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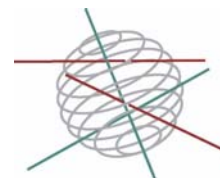
STATUS, CONTROL AND ROLE OF THE PELAGIC DIVERSITY OF THE AUSTRAL OCEAN (PELAGANT)

J.H. HECQ, F. VOLCKAERT



PART 2
GLOBAL CHANGE, ECOSYSTEMS AND BIODIVERSITY

-  ATMOSPHERE AND CLIMATE
-  MARINE ECOSYSTEMS AND BIODIVERSITY
-  TERRESTRIAL ECOSYSTEMS AND BIODIVERSITY
-  NORTH SEA
-  ANTARCTICA
-  BIODIVERSITY



Part 2:
Global change, Ecosystems and Biodiversity



FINAL REPORT



**STATUS, CONTROL AND ROLE OF THE PELAGIC
DIVERSITY OF THE AUSTRAL OCEAN
(PELAGANT)**

EV/30

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TABLE OF CONTENT

ABSTRACT	7
1. Introduction, objectives and strategy	9
2. Determination of planktonic key- species (including Ichthyoplankton) and assemblages of the Terre Adélie sector of THE East Antarctic Shelf (139°E – 145°E), their spatial and temporal and links with the habitats	11
2.1. Introduction. Hydrological and abiotic characteristics of the shelf waters from Terre Adélie to the Mertz Glacier, Antarctica (139°E - 145°E)	11
2.2. Nutrients, Chlorophyll and Microplankton in shelf waters from Terre Adélie to the Mertz Glacier, Antarctica (139°E - 145°E)	15
2.3. Zooplankton distribution in the Terre Adélie sector of East Antarctic Shelf ecosystem.....	29
2.4. Ichthyoplankton distribution and Trophic status of larvae of <i>Pleuragramma antarcticum</i> in the Terre Adélie sector of East Antarctic Shelf ecosystem	37
2.5. Sea ice zone ecology and the life cycle of copepods in the coastal zone of Dumont d'Urville	43
2.6. Synthesis and conceptual approach of the Pelagic Ecosystem of the Terre Adélie sector of East Antarctic Shelf	45
2.7. Conclusion and perspectives	48
3. Antarctic PELAGIC Fish Diversity and Ecology	49
3.1. Structuring of the pelagic ichthyofauna in the Lazarev Sea and the West-Indian sector of the Southern Ocean.....	49
3.2. Seasonal variations in energy content in <i>Electrona antarctica</i>	59
3.3. A referential database for the molecular identification of Antarctic fish species and its application in ecological research	65
3.4. Historical evolution of the lanternfish <i>Electrona Antarctica</i>	70
3.5. Evolutionary analysis of large and small-scale population structure and dispersal of the dusky notothen <i>Trematomus newnesi</i> and the yellowbelly rockcod <i>Notothenia coriiceps</i>	72
4. State dependent energy allocation in the pelagic Antarctic silverfish <i>Pleuragramma antarcticum</i>: trading off between winter reserves and buoyancy	77
5. General conclusions and perspectives	83
6. Acknowledgements	89
7. Bibliography	91

ABSTRACT

The PELAGANT project addressed the key components of the Austral Ocean Pelagic Ecosystem and dealt with the criteria for the appearance, maintenance and modification of biodiversity from an interdisciplinary perspective.

The specific objectives of PELAGANT were (i) data collection and data banking to determine the distribution of Antarctic pelagic key-species in relation to the biotic and abiotic factors of the environment; (ii) analysis of the pelagic diversity at the species, population and ecosystem levels; (iii) development and application of a conceptual and numerical ecohydrodynamical model to the Austral Ocean Pelagic Ecosystem in view of determining the stability of biotic assemblages, their sensitivity to environmental constraints and especially the response to climate changes.

Planktonic key-species (including ichthyoplankton) of the Terre Adélie sector of the East Antarctic Shelf (139°E – 145°E) and their spatial and temporal distributions have been studied in collaboration with the French programme ICOTA (Ichtyologie Côtière en Terre Adélie) funded by the Institut Polaire Paul Emile Victor (IPEV). The major pelagic assemblages and links with the habitats have been recognized. At the spatial and temporal scale we are working on, the pelagic realm in the shelf zone can be monitored by a limited number of key pelagic species, which are mainly one species of euphausiids, *Euphausia crystallorophias*, and the pelagic fish, *Pleuragramma antarcticum*. The krill *Euphausia superba* is only abundant over deeper areas. These two species can highly dominate the micronekton and macroplankton and are good indicators, which respond at several time scales of variations in the marine environment. They depend on phyto- and mesozooplankton for their foraging and are preys of top-predators.

Larval and post-metamorphous fish have sampled studied during expeditions with RV *Polarstern* and RV *Aurora Australis*. The communities of fish observed during both campaigns are congruent with previous observations in the Southern Ocean. The strongest differentiation was observed between the coastal nototheniid community and the mesopelagic oceanic community. The currently analyzed data in both areas preclude a distinction between geographical, seasonal and climatological effects. The energy metabolism of the myctophid *Electrona antarctica* has been put in een ecological perspective. A referential database for the molecular identification of Antarctic fish species and its application in ecological research has been established and integrated in the Barcoding of Fish project. The genetic diversity of *E. antarctica* in the Southern Ocean seems low. The evolutionary analysis of the large and small-scale population structure and dispersal of the dusky notothen *Trematomus newnesi* and the

yellowbelly rockcod *Notothenia coriiceps* is in progress. Microsatellite DNA markers of *Trematomus newnesi* show a high diversity, which is characteristic for marine species.

A 1D coupled physical biological model has been used to simulate the vertical gradients in water temperature, optical properties, food availability and predation risk as input for a model of growth of *P. antarcticum*. That dynamic state variable model investigates the partitioning of ingested energy over three state variables: lipid reserves, structural protein body mass and egg development. It predicts the habitat preferences by age group.

1. INTRODUCTION, OBJECTIVES AND STRATEGY

The PELAGANT project addresses from an interdisciplinary perspective the key components of the Austral Ocean Pelagic Ecosystem and dealt with the criteria for the appearance, maintenance, and modification of biodiversity. The diversity and dynamics of this ecosystem are particularly sensitive to variations in physical structure of the ocean and in ice coverage, and are affected by climate changes.

Although the pelagic diversity of the Austral Ocean remains poorly documented, it is probably larger than estimated initially. Many pelagic species, including macrozooplankton, ichthyoplankton and pelagic fishes, have been ignored, especially in ecological and biogeochemical studies and in modelling (Hecq, 2003). The diversity of the pelagic system is essential to guarantee the fitness of the consumers. In response to a dominant plankton community, specific communities of consumers will evolve. This is particularly true for the various life stages of fishes (larvae, juvenile and adults), which require specific plankton nutrition. Thus, it can be expected that larvae and juvenile fish considerably affect the zooplankton biomass and should be included as zooplankton sinks in ecosystem models.

The pelagic species are organised in habitat-specific assemblages. The diversity and structure of these pelagic assemblages is caused by the spatio-temporal heterogeneity of abiotic factors, especially the physical structure of the water masses and ice coverage (Goffart *et al.* 2000, Hecq *et al.* 1999, Hecq 2003). This influences the availability of food, the stability of the water column and the variability of habitats. Species composition of fish and ichthyoplankton in the pelagic realm is not random as they migrate between locations with favourable conditions, resulting in distinct distributions and assemblages (Kock 1992, Loots *et al.* 2007). Vertical distributional differences may be related to ontogenetic shifts within species.

During the previous Belgian Antarctic programme in the Austral Ocean, we have verified experimentally and by modelling the impact of variations in temperature, ice coverage dynamics, solar irradiation and the vertical structure of the water column on the dynamics of the most important Antarctic plankton groups. Many recent publications have hypothesised that climate changes modify the temperature and the wind conditions, influence the ice-edges and thus indirectly affect the dynamics and diversity of pelagic food webs (Goffart *et al.* 2002, Hays *et al.* 2005, Costello *et al.* 2006). Species-specific differential responses to climate warming that alter phenologies can dramatically affect community function. The knowledge of those assemblages and of their control remains to be acquired.

Two distinct fish assemblages characterize the pelagic Southern Ocean (Efremenko and Pankratov, 1988). The oceanic assemblage is dominated by meso- and bathypelagic fish, while the coastal and shelf assemblage are characterized by the dominance of notothenioid juveniles (Kock 1992, Koubbi *et al.* 1991, Pakhomov *et al.* 1995). The pelagic Antarctic shelf zone is dominated by the nototheniid *Pleuragramma antarcticum* and pelagic larvae and juveniles of four notothenioid families: Artedidraconidae, Bathydraconidae, Nototheniidae and Channichthyidae (Williams and Duhamel 1994, Hoddell *et al.* 2000).

The general objective of the project is to analyse the status, control and role of the pelagic components of system of the Southern Ocean Ecosystem. In the long term this may contribute to assess the impact of global climate changes on the pelagic biodiversity and structure. The project benefited of the usefull collaboration between the University Liège (Laboratory of Oceanology) and Catholic University of Leuven (Laboratory of Animal Diversity and Systematics) to achieve the objectives.

The specific objective of PELAGANT was (i) data collection and data banking to determine the distribution of Antarctic pelagic key-species in relation to the biotic and abiotic factors of the environment; (ii) to analyse the pelagic diversity at the species, population and ecosystem levels; (iii) and to apply a conceptual and numerical ecohydrodynamical model of the Austral Ocean Pelagic Ecosystem in view of determining the stability of biotic assemblages, their sensitivity to the environmental constraints and especially the response to climate changes. To facilitate visibility, each task corresponding to a manuscript submitted, accepted or published, has been presented and discussed separately.

This research is a contribution of Belgian science to international conventions on the maintenance and monitoring of the Antarctic ecosystem in a context of environmental and climatic changes (CCAMLR, SCAR, SO-GLOBEC). The research follows the recommendations of the international conventions and programmes in which Belgium is involved (Antarctic Treaty, Law of the Sea Convention and Rio Convention on Biological Diversity; DIVERSITAS programme) by identifying key components of the Antarctic pelagic ecosystem and the criteria for the appearance, maintenance, evolution and anthropogenic modification of biodiversity. The project will benefit the interdisciplinary collaboration that we have developed with international Antarctic scientific programs (e.g. France, Germany, Australia and Japan) and in which we are involved.

2. DETERMINATION OF PLANKTONIC KEY- SPECIES (INCLUDING ICHTHYOPLANKTON) AND ASSEMBLAGES OF THE TERRE ADÉLIE SECTOR OF THE EAST ANTARCTIC SHELF (139°E – 145°E), THEIR SPATIAL AND TEMPORAL AND LINKS WITH THE HABITATS

Contributors: Jean-Henri Hecq, Anne Goffart and Philippe Koubbi

2.1. Introduction. Hydrological and abiotic characteristics of the shelf waters from Terre Adélie to the Mertz Glacier, Antarctica (139°E - 145°E)

Contributors: Anne Goffart, Cristina Beans, Philippe Koubbi and Jean- Henri Hecq

Most of Antarctic pelagic studies concern the offshore krill dominated areas. On the contrary, surveys are rare in Antarctic Shelf Zones where the habitats are complex. The Eastern Antarctic Continental Shelf and specifically the Terre Adélie sector, is under the influence of seasonal sea ice, complex bathymetry with innershelf depressions and relative small shelf extent. The mesoscale shelf waters circulation is influenced by shelf-break fronts, formation of deep Antarctic waters and variations of the mixed layer depth. The icebergs act as stress for benthic ecosystem - by scouring - or possibly positive for pelagic ecosystems and dynamics of glacier tongue. That complexity of the Terre Adélie Continental Shelf, assumes a large pelagic diversity of habitats and gives the possibility to study the impact on biotic assemblages specifically plankton and fish larvae.



Figure 1. The R.V. "Astrolabe" of the French Institut Polaire Paul Emile Victor (IPEV).

Our research has been realised in a strong collaboration with the French programme ICOTA (Ichtyologie Côtière en Terre Adélie) of Institut Polaire Paul Emile Victor (IPEV)

and integrated in the international Antarctic scientific network programme CEAMARC (Collaborative East Antarctic Marine Census) (Australia, France and Japan) where the pelagic diversity in the Austral Ocean is studied in an environmental and biological context.

Annual surveys onboard the R/V "l'Astrolabe" (fig.1) occurred yearly from 2003 to 2007 and include (1) hydrological conditions (mixed layer depths, variations of density linked to sea ice melting), (2) sea ice and positions of polynias, (3) nutrients, pigments and phytoplankton composition, (3) annual changes in mesozooplankton, krill and pelagic fish, and (4) foraging performances of the fish *P. antarcticum* that will influence its population recruitment in the area. All the data are treated and banked in SCAR-MARBIN databank. However, in the present report, only data of summer 2004 will be discussed in depth.

Environmental variability in the pelagic ecosystem operates at various temporal and spatial scales (Haury *et al.*, 1978). At the spatial and temporal scale we are working on, the pelagic realm in the neritic zone can be monitored by a limited number of key pelagic species which are mainly one species of euphausiids, *Euphausia crystallorophias* and one species of pelagic fish, *Pleuragramma antarcticum*. The species *Euphausia superba* is only abundant over deeper areas (Hecq 2003). These two species can highly dominate the micronekton and macroplankton and are good indicators, which respond at several time scales of variations in the marine environment. They depend on phyto- and mesozooplankton for their foraging and are preys of top-predators.

Prominent features along the coast are three large bays (Commonwealth, Watt and Buchanan Bays), the presence of small glaciers (the Astrolabe and the Zélée), as well as the largest glacier in the region: the Mertz Glacier (Fig. 2).

Relatively shallow waters can be found over a large plateau (~200m depth) between the Astrolabe Glacier and Commonwealth Bay. On either side of this plateau, deeper areas are found, most notably near the Astrolabe and Mertz Glaciers. The deepest (with depths reaching 1200m) is known as the Adélie Depression, and is located between the Mertz Glacier and Watt Bay (142°E – 146°E). During the campaign, the water was free of sea ice, with icebergs observed only near the glaciers. We sampled at a total of 38 stations in the waters over the continental platform between 139°E – 145°E and 66°S – 67°S (Fig. 2).

The area is characterized by strong katabatic winds that influence surface water currents (Wendler *et al.*, 1997). Water mass characteristics depend on both bathymetry and advection linked to wind and ice cover.

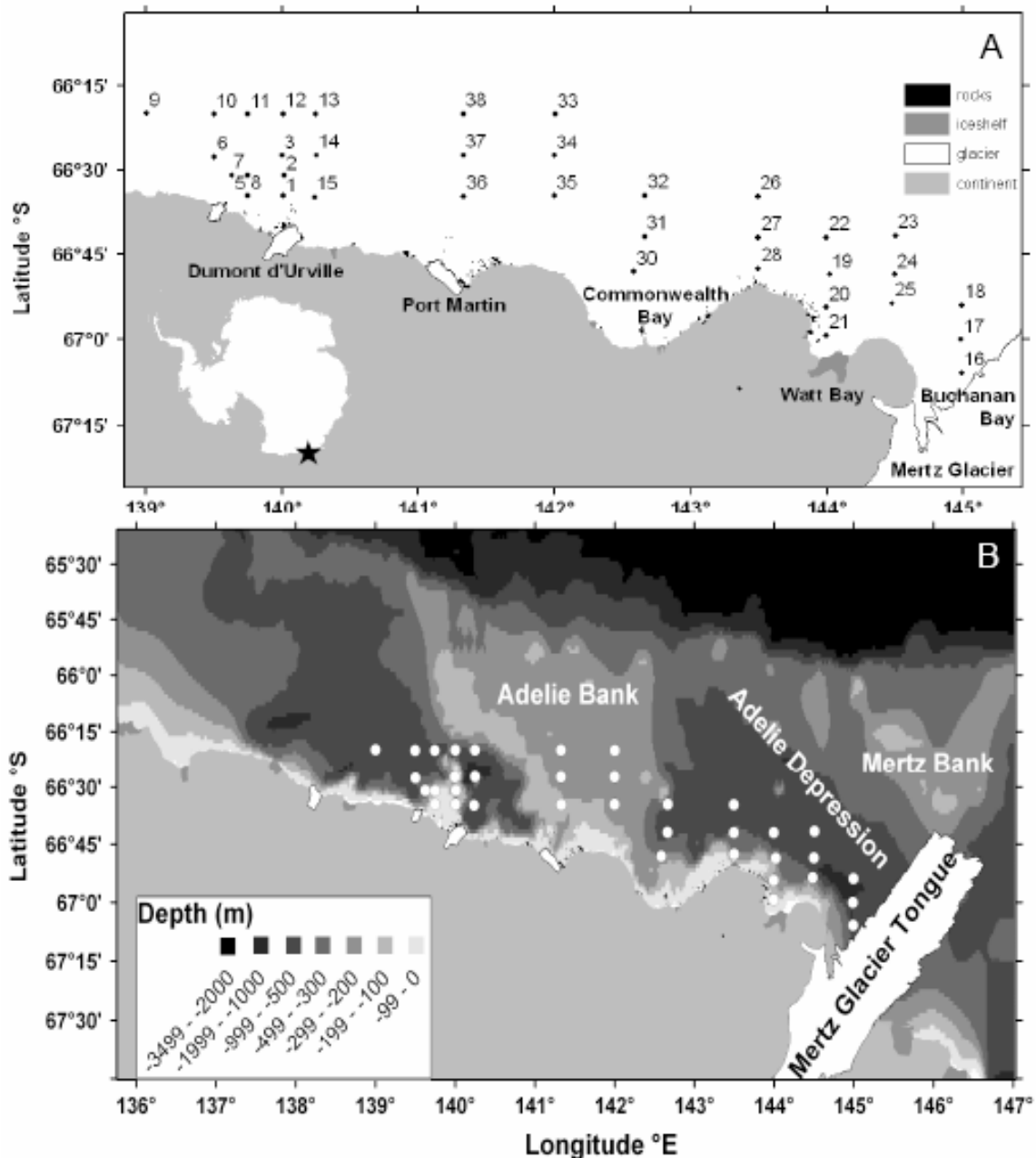


Figure 2. Bathymetry of the study area and localisation of sampling stations from the 2004 survey. A. Shows sampling stations. Inset shows location of study region. B Bathymetry (data source: ETOPO2v2, NOAA, GDC) (Swadling *et al.* submitted).

Two major areas (fig. 2) can be observed over the shelf (Sultan *et al.*, unpublished; Swadling *et al.*, submitted, Beans *et al.* submitted). The first one is west of Commonwealth Bay (143°E), which has less vertical stratification compared to the second zone east of this bay. East of it, the Adélie Depression is identified as an important source of deep water (Adélie Land Bottom Water - ALBW) studied by the

ALBION project. The densest part of the water column is trapped within the depression. The MGT isolates the Adélie Depression from the East Drift, allowing the Mertz Glacier Polynia to be formed and maintained throughout the entire winter (Williams and Bindoff 2003). An important cyclonic gyre transports water within the depression. A gradient of density (σ_t) was observed in surface waters over this region, following quite closely the gradient in sea surface salinities (SSS) (Fig.3). In general higher densities were observed closer to shore than further out to sea. Denser waters (and saltier, $SSS > 34.2$) were to be observed around and offshore from the Astrolabe Glacier, and east along the coast until Commonwealth Bay from where less dense (and fresher, $SSS < 33.9$) waters predominated towards the Mertz Glacier and further offshore. Waters were coldest ($SST < -1.5^\circ\text{C}$) in the proximity of the Mertz Glacier, whereas relatively warm waters were observed over the plateau ($SST > 0.4^\circ\text{C}$).

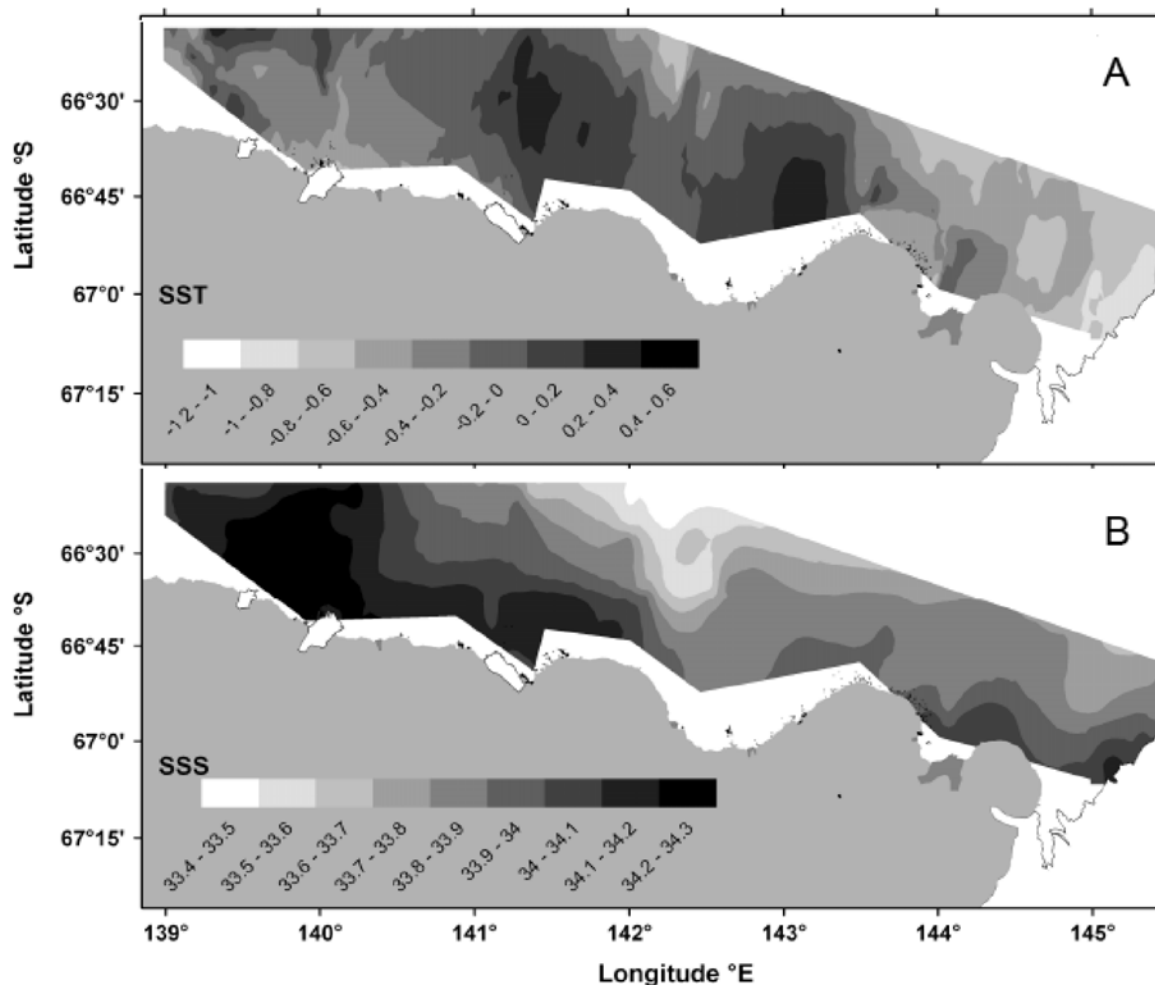


Figure 3. Sea Surface (A) temperature and (B) salinity.

2.2. Nutrients, Chlorophyll and Microplankton in shelf waters from Terre Adélie to the Mertz Glacier, Antarctica (139°E - 145°E)

Contributors: Anne Goffart, Cristina Beans, Philippe Koubbi and J H Hecq

This text contains excerpts from the following papers:

Beans C., Hecq J.H., Chalon C., Koubbi P., Vallet C., Wright S., Goffart A. An initial study of the diatom-dominated microplankton summer assemblages in coastal waters from Terre Adélie to the Mertz Glacier, Antarctica (139°E - 145°E). Submitted to: Polar Biology

Introduction

The shelf waters of Terre Adélie and King Georges V Land (from 139°E – 146°E) are of interest notably due to the formation of Antarctic Deep Water in the Mertz Glacier region (Bindoff *et al.* 2000) and to the presence of two coastal polynyas, biologically productive areas of open water or reduced sea-ice cover within the ice pack, near Dumont D'Urville and the Mertz Glacier (Arrigo and van Dijken 2003; Sambrotto *et al.* 2003). In the Mertz Glacier Polynya, which opens up before the Dumont D'Urville Polynya, the phytoplankton bloom has been observed to last three months, although there are usually two peaks: late December and early March (Arrigo and van Dijken 2003).

Early studies of the phytoplankton in Terre Adélie by Manguin in 1949-50 and Franguelli in 1950-52 (Riaux-Gobin *et al.* 2003) were centred on diatom taxonomy. Since then, subsequent surveys in the region have studied the microplankton community in offshore waters north of the shelf break and close to the Polar Front (Chiba *et al.* 2000; Waters *et al.* 2000) or, if near the coast, have centred on the sea-ice communities (Delille *et al.* 1995; Riaux-Gobin *et al.* 2000; Riaux-Gobin *et al.* 2003; Riaux-Gobin *et al.* 2005) or concentrated on phytoplankton biomass and primary production in the Mertz Polynya (Sambrotto *et al.* 2003; Vaillancourt *et al.* 2003).

From the 2004 to 2007 survey, we studied the microplankton community from the coastal waters of Terre Adélie and Georges V Land in terms of biomass and species composition, in relation with spatio-temporal variations in abiotic factors such as frontal structures, bathymetry, water column stratification, ice conditions and nutrient availability. Here we discuss the microplankton results from the January 2004 which took place on board the Astrolabe campaign (Beans *et al.*, submitted).

Material and method

Four 8-liter Niskin bottles were used to obtain samples from the water column for each station (at 5, 25, 75 and 150 m depth) in order to study levels of nutrients, photosynthetic pigments and the microplankton community. Further samples (for microplankton) were obtained from an onboard pump that provided water from 3 m depth. Maps presented in this paper will centre around data from samples obtained at 5 m depth, with statistics on all depths.

Water samples for nitrate, nitrite and silicate (20 ml) were collected directly from the Niskin Bottles using polyethylene syringes. Polyethylene flasks were filled ca. 2/3 full, immediately frozen vertically and stored at -20°C until analysis. Syringes and flasks had previously been soaked in 10% HCl for 24h and rinsed thrice with Milli-Q water and sample water. Nutrients were determined by means of a Technicon Auto-Analyser II. Nitrate and nitrite were analysed according to working procedures of Tréguer and Le Corre (1975), while silicate was determined according to Gordon *et al.* (1993). OSIL marine nutrient standards were used for calibrations.

Phytopigment analysis has been described in Swadling *et al.* (submitted). In brief, seawater was filtered through 13 mm GF/F filters and then frozen in liquid nitrogen for return to Australia where pigments were extracted and analysed by HPLC (Zapata *et al.* 2000).

Microplankton samples were obtained at each station by filtering seawater through a 20µm mesh net. The resulting sample was collected in a flask and preserved in 2.5% buffered formalin. The volume of water filtered varied depending on the source: between 30-50l of water for surface samples (via the on-board pump), whereas for vertical profiles (sampling at 5, 25, 75 and 150 m depth), it was between 2-5 l (all the water remaining in the Niskin bottles after samples had been collected for other analyses). The microplankton assemblages were later studied in the laboratory of the university of Liege, using an Olympus IX50 inverted microscope. Subsamples were collected (between 1-5 ml for pump samples and 10-15 ml for Niskin samples) and allowed to sediment in a 20 ml chamber for at least 18h and then observed using a 20x and 40x objectives. An initial qualitative approach was done to identify taxa present using the recent work published by Scott and Marchant (2005). Community diversity based on abundances was estimated by calculating the Shannon-Weaver diversity index H' (log-base).

Geographic Information Systems (GIS) (ArcGis 8; ESRI; Golden Software Surfer8) were used to produce distribution maps of the microplankton and environmental variables. Environmental and biological data were imported into the GIS as point georeferenced data. Interpolations of surface temperature and salinity were calculated

to generate raster layers (based on pixels) using the Geostatistical Analyst extension of ArcGis. Geostatistics are methods which allow the estimation of a value at unsampled locations (Rivoirard *et al.* 2000). Correspondence Analysis was done on 26 stations and on the abundances of principal diatom taxa. Prior to this data were normalised (using the square root).

Results

Nutrients measured, NO_2^- , NO_3^- and SiO_3^{2-} , showed both horizontal (Fig. 4) and vertical variations throughout the site. NO_2^- concentrations decreased with depth, whereas both NO_3^- and SiO_3^{2-} concentrations showed a tendency to increase. At 5 m depth, both NO_3^- and SiO_3^{2-} showed a gradient from higher concentrations in the west (maxima of $34.37 \mu\text{M}$ at station 8 and $56.08 \mu\text{M}$ at station 5 respectively) to lower ones over the plateau and the Adélie Depression (minima of $30.38 \mu\text{M}$ at station 16 and $50.22 \mu\text{M}$ at station 31 respectively). NO_2^- on the other hand, showed highest concentrations over the plateau ($0.24 \mu\text{M}$ at station 33), with values slightly decreasing both to the east and west of this area (minimum of $0.15 \mu\text{M}$ at station 7).

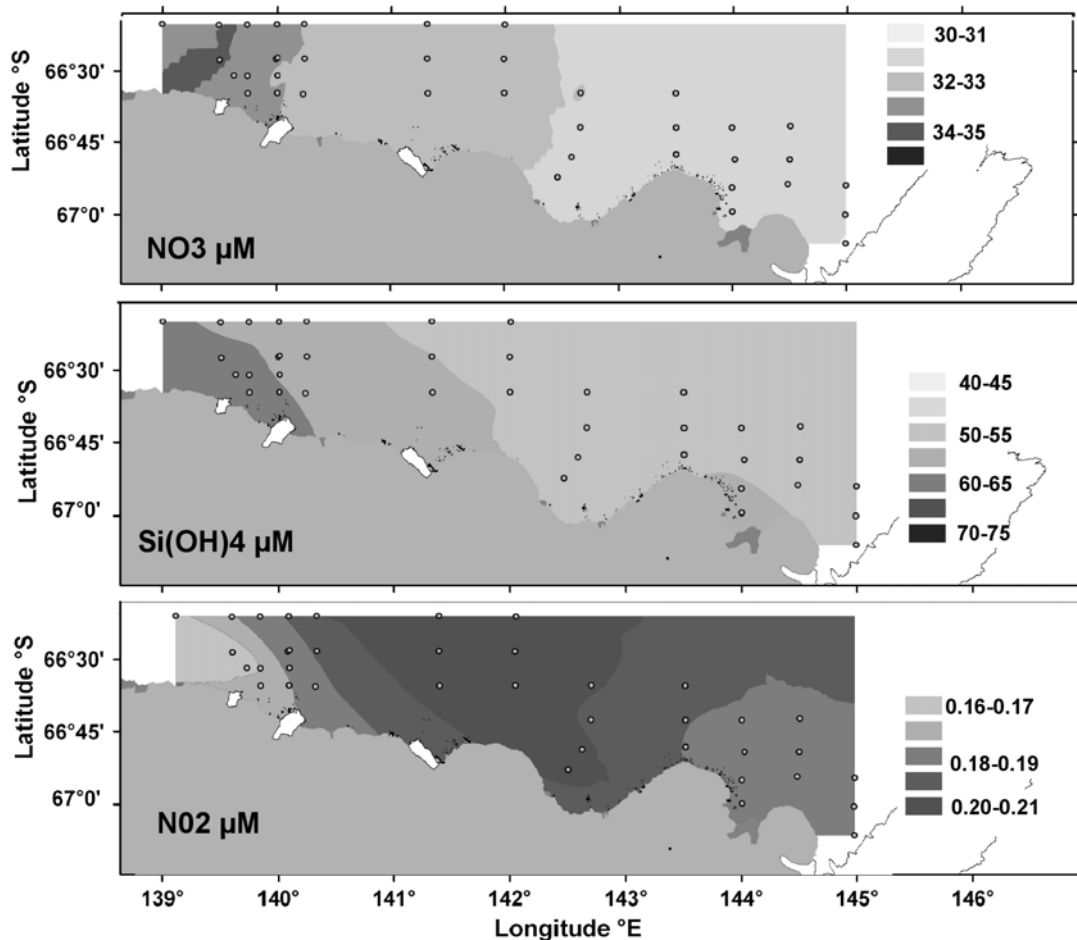


Figure 4. Nutrient concentrations at 5 m depth January 2004

Chlorophyll concentrations at 5 m depth (Fig. 5) were highest near the Astrolabe and Mertz Glaciers and over the Adélie Depression, with maximum peak in proximity to the Mertz Glacier ($1.57 \mu\text{g l}^{-1}$ at station 16). Much lower values were observed over the plateau (minimum $0.21 \mu\text{g l}^{-1}$ at station 35). Vertically there was little variation in concentrations in the waters surrounding the Astrolabe Glacier, whereas in the eastern region concentrations dropped considerably with depth.

From Terre Adélie to the Mertz Glacier, the microplankton community was completely dominated by diatoms, with abundances 1-2 orders of magnitude greater than the other components: dinoflagellates, silicoflagellates and ciliates (Beans *et al.* Submitted). In general, microplankton abundances varied widely, both on horizontal and vertical levels. The results presented here will centre around 5 m depth as this is where abundances were highest.

Total microplankton abundances averaged $11\,754 \pm 15\,312 \text{ cells l}^{-1}$ with a maximum of $71\,154 \text{ cells l}^{-1}$ (station 23) over the Adélie Depression. Values then decreased towards the coast and the west, with a minimum of 417 cells l^{-1} (station 9) in the westernmost region. The Shannon index H' values were minimal near the Mertz Glacier and over the Adélie Depression (0.12 in stations 17 and 23) but then increased towards the west with a maximum of 1.01 near the Astrolabe Glacier (station 2) and varied little in the surrounding waters or over the plateau.

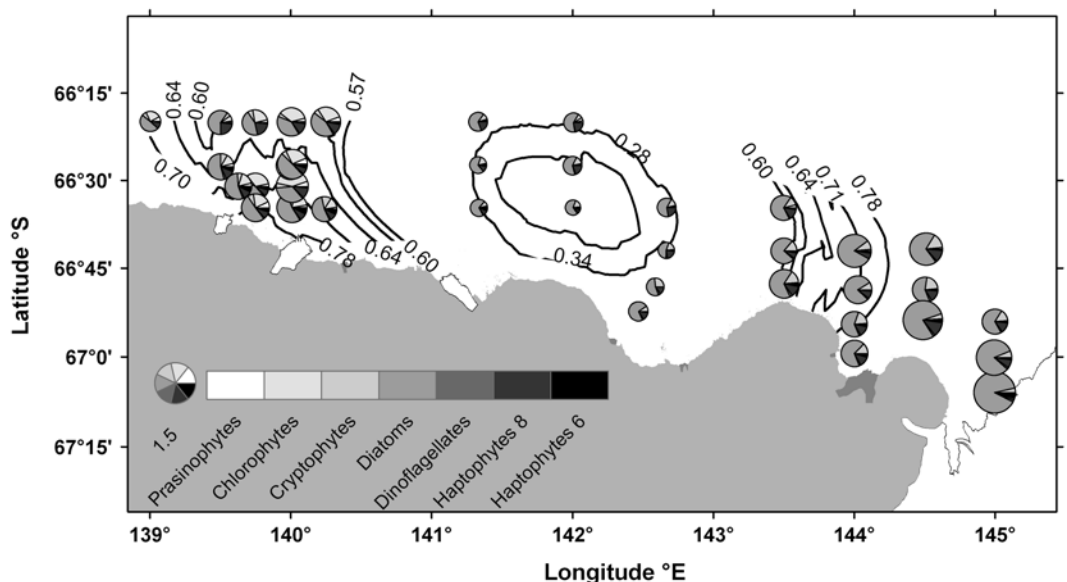


Figure 5. Concentrations of pigments ($\mu\text{g l}^{-1}$) at each station: Distributions of major groups at 5 m based on pigment biomarkers (Swadling *et al.*, submitted).

(i) *Non-diatom microplankton*. Dinoflagellates identified included members of the genera *Dinophysis*, *Gymnodinium*, *Gonyaulax*, and *Protoberidinium*. Results from dinoflagellates have all been pooled into a single category. Dinoflagellate abundances (Fig. 6a) showed highest levels at 5 m ($218 \pm 178 \text{ cells l}^{-1}$) and then tended to

decrease with depth. In general, higher concentrations were seen close to shore in Commonwealth Bay and over the Adélie Depression (with a maximum of 625 cells l⁻¹ at station 29). Cell concentrations were lowest away from the coast, west of the Astrolabe Glacier (indeed, no dinoflagellates were observed in several samples from this area).

Dictyocha speculum was the only silicoflagellate observed. This group presented the lowest abundances of all the microplankton, 35 ± 86 cells l⁻¹ at 5 m, except in the surface waters just west of the Astrolabe Glacier where they frequently outnumbered dinoflagellates and ciliates (Fig. 6b). In general, silicoflagellates were most abundant in surface waters near the Astrolabe Glacier (maximum of 460 cells l⁻¹ at station 6). Their numbers decreased drastically both towards the east and with depth, excepting a peak at 75 m near the Astrolabe Glacier. They were very rarely observed in samples obtained from 75 – 150m depth.

A large majority of the ciliates observed during this study were tintinnids ($71.6 \pm 32\%$ of all ciliates), amongst which the genus *Codonellopsis* was abundant. At 5 m, ciliates averaged 102 ± 126 cells l⁻¹, with a maximum of 628 cells l⁻¹ at station 2 close to the Mertz Glacier (Fig. 6c). There were several samples in which no ciliates were observed. In general ciliate abundances were highest at 5 m depth, and then decreased to become minimal at 150m. At all depths higher levels were observed just off the Astrolabe and Mertz Glaciers (in particular over the Adélie Depression), and then lower over the plateau.

(ii) *Diatom abundances and species composition.* As stated previously, diatoms were the overwhelmingly dominant component of the microplankton community. Abundances varied widely, with maxima found at 5 m, and then decreasing with depth. Results at 5 m depth (Figure 6d), averaging $11\,398 \pm 15\,161$ cells l⁻¹, showed large variations over the area surveyed, with very high abundances observed over the Adélie Depression (maximum of 70 275 cells l⁻¹ at station 23) and in general in the waters neighbouring the Mertz Glacier; whereas in the waters over the plateau and the western part of the region the diatom population showed a marked decrease in numbers (minimum of 48 cells l⁻¹ at station 38).

The commonest diatom species, counted and identified using optical microscopy, are listed in Table 1, along with their frequency of occurrence. Among the most widespread groups, only four ever individually constituted more than 10% of the diatom population at any one station and could be considered a dominant group. These were *Fragilaropsis* spp., *Chaetoceros criophilus*, *Rhizosolenia* spp., *Corethron pennatum*. On occasion *Thalassiothrix antarctica* also approximated this 10% level (at 25 m or 75 m from stations 10, 11, 15, 36 and 37). The use of SEM showed the

presence of other diatom species that weren't included in the counts. These included the centric diatoms, *Chaetoceros atlanticus*, *Coscinodiscus bouvet*, *Stellarima microtrias*, several *Thalassiosira* species (such as *T. ritscheri*, *T. lentiginosa*, *T. gravida*, *T. gracilis*, *T. tumida*, *T. ritscheri*), *Porosira glacialis*, *Asteromphalus hookeri*, *Actinocyclus actinochilus*, *Rhizosolenia antennata* and the pennate diatoms, *Achnanthes vicentri*, and *Cocconeis spp.*, as well as several *Fragilariopsis* species (such as *F. kerguelensis*, *F. curta*, *F. pseudonana*, *F. rhombica*).

Table 1: Frequency of occurrence of common diatom species found in samples (all depths) from Terre Adélie to the Mertz Glacier

Taxon	FO (%)
<i>Acinocyclus spp</i>	98.9
<i>Thalassiothrix antarcticum</i>	97.1
<i>Fragilariopsis spp.</i>	96.6
<i>Rhizosolenia spp.</i>	96.6
<i>Thalassiosira spp.</i>	91.4
<i>Chaetoceros spp.</i>	90.2
<i>Chaetoceros criophilus</i>	88.5
<i>Corethron pennatum</i>	88.5
<i>Asteromphalus spp.</i>	72.4
<i>Nitzschia, Pseudo-nitzschia, Navicula group</i>	67.8
<i>Chaetoceros dichæta</i>	61.5
<i>Coscinodiscus spp.</i>	41.4
<i>Eucampia antarctica</i>	33.9
<i>Banquisia belgica</i>	25.3
<i>Odontella spp.</i>	14.9
<i>Chaetoceros curvisetus</i>	9.2

The small, rectangular-shaped, colonial pennate diatom *Fragilariopsis spp.* (sizes usually +/- 5*30 µm, with occasional larger forms reaching up to 8*100 µm) was by far the most widely distributed and abundant group (Fig. 6e). Abundances (often an order of magnitude greater than other groups) varied a lot throughout the zone, with an average of $9\,335 \pm 15\,170$ cells l⁻¹ at 5 m depth, and a maximum of 68 222 cells l⁻¹ at station 23. Generally *Fragilariopsis spp.* comprised > 80% of the diatoms, (ranging between 60 – 90%), in the eastern region of our site, in particular over the Adélie Depression. In the western region, although they frequently remained abundant (but an order of magnitude less), they were no longer as dominant (ranging between 0 – 50% of diatoms) due to the large number of other species present. None were observed in two offshore stations (10 and 11).

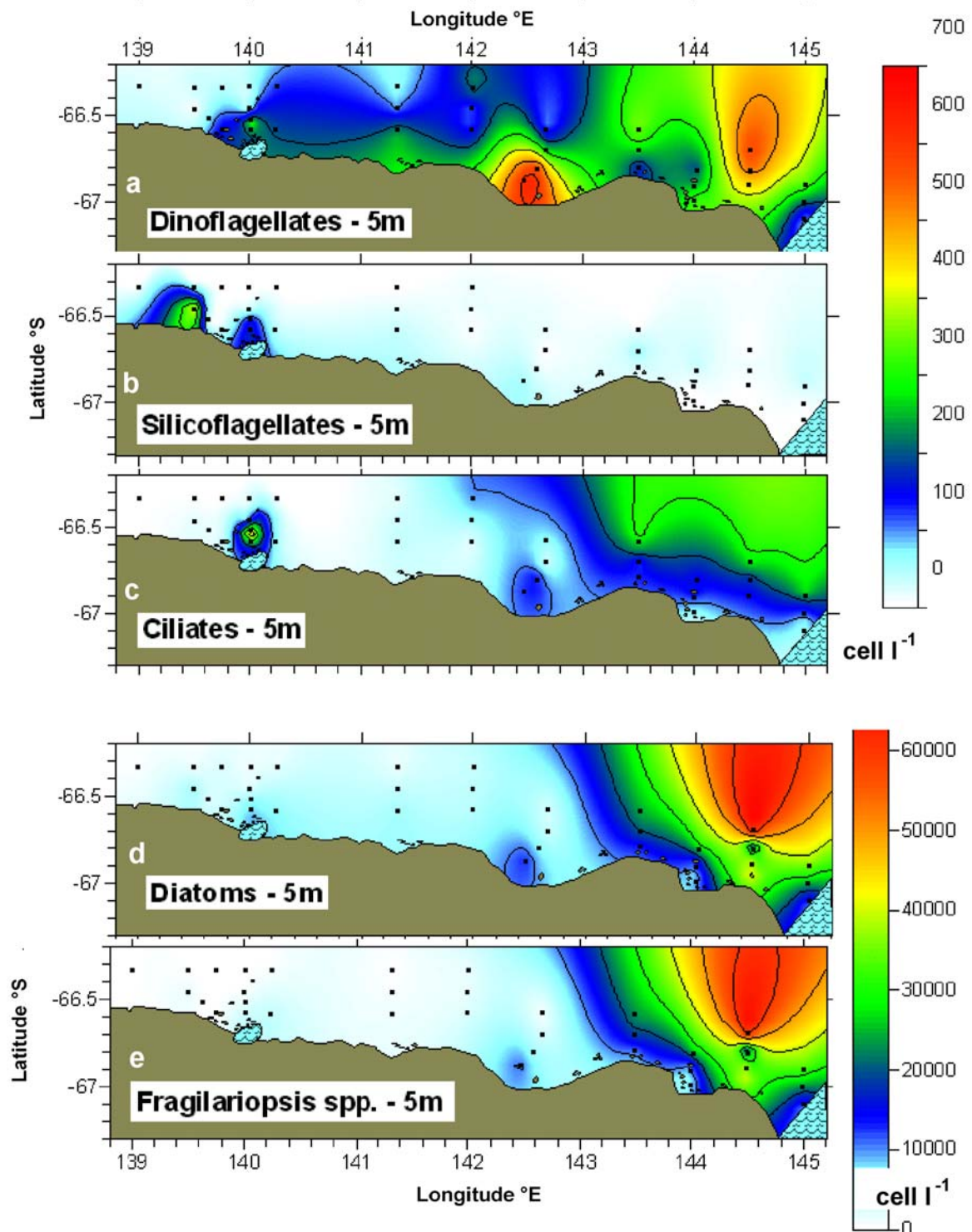


Figure 6. Microplankton abundances (cells l⁻¹) at 5 m depth. (a) Dinoflagellates, (b) Silicoflagellates, (c) Ciliates, (d) Diatoms (e) *Fragilariopsis* spp. (Beans *et al.* submitted)

The chain-forming central diatom *Chaetoceros criophilus* (+/- 25*30 µm) was also present throughout the region (Fig. 6f), with an average abundance of 478 ± 422 cells l⁻¹ at 5 m. At this depth, *C. criophilus* were most abundant close to the coast over the plateau (maximum of 1 701 cells l⁻¹ at station 36) and near the Astrolabe Glacier (peak of 1 344 cells l⁻¹ at station 6). Further offshore and to the east, abundances decreased,

to the point that none were observed at certain stations (16, 17 and 25). Several other *Chaetoceros* species were observed (Table 1), but the only other one to reach relatively high abundances was *Chaetoceros dictyota* (51 ± 54 cells l^{-1}).

The centric diatoms *Rhizosolenia spp.* and *Corethron pennatum*, with sizes ranging from 5×140 to 40×500 μm and 20×90 to 50×350 μm respectively, were two of the largest species present (with the exception of a few *Thalassiosira spp.* of $\phi > 100 \mu m$). They showed similar distributions and abundances (Fig. 6g and h), averaging at 5 m 378 ± 359 cells l^{-1} and 206 ± 281 cells l^{-1} respectively, and were frequently dominant species (maximum 24.3% of all diatoms for *Rhizosolenia spp.* and 31.3% for *C. pennatum* at 5 m).

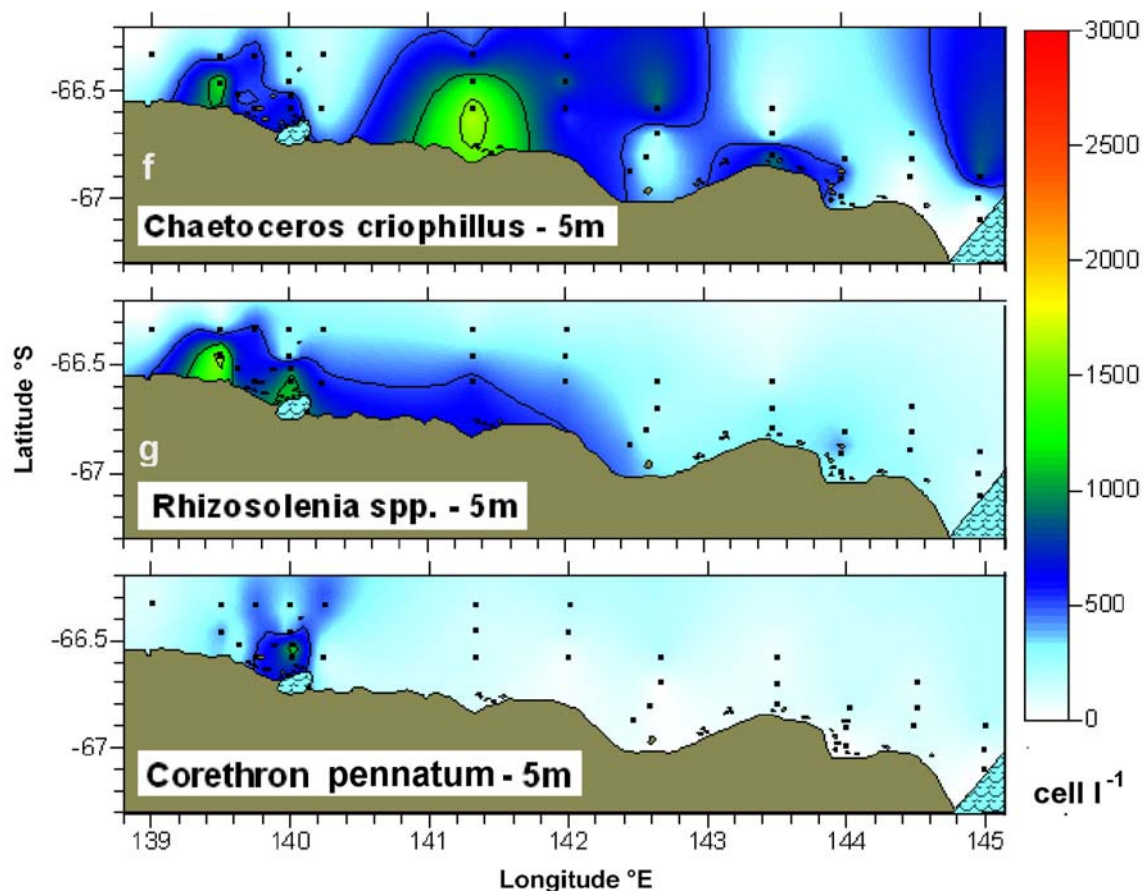


Figure 6. (continued) : Abundances (cells l^{-1}) of dominant diatoms at 5 m depth: (f) *Chaetoceros criophilus*, (g) *Rhizosolenia spp.*, (h) *Corethron pennatum*. (Beans et al. submitted)

Both groups showed their highest abundances close to the Astrolabe Glacier (1841 cells l^{-1} for *Rhizosolenia spp.* at station 6 and 1395 cells l^{-1} for *C. pennatum* at station 2), but where *Rhizosolenia spp.* distribution seemed to remain close to the coastline, continuing eastward a bit over the plateau, *C. pennatum* abundances peaked directly to the north of the Astrolabe Glacier. A similar pattern was observed for the remaining depths, with decreases in abundances. Over the plateau, *Rhizosolenia spp.* could

constitute approximately 10% of the diatom population, whereas in this same area *C. pennatum* was always below 10%. Both groups were occasionally present in the east, but were rare (between 0.3 - 7% of diatoms for *Rhizosolenia spp.* and 0 - 1% for *C. pennatum*).

Other diatoms of interest whose abundances were estimated include the pennate *Thalassiothrix antarctica* and the centric *Eucampia antarctica* and *Odontella sp.* *T. antarctica*, although frequently considered an open-ocean species (Crosta et al 2005), was quite abundant in certain areas (albeit to a lesser degree than the four groups mentioned previously), sometimes representing >10% of the diatom population over the plateau. The average abundance at 5 m was 236 ± 191 fragments.l⁻¹, with a rather uniform distribution throughout the region, excepting the presence of peaks of abundance close to shore near the Astrolabe Glacier and at either side of Watt Bay (maximum of 755 fragments.l⁻¹ at station 28). In general abundances increased with depth to 25 m, with maxima observed near the Mertz and Astrolabe Glaciers, and then decreased.

Eucampia antarctica and *Odontella sp.* are known as ice-associated species (Palmisano in Gomi et al. 2005). *Odontella sp.* was extremely rare (2.8 ± 8 cells l⁻¹ at 5 m), but could have been underestimated due to the difficulty of observing its weakly silicified cells with the optical microscope. It was more noticeably present near the Astrolabe Glacier. *Eucampia antarctica* averaged 8.3 ± 24 cells l⁻¹, and was most abundant near the Astrolabe Glacier (maximum 127 cells l⁻¹ at station 1) and to a lesser degree near the Mertz Glacier. In the former region it comprised up to 3% of the diatom population.

(iii) *Diatom assemblages.* Correspondence analysis was done on the abundances of the principal diatom taxa for all five depths (Fig. 7) taken together. The first two axes accounted for 71,94 % of the variation. These results allowed similar stations to be gathered into three groups, each characterised by the dominance of a certain group. The first axis, which accounted for 61.32 % of the variation, shows a clear separation between the stations in the Mertz Glacier and Adélie Depression region (stations 16-28) as well as the two coastal Commonwealth Bay stations (29 and 30) and the rest of the study site. In these stations *Fragilariopsis spp.* is the overwhelmingly abundant and dominant taxon. The second axis (10.62 % of the variation) allows for the separation of the stations over the plateau (31 – 38) from those near the Astrolabe Glacier and further east. The former group appears to have been determined by the presence of *Chaetoceros criophilus*, whereas the latter by the larger species *Corethron pennatum* and *Rhizosolenia spp.* Based on this grouping of stations, average abundances of the main microplankton groups for each zone have been presented in Table 2

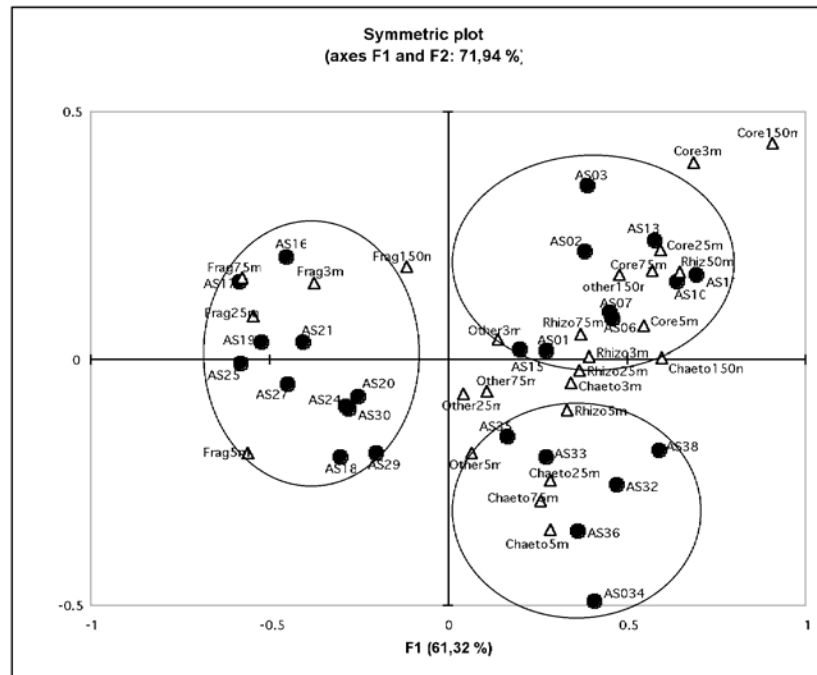


Figure 7. Correspondence analysis of dominant diatom groups and sampling stations

Discussion and Conclusions

With chlorophyll *a* concentrations averaging $0.64 \mu\text{g l}^{-1}$ at 5 m depth, and ranging between 0.04 and $1.57 \mu\text{g l}^{-1}$ throughout the zone (at all depths), the waters from Terre Adélie to the Mertz Glacier appear to support a significant summer standing crop of phytoplankton, comparable to the $0.6 \mu\text{g l}^{-1}$ yearly average observed around Antarctica (Table 3). Nevertheless, although presenting similar diatom cell abundances to neighbouring regions (Table 3), these values are lower than those observed in the coastal waters of the not too distant Prydz Bay ($2.1 \mu\text{g l}^{-1}$) (Jacques *et al.* 1994) and Terra Nova Bay ($0.1 - 4 \mu\text{g l}^{-1}$) (Goffart *et al.* 2000, Hecq 2003). And although it could be possible that we missed the peak of the summer bloom, similar levels were presented by Arrigo (2003), Sambrotto (2003) and Vaillancourt (2003) at the peak of the blooms in the Dumont d'Urville Polynya, Commonwealth Bay and the Mertz Polynya. Also, in a major survey of the region, Wright and van den Enden (2000) found that waters from $128 - 150^\circ\text{E}$ were considerably less productive than waters from $93 - 120^\circ\text{E}$. It appears then that phytoplankton biomasses are lower in the Terre Adélie – George V Lands than in those neighbouring regions. The Chl *a* concentrations measured during this study were higher than those of the waters north of the Terre Adélie shelf break (yet still south of the Polar Front) as studied by Chiba in 1996 and Gomi in 2000 (Table 3), indicating that the shelf waters remain an important location for primary production in the region.

Table 2: Nutrients (μM), Chl *a* ($\mu\text{g l}^{-1}$) and microplankton (cells l^{-1}) in Terre Adélie and Georges V Land surface waters (5 m depth) (average \pm standard deviation, maximum – minimum)

	Astrolabe Glacier	Plateau	Mertz Glacier + Adélie Depression
Nitrite	0.19 \pm 0.02 (0.15 – 0.22)	0.21 \pm 0.01 (0.19 – 0.24)	0.19 \pm 0.02 (0.16 – 0.22)
Nitrate	33.45 \pm 0.84 (31.65 – 34.37)	32.22 \pm 0.4 (31.38 – 32.64)	31.29 \pm 0.48 (30.38 – 31.91)
Silicate	54.42 \pm 1.05 (51.51 – 58.08)	51.81 \pm 1.21 (50.22 – 53.23)	52.23 \pm 0.80 (51.15 – 54.21)
Chl <i>a</i>	0.68 \pm 0.14 (0.38 – 0.94)	0.29 \pm 0.05 (0.21 – 0.35)	0.79 \pm 0.37 (0.28 – 1.57)
Ciliates	80 \pm 180 (0 – 628)	42 \pm 30 (14 – 97)	156 \pm 82 (40 – 312)
Dinoflagellates	102 \pm 105 (0 – 352)	154 \pm 82 (61 – 269)	354 \pm 180 (78 – 624)
Silicoflagellates	71 \pm 139 (0 – 460)	12 \pm 12 (0 – 35)	17 \pm 22 (0 – 67)
Diatoms	3317 \pm 2790 (394 – 9058)	3360 \pm 1271 (1190 – 5432)	22919 \pm 18249 (6507 – 70274)
<i>Fragilariopsis</i> spp.	954 \pm 1346 (0 – 3669)	1216 \pm 850 (76 – 2459)	21159 \pm 18064 (4448 – 68222)
<i>Rhizosolenia</i> spp.	608 \pm 516 (56 – 1841)	298 \pm 142 (145 – 555)	226 \pm 115 (76 – 456)
<i>Corethron pennatum</i>	433 \pm 380 (72 – 1395)	107 \pm 64 (0 – 183)	70 \pm 53 (0 – 187)
<i>Chaetoceros criophilus</i>	444 \pm 380 (72 – 1395)	821 \pm 488 (168 – 1701)	312 \pm 331 (0 – 989)
Other <i>Chaetoceros</i> spp.	311 \pm 307 (18 – 973)	385 \pm 331 (139 – 1463)	434 \pm 356 (34 – 1145)
<i>Thalassiothrix antarctica</i> (fragments II)	204 \pm 215 (0 – 696)	171 \pm 123 (42 – 425)	300 \pm 193 (96 – 755)
<i>Eucampia antarctica</i>	12 \pm 36 (0 – 127)	0	10 \pm 15 (0 – 44)
<i>Asteromphalus</i> spp	37 \pm 54 (0 – 175)	58 \pm 66 (0 – 208)	81 \pm 54 (0 – 160)
<i>Acinocyclus</i> spp.	97 \pm 96 (0 – 316)	101 \pm 63 (17 – 215)	139 \pm 84 (16 – 323)
<i>Thalassiosira</i> spp.	69 \pm 95 (0 – 337)	41 \pm 34 (0 – 97)	61 \pm 42 (0 – 161)
<i>Coscinodiscus</i> spp	16 \pm 33 (0 – 105)	8 \pm 11 (0 – 28)	11 \pm 15 (0 – 54)
<i>Odontella</i> spp.	6 \pm 13 (0 – 37)	0	1 \pm 5 (0 – 18)
<i>Nitzschia</i> / <i>Pseudo-</i> <i>nitzschia</i> group	6 \pm 21 (0 – 74)	0	0
Other diatoms	120 \pm 130 (0 – 337)	107 \pm 109 (0 – 334)	164 \pm 110 (0 – 418)

Table 3: Chlorophyll a and microplankton abundance in the region

Location	Period	Chl a ($\mu\text{g}\cdot\text{l}^{-1}$)	Diatom abundances ($\text{cells}\cdot\text{l}^{-1}$)	Reference
Southern Ocean	Yearly average	0.6		El Sayed, (2005)
Prydz Bay	Summer	2.1		Jacques & Fukuchi, (1994)
Terre Adélie + Georges V Land	January 2004	0.21 – 1.57	1.14×10^5	This study
Dumont d'Urville Polynya	November 1995	0.69	2×10^3	Riaux-Gobin et al. (2000, 2003)
Dumont d'Urville Polynya Mertz Polynya	Summer peak	1.17 0.93		Arrigo & van Dijken, (2003)
Terre Adélie + Commonwealth Bay Mertz Region	December 2000 – January 2001	1.33 1.03		Sambrotto et al (2003) & Vaillancourt et al (2003)
Terre Adélie – offshore	January – February 1996	0.4 – 0.6		Chiba et al. (2000)
Terre Adélie – offshore	February – March 2000	0.3 – 0.5		Gomi et al. (2005)
Terra Nova Bay (Ross Sea)	January – February 1998		Maximum 6×10^5	Fonda Umani et al. (2005)
Western Ross Sea	January 1990	0.1 – 4		Goffart et al. (2000)

As in other shelf waters around Antarctica (Jacques and Fukuchi 1994, Chiba *et al.* 2000, Waters *et al.* 2000, Fonda Umani *et al.* 2005), the microplankton communities in Terre Adélie are strongly dominated by diatoms (over 80% of the microplankton). Within this group, the dominance of pennate diatoms (in particular *Fragilariopsis spp*) is consistent with other eastern Antarctic and Ross Sea studies (Kopczynska *et al.* 1986, Goffart *et al.* 2000, Waters *et al.* 2000).

Previous studies in the waters just north of the shelf break also noted the importance of *Fragilariopsis spp.* and related species in the region, with abundances similar to those reported here ($0 - 6.8 \cdot 10^5$ cells l^{-1} at 5 m): in Gomi's study (Gomi *et al.* 2005) the dominant diatoms were *Fragilariopsis spp* ($0.5 - 1 \cdot 10^5$ cells l^{-1}); (Waters *et al.* 2000) noted the most frequent diatoms in our zone were a group composed of *F. curta*, *Nitzschia lecontei* and other related species larger than $20 \mu\text{m}$ ($3.6 \cdot 10^4 - 5.6 \cdot 10^5$ cells l^{-1}), while in the Terre Adélie waters close to the Antarctic Convergence (Chiba *et al.* 2000), the dominant diatom was *F. kerguelensis*. These authors also mentioned the presence of *Corethron pennatum*, *Rhizosolenia spp.* and the frequently abundant *Thalassiothrix antarctica* and *Chaetoceros criophilus*, which are all abundant species in our study.

We compared the distribution of the four dominant taxa observed in this study (*Corethron pennatum*, *Rhizosolenia spp.*, *Chaetoceros criophilus* and *Fragilariopsis*

spp) with the surface water densities (Fig. 8). *Corethron pennatum*, *Rhizosolenia spp* and *Chaetoceros criophilus* abundances had a significant relationship with SigmaT values ($p < 0.01$), showing a distinct preference for the more mixed waters with higher surface densities (although *C. criophilus* was also abundant in slightly less dense and more stratified waters). *Fragilariopsis spp*, on the other hand, although no clear relationship was observed between abundances and SigmaT values ($r = -0.15$, $p = 0.37$), did show a tendency to be more abundant in more stratified waters with lower surface density.

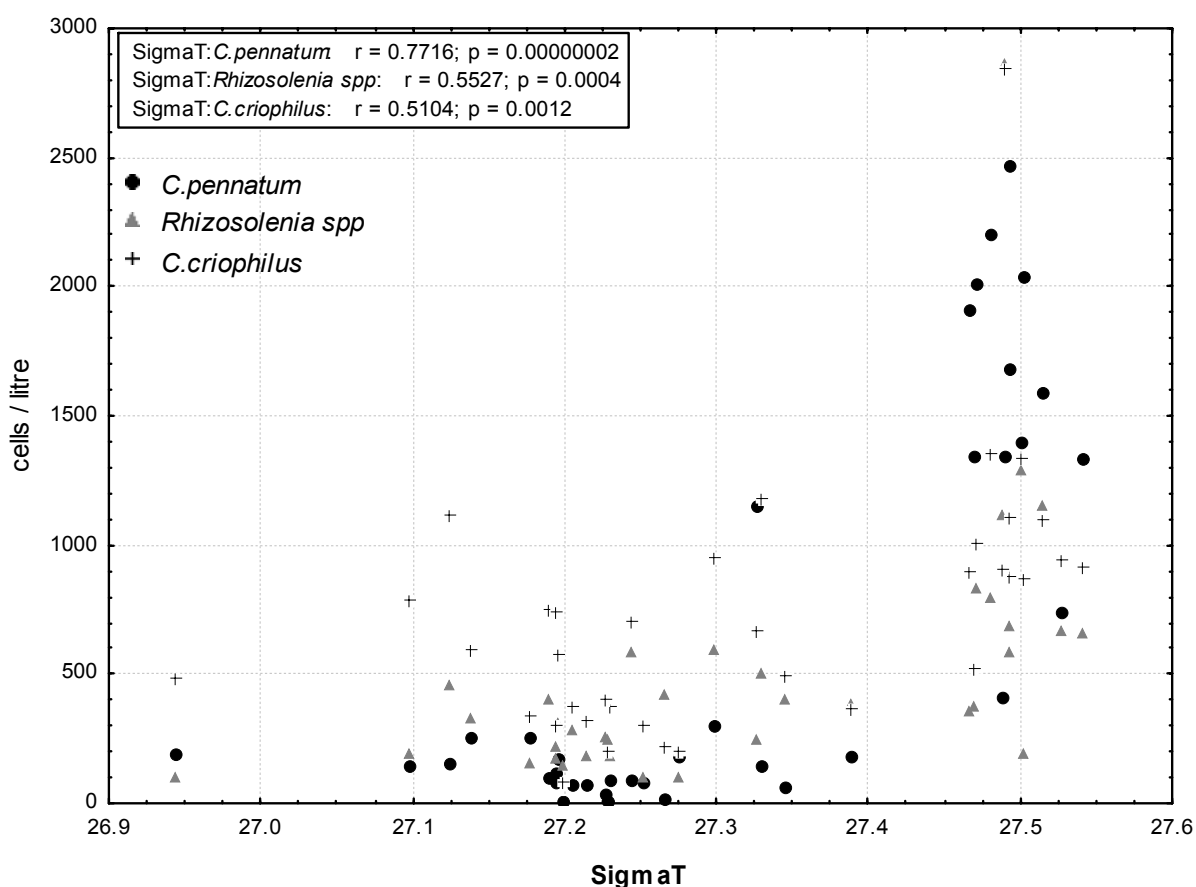


Figure 8. Surface water density (sigmaT) vs. abundances of three diatom species: *Chaetoceros criophilus*, *Rhizosolenia spp.* and *Corethron pennatum*

Both the cartographic representations and the correspondence analysis done on the abundances of the principal diatom species allowed us to distinguish three separate zones in our region (cfr 2.7 fig 14): the Mertz Glacier and Adélie Depression zone, the Astrolabe Glacier zone, and the shelf waters over the plateau in between these two.

Beginning in the East, the Mertz Glacier and Adélie Depression stations are shown to be very different from the remaining zones. The region is characterised by the presence of a polynya which begins to open in mid-September and is usually fully developed by mid-October, allowing for a phytoplankton bloom early in the season (Sambrotto *et al.* 2003; Vaillancourt *et al.* 2003). During our study we found there was

maximum depletion of nutrients in this region and a stratified water column, probably due to the ice melt. Diatom, ciliate and dinoflagellate abundances were at a maximum (70 274 cells l⁻¹, 312 cells l⁻¹ and 624 cells l⁻¹ respectively). Among the diatom community, a very low diversity of principally small diatoms was observed (*Fragilariopsis spp.* dominated the community, *Chaetoceros spp.* were also relatively abundant). In a classification by (Sambrotto *et al.* 2003), this region was also separated from the rest based on bathymetry, distribution of pack-ice and fast-ice, and chlorophyll levels. Studies by Samyshev in 1991 (*in Waters et al.* 2000) have suggested that the smaller ice-seeded diatoms *Fragilariopsis spp.* and *Chaetoceros spp.* are typical of spring / early summer, when the sea-ice begins to melt and the waters are stratified. Other authors have also mentioned the importance of stratified waters for diatoms, noting that diatoms showed a positive correlation with water column stability, as stratification increases the time a cell spends in an environment with high available light for photosynthesis (Gibson *et al.* 1997; Goffart *et al.* 2000; Moro *et al.* 2000). In their studies diatom blooms appeared to be much more abundant in stratified waters and were frequently dominated by small pennate diatoms such as *Fragilariopsis spp.* or *Nitzschia spp.*. Cores taken from the sediment near the Mertz Glacier showed signs of abundant *Fragilariopsis* species, making this group the dominant diatom in recent times (Maddison *et al.* 2006).

The remaining stations in the other two zones were in a less stratified region with more mixed surface waters which could be the result in part of the summertime katabatic winds which are more frequent and intense in Terre Adélie and Commonwealth Bay than near the Mertz Glacier (Sambrotto *et al.* 2003; Vaillancourt *et al.* 2003). They showed similar abundances and diversity, but were separated into two groups based on the importance of certain diatom taxa.

The Astrolabe Glacier zone comprised 15 stations with less nutrient-depleted waters than elsewhere in the region, and with little vertical change observed in the concentrations. This zone was characterised by average Chl *a* concentrations (0.68 ± 0.14 µg l⁻¹ at 5 m), high diatom diversity and average abundances (3317 ± 2790 cells l⁻¹ at 5 m), and dominated by predominantly larger species such as *Corethron pennatum* and *Rhizosolenia spp.* These are typically associated with open ocean conditions (Armand *et al.* 2005; Crosta *et al.* 2005; Maddison *et al.* 2006) and would thrive better in these mixed waters than the smaller pennate diatoms due to adaptations which reduce their sinking rate by drag such as long appendages (in the case of *C. pennatum*) or their needle-like morphology (for *Rhizosolenia spp.*). It is also in this zone where maximum abundances of silicoflagellates were found (maximum 460 cells l⁻¹).

The third zone comprised stations that were located over the shallower and warmer shelf waters and were characterised by having similar nutrient concentrations to the Astrolabe Glacier zone, and yet much lower Chl *a* concentrations ($0.29 \pm 0.05 \mu\text{g l}^{-1}$ at 5 m) and average diatom abundances ($3360 \pm 1271 \text{ cells l}^{-1}$ at 5 m) with a high diversity. These stations seem to be characterized by the presence and high abundance of *Chaetoceros spp.*, in particular *C. criophilus*. The similarity between the surface water densities and nutrient concentrations of this zone and those of the Astrolabe Glacier zone suggest that differences in diatom abundances between the two zones must be due to another factor. Studies by Swadling *et al.* (in press) and Koubi *et al.* (in press) found the waters over the plateau to hold the largest abundances of potential grazers in the region. These include various copepods (calanoid and cyclopoid), appendicularians, euphausiids (Vallet, pers. communication) and fish larvae (particularly *Pleuragramma antarcticum*) which have been known to prey on microplankton. The low biomass observed here may therefore very well be due to the larger grazing pressure in this zone.

Conclusions

The microplankton communities in the coastal waters between Terre Adélie and the Mertz Glacier were dominated by diatoms. Correspondence analysis of the species composition allowed the region to be separated into three zones each represented by a dominant group: the Mertz Glacier – Adélie Depression zone with stratified waters characterised by low diversity due to very high abundances (chl *a* 0.79 ± 0.37 ; diatoms $22\,919 \pm 18\,249 \text{ cells/l}$ at 5 m) dominated by the small colonial *Fragilariopsis spp.*; the Astrolabe Glacier zone where diversity was high, abundances average (chl *a* $0.68 \pm 0.14 \mu\text{g/l}$; diatoms $3317 \pm 2790 \text{ cells/l}$ at 5 m) and the diatom community was principally composed of larger species such as *Corethron pennatum* and *Rhizosolenia spp.*; and finally an intermediate zone between the two over the shallower shelf waters where biomasses were lower (chl *a* $0.29 \pm 0.05 \mu\text{g/l}$; diatoms $3360 \pm 1271 \text{ cells/l}$ at 5 m), coinciding with a large presence of herbivorous zooplankton, and where the small chain-forming *Chaetoceros criophilus* and similar species were dominant.

2.3. Zooplankton distribution in the Terre Adélie sector of East Antarctic Shelf ecosystem

Contributors: Jean-Henri Hecq, Anne Goffart, Philippe Koubbi and Kerry Swadling

This text contains excerpts from the following paper:

Swadling K.M., Koubbi P., Hecq J.H., Wright S.W., Sultan E., Goffart A. Zooplankton-environment relationships along the East Antarctic coast (139°E – 145°E) in summer. Submitted to Deep Sea Res II.

There have been few studies of zooplankton distribution on the continental shelf between 139°E and 146°E (Hosie *et al.*, 2000; Chiba *et al.*, 2001); generally the focus has been further offshore or near the shelf break where *E. superba* dominates (Nicol *et al.*, 2000; Hosie *et al.*, 2000). Planktonic fauna are key components of the Antarctic marine ecosystem. While the general distributions of zooplankton in the Southern Ocean are apparent, the underlying factors controlling these distributions are still poorly understood.

To elucidate those features that were important in structuring planktonic communities we investigated associations between zooplankton species composition and physical and chemical oceanography at 36 sites along the coast of Terre Adélie (139°E to 145°E), during January 2004 (Swadling *et al.* Submitted). A WP2 net (Hydrobios), with mesh size 200 µm and 600 mm diameter (260 cm length), was used to sample the zooplankton. Single vertical hauls from 200 m or close to the seafloor for shallower waters were taken from 36 sites. A flowmeter (Hydrobios) at the entrance of the net allowed the filtered volume of water to be calculated. Samples were preserved in 5% formaldehyde seawater buffered with sodium tetraborate at sea water pH. Samples were split with a Folsom Splitter in the laboratory so that at least 1000 animals were counted per sample. Animals were identified to the lowest taxon possible and, in the case of most copepods, to sex and stage. Copepod nauplii could not be identified to species and were pooled as cyclopid or calanoid nauplii.

We identified 28 zooplankton taxa in the coastal and shelf waters between 139°E and 145°E. Total zooplankton abundance was variable between the sites, ranging from 55 to 1280 individuals m⁻³ (mean: 290 individuals m⁻³). The assemblages were dominated by appendicularians and small copepods, in particular *Oithona similis* and *Oncaea curvata*. Common calanoid copepods included *Stephos longipes*, *Calanus simillimus*, *Metridia gerlachei* and *Calanoides acutus*.

The dominant forms were small copepods, particularly cycloids, and appendicularians for which we have less information. In 2004, the zooplankton abundance ranged from 55 to 1280 individuals m⁻³. The highest abundances were found over the Adélie Bank, which is delineated to the east and west by deep depressions (figure 9). This area also exhibited the warmest surface temperatures and had the lowest pigment concentrations, suggesting increased grazing activity by the zooplankton.

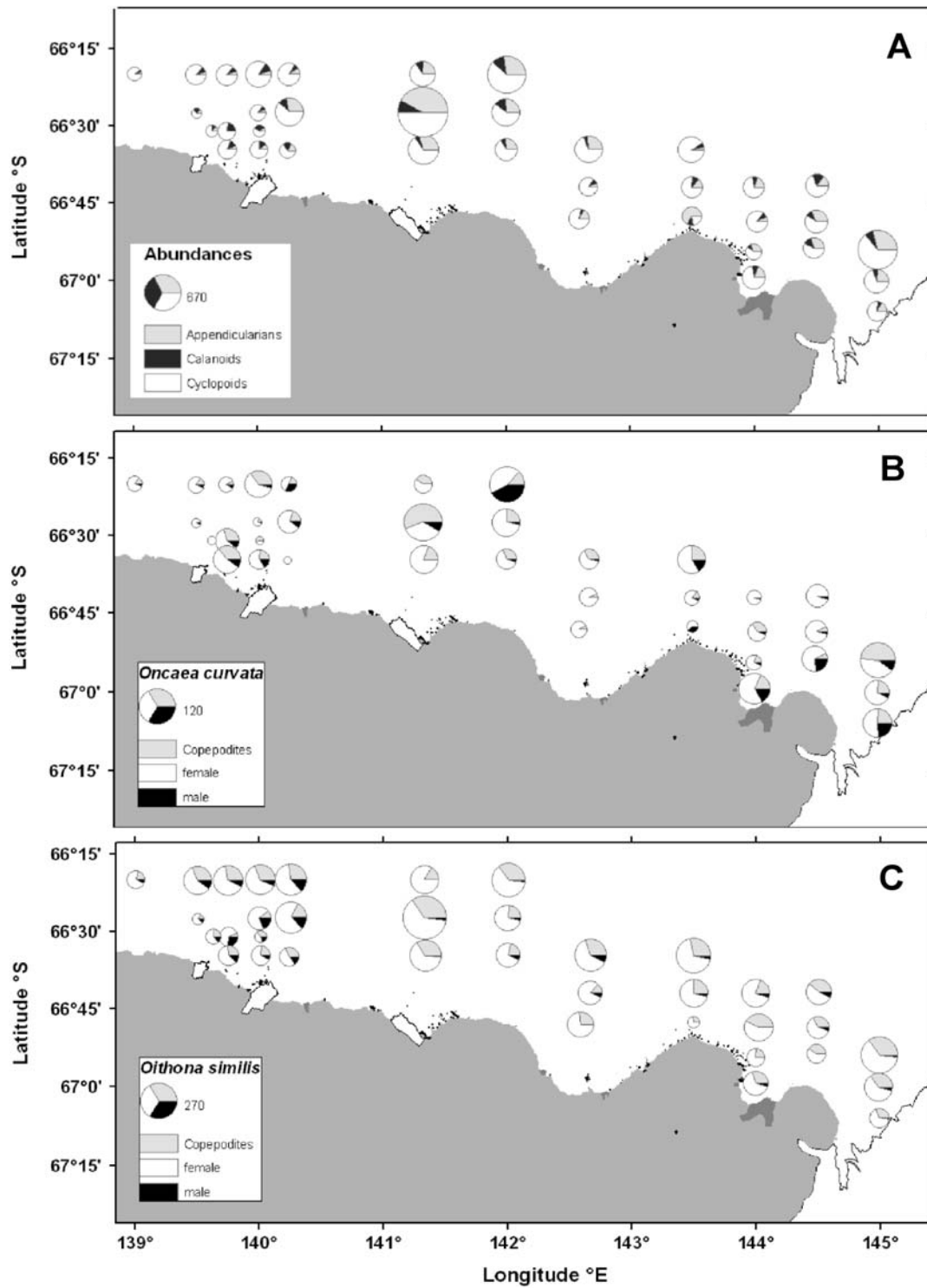


Figure 9. (A) Total abundance (individuals m⁻³) of zooplankton during the 2004 survey showing the proportions of cyclopoid copepods, calanoid copepods and appendicularians at 36 sampling sites. Abundance of development stages of (B). *Oncaea curvata* and (C). *Oithona similis* (Swadling *et al.*, submitted).

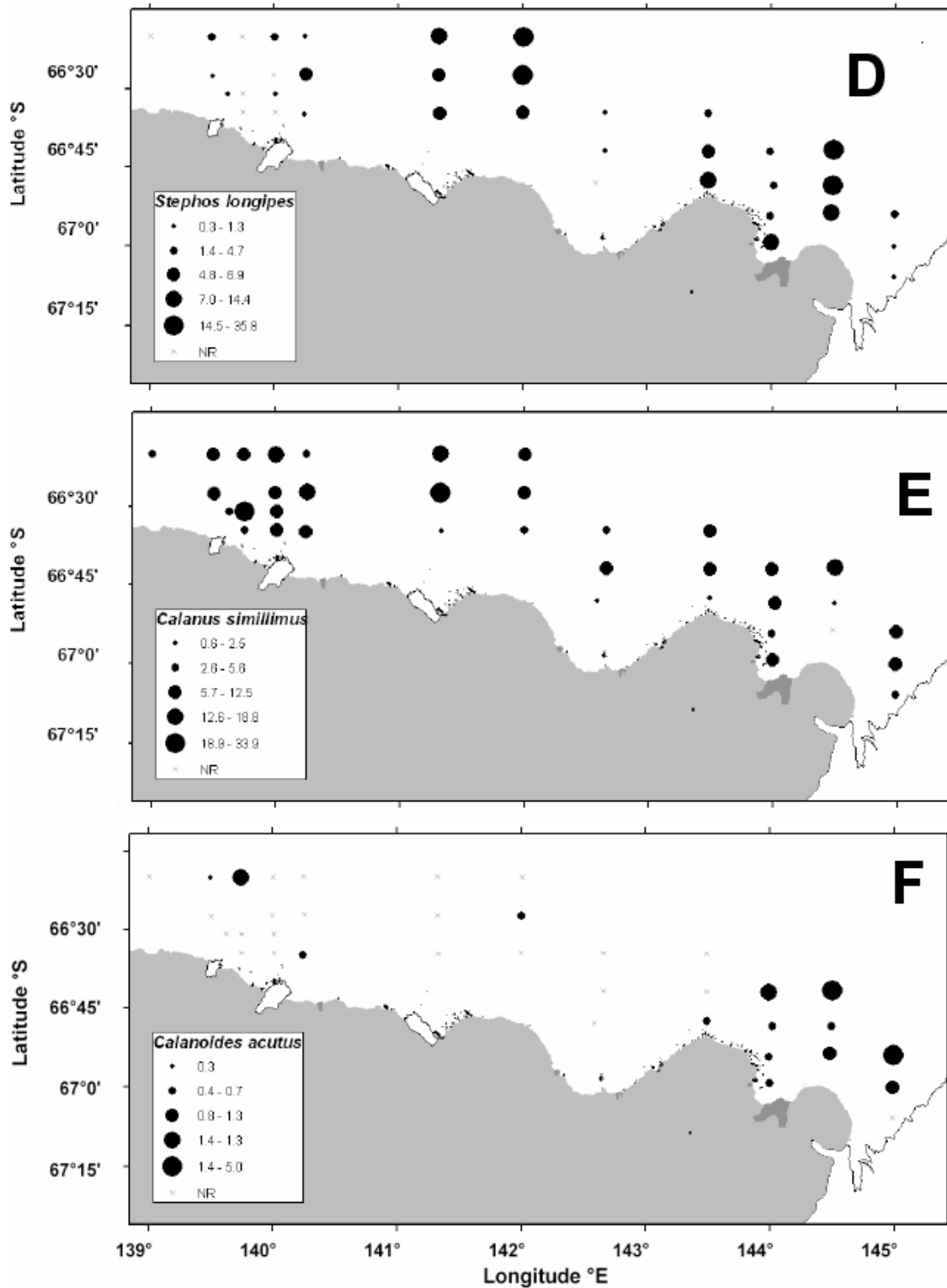


Figure 9. (continued) Abundances (individuals m⁻³) of common calanoid copepods at 36 sampling sites. D. *Stephos longipes*, E. *Calanus simillimus*, F. *Calanoides acutus*, NR: not recorded.

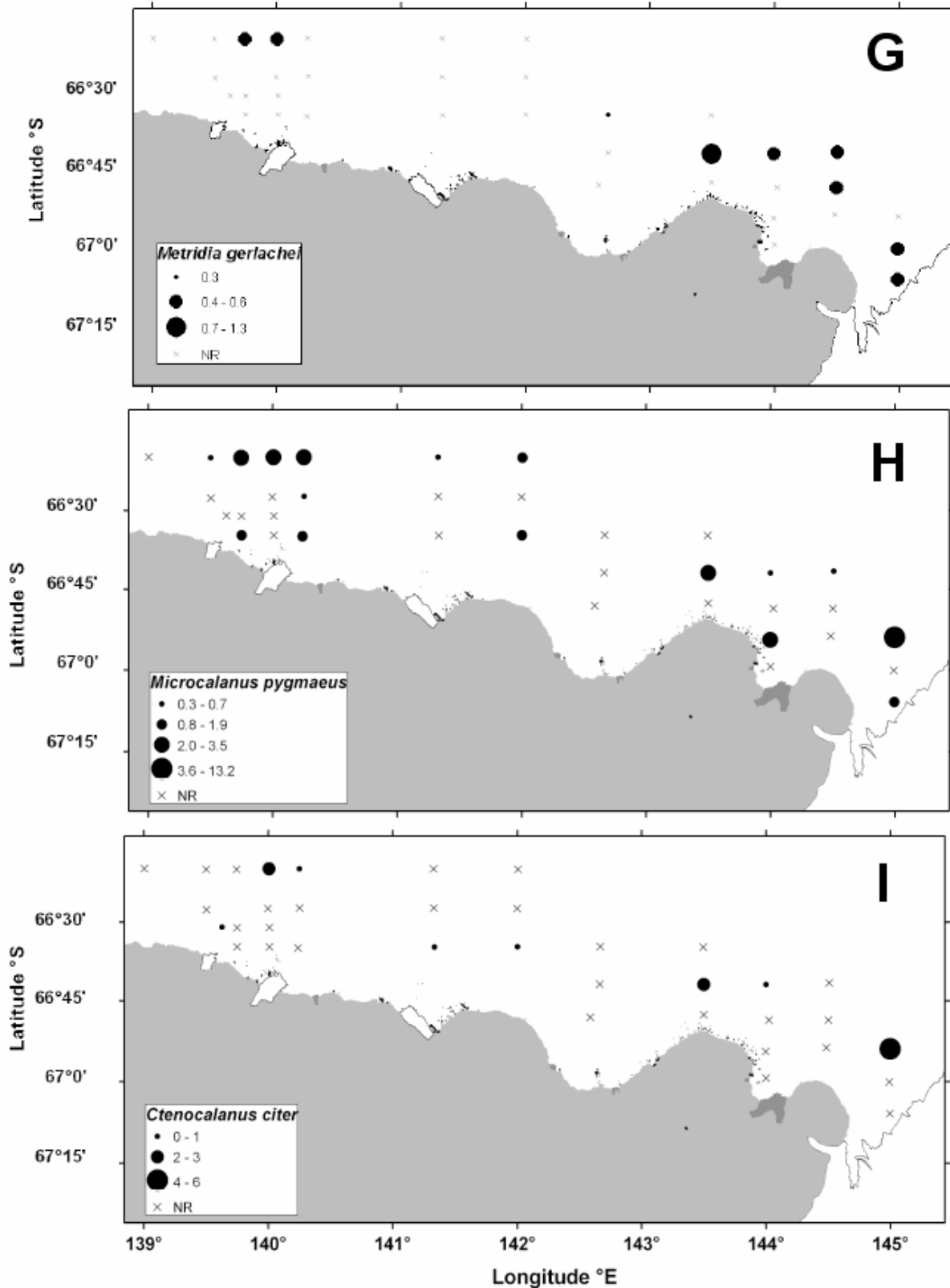


Figure 9. (continued) Abundances (individuals m⁻³) of common calanoid copepods at 36 sampling sites. G. *Metridia gerlachei*, H. *Microcalanus pygmaeus* and I. *Ctenocalanus citer*. NR: not recorded.

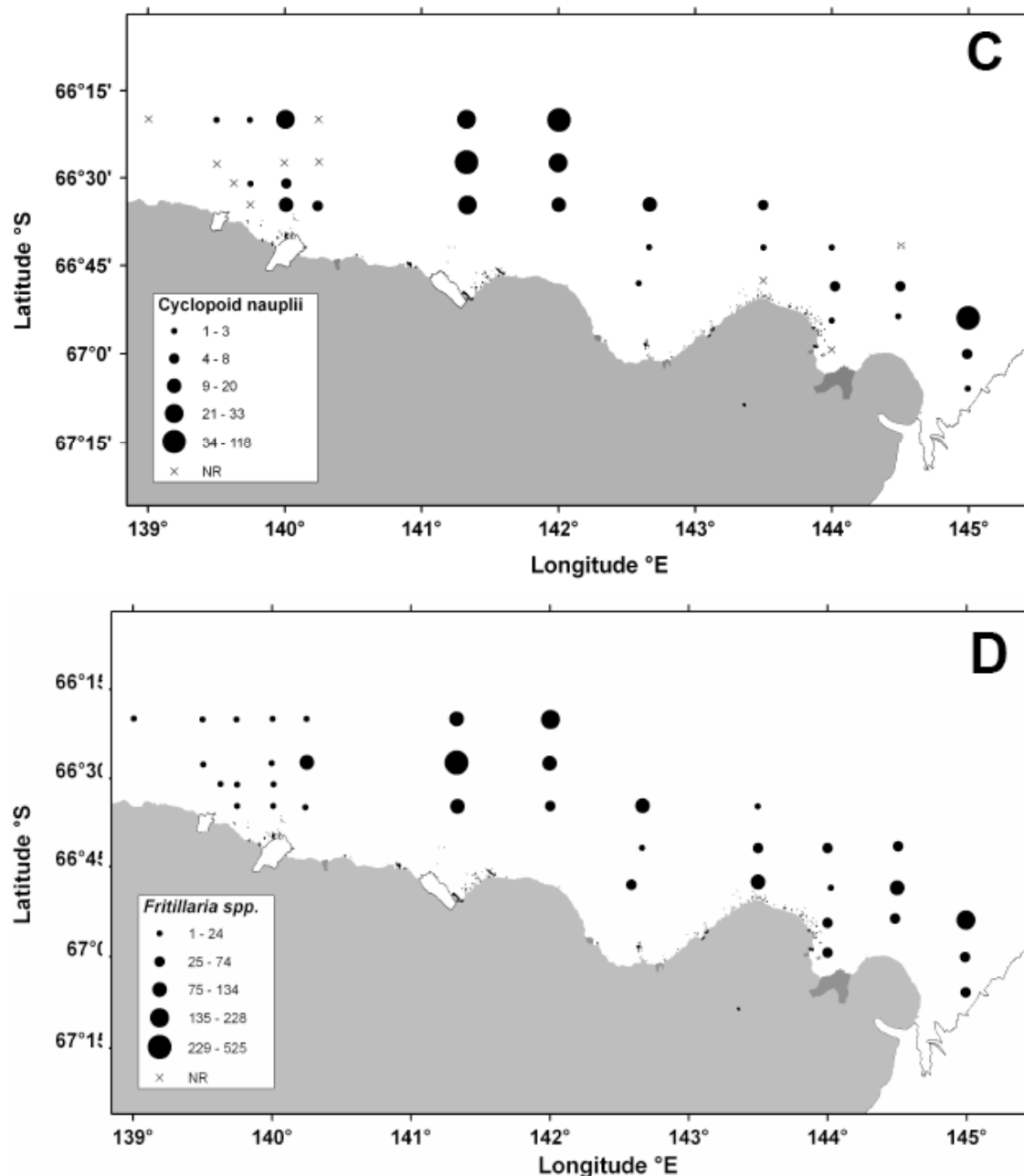


Figure 9. (continued) Abundances (individuals m⁻³) of J. Cyclopoid nauplii and K. Fritillaria spp. NR: not recorded. (Swadling et al., submitted)

The composition of the zooplankton assemblage was generally consistent across the sampling region, although diversity tended to be higher over the deeper waters associated with the Adélie Depression and MGT. Among copepods, *Oithona similis* is widely distributed. This species is believed to be cosmopolitan (Galliène and Robins, 2001) and accounted for between 15 and 80% of numerical abundance in the studied area. It is a generalist feeder, which might explain its success in so many marine environments and its ability to reproduce during times of low primary productivity in the southern ocean. *Oncaea curvata* is also widely distributed in the southern ocean and can be particularly abundant at coastal sites. A generalist diet, which includes diatoms, aggregates and detritus, as well as possible carnivorous input, would assist *O. curvata*

in maintaining high abundances throughout the year. Large calanoid copepods, such as *Euchirella rostromagna*, *Calanoides acutus* and *Metridia gerlachei*, were found in deeper water.

An ordination method, Redundancy Analysis (RDA), was used to assess the influence of environmental factors on the distribution of zooplankton. The first two axes of the RDA explained 80% of the variation in the zooplankton-environment relationships, although only surface salinity explained a statistically significant ($p < 0.5$) proportion (42%) in the zooplankton assemblages along the coast of Terre Adélie (Fig. 10).

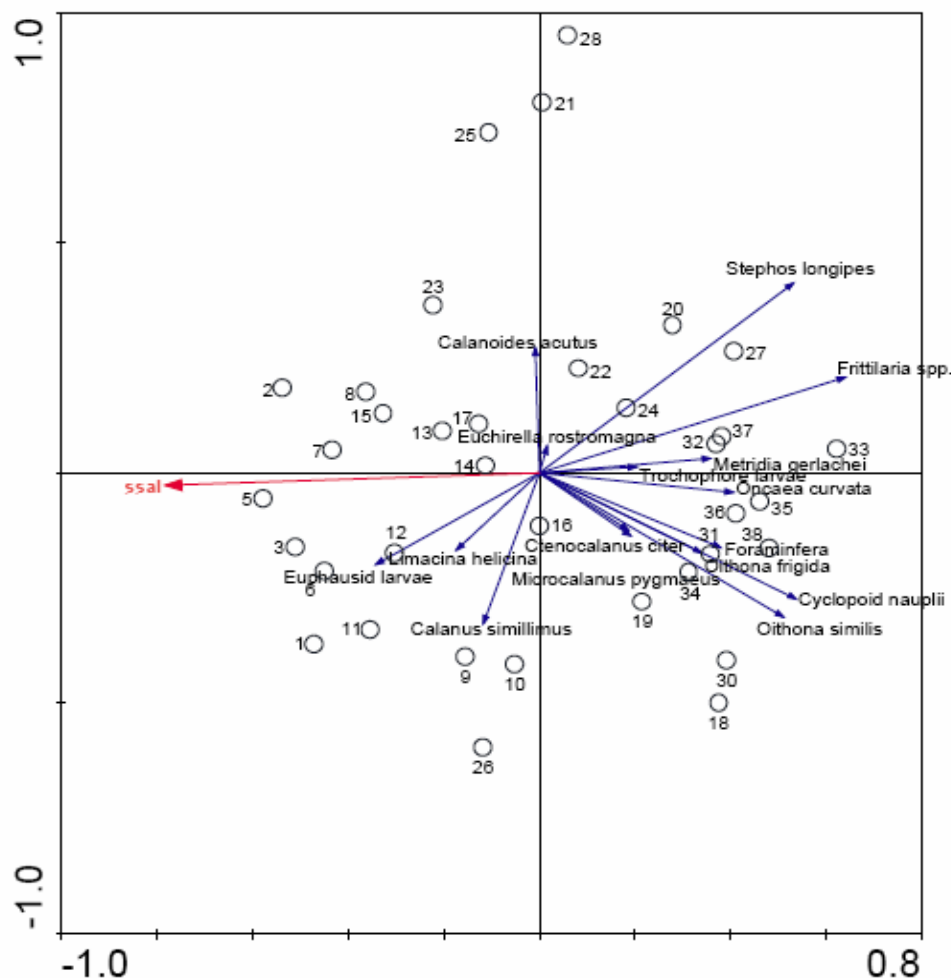


Figure 10. Redundancy analysis of zooplankton-environment relationships. Triplot shows surface salinity (thick arrow), zooplankton taxa (thin arrows) and sampling sites (circles) (Swadling et al., submitted) .

In point of view mesozooplankton distribution, the study region encompassed two main water bodies: those in the west were shallower, less stratified and had higher surface salinities and temperatures than waters further east towards the Mertz Glacier Tongue. Furthermore, waters in the west had generally lower concentrations of phytoplankton and exhibited less zooplankton diversity than observed further east.

Since 2004, the surveys carried out from Terre Adélie to Mertz glacier tongue allowed to study the distribution of euphausiids within the neritic zone (Vallet *et al.*, in-prep). *Euphausia crystallorophias* form a significant component of zooplankton biomass replacing *E. superba* in the neritic zone and represent an important alternative pathway in the Antarctic food web for top predators (figure 11).

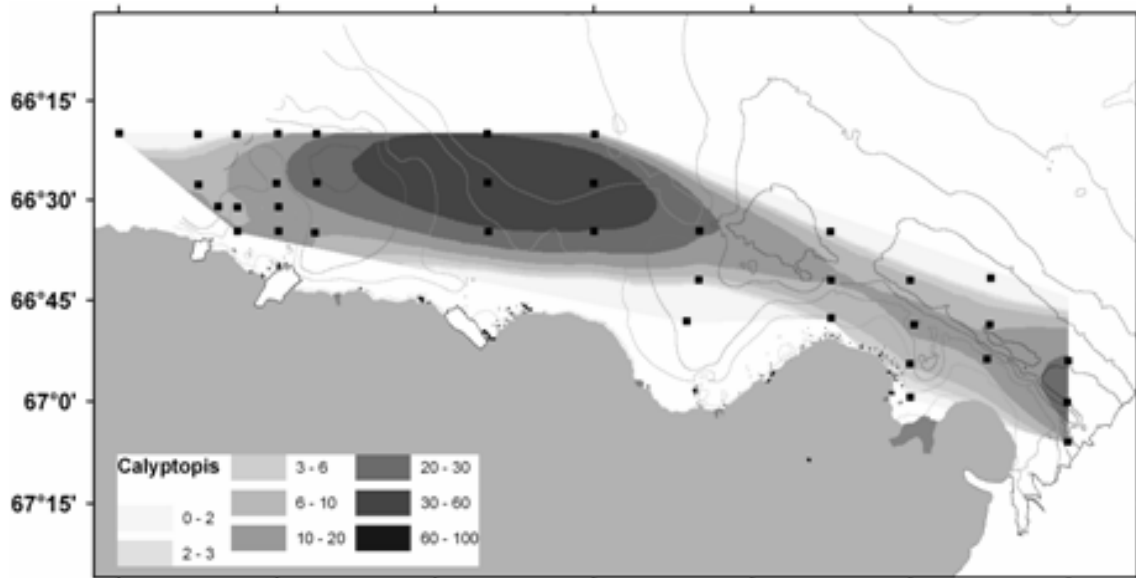


Figure 11. Abundances of calyptopis stages of *E. crystallorophias* during the 2004 survey.

Abundances of young stages (metanauplius and calyptopis) were the highest in our samples and maxima were observed over the Adélie Bank. But other smaller swarms were observed near the MGT for calyptopis and West of the Adélie Bank for metanauplius. Adults showed a quite different repartition with highest abundances over the slopes of the main depressions. Beside depth explaining the life stages distribution, the correlations are not too high between life stages and environmental values showing here that secondary swarm locations are probably related to biotic factors such as food availability, presence of predators or due to mixing effect during strong wind events.

2.4. Ichthyoplankton distribution and Trophic status of larvae of *Pleuragramma antarcticum* in the Terre Adélie sector of East Antarctic Shelf ecosystem

Contributors: Jean-Henri Hecq, Anne Goffart and Philippe Koubbi

This text contains excerpts from the continued papers:

Koubbi P., Duhamel. G, Hecq J.H., Beans C., Loots C, Pruvost P., Tavernier E., Vacchi M., C. Vallet. Ichthyoplankton in the neritic and coastal zone of Antarctica and Subantarctic islands. In: 38th International Liège Colloquium on Ocean Dynamics - Revisiting the role of zooplankton in pelagic ecosystems, Liège (Belgique). *J. Mar. Syst.* Accepted for publication

Frangoulis C., Christou E.D. Hecq J.H. 2005, Comparison of marine copepod outfluxes: nature, rate, fate and role in the carbon and nitrogen cycles. *Advances in Marine Biology*, 47:253-309

P. antarcticum larvae dominate the neritic assemblages over the Eastern Antarctic continental shelf with values sometimes greater than 90% (Koubbi *et al.*, 1997 and accepted, Hoddell *et al.*, 2000). Spawning is supposed to occur in deep coastal canyons or in coastal zones near ice-shelves or glaciers. ROV explorations in coastal innershelf depressions in 2007 in Dumont D'Urville showed high abundances of larvae near the bottom at depth greater than 150 m. Hatching might occur in November-December. The spatial segregation of life stages of this species is clearly explained in the Weddell sea where gyres and currents are clearly described (Kellermann 1987, Hubold 1984, 1985) (figure 12 A).

Since 2004, *P. antarcticum* larvae are monitored between Terre Adélie and the MGT. Young larvae are very abundant over the Adélie Bank as *E. crystallorophias* or copepods (figure 12 B) (Koubbi *et al.*, accepted). Larvae of other species such as the icefish *Chionodraco hamatus* are also dominant in this area. For *P. antarcticum*, Hubold (1992) and our results from Terre Adélie show that the segregation of life stages seemed to follow the scheme of Harden-Jones (1968). Regional oceanography induces spatial segregation of life stages and reduces intraspecific competition. Katabatic winds are very important; they might allow larvae to reach nursery areas near the shelf break (figure 13).

Are *P. antarcticum* larvae dispersed all over the eastern antarctic shelf in relation to the Eastern Coastal Current and what are the consequences on population exchanges? Two ARGOS buoys, launched from the coastal zone of Terre Adélie, were tracked in 1998 (figure 13).

During the first two months, they clearly drifted offshore and to the West due to major currents and during the first days to strong katabatic events. After this period, the direction of the remaining buoy changed to the East showing in some areas the presence of gyres such as those present to the North of Terre Adélie. From these observations, we can assume that larval drift of *P. antarcticum* larvae is possible between areas of the Eastern Antarctic shelf but that gyres may also limit emigration. However, Bargelloni *et al.* (2000) could not differentiate populations or subpopulations between sectors but this should be restudied with new molecular markers.

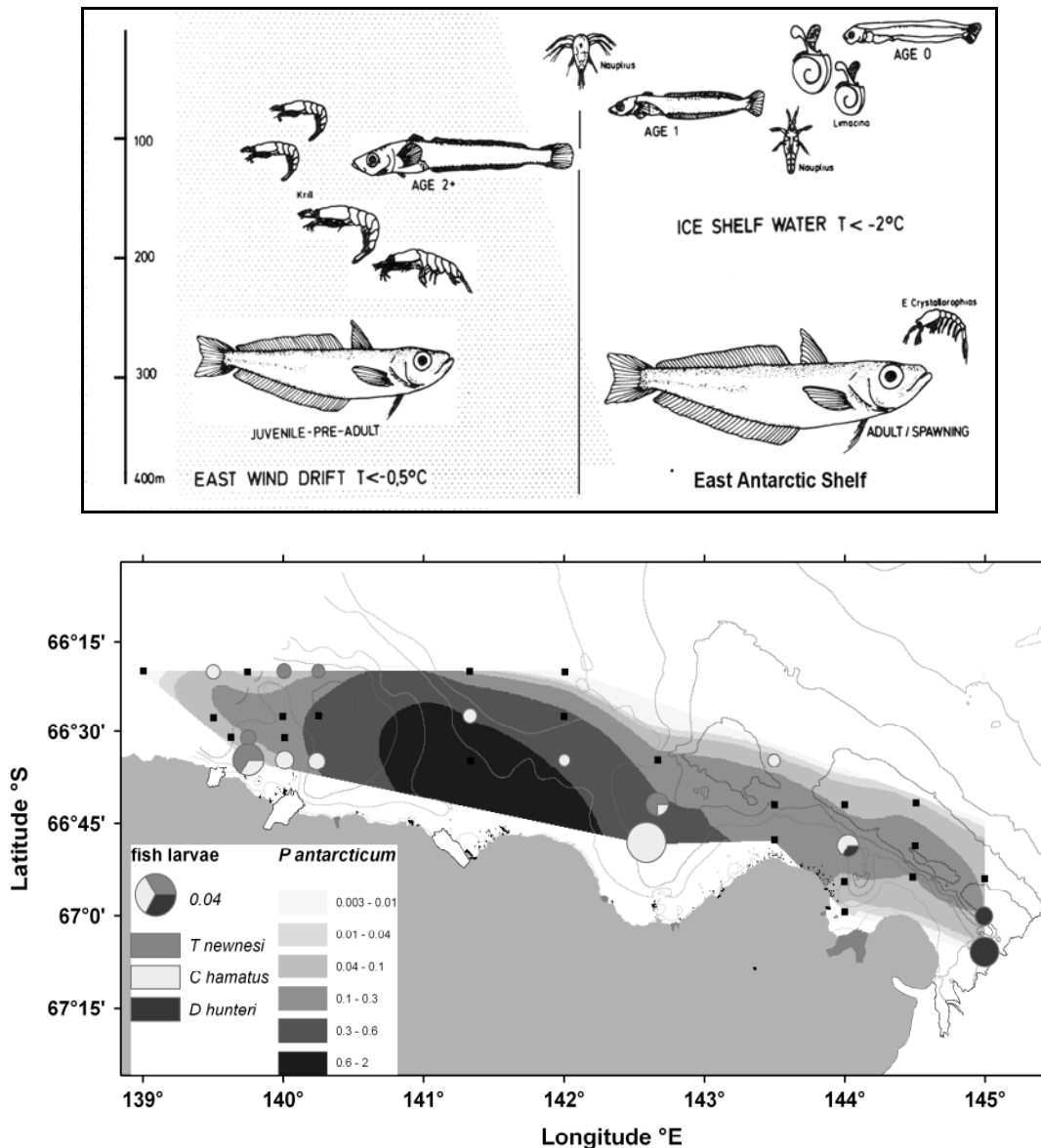


Figure 12. (A) superposition of the life cycle of *P. antarcticum* with the distribution of its preys in the Weddell sea (from Hubold, 1985). However, young larvae live also near the bottom in coastal waters (pers. observ.). (B) Abundances of the main fish larvae species during summer 2004. (Koubbi *et al.*, accepted).

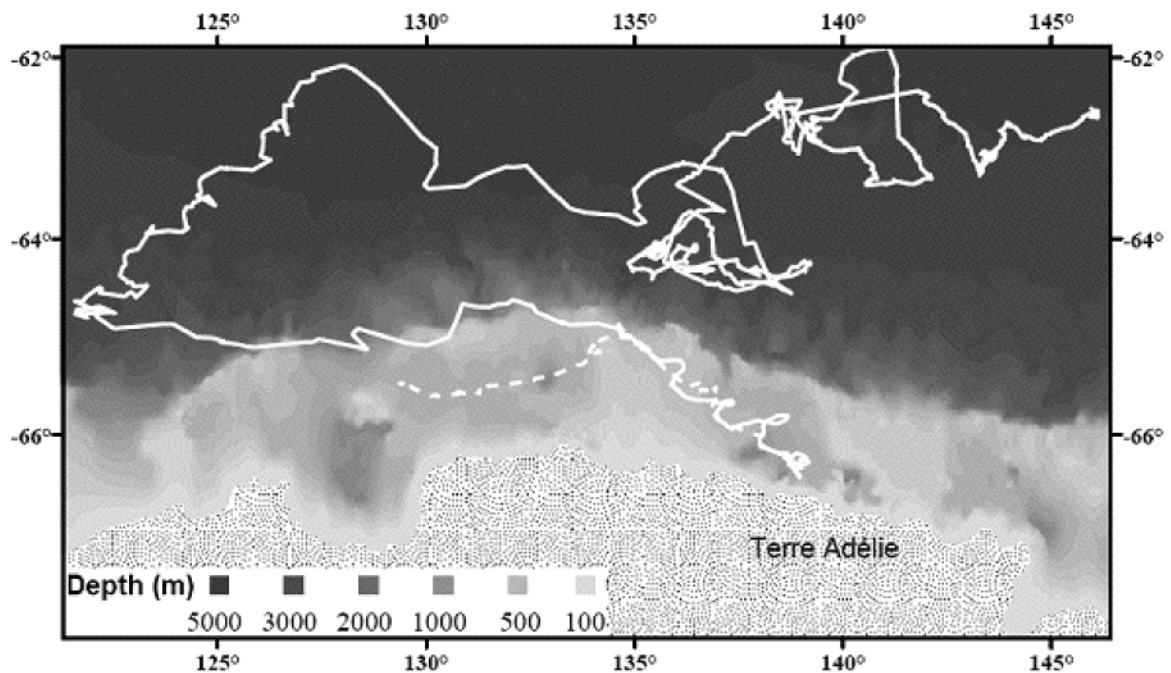


Figure 13. drift tracks of two ARGOS buoys deployed in Terre Adélie during the summer 1998 (Koubbi et al. accepted).

The production of fish larvae in time should be matched or mismatched to that of their food Cushing (1975). If matched, recruitment would be high within the limits of variation of the primary production. If mismatched, recruitment will be low- more so if primary production is low, but less so if it is high. In the study area, the stability of the surface waters is influenced by the winter conditions and by the frequency and intensity of katabatic winds or depressions. As stated by Lasker (1984) in its stable-ocean hypothesis, food patches form in stable oceans and will result in strong year class of fish populations.

First-feeding larvae require an abundance of food or they will starve but once this critical period (Hjort, 1914) achieved with success, the optimal environmental window for small pelagic fish will probably depend upon a triad of physical factors.

Those factors, known as Bakun Ocean triad (Bakun 1996), are:

- (i) Enrichment processes of surface waters lead to the production of the (zoo)plankton upon which the young stages depend for food. The physical processes implied are: upwelling of nutrients rich waters from deeper layers and mixing.
- (ii) Concentration processes aggregate planktonic organisms on which larvae feed and increase good conditions for larval growth. The physical processes implied are convergence, stability, dynamics of fronts and viscosity / larvae. Life cycles of marine organisms tend to include at least one stage of passive larval drift.
- (iii) Retention processes that keep the young in their favoured nursery habitat. Physical processes are transport, enclosed gyral circulation and recirculation associated with topographical features.

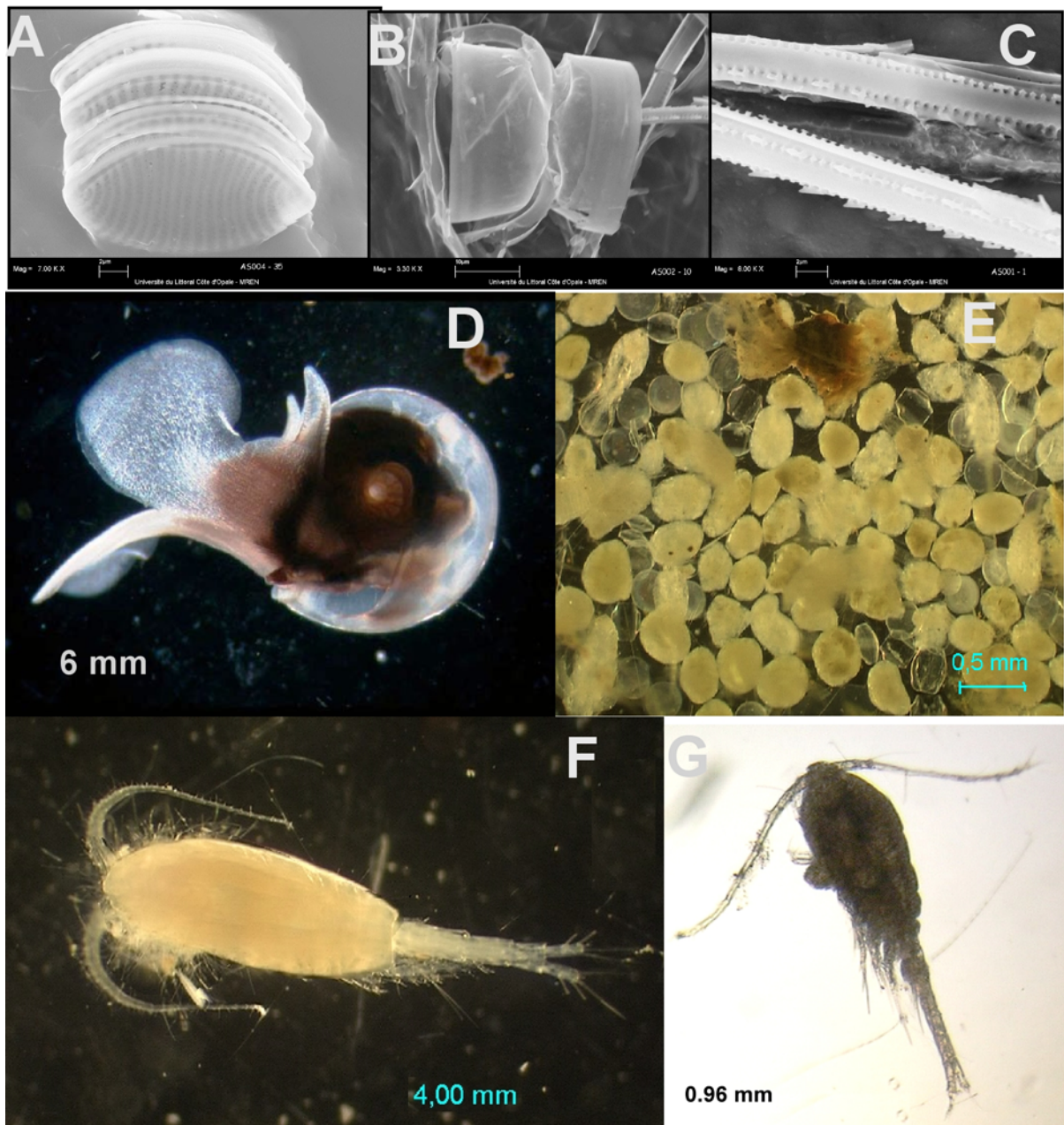


Figure 14. Diatoms found in gut of *P. antarcticum*, S.E.M., from left to right: group of (A) *Fragillariopsis rhombica*, (B) *Chaetoceros criophilus*, (C) *Thalassiothrix antarcticum*. Potential preys of *Pleuragramma antarcticum* (D) *Limacina helicina* and (E) its faecal (oval) pellets. (F) *Metridia gerlachei*, G *Oithona similis* (photo ABC by L. Courcot, photo DEFG, by JH Hecq).

As shown in the presentation of the regional oceanography of the area, many of these factors are observed such as stability over the Adélie Bank which may favour zooplankton and ichthyoplankton survival, upwelling in the western part of the Adélie Bank, gyral circulations either in the eastern part (Adélie Depression) or offshore as shown by Argos buoys drift. Finally, complex topography of the shelf with banks and innershelf depressions creates fronts and retention areas that can be disrupted by strong katabatic winds.

Foraging success of fish larvae in relation to prey composition and oceanographic features can be estimated by the use of condition index which can explain interannual variations of recruitment.

P. antarcticum has a long pelagic larval phase of over one year (Kellermann, 1987). The larvae have to survive the critical period and also through winter when planktonic resources are low (Longhurst, 1998). Consequently, it is important to determine if the plankton bloom will enable larval fish survival or not. Spatial segregation of life stages allows each stage to forage on the most suitable size of prey since young larvae are inshore as they are their prey on small copepods (e.g., *Oithona* sp., *Oncea* sp.) or *Euphausia crystallorophias*. Older stages and juveniles are offshore as is *Euphausia superba* on which they forage.

Table 4: Common prey of *P. antarcticum* post larvae

Prey	Reference
<i>Euphausia superba</i> (Krill) eggs	Kellerman (1987)
Copepod nauplii	Wöhrmann et al. (1997)
Cyclopoïd copepods	Wöhrmann et al. (1997)
<i>Limacina</i> spp. (small pteropod molluscs)	Hubold (1985), Kellerman (1986), Miller (1993)
<i>Oncaea</i> spp., calanoïd copepod eggs, tintinids and <i>Euphausia superba</i> eggs	Kellerman (1987)
Diatoms	Koubbi et al. (in press)

In two studies, we have shown (Koubbi *et al.*, 2007 and Beans *et al.*, pers. comm.) that in January-February, *P. antarcticum* larvae fed essentially on diatoms and eggs and sometimes on copepods. It can be hypothesized that during the phytoplanktonic bloom in summer, diatoms probably stabilize the nutritional conditions of larvae, which can wait for a better time to feed on copepods, their most common prey. Phytoplankton, especially diatoms, may provide a direct supply of nutrients and free amino acids, which are contained in large amounts in diatoms and which played an important role in energy production and protein synthesis (Fig. 14). It could be possible that in extreme conditions as in the Antarctic, *P. antarcticum* larvae need to feed on phytoplankton in order to get a better digestion and assimilation of large prey such as copepods. This means that these larvae are omnivorous.

Estimation of Condition Indices provide a superior means of predicting larval nutritional status and survival probability than only looking at diets. Diets are only

instantaneous index whereas condition index tell us about the nutritional conditions that the larvae faced.

Among biochemical indices, lipid class composition have been used to assess the nutritional condition of fish larvae (Fraser *et al.*, 1987; Hakanson, 1989). The duration of the larval period being correlated to the nutritional status and the larval condition being primarily influenced by food availability, analysis of lipid components is one of the criteria advantageously used to monitor the larval condition and can thus provide useful information on larval survival.

Zooplankton faecal pellets may act as a food source for pelagic as well as for benthic and epibenthic organisms. We have compared the nature of copepod outfluxes of non-living matter, the factors controlling their rate and their fate, and finally their role, particularly their relative importance in the carbon and nitrogen cycle (Frangoulis *et al.* 2006). Copepods release dissolved matter through excretion and respiration, and particulate matter through production of faecal pellets, carcasses, moults and dead eggs. Generally the most important factors controlling the production of pellets are: temperature, body mass, food concentration, food quality and faunistic composition. Physical and biological factors govern the vertical fate of copepod products, by affecting their sedimentation speed and concentration gradient. The physical factors are sinking speed, advection, stratification, turbulent diffusion and molecular diffusion. They influence the sedimentation speed and degradation of the copepod products. The biological factors are production, biodegradation (by zooplankton, nekton and microorganisms) and vertical migration of copepods (diel or seasonal). Physical degradation and biodegradation by zooplankton and nekton are faster than biodegradation by microorganisms. The evaluation of the role of copepod products in the transport and recycling of elements and compounds requires a quantification of all copepod products and their different fates, particularly detritiphagy, remineralisation or integration as marine snow.

2.5. Sea ice zone ecology and the life cycle of copepods in the coastal zone of Dumont d'Urville

Contributors: Jean- Henri Hecq, Anne Goffart, Christophe Loots and Philippe Koubbi

This text contains excerpts from the following papers:

Hecq J.H., 2003. Modélisation conceptuelle et numérique de l'écosystème planctonique océanique. Bull. Soc. Roy. Sci. Liège, 72 : 93-302.

Loots C., Swadling K.M., P. Koubbi, accepted. Annual cycle of distribution of three ice-associated copepods along the coast near Dumont d'Urville, Terre Adélie (Antarctica). In: 38th International Liège Colloquium on Ocean Dynamics - Revisiting the role of zooplankton in pelagic ecosystems, Liège (Belgique). *J. Mar. Syst.*

The northern position of Terre Adélie and the small extent of the seaice compared to other areas in Antarctica is a good place to study the effect of climate change on the seaice zone ecosystem. In the studied area, polynias are observed with a large permanent one from Commonwealth bay to the Mertz Glacier Tongue and non-permanent smaller ones offshore Terre Adélie that can last from few days to many weeks or months depending on the year. At the end of winter, polynia opens slowly by ice melting and opening of leads (Hecq 2003). After different wind events, it continues its opening by a northward transport of ice floes. That phase is very fast and does not take the time to ice melting. Then, the polynia opens to the Southern Ocean.

The discontinuity in the progress of the polynia ice front will develop a strong variability in the light, the stability of the water column and the algae releasing in the water column. The consequences will be a spatial heterogeneity of ice cover and thus different timing of seasonal plankton cycle.

This spatial variability has repercussions in the distribution of the biotic assemblages that we have identified. Variations in ecosystem patterns characterized by specific biota assemblages were identified on the basis of plankton composition in diverse areas. A « diatom-krill » assemblage dominated by *Euphausia superba* occurs in the Adélie offshore area along the periantarctic marginal ice-edge. A « multivorous food web» assemblage is present on the Adélie shelf, where continuous ice melting determines a temporary vertical stability favorable to phytoplankton productivity. All groups are present: diatoms, flagellates, copepods, krill (*Euphausia cristallarophias*) including birds and whales.

The « coastal diatom» assemblage encountered in the Terre Adélie coastal area where *Limacina helecina* is the dominant herbivorous plankton. In that coastal area a mesozooplankton herbivorous food chain (diatoms, copepods, ostracods) is observed but the plankton ecosystem is mainly dominated by the macrozooplankton food chain (diatoms - molluscs - amphipods). Larvae stages of *Pleurogramma* represent the carnivorous level.

We have described the sequence of phyto and zooplanktonic events in the Antarctic Ice zone as a sequence of events tributary to the melting of the ice and the stability of the water column (Hecq 2003).

This growth and planktonic ecosystem sequence are not simultaneous in all the Terre Adélie area. Different biotic assemblages will correspond to local particularities and seasonal successions of different phases of the whole Southern Ocean seasonal ice zone ecosystem controlled by specific physical conditions. They are not to be taken as different ecosystems but more realistically as different states of a typical ecosystem locally controlled by specific constraints or progressing from pack-ice to ice-free waters. This typical ecosystem has been summarized as a conceptual model.

Sea ice provides important habitat for small grazers, such as copepods. During the prevcruises, an intensive sampling of the plankton and fish in the water column and in the sea ice has been achieved (Loots *et al.*, accepted). Three species of ice-associated copepods were found: two calanoid copepods *Paralabidocera antarctica* and *Stephos longipes* and the harparcticoid copepod *Drescheriella glacialis*. *P. antarctica* was the most abundant of the three and was closely associated with the sea ice during most of the year. This species had a one year life cycle with a long overwintering period in the sea ice as nauplii and a short copepodite phase in spring. Reproduction and spawning occurred in early summer. A comparison with two other populations (near Syowa and Davis stations) along the east coast of Antarctica showed that there was a temporal shift in the life cycles of the three populations that was linked to variability in sea ice conditions (figure 15).

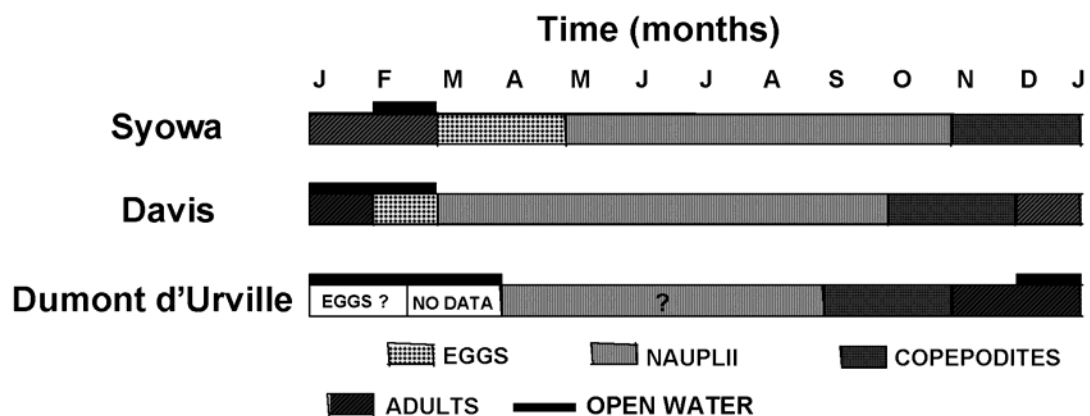


Figure 15. Comparison of the life cycle of the copepod *P. antarctica* at three sites along the east coast of Antarctica. This species pass the winter as naupliar stages and the copepodite phases are short. There are some differences between sites highlighting a temporal shift of 1 month implicating that the life cycle is achieved earlier at Dumont d'Urville than at Syowa with Davis as intermediate. This shift can be linked to time of sea-ice break that is earlier in Dumont d'Urville. Developmental growth and time of reproduction seemed to be flexible and related to time of the seaice break out (Loots *et al.*, accepted).

Drescheriella glacialis was the second most abundant copepod and was more common during the winter than during summer, indicating its preference for the sea ice habitat. In autumn, the presence of *D. glacialis* in the deeper part of the water column suggested that this species colonised the sea ice from the benthos. *Stephos longipes* was found only in the water column near Dumont d'Urville and was not very abundant.

Because of the strong katabatic winds, Terre Adélie experiences longer periods of open water in summer than other sites along the east coast and the ice is more subject to unpredictable break-out at other times of the year. This means that any copepods trying to establish populations must be able to cope with the ephemeral nature of the sea ice. Further, unstable sea ice in autumn, coupled with the presence of polynias during winter, probably has substantial impacts on the mortality rates of the early naupliar stages and on the presence of individuals in the water column. This might explain, in part, why the abundances of ice-associated copepods in this region are low compared to other sites around Antarctica.

2.6. Synthesis and conceptual approach of the Pelagic Ecosystem of the Terre Adélie sector of East Antarctic Shelf

Contributors Anne Goffart, Jean-Henri Hecq, Philippe Koubbi

Through a multidisciplinary effort in Terre Adélie area, we have identified the key-species governing the pelagic ecosystem over the Eastern Antarctic continental shelf. Key species or assemblages have been monitored in relation to environmental variability including seaice variability.

For the pelagic realm, the study focussed on the control of the pelagic ecosystem by few species of euphausiids, micronekton and plankton.

Environmental variability in the pelagic ecosystem operates at various temporal and spatial scales. At the spatial and temporal scale we are working on, the pelagic realm in the neritic zone can be monitored by a limited number of key pelagic species which are mainly one species of euphausiids, *Euphausia crystallorophias* and one species of pelagic fish, *Pleuragramma antarcticum*. The species *Euphausia superba* is only abundant over deeper areas. These two species can highly dominate the micronekton and macroplankton and are good indicators, which respond at several time scales of variations in the marine environment. They depend on phyto- and mesozooplankton for their foraging and are preys of top-predators.

Water masses, sea ice cover and life history strategies combine to influence broad-scale trends in plankton distribution. Surface density explains plankton abundance. Salinity might be more stable spatially than any other parameters in the neritic zone during the summer period as it is mainly related to the winter and spring conditions. During spring, ice melt and summer is influenced by the extent of the ice sheet during the previous winter: a more extensive ice sheet will result in lowered salinity. Katabatic wind modify the characteristics of the surface water masses by modifying water circulation, cooling the surface layer and creating upwelling that could bring up cold and salty waters to the surface. They are probably responsible of life stages segregation of fish larvae with younger larvae inshore and older ones and juveniles offshore. Bathymetry also has a significant influence on water masses in the area. In the Eastern part and in Commonwealth bay, deep antarctic waters are formed. However, one of the main results is related to the Adélie Bank as slope front is observed along the Eastern side of the bank. This front is not a sharp biological boundary. Its structure might be influenced by katabatic winds or storms which allow plankton and nutrients exchange between the western and eastern part of this area. As a consequence, plankton assemblages only differ by slight changes of species compositions or abundances.

The study area can be regionalised into three zones (Fig. 16):

To the East over the Adélie Depression and near the MGT. The region is characterized by the presence of a polynia which begins to open in mid-September and is usually fully developed by mid-October, allowing for a phytoplankton bloom early in the season. Phytoplankton and zooplankton show high biomass but phytoplankton diversity was low. During the January 2004 study, stratified water column, probably due to the ice melt and maximum depletion of nutrients were found in this region.

To the West of the Adélie Bank, the zone comprises nutrient-rich waters, with little vertical change observed in the upper water column structure. In January 2004, this zone was characterized by average chlorophyll a concentrations, high diatom diversity and average abundances. Zooplankton was not maximum but higher abundances can be observed near the edges of banks and depressions.

Over the Adélie Bank, the low biomass observed may therefore be due to the larger grazing pressure in this zone where we observed maximum abundances of various copepods, appendicularians, euphausiids and fish larvae (particularly *P. antarcticum* and *C. hamatus*) which have been known to prey on plankton.

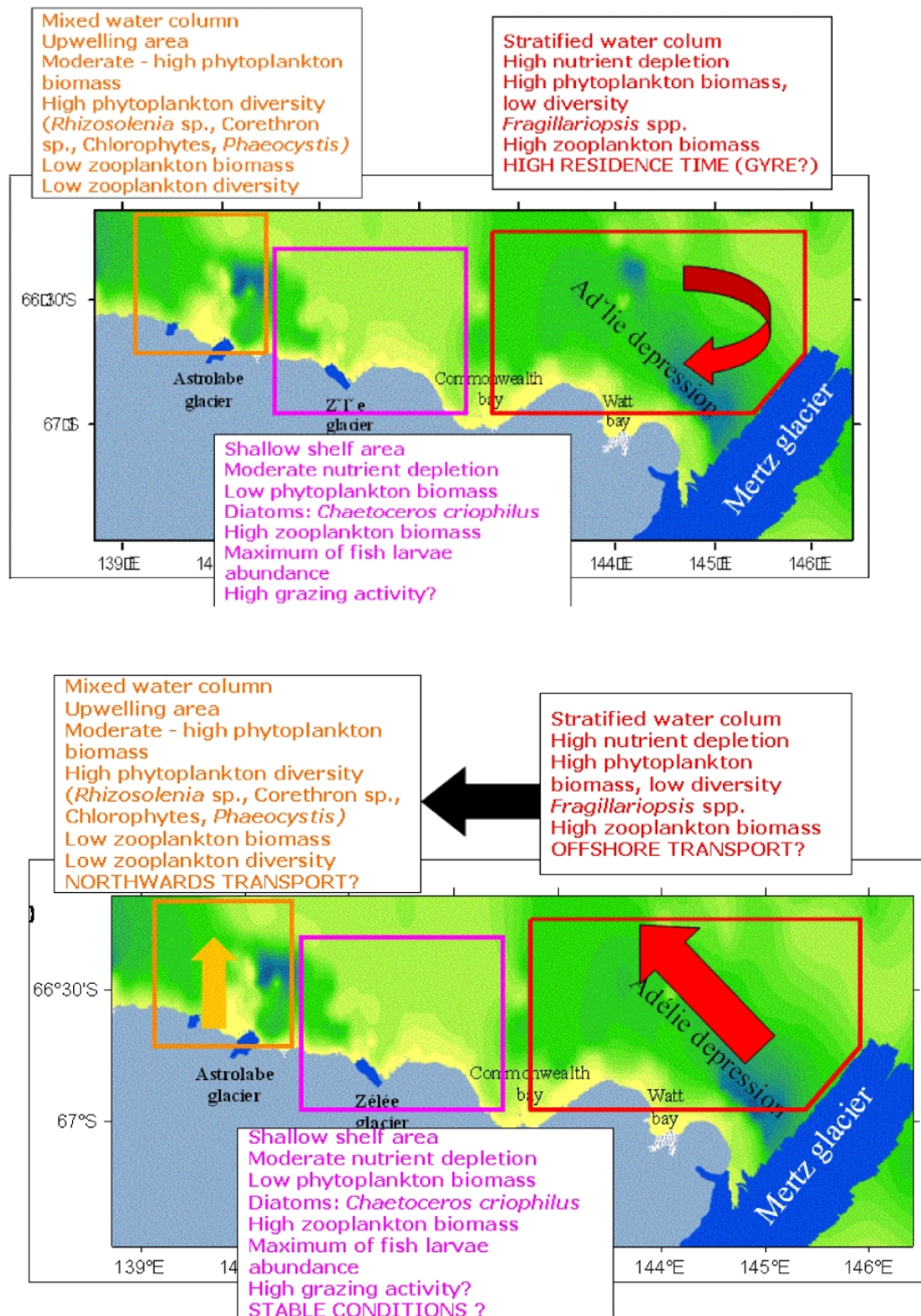


Figure 16. Hypothesis of ecosystem functioning during weak wind (top) and SE strong wind (bottom). Goffart unpublished

2.7. Conclusion and perspectives

Through a multidisciplinary effort in Terre Adélie area, we have identified the key-species governing the pelagic ecosystem over the Eastern Antarctic continental shelf. Key species or assemblages have been monitored in relation to environmental variability including seaice variability. For the pelagic realm, the study focussed on the control of the pelagic ecosystem by few species of euphausiids, micronekton and phyto and zooplankton.

Environmental variability in the pelagic ecosystem operates at various temporal and spatial scales. At the spatial and temporal scale we are working on, the pelagic realm in the neritic zone can be monitored by a limited number of key pelagic species which are mainly one species of euphausiids, *Euphausia crystallorophias* and one species of pelagic fish, *Pleuragramma antarcticum*. The species *E. superba* is only abundant over deeper areas. These two species can highly dominate the micronekton and macroplankton and are good indicators, which respond at several time scales of variations in the marine environment. They depend on phyto- and mesozooplankton for their foraging and are preys of top-predators.

By the diversity of habitats, as well as of species, the Terre Adélie area has enormous scientific potentials as shown by the intensity of previous and future CAML surveys (e.g. CEAMARC : Collaborative East Antarctic Marine Census). Three identified major reasons are: the formation of deep Antarctic waters; the influence of the large Mertz Glacier Tongue on the oceanography of the area; the northern position of Terre Adélie and Georges V Land in Eastern Antarctica.

A practical reason is that Dumont d'Urville is the only permanent station in this part of the coast and will be a good candidate for integrating the Southern Ocean Observing System.

In the future, a pluriannual survey will be necessary to assess the long-term spatial variability of phytoplankton assemblages and will focus on stations sampled at 5 m depth (i.e. highest recorded abundance). The taxonomic studies of phytoplankton communities started in 2004 need to be continued at a pluriannual scale and completed by the estimation of phytoplankton standing stocks in terms of carbon biomass. This will permit to give further insights into the role played by phytoplankters as a trophic resource for higher levels within the trophic food web.

Microzooplankton protozoans will be studied and their importance in terms of abundance and biomass will be estimated by inverted microscopy.

Zooplankton will be studied on every station by various nets (see annual programme) from the surface to 200 m. Analysis will be held to the species level for copepods. Euphausiids life stages will be evaluated at each station from the surface to 200 m.

3. ANTARCTIC PELAGIC FISH DIVERSITY AND ECOLOGY

3.1. Structuring of the pelagic ichthyofauna in the Lazarev Sea and the West-Indian sector of the Southern Ocean

Contributors: Anton P. Van de Putte, Filip A. Volckaert, Hauke Flores, Jan-Andries Van Franeker, Volker Siegel

This text contains excerpts from the following papers:

Van de Putte A. P., Jackson G., Pakhomov E., Flores H., Volckaert F.A.M., (submitted) Deep Sea Research II, Distribution of squid and fish in the pelagic zone of the Cosmonaut Sea and Prydz Bay region during BROKE-west, January-March 2006

Flores H., Van de Putte A.P., Siegel V., Pakhomov E., van Franeker J.A., Meesters E., Volckaert F.A.M.. (in prep.) The distribution of pelagic fish and larvae in the Lazarev Sea with special focus on the ecological role of *Electrona antarctica*.

Introduction

Species composition of fish and ichthyoplankton in the pelagic realm is not random as they migrate between locations with favourable conditions, resulting in distinct distributions and assemblages (Kock 1992). These differences in distribution are often related to hydrographical properties such as water depth, density, temperature, the presence of seamounts or islands, or the position of fronts (Loots *et al.* 2007). Vertical distributional differences may be related to ontogenetic shifts within species. Often larval stages prefer the pelagic zone to enhance early development and survival by niche separation and dispersal by surface currents. On a small temporal scale, species with nocturnal migration may display considerable diurnal shifts in distribution related to metabolic optimisation, predator avoidance and feeding.

Two distinct fish assemblages characterize the pelagic Southern Ocean (Efremenko and Pankratov 1988). The oceanic assemblage is dominated by meso- and bathypelagic fish, while the coastal assemblage is characterized by the dominance of notothenioid juveniles (Kock 1992; Koubbi *et al.* 1991, Pakhomov *et al.* 1995). The pelagic Antarctic shelf zone is dominated by the nototheniid *Pleuragramma antarcticum* and pelagic larvae and juveniles of four notothenioid families: Artedidraconidae, Bathydraconidae, Nototheniidae and Channichthyidae (Williams and Duhamel 1994, Hoddell *et al.* 2000). While larval and juvenile stages may have a pelagic phase lasting up to two years (Kock *et al.* 1985, Hoddell *et al.* 2000), adults of these species are generally small benthic fishes except for the partially mesopelagic *Champocephalus gunnari*, *P. antarcticum* or *Dissostichus mawsoni* (Kock 1992). The widely distributed and locally abundant *P. antarcticum* plays an important role in the coastal ecosystem (Hubold *et al.* 1985). Larvae and fingerlings live close to the surface, often in

association with krill swarms, while adults stay in proximity of the bottom (Hubold *et al.* 1985). Locally the food spectrum of *P. antarcticum* may differ considerably, but euphausiids and copepods generally dominate (Kellermann 1986, Sabourenkov 1991, Pakhomov *et al.* 1995). *P. antarcticum* can also be an important prey in the diet of various seals (Hubold *et al.* 1985), other fish (Eastman 1985) and seabirds (Van Franeker *et al.* 2001).

In the oceanic zone south of the Antarctic Polar front (APF) lanternfish (family Myctophidae) of the genus *Electrona* and Paralepididae of the genus *Notolepis* are the most numerous in terms of biomass and numbers (Kock 1992, Efremenko and Pankratov 1988). Larvae of *Electrona antarctica* and *Notolepis coatsi* are abundant in the surface layers (Hoddell *et al.* 2000, Efremenko and Pankratov 1988). Older individuals are mainly distributed between 200 and 600 m depth during daytime and shift upward above 200 m at night (Torres and Somero 1988). *E. antarctica* migrates to the upper 100 m and has been reported close to the surface. It is an important predator on mesozooplankton (Pakhomov *et al.* 1996, Pusch *et al.* 2004) and is frequently caught by seals and birds (Quillfeldt 2002, Casaux *et al.* 2003). *N. coatsi* preys almost exclusively on krill (Pakhomov 1997) but larval stages prey on a range of small zooplankton (Lipskaya *et al.* 1991). It is found in the stomachs of Antarctic fur seals and Antarctic petrels where it may be one of the main fish components (Klages *et al.* 1990, Daneri and Carlini 1999, Ciaputa and Siciski 2006).

The Lazarev Sea is one of the least investigated areas in the Southern Ocean; it lies at the eastern border of the Weddell Sea and is influenced by the Eastern limb of the Weddell gyre (Fig. 17). The general flow of the Weddell in The Lazarev Sea is from the north to the east, with several braches of warmer water flowing around Maud rise. The coldest water mass is found closest to the continent in the Antarctic Slope Current (ASC) (Osri *et al.* 1993, Klatt *et al.* 2005, Cembella *et al.* 2005). To the east of the Lazarev Sea lies the Cosmonaut Sea, to the west and further to the east the Cooperation Sea and the Prydz Bay area. The Cosmonaut Sea is influenced by an intrusion of the eastern boundary of the Weddell Gyre. To the east there is the Cooperation Sea characterized by the Prydz Bay Gyre. To the south both gyral systems are bordered by the fast and narrow westward flowing ASC. The eastward flowing Antarctic Circumpolar Current (ACC) forms the northern boundary of the two gyral systems but had a more southern extension in Cooperation Sea. The ACC is characterized by the southern ACC front and its southern limit is formed by the Southern Boundary (SB).

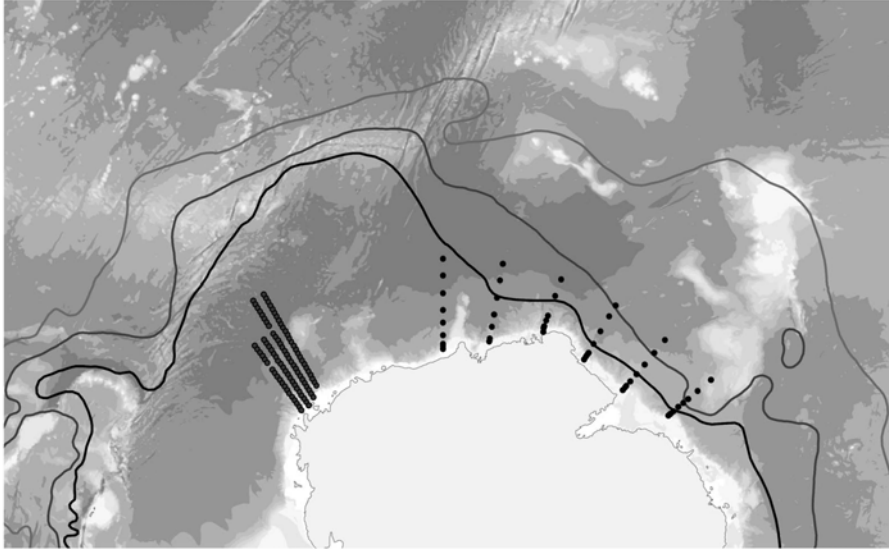


Figure 17. Sampling locations during the LAKRIS (ANTXXI-4) and BROKE west campaigns. Hydrographic features according to Orsi *et al.* (1993); from north to south: Polar Front (-), Southern Antarctic Circumpolar current (-), Southern Boundary of the Antarctic circumpolar current (-)

Here we present a subset of data gathered in the framework of the LAKRIS (LAzarev Sea KRill Survey) and BROKE-west (Baseline Research on Oceanography, Krill and the Environment) programmes. These international research efforts were respectively coordinated by the Alfred Wegener Institute for polar and marine research (AWI) and the Australian Antarctic Division (AAD). Both campaigns focus on the population structure, survival and reproduction of Antarctic krill in the Lazarev Sea and the Cosmonaut & Cooperation Sea. In addition to krill sampling, a wide range of oceanographic and ecological data was collected in order to obtain as complete a picture as possible of the pelagic ecosystem. Here we limit ourselves to the results of the fall data from the first LAKRIS campaign (ANT XXI-4) and the BROKE-west campaign in summer.

Material and Methods

Sampling procedure

Larval and post-metamorphous fish were collected between 7 and 26 April 2004 during an expedition with RV *Polarstern* (Lakris (ANT XXI-4)) and the BROKE-west cruise of RV *Aurora Australis* (05/06 V3), between January 2 and March 17, 2006. The station grid in the Lazarev Sea (CCAMLR statistical subarea 48.6) resembled four longitudinal transects, ranging from 61° - 71° S and 0° - 6° W. Latitudinal spacing between stations was 20 nm (37.6 km). The sampling grid during BROKE-west consisted of eleven longitudinal transects between 30° and 80° E and 58°S down to the Antarctic coastline (CCAMLR statistical subarea 58.4.2) (Fig. 17).

Fish were caught using Rectangular Midwater Trawl nets (RMT 8 + 1), consisting of a RMT 1 mounted above a RMT 8 with a mouth area of 1 and 8 m and a cod end mesh size of 0.33 and 0.85 mm, respectively. Hauls consisted of a standard double oblique tow from the surface down to 200 m and back again to the surface. Towing speed was approximately 2.5 knots (4.5 km. h⁻¹).

Fish were sorted from the total catch of the RMT 8 and identified to species level wherever possible. Fish standard length was measured onboard to the lowest mm and fish were preserved on absolute ethanol, formalin or initially frozen at -80°C and stored at -20°C.

Data analysis

1. Community structure

Fish community structure was investigated in both areas by hierarchical cluster analysis for routine and target trawls separately. Clustering was done based on a Bray-Curtis dissimilarity matrix on presence-absence data of each species per station with catch, using the Unweighted Pair Group Method with Arithmetic mean (UPGMA). Unidentified specimens and stations where no larvae were caught were excluded from analysis.

2. BROKE-west: Redundancy Analysis

For the most abundant and frequent species caught during BROKE-west, association with environmental variables was analysed using a direct gradient analysis. Redundancy Analysis (RDA) was the optimal method based on the methodology of Leps & Smilauer (2003). RDA is an extension of Principal Component Analysis that explicitly models response variables as a function of explanatory variables. In order to meet the requirements for redundancy analysis only the random routine stations were included. Species abundance data for each station was log(X+1) transformed.

The RMT net used for sampling during BROKE-west was equipped with a CTD, providing detailed data on conductivity, temperature (C°), salinity (PSU), pressure (dBar) and fluorescence (Gorton 2006). Additional oceanographic information such as mixed layer depth (MLD) and position of fronts was provided by Williams *et al.* (2007). Solar azimuth, elevation and day length were calculated as a measurement of light conditions, according to the procedure provided by NOAA. (Earth System Research Laboratory 2007).

3. LAKRIS (ANTXXI-4): GAM modelling

The higher number of (nighttime) sampling stations with *E. antarctica* adults allowed a different analytical method. The relationship of the individual density of adult *E. antarctica* caught in nighttime hauls during LAKRIS (ANTXXI-4), with a set of environmental variables was explored with a Generalized Additive Model (GAM: Hastie and Tibshirani 1990). GAMs can be considered as an extension to Generalized Linear Models (GLM: McCullagh and Nelder, 1989). They extend the implicit linear

relationship between response and explanatory variables of GLMs by fitting higher order smooth functions to explanatory variables.

A suite of environmental variables were continuously recorded by shipboard sensors: ocean depth, surface sea temperature and surface salinity were. Euphausiid larval and post-larval abundance data [N 1,000 m^{-3}] were collected following the procedures described in Siegel *et al.* 2004). Surface water global chlorophyll [$mg\ m^{-3}$] at each sampling station was obtained from a public database based on the NASA Ocean Biogeochemical model (NOBM: Gregg and Casey in press; NASA 2007). The proportional total ice coverage was monitored by a shipboard observer while the ship was steaming between stations. For more details on the analytical methodology and the collection of environmental data we refer to Flores *et al.* (in prep.). Statistical calculations were performed with the R (R-Development-Core-Team 2006), Brodgar (Highland Statistics 2006), PRIMER 5 and STATISTICA software packages.

Results

Ninety-three stations were sampled for fish during LAKRIS (ANT XXI-4). At 74 of these stations, 903 fish larvae and 1094 post metamorphic fish were collected. They comprised at least 10 species belonging to 7 families. *Electrona antarctica*, *Notolepis coatsi* and *Pleuragramma antarcticum* dominated the species community, altogether accounting for 93% of the larvae caught (Table 5). During BROKE-west 50 stations were sampled. At 37 of these stations, a total of 183 fish was collected; 14 species belonging to 7 families were identified. The community was dominated by three species, *E. antarctica*, *Notolepis coatsi* and *P. antarcticum* accounting for 89% of the species.

1. Community structure

Following exclusion of stations lacking fish, analysis was performed on both datasets. There where both adult and larval data were used to investigate the BROKE-west dataset, only larval data were used for the LAKRIS data. The cluster analysis of the BROKE-west (Fig. 18A) showed a cluster of outliers above the 98% dissimilarity level. These outliers were the result of uniquely occurring species. Below this level the stations were further subdivided at 85% dissimilarity into a cluster corresponding to coastal stations and a larger cluster representing oceanic stations composed of two smaller subclusters (Oceanic 1 & 2) at the 67% dissimilarity level. *Pleuragramma antarcticum* had a higher abundance in the coastal stations, and a variety of notothenioids was found in the coastal stations.

Table 5: Catch statistics of fish caught during LAKRIS (ANTXXI-4) and BROKE-west. F_o = frequency of occurrence (percentage of stations where fish larvae were caught); N = number of fish larvae caught

	Lakris (ANTXXI-4)			BROKE-west		
	N	No of stations	F _o [%]	N	No of stations	F _o [%]
Artedidraconidae						
<i>Artedidraco scottsbergi</i>	-	-	-	1	1	2
<i>Pogonophryne marmorata</i>	-	-	-	1	1	2
Bathydraconidae						
<i>Bathydraco sp.</i>	-	-	-	2	2	4
	-	-	-	1	1	2
<i>Gerlachea australis</i>	-	-	-	1	1	2
<i>Gymnodraco acuticeps</i>	-	-	-	3	3	6
Bathylagidae						
<i>Bathylagus antarcticus</i>	16	8	8.60	-	-	-
<i>Bathylagus antarcticus</i> post-larval	40	7	7.53	-	-	-
Macrouridae						
<i>Macrouridae sp.</i>	-	-	-	1	1	2
Myctophidae						
<i>Electrona antarctica</i> larvae	262	55	59.14	48	16	32
<i>Electrona antarctica</i> post-larval	987	42	45.16	25	8	16
<i>Electrona antarctica</i> all	1249	73	78.49	73	21	42
<i>Gymnoscopelus braueri</i> post-larval	65	20	21.51	-	-	-
<i>Gymnoscopelus nicholsi</i> post-larval	2	2	2.15	-	-	-
<i>Protomyctophum bollini</i>	-	-	-	1	1	2
Muraenolepidae						
<i>Muraenolepis sp.</i>	1	1	1.08	-	-	-
Paralepididae						
<i>Notolepis coatsi</i>	362	60	64.52	77	24	48
Bathydraconidae						
<i>Akarotaxis nudiceps</i>	1	1	1.08	-	-	-
<i>Racovitza glacialis</i>	1	1	1.08	-	-	-
Channichthyidae						
<i>Chionodraco sp.</i>	-	-	-	2	2	4
<i>Cryodraco antarcticus</i>	-	-	-	0	0	0
<i>Pagetopsis maculates</i>	-	-	-	1	1	2
Channichthyidae spp.	4	3	3.23	-	-	-
Nototheniidae						
<i>Notothenia kempfi</i>	2	2	2.15	-	-	-
<i>Pleuraagramma antarcticum</i>	248	7	7.53	13	6	12
Nototheniidae sp.	1	1	1.08	-	-	-
<i>Trematomus sp.</i>	-	-	-	1	1	2
Unidentified	5	3	3.23	5	3	6
Empty		7			13	26
Total	1997	93	-	183	50	-

2. Redundancy analysis

An RDA analysis was used to explore the association between the main species and environmental variables (Fig. 19). Significance of the first axis and all axes was confirmed using a Monte Carlo test ($P=0.002$ in both cases). The first axis corresponds to the division into a coastal and oceanic community and explains 31.2% of the total variability in the species data. *P. antarcticum* was strongly correlated with shallow waters and high primary production. The oceanic larvae of *N. coatsi* and *E. antarctica* grouped together as well, as did the paralarvae of the squid *G. glacialis*. All were strongly positively correlated with temperature and salinity, and to a lower extent mixed layer depth. The distribution of *E. antarctica* juveniles and adults was unrelated to the other species. On the second axis that explained 5% of total variability, *E. antarctica* showed a strong negative correlation with solar elevation, corresponding to a pronounced night time occurrence in the catches. The extent of the Mixed Layer Depth was positively correlated with all oceanic species.

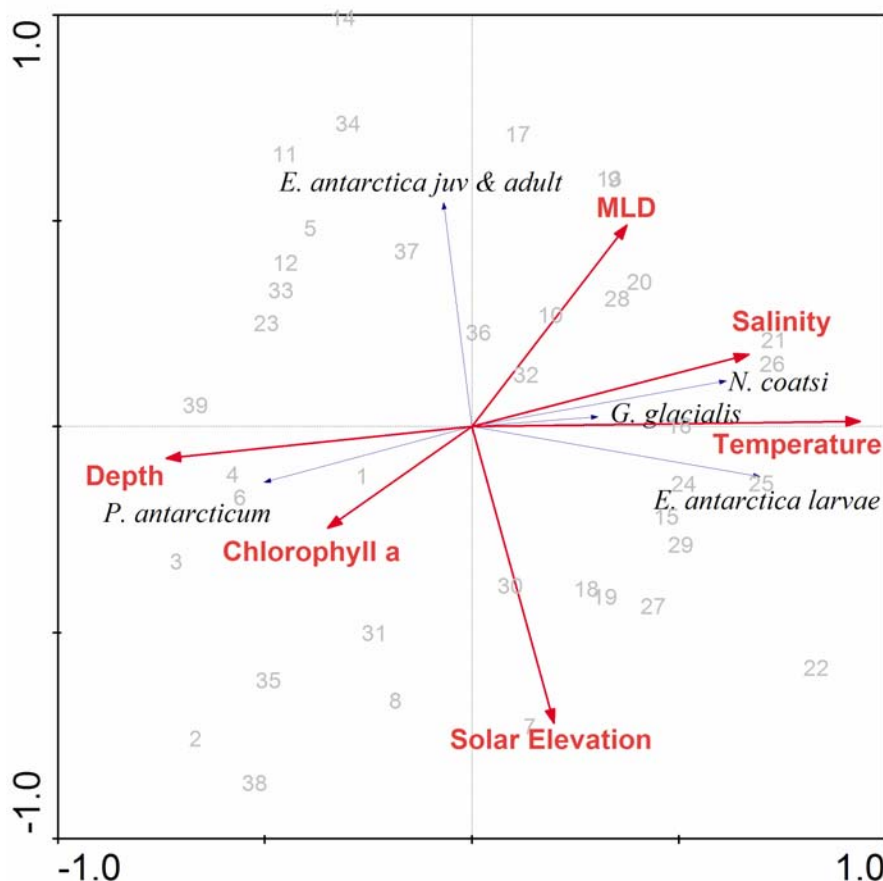


Figure 19. Species-environment biplot diagram summarizing the effect of environmental variables on the abundance of *Electrona antarctica* larvae and juvenile and adult stages, *Notolepis coatsi*, *Pleuogramma antarcticum*. The first explanatory variable is displayed on the X-axis, the second on the Y-axis, (MLD = Mixed Layer Depth).

3. GAM modeling- relationship of *Electrona antarctica* density with environmental variables

In order to meet the analysis requirements depth data were log-transformed and a fourth-root transformation was applied to the euphausiid abundance data. The model with the lowest deviance included abundance of post-larval *Euphausia superba*, depth and abundance of larval *E. superba* (Table 6). The smoother for *E. superba* larval abundance, however, was highly insignificant (approximate $P > 0.2$), while decrease in deviance was close to the significance threshold of 0.05 when this variable was added (F-test: $P = 0.497$), suggesting that a combination of post-larval krill abundance and depth was the most meaningful predictor of the density of *E. antarctica*. This model could explain 54 % of the deviance (Table 6). Inclusion of either total ice coverage or floe coverage did not contribute to a significant decrease in deviance.

Table 6: *Electrona antarctica* – Comparison of models relating the density of fish to different combinations of environmental variables. P indicates F-test significance of change in deviance compared to model in row above

Environmental variables	Deviance	Explained deviance	P
Post-larval krill abundance	624.1	42.1 %	0.0030
Post-larval krill abundance, ocean depth	498.0	53.8 %	0.0082
Post-larval krill abundance, ocean depth, larval krill abundance	443.7	58.8 %	0.0497

Post-larval krill abundances above two individuals.1000 m⁻³ and depths between 3,000 and 5,000 m had a positive effect on the modeled density of *E. antarctica*. Conversely, shallower and greater depths in and low abundance of post-larval krill had a negative effect on the modeled density of the lanternfish (Fig. 22).

Discussion

With at least 17 species comprising a mixture of notothenioids and mesopelagic fish such as myctophids and paralepids, species diversity observed during BROKE-west was slightly lower in comparison to other studies in the Southern Ocean (Hubold 1990, Morales-Nin *et al.* 1995). Species composition is in accordance with Efremenko and Pankratov 1988) in the same area, although these authors reported a larger variety of oceanic species. Only 12 species were identified in the Lazarev Sea. The taxonomic richness was small compared to reports from nearby areas in Weddell Gyre, such as Efremenko (1991), who found 25 species of eight families, and White and Piatkowski 1993) who reported 18 species of eight families. The high diversity reported by these authors is mainly attributed to a rich shelf-associated species community. While

species diversity was low in the Lazarev Sea, compared to other studies, densities weren't. This was in contrast with the results from BROKE-west. Overall numbers and densities of fish species were among the lowest observed in the Southern Ocean (Hubold 1990, Morales-Nin 1995). Total fish density for routine trawls was more than ten times lower than during BROKE (Hoddell *et al.* 2000) and in the Lazarev Sea.

Both cluster analyses identified a coastal and an oceanic community. This pattern was also observed during BROKE both for fish and other zooplankton (Hoddell *et al.* 2000, Hosie *et al.* 2000). The coastal pelagic community sampled during BROKE-west had the highest diversity, consisting of a range of notothenioid species dominated by *P. antarcticum*. In the Lazarev Sea the coastal community was also dominated by *P. antarcticum*. The oceanic community was composed of various combinations of *E. antarctica* and *N. coatsi*.

The RDA analysis performed on the LAKRIS data was consistent with the grouping of the cluster analysis. Stations on the shelf and with higher primary production were associated with the occurrence of *P. antarcticum*. This confirms previous reports. Within deeper, oceanic regions of the sampling area larvae of *E. antarctica* and *N. coatsi* were, to various degrees, positively correlated with temperature and salinity with little or no correlation with the solar elevation. Abundance of juveniles and adult stages of *E. antarctica* on the other hand were strongly correlated with the solar elevation and mostly independent of any other variables under analysis.

Ocean depths between about 3,000 m and 5,000 m and elevated abundances of post-larval krill had a positive effect on the density model of *E. antarctica* (Fig. 20). A positive correlation between density of *E. antarctica* and post-larval krill abundance probably indicates that both species responded to similar environmental signals. It is unlikely to reflect a predator-prey relationship, because post-larval krill are not a typical prey item of the mostly small fish encountered in this study (Lancraft *et al.* 1991, Pusch *et al.* 2005). Ocean depth was the only significant abiotic variable of the model. Below depths of about 3,000 m, modeled density of *E. antarctica* decreased towards shallower waters. A similar relationship was also reported by Loots *et al.* 2007), agreeing with the common perception that *E. antarctica* prefers offshore waters. A negative effect of increasing depth on modeled fish density at depths greater than 5,000 m suggests that other factors influenced the myctophid distribution in these waters. The deeper waters in the north of the area of investigation were influenced by the eastward-flowing northern limb of the Weddell Gyre, which might have carried lower densities of *E. antarctica* (Orsi *et al.* 1993).

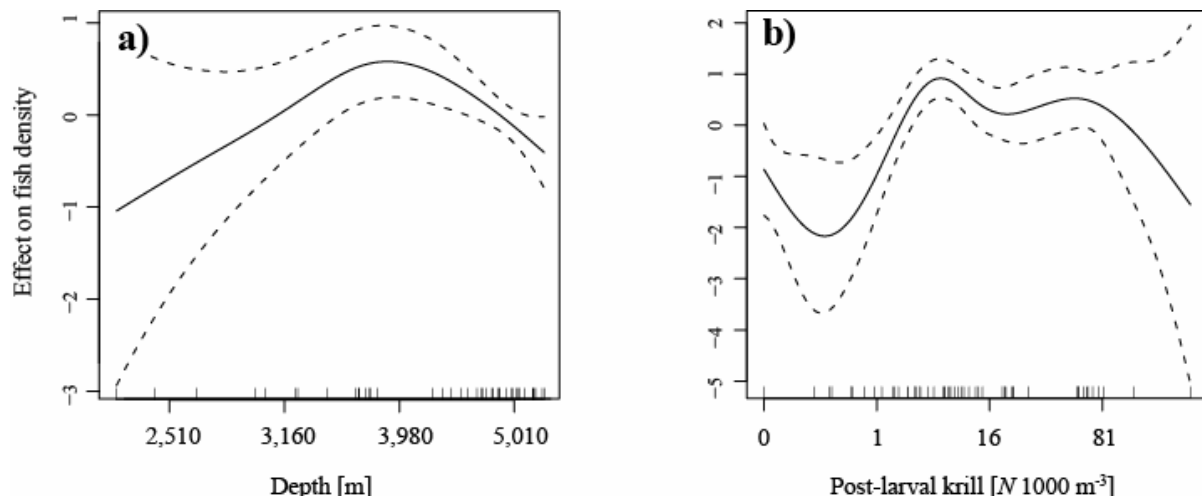


Figure 20. Generalized Additive Model of the numerical density of post-larval *Electrona antarctica*. Effect of additive smoothing functions of post-larval krill (*Euphausia superba*) abundance and ocean depth on the modeled density of fish. Dashed lines show 95 % confidence interval of smoothers.

In conclusion, the communities of fish observed during both campaigns are congruent with previous observations in the Southern Ocean. The strongest differentiation was observed between the coastal nototheniid community and the mesopelagic oceanic community. Distribution of fish in both sampling areas was influenced by environmental factors. As such RDA and GAM modelling are valuable tools for extending our knowledge of pelagic ecosystems. However the marked differences in densities between both areas can't be explained easily within the context of these data. The currently analysed data in both areas preclude a distinction between geographical, seasonal and climatological effects. Additional analysis of data collected during the LAKRIS programme during summer (2005-2006) and winter (2007), will improve our understanding of the ecosystem in both areas.

3.2. Seasonal variations in energy content in *Electrona antarctica*

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This text contains excerpts from the following papers:

Van de Putte A. P., Jackson G., Pakhomov E., Flores H., Volckaert F. A.M., (submitted), Distribution of squid and fish in the pelagic zone of the Cosmonaut Sea and Prydz Bay region during BROKE-west, January-March 2006. Deep Sea Research II

Van de Putte, A., Flores, H., Volckaert, F., van Franeker, J.A., 2006. Energy content of Antarctic mesopelagic fishes: Implications for the marine food web. Polar Biology 29 (12), 1045-1051.

Introduction

Energy content of prey is a key factor controlling the structure of food webs and the relationships between their components. Accurate measurements of the calorific value of prey and predators allow estimates of food requirements and energy-flow from lower to higher trophic levels and are as such valuable for the development of ecosystem models. In this manner they play an important role in ecosystem management. As evidence is increasing that the classic diatom-krill-consumer model for the Southern Ocean is more complex than initially assumed, there is a need to better understand the role and position of other organisms, such as squid and mesopelagic fish, in the Southern Ocean ecosystem (Ainley *et al.* 1992, Ainley *et al.* 1994, Van Franeker *et al.* 1997, Barrera-Oro 2002).

Lanternfishes (family Myctophidae) are the most abundant mesopelagic fish of the Antarctic Ocean, both in numbers and biomass (Kock 1992). Myctophids are major predators on mesozooplankton (Pakhomov *et al.* 1996, Pusch *et al.* 2005). Among them, *Electrona antarctica* (Günther 1878) is considered a key species due to its high abundance, almost circumpolar distribution and vertical migration (Hulley 1990, Sabourenkov 1991, Hopkins *et al.* 1993, Barrera-Oro 2002). It displays a diel migration between 200 and 650 m during the day and close to the surface layer at night. *E. antarctica* is also an important prey for birds and seals (Lea *et al.* 2002a, Quillfeldt 2002, Casaux *et al.* 2003).

Energy content of Southern Ocean fish species has been estimated in the context of various questions, such as the energy content in relation to depth, season or region (Donnelly *et al.* 1990, Tierney *et al.* 2002), or in the context of diet studies (Clarke and Prince 1980, Eder and Lewis 2005). However, most of these studies were based on relatively small sample sizes.

Here we present data on energy content of *E. antarctica* of which a large number of individuals were investigated over a wide size range in two different regions. There where enough samples were available, data on other mesopelagic species such as *Bathylagus antarcticus*, *Gymnoscopelus braueri*, *Pleuragramma antarcticum* and *Notolepis coatsi* were included. The results of this study are put into perspective through comparison with published data on ecology, proximate composition and energy content.

Material and Methods

Sampling

Sampling of mesopelagic fish was performed in two campaigns, onboard RV *Polarstern* in the Lazarev Sea (Fall 2004) and RV *Aurora Australis* in the Cooperation Sea and Cosmonaut Sea (summer 2005-2006). On both campaigns samples were

routinely collected from Rectangular Midwater Trawls. The Rectangular Midwater Trawl nets (RMT 8+1) consist of an RMT 1 mounted above an RMT 8 with a mouth area of 1 and 8 m² and a cod end mesh size of 0.33 and 0.85 mm, respectively. Each Routine RMT (R-RMT) haul consisted of a standard double oblique tow from the surface down to 200 m (450 m cable length) and back to the surface. Towing speed was approximately 2.5 knots. Additionally target trawls were used. Target trawls were not pre-planned and were aimed at acoustically detected aggregations. The net was lowered to the depth of the aggregation and opened and closed remotely.

Fish were sorted from the total catch of the RMT 8 and identified to species level wherever possible. Fish standard length was measured onboard to the lowest mm and samples for energy content analysis were initially frozen at -80°C and stored at -20°C.

Water and energy content

Dry mass and energy content was determined from frozen specimen. To prevent errors due to the loss of body fluids during dissection, water and energy content was determined for whole individuals only. For the few larger specimens caught during BROKE-west stomach content was analysed before desiccation. After the stomach content was analysed fish and stomach were further processed according to the protocol. Frozen fish were thawed, blotted dry and total wet weight (WW) was determined to the nearest 0.1 mg. Fish were dried until complete desiccation (constant mass). After drying, they were re-weighed to determine the total dry weight (DW). Water content was calculated as the difference between WW and DW, expressed as %WW. Individual DW and WW energy content, expressed as kJ g⁻¹, was determined by an isoperibol bomb calorimeter calibrated with benzoic acid. After homogenizing, either the whole fish or a subsample (0.1 – 0.6 g) was used for calorimetry, depending on the size of the fish.

Data analysis

Mean energy and water content with standard deviations (SD) were calculated for each species. Various regression analyses were performed in order to estimate the effect of size on energy content. Significance threshold was 0.05 for all statistical tests.

Results

During both campaigns *Electrona antarctica* was sampled most commonly. A high number of samples was collected during LAKRIS. While a lower number was sampled during BROKE-west the size range was well covered (table1). *N. coatsi*, *P. antarcticum*, *G. braueri* and *B. antarcticus* were caught infrequently; their potential size range was covered incompletely. Only the upper portion of the natural size range was obtained for *G. braueri* and *N. coatsi*. For *P. antarcticum* all samples were in lower

size range. *B. antarcticus* was represented by a low number of samples spread over a wide size range (Table 7).

Table 7: Samples size, mean values for size, water content, wet (WW) and dry weight (DW) energy density of all investigated species. Species sampled during LAKRIS (ANTXXI-4) are indicated with L, during BROKE-west with BW

Species		Known range [mm]	N	Size range [mm]	Mean size [mm]	Water content [%]	WW Energy density [kJ g ⁻¹]	DW energy density [kJ g ⁻¹]
<i>Bathylagus antarcticus</i>	L	0-170	12	36 – 123	71.6 (23.42)	85.6 (2.46)	2.92 (0.421)	20.36 (1.319)
<i>Electrona antarctica</i>	L	0-102	113	16 – 83	47.6 (15.90)	68.4 (4.14)	9.35 (1.575)	29.40 (1.800)
<i>Electrona antarctica</i>	BW	0-102	24	15-90	57.38 (21.15)	73.67 (3.98)	7.26 (1.68)*	27.21 (2.76)*
<i>Gymnoscopelus braueri</i>	L	0-132	20	64 – 132	87.3 (18.05)	69.5 (3.96)	8.86 (1.421)	29.37 (1.509)
<i>Notolepis coatsi</i>	BW	0-380	3	108-203	168 (52.20)	79.82 (1.25)	4.42 (0.33)	21.90 (0.73)
<i>Pleuragramma antarcticum</i>	BW	0-250	16	57-124	72.75 (19.12)	85.72 (7.13)	3.27 (1.91)	22.29 (2.05)

The myctophids *E. antarctica* and *G. braueri* had the highest energy content and the lowest water content. Their energy content was significantly different from the non-myctophids sampled. Average energy content of *E. antarctica* was lower during BROKE-west (Table 7). The lowest energy content was found in *B. antarcticus* while *N. coatsi* and *P. antarcticum* had slightly higher energy contents (Table 7).

Size and age effects on energy content in E. antarctica

In *E. antarctica*, the number of samples and their widespread size distribution allowed the analysis of the effect of size, DW and WW on energy density. Continuous size effects in the other species were not investigated because of the fragmented size cover. Among the models tested, a linear regression of the ln-transformed data proved to deliver the statistically most robust results for both campaigns. Energy content in the BROKE-west area was constantly lower during LAKRIS (ANTXXI-4). Fig. 23 exemplifies the relationship between energy content and dry weight for both campaigns. The corresponding power function exhibits a steep increase of energy density with size, DW and WW in young of the year and age group 1 fish, and a gradual increase in older fish. The model parameters for energy content as a function of size, DW and WW are listed in Table 8.

Table 8: *Electrona antarctica* Energy density (y) of dry weight (DW) and wet weight (WW) as a function of size and DW (x)

X		y [kJ g⁻¹]	A	b	p	r²	e²
Size [mm]	L	DW	2.94	0.1164	< 0.01	0.40	18.8422
	L	WW	0.79	0.3745	< 0.01	0.47	2.2127
	BW	DW	2.61	0.173	< 0.01	0.55	13.6345
	BW	WW	0.34	0.4076	< 0.01	0.50	1.3999
DW [g]	L	DW	3.42	0.0347	< 0.01	0.46	30.5114
	L	WW	2.35	0.116	< 0.01	0.58	10.4856
	BW	DW	3.35	0.0537	< 0.01	0.67	28.4629
	BW	WW	2.07	0.1269	< 0.01	0.61	7.93037
WW [g]	L	DW	3.38	0.0367	< 0.01	0.44	29.3062
	L	WW	2.22	0.1165	< 0.01	0.50	9.16507
	BW	DW	3.23	0.0236	< 0.01	0.61	25.1964
	BW	WW	1.9	0.129	< 0.01	0.54	6.67854

Discussion

Estimates of average water content and energy content of the three species investigated are within the range of previous publications (for an overview see Van de Putte *et al.* 2006). For *B. antarcticus* and *G. braueri*, our values closely resemble autumn energy densities found by Donnelly *et al.* (1990) in the Weddell Sea, by calculating energy content from proximate composition. Energy measurements of *E. antarctica* during LAKRIS (ANT XXI-4) were at the high end of the reported range. It was exceeded only by values reported by Lea *et al.* 2002b). However, the reported data differ sometimes widely in size ranges of fish, time of year, geographic location and methodology. Each factor can have a strong influence on the energy / water content itself (Donnelly *et al.* 1990).

The mean energy content of the *E. antarctica* samples collected during BROKE-west was in the low range of the published data (Van de Putte *et al.* 2006). WW energy content was of the same order of magnitude as the spring data collected by Donnelly *et al.* 1990).

Investigation of the effect of size on energy content based on a large number of *E. antarctica* yielded significant results. These trends correspond to the size effect found by Donnelly *et al.* 1990), while contradicting the size effects observed by Tierney *et al.* 2002). The difference in energy content between *E. antarctica* from BROKE-west and LAKRIS correspond to the differences between seasons observed by Donnelly *et al.* (1990).

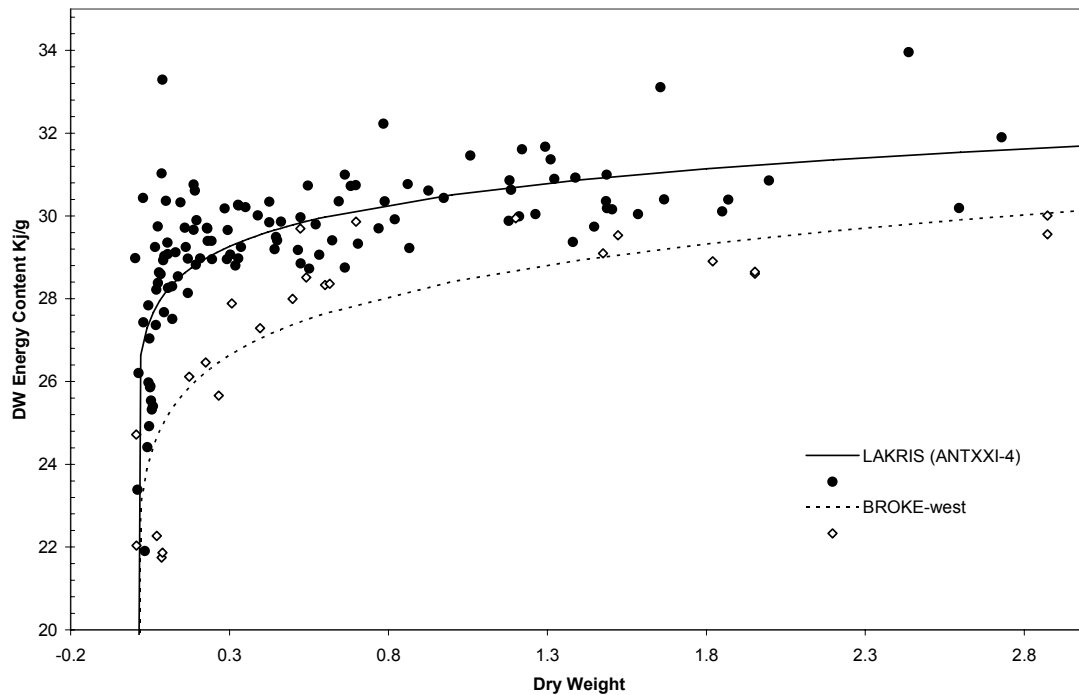


Figure 21. *Electrona antarctica*. Relationship between dry weight (g) and dry weight energy density (KJ.g^{-1}) for both campaigns. Regression parameters of power function provided in Table 8.

These results are consistent with a reduction in energy content after reduced food availability during the winter months or spawning at the end of winter (Donnelly *et al.* 1990). Another factor contributing to the observed differences may be the lower productivity in the BROKE-west area compared to the productive Scotia Sea. DW energy measurements for age class 0 individuals were relatively high in comparison with the fitted power function, which can be attributed to the high energy reserves at spawning or feeding on phytoplankton at the onset of the spring primary production peak. However it can not be excluded that this is a geographic rather than seasonal effect. Productivity in the Cosmonaut and Cooperation Sea was very low and as such food availability and energy build-up could have been reduced.

The size - energy density relationship of *E. antarctica* suggests that the smallest fish invest proportionally more energy in growth and locomotion than older individuals (Fig. 21). Our results confirm the common notion that there is a strong drive for young fish to grow quickly in order to escape predation pressure (Anthony *et al.* 2000). Outgrowing potential predators would allow them to invest subsequently more energy in building reserves (Calow and Townsend 1981). The need of an abundant species such as *E. antarctica* to build up high energy reserves over a short time may partly explain the high predatory impact of mesopelagic fishes, which has been suggested to

reach up to 40% of the secondary production in the Antarctic Ocean (Pakhomov *et al.* 1996).

While the energy content of *P. antarcticum*, an important food source for top predators in the coastal zone, was comparable to Antarctic krill (Torres *et al.* 1994b), the significantly higher energy content of *E. antarctica* suggests that it may be considered the off-shelf counterpart of Antarctic silverfish *Pleuragramma antarcticum*, the primary prey of many top predators in Antarctic shelf waters (Green and Williams, 1986; Arnould and Whitehead 1991, Creet *et al.* 1994). Stocks of *E. antarctica* represent a large reserve of energy through their high abundance and circumpolar distribution (Lancraft *et al.* 1989, Kock 1992). The myctophid has more than twice the energy density of Antarctic krill *Euphausia superba* (Clarke and Prince 1980, Torres *et al.* 1994a). Although being usually much lower in biomass than krill (Lancraft *et al.* 1989), it represents a valuable prey for top predators: The average lanternfish is significantly larger than an average krill, and would thus optimize the energy yield per prey item of a potential predator. In fact, the proportional mass of myctophid fish often dominates, or at least equals euphausiids in the diet of many Antarctic top predators (Ainley *et al.* 1992, Van Franeker 2001; Casaux *et al.* 2003).

3.3. A referential database for the molecular identification of Antarctic fish species and its application in ecological research

Contributors: Van Houdt J., Van de Putte A., Obbels D., Volckaert F.A.M.

Introduction

In the field and the laboratory individuals are assigned to a taxon on the basis of their morphological characteristics. Increasingly complementary information, such as molecular markers and ecology, is used for proper taxonomic assignment. DNA sequence diversity, whether assessed directly or indirectly through protein analysis, can be used to discriminate species. The Fish Barcoding of Life initiative (Ward *et al.* 2005; www.fishbol.org) is a global effort to coordinate an assembly of a standardised reference sequence library for all fish species. The benefits of barcoding fishes include facilitating species identification; highlighting specimens that represent a range expansion of known species; flagging previously unrecognized species; and enabling identifications where traditional methods are not applicable.

The Antarctic fish fauna (Teleostei) counts an estimated 300 species and is dominated by the endemic suborder of the Notothenioidei. It includes 35% of the “fish” species of the Southern Ocean, for which 97% are endemic and represent 46% of the fish

species and 90% of the fish biomass of the continental shelf and upper slope (Eastman and Clarke 1998). The Nototheniidae is the most speciose family of the Notothenioidei (qualified as species flock) and is adapted to life in temperature constrained environments. In the process of cold adaptation, the evolution of notothenioids has produced unique specialisations, including modification of hematological characteristics. Very special is that the crown group of the Channichthyidae is devoid of hemoglobin (di Prisco *et al.* 2007). Other remarkable characteristics are the presence of antifreeze glycoproteins, the absence of a swim bladder and adaptations to blood viscosity. Identification of adults is feasible from morphological traits (Miller *et al.* 1993), but the correct assignment of fish eggs and larvae, stomach contents and fish products at the species level (fisheries enforcement) remains problematic. Molecular markers provide a valid and highly successful alternative.

Our aim is to contribute to a reference database of Antarctic fish species that contains information on various mitochondrial and nuclear markers allowing DNA barcoding. The DNA sequence of the mitochondrial 12S and 16S rDNA genes have been published for a number of Antarctic fish species and might be suitable markers for the identification of most Antarctic fish. We evaluate the suitability of the mitochondrial COI gene (Ward *et al.* 2005) as a complementary source of information to identify species at the molecular level.

Material and Methods

Samples

The first challenge was to collect well identified reference specimens for the DNA based identification. Fresh and preserved biological material was collected through numerous international collaborations and ship-based sampling campaigns. The archiving and curation of voucher specimens was coordinated with the Muséum Nationale d'Histoire Naturelle (C. Ozouf-Costaz and G. Lecointre, Paris, F). An inventory of the 19 Antarctic fish species (adults, juveniles and larvae) for which we collected reference samples is listed below (Table 9).

Table 9: Overview of the Antarctic fish species collected by the KULeuven and managed with the Muséum Nationale d'Histoire Naturelle (Paris, F)

Genus	Species	adult	juvenile	larvae
<i>Artedidraco</i>	<i>skottsbergi</i>	■		
<i>Chionodraco</i>	<i>myersi</i>	■		
<i>Electrona</i>	<i>antarctica</i>	■	■	■
<i>Gymnodraco</i>	<i>acuticeps</i>	■		
<i>Lepidonotothen</i>	<i>larseni</i>	■		
<i>Notolepis</i>	<i>sp.</i>		■	■
<i>Notothenia</i>	<i>coriiceps</i>	■		
<i>Pagetopsis</i>	<i>macropterus</i>	■		
<i>Pleuragramma</i>	<i>antarcticum</i>	■		■
<i>Prionodraco</i>	<i>evansi</i>	■		
<i>Trematomus</i>	<i>eulepidotus</i>	■		
<i>Trematomus</i>	<i>lepidorhinus</i>	■		
<i>Trematomus</i>	<i>scotti</i>	■		
<i>Trematomus</i>	<i>pennellii</i>	■		
<i>Trematomus</i>	<i>nicolai</i>	■		
<i>Trematomus</i>	<i>newnesi</i>	■		
<i>Trematomus</i>	<i>juv.</i>		■	
<i>Gymnoscophelus</i>	<i>braueri</i>	■		
<i>Gymnoscophelus</i>	<i>nicolesai</i>	■		
<i>Bathylagus</i>	<i>antarcticus</i>		■	■

Molecular characterization

Historically, a suitable marker for the molecular identification of most Antarctic fishes is the DNA sequence of the mitochondrial 12S and 16S rRNA genes (Near *et al.* 2004). In the recently initiated DNA bar coding project (<http://www.fishbol.org>) the mitochondrial COI gene was chosen (Ward *et al.* 2005). Sequences were aligned with Clustal X multiple sequence alignment programme (Thompson *et al.* 1997) and clustered with the UPGMA method through the phylogenetic software package MEGA 3.1 (Kumar *et al.* 2004).

Results

We sequenced the samples and a set of (un)identified larval specimen available (see Table 5) at the 12S and 16S rRNA genes for a 300 to 500 and 1000 to 1500 bp fragment respectively (for primer sequences see Near *et al.* 2004, and the mitochondrial COI gene for a 655 bp fragment (for primer sequences see Ward *et al.* 2005).

Additional sequences were collected from GenBank. The results of only the former DNA fragment are presented here, since they provided the best available at the time. Notothenioids form a distinct clade from *Electrona antarctica*, *Protomyctophum crockeri* and several unidentified fishes from stomach content samples (Fig. 22). The UPGMA analysis of only the Notothenioidei differentiates most species, and was able to genetically identify the majority of larval stages although *Trematomus* conspecifics separate weakly while the genus *Dissostichus* is split over two clades (Fig. 23).

Discussion

Barcoding of Antarctic fishes is a realistic option, provided that high quality biological material is available. However, it is a huge challenge to collect material in the harsh and immense Southern Ocean. The project has been merged for the sake of efficiency with the barcoding project at the MNHN; curation of all biological material is done at MNHN. Our biological material contributes to the Fishbol regional barcoding survey (see Ward *et al.* 2005). COI sequencing is in progress and data are being entered into the Fishbol database.

Phylogenetically the 12S and 16S rDNA markers do not suffice to discriminate between the species of the *Trematomus* group. Only a multimarker approach has been able to prepare a well resolved tree (Sanchez *et al.* 2007). *Trematomus newnesi* turns out to be fairly basal in the tree.

Interesting is that preliminary results from this and other studies point to a genetic diversity within species meriting further phylogeographical analysis (e.g., Zane *et al.* 2006; see later).

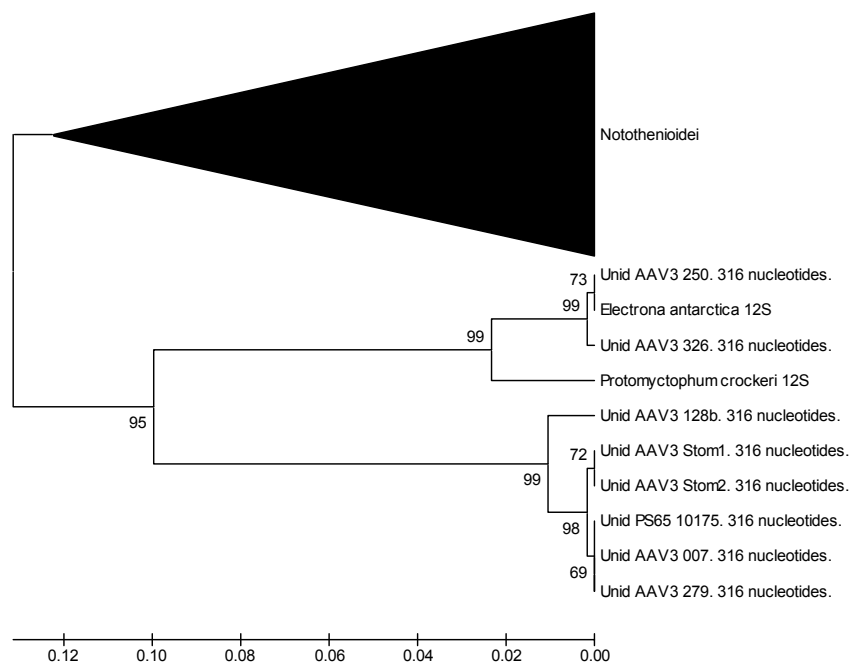


Figure 22. UPGMA tree (including bootstrap value) of the 12S rRNA gene of fishes of the Southern Ocean. Bootstrap values are indicated at the nodes.

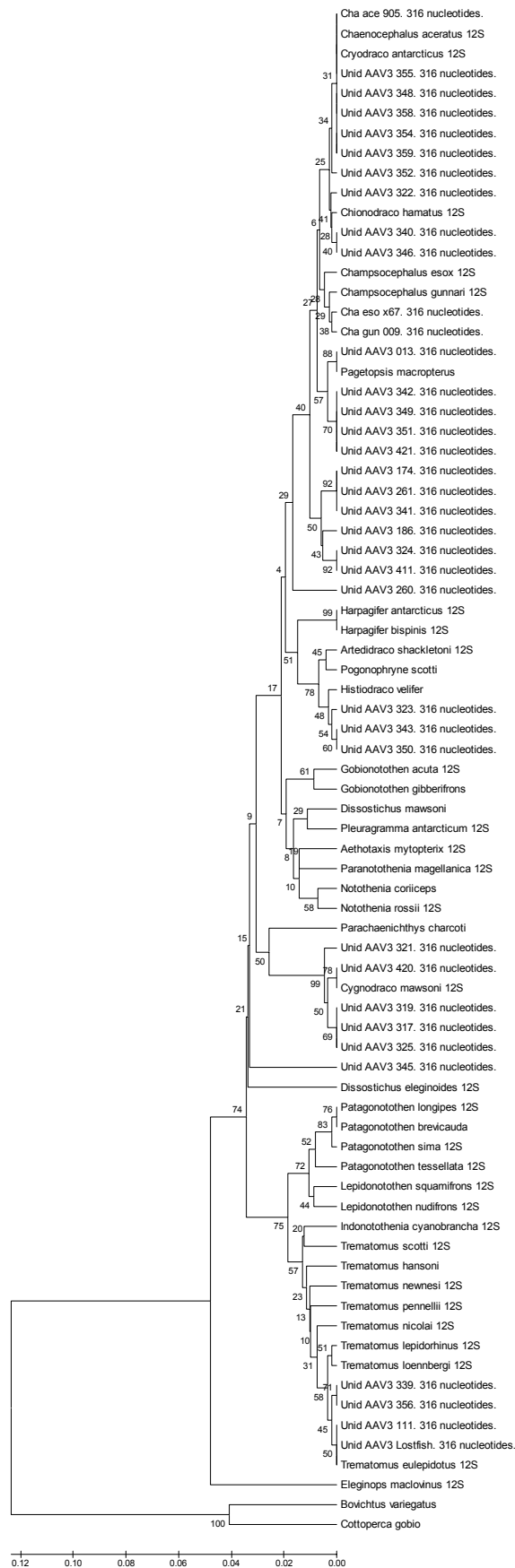


Figure 23. UPGMA tree (including bootstrap value) of the 12S rRNA gene of the Notothenioidei. Outgroups are *Bovichtus variegatus* and *Cottoperca gobio*. Bootstrap values are indicated at the nodes.

3. 4. Historical evolution of the lanternfish *Electrona Antarctica*

Contributors: Anton P. Van de Putte, Filip A.M. Volckaert, Jeroen Van Houdt, Bart Hellemans

Introduction

Origin and maintenance of genetic diversity is a central issue in evolutionary biology. Understanding these processes in the ocean realm is particularly difficult because barriers to gene flow are far less obvious in marine compared to continental species. Vicariance is usually invoked as the most likely model of speciation promoting genetic discontinuities across geographic ranges (Cunningham and Collins 1998). However, historical environmental factors related to habitat, currents and glaciations (Wares 2002) combined with species-specific traits play a pivotal role in shaping the pattern of intra-specific differentiation. Their relative contribution remains hard to disentangle. These ancestral interactions combined with present day environmental patterns are the focus of marine phylogeographic investigations. The few historical patterns analysed in the Southern oceans show weak differentiation, so typical of marine organisms (Zane *et al.* 1998, 2006).

The commonly occurring *Electrona antarctica* (Teleostei: Myctophidae) is considered as the only endemic lanternfish of the Southern Ocean and the only circumpolar species which occurs exclusively south of the Antarctic Polar Front (Greely *et al.* 1999) (Fig. 26). *E. antarctica* has a strong nyctemeral migration pattern, is planktonic during the larval phase such that the distribution is strongly influenced by patterns of ocean circulation. The diet includes copepods, ostracods and euphausiids including the krill, *Euphausia antarctica* (Pakhomov *et al.* 1996). It is an important prey for offshore birds. The aim of the study is the analysis of the historical evolution across the Southern Ocean based on genetic patterns (named phylogeography). This will provide information on historical differentiation (including the identification of evolutionary significant units), the influence of the environment on distribution and connectivity, and historical population dynamics. The phylogeographical analysis provides a starting point for a more detailed population genetic analysis (see further).

Material and methods

Samples

Biological material was collected during cruises with R.V. *Polarstern* (LAKRIS XXI-4, XXIII-4 and XXIII-6) and R.V. *Aurora australis* (Broke-West) and through exchanges with musea and colleagues (see acknowledgements). About 2000 frozen *Electrona*

antarctica from three sites, 120 ethanol preserved samples from four locations and 150 formalin preserved fishes from three sites are available.

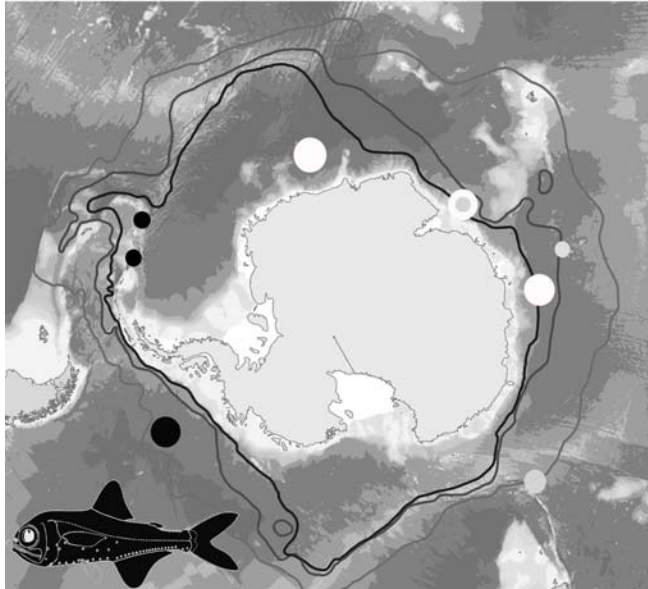


Fig. 24. Distribution of samples of *Electrona antarctica* used for phylogeographical analysis.
Frozen samples (□),
ethanol preserved samples (■),
formalin preserved samples (■)

Molecular characterisation

The mitochondrial DNA markers D-loop (500 bp) and cytochrome *b* (800 bp) were optimized on fresh material. For the formalin preserved material, a strategy based on the selective amplification of shorter molecular fragments was developed.

Results

Fresh collected material

An initial analysis of molecular variability in a 800 bp sequence of cytochrome *b* for 100 individuals showed little (< 5%) variance. Consequently additional primers were developed for the D-loop region. However variance in the D-loop region remains to be analyzed.

Museum material

Various techniques for recovering DNA from formalin preserved material were tested (for an overview of methods see Tang 2006). Of these techniques the modified protocol of Klanten *et al.* (2003), using a nucleospin extraction kit instead a phenol-chloroform extraction was selected. Additional internal primers are under development to sequence shorter fragments within the selected regions.

Discussion

Genetic diversity of *Electrona antarctica* in the Southern Ocean seems low from the small number of samples analysed so far. Given the large population sizes inhabiting the Southern Ocean (for some time a commercial fishery targeted *E. antarctica*) this is remarkable.

It is too early to discriminate between a fragmented or continuously distributed historical pattern. But again given the large population sizes, it is more likely that populations are continuous. It is also too early to detect evidence for population expansions or contractions during the Pleistocene. Although such expansions have been observed for amongst others the Antarctic silverfish (Zane *et al.* 2006), each species has responded uniquely to the cycling of the Pleistocene glaciations. Further analysis of more variable markers (D-loop, microsatellite markers) is underway and will resolve these questions. These preliminary results are part of a PhD thesis to be completed by the spring of 2008.

3.5. Evolutionary analysis of large and small-scale population structure and dispersal of the dusky notothen *Trematomus newnesi* and the yellowbelly rockcod *Notothenia coriiceps*

Collaborators: Jeroen Van Houdt, Bart Hellemans, Anton Van de Putte, Filip A.M. Volckaert, Philippe Koubbi, Guillaume Lecointre.

This text is based on the following paper:

Van Houdt J., Hellemans B., Van de Putte A., Koubbi P., Volckaert F.A.M. (2006) Isolation and multiplex analysis of six polymorphic microsatellites in the Antarctic notothenioid fish, *Trematomus newnesi*. *Molecular Ecology Notes* 6: 157-159

Introduction

One of the most interesting challenges in evolutionary biology is to assess the processes responsible for genetic differentiation of distantly or closely related populations without any obvious barriers. Marine organisms with a pelagic larval stage have a high potential for gene flow resulting in a lower degree of genetic differentiation than freshwater or anadromous species. However, the marine environment, although physically less structured than freshwater or terrestrial ecosystems, is not homogeneous. In recent years microsatellites have yielded evidence for a subtle but significant genetic structure. However, most studies have been carried out on a large geographic scale of hundreds or thousands of kilometers on species migrating over

vast distances. Thus, little world-wide information and almost none from the Southern Ocean are available as to whether small-scale systems of larval retention in the ocean exist and influence dispersal. Two common shelf fishes of the Southern Ocean are used here for understanding the dynamics of genetic structure.

Notothenia coriiceps (Nototheniidae; max. 62 cm) is found on the shelf of the Southern Ocean (<200 m) and is of potential fisheries interest. *Trematomus newnesi* (Nototheniidae; max. 20 cm) is found in shallow near shore areas and more commonly in the intertidal zone of the Southern Ocean. It feeds mainly on amphipods, polychaetes, gastropods, isopods, copepods, and euphausiids (*Euphausia superba*). It is often seen feeding in the water column or at the undersurface of ice. Phylogenetically it has been placed close to the root of the *Trematomus* species flock (Sanchez *et al.* 2007).

The aim of the study is twofold: to analyse the contemporaneous population structure in order to understand the differences between the historical patterns (see above) and those currently present. This will provide a basis for the identification of fish stocks (important for fisheries science) and more advance analyses of adaptive features. Second we quantify the gene flow between populations to identify “source-sink” dynamics. This will be helpful for taking conservation measures in the Southern Ocean.

Materials and methods

Samples

Notothenia coriiceps and *Trematomus newnesi* were collected in the coastal zone of Terre-Adélie during the years 2004-2006. Additional samples from other locations in the vicinity of the Antarctic Peninsula were obtained through exchanges with musea and colleagues (see acknowledgements). (Fig. 25)

Molecular characterization

A microsatellite enrichment protocol and selective hybridization with di-, tetra- and penta-repeat probes were used to isolate the microsatellite markers (for details see Van Houdt *et al.* 2006).

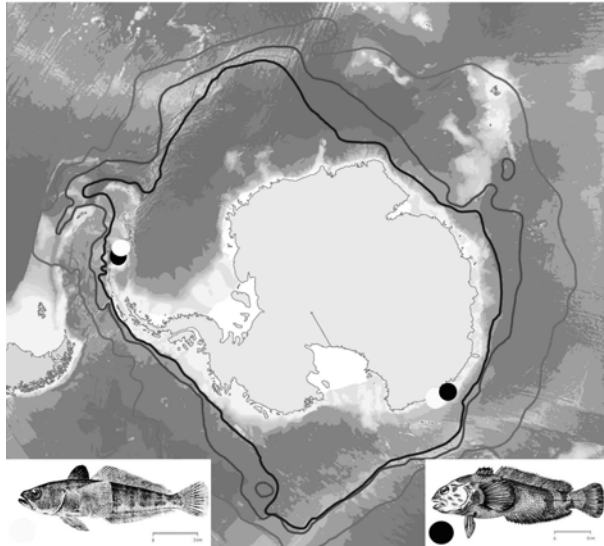


Fig. 25. Distribution of samples of *Notothenia coriiceps* and *Trematomus newnesi* used for population genetic analysis

Results

Six polymorphic microsatellites were isolated from *Trematomus newnesi*. Five loci were screened in 48 individuals captured in the Southern Ocean (coastal zone of Terre-Adélie). They reveal eight to 22 alleles per locus and an observed heterozygosity ranging from 0.70 to 0.92 (see Table 10).

Table 10: Diversity indices for microsatellites isolated from *Trematomus newnesi* based on a sample of 48 individuals from Terre-Adélie (Antarctica 66°40'13"S; 140° 01' 12" E) (source: Van Houdt *et al.* 2006).

Locus	Primer sequence (5_3_)	Conc (μ m)	Core motif	Size (bp)	T _a (°C)	n _A	H _O	H _E	F _{IS}	P
Trne20	F:GCCTCGCTAAACCCCTTGTGA	0.16	(CA) ₁₃	151	57	22	0.917	0.925	0.02	0.278
	R:AGCTGTCAGTCTGCTGG	0.16								
Trne35	F:ACTGAAGCATGCTGGGAACT	0.04	(TG) ₁₅	240	57	16	0.702	0.86	0.194	0.007
	R:CGTGTGAGGCCCGTCAG	0.04								
Trne37	F:AGGTGAGTGCTTGCGTGTGAG	0.04	(TG) ₁₁	167	57	9	0.896	0.812	_0.093	0.005
	R:GCACTCCATACAGACAAGCACGCT	0.04								
Trne53	F:ACACTCCCACAGCAACC	0.16	(AC) ₁₆	309	57	21	0.854	0.902	0.064	0.212
	R:GCCTTGTGACAGCCTGGAC	0.16								
Trne55	F:TCACACTGACACAGGGCAG	0.04	(TG) ₁₄	194	57	8	0.729	0.779	0.075	0.235
	R:GTGTACATTGGTGCCTGTGG	0.04								
Trne66	F:TGCTTGGACAGACTCCAGC	0.16	(CA) ₂₀	303	57	18	0.792	0.856	0.085	0.268
	R:TGGTAGTGGAGACATGCACAC	0.16								

T_a, annealing temperature; n_A, number of alleles; H_O, observed heterozygosity; H_E, expected heterozygosity; F_{IS}, fixation index; P, probability (based on 1000 permutations) of observing a more extreme F_{IS} value under the assumption of Hardy-Weinberg equilibrium (Bonferroni corrected 5% significance level = 0.00833). Clone sequences used for primer development have GenBank Accession nos DQ119759SDQ119764.

Currently five microsatellite markers for *N. coriiceps* have been developed and are being tested for variability. Additional testing of the *T. newnesi* markers on *N. coriiceps* samples revealed primers that could be used for *N. coriiceps* (Table 11).

Table 11: Microsatellites isolated from *Notothenia coriiceps* based on a sample of 48 individuals from Terre-Adélie (Antarctica 66°40'13"S; 140° 01' 12" E) and *Trematomus newnesi* microsatellites suitable for *N. coriiceps*.

Locus	Size (bp)	T _a (°C)	Cycles
Designed for <i>N. coriiceps</i>			
Noco_43	400	54	30
Noco_52	140	54	30
Haan_1	250	54	30
CHMY_1	155	54	30
CHMY_2	135	54	30
Compatible <i>T. newnesi</i> markers			
Trne37	175	54	30
Trne38	300	54	30

Discussion

The microsatellite markers of *Trematomus newnesi* show a high diversity, which is characteristic for marine species. The markers provide a tool to study the relationships between the various morphs observed. The species-specific markers can also be used for population genetic analysis, stock and gene flow analyses, and biodiversity studies in both species. For example, spatio-temporal metapopulation dynamics on the shelf area off Terre-Adélie is a focus of ongoing research.

Genetic markers for *N. coriiceps* and *E. antarctica* have been developed and will be further tested.

4. STATE DEPENDENT ENERGY ALLOCATION IN THE PELAGIC ANTARCTIC SILVERFISH *PLEURAGRAMMA ANTARCTICUM*: TRADING OFF BETWEEN WINTER RESERVES AND BUOYANCY

Contributors: Joachim Maes, Anthon Van de Putte, Jean-Henri Hecq, Filip A.M. Volckaert.

This text contains excerpts from the following paper:

Maes J., Van de Putte A., Hecq J.H., Volckaert F.A.M. (2006) State-dependent energy allocation in the pelagic Antarctic silverfish *Pleuragramma antarcticum*: trade-off between winter reserves and buoyancy Marine Ecology-Progress Series 326: 269-282 2006

Introduction

Pelagic species often possess hydrodynamically streamlined, compressed bodies with a silvery colour and forked tails. They exhibit several physiological adaptations enabling them to swim continuously, mostly in schools. They facilitate life in an environment which offers relatively little physical structure and, particularly in temperate and high latitude ecosystems, periodic food availability.

Few notothenioid Antarctic fish species radiated into meso-, epi- or cryopelagic niches, including the abundant Antarctic silverfish *Pleuragramma antarcticum*, the most abundant fish species in the High-Antarctic shelf areas of the Southern Ocean (Hubold 1984). It has achieved neutral buoyancy through a combination of skeletal reduction and lipid deposition in large subcutaneous and intermuscular lipid sacs (Eastman 1993). Fat reduces the density of the fish such that buoyancy increases. Negatively buoyant fish must spend energy to maintain a vertical position.

Lipid content in *Pleuragramma* ranges between 15 and 40% of the dry body mass and represents among the largest observed for teleosts (Hagen *et al.* 2000). Many animals use their fat reserves rather than proteins or sugars as an energy source whenever demands exceed intake (Noren and Mangel 2004). In *Pleuragramma*, it is unclear whether lipid storages are metabolically active and supply energy to maintain body functions during the austral winter when productivity is low. Lipid sacs are surrounded by cells which possibly regulate lipid transport (Eastman 1988). Lipid reserves in *Pleuragramma* may thus represent an energy source to be used in periods of critically low food intake as well as a buoyancy aid, which should be conserved.

We model an optimal allocation strategy of resources and habitats taking into account fitness consequences. We focus on the lipid metabolism and impose different constraints with respect to the accumulation or utilization of lipid reserves. We use the framework of a dynamic state variable model, introduced by Mangel and Clark (1988). We explore how different constraints on the energy dynamics affect lipid deposition, expected fitness, fecundity and habitat use in *P. antarcticum*. Under

plastic energy allocation, individuals may store fat reserves but incur increased metabolic costs. A second strategy consists of lipid accumulation at zero maintenance costs but once lipids are stored, they are unavailable for oxidation when food is scarce. The two strategies are compared with field data of fat content and fecundity.

Material and methods

Model structure The model simulates optimal habitat selection and an optimal energy allocation strategy using a time step of one week. We consider three different vertical habitats that vary in water temperature, optical properties, food availability and predation risk. Fish choose between a non-visual and a visual feeding strategy depending on ambient light conditions and plankton concentration. Assimilated energy is used to offset metabolic costs first. Energy in excess may be used to invest in structural protein mass, lipid reserves or reproductive tissue. Likewise, energy in shortage can be paid from any of these state variables. The model predicts optimal habitat use and energy allocation strategy for *Pleuragramma* by evaluating lifetime reproductive success using a dynamic state variable model (Clark and Mangel 2000).

The environment is simulated using a 1-D physical model coupled to a 1-D ecosystem model that has been parameterised for different regions of the Ross Sea. For a description of the full model, we refer to Hecq (2003). The state of an individual fish with total wet mass $W(t)$ is at any time t characterized by its structural body mass $B(t)$, its lipid mass $L(t)$ and its gonad mass $G(t)$. In the model, metabolic demands $M(t)$ are the sum of basic metabolism $M_1(t)$ and costs due to activity in order to maintain vertical position $M_2(t)$. For each habitat h , we model the number of prey eaten per second $F(t)$ as a type 2 functional response to food concentration $N(h,t)$ (number m^{-3}). In the model, the probability of individual *Pleuragramma* to survive $S(t)$ from time t to time $t+1$ is the product of size dependent survival $S_B(t)$ and habitat dependent survival $S_H(t)$. We assume that *Pleuragramma* reproduce annually at the end of the winter. Details on the expected lifetime reproductive success and the above mentioned variables can be found in Maes *et al.* (2006).

The solution of the dynamic fitness model predicts for all combinations of state the time dependent optimal habitat use and energy allocation strategy. We have used the model to conduct two theoretical experiments. In plastic allocation models (PAM), energy in excess can be allocated to each type of tissue while energy in shortage can be derived from each type of tissue. In fixed allocation models (FAM), we have put constraints on the allocation rule (Noren and Mangel 2004).

Results

We have run models over two years but we base our results solely on the first 52 weeks to avoid terminal fitness effects. The model starts at the onset of spring (1 September) and ends 52 weeks later with a spawning event for mature fish. Results summarize model data for 850 different states of individual *Pleuragramma* ranging between 0.5 and 100 g total wet body mass. In premature fish, we consider only states for which $G(t) = 0$.

All models predict ontogenetic changes in the allocation of assimilated energy to different tissues. The importance of energy allocation to structural body mass decreases with increasing size. Larger fish invest proportionally more energy in eggs.

Both plastic and fixed allocation models predict similar patterns of habitat use. Briefly, the use of shallow water is predicted to decrease with increasing size (Fig. 26). The use of deep water increases with increasing size. Mid water use is predicted to be the most favourable habitat throughout the life history. Models predict that all life history stages use shallow, ice-covered water during winter. Habitat distribution is mainly regulated through mortality, but patterns are similar among the models since shallow waters are annually covered by pack ice and snow offering a safe refuge from visual predators during winter. Doubling light related mortality via parameter ρ in equation 10 results in a slightly increased use of deeper waters.

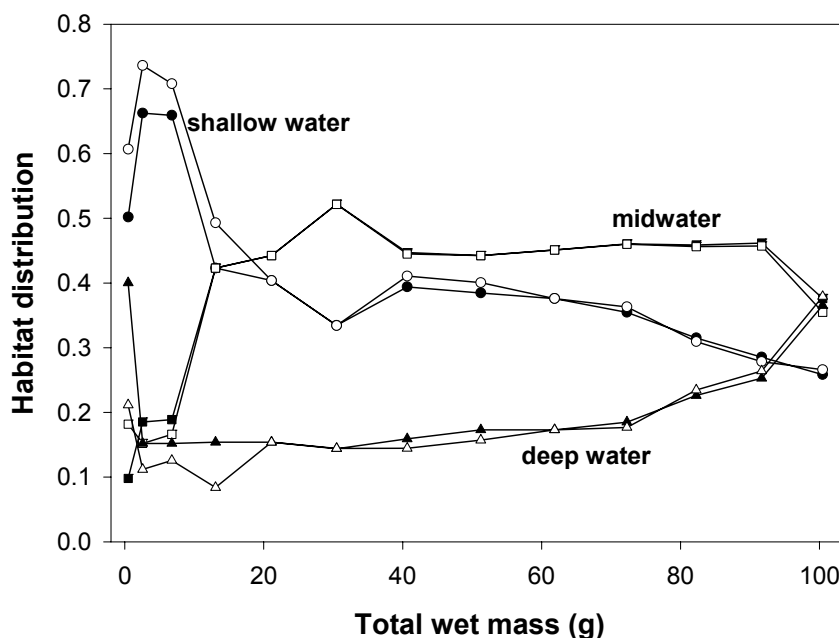


Figure 26. Size dependent proportional habitat use predicted by the plastic allocation model (black dots) and by the fixed allocation model 1 (FAM1), (white dots). Model results for FAM2 were almost similar as for FAM1. Circles represent shallow water; squares midwater and triangles deep water.

The array of decisions for energy allocation to different tissues can be used in a forward iteration procedure to estimate average, state dependent fecundity and lipid content. All models predict that fecundity correlates positively with fish size, following field data presented by Gerasimchuk (1987). The modelled slope of the relation between fish size and fecundity is steepest in the plastic allocation model. With respect to field observations, models underestimate fecundity in recently matured individuals (30 g) and overestimate fecundity for larger fish (100 g).

Under plastic allocation of resources, lipid content per gram wet mass averages 1.9%. Assuming a water content of 80% (Friedrich and Hagen 1994), fat content is close to 10% of the dry mass throughout the life history and does not accumulate. In the FAMS, lipid contents are predicted to accumulate steadily and contributed to a maximum of 14% of the fish's wet mass. Contrary to the PAM, models with a fixed allocation scheme replicate well observations of lipid content of *Pleuragramma* in the wild (Fig. 27).

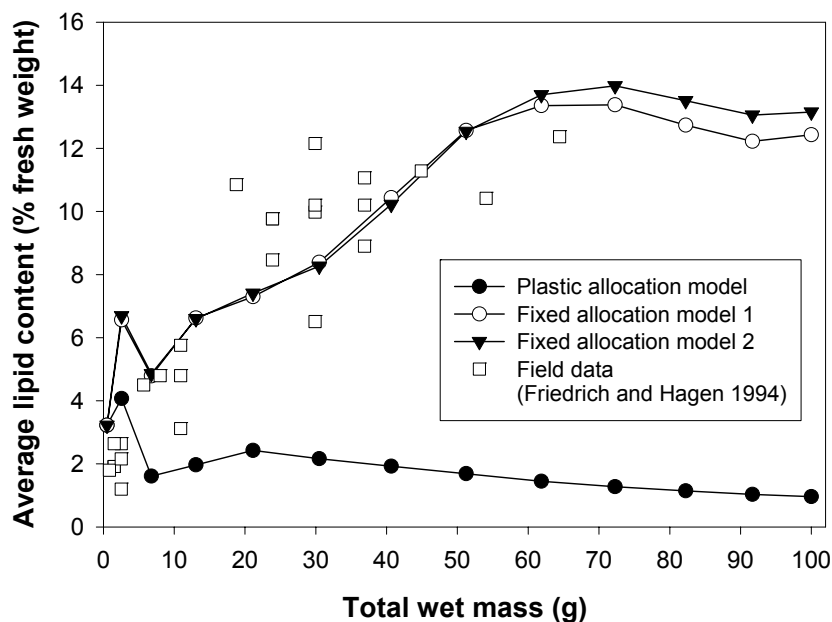


Figure 27. Size dependent patterns of relative fat content (% total wet mass) predicted by plastic and fixed allocation rules and comparison of model predictions with field data. Field data of fecundity are redrawn from Gerasimchuk (1987). Field data of relative fat content are redrawn from Friedrich and Hagen (1994).

Discussion

Field measurements of fat content in *Pleuragramma antarcticum* show a pronounced ontogenetic lipid accumulation with increasing size, without any notable variation among seasons (Hubold and Hagen 1997). These data are in close agreement with model predictions of fat content relative to wet mass based on a fixed allocation scheme of resources to different tissues. The fixed allocation model was constrained

to allow only the deposition of lipids. Such a strategy requires that, throughout the life history, a part of ingested energy is continuously and permanently fixed into lipid reserves, at the cost of somatic growth and fecundity. The award is a higher individual fitness, relative to a plastic allocation strategy, which allocated more resources into somatic and reproductive growth. It seems contradictory that plastic allocation of ingested energy results in lower fitness than an allocation strategy that is bound to follow predefined constraints. The essential difference between the two models is, however, the exclusion of accumulated lipid reserves from the calculation of metabolic costs. In the PAM, individuals are allowed to accumulate fat reserves but pay off with increased metabolic costs to maintain reserves during periods when resources are abundant. In the FAM, lipids may only be accumulated but no maintenance costs are considered. The latter assumption is not entirely justified. *Pleuragramma* do have small amounts of adipose tissue, which possibly is metabolically active (Eastman 1993). However, most fat reserves are stored in 100-200 large subcutaneous and intramuscular lipid sacs. Sacs are present at all 53 vertebral levels and vary between 0.2 and 3 mm in diameter. Histological section of the sac wall suggests that lipid transport to (and from) the sacs occurs via adipose cells. However, the organisation of lipids in large aggregations rather than in individual cells clearly limits the possibilities of rapid lipid mobilization in case of food deprivation (Eastman 1993).

The model results provide quantitative support to the hypothesis that lipid sacs are a buoyancy adaptation in order to save energy (DeVries and Eastman 1978). Through lipid deposition in metabolically inactive or low active structures, *Pleuragramma* may reduce its basal metabolism.

Energy saving mechanisms may represent a particular advantage in sluggish fish (Johnston *et al.* 1988). *Pleuragramma* has a presumed low scope for activity, due to the low incidence of red muscle (Kunzman 1990). The energy that becomes available through energy saving adaptations may be used for the exploitation of the food rich top waters of the high Antarctic zone.

Although this paper focussed mainly on the role of lipids, we note that model predictions with regard to habitat distribution more or less match with observed patterns (Hubold 1984). Especially the role of sea ice in the life history of *Pleuragramma antarcticum* warrants further studies. The dark, shallow waters under pack ice may offer a permanent food supply and probably provide a refuge against predators for all life history stages of *Pleuragramma*. If true, annual extension of the pack ice zone would influence the population dynamics of *Pleuragramma*, similar as observed in krill (Atkinson *et al.* 2004).

5. GENERAL CONCLUSIONS AND PERSPECTIVES

During the PELAGANT project we have analysed the status, the control and role of the pelagic components of system of the Southern Ocean Ecosystem. Three major tasks have been used to achieve the objectives:

The first task concerned data acquisition and analysis, data compilation of historical collections and data banking of the relevant pelagic organisms (especially microplankton, mesozooplankton, ichthyoplankton and fishes). The research was done on the Terre Adélie Continental Shelf, in the Ross Sea, in the Lazarev Sea and in the West-Indian sector of the Southern Ocean. The first aim of this proposal was the compilation of all the relevant data necessary to construct or calibrate the models. These data, which include information on the population dynamics of micro-, meso- and macroplankton and fishes, have been stored in dedicated databases (SCAR-MARBIN), CAML (Census of Marine Life), FishBol (Barcoding of Fish) and CEAMARC (Collaborative East Antarctic Marine Census).

The second task was to conceptualise the pelagic diversity and its spatio-temporal variation. The pelagic biodiversity has been analysed at three levels: ecosystem, species and population, by means of genetic, morphological, ecophysiological and ecosystemological tools. The large and small-scale evolution (genetic diversity and structure) of “umbrella” fish species has been determined with complementary molecular markers and a very complete statistical analysis. A functional morphological and a nutritional approach has assessed the relation between the developmental stages and the selection and exploitation of planktonic preys. The pelagic diversity status has been determined by analysing the spatio-temporal distribution of organisms in function of the abiotic factors. The pelagic assemblages have been explored with statistical models in search for consistent patterns or systematic relationships between variables using several statistical tools (data exploration).

Planktonic key- species (including Ichthyoplankton) of the Terre Adélie sector of East Antarctic Shelf (139°E – 145°E) and their spatial and temporal distribution have been studied in collaboration with the French programme ICOTA (Ichtyologie Côtière en Terre Adélie) of the Institut Polaire Paul Emile Victor (IPEV) and integrated in the international Antarctic scientific network programme CEAMARC (Collaborative East Antarctic Marine Census).

Larval and post-metamorphous fish have been collected during the expedition with RV *Polarstern* (Lakris (ANT XXI-4)) and the BROKE-west cruise of RV *Aurora Australis* (05/06 V3). The communities of fish observed during both campaigns are congruent with previous observations in the Southern Ocean. The strongest differentiation was observed between the coastal nototheniid community and the

mesopelagic oceanic community. Distribution of fish in both sampling areas was influenced by environmental factors. As such RDA and GAM modelling are valuable tools for extending our knowledge of pelagic ecosystems. However the marked differences in densities between both areas can't be explained easily within the context of these data. The currently analysed data in both areas preclude a distinction between geographical, seasonal and climatological effects. Additional analysis of data collected during the LAKRIS programme during summer (2005-2006) and winter (2007), will improve our understanding of the ecosystem in both areas.

The energy content of *Electrona Antarctica*, of which a large number of individuals was investigated over a wide size range in two regions, points to an asymptotic increase with age. There where enough samples were available, data on other mesopelagic species such as *Bathylagus antarcticus*, *Gymnoscopelus braueri*, *Pleuragramma antarcticum* and *Notolepis coatsi* were included. The results of this study are put into perspective through comparison with published data on ecology, proximate composition and energy content.

A referential database for the molecular identification of Antarctic fish species and its application in ecological research has been established. Genetic diversity of *Electrona antarctica* in the Southern Ocean seems low from the small number of samples analysed so far. Given the large population sizes inhabiting the Southern Ocean (for some time a commercial fishery targeted *E. antarctica*) this is remarkable. It is too early to discriminate between a fragmented or continuously distributed historical pattern. But again given the large population sizes, it is more likely that populations are continuous.

Evolutionary analysis of large and small-scale population structure and dispersal of the dusky notothen *Trematomus newnesi* and the yellowbelly rockcod *Notothenia coriiceps* were developed. The microsatellite markers of *Trematomus newnesi* show a high diversity, which is characteristic for marine species. The markers provide a tool to study the relationships between the various morphs observed. The species-specific markers can also be used for population genetic analysis, stock and gene flow analyses, and biodiversity studies in both species. For example, spatio-temporal metapopulation dynamics on the shelf area off Terre-Adélie is a focus of ongoing research. Markers for *N. coriiceps* and *E. antarctica* have been developed and will be further tested.

The third task was to model the dynamics of the pelagic assemblages by the development and implementation of a one-dimensional coupled biological/physical plankton model developed by our team during the previous phase of the Belgian

Antarctic Programme. The expanded version of the model includes the species identified and the selected trophodynamic concepts. The model will be used to determine the stability of biotic assemblages, their sensitivity to the environmental constraints and specially the response to climate changes.

The model has been used to simulate the vertical gradients in water temperature, optical properties, food availability and predation risk as input for a model of growth of *Pleuragramma antarcticum*. That dynamic state variable model investigates how ingested energy is partitioned over three state variables: lipid reserves, structural protein body mass and egg development. Two forms of the model differed in that lipid reserves were either included in or excluded from the total metabolic energy budget of an individual. The model was parameterised for the Antarctic silverfish *Pleuragramma antarcticum*. In that species, lipids are stored in unique extracellular lipid sacs, which are thought to serve as buoyancy aids and energy reserves. The model predicts optimal habitat selection and an optimal energy allocation strategy by maximizing future reproductive output. The environment is simulated using vertical gradients in water temperature, optical properties, food availability and predation risk. The form of the model that considers lipids as metabolically inactive reserves best replicates field measurements of fat content and yields high values for fitness in *Pleuragramma*. Uncoupling fat reserves from metabolism, through the development of extracellular lipid sacs, probably represents a key adaptation in the evolution towards a pelagic lifestyle in a fish species with a low scope for activity.

Through a multidisciplinary effort in Terre Adélie shelf area, we have identified the key-species governing the pelagic ecosystem over the Eastern Antarctic continental shelf. Key species or assemblages have been monitored in relation to environmental variability including seaice variability. The major pelagic assemblages and links with the habitats have been recognised. For the pelagic realm, the study focussed on the control of the pelagic ecosystem by few species of euphausiids, micronekton and phyto and zooplankton. Environmental variability in the pelagic shelf ecosystem operates at various temporal and spatial scales. At the spatial and temporal scale we are working on, the pelagic realm in the shelf zone can be monitored by a limited number of key pelagic species, which are mainly one species of euphausiids, *Euphausia crystallorophias* and one species of pelagic fish, *Pleuragramma antarcticum*. The krill *E. superba* is only abundant over deeper areas. These two species can highly dominate the micronekton and macroplankton and are good indicators, which respond at several time scales of variations in the marine environment. They depend on phyto- and mesozooplankton for their foraging and are preys of top-predators. By the diversity of habitats, as well as of species, the Terre Adélie shelf area has enormous scientific potential as shown by the intensity of

previous and future CAML surveys (e.g. CEAMARC : Collaborative East Antarctic Marine Census). Three identified major reasons are: the formation of deep Antarctic waters; the influence of the large Mertz Glacier Tongue on the oceanography of the area; the northern position of Terre Adélie and Georges V Land in Eastern Antarctica.

To conclude, it appears that information on the spatial distribution of key-species and their relationships to habitats is crucial for the effective protection of the Antarctic marine environment and biodiversity and the management of activities that could impact natural resources.

At the level of the Antarctic Treaty, work has started that will lead to the establishment of a system of Marine Protected Areas (MPAs) harmonised for the protection and sustainability of the Antarctic marine environment. A bioregionalisation analysis of the Southern Ocean will be of relevance for the selection of representative areas, and areas containing features critical to ecosystem function, with the overarching goal of maintaining biological diversity and ecosystem processes. Bioregionalisation will also have relevance as a scientific foundation to identify scientific and vulnerable areas and to provide a framework for management decisions on the basis of spatial and ecological criteria.

Until now, work on bioregionalisation permitted to divide the Southern Ocean into large-scale regions. The next challenge is to refine this broad scale regionalisation by better understanding how pelagic biodiversity and ecosystem stability are related to the major environmental drivers. In this context, results obtained during the PELAGANT project contribute to the development of a further fine-scale bioregionalisation of the Southern Ocean.

Within the PELAGANT project results focused on the Antarctic pelagic biodiversity and its control by physical, chemical and biological factors. Different biological levels were taken into account (species, population and ecosystem levels) as well as the functional aspects of biodiversity. Results emphasized that the concept of short, low diversity Antarctic pelagic food webs is overly simplistic. At different spatial scales, they allowed to identify Antarctic pelagic key-species and to determine their distribution in relation to the biotic and abiotic factors of the environment.

Of particular interest for bioregionalisation is the first attempt carried out to define ecological regions according to the range of plankton and fish communities that inhabit them. Special attention was paid to understand how environmental factors (meteorological conditions, sea ice extent, stratification of the water column and nutrient availability) control the spatial and temporal evolution of the Ross Sea and

Terre Adélie pelagic ecosystem and its functioning. Information obtained in the Terre Adélie area is particularly useful because this region is still poorly documented as compared to the Indian and Atlantic sectors of the Southern Ocean.

Another important contribution for the purpose of bioregionalisation are the biogeographic and phylogeographic patterns established during the PELAGANT project. The former are based on regional species lists and the latter on genetic patterns of a pelagic key species.

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