturbance, especially by wind induced wave violence.

- Two sites were sampled to study the third habitat type, sublittoral soft bottoms: the first in the eastern Straits of Magellan (Segunda Angostura), between 30 and 50 m depth, applying a quantitative McIntyre grab on 6 occasions during a period of two years, and the second in the central and western Straits and off the South Patagonian Icefield (SPI), between 66 and 723 m, using an Agassiz trawl. The main environmental factor influencing the sublittoral communities in the Straits are semidiurnal tidal currents, whereas the benthic community off the SPI suffers the effect of glaciers, i.e. high sedimentation rates, freshwater input and stratification. A total of 301 macrobenthic species and higher taxa was obtained from the quantitative samples in the Segunda Angostura. Although this value is higher than that of any other community considered here, it is far from the total number of species registered so far in the area (see below). Again low sample species richness, relatively low abundances and strong dominance of few species were found. Lumping all samples over the two-year period a relatively high species richness and diversity resulted. Species richness and the abundances of single species populations varied considerably during the study period. The AGT transect from the SPI to the central Straits cannot be compared directly to the eastern grab samples because of methodological differences, but analyses based on species presence/absence reveal differences between the stations in front of the SPI and those in the rest of the Straits. The AGTs revealed rather low catches bringing up from 30 hauls just 1,895 benthic specimens. A total of 131 species/taxa were separated from all catches. Species richness in both areas was about the same (SPI 85, SM 88 species/taxa), but the abundances in the channels were consistently higher than in the SPI area influenced by glaciers. Both areas share 26 species and were dominated by few species.
- 250 species (83%) of the benthic fauna in the sublittoral zone of the eastern part of the Straits of Magellan were found only in this habitat type. The second diverse holdfast associated fauna shared 48 of the totally registered 114 species with the other types of habitat, whereas the intertidal cobble and boulder terraces as the habitat with the lowest species number (66) shared 16 species with the other habitats. From these figures it is

obvious that the two shallow water habitats, which are characteristic habitats of the entire Magellan region, contributed a greater share of their fauna to the diversity of the sublittoral benthic communities than vice versa.

- The coexistence of a variety of different habitats with specific communities makes it difficult to define any latitudinal gradients, i.e. more or less continuous changes in community parameters in the Magellan region. It rather enhances abrupt changes in species richness. Changes in community structure were found to be abrupt also over short distances due to the existence of sharp environmental/ morphological differences in habitat structures.

These results are discussed in more detail below and related to the findings of other authors.

#### ● **Heterogeneity in benthic communities**

The question whether the enormous environmental heterogeneity of the Magellan area is reflected in a similar heterogeneity of its benthic communities can be positively answered from my investigations, although detailed descriptions and comparisons of many benthic communities inhabiting different types of habitats in the Magellan region are still lacking. Considerable variability in community structure, i.e. densities, biomasses, species composition, dominance of certain species, species richness and diversity was observed in all the studied Magellan habitats.

In the boulder and cobble fields patchiness was evidenced inside sites by zonation patterns along the intertidal profiles but also in distinct differences between study sites in the Straits of Magellan and those in the Cape Horn Archipelago (Publ. N° I and Data Report N°II). In terms of biomass molluscs appeared highly dominant in this habitat at all study sites. Concerning the abundance of dominating species the more sheltered intertidal areas in the Straits of Magellan house a different fauna dominated by big and sessile molluscs as compared to the unprotected and exposed habitats at Cape Horn, where tiny and motile crustaceans (e.g. *Exosphaeroma gigas* and *Paramoera fissicauda*) dominate, probably because these species are able to escape from this frequently highly disturbed habitat into deeper, more stable parts of the system. The community parameters abundance, biomass, species richness and diversity and evenness appeared highly variable both at Bahía Laredo and Caleta Toledo, which are more than 350 km apart from each other.

The inside site zonation patterns described by me follow the depth profiles and can be divided roughly into three depth zones at all the intertidal study sites. These patterns coincide with patterns from previous studies in Magellan intertidal boulder and cobble fields (e.g. Langley et al. 1980; Guzmán 1981; Ríos & Gerdes 1997). Similar results are reported also from intertidal boulder and cobble fields in Australia (McGuinness & Underwood 1986; Chapman 2002), western Brittany, France (Le Hir & Hily 2005) and for several Subantarctic and Antarctic areas (Arnaud 1974). On the other hand, our results contrast with results obtained by Benedetti-Cecchi & Cinelli (1997), who did not find any zonation patterns at all in their Magellan studies. I believe that these differences exist because of different sampling procedures, i.e. the resolution of the different depth horizons by their sampling stations probably did not allow to recognize such patterns, which are well known from this type of habitat worldwide as mentioned already above.

Sublittoral soft bottoms were studied qualitatively by using samples obtained with AGT (Publ. N° III) and quantitatively with samples from a McIntyre grab (Publ. N° IV). Both methods show the sublittoral habitats between the South Patagonian Icefield (SPI) and the first and second Angostura in the eastern Straits of Magellan (SM) to host the most diverse benthic communities of all studied habitats (Fig. 2). The 270 quantitative samples obtained from the sublittoral in the eastern Straits brought up 301 macrozoobenthos species and major taxa with a mean number of 105 species per station. Due to the method applied polychaetes were the most diverse and dominant taxon in the grab samples in terms of species numbers (119), followed by crustaceans (68), gastropods (44) and bivalves (21). As documented also for the intertidal boulder and cobble fields few species such as *Astarte longirostris*, *Eurhomalea exalbida* and *Cyamiocardium denticulatum* (bivalves), *Trochita pileolus* (gastropod), *Themiste sp.* (sipunculid), *Hemipodus simplex* and *Notocirrus lorum* (polychaetes), *Magellania venosa* (brachiopod) and *Euvallentinia darwini* (isopod) were numerically dominant.

The AGT samples in the western Magellan region discriminated two groups of stations based on presence-absence data. One group included all the stations from the SPI and the second one comprised stations from the SM area. The catch efficiency of the AGT was comparable in both areas, i.e. 44 % of all specimens were caught at SPI stations. This is somewhat surprising, because from quantitative samples the SPI showed the mean

abundance ( $627 \text{ ind m}^{-2}$ ; Thatje & Mutschke, 1999) to be 3 times lower as compared to SM data.

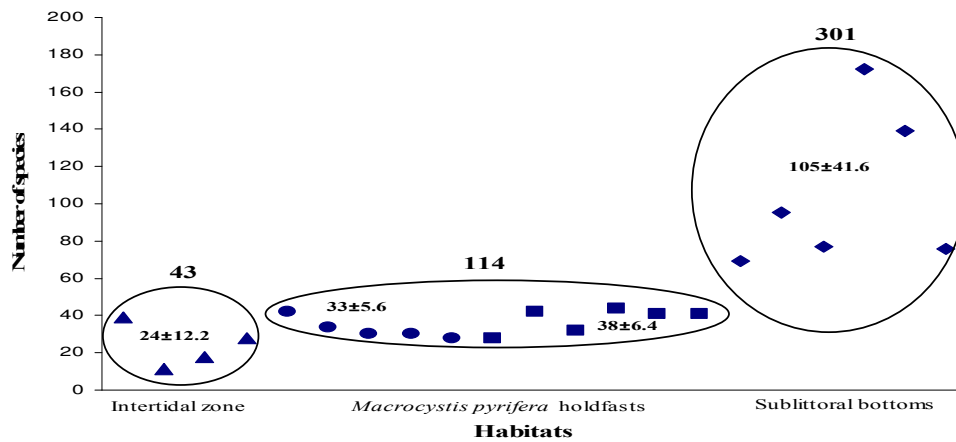


Fig 2. Sample species richness and standard deviation in quantitative samples of different habitat types. In bold the total number of macrofaunal species and taxa identified in each of the habitats.

Despite these lowest organism densities the species richness in front of the SPI was almost in the same order of magnitude as the mean number of species in the SM sublittoral habitats, thus not evidencing a community impoverished in species as one would suggest because of the unfavourable environmental conditions in front of the glaciers. Comparing organism densities higher mean abundances resulted from multibox corer stations in the Paso Ancho ( $1591 \text{ ind m}^{-2}$ ), in the Beagle Channel ( $4467 \text{ ind m}^{-2}$ ) and on the open continental shelf and slope of its eastern entrance ( $2319 \text{ ind. m}^{-2}$ ; Gerdes & Montiel 1999) resulted. These data suggest the existence of a numerically impoverished fauna living in the inner fjords directly in front of the glaciers of the SPI.

The AGT as a towed gear collected epibenthic organisms as echinoderms much more efficiently and brought up 47 different species with asteroids (25) and ophiuroids (13 species) being best represented. Polychaetes were the second dominant group with 46 species, followed by molluscs with 26 species. *Harmothoe campoglacialis* and *Polyeunoa laevis*, two carnivorous polychaetes were numerically dominant within the 29 species found in the SPI, whereas 16 species occurred in the SM area with *Eunereis patagonica* and *Chaetopterus sp.* as the numerical dominants. Echinoderms were the most diverse taxon in the SM, occurring there with 36 species whereas 22 species were found at the SPI sampling sites. Based on the presence/absence data matrix 10 species contributed  $> 50\%$  of the dissimilarity between both areas: five echinoderms (*C. procurator*, *O. lymani*, *P.*

*magellanicus*, *P. patagonicus*, Holothuroidea sp.), mostly omnivorous deposit feeders, the 3 molluscs *L. marionensis*, *Dentalium majorinum*, *C. subhyalinus*, the isopod *Acanthoserolis schythei* and the brachiopod *Magellania venosa*. All these main discriminating species dominate the SM fauna more than the SPI community.

The kelp holdfast has to be regarded as a rather dynamic habitat of high importance for the diversity of the Magellan benthos. The comparatively rich benthic fauna exhibited many species occurring exclusively in the holdfasts and not in the surrounding sediments. Comparing, e.g. the polychaetes as the dominating and best studied faunal taxon, almost 90 % of the 43 polychaete species found in holdfasts were absent in the surrounding sediments, however, known from other parts of the region (Montiel, pers. comm.). It is interesting to note that this taxon was practically absent in samples obtained by Ojeda & Santelices (1984) in the southern Beagle Channel and by Adami & Gordillo (1999) in the northern Beagle. In the case of echinoderms nine out of twelve species occurred also in the surroundings (Mutschke & Ríos 2006).

*Macrocystis pyrifera* as an ecosystem structuring species covers almost 30% of the entire Magellan shallow coastal waters. Kelp forests are important habitats for several reasons. The plants consist of different parts, all of which play substantial roles for benthic organisms, e.g. as sheltered refuges for reproduction, as feeding grounds, or as dispersal tools for benthic species. Particularly the holdfasts host a rich and diverse associated benthic fauna. *Macrocystis* in the Magellan area probably plays an outstanding role for the successful dispersal of benthic species by means of the West Wind Drift (WWD) and the Antarctic Circumpolar Current. Mortensen (1925) first indicated the significance of this unidirectional eastward flowing “transport system” for the dispersal of benthic species, which due to their reproduction modes normally do not own wide distribution ranges within the southern hemisphere. Helmuth et al. (1994) provided evidence for long-distance dispersal (up to 2000 km) of brooding *Gaimardia trapesina* on floating dislodged rafts of *Macrocystis pyrifera* from Magellan waters. Recent studies of the Bouvet Island benthic fauna have raised further speculations about a possible eastward expansion of the South American fauna to this island with its remote position directly within the WWD (Arntz 2006). It is interesting to mention that according to Linse (2006) the mollusc fauna of Bouvet Island shows more affinities to the Magellan mollusc fauna than to high Antarctic molluscs.

Looking back at the first three hypothesis presented in the Introduction I conclude,

- the enormous habitat heterogeneity of the marine realm in the Magellan region is reflected in density, biomass and diversity patterns of the benthic communities studied in different habitats.
- abundance, biomass and species richness increase with increasing depth. The sample species richness appeared highly heterogeneous in all habitats/depths and also seasons. These findings suggest non-equilibrium communities in all habitat types maintained by different effective disturbance regimes. High local species richness is maintained by higher heterogeneity patterns among samples, both in a spatial and temporal sense. These findings agree with Picken's (1985) assumption that environmental stability might explain benthic diversity.
- the highly complex *Macrocystis pyrifera* holdfasts with their considerable species richness contribute significantly to local (beta) diversity.

- **Latitudinal patterns**

Because of its exposed position directly adjacent to Antarctica the Magellan region is a key region for the analysis of biogeographic units in the southern hemisphere, for studies of species richness along latitudinal gradients and for global comparisons of benthic community structure and functioning in ecosystems. In fact, the more uniform temperate Pacific coastline off north and central Chile might be better suited than the Magellan region to define latitudinal gradients in benthic community parameters. However, between a well-colonized coastal strip (Tarazona et al. 2003) and fairly rich deep-water communities (Palma et al. 2005) the Oxygen Minimum Zone (OMZ) hosts impoverished benthos communities in a rather monotonous way along several latitudes of coastline (Tarazona et al. 2003; Gallardo et al. 2004; Palma et al. 2005; Quiroga et al. 2005; Arntz et al. 2006; Laudien et al. 2007). Unfortunately no latitudinal benthic inventories along the entire Chilean coastline have been performed so far (cf. also Fernández et al. 2000 and Escribano et al. 2003).

Although one might suggest a gradient of increasing benthic abundance and biomass within the Magellan waters from north to south (Gerdes & Montiel 1999), these data probably reflect local environmental conditions and gear differences rather than a latitudinal gradient. Despite high variability in dominant species between Bahía Laredo and Caleta Toledo, 3° of latitude apart, there was no evidence of any trend or gradient,



although the observed difference between these sites turned out to be significant. I suggest the response of benthic organisms at the different sites to specific local environments to be too strong to allow the recognition of such gradients; they might exist but overlaid by local characteristics. This statement is corroborated by data of Gerdes & Montiel (1999) who compared benthos community parameters from the high Antarctic Weddell Sea shelf and the Magellan region. They detected differences in species composition but no latitudinal gradient in densities and biomasses. Piepenburg et al. (2002), working on benthic assemblages off King George Island, (Antarctic Peninsula), provided further evidence that no distinct latitudinal gradients in benthic abundance and biomass exist between Antarctica and the Magellan region.

Information available on diversity aspects for the benthic systems is similarly unsatisfactory. The few studies available seem to indicate local hotspots of diversity and species richness rather than any latitudinal gradients, although Escribano et al. (2003) reported after a decrease of species richness from northern Chile to about 40/45° S a “dramatical increase” to the southern tip of South America. Abrupt changes in species richness have been commented, too, in molluscs (Valdovinos et al. 2003), polychaetes (Montiel et al. 2002, 2004), sea anemones (Häussermann & Försterra 2005), echinoderms (Mutschke & Ríos 2006), among other taxa (see Arntz & Ríos 1999 for further details). These changes did not reveal any consistent trend. Clear differences, however, exist in species composition and relative importance of higher taxa along latitudes, without showing a common pattern with decreasing species numbers towards higher latitudes as predicted by the ‘bell shaped curve’ (Arntz et al. 2005). Only some taxa follow this concept at least partly and show lower species numbers in the high Antarctic Weddell Sea (e.g. macroalgae, decapods, stomatopods, cirripeds) than in Magellan waters, whereas other taxa (e.g., sponges, amphipods, isopods, polychaetes, echinoderms) occur with higher species numbers in Antarctic waters.

**Summarizing my results and further data from literature, the answer to the fourth hypothesis is,**

- **my results do not evidence any clear latitudinal gradients in benthic abundance, biomass, species richness and diversity.**
- **however, different local disturbance regimes at sites in the sheltered Straits of Magellan and the exposed sites off Cape Horn determine a different composition in**

**the dominant species with tiny motile crustaceans in the Cape Horn Archipelago versus large sessile bivalves being the dominants in the SM.**

● **Disturbance**

During my studies in different typical habitats types in the Magellan region I identified glaciers, wind and high water currents as disturbance agents impacting benthic communities on local and regional scales.

Directly in front of glaciers, particularly after calving events, ice may destroy benthic communities locally. More important, with effects on larger scales, are indirect influences through mass transport of fine sediments and terrestrial runoff of freshwater with various chemical compounds towards the marine realm. These conditions affect processes in the water column and at the seafloor in a similar way. I identified one impoverished benthic community living under these conditions directly off the glacier tongues. It differed in its composition from the richer channel community living at a greater distance from the glaciers, as is confirmed by Thatje & Mutschke (1999). Due to high sedimentation loads in the water column, suspension feeding species were rare with few specimens; mostly burrowing, large-sized species, which can cope with the soft sediments, contributed the bulk of the biomass.

Wind, tides, wind induced surface currents and wave actions affect benthic communities in intertidal boulder and cobble terraces and Magellan kelp forests alike. The variability in species composition and richness in intertidal boulder and cobble terraces has been explained with sediment characteristics (e.g. grain size) and the degree of compactness of the fine soft-sediment below the boulders and cobbles. This matrix can be disturbed severely by tidal-wave force and fine-scale hydrodynamic flow patterns around single boulders and rocks (Sousa 1979; McGuinness 1987; Archambault & Bourget 1996; Cusson & Bourget 1997; Chapman 2002). This impact may locally cause extreme heterogeneous inside-habitat patterns (zonations), it may contribute also to distinct differences between different intertidal terraces. Locally differing disturbance intensities related to more exposed or sheltered specific locations may explain the variability observed in the boulder and cobble benthic community structure in this characteristic habitat of the Magellan region.

The distribution of *Macrocystis pyrifera* kelp forest in the Magellan region is determined greatly by these physical factors. Kelp forests are not found in areas heavily affected by

glacier related disturbances and they also do not grow in the easternmost sector of the Straits of Magellan with prevailing much higher current velocities and probably higher tidal amplitude (own observation). They prefer more or less sheltered locations, although some forests also grow on exposed beaches (Dayton 1985). The associated holdfast fauna, too, is impacted by wind induced violence in surface waters. According to Santelices & Ojeda (1984b) or Barrales & Lobban (1975) the kelp forests in Magellan waters are regularly destroyed by heavy storms every 3 to 4 years. Most beaches of the Straits of Magellan are totally covered by numerous destroyed holdfasts lying around, demonstrating these catastrophic events (Fig. 3).



Fig. 3: Piles of *Macrocystis pyrifera* holdfasts washed ashore in Bahía Laredo, Straits of Magellan

The mismatch between the longevity of kelp as a habitat and the inhabiting benthic species with much longer lifespans suggests that the holdfast communities have to be regarded as immature communities. Both sites off Fuerte Bulnes and in Bahía Laredo in the Straits of Magellan, however, can be regarded as more or less sheltered bays where predominantly south-easterly winds create less disturbance to the plants, thus suggesting the benthic holdfast communities to be more stable as indicated by higher species richness and diversity. In fact, Ojeda & Santelices (1984) described the holdfast fauna in less sheltered kelp forests off Isla Navarino at the eastern entrance of the Beagle Channel to be less diverse, with lower species numbers (42 taxa plus one fish species) as also do Adami

& Gordillo (1999) for a wind exposed *M. pyrifer* forest off Ushuaia with 54 holdfast associated species:

There are some hints in my data that high current velocities, too, have to be regarded as a physical disturbance. The Segunda Angostura (second embayment) in the eastern SM sector has mean tide amplitudes of 7.1 m and strong currents related with the large semi-diurnal tidal wave entering from the Atlantic Ocean (Medeiros & Kjerfve 1988) which often exceed  $80 \text{ cm s}^{-1}$  and may reach near surface maxima of  $125\text{-}130 \text{ cm s}^{-1}$ . In the adjacent Paso Ancho the currents appear drastically reduced. Strong currents might interfere with the whole marine system by determining e.g. processes of erosion and resuspension of the bottom sediments, thus making medium to coarser sand and gravel the main sediment fractions, whereas finer fractions are washed out. This situation holds true also for the seafloor in the Segunda Angostura.

The Segunda Angostura with high current velocities and the Paso Ancho as a habitat with distinctly lower current velocities reveal differences in benthic community organism densities, biomasses and composition (Tab. 1, Fig. 4).

Table 1. Mean abundance and biomass data obtained quantitatively at different sites (< 100 m water depth) with distinctly different current regimes in the Magellan region. <sup>1)</sup>near-bottom mean current velocities after Michelato et al. (1991)

	Paso Ancho (Straits of Magellan)	Second Embayment (Straits of Magellan)
abundance (ind m <sup>-2</sup> )	2695	245
biomass (mg AFDW m <sup>-2</sup> )	18.04	11.03
current speed (cm s <sup>-1</sup> )	20 <sup>1)</sup>	64 <sup>1)</sup>

In the second embayment the benthic fauna was clearly less abundant as compared to the adjacent Paso Ancho stations. The holothurians *Athyonidium chilensis* and *Pseudocnus dubiosus leoninus* dominate the community in terms of biomass followed by molluscs whereas bivalves, polychaetes, brachiopods and the sipunculid *Themiste sp.* were dominating in terms of organism densities.

The Paso Ancho stations showed a rather different community composition with crustaceans, especially cirripedes being dominant in terms of biomass and almost 10 times higher mean abundance of organisms. These few data suggest that high current velocities might contribute to the structure of benthic communities. AGT samples collected directly

in the eastern Atlantic entrance of the Straits of Magellan, where extreme current velocities are measured, underline this impression by extremely low catch volumes from which  $< 10 \text{ ind. m}^{-2}$  were calculated (own unpubl. data).

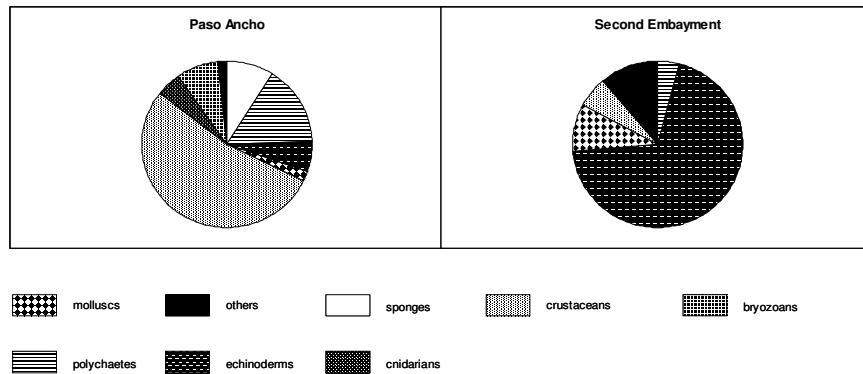


Fig. 4: Composition of benthic communities living under different current regimes in the Magellan region

#### Summarizing I conclude that

- the benthic fauna in glaciated areas appeared impoverished in terms of abundance and biomass, however not in species richness. Abundance and biomass differed from a richer channel community living at more distance from the glaciers. Filter feeding species in waters with high sedimentation loads were rare.
- wind induced wave violence affects the sediment matrix in intertidal boulder and cobble terraces and causes heterogeneous within-habitat patterns as well as differences between sites in benthic communities.
- the distribution of *Macrocystis pyrifera* beds is also determined by physical factors such as strong winds and currents. Frequent disturbance destroys the plants and affects the associated holdfast fauna, thus keeping it in an immature status.
- subtidal benthic communities living under high current velocities appear impoverished in terms of abundance and biomass and show a different composition as compared to communities in areas with lower currents.

#### ● “Magellan benthos” in a “Magellan Province”?

Benthic research in waters at the tip of South America has been intensified considerably in the last decades, providing improved benthic species inventories and important insights into the relationships between species and the environment. Nevertheless, we are far from understanding the complex benthic structures and processes in this heterogeneous region.

Above all, the question which zoogeographical position is held by “the Magellan Province” is still controversially discussed in the scientific community (see Introduction). Different approaches and criteria impede a clear definition of specific borders of a distinctive “ typical Magellan benthic regime” thus including on the one hand the entire tip of South America south of Rio de la Plata on the Atlantic side to Chiloé Island on the Pacific coast (e.g. Stuardo 1964), whereas Montiel et al. (2005a) restricted the Magellan Province exclusively to waters around the tip of the Cono Sur, including waters off the South Patagonian Icefield, the Straits of Magellan, the Beagle Channel and the Cape Horn Archipelago. Camus (2001) described from literature studies at least 27 different definitions to discriminate zoogeographical units along the Chilean coastline. Why are precise definitions of a “ Magellan Province” so difficult to make?

Such definitions rely on the structure and the species inventories of benthic communities in specific areas. These communities are shaped by the specific environments, i.e. mainly by their topography and hydrography. In areas with relatively homogeneously structured environments the definition of zoogeographic units appears rather clear. Examples are e.g. the Peruvian Province along the relatively simply structured shelf areas off Peru and north/central Chile or the isolated high Antarctic Province with its unique communities. The Magellan region, however, is a highly heterogeneous and patchy realm with thousands of fjords, channels, lakes, all different in topography and hydrography, exposed to totally different disturbance regimes and influenced by different current systems. I doubt that within this complicate region the definition of a Magellan Province is possible. All benthic studies performed up to now evidence the fauna in this region to be a melting pot of faunistic element from the northern Peruvian Province, from high Antarctic waters and from both adjacent oceans. The Magellan waters with the inhabiting benthic communities thus appear to be rather a transitional zone of species from adjacent provinces than as a distinct zoogeographic unit on its own with typical characteristic benthic inventories.

**Answering hypothesis 6, my thesis shows**

- **the Magellan waters to be a transitional, highly heterogeneous zone between cold water and temperate ecosystems with local disturbance regimes, which are reflected in very different benthic subsystems and communities. All of these systems contribute to the high overall biodiversity of the region.**

- **the non-existence of a typical “Magellan zoobenthos”, rather a mixture of faunistic elements from Pacific, Atlantic and Antarctic waters.**

• **Are young ecosystems necessarily poor in species? Young Magellan benthos vs. young benthos elsewhere**

The Magellan region was recolonized by marine benthic species only about ten thousand years ago after the retreat of the LGM ice sheet (cf. McCulloch et al. 1997). Comparable young systems in the northern hemisphere are the southern North Sea and the Baltic Sea. The North Sea is a marginal sea of the Atlantic Ocean with a surface area of 575,000 km<sup>2</sup> and a mean depth of 70 m. Its southern part up to the Doggerbank is shallow, mostly less than 30 m, and only slowly recovered a marine character after the last glaciation. The salinity of the water depends on the locality and time of the year and lies in the range of 15 to 25 o/oo around river mouths and up to 32 to 35 o/oo in the central North Sea. The surface water temperature can reach up to 25°C in summer, whereas winter temperatures normally decrease to about 3°C except in ice winters, when they may reach below 0°C (Dekker & de Bruin 2000). Also the Baltic Sea, formed after the latest glaciation by a series of transitional stages part of which were freshwater, is a young ecosystem. It is an enclosed, non-tidal sea with low winter temperatures accompanied by surface ice in the north and east and steep latitudinal and vertical salinity gradients. The western parts are connected via the shallow Kattegat and the deep Skagerrak with the open ocean and have salinities between 25 and 30 o/oo at the seafloor. Within a few hundred km east- and northward these values drop to 5 o/oo and finally towards more or less freshwater conditions (Zettler et al. 2007). As a consequence of this strong gradient the number of macrozoobenthic species decreases significantly towards the east and north. Whereas in the sublittoral of Kiel and Mecklenburg Bay 150-240 species may occur regularly (Zettler et al. 2000, Arntz & Gili 2001), only around 100 species are known from the Pomeranian Bay further east (Zettler et al. 2007). The relatively high number of about 600 macrofaunal species compiled by Gerlach (2000) for the western Baltic includes all the occasional immigrants from the Kattegat ever registered in this area over 135 years as well as the intertidal and brackish-water fauna. Species numbers are high from the Norwegian Sea (Gray 2001) to the Skagerrak and then decline rapidly towards the inner parts of the Baltic. This decline in the overall number of benthic species, from > 1600 in the open

Skagerrak to < 20 species in the northern Baltic region has been illustrated again by Bonsdorff (2006).

According to Hayward & Ryland (1995) appr. 1500 species make up the north-west European marine macrofauna. As is the case in the Baltic Sea the North Sea macrozoobenthos, too, has to be regarded as species poor. Salzwedel et al. (1985) identified in the German Bight 219 species, Kühne & Rachor (1996) distinguished 289 species in a stony area northeast of the island Helgoland. Harms (1993) extracted from recent publications 666 macrobenthic species for intertidal and subtidal hard-bottom communities around Helgoland. More recently, Daan & Mulder (2000) monitored the Dutch sector of the North Sea and arrived at about 200 macrofaunal species

A preliminary checklist of the marine macrozoobenthic taxa reported for the Magellan area from the available literature indicates the existence of at least 1400 species (this checklist is available upon request from the author of the thesis). For the remainder of Chile further north Lancellotti & Vásquez (2000) registered almost 1600 macrozoobenthic species in <100 m water depth. As a reference, Gutt et al. (2004) estimated for the entire Antarctic shelf (as a much older system) a total number of macrozoobenthic species ranging between 11,000 and 17,000 species.

Obviously the Magellan marine benthic ecosystem, although being as young as the Baltic and North seas, appears to be richer in macrozoobenthic species numbers than both ecosystems in the northern hemisphere, although the species numbers in the Skagerrak, the only natural invasion corridor for benthic species to the Baltic Sea from the open North Atlantic, were comparably high. Furthermore, unlike the Baltic and the southern North Sea, this deep area suffered less the impact of the last glaciation (Dietrich & Köster 1974).

The above mentioned comparisons suggest that young ecosystems are not necessarily low in species number. I suppose several factors to be important for the recolonization of glacially defaunated marine realms and the successful establishment of communities. Among these are environmental heterogeneity and stability (constancy of physical conditions) of a specific region and biogeographic isolation. For example, a striking difference between the Magellan region and the two northern hemisphere systems is that the region at the southernmost tip of South America is influenced by very different systems such as the West Wind Drift from the Pacific Ocean, by high- and Subantarctic waters and also from the Atlantic Ocean, whereas the southern North Sea and especially the Baltic are sparsely connected just with the (north) Atlantic water masses and their



fauna. This means that the Magellan region is provided with potential new species from a much bigger reservoir of all different systems surrounding the Magellan region as compared to both northern hemisphere systems. Another reason for higher species numbers in the Magellan region probably is a greater habitat heterogeneity which enhances colonisation success of a broader variety of species and living modes on very different spatial scales. This is to some extent shown by my community studies in the different Magellan habitats; Bonsdorff et al. (2003), too, described the heterogeneous local conditions to have clear implications on the benthic communities in the western Gulf of Finland.

In recent decades the benthic communities in the southern North Sea and the Baltic Sea have shown stress symptoms due to eutrophication and pollution (Ducrottoy et al. 2000; Falandysz et al. 2000; Karlson et al. 2002), fishery impact (De Groot & Lindeboom 1994; Jennings & Kaiser 1998; Lindeboom & De Groot 1998; Frid et al. 2000), dumping of harbour sludge, constructions in coastal habitats, etc. With increasing levels of stress benthic communities may respond with alternating community structures towards a dominance of small, opportunistic species, which, e.g. replace larger, long-lived organisms that can be used commercially (Pearson & Rosenberg 1978; Thatje & Gerdes, 1997).

Relationships between benthic community development and eutrophication effects, but also changing climatic conditions, food supply and disturbance regimes such as extreme weather conditions were described by Schröder (2005) for the German Bight (North Sea). Stress imposed by eutrophication effects has modified benthic communities also in the Baltic Sea; above the halocline and in coastal waters biomass increased (Brey, 1986) whereas in deeper parts it collapsed due to hypoxia or anoxia (Arntz 1981; Diaz & Rosenberg 1995; Karlson et al. 2002). Further changes observed in benthic communities include the invasion of non-native species (Gollasch et al. 1999; Nehring & Leuchs 1999; Leppäkoski et al. 2002; Franke & Gutow 2004) some of which may be considered as indicators of a warming trend, and a poleward shift of species due to climate change induced warming as recently recorded for marine fish by Pörtner & Knust (2007).

Basic requisites to follow such developments in benthic communities induced by natural or anthropogenic disturbance are long-term data sets both for environmental parameters and the benthos. Sublittoral benthic communities are less affected by short-term events,

because they live in an ecologically more stable environment than intertidal communities. They may therefore be expected to reveal true long-term trends in ecological parameters easier and more reliably. Unfortunately the hitherto performed benthic and environmental studies in Magellan waters have been more of a snapshot character than representing long-term monitoring campaigns. Such campaigns, however, are urgently needed to allow to monitor natural and anthropogenic environmental changes and the response of benthic communities to these. In comparison to the North Sea and the Baltic the Magellan waters have to be regarded as less disturbed by human activities, although natural disturbance factors such as wind, wave action and ice have clearly been identified by this thesis. Oxygen deficiency does not occur in the Magellan region (Silva & Prego 2002), eutrophication is low, and marine pollution is restricted to occasional tanker accidents (Guzmán & Campodonico 1981). Bottom trawling is insignificant in this area where the major fisheries targets (king crabs, echinoids, gastropods and demersal fish, SERNAPESCA reports 1998-2005; Arntz et al. 2005) are caught by baited traps, divers and longlining. Conversely, certain areas in the North Sea are trawled by heavy bottom or beam trawls up to 10 times per year (Arntz & Laudien 2006). Climate change induced sea surface temperature increase (Fig. 5) reveals obvious changes during the last century. Monitoring and long-term time series are urgently required to recognize responses of the environment and the biota.

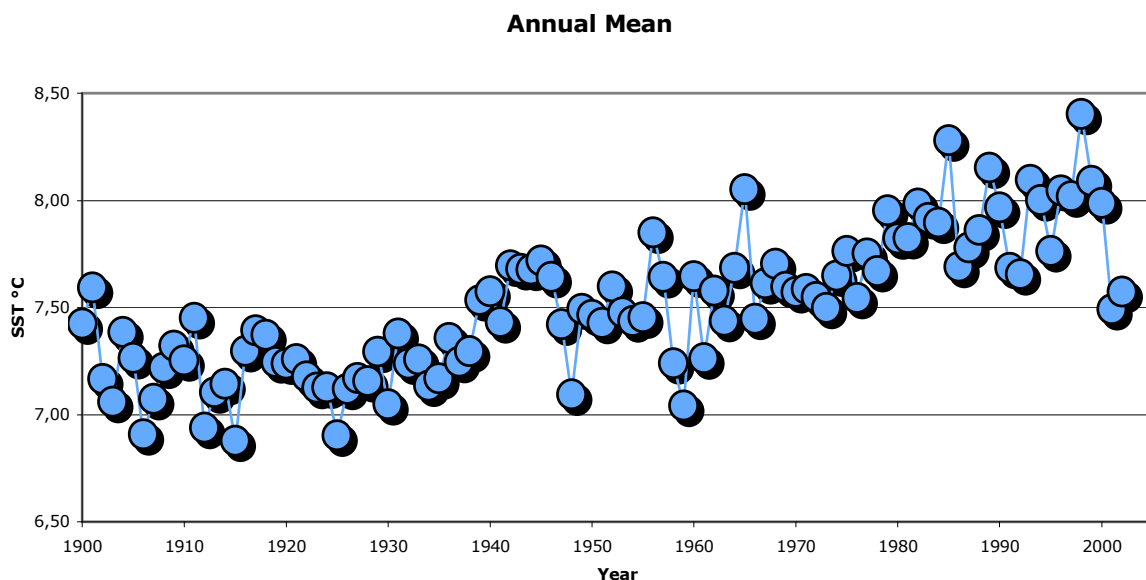


Fig. 5: Sea surface temperature (SST °C) for the area of Ushuaia (Tierra del Fuego, Argentina) reconstructed using the most recently available comprehensive Ocean-Atmosphere data set. After Smith & Reynolds (2004).

**In conclusion, hypothesis 7 can be answered as follows,**

- **young systems of comparable age are not necessarily poor in species numbers. The Magellan waters are species richer than the southern North Sea and the Baltic Sea.**
- **different species numbers can be explained to some extent by the degree of isolation of the specific system.**
- **different species numbers most likely also reflect differences in the kind and intensity of disturbance regimes, both natural and man made.**
- **due to the lack of long-term environmental and benthos data sets in Magellan waters it is almost impossible to refer benthic responses with any degree of certainty to climate change, natural or anthropogenic stress. It is obvious, however, that the Magellan system is subject to less disturbance from fisheries, eutrophication and pollution than the two young seas in the northern hemisphere.**

#### ● **Perspectives**

Work during the preparation of this thesis has shown that the inventory of the Magellan benthic ecosystem is far from complete. Many more studies are required to integrate those parts, which have so far received little attention, including the two internal seas (Seno Otway, Seno Skyring) and most of the narrow channels and fjords of the Cape Horn Archipelago and the South Patagonian Icefield. Also on the Argentinean side there are large areas needing further investigation, e.g. the Isla de los Estados. Including these areas will provide a much improved picture of the Magellan region as a whole, which is necessary to arrive at final conclusions about the region as a biogeographic entity and latitudinal faunal gradients. It will also facilitate the comparison with the Antarctic benthos, which was initiated in the frame of the IBMANT activities (Arntz & Ríos 1999, Arntz et al. 2005). The Magellan region is ideal to continue these studies on faunistic relationships especially with the Antarctic, but also with other fragments of former Gondwana.

Environmental changes due to climate change are expected to become more and more evident in areas such as the Magellan region, which are especially sensitive because of their geographical position at the edge of the big ice masses. The ecology of non-equilibrium benthic communities can be strongly negatively affected, with shifts in their composition from long-lived, in some cases also economically important species to opportunistic species. However, temporal variability of the most relevant

species/communities in the Magellan region is virtually unknown. We need to study community parameters (species richness, dominance, diversity, abundance, biomass) in time series in order to allow the monitoring of responses of marine biota to natural and anthropogenic changes in the environment, in particular to global climate change. These studies have to be planned as long-term studies together with other disciplines (oceanography, geology) to provide the necessary physical and geological background for the biological patterns and processes. While traditional approaches should continue to complement the faunal inventory, new methods, e.g. in molecular genetics and the use of stable isotopes, should also be included for the solution of questions such as cryptic species, the identity of disjunct populations and biogeographic connections, or of age and growth of species that cannot be aged from growth rings or other marks.

These studies should also have an applied aspect. For example, intensified aquaculture already under way (e.g. salmon) and extended fishery activities on crustaceans, molluscs, echinoderms, as well as ideas to use *Macrocystis pyrifera* as an alimentary source, might alter the marine Magellan system significantly. *Munida* spp. are a potential resource for the future, gastropods such as *Adelomelon* spp. and *Trophon geversianus* as well as the bivalve *Ensis macha* are presently exploited. There already is evidence of overexploitation of economically important Magellan benthic species such as *Loxechinus albus*, *Lithodes santolla* and *Chlamys patagonica*. Accompanying new research activities have to be developed in order to allow the sustainable use of the rich marine resources and to enable their management.

## 5. ACKNOWLEDGEMENTS

This thesis had not been possible without the generous support and permanent encouragement given for several years by a special German ecologist interested in studying the – sometimes ignored – marine benthos. This is my “Doktorvater” Prof. Dr. Wolf E. Arntz who, as only a few Chilean have done so, has been encouraging for more than a decade the study of the marine ecosystem of the great southernmost region of Magellan (and its relation with Antarctica!).

The generous support offered by Dr. Dieter Gerdes was the essential complement to achieve this goal. Dr. Gerdes put all his tolerance at stake to overcome, during the whole period of difficult work, difficulties with the language, the varied insufficiencies in the depth of the analyses and my very long paragraphs derived from Spanish.

This is a good opportunity to point out that, on the ideas aspect, many times one does not realize well when our own ideas start and when those of influential persons finish in that aspect. Although imperfect, this thesis is an example of the above.

To both of you my sincere thanks for this great opportunity!

I would like to thank Prof. Dr. Matthias Wolff for taking over the co-promoter in a very final stage of this work.

Many suggestions and many ways of contribution for the development of this thesis came from Dr. habil. T. Brey and Dr. R. Knust. My appreciation for all of them.

At certain levels of life it must exist persons that with their permanent support to overcome the work obligations, have also contributed to finish this stage. That is why I show my appreciation to my colleagues from the Laboratorio de Hidrobiología, Instituto de la Patagonia, Universidad de Magallanes, Lic. Erika Mutschke and Dr. Américo Montal SM. Also from the same Laboratory are Cristian Muñoz, Claudia Andrade, Luís Vladilo, Daniel-W Antúnez and Jorge Capitano Ramírez; thanks for your rapid answers to the several requests of data, reports, drawings, figures, for your good sense of humor and trying to keep the idea of a Laboratory with more emphasis in labor than in oratory.

I also want to express my gratitude to my wife Erika Mutschke. All this time she could bear not only her own mood and strength of character, but those of our dear Ignacio and Antonieta and, as it that were not enough, also mine. In the last months that task was very critical and allowed me an invaluable time to pay all possible attention to only one task. Thanks to the three of you for waiting for me. For Rosita also my gratitude.

I also want to emphasize the generous friendship received for a long time in the North of Germany. Those deep gestures are also part of this thesis. The Gerdes-Schröder family (Dieter, Sabine, Ella Gesine und Berta) not only opened their home to me, but also their ways of life. My deepest appreciation to all of them and their many and good friends I could meet during my many trips to Sorgenfrei (Bremen) and the Weserstadion.

The highest authority in my University, the Chancellor Prof. Dr. Victor Fajardo, gave all his support to this thesis and made it possible for me to have the maximum support from Universidad de Magallanes in the last period in order to finish this thesis. I also thank the personal interest and support of the Director of the Instituto de la Patagonia, Prof. Claudio Venegas, to get all the necessary leave of absence required to fulfill this task and for his words of friendly encouragement.

A big part of the biological material included in this thesis came from several site campaigns in the Magellan region. These campaigns were partially or completely financed by the Comité Oceanográfico Nacional – CONA, the Research Office of Universidad of Magallanes and also the Laboratorio de Hidrobiología through their agreements with several private companies. Also, some of the academic exchanges both to Chile and to Germany that took part in this thesis were financed by the International Bureau of the BMBF, Germany.

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## **APPENDIX I**



**Appendix 1.** Partial list of scientific articles related specifically with the benthic assemblages in the Magellan region marine ecosystem. Arbitrary divisions consider articles referred to community and species population level. Also included are key articles which incorporate into the analysis the Magellan biogeographical Province. Source ranking by year of publication within each level category considered.

	Level	Habitat type	Depth range	Objectives	Sources
	<b>COMMUNITY</b>				
1		boulder and cobbles	intertidal	community structure, zonation pattern, epi & infauna	Guzmán & Ríos 1981
2		boulder and cobbles	intertidal	community structure, zonation pattern, epi & infauna	Ríos & Guzmán 1982
3		<i>Macrocystis pyrifera</i> kelp forest	sublittoral	fish assemblage, diet of the fishes	Moreno & Jara 1984
4		<i>Macrocystis pyrifera</i> kelp forest	sublittoral	community structure, effects of canopy removal	Santelices & Ojeda 1984a
5		<i>Macrocystis pyrifera</i> holdfasts	sublittoral	Community structure, species richness	Ojeda & Santelices 1984
6		<i>Macrocystis pyrifera</i> kelp forest	sublittoral	distribution patterns, diet of sea urchins	Vásquez et al. 1984
7		<i>Macrocystis pyrifera</i> kelp forest	sublittoral	food webs structure	Castilla 1985
8		boulder and cobbles	intertidal	community structure, zonation pattern, epi & infauna	Guzmán & Ríos 1986
9		boulder and cobbles	intertidal	algal and fauna species composition	Mazella et al. 1991
10		boulder, cobbles & rocky shore	intertidal	community structure, zonation pattern, epibenthic fauna	Benedetti-Cecchi & Cinelli 1997
11		boulder and cobbles	intertidal	community structure, zonation pattern, species richness, epibenthic fauna	Ríos & Gerdes 1997
12		boulder and cobbles	intertidal	species composition and richness	Mutschke et al. 1998
13		boulder and cobbles	intertidal	community structure, species richness, epi & infauna & flora	Ríos & Mutschke 1999
14		<i>Macrocystis pyrifera</i> kelp forest	sublittoral	macrobenthic associated fauna, temporal variability	Adami & Gordillo 1999
15		soft-bottom	sublittoral	macrobenthic biomass, productivity	Brey & Gerdes 1999
16		soft-bottom	sublittoral	pelagic-benthic coupling	Cattaneo-Vietti et al. 1999
17		soft-bottom	sublittoral	meiobenthic community structure, spatial distribution	Chen et al. 1999
18		soft-bottom	sublittoral	community structure, abundance, biomass	Gerdes & Montiel 1999
19		soft-bottom	sublittoral	community structure, biodiversity, spatial distribution	Gutt et al. 1999
20		soft-bottom	sublittoral	abundance and biomass, macrozoobenthic productivity	Thatje & Mutschke 1999
21		soft-bottom	sublittoral	macrozoobenthic abundance, biomass	Montiel et al. 2001
22		soft-bottom	sublittoral	species composition, species richness, abundance, diversity	Ríos et al. 2003
23		rocky-shore	intertidal	Species composition and richness, abundance, biogeography	Ingólfsson 2005
24		soft-bottom	sublittoral	species composition, species richness, abundance, diversity	Ríos et al. 2005
25		general	shelf & upper slope	benthic ecology, progress report	Arntz et al. 2005
26		soft-bottom	sublittoral	benthic ecology, progress report	Mutschke 2006
27		soft-bottom	sublittoral	species composition, species richness	López & Sueiro 2007
28		<i>Macrocystis pyrifera</i> kelp forest	sublittoral	fish assemblage, effects of canopy removal	Vanella et al. 2007
29		<i>Macrocystis pyrifera</i> holdfasts	sublittoral	community structure, spatial and temporal comparison	Ríos et al. 2007
	<b>SPECIES</b>				
30	Polychaetes	soft-bottom	sublittoral	taxonomy	Hartmann-Schröder 1965
31	Crustacea	soft-bottom	sublittoral	taxonomia	Campononico & Guzmán 1972a
32	Crustacea	soft-bottom	sublittoral	reproductive biology	Campononico & Guzman 1972b
33	Macroalgae	hard-bottom	intertidal sublittoral	distribution pattern, abundance	Alveal et al. 1973
34	Decapods	soft-bottom	sublittoral	taxonomy, distribution pattern	Retamal 1974

35	Molluscs	hard-bottom	intertidal	spatial distribution, density	Guzmán 1978
36	Molluscs	hard-bottom	sublittoral	individual age and growth, population structure	Miranda & Acuña 1979
37	Molluscs	boulder & cobbles	intertidal	spatial distribution, density patterns	Langley et al. 1980
38	Bryozoans	hard-substrates	sublittoral	taxonomy, diversity, zoogeography	Moyano 1982
39	Polychaetes	soft-bottom	sublittoral	taxonomy	Hartmann-Schröder 1983
40	Macroalgae	<i>Macrocystis pyrifera</i> kelp forest	sublittoral	kelp forest population dynamics	Santelices & Ojeda 1984b
41	Asteroids	<i>Macrocystis pyrifera</i> kelp forest	sublittoral	trophic relationship	Vásquez & Castilla 1984
42	Echinodermata	<i>Macrocystis pyrifera</i> kelp forest	sublittoral	distributional pattern, diets	Vásquez et al. 1984
43	Molluscs	boulder & cobbles	intertidal	larval development	Ríos et al. 1987
44	Molluscs	boulder & cobbles	intertidal	individual age and growth	Guzmán & Ríos 1987
45	Isopods	Soft-bottom	sublittoral	taxonomy,	Wägele & Bruce 1989
46	Copepods	soft-bottom	sublittoral	faunistic study	Mazzochi & Ianora 1991
47	Isopods	soft-bottom	sublittoral	taxonomy	Winkler 1992
48	Mollusc	hard-bottom	intertidal	individual growth	Morriconi & Calvo 1993
49	Isopods	Soft-bottom	sublittoral	taxonomy	Winkler 1994
50	Macroalgae	hard-bottom	Intertidal	taxonomy	Cornejo 1996
51	Amphipoda	hard-bottom	sublittoral	taxonomy	Rauschert 1996
52	Amphipods	soft-bottom	sublittoral	taxonomy, zoogeography	De Broyer & Jazdzewski 1996
53	Molluscs	soft-bottom	sublittoral	population dynamics	Urban & Tesch 1996
54	Polychaetes Isopods	soft-bottom	sublittoral	diversity, distribution, biogeography	Mariani et al. 1996
55	Peracarids	soft-bottom	sublittoral	abundance pattern, diversity	Brandt et al. 1997
56	Isopods	soft-bottom	sublittoral	diversity, structure of the assemblage	Lorenti & Mariani 1997
57	Molluscs	hard-bottom	intertidal	geographic distribution	Schrödl 1997
58	Molluscs	soft-bottom	sublittoral	spatial distribution	Linse & Brandt 1998
59	Molluscs	boulder & cobbles	intertidal	larval development, reproduction	Santana 1998
60	Isopods	soft-bottom	sublittoral	taxonomy, geographical distribution	Brandt 1998
61	Molluscs	soft-bottom	sublittoral	faunistic study	Osorio 1999
62	Macroalgae	hard-bottom	intertidal sublittoral	taxonomy, distribution pattern	Mendoza 1999
63	Polychaetes	soft-bottoms	sublittoral	distribution, abundance, biogeography	Cañete et al. 1999
64	Decapods	soft-bottom	sublittoral	species composition and abundance, biogeography	Arntz et al. 1999
65	Decapods	soft-bottom	sublittoral	reproductive biology, latitudinal cline	Werthman & Lardies 1999
66	Decapods	soft-bottom	sublittoral	egg production, energy allocation	Navarrete et al. 1999
67	Decapods	soft-bottom	sublittoral	sex composition, size structure	Soto et al. 1999
68	Decapods	soft-bottom	sublittoral	reproductive biology, life history traits	Lovrich & Vinuesa 1999
69	Decapods	soft-bottom	sublittoral	feeding habit, natural diet	Comoglio & Amin 1999
70	Decapods	soft-bottom	sublittoral	biogeography, species composition	Gorny 1999
71	Decapods	soft-bottom	sublittoral	species composition, abundance	Mutschke & Gorny 1999
72	Decapods	soft-bottom	sublittoral	geographical distribution	Vinuesa et al. 1999
73	Amphipods	soft-bottom	sublittoral	biodiversity, biogeography	De Broyer & Rauschert 1999
74	Copepods	soft-bottom	sublittoral	taxonomy, biogeography	George & Schminke 1999
75	Tanaidacea	soft-bottom	sublittoral	taxonomy, biogeography	Schmidt & Brandt 2001

76	Polychaetes	soft-bottom	sublittoral	species composition, biogeography	Gambi & Mariani 1999
77	Polychaetes	soft-bottom	sublittoral	reproductive biology, larval development	Gambi & Patti 1999
78	Echinoderms	soft-bottom	sublittoral	species composition and biomass individual age and growth, diet	Dahm 1999
79	Echinoderms	soft-bottom	sublittoral	species composition	Larraín et al. 1999
80	Echinoderms	soft-bottom	sublittoral	reproductive cycle	Oyarzún et al. 1999
81	Molluscs	soft-bottom	sublittoral	species richness and abundance, feeding mode	Linse 1999a,
82	Molluscs	soft-bottom	sublittora	species composition, biogeography	Linse 1999b
83	Molluscs	soft-bottom	sublittoral	species composition, zoogeography	Schrödl 1999
84	Molluscs	Hard-substrate	intertidal	reproductive cycle	Morriconi 1999
85	Peracarids Molluscs	soft-bottom	sublittoral	biogeography	Brandt et al. 1999
86	Cumaceans	soft-bottom	sublittoral	species composition, biogeography	Mühlenhardt-Siegel 1999
87	Demosponges	soft-bottom	sublittoral	taxonomy, biogeography	Pansini & Sarà 1999
88	Sipunculids	soft-bottom	sublittoral	taxonomy, zoogeography	Saiz-Salinas & Pagola-Carte 1999
89	Hydroids	soft-bottom	sublittoral	taxonomy, biogeography	Peña-Cantero & García-Carrascosa 1999
90	Bryozoans	hard-substrates	sublittoral	taxonomy, diversity, zoogeography	Moyano 1999
91	Bryozoans	hard-substrates	sublittoral	taxonomy, diversity, zoogeography	Moyano 2000
92	Polychaetes	soft-bottoms	sublittoral	taxonomy	Hilbig & Montiel 2000
93	Polychaetes	soft-bottom	intertidal sublittoral	larval development, diversity	Gambi et al. 2000
94	Picnogonida	soft-bottom	sublittoral	Body morphology, feeding habit, reproductive traits	Gusso & Gravina 2001
95	Isopods	<i>Macrocystis pyrifera</i> holdfasts	sublittoral	species abundance	Cariceo et al. 2002
96	Polychaetes	soft-bottoms	sublittoral	taxonomy	Montiel et al. 2002
97	Molluscs	soft-bottoms	sublittoral	growth and production	Lomovasky et al. 2002
98	Echinoidea	<i>Macrocystis pyrifera</i> holdfasts	sublittoral	size frequency distribution, abundance	Ríos et al. 2003
99	Ascidians	soft-bottoms	sublittoral	species composition, biogeography	Sanamyan & Schories 2003
100	Polychaetes	soft-bottoms	sublittoral	species composition, taxonomy	Montiel et al. 2004
101	Polychaetes	soft-bottoms	sublittoral	taxonomy	Montiel & Hilbig 2004
102	Echinodermata	soft-bottom	sublittoral	molecular phylogeny, vicariante	Lee et al. 2004
103	Gastropoda	n. i.	intertidal	juvenile nutrition,	Gallardo et al. 2004
104	Gastropoda	n. i.	sublittoral	taxonomy	Pastorino 2005
105	Decapods	soft-bottom	sublittoral	species composition, biogeography	Boschi & Gavio 2005
106	Molluscs	soft-bottoms	sublittoral	reproductive cycle	Morriconi et al. 2005
107	Isopods	soft-bottom	sublittoral	species composition, taxonomy, zoogeography	Doti et al. 2005
108	Copepods	soft-bottom	sublittoral	species composition, species diversity, zoogeography	George 2005
109	Amphipoda	soft-bottom	sublittoral	species composition, zoogeography	Chiesa et al. 2005
110	Ascidians	soft-bottom	sublittoral	species composition, zoogeography	Ramos-Espla et al. 2005
111	Actinians	hard-bottom	sublittoral	distribution pattern, taxonomy zoogeography	Häussermann & Fösterra 2005
112	Polychaetes	soft-bottoms	sublittoral	species composition, biogeography trophic guild	Montiel et al. 2005a
113	Polychaetes	soft-bottoms	sublittoral	distribution patterns, zoogeography	Montiel et al. 2005b
114	Echinoderms	soft-bottom	sublittoral	species composition, distribution pattern, relative abundance	Mutschke & Ríos 2006
115	Macroalgae	hard-bottom	sublittoral	taxonomy, geographical distribution	Mansilla et al. 2006
116	Molluscs	soft-bottom	sublittoral	biodiversity and biogeography	Linsey et al. 2006


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	GLOBAL ANALYSIS				
117				zoogeography	Brattström & Johannsen 1983
118				benthic ecology, summary review	Arntz 1999
119				biogeography, conservation topics	Fernández et al. 2000
120				zoogeography	Lancellotti & Vásquez 2000
121				Thorson's rule, gastropods reproduction	Gallardo & Penchaszadeh 2001
122				biogeography	Camus 2001
123				Thorson's rule, molluscs	Valdovinos et al. 2003
124				Rapoport's rule, polychaetes	Hernández et al. 2005
125				biogeography, polychaetes	Moreno et al. 2005

Disclaimer

Herewith I assure that I wrote this thesis independently and that I did not use any additional help except to the extend and the manner stated. References are cited in compliance with guidelines on safeguarding good scientific practice.

Bremen, August 20<sup>th</sup> 2007

A handwritten signature in black ink, consisting of a large, stylized 'C' followed by 'Ríos' and 'Cardoza' in a cursive script. The signature is underlined with a single horizontal line.

Carlos Ríos Cardoza