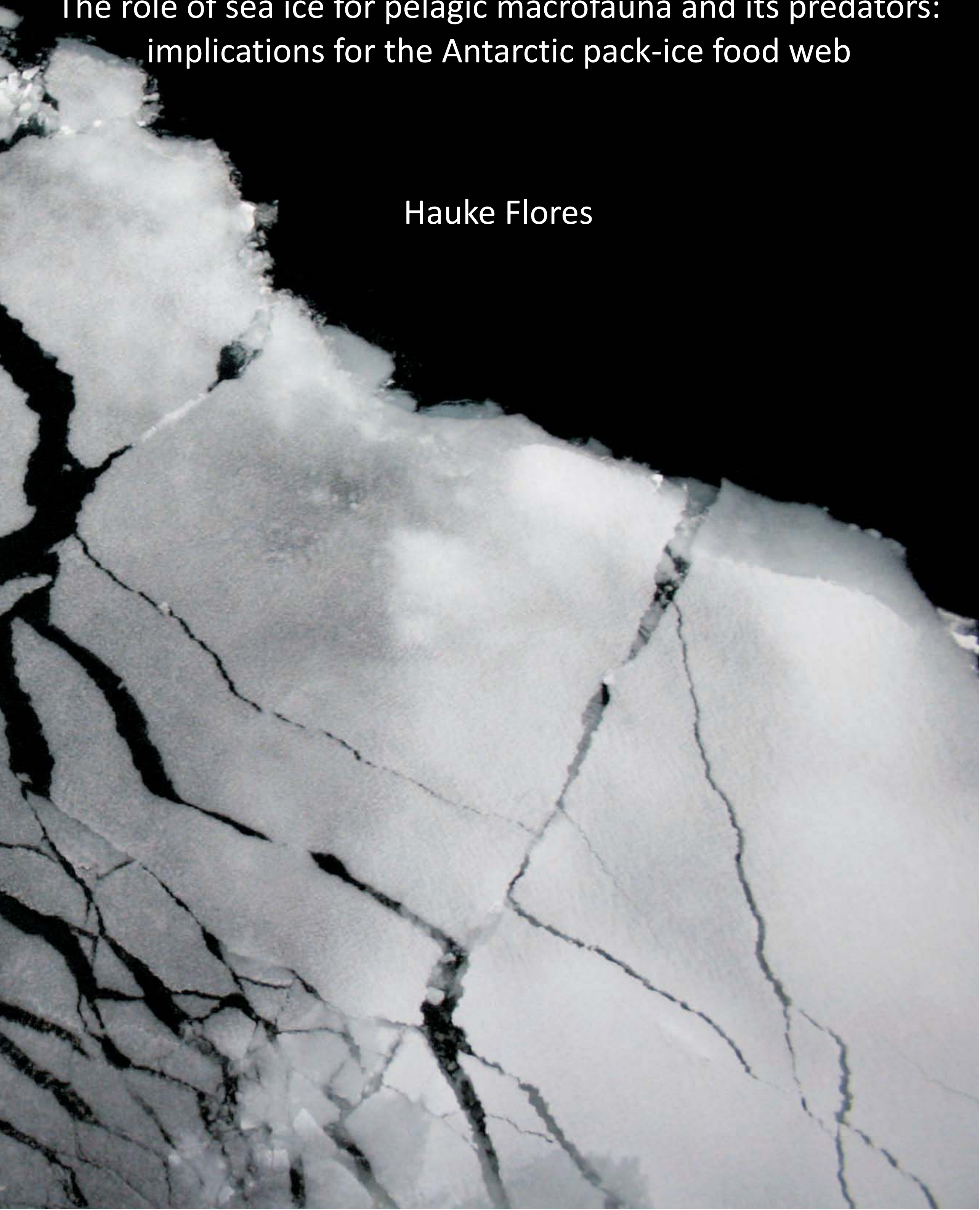
Frozen Desert Alive

The role of sea ice for pelagic macrofauna and its predators: implications for the Antarctic pack-ice food web

Hauke Flores



Frozen Desert Alive

The role of sea ice for pelagic macrofauna and its predators:
implications for the Antarctic pack-ice food web

Printed by Ponsen & Looien b.v., Ede

Electronic version available at:

http://www.rug.nl/bibliotheek/catalogibestanden/elekpubrug/dissertaties/index

ISBN: 978-90-6464-339-2

RIJKSUNIVERSITEIT GRONINGEN

Frozen Desert Alive

The role of sea ice for pelagic macrofauna and its predators: implications for the Antarctic pack-ice food web

PROEFSCHRIFT

ter verkrijging van het doctoraat in de
Wiskunde en Natuurwetenschappen
aan de Rijksuniversiteit Groningen
op gezag van de
Rector Magnificus, dr. F. Zwarts,
in het openbaar te verdedigen op
vrijdag 1 mei 2009
om 13.15 uur

door

Hauke Flores

geboren op 18 september 1974
te Bremerhaven

Promotor : Prof.dr. W.J. Wolff

Copromotor : Dr. J.A. van Franeker

Beoordelingscommissie : Prof.dr.ir. H.J.W. de Baar
Prof.dr. U.V. Bathmann
Prof.dr. F.A.M. Volckaert

In memory of my grandmother
In Gedenken an meine Großmutter

Gisela Flores
(24 Sep. 1921 - 26 Jan. 2008)

Contents

English summary

In the ocean around Antarctica, an area twice as large as Europe is periodically covered by sea ice each year. This area is known as the Antarctic Seasonal Sea Ice Zone (SIZ). Humans often perceive the pack-ice as a ‘frozen desert’. In spite of its harshness, however, the Antarctic SIZ features a remarkable biodiversity and hosts globally significant biological resources, such as the shrimp-like Antarctic krill (*Euphausia superba*). Large populations of penguins, other birds, seals and whales symbolize the biological richness of the SIZ ecosystem. Many of these animals are unique to the Antarctic Ocean, and as such have a high conservation status. Today, due to global warming the distribution of sea ice is beginning to alter in some Antarctic regions. It is therefore imperative to understand the ecological significance of sea ice in order to better predict future changes of Antarctic marine ecosystems. This thesis compiles eight studies focusing on the food web structure, the species composition and the spatial distribution of organisms in the Antarctic SIZ. Special attention is paid to the role of the ice-water interface layer for organisms that can transfer biomass and energy from the sea ice into the food chains ultimately sustaining the birds and mammals of the SIZ.

The biomass in offshore marine ecosystems is predominantly produced by microscopic algae suspended in the water (phytoplankton). In marine food chains, phytoplankton is fed on by small animals (zooplankton) that in turn are eaten by fish or squid, which are the prey of birds and mammals or larger fish. In the Antarctic Ocean, Antarctic krill can replace the usual zooplankton – fish/squid step of the food chains. In the South Shetland Islands, a high share of Antarctic krill in the food web was apparent from a study on the feeding ecology of mackerel icefish (*Champsocephalus gunnari*) and Scotia Sea icefish (*Chaenocephalus aceratus*). The diet of the mackerel icefish consisted almost exclusively of Antarctic krill in three consecutive summers. Juvenile Scotia Sea icefish also fed predominantly on krill. Their older congeners, however, clearly preferred fish (**Chapter 2**).

The South Shetland Islands belong to a highly productive region in the vicinity of the Antarctic Peninsula where Antarctic krill is concentrated by the prevailing currents. Based on investigations conducted in this region, it has generally been assumed that Antarctic krill is the key energy transmitter of the Antarctic marine food web. This assumption, however, does not agree with an increasing number of diet investigations finding that fish and squid dominate the food of birds and mammals. The role of organisms in the food web depends much on their nutritional value. Therefore, the energy content of three abundant fishes from the Lazarev Sea was investigated in **Chapter 3**. It was shown that individuals of the lanternfish *Electrona antarctica* quickly build up high energy reserves during their first year. The average energy content of the lanternfish was more than twice as high as that of Antarctic krill.

Specimens for energy measurements were sampled during a study on the species composition, distribution and abundance of fishes and their larvae in the upper 200 m of the Lazarev Sea (**Chapter 4**). *Electrona antarctica* was clearly the most abundant species in deep waters. The most important diet items of the lanternfish were small crustaceans other than krill. It was calculated that *Electrona antarctica* dwelling in the upper 200 m represent more than one-third of the energy bound in the population of Antarctic krill in the Lazarev Sea. Since large parts of the lanternfish population are usually distributed below 200 m, it can be assumed that the amount of energy bound in the total stock of *Electrona antarctica* was possibly similar to that of Antarctic krill. Such high contribution of fish to the energy household of the ecosystem challenges the classic krill-centered concept of the Antarctic marine food web.

The growth of algae depends on the availability of light. Because phytoplankton is often mixed into deeper water layers, it can hardly grow at all when the available light is additionally dimmed by a pack-ice canopy. However, a high food demand of birds and mammals persists in pack-ice areas even hundreds of kilometres away from open water, indicating substantial biological production in the ice. In contrast to phytoplankton, microalgae growing at the underside of ice floes always stay near the well-lit surface. The biomass and energy produced by these ice algae can be passed on through the food chains, ultimately feeding all animals of the SIZ. The perception that the sea ice area can sustain considerable abundances of birds and mammals was supported by the results of a penguin and seal census conducted in the seldom investigated pack-ice of the inner Weddell Sea (**Chapter 5**). The abundance of seals and penguins in the dense pack-ice was similar to what is known from northerly, more open waters. The most abundant species was the crabeater seal (*Lobodon carcinophaga*). In a novel approach, census data of this species were combined with ice thickness measurements collected in parallel. The statistical analysis of these data indicated that the distribution of crabeater seals was significantly related to ocean depth and ice thickness. This observation exemplifies the influence of sea ice characteristics on the distribution of animals.

If the Antarctic SIZ ecosystem depends largely on sea ice production, the biological resources of the ice must be transferred into the food web of the water column at the ice-water interface. The underside of ice floes, however, is inaccessible for conventional net-based and hydro-acoustic sampling techniques. A novel under-ice sampling device was therefore developed at Wageningen IMARES, the *Surface and Under Ice Trawl* (SUIT). In Antarctic coastal waters, several crustaceans of the order Amphipoda live in close association with the undersurface of ice. During a study conducted mostly in offshore areas of the Weddell Sea and the Lazarev Sea, amphipods were collected by means of baited traps, by SCUBA diving and with SUIT (**Chapter 6**). The six species found at the underside of ice floes are first evidence of an ice-associated mode of life from amphipods living in Antarctic deep waters.

A multi-seasonal SUIT study provided the first quantitative account of under-ice species composition at a large spatial scale (**Chapter 7**). An unexpectedly large number of species were collected in the two-metre surface layer, both in open water and under ice. In an analysis using multiple environmental parameters it was shown that, next to few other factors, the species composition significantly responded to sea ice properties in autumn and summer. The results of this study indicated that the ice-water interface layer attracts a surprising diversity of species, indicating intense biological interaction between ice-associated life and the food web of the underlying water column.

Chapter 8 represents the first record of the distribution and abundance of Antarctic krill in the two-metre surface layer both under ice and in open water during three different seasons. The average abundance of Antarctic krill in the upper two metres as estimated by SUIT was highest under ice in winter and lowest in the largely ice-free autumn. In summer, krill was more abundant in the surface layer under ice than in open water. Comparison with data from concurrently deployed midwater nets demonstrated that the average per-m^2 abundance of Antarctic krill was higher in the two metres under the ice than in the entire 0-200 m depth range in winter and summer. These results indicate that the biological capacity of ice-covered waters can be much higher than estimated by the usually applied midwater sampling using nets or sonar. More importantly, the high relevance of the ice habitat demonstrated for Antarctic krill and other species highlights the vulnerability of the Antarctic SIZ ecosystem to changes in the structure and the spatial and temporal extent of sea ice.

These studies demonstrated the value of the newly developed SUIT for providing new insights in the structure of the SIZ ecosystem that could not be obtained with conventional technology. In **Chapter 9**, the ability of SUIT to sample zooplankton, fish and squid in a representative manner was investigated based on real-time current measurements in the net opening, the species composition and the size distribution of SUIT catches. The measurements indicated a steady flow into the net allowing standardized abundance estimates. SUIT catches comprised species ranging in size from crustaceans smaller than 1 mm to fully grown fish and squid. The size distribution of Antarctic krill was almost identical to that from midwater trawls using a similar mesh size. Although some adult fishes and squid may be able to avoid the net, SUIT can be assumed to be a reliable quantitative sampling device at least up to the size of adult Antarctic krill.

The results of this thesis provide new and direct evidence that sea ice is crucially important for the productivity and the biodiversity of the Antarctic SIZ. In addition, further evidence was found that the offshore food web of the Antarctic SIZ is more complex than suggested by traditional krill-centered food web models. These insights may contribute to better estimates of the response of Antarctic marine ecosystems to changing sea ice characteristics caused by global warming. A better understanding of future ecological changes in the Antarctic SIZ is important for both, biological resource management and conservation.

Nederlandse samenvatting

De oceaan rond Antarctica bevriest ieder jaar opnieuw over een gebied twee keer zo groot als Europa. Dit gebied is bekend als de Antarctische Seizoens IJszone (Antarctic Seasonal Sea Ice Zone, of SIZ). Het daar voorkomende pakijs wordt vaak beschouwd als een kale ijswoestijn zonder leven, maar niets is minder waar. Ondanks de barre omstandigheden kent het gebied een opmerkelijke biodiversiteit en is rijk aan biologische hulpbronnen zoals het garnaalachtige Antarctische krill (*Euphausia superba*). Grote aantallen pinguïns, andere zeevogels, zeehonden en walvissen zijn kenmerkend voor de biologische rijkdom van het ecosysteem. Veel van deze soorten zijn uniek voor de Antarctische Oceaan en hebben daarom een hoge beschermingswaarde. Door de opwarming van de aarde verandert de verspreiding van het zee-ijs in bepaalde delen van Antarctica. Het is daarom van groot belang om te begrijpen wat de ecologische betekenis van zee-ijs is om toekomstige veranderingen in het Zuidpoolecosysteem te voorspellen. Dit proefschrift omvat acht hoofdstukken die zich richten op de structuur van de voedselketen, op de soortensamenstelling en op de ruimtelijke verspreiding van dieren in het zee-ijs. Een tot nu toe onbekende wereld bevindt zich op het grensvlak tussen het drijvende ijs en het zeewater eronder. Verschillende hoofdstukken besteden speciale aandacht aan deze ijs-water grens, waar organismen leven die van groot belang zijn voor Antarctische vogels en zeezoogdieren.

In zee vervullen microscopisch kleine algen (fytoplankton) eenzelfde rol als planten op land. Ze dienen als voedsel voor dierlijk plankton (zoöplankton), dat weer de energiebron vormt voor vissen en inktvissen. Aan het eind van de voedselketen staan vogels, zoogdieren en grotere vissen. In de Antarctische Oceaan kan Antarctisch krill de rol van zoöplankton, vissen en inktvissen in de voedselketen overnemen. Rond de Zuidelijke Shetlandeilanden vormt krill een belangrijke schakel in de voedselketen. Uit een driejarige dieetstudie bleek dat Antarctisch krill veruit de belangrijkste voedselbron van de ijsvis *Champsocephalus gunnari* vormt (**Hoofdstuk 2**). Ook jongere exemplaren van de verwante soort *Chaenocephalus aceratus* aten voornamelijk krill. De volwassen dieren van deze soort prefereerden echter duidelijk vis.

De Zuidelijke Shetlandeilanden maken deel uit van het biologisch zeer productieve gebied rond het Antarctisch Schiereiland, waar krill onder invloed van zeestromingen wordt geconcentreerd. Er is altijd aangenomen dat Antarctisch krill een centrale rol vervult binnen de voedselketens rond de Zuidpool. Een groeiend aantal dieetstudies laat echter zien dat ook vis en inktvis een belangrijk deel van het voedsel van vogels en zoogdieren uitmaken. De rol van organismen in het voedselweb hangt nauw samen met hun energetische inhoud. Daarom zijn de energie-inhouden van drie vissoorten onderzocht in de Lazarev Zee (**Hoofdstuk 3**). De lantaarnvis *Electrona antarctica* legt tijdens het eerste levensjaar grote energievoorraden aan, waardoor de vissoort een rijke bron van energie vormt voor predatoren. De gemiddelde energie-inhoud van deze lantaarnvis bleek maar liefst twee keer zo hoog als die van Antarctisch krill.

Hoofdstuk 4 beschrijft een studie naar de verspreiding en dichtheid van vissen en vislarven in de bovenste tweehonderd meter van de waterkolom in de Lazarev Zee. *Electrona antarctica* was duidelijk de meest voorkomende vissoort. Uit maagonderzoek bleek dat de belangrijkste prooidieren van de lantaarnvis roeipootkreeftjes waren. Naar schatting heeft het totale bestand van de lantaarnvis in de bovenste tweehonderd meter een voedingswaarde die vergelijkbaar is met meer dan 1/3 van die van het krillbestand. Omdat lantaarnvissen juist vaak dieper dan tweehonderd meter voorkomen, is het waarschijnlijk dat de voedingswaarde van het totale lantaarnvisbestand even groot is als die van het krillbestand. Een dermate belangrijke rol van vis in het ecosysteem zet vraagtekens bij het klassieke model van een sterk op krill gebaseerd Antarctisch voedselweb.

Zee-ijs vangt extra veel licht weg waardoor zwevende algen als zij in diepere lagen terecht komen, nog maar nauwelijks kunnen groeien en geen bijdrage meer kunnen leveren aan de voedselketen in de zee-ijsgebieden. Toch blijkt dat tot ver in het zee-ijs, honderden kilometers weg van open water, zeer hoge dichtheden vogels en zeezoogdieren voorkomen die daar blijkbaar voldoende voedsel kunnen vinden. Waarschijnlijk ligt de oplossing van dit raadsel in microscopisch kleine algen die tegen de onderkant van het ijs groeien, en zo optimaal gebruik maken van het doordringende licht van het oppervlak. De biomassa en energie van deze ijs-algen worden via de voedselketen doorgegeven aan alle andere organismen in het zee-ijs gebied. Aanwijzingen voor een dergelijke voedselketen werden gevonden in het weinig onderzochte centrale deel van de Weddell Zee dat met pakijs is bedekt (**Hoofdstuk 5**). De aantallen pinguïns en zeehonden waren er gelijk aan die aan de rand van het zee-ijs, bij het open water. Dankzij een nieuwe techniek kon de dikte van zee-ijs gemeten worden tijdens de vogel- en zeezoogdiertellingen. De verspreiding van de krabbeneter (*Lobodon carcinophaga*), de meest algemene Antarctische zeehond, bleek significant gerelateerd aan oceaandiepte en ijsdikte. Dit laat zien dat ijs een duidelijke invloed heeft op de verspreiding van dieren in de SIZ.

Aangezien de biologische productie vlak onder het zee-ijs zo cruciaal lijkt binnen het ecosysteem is het belangrijk om deze zone goed onder de loep te nemen. De onderkant van ijsschotsen is echter niet bepaald gemakkelijk te bestuderen met conventionele onderzoeksmethoden. Binnen Wageningen IMARES is daarom een visnet ontwikkeld dat wel onder het ijs kan bemonsteren, het ‘Surface and Under Ice Trawl’ (SUIT). Het SUIT is, naast andere technieken zoals vallen met aas en duikend onderzoek, ingezet om vlokreeften te bestuderen in diepzeegebieden van de Weddell Zee en de Lazarev Zee (**Hoofdstuk 6**). Zes onder het ijs gevonden soorten vormen het eerste bewijs van vlokreeften uit diepere Antarctische wateren die afhankelijk zijn van het zee-ijs.

Met SUIT werd een onverwacht groot aantal diersoorten gevangen in de bovenste twee meter van de waterkolom, zowel onder het zee-ijs als in open water (**Hoofdstuk 7**). De soortensamenstelling hangt sterk samen met de eigenschappen van het zee-ijs in de zomer en in de herfst, bleek uit een analyse met verschillende omgevingskenmerken. De waterlaag direct onder het ijs trekt een verbazingwekkende diversiteit van soorten aan. Deze resultaten tonen aan dat de voedselketen in de onderliggende waterkolom sterk verbonden is aan de biologische productie vlak onder het ijs.

Hoofdstuk 8 laat dankzij het SUIT voor het eerst zien in welke hoeveelheden Antarctisch krill in de bovenste 2 m van de waterkolom voorkomt, zowel onder het zee-ijs als in open water. In de winter was krill het meest talrijk aanwezig aan het wateroppervlak vlak onder het ijs. In de bijna ijsvrije herfst was krill het minst aanwezig in het oppervlaktewater. In de zomer prefereerde het krill duidelijk het water vlak onder het ijs en niet het open water. Uit vergelijking met een dieper vissend net bleek dat de gemiddelde dichtheid van krill (dieren per m^2) in de bovenste twee meter onder het ijs in de zomer en in de winter hoger was dan in de tweehonderd meter eronder. Deze resultaten wijzen erop dat de biologische productie in wateren die met ijs bedekt zijn veel groter kan zijn dan tot nu toe met gewone visnetten of sonar is waargenomen. Het zee-ijs is dus enorm belangrijk voor Antarctisch krill en andere soorten waardoor dit ecosysteem kwetsbaar is voor veranderingen in de structuur en de verspreiding van het ijs.

Het SUIT is van grote waarde voor het in kaart brengen van de structuur van Antarctische voedselketens. Met conventionele vistechnieken is dat niet mogelijk. In **Hoofdstuk 9** is de geschiktheid van het SUIT voor kwantitatieve bemonsteringen kritisch onderzocht. Metingen van de stroomsnelheid van water in het net tijdens het vissen lieten zien dat de waterstroom door het SUIT constant was, waardoor je inderdaad gestandaardiseerde metingen kunt doen. Het SUIT ving zowel kreeftachtigen kleiner dan 1 millimeter als volgroeide vissen en inktvissen. De grootteverdeling van het Antarctisch krill uit SUIT was bijna identiek aan die van het krill in een gestandaardiseerd net met vergelijkbare maaswijdte. Hoewel snel zwemmende vissen en inktvissen het net mogelijk kunnen ontwijken, tonen de resultaten aan dat het SUIT betrouwbare kwantitatieve metingen kan doen van soorten tot tenminste de grootte van volwassen Antarctisch krill.

De resultaten in dit proefschrift leveren nieuw en direct bewijs dat zee-ijs cruciaal is voor het ecosysteem in de Antarctische SIZ. Daarnaast blijkt het traditionele beeld dat krill het middelpunt van het voedselweb vormt een te eenvoudige voorstelling van de werkelijkheid. Deze kennis draagt hopelijk bij tot betere inzichten in de reactie van Antarctische mariene ecosystemen op veranderende kenmerken van het zee-ijs veroorzaakt door de opwarming van de aarde. Zulke inzicht is belangrijk voor de bescherming van de natuur en een verantwoord beheer van de visserij rond Antarctica.

Deutsche Zusammenfassung

Auf dem Meer um die Antarktis erstreckt sich alljährlich eine Eisdecke, die doppelt so groß ist wie Europa. Das Packeis dieses als saisonale Meereiszone (SMZ) bezeichneten Gebiets wird von Menschen oft als eine lebensfeindliche Eiswüste wahrgenommen. Trotz der extremen Bedingungen aber beherbergt die SMZ eine bemerkenswerte Vielfalt an Lebensformen und biologische Ressourcen von globaler Bedeutung, wie den antarktischen Krill (*Euphausia superba*). Der biologische Reichtum der SMZ ist deutlich erkennbar an den großen Beständen von Pinguinen, anderen Vögeln, Robben und Walen in diesem Gebiet. Viele dieser Tiere kommen allein im antarktischen Ozean vor und sind international geschützt. Durch die globale Erwärmung beginnt sich die Ausdehnung des Meereises in manchen Regionen der Antarktis bereits zu verändern. Es ist also dringend notwendig, die ökologische Bedeutung des Meereises zu verstehen, um zukünftige Reaktionen des Ökosystems besser vorhersagen zu können. In dieser Dissertation sind acht Studien zusammengestellt, die sich mit der Struktur des Nahrungsnetzes, der Artzusammensetzung und der räumlichen Verbreitung von Tieren in der antarktischen SMZ auseinandersetzen. Ein besonderes Augenmerk gilt der Rolle der Eis-Wasser-Grenzschicht für Organismen, die Biomasse und Energie vom Meereis in jene Nahrungsketten transferieren, von denen die Vögel und Säugetiere der SMZ abhängig sind.

Frei driftende, mikroskopisch kleine Algen (Phytoplankton) produzieren fast die gesamte Biomasse des offenen Ozeans. In ozeanischen Nahrungsketten werden diese planktonischen Algen von tierischem Plankton (Zooplankton) gefressen, das wiederum als Nahrung für Fische und Tintenfische dient, die ihrerseits die Beute der Meeresvögel und Säugetiere oder großer Raubfische sind. Im antarktischen Ozean kann antarktischer Krill die Funktion von Zooplankton und Fisch bzw. Tintenfisch in der Nahrungskette übernehmen. Nahrungsuntersuchungen am Bändereisfisch (*Champsocephalus gunnari*) und am Scotia-See-Eisfisch (*Chaenocephalus aceratus*) aus dem Gebiet der Süd-Shetland-Inseln deuten darauf hin, dass Krill eine wesentliche Rolle im dortigen Nahrungsnetz spielt. In drei aufeinanderfolgenden Sommern bestand die Nahrung der Bändereisfische fast ausschließlich aus antarktischem Krill. Auch junge Scotia-See-Eisfische fraßen vor allem Krill. Ihre älteren Artgenossen allerdings zogen Fisch als Nahrungsquelle vor (**Kapitel 2**).

Die Süd-Shetland-Inseln gehören zu einer biologisch hochproduktiven Region an der antarktischen Halbinsel, in der antarktischer Krill durch Meeresströmungen stark angereichert wird. Aufgrund von Untersuchungen in diesem Gebiet nimmt man allgemein an, dass antarktischer Krill der Schlüsselorganismus für die Energieübertragung im antarktischen Nahrungsnetz ist. Zweifel an dieser Annahme aber werden von einer wachsenden Anzahl nahrungsökologischer Untersuchungen hervorgerufen. Diese Arbeiten zeigen, dass die meisten Vögel und Säugetiere der SMZ vor allem von Fisch und Tintenfisch leben. Die nahrungsökologische Bedeutung eines Organismus hängt sehr von seinem Nährwert ab. In **Kapitel 3** wurde deshalb der

Energiegehalt von drei häufig vorkommenden Fischarten in der Lazarevsee untersucht. Es konnte gezeigt werden, dass Fische der Leuchtsardinenart *Electrona antarctica* während ihres ersten Lebensjahres sehr schnell Energiereserven aufbauen. Bemerkenswerterweise war der durchschnittliche Energiegehalt der Leuchtsardinen mehr als doppelt so hoch wie der des antarktischen Krill.

Die Proben für die Energiebestimmungen wurden im Rahmen einer Studie zur Artzusammensetzung, räumlichen Verteilung und Abundanz von Fischen und Fischlarven in den oberen 200 m der Lazarevsee gewonnen (**Kapitel 4**). *Electrona antarctica* war mit Abstand die häufigste Fischart im offenen Ozean. Die Nahrung der Leuchtsardinen bestand vor allem aus Ruderfußkrebsen. Berechnungen ergaben, dass die in den Leuchtsardinen der oberen 200 m gespeicherte Energiemenge mehr als ein Drittel so groß war wie die der Krillpopulation in der Lazarevsee. Da sich aber viele Leuchtsardinen unterhalb 200 m Tiefe aufhalten, war die Energiemenge der gesamten Fischpopulation womöglich ebenso groß wie die des Krillbestandes. Dieses Ergebnis deutet darauf hin, dass Fische einen hohen Anteil im Energiehaushalt des Ökosystems ausmachen und stellt das klassische, krillzentrierte Modell des antarktischen Nahrungsnetzes in Frage.

Das Wachstum von Algen ist von Licht abhängig. Da aber das Phytoplankton oft in lichtarme Tiefen sinkt, kann es kaum wachsen, wenn der Lichteinfall zusätzlich durch die Packeisdecke vermindert wird. Trotzdem zeigt ein anhaltend hoher Nahrungsbedarf von Vögeln und Meeressäugetieren auch hunderte Kilometer entfernt vom Eisrand hohe biologische Produktivität an. Im Gegensatz zu Phytoplankton bleiben Mikroalgen, die an der Unterseite der Eisschollen wachsen, immer in der lichtdurchfluteten Oberflächenschicht. Diese Eisalgen produzieren wahrscheinlich genug Biomasse, um die reichhaltigen Lebensgemeinschaften der SMZ zu unterhalten. Die Ergebnisse eines Pinguin- und Robben-Surveys im selten untersuchten Packeisgebiet des inneren Weddellmeeres bestätigten die Annahme, dass das tiefe Packeis beträchtliche Bestände von Warmblütern beherbergen kann (**Kapitel 5**). Die Abundanz von Pinguinen und Robben war hier ebenso hoch, wie es von weiter nördlich gelegenen, offeneneren Gewässern bekannt ist. Die Krabbenfresserrobbe (*Lobodon carcinophaga*) war die häufigste Art. In einem neuartigen Ansatz wurde der Robben- und Pinguinsurvey mit kontinuierlichen Eisdickenmessungen kombiniert. Die statistische Auswertung ergab, dass die räumliche Verteilung von Krabbenfresserrobben in starkem Zusammenhang mit Wassertiefe und Eisdicke steht. Dieses Ergebnis veranschaulicht den deutlichen Einfluss des Meereises auf die räumliche Verteilung von Tieren in der Antarktis.

Wenn das Ökosystem der SMZ in großem Maße von der Produktion der Eisalgen abhängt, müssen biologische Ressourcen vom Meereis über die Eis-Wasser-Grenzschicht in das Nahrungsnetz der Wassersäule gelangen. Die Unterseite des Eises aber ist unerreichbar für konventionelle Netze oder Sonare. Aus diesem Grund wurde bei Wageningen IMARES ein neuartiges Beprobungsgerät entwickelt, das *Surface and Under-Ice Trawl* (SUIT; engl.: Oberflächen- und Unter-Eis-Schleppnetz). In küstennahen Gewässern der Antarktis leben einige Flohkrebsarten an der Unterseite des Eises. Während einer Studie, die großenteils in den Hochseegebieten des Weddellmeeres und der Lazarevsee durchgeführt wurde, wurden Flohkrebse in Köderfallen, von Tauchern und mit dem SUIT gesammelt (**Kapitel 6**). Die sechs in der Eis-Wasser-Grenzschicht gefundenen Flohkrebsarten sind der erste Nachweis eisassoziierter Flohkrebse im offenen Ozean der Antarktis.

Die Zusammensetzung der Lebensgemeinschaft in der Eis-Wasser-Grenzschicht wurde mit dem SUIT erstmalig quantitativ und weiträumig zu verschiedenen Jahreszeiten untersucht (**Kapitel 7**). Überraschend viele Arten wurden in den oberen zwei Metern sowohl unter Eis als auch im offenen Wasser vorgefunden. Unter Berücksichtigung zahlreicher Umweltparameter konnte mit einer statistischen Analyse gezeigt werden, dass die Artzusammensetzung der Oberflächenschicht im Sommer und im Herbst vor allem durch Eigenschaften des Meereises bestimmt wird. Die Ergebnisse dieser Studie zeigen, dass die Eis-Wasser-Grenzschicht eine überraschende Vielfalt von Lebensformen anzieht. Dies legt eine starke Wechselwirkung zwischen der eisassoziierten Artgemeinschaft und dem Nahrungsnetz in der Wassersäule nahe.

Eine zweite SUIT-Studie erbrachte den ersten jahreszeitenübergreifenden Nachweis der räumlichen Verteilung und Abundanz von antarktischem Krill in den oberen zwei Metern der Wassersäule unter Eis und im offenen Wasser (**Kapitel 8**). Die höchste durchschnittliche Abundanz von antarktischem Krill wurde unter winterlichem Packeis gemessen. Der niedrigste Wert wurde im nahezu eisfreien Herbst erreicht. Im Sommer war die Abundanz des Antarktischen Krill in der Eis-Wasser-Grenzschicht deutlich höher als in der eisfreien Oberflächenschicht. Ein Vergleich mit Daten von tiefer fischenden Netzen zeigte, dass die durchschnittliche Abundanz (Krill pro m^2) in den zwei Metern unter dem Eis im Winter und Sommer höher war als im gesamten 0-200 m Tiefenbereich. Diese Ergebnisse legen nahe, dass eisbedeckte Gewässer wesentlich mehr biologische Ressourcen enthalten können, als aus den üblichen Beprobungen der Wassersäule mit Netzen oder Sonaren hervorgeht. Darüber hinaus unterstreicht die große Bedeutung des Meereises für antarktischen Krill und viele andere Arten die Empfindlichkeit des Ökosystems für Veränderungen von Struktur und Ausdehnung der Eisbedeckung in Raum und Zeit.

Diese Studien zeigen, dass das speziell entwickelte SUIT wertvolle neue Einsichten in die Struktur des Ökosystems der antarktischen SMZ ermöglicht, die mit konventioneller Beprobungsmethodik nicht gewonnen werden können. In **Kapitel 9** wurde die Eignung des SUIT zur repräsentativen Beprobung von Zooplankton, Fischen und Tintenfischen kritisch untersucht. Zu diesem Zweck wurden Echtzeit-Strömungsmessungen in der Netzöffnung, die Artzusammensetzung und die Größenzusammensetzung des Fanges herangezogen. Die Strömungsmessungen zeigten einen gleichmäßigen Einstrom von Wasser in das Netz, der standardisierte Abundanzbestimmungen ermöglicht. Die Fangzusammensetzung des SUIT beinhaltete Tiere in der Größenordnung von Kleinkrebsen (unter 1 mm) bis zu ausgewachsenen

Fischen und Tintenfischen. Die Längenverteilung von antarktischem Krill aus dem SUIT war nahezu identisch mit derjenigen aus parallel eingesetzten etablierten Netzen mit ähnlicher Maschenweite. Obwohl einige Fische und Tintenfische vielleicht in der Lage sind, dem Netz zu entkommen, kann angenommen werden, dass SUIT ein verlässliches quantitatives Beprobungsgerät für Tiere bis mindestens zur Größe von ausgewachsenem antarktischem Krill ist.

Die Ergebnisse dieser Forschungsarbeiten liefern neue und direkte Daten, die auf eine entscheidende Bedeutung des Meereises für die Produktivität und die Biodiversität der SMZ hindeuten. Daneben wurden starke Hinweise auf ein deutlich komplexeres Nahrungsnetz in der ozeanischen SMZ gefunden, als es herkömmliche krillzentrierte Modelle nahelegen. Im Rahmen globaler Klimaveränderungen können diese Erkenntnisse zu einer besseren Einschätzung der Reaktion antarktischer mariner Ökosysteme auf Veränderungen des Meereislebensraums beitragen. Ein besseres Verständnis der zukünftigen Entwicklung mariner Ökosysteme ist sowohl bedeutsam für die nachhaltige Nutzung biologischer Ressourcen als auch für den Naturschutz in der Antarktis.

A layer of ice algae grows at the underside of this overturned ice floe.

CHAPTER 1
General introduction

"It was a packed day full of wondrous experiences (..). A day with blue sky, the bluest of my life. With philosophical emperor penguins which (…) seem to ponder how those crippled, oversized, non-swimming penguins will ever cope here. A packed day with light glowing from within stacked ice floes: a Mediterranean grotto blue, only more glowing, more intense, more magical."

Journalist **Claus-Peter Lieckfeld** (Arndt & Lieckfeld 2005; translated from German)

1.1 The human interest in Antarctica

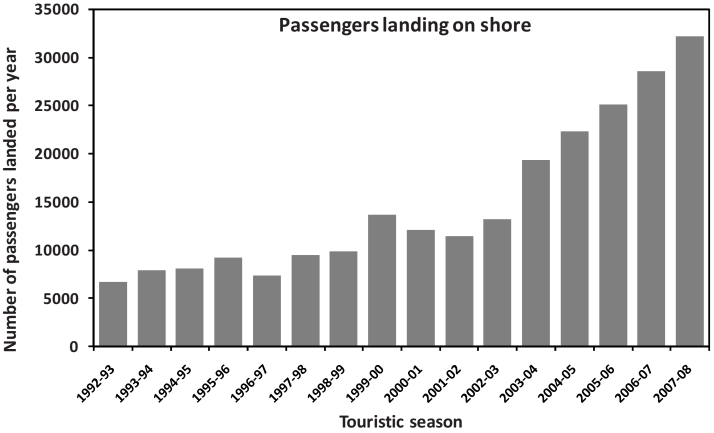
The quote of a modern-days journalist shown on the title page of this chapter exemplifies the many attempts to paraphrase the touching experience of Antarctic nature on those who witness it. Besides the beauty of its harsh physical nature, Antarctica hosts an impressive wildlife that appears to contrast with the seemingly hostile environment. Although few people get the possibility to experience Antarctic nature in reality, Antarctic animals have obtained an almost archetypal status in global consciousness. Antarctic nature features in a flourishing market of literature and TV productions and has become a common inventory of top-selling Hollywood productions (Figure 1).

To date, about 50 charter companies offer trips into the South Polar Region, sending at least 55 ships on about 300 voyages per year (IAATO 2008). Antarctic tourism has increased from about 7,000 ship-based tourists setting foot on the Antarctic continent and islands per year in the 1992 / 1993 season to a present number of approximately 33,000 (Figure 2). This enormous increase of touristic activities reflects the fascination Antarctic nature evokes in humans.

The growing tourism illustrates the economical relevance of the South Polar Region, which was initially based purely on the harvesting of biological resources. The Southern Ocean has witnessed a long history of exploitation (reviewed in Knox 2007). In the nineteenth century, predominantly seals were taken. This phase was followed by a period of whale hunting in the twentieth century that led to the depletion of most Antarctic baleen whale populations to near-extinction levels by the 1960s (Figure 3).

Due to the near-fatal reduction of whale stocks in the Southern Ocean and elsewhere, the International Whaling Commission (IWC) introduced a worldwide moratorium on commercial whaling in 1982.

▲ **Figure 1.** A journalist putting an emperor penguin *Aptenodytes forsteri* into the picture.

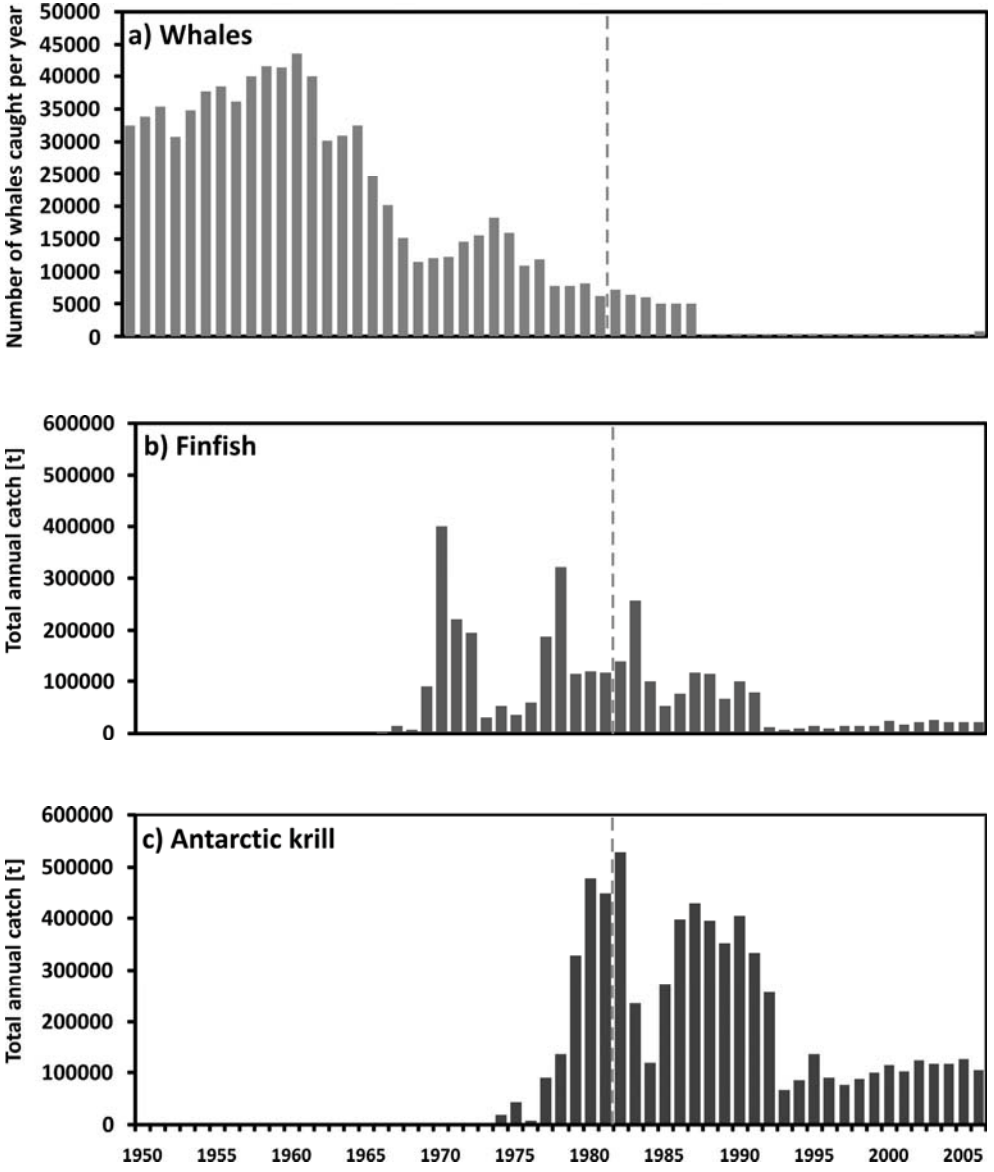


▲ **Figure 2.** Numbers of tourists landed on the Antarctic continent and islands south of 60°S between 1992 and 2008. Source: IAATO (2008).

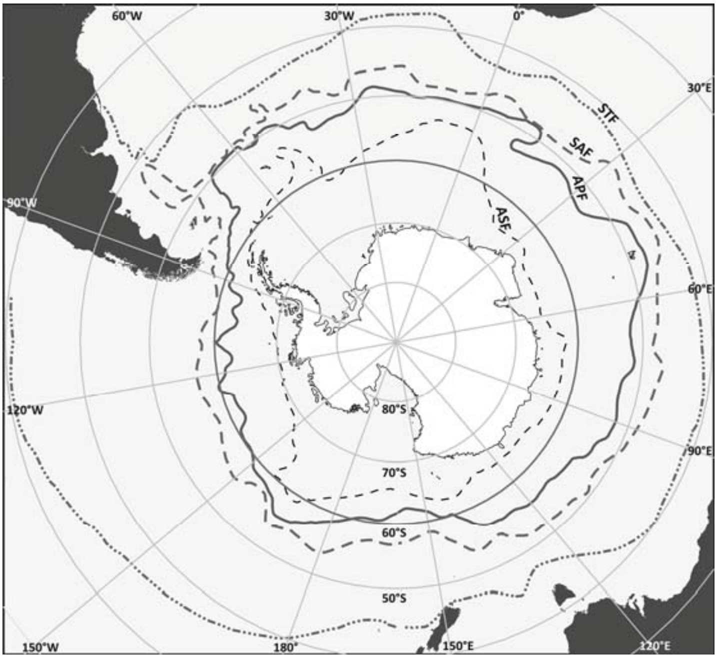
The last quarter of the twentieth century saw the development of fisheries on finfish and Antarctic krill *Euphausia superba* (Figure 3). However, like it had happened to the stocks of fur seals and whales previously, also fish stocks were depleted below economically meaningful levels only shortly after exploitation had begun (Kock 1992). Under this impression and in the light of a growing krill fishery, the "Convention on the Conservation of Antarctic Marine Living Resources" (CCAMLR) was established in 1982. To date, CCAMLR counts 25 members (24 states and the EU), including nations with major fisheries in the Southern Ocean, such as Japan, Korea, Poland and Russia.

The Netherlands have the status of an advisory party to the convention and are currently considering full membership. The primary goal of CCAMLR is "the conservation of Antarctic marine living resources", albeit including their "rational use" (CCAMLR 1982, Article II). To achieve this goal, an unprecedented ecosystem approach was introduced to fisheries management (reviewed in Hewitt & Linen Low 2000). The ecosystem approach not only focuses on managing the harvesting of certain species, but also aims to ensure that other species related to or dependent on the target species are not irreversibly affected.

Today, CCAMLR combines a precautionary approach to management with a multi-species ecosystem monitoring programme that is still unique among the fisheries managements of the world (Hewitt & Linen Low 2000). However, illegal unreported fisheries are a serious problem, probably accounting for catches well in excess of the reported statistics (CCAMLR 2008).



▲ **Figure 3**. Exploitation of biological resources in the Southern Ocean. Catch statistics of (a) whales, (b) finfish and (c) Antarctic krill taken in the Southern Ocean between 1950 and 2006. Source: FAO (2008). The dashed line indicates the implementation of the whaling moratorium by the IWC and the establishment of CCAMLR in 1982.

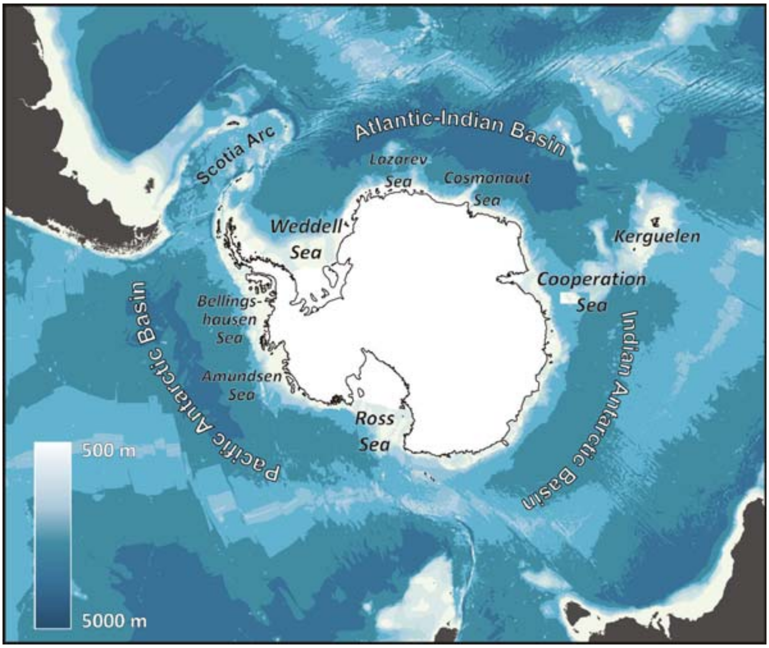


▲ **Figure 4.** Frontal systems in the Southern Ocean after Orsi et al. (1995). **APF** = Antarctic Polar Front; **ASF** = Antarctic Slope Front; **SAF** = Subantarctic Front; **STF** = Subtropical Front. The 60°S northern perimeter of the Southern Ocean applied by the International Hydrographic Organization is shown in bold.

1.2 The Southern Ocean

Much of the biological uniqueness as well as the complex relationships among Antarctic lifeforms are related to the oceanographic peculiarities and the paleo-geographical history of the Southern Ocean. Numerous descriptions of the Southern Ocean exist (e.g. Kock 1992, Orsi et al. 1995). For the purpose of this introduction, only major characteristics are summarized, largely following the reviews by Knox (2007), and Lutjeharms (1990).

The Southern Ocean comprises the sea around the Antarctic continent. Because it is confined by no other land mass in the north, the northern limits have long been subject of debate. In 2000, the International Hydrographic Organization has promulgated 60°S as its northern perimeter. This limit is also applied by the Antarctic Treaty. This simple geographic boundary may be suitable for political and diplomatic purposes, but is inadequate for natural sciences. This thesis rather refers to the natural boundaries represented by a series of distinct circumpolar frontal systems that characterize the transition from Antarctic waters to the northerly adjacent Atlantic, Indian and Pacific Oceans (Figure 4). From these, the Antarctic Polar Front (APF) marks a northern limit for the distribution of many non- migratory Antarctic species. Because of this function as a habitat boundary and a relatively stable geographic position, the Antarctic Polar Front is often considered the northern border of the true Antarctic Ocean (Figure 4). The limits of the CCAMLR conven-

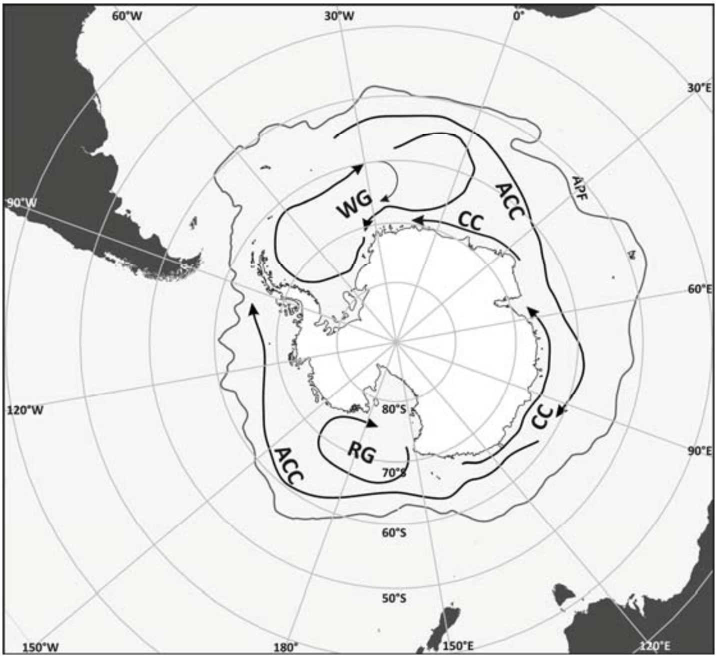


▲ **Figure 5.** Bathymetry of the Southern Ocean with major ocean basins and sea areas.

tion area roughly follow the average position of the Antarctic Polar Front. The waters south of the Antarctic Polar Front cover an area of approximately 35 million km^2. This area compares to about four times the size of Europe, three times the Arctic Ocean or 15 times the Mediterranean Sea.

During the Cretaceous (150 – 100 million years ago), Antarctica was part of the southern supercontinent Gondwana. It was already situated close to the South Pole at that time. The subsequent separation from the other continents and the formation of the circumpolar Southern Ocean was completed by the opening of the Drake Passage 39 – 35 million years ago. An intense cooling of the southern hemisphere and the glaciation of Antarctica occurring during this period set the scene for the prevalent cold climate.

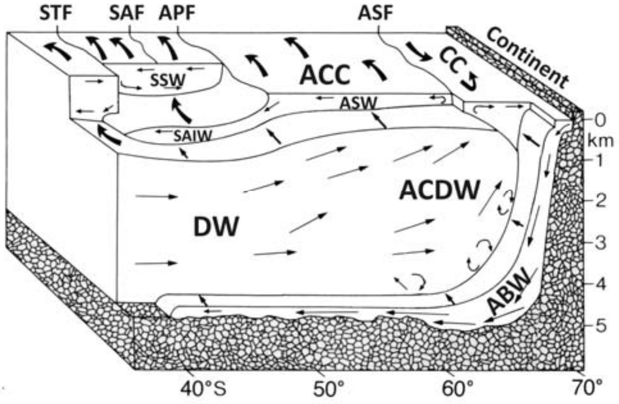
The largest parts of the Southern Ocean cover three deep-sea basins: the Atlantic-Indian basin, the Indian Antarctic Basin and the Pacific Antarctic Basin (Figure 5). These basins are separated by various oceanic ridges and plateaus bearing a number of smaller islands and archipelagos. Among them, the island groups of the Scotia Arc are a key area of fishing and touristic activities. They rise along a system of oceanic ridges connecting the Antarctic Peninsula with the Patagonian Shelf (Figure 5). The Antarctic continental shelf is mostly narrow and almost twice as deep as in other oceans. Where the shelf broadens in the Weddell and Ross Seas, it is covered by ice shelves several hundreds of meters in thickness.As noticed before, the Southern Ocean is characterized by the presence of several strong and persistent circumpolar fronts. They mark drastic changes in salinity and temperature of surface waters accompanied by distinct biological changes and often enhanced primary production. These fronts



▲ **Figure 6.** Major surface currents of the Southern Ocean (after Lutjeharms 1990, van de Putte 2008). **ACC** = Antarctic Circumpolar Current; **APF** = Antarctic Polar Front; **CC** = Coastal Current; **RG** = Ross Gyre; **WG** = Weddell Gyre.

are from north to south: the Subtropical Convergence, the Subantarctic Front, the Antarctic Polar Front and the Antarctic Slope Front (Figure 4; Figure 7). The Antarctic Polar Front and the Antarctic Slope Front are also known as the Antarctic Convergence and the Antarctic Divergence, respectively. At the Antarctic Polar Front a steep drop in sea surface temperature (2.8 – 5.5 °C) marks the transition from the relatively warm subantarctic to the cold Antarctic surface water. Along with the change in surface temperature, abrupt changes in weather conditions and the distribution of phytoplankton, zooplankton and seabirds occur. The Antarctic Polar Front isolates the cold water and climate regime of the Antarctic realm from northerly influences. In this way it forms an effective hydrographical barrier to the latitudinal dispersal of species.

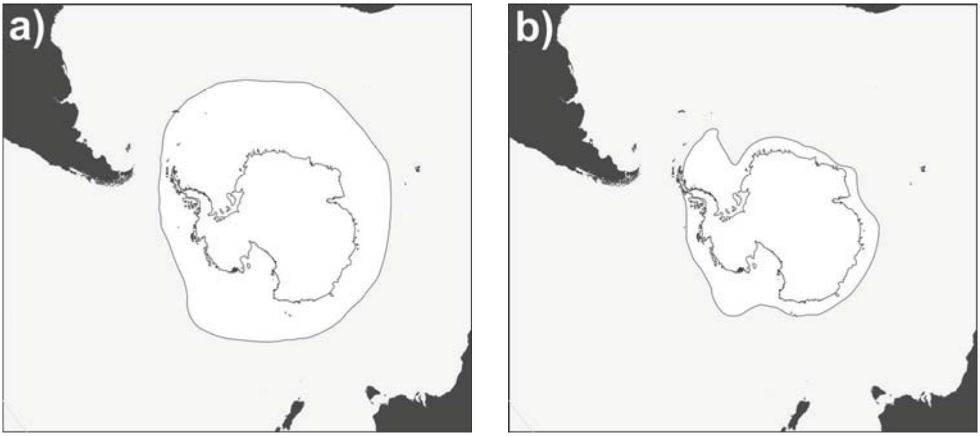
The surface water mass distribution in the Southern Ocean and the associated position of fronts are largely caused by the prevailing winds. Strong westerly winds drive the dominating current system of the Southern Ocean, the Antarctic Circumpolar Current. The Antarctic Circumpolar Current is virtually unobstructed by land barriers, forming the only circumglobal zonal current on earth. The latitudinal extent of this current band ranges from a width of 200 km south of Australia to more than 1000 km in the Atlantic sector, roughly comprising the area between the Subtropical Front and 60°S (Figure 6). In the region of the Antarctic Peninsula and the Scotia Arc the eastward flowing Antarctic Circumpolar Current is deflected northwards. The oppo-



▲ **Figure 7.** Schematic representation of the distribution of water masses, fronts and currents in the Southern Ocean. *Currents*: **ACC** = Antarctic Circumpolar Current; **CC** = Coastal Current. *Fronts*: **APF** = Antarctic Polar Front; **ASF** = Antarctic Slope Front; **SAF** = Subantarctic Front; **STF** = Subtropical Front. *Water masses*: **ABW** = Antarctic Bottom Water; **ACDW** = Antarctic Circumpolar Deep Water; **ASW** = Antarctic Surface Water; **DW** = Deep Water; **SAIW** = Subantarctic Intermediate Water; **SSW** = Subantarctic Surface Water. Modified after Kock (1992).

site flow direction is characteristic of the rather discontinuous east wind-driven Coastal Current along the margins of the Antarctic continent south of 65°S (Figure 6). Eddies of variable size characterize the region between the Antarctic Circumpolar Current and the Coastal Current. The Coastal Current joins the southern limbs of the two conspicuous cyclonic gyres of the Southern Ocean, the Weddell Gyre and the Ross Gyre.

The Southern Ocean plays a key role in the formation and transport of water masses through the world ocean driven by differences in temperature and salinity. The Antarctic Bottom Water takes a central function in this process known as thermohaline convection. This water mass produced mainly under the ice shelves of the Weddell Sea has a high density due to its low temperature and high salinity. The Antarctic Bottom Water flows down the Antarctic shelf and sinks to the ocean bottom, where it spreads northwards and fills all ocean basins. In the global thermohaline convection, the northward flow of the Antarctic Bottom Water is counterbalanced by the southward movement of North Atlantic Deep Water that rises at the Antarctic Slope Front as Antarctic Circumpolar Deep Water. Figure 7 shows a simplified visualization of the distribution of these two principal Antarctic water masses and the surface waters in conjunction with major currents and oceanographic fronts.



▲ **Figure 8.** Average maximum (a) and minimum (b) sea ice cover in the Southern Ocean.

1.3 Sea ice

The Southern Ocean is distinct from most other oceans through its extreme seasonality in light regime, weather conditions and surface water characteristics. The most conspicuous and most influential seasonal factor, however, is the huge annual variability in ice cover (Figure 8). Each winter, sea ice covers about 18 million km^2 of the Southern Ocean. This vast area is known as the Antarctic seasonal sea ice zone. It compares to almost twice the area of Europe or 1.5 times the size of the Arctic Ocean. The ice recedes to a residual of almost 20 % of the winter extent (3 million km^2) in summer (Parkinson 2004). Small areas of multi-year sea ice remain mainly in the Weddell Sea and the Bellingshausen and Amundsen Seas. A narrow belt of fast ice (sea ice attached to the coast or ice shelves) persists along parts of the Antarctic coast line and shelf ice edges (Parkinson 2006).

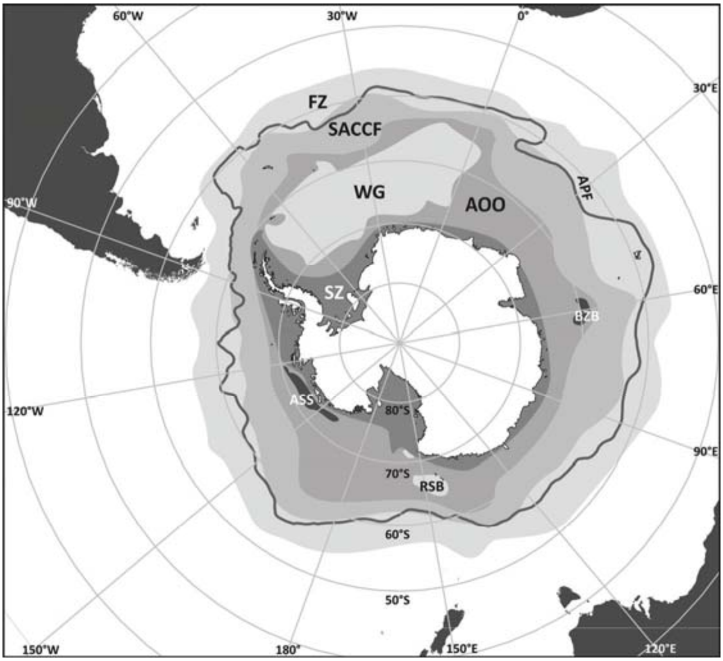
It is evident that distribution, structure and extent of sea ice are highly sensitive to climatic conditions. To date, Global Warming has most severely affected the Arctic Ocean. The average extent of the annual sea ice cover in the Northern Polar Region in summer has declined by 21 % between 1979 and 2000, and ice-free summers are expected from 2040 onwards (Serreze et al. 2007). This dramatic trend is not resembled in the southern hemisphere until now. Rather, a slight increase in total ice cover has been observed in the Southern Ocean over the past decades. This tendency, however, differs drastically on a regional scale. In the Antarctic Peninsula and Scotia Arc region, the annual sea ice cover is declining and the duration of the ice season is shortening dramatically. In this area, the worldwide strongest increase of winter temperatures has occurred. A negative trend in sea ice extent was also observed in the Bellingshausen and Amundsen Seas. This decline was compensated mainly by an increase of average ice cover in the Ross Sea sector (Parkinson 2004).

1.4 Life in the Southern Ocean

The Antarctic marine fauna is clearly distinct from the species communities of the adjacent oceans. It combines a high degree of endemism with surprisingly high species richness (e.g. Arntz et al. 1997; Brandt et al. 2007). The species richness of metazoans has generally been considered to be high at the Equator and decline towards the Poles. There is increasing and strong evidence, however, that this assumption does not hold for the marine fauna of the southern hemisphere. For example, a recent in-depth analysis of the fauna of the South Orkney Islands demonstrated that metazoan species richness on the shelf of this Antarctic archipelago was higher than on the Ecuadorian shelf including the Galapagos Islands (Cruz et al. 2003; Barnes et al. 2008).

Antarctica has been described as an “evolutionary hot spot” (Eastman 2005), because the combined forcing of an extreme environment and hydrographic isolation enhance the evolution of endemic species in many taxa, e.g. cephalopods, crustaceans, fishes and penguins (Kooyman 2002; Brandt 2005; Eastman 2005; Collins & Rodhouse 2006). The beginning of adaptive radiations in a number of taxa coincides roughly with the opening of the Drake Passage (e.g. Eastman & Clarke 1998; Wilson 1998; Jarman et al. 2000). One closely investigated radiation occurred in the Notothenioidei, a group of perch-like (perciform) fishes originating from Antarctic coastal habitats. Today, the fish fauna of the Antarctic shelves is dominated in species numbers, abundance and biomass by this taxon (Kock 1992). The Notothenioidei underwent a remarkable diversification over the past 40 million years (Eastman 2005). This process was probably enhanced by the demise of competing taxa through the harsh climate combined with the isolation from intruders by the Antarctic Polar Front. Notothenioidei are primarily demersal and lack a swim bladder, but adapted various life strategies, including a pelagic mode of life (Klingenberg & Ekau 1996; Kock 2005a; Kock 2005b). Among the unique traits that evolved exclusively in the Notothenioidei is a suite of antifreeze glycopeptides that allow the fish to survive the extremely low water temperatures of the Antarctic shelf (Chen et al. 1997). Another remarkable adaptation to the cold environment is the complete loss of hemoglobin in the blood of the family Channichthyidae (di Prisco et al. 2002).

Species and communities are not equally distributed over the Antarctic marine habitats. Attempts to define biogeographical regions have been made based on hydrography (Orsi et al. 1995; Longhurst 1998), nutrients and ice cover (Tréguer & Jacques 1992) and distribution of fish stocks (Everson 1977). Various authors classified the biogeography of Antarctic benthos (e.g. Dell 1972; Linse et al. 2006; Griffiths et al. 2008). However, to date there is no generally accepted concept of the biogeographical zonation of the Southern Ocean.



▲ **Figure 9.** Bioregionalization of the Southern Ocean. The primary biogeographical regions are the Frontal Zone (**FZ**) and the southerly adjacent Antarctic Zone. The latter is divided into the Shelf Zone (**SZ**) and the Antarctic Open Ocean (**AOO**). The AOO has several subsystems: The Weddell Gyre (**WG**) and Ross Sea Banks (**RSB**), the Antarctic Shelf Slope (**ASS**) and Banzare Bank (**BZB**), and the Southern Antarctic Circumpolar Current Front (**SACCF**). **APF** = Antarctic Polar Front. Modified after Grant et al. (2006).

The most recent approach towards a concise bioregionalization of the Southern Ocean applied a combined analysis of physical (e.g. bathymetry, sea ice concentration) and biologically relevant (e.g. chlorophyll concentration, nutrient concentration) remote sensing data (Grant et al. 2006). The distribution of major biogeographic regions proposed by this approach is shown in Figure 9. The most conspicuous partition separates the Southern Ocean into a frontal and an Antarctic province. The frontal province comprises the Antarctic Polar Front, Subantarctic Front and the Kerguelen Plateau. The species assemblage of the frontal region is strongly influenced by temperate components (e.g. Kock 1992; Pakhomov & Froneman 2000; Collins & Rodhouse 2006). The typical dominance of endemic Antarctic species characterizes the Antarctic province. It is subdivided in an oceanic and a shelf zone, reflecting the significant faunal difference between these habitats. The coastal areas usually host higher species numbers than the oceanic realm. The oceanic zone may be further split in an open ocean, Weddell Gyre and Ross Sea banks, shelf slope and Banzare Bank, and a Southern Antarctic Circumpolar Current Front region. The latter area largely coincides with the permanently ice-free part of the Southern Ocean. A longitudinal division is virtually absent due to the circumantarctic movement of water masses facilitating the zonal transport of animals and their larvae. Benthic species, especially those without pelagic larvae, disperse less easily over large distances. Hence, the biogeography of benthic habitats is more assorted (Griffiths et al. 2008).

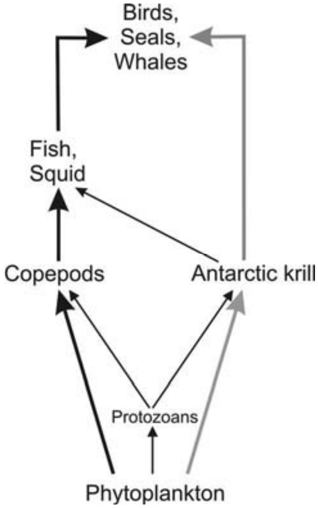
This preliminary regionalization agrees well with the major distribution patterns of pelagic species (e.g. Loeb 1991; Pakhomov et al. 2000; Collins & Rodhouse 2006; Atkinson et al. 2008). Antarctic krill can be considered a character species of the Antarctic oceanic province. It has a northern distribution limit at the Antarctic Polar Front, and 87% of the total stock is found in deep water habitats (Atkinson et al. 2008). Its circumpolar distribution, however, is asymmetric, with an estimated 70% of the total stock concentrated in the Antarctic Peninsula / Scotia Arc and adjacent regions (0° - 90° W). Thorpe et al. (2007) demonstrated that krill distribution is mainly determined by current patterns. Particularly in the Antarctic Peninsula / Scotia Arc region, the convergence of water advected from the west by the Antarctic Circumpolar Current with the easterly water of the Coastal Current / Weddell Gyre system enhances the concentration of krill. It should be noted, however that besides advection also sea ice distribution, food availability, life history, behaviour and predation pressure determine the distribution of *E. superba* (Nicol 2006; Atkinson et al. 2008).

Due to its high abundance and economical importance, Antarctic krill has received much attention with respect to its distribution, population dynamics, productivity, ecological impact and the factors that control these properties. The bioregionalization of the Southern Ocean may be further improved when other indicative species are considered with comparable effort. For example, the distribution of lanternfishes closely resembles the spatial patterns implied by the bioregionalization approach of Grant et al. (2006) (Hulley 1990).

1.5 The Antarctic pelagic food web

The trophic transfer of energy through an ecosystem is usually visualized by the food chain concept. In food chains, energy in the form of organic carbon is mostly assimilated by photosynthesis and then transmitted through a series of consumers feeding on each other. The different steps in the trophic hierarchy of food chains are referred to as trophic levels. At each increase in trophic level, typically, 80 – 90 % of the energy and biomass are lost (Knox 2007). The food web comprises the complex suite of food chains interacting with each other in an ecosystem. The top predators are at the highest trophic level of the food web.

Marine food webs are usually highly complex systems characterized by multiple trophic interactions at various levels. One should therefore keep in mind that any conceptual description of the fundamental trophic patterns cannot avoid substantial simplification. In marine food webs, planktonic algae usually provide the bulk of the primary production. The food chains typically follow the phytoplankton – zooplankton – nekton – top predator trajectory. At the lower trophic levels a “detritus food chain” along a particulate organic matter – bacteria – zooplankton trajectory is probably



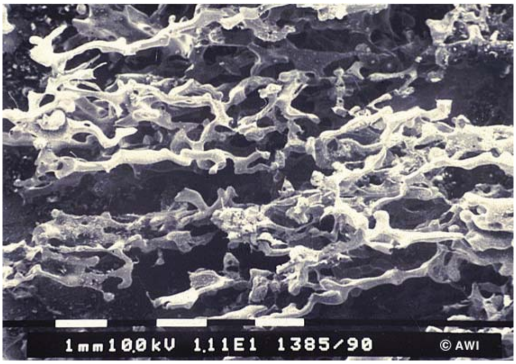
▲ **Figure 10:** Major pathways of the pelagic food web in the oceanic seasonal sea ice zone of the Southern Ocean. The copepod – fish / squid trajectory is indicated by black, the krill trajectory by grey arrows.

equally important (Knox 2007). Knox (2007) provided an extensive review of the food webs of the Southern Ocean. In this thesis the focus will be on the pelagic food web in the oceanic seasonal sea ice zone, where most of the included investigations were conducted.

The pelagic ecosystem of the Southern Ocean does not generally differ from the basic pattern of marine food webs. However, a characteristic peculiarity is the unusual abundance of a micronektonic phytoplankton consumer, the Antarctic krill. Thus, energy flow through the intermediate trophic levels (the zooplankton – nekton step of the oceanic food chain) can follow two pathways in the Southern Ocean (Figure 10):

- Antarctic krill is the major trophic link between the primary producers and the upper trophic levels.
- Energy is transmitted via a mesozooplankton (mainly copepods) and fish / squid trajectory. This resembles the typical pattern of trophic transfer of most marine ecosystems.

Antarctic krill is an extremely effective grazer capable of depleting phytoplankton blooms in short time (e.g. Ross et al. 1998). It constitutes an important diet component of various fishes and squid species and is frequently taken by a range of birds and mammals (reviewed in Ainley & DeMaster 1990). Due to the apparent dominance of *E. superba* in the pelagic ecosystem it was concluded that the food web has a simple structure, in which the assimilation products of planktonic algae are predominantly channeled to higher trophic levels through Antarctic krill alone. This concept cumulated in the often-quoted example of the algae – krill – whale food chain. It has thus been assumed that the short food chains of the Antarctic krill-centered food web are highly efficient in energy transmission to the top predators (e.g. Hempel 1985).



▲ **Figure 11**. Scanning Electron Microscope image of brine channels in the ice. The cavities in the ice had been filled with a polymer before thawing for microscopy (Source: AWI; www.awi.de).

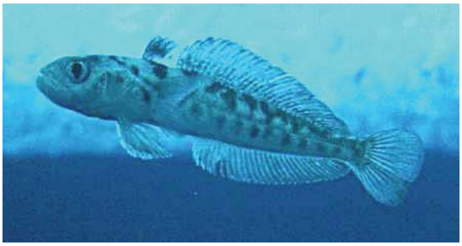
▲ **Figure 12**. *Tergipes antarcticus*, the first mollusc species known to live in Antarctic sea ice (Kiko et al. 2008a). Photo: M. Nicolaus.

Such view of the Antarctic marine ecosystem took shape in the early phase of intensive Antarctic research during the 1970s and 1980s. In that time, major ecosystem studies concentrated in the economically important Antarctic Peninsula / Scotia Arc region (e.g. El-Sayed 1994). As explained above, bathymetry and current patterns enhance the concentration of Antarctic krill in this area, which may have caused some bias in the perception of the overall ecological relevance of krill. It is generally agreed that Antarctic krill constitutes about 50 % of the standing stock of zooplankton in the Southern Ocean (Voronina 1998). This population is capable to graze not more than 5 % of the primary production (Knox 2007). This leaves ample resources for the copepod – nekton pathway of energy transmission. A concise estimate of the relative importance of the krill-dominated versus the copepod – fish / squid food chain is complicated by the manifold interactions of these two trophic pathways with each other (e.g. Hopkins et al. 1993).

1.6 The ecological importance of sea ice

Sea ice constitutes a habitat for a diversity of life specifically adapted to this environment, ranging in size from microscopic bacteria and algae to the large penguins, seals and whales of the seasonal sea ice zone. A comprehensive review of the ecology of the sea ice system was provided by Brierley & Thomas (2002).

Much of the versatility of the sea ice habitat roots in its peculiar microstructure. The ice crystal structure allows only a small amount of salt ions to be incorporated (Eicken 2007). Salts are thus expelled during crystallization and concentrate in the surrounding water. This extremely saline brine constitutes a complex matrix of brine pockets and channels (Figure 11). Bacteria, microalgae and protozoa scavenged from the water during freezing are the first inhabitants of the brine labyrinth. They make up the trophic fundament of the sympagic (i.e. ice-associated) meiofauna community.



▲ **Figure 13.** *Pagothenia borchgrevinki*. This fish lives in the ice-water interface layer near the Antarctic coast. Photo: R.W. Davis. Source: www.bio.research.ucsc.edu.

▲ **Figure 14**. The Ross seal *Ommatophoca rossii* is the rarest known pack-ice seal.

This community consists of foraminiferans, ciliates, flatworms, copepods and gastropods (Figure12; Brierley & Thomas 2002; Kiko et al. 2008a).

A variety of macroscopic animals dwell in the ice-water interface layer. They at least temporarily depend on sea ice biota as a food source. Macrofauna of the ice-water interface layer includes copepods, amphipods, Antarctic krill and fish (Figure 13; Gulliksen & Lonne 1991; Schnack-Schiel 2003; Arndt & Swadling 2006). The life cycle of *E. superba* is closely linked with sea ice (Siegel & Loeb 1995). Antarctic krill were repeatedly reported feeding at the underside of ice (e.g. Marschall 1988; Siegel et al. 1990). Feeding on ice algae during winter is especially important for the larvae (Daly 2004). It was demonstrated that krill recruitment is positively correlated with the extent of the sea ice cover in the preceding winter (Atkinson et al. 2004).

Finally, the ice floes serve as a resting or breeding platform for several penguin and seal species that also use the sea ice habitat as a foraging ground (Figure 14). The pack-ice is further temporarily frequented by a variety of penguins, seabirds, seals and whales that forage between and under the ice floes (Ainley et al. 2003b; Knox 2007).

The seasonal growth and decay of the pack-ice cover constitutes a strong annual pulse that acts as a major driver of the Antarctic marine ecosystem. The ecological significance of this pulse is especially pronounced in the marginal ice zone in summer. Here, the melting of sea ice promotes a range of dynamic processes. Because salt was expelled during freezing, melting sea ice is comparatively fresh and thus less dense. The lighter melt water overlays the water column. The resulting stable stratification confines phytoplankton to the well-lit surface layer, enhancing photosynthetic productivity. Algal production is further augmented by the release of ice algae and nutrients from the melting ice. The primary production of the marginal ice zone has been estimated to be about 3 – 4 times higher than in adjacent open waters (Smith & Nelson 1986). The marginal ice zone was reported to be associated with increased abundances of zooplankton, nekton and a range of top predators (e.g. Ainley & Jacobs 1981; Ribic et al. 1991; Siegel et al. 1992; Donnelly 2006). The spatially limited but highly productive marginal ice zone propagates southward during the melting season, ultimately crossing the entire seasonal sea ice zone each year. The fecundity of the marginal ice zone has been attributed a key role in the overall carbon budget of the Southern Ocean, possibly contributing about 60 % of the gross annual production (Smith & Nelson 1986).

These figures, however, do not reflect variations in the spatial extent of ice edge blooms and seasonal changes in their assimilation rate. It is also important to take into account the increasing evidence that the entire pack-ice area rather than its margin is an important site of biological production. Ice algal assimilation has been estimated to reach 1 g C m^{-2} d^{-1}, a value that is similar to an intense marginal ice zone bloom (Wilson et al. 1986; Arrigo et al. 1993; Arrigo et al. 1995). Due to their constant exposure to near-surface light intensities, ice algae can provide primary production year-round (Arrigo et al. 1997). Thus, the benefit of the sea ice habitat for algae is particularly evident in winter and spring, when low light availability and deep mixing suppress phytoplankton assimilation.

1.7 Objectives of this thesis

Until today, the richness of the Antarctic seasonal sea ice zone in penguins, flying birds, seals and whales has largely been attributed to the fecundity of the marginal ice zone in combination with an energy-efficient, krill-dominated food web (e.g. Smetacek & Nicol 2005; Gross 2007). This simplistic view of the Southern Ocean ecosystem, however, was challenged by investigations on top predators that can be summarized in two paradoxes:

- The krill paradox: A growing number of diet studies indicates that fish and squid rather than Antarctic krill constitute the baseline diet of most Antarctic birds and mammals (e.g. Hopkins et al. 1993; Van Franeker et al. 2001; Ainley et al. 2003a). These observations are in strong contrast with the short food chain concept, in which krill is considered the key energy source of the top predators.
- The sea ice paradox: In spite of incidental reports of top predator aggregations in the marginal ice zone, comprehensive censuses demonstrated repeatedly that top predator abundances remained on a high level or even increased hundreds of kilometers into the pack-ice (e.g. Joiris 1991; Van Franeker 1992; Ainley et al. 1994; Van Franeker et al. 1997). These observations indicate that resource availability is high throughout the entire pack-ice zone rather than only in areas of high phytoplankton productivity, such as the marginal ice zone.

The objective of this thesis is to challenge the classic krill- and phytoplankton dominated Antarctic food web concept by critically investigating the importance of Antarctic krill in relation to other prey species in the pelagic habitat and exploring the availability of prey for higher level predators in the surface layer throughout the entire pack-ice zone at different seasons.

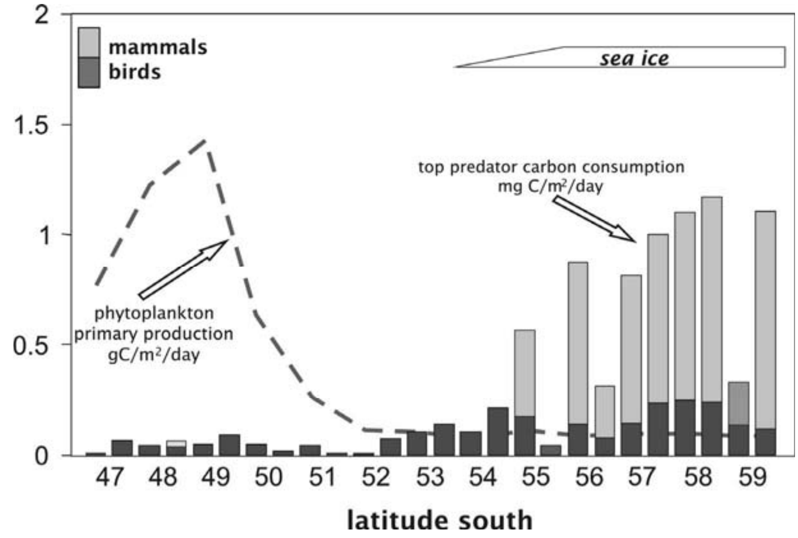
Due to the considerations expressed by the krill paradox (1), the perception that *E. superba* is the key energy transmitter in the Antarctic food web has gradually been changing over the past decade. Nowadays, consensus is growing that the pelagic food web of the Southern Ocean is not radically different from that of other pelagic ecosystems. In spite of such awareness, even recent textbooks, such as Knox (2007) still state that "krill (...) provides the food base for large populations of baleen whales, crabeater and fur seals and penguins".

The paradigm of the dominant role of krill in the Southern Ocean food web is thus still persistent, probably enhanced by the ongoing concentration of research activities in the Antarctic Peninsula / Scotia Arc region during the season when krill is superabundant in this area. Therefore, it appears necessary to intensify research that puts the ecological role of krill in proportion to other potentially relevant energy transmitters, such as zooplankton, fish and squid. The present thesis addresses this issue by:

- A diet investigation of abundant fishes in a krill-dominated shelf habitat (Chapter 2);
- An analysis of the energetic value of pelagic fish important in the diet of top predators in the seasonal sea ice zone (Chapter 3);
- A study on the distribution of pelagic fish and larvae in the oceanic seasonal sea ice zone in relation to the physical and biological environment with an assessment of their relevance in the pelagic food web compared to Antarctic krill (Chapter 4);

The enhanced abundance of top predators in ice-covered waters with seemingly negligible primary production is referred to in the sea ice paradox (2). Figure 15 shows results from top predator studies conducted by van Franeker et al. (1997) in the Weddell-Scotia confluence zone. These data illustrate how the food demand of the top predator community increases in the pack ice area with increasing distance from the ice edge. This tendency was not mirrored in the phytoplankton distribution which was highest in the open ocean and low in waters covered by ice. This indicates that the food web of the inner pack-ice relies on high productivity of ice algae instead. The productive sea ice would attract zooplankton, fish and squid in the ice-water interface layer, providing sufficient resources for the observed high abundances of birds and mammals. This hypothesis was supported by reports of an upward shift in the vertical distribution of macrozooplankton and nekton in the presence of a sea ice canopy (Ainley et al. 1986; Kaufmann et al. 1995).

Today, sea ice production is increasingly accepted as the 'motor' of the Antarctic pack-ice ecosystem (Brierley & Thomas 2002). It has been demonstrated that pelagic copepods and krill larvae are abundant in the ice-water interface layer (Daly 2004; Schnack-Schiel et al. 2008b; Tanimura et al. 2008). Macrozooplankton and nekton that feed (and are fed on) in the ice-water interface layer would constitute the most direct energy transmitters from the sea ice to the top predators, but they are difficult to quantify under ice. A variety of studies attempted to link the distribution of adult Antarctic krill and other pelagic macrofauna to sea ice. These studies used various



▲ **Figure 15.** Distribution of the food demand of top predators in the Weddell Sea expressed as daily carbon consumption in relation to latitude and sea ice distribution. The hatched line indicates the primary production in the water column. Redrawn after van Franeker et al. (1997).

techniques to sample the sea ice habitat, such as diving (e.g. Hopkins & Torres 1988);under water cameras mounted on remotely operated vehicles (ROV) (Marschall 1988), baited traps (Kaufmann et al. 1993) and sonar technology (Kaufmann et al. 1995; Brierley et al. 2002). However, these studies were either hampered by limited spatial coverage (diving, traps, ROV), or could not resolve the immediate ice-water interface layer (sonar).

How the sea ice system interacts with the pelagic macrozooplankton and nekton that ultimately support the birds and mammals of the seasonal sea ice zone is understood at best in qualitative terms to date. To overcome this shortcoming, the Surface and Under Ice Trawl (SUIT) was developed at Wageningen IMARES to quantify the abundance of macrofauna in the upper two meters of the water column both under ice and in open water. This new device was constructed as a floating rectangular fishing net protected against ice impact by a heavy steel frame.

This thesis aims to unravel the sea ice paradox with five studies focusing on:

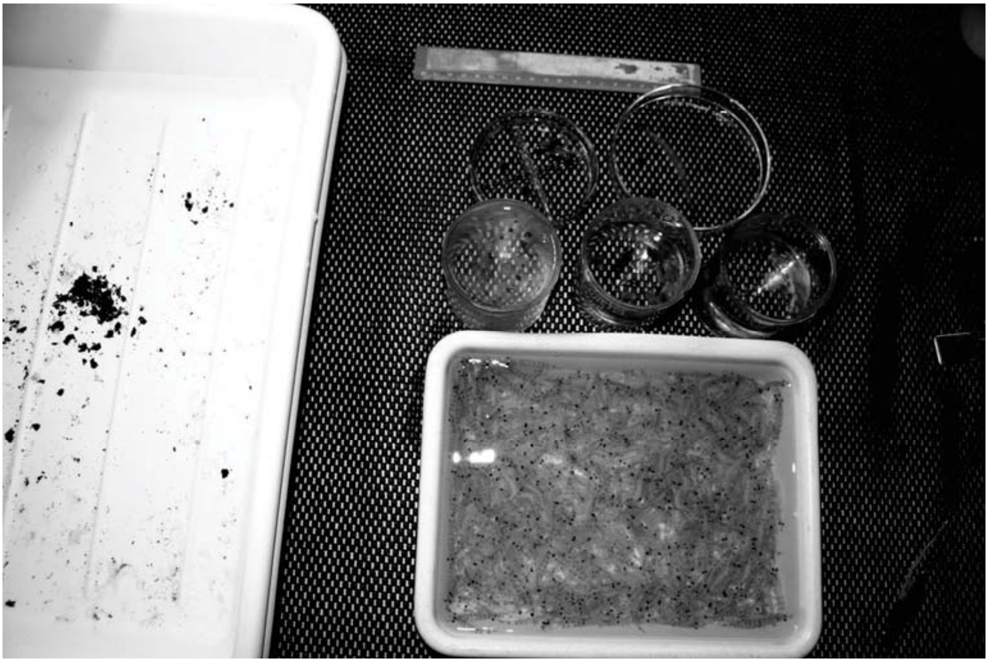
- the distribution of top predators in relation to sea ice properties in the pack-ice (Chapter 5);
- the importance of the ice-water interface as a critical habitat for potentially sympagic amphipods (Chapter 6);
- the diversity and faunal composition of the surface layer under ice and in open water and the environmental factors that influence the community structure (Chapter 7);

- the distribution of krill species (Euphausiidae) in the surface layer under ice and in open water, the environmental factors that drive their distribution in this habitat, and a comparison of these results to the presence of euphausiids in the underlying water column (Chapter 8);
- the performance of the SUIT as a quantitative sampling device of surface layer macrofauna under ice and in open water (Chapter 9).

The present thesis combines the results obtained with SUIT with a range of conventional approaches from various disciplines. With new insights in the functionality of the seasonal pack-ice ecosystem, it hopefully contributes to a better view of the ecological importance of an Antarctic habitat that is likely to face drastic changes in the future.

Key references

- Brierley AS, Thomas DN (2002) Ecology of Southern Ocean pack ice. Advances in Marine Biology 43:171-276.
- Knox GA (2007) Biology of the Southern Ocean. Taylor & Francis Group, LLC. 621p
- Parkinson CL (2006) Earth's cryosphere: Current state and recent changes. Annual Review of Environment and Resources 31:33-60.
- Orsi, A.H., T. Whitworth III and W.D. Nowlin (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. Deep-Sea Research, 42, 641-673.
- van Franeker JA, Bathmann UV, Mathot S (1997) Carbon fluxes to Antarctic top predators. Deep Sea Research II 44:435-455.



Sorting samples. In the foreground: Antarctic krill *Euphausia superba.*

CHAPTER 2

Diet of two icefish species from the South Shetland Islands and Elephant Island, *Champsocephalus gunnari* and *Chaenocephalus aceratus* in 2001 - 2003

Hauke Flores, Karl-Herman Kock, Sunhild Wilhelms
& Christopher D. Jones

Abstract The summer diet of two species of icefishes (Channichthyidae) from the South Shetland Islands and Elephant Island, *Champsocephalus gunnari* and *Chaenocephalus aceratus*, was investigated from 2001 to 2003. *Champsocephalus gunnari* fed almost exclusively on krill (*Euphausia superba*) in all years. The importance of other taxa (*Themisto gaudichaudii*, mysids, myctophids) in the diet was negligible. The average feeding rate of *Champsocephalus gunnari* inferred from an exponential gastric evacuation model was between 1.0 and 1.5% body weight per day. Most of the stomachs of *Chaenocephalus aceratus* were empty. Stomachs with food contained mainly krill, mysids and fish. Among the fish taken, locally abundant species formed the bulk of the diet. They were *Gobionotothen gibberifrons* in 2001, *Lepidonotothen larseni* and *Champsocephalus gunnari* in 2002 and *L. larseni* in 2003. An ontogenetic shift in feeding preference of *Chaenocephalus aceratus* was observed: Fish smaller than 30 cm fed on krill and mysids, while larger animals relied primarily on fish.

Polar Biology 27 (2004): 119-129

2.1 Introduction

The Antarctic fish fauna is dominated by the perciform suborder Notothenioidei which comprises the majority of species in shelf waters down to 500 m depth and account for more than 90% of the fish biomass in most regions of the Southern Ocean (Eastman and Clarke 1998). Among the eight notothenioid families, icefishes (Channichthyidae) are peculiar in that their blood does not contain haemoglobin (Ruud 1954).

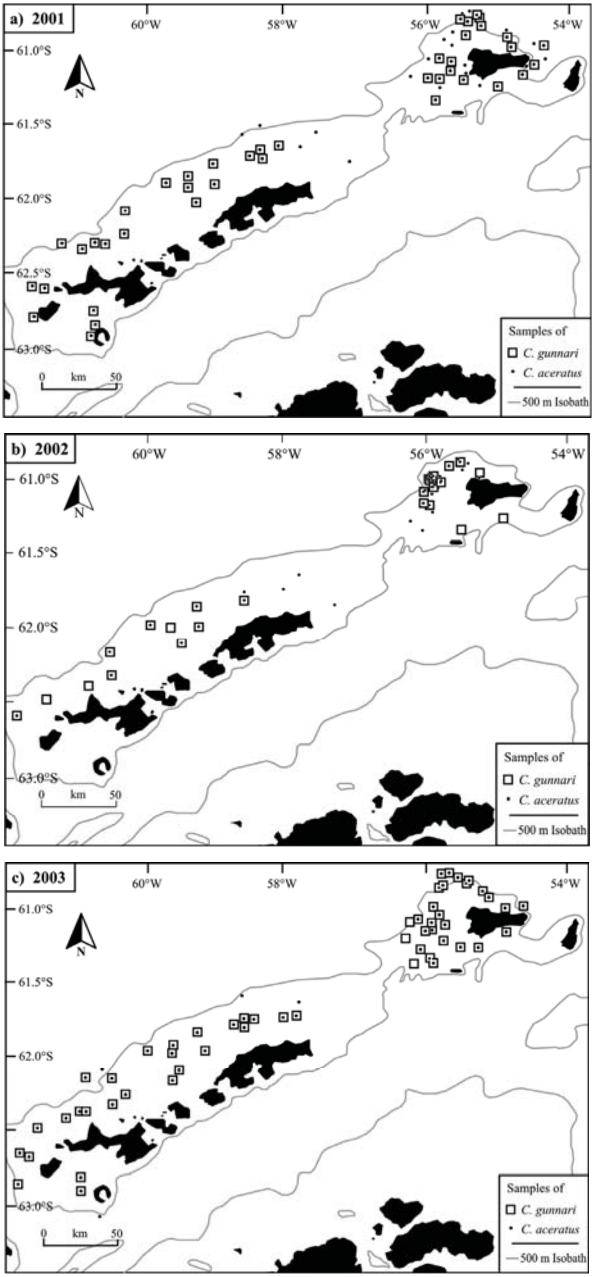
The South Shetland Islands are located north of the Antarctic Peninsula. They are part of the low-Antarctic zoogeographical province, or seasonal pack-ice zone (Kock 1992). Krill (*Euphausia superba*) is considered the key species of the marine food web in this province (Hempel 1985, Verity and Smetacek 1996). Many demersal fish species depend directly or indirectly on krill (Gröhsler 1992).

Only four of the 15 Antarctic icefish species (Eastman and Eakin 2000) are found in some abundance in the low-Antarctic Province. Two of these, mackerel icefish (*Champsocephalus gunnari*) and Scotia Sea icefish (*Chaenocephalus aceratus*), are among the most abundant fish species on the continental shelf of Elephant Island and the South Shetland Islands (Kock 1998, Kock and Stransky 2000). Some biological features of the two species have been well documented, including reproduction (Kock 1981, Kock and Kellermann 1991, Kock et al. 2001, Kock and Jones 2005) and the composition of their diet (Taverdieva and Pinskaya 1980, Kock 1981, 1982; Sosinski 1985, Kozlov et al. 1988, McKenna 1991, Takahashi and Iwami 1997, Kock and Jones 2005). However, these studies either concentrated on a limited number of samples from a limited number of stations and / or a comparatively small area of investigation. The only extensive analysis available is an early winter study conducted around Elephant Island in May / June 1986 by Gröhsler (1992).

In the investigation reported here, we present data on stomach contents of *C. gunnari* and *C. aceratus* collected over the whole shelf in three consecutive years in order to provide a more comprehensive picture of the summer diets and feeding habits of these species.

▾ **Table 1.** Number of stomachs sampled from *Champsocephalus gunnari* and *Chaenocephalus aceratus* in each depth stratum at the South Shetland Islands

Depth	**2001**		**2002**		**2003**	
Stratum [m]	***C. gunnari***	***C. aceratus***	***C. gunnari***	***C. aceratus***	***C. gunnari***	***C. aceratus***
> 50 – 100	133	46	31	10	143	68
> 100 – 200	622	347	356	254	499	414
> 200 – 300	124	133	34	251	101	232
> 300 – 400	39	58	-	64	65	52
> 400 – 500	-	11	-	18	14	38
Total	918	595	421	597	822	804



▲ **Figure 1.** Positions of sampling stations for *Champsocephalus gunnari* and *Chaenocephalus aceratus* in 2001 (a), 2002 (b) and 2003 (c). Stations at which stomachs of *C. gunnari* were analysed are indicated by open squares; stations at which *C. aceratus* was sampled are shown as black dots.

2.2 Material and Methods

Material was collected during three demersal finfish surveys conducted by the US AMLR (Antarctic Marine Living Resources) programme in 2001 and 2003 and the German Antarctic Marine Living Resources Programme in 2002 under the auspices of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) at Elephant Island and the South Shetland Islands. Samples were taken aboard R.V. “Yuzhmorgeologiya” from 12 to 31 March 2001, aboard R.V. “Polarstern” from 29 January to 19 February 2002 and aboard “Yuzhmorgeologiya” from 7 March to 4 April 2003 from the waters around Elephant Island and the South Shetland Islands. The distribution of stations where material was collected is provided in Figure 1a - 1c. Fish were caught during daylight hours, using a commercial size bottom trawl. Fishing depths ranged from 50 to 500 m. A detailed description of the trawling operations was provided in Jones et al. (2001, 2003), and Kock et al. (2002). The number of samples per depth stratum collected during the cruises is shown in Table 1. Whenever the number of fish caught was sufficient, at least 40 (2001) or 30 (2002, 2003) individuals of *Champsocephalus gunnari* and *Chaenocephalus aceratus* were collected on each station. The samples covered the complete spectrum of length ranges obtained from both species.

The following information was recorded directly after capture:

- length (total length to the nearest cm below),
- sex, maturity (according to a 5 point scale: Kock and Kellermann 1991),
- total weight (to the next gram below, by means of an electronic scale),
- gonad weight in adult fish,
- wet weight of the stomach.
- Stomachs collected in 2001 were frozen immediately after capture for further analysis in the home laboratory. Stomachs collected in 2002 and 2003 were analysed on board. Stomach fullness was classified according to a six-point scale: 0 (empty), 1 (> 0 – 24 % full), 2 (> 25 – 49 % full), 3 (> 50 – 100 % full), 4 (> 100 % full), 5 (regurgitated). The degree of digestion (DOD) was estimated following a four-point scale: 1 (fresh - no signs of digestion), 2 (slightly digested), 3 (advanced stage of digestion) and 4 (heavily digested).

The composition of the stomach contents from both species was identified to the lowest taxon possible by means of a stereo microscope. Food composition in all years was expressed as frequency of occurrence. In 2001, items in each prey category were counted, whenever possible. In cases of advanced decay, the minimum number of crustaceans in each sample was estimated as half the number of eyes detected. Total weight of the stomach content and wet weight of each fraction of the stomach content were determined to an accuracy of 0.1 g. In 2002 and 2003, accuracy was only to the nearest gram below, food fractions were not weighed, and items were not counted.

Data collected in 2001 allowed the calculation of the proportion of total food weight for each prey taxon as well as their dietary coefficient, *Q* (Hureau 1969):

(1) $$Q = h_i * g_i;$$

where *Q* is the dietary coefficient, h_i is the relative abundance and g_i is the relative weight of the prey category *i*. Based on this index, prey items can be separated into three classes: $Q > 200$ (main prey), $200 > Q > 20$ (secondary prey) and $Q < 20$ (occasional prey). The calculation of *Q* values for *C. gunnari* turned out to be dispensable since the diet of this species was dominated by one prey species only. Relative feeding rates of *C. gunnari* were calculated based on a gastric evacuation model. Since there is little knowledge about the process of digestion in channichthyids and experimental data on feeding rates of notothenioids are scarce and somewhat inconsistent (Kock 1992), a model of gastric evacuation was chosen which was as simple as possible. Elliott and Persson (1978) proposed an exponential model in a generalized form. It was found to describe the evacuation process in most fish species, though it has been refined by a number of authors (e.g. Persson 1986, Andersen 1999, 2001). Hop and Tonn (1998) showed that this model was applicable to cold adapted polar cod (*Boreogadus saida*). Results from experimental studies on other notothenioids, e.g. *Pagothenia borchgrevinki* (Montgomery et al. 1989) or *Harpagifer antarcticus* (Boyce et al. 2000), agree with an exponential mode of stomach evacuation.

Feeding rate was assumed to equal stomach evacuation rate *R* which was calculated as follows:

(2) $$R = a * e^{bT}$$ (Elliott and Persson 1978);

where *R* is the gastric evacuation rate and *a* and *b* are absolute terms.

For the purpose of this paper *a* and *b* were considered to be close to values determined for polar cod. *R* was calculated as $a = 0.018$ and $b = 0.14$ (Hop and Tonn 1998):

(3) $$R = 0.018 * e^{0.14} = 0.0207$$

Mean daily consumption (*R'*) and relative daily feeding rate (*r'*) were calculated for each 5 cm length class of the *C. gunnari* investigated:

(4) $$R'(L) = 24 * \overline{W_{SC}}(L) * 0.0207;$$

where *R'(L)* is the consumption in g per day, and $\overline{W_{sc}}$ *(L)* is the mean stomach content wet weight in g in each length class *L*:

(5) $$r'(L) = 100 * 24 * \frac{\overline{W_{SC}(L)}}{\overline{TW}(L)} * R \;;$$

where *r'(L)* is the relative feeding rate in % body weight per day, and $\overline{TW}(L)$ is the mean total weight of the fish in g in each length class *L*.

The resulting daily rations were taken to estimate the total stock's consumption of krill in the area of investigation. In order to perform these calculations, we used the data available on stock sizes from 2001 (Jones et al. 2001) and 2002 (Kock et al. 2002). Since the daily differed between length classes, the consumption was first calculated for each length class separately before adding up the amounts of krill consumed in each length class. The total number of individuals per length group in the population was calculated as follows:

$$N_T(L) = \frac{B_T * N_C(L)}{B_C}; \tag{6}$$

where $N_T(L)$ is the total stock number of individuals in length group *L*, B_T is the standing stock biomass in the area of investigation, $N_C(L)$ is the number of individuals caught in length group *L* and B_C is the biomass of the total catch of *C. gunnari*.

The daily krill consumption of the standing stock was then estimated:

$$B_K = \sum \frac{R'(L) * P_K(L) * N_T(L)}{10^3}; \tag{7}$$

where B_K is the biomass of krill consumed by the standing stock of *C. gunnari* per day in metric tonnes (t) and $P_K(L)$ is the proportion of krill in the diet of length group *L*.

Most of the stomachs of *C. aceratus* were empty. Consequently, no feeding rates were calculated for these fish because gastric evacuation models usually assume a continuous food intake.

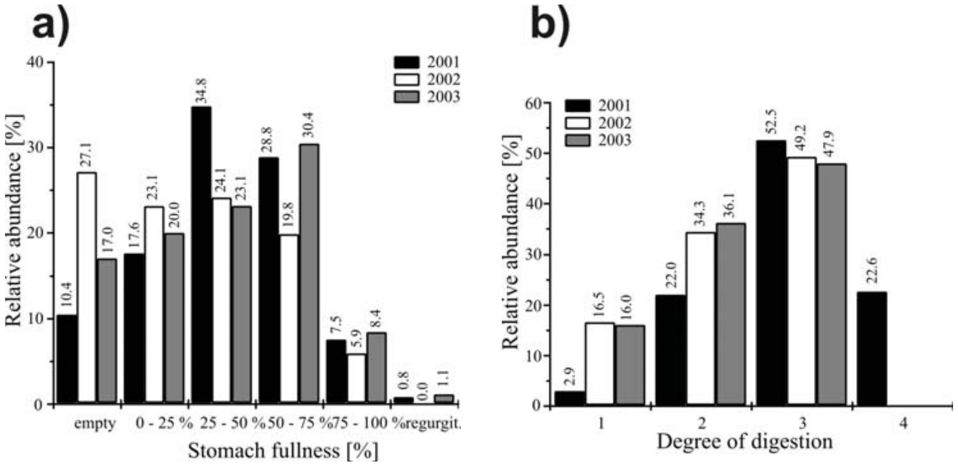
2.3 Results

2.3.1 *Champsocephalus gunnari*

Stomach fullness and degree of digestion

In samples collected in 2001, the proportion of empty stomachs was low (10%), and few appeared to be regurgitated (1%). Most of the stomachs (71%) were in filling degree 2 or higher. In 2002, the proportion of empty stomachs was considerably higher (27%). The majority of stomachs (50%) were in filling degree 2 or higher, and no stomachs were found to be regurgitated. In 2003, the distribution was somewhat intermediate: The proportion of empty stomachs was higher than in 2001 but lower than the preceding year (17%). The proportion of stomachs which were at least in filling degree 2 was also in-between the two other years (62%) (Figure 2 a).

In 2001, most of the stomach contents (75%) were considerably digested (DOD 3 or 4). The proportion of stomach contents that was fresh or only slightly digested (DOD 1



▲ **Figure 2.** *Champsocephalus gunnari* – distribution of stomach fullness (a) and degrees of digestion (b) in 2001 (*dark columns*), 2002 (*white columns*) and 2003 (*grey columns*). The percentages of abundance of stomachs in each category are indicated *above* the columns.

or 2) was higher in 2002 and 2003 (50% and 52%, respectively), when no stomach contents were judged to be heavily digested (Figure 2 b).

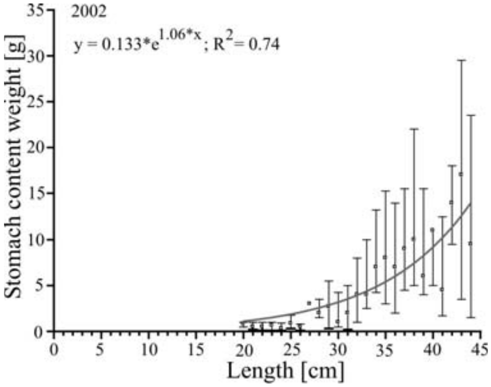
Stomach content weight

Overall mean stomach content weight in 2001 was 6.8g (SD = 9.31). It was lower in 2002 (5.3g (SD = 8.75). In 2003, mean stomach content weight was as high as 8.3 g. (SD = 10.65). Maximum stomach content weight was 75g in 2001, 65g in 2002 and 74g in 2003.

Stomach content weight was positively correlated with fish length. The relationship of stomach content weight to total length of fish approximately followed an exponential function of the form:

$$(8) \qquad W_{st} = a * e^{bTL};$$

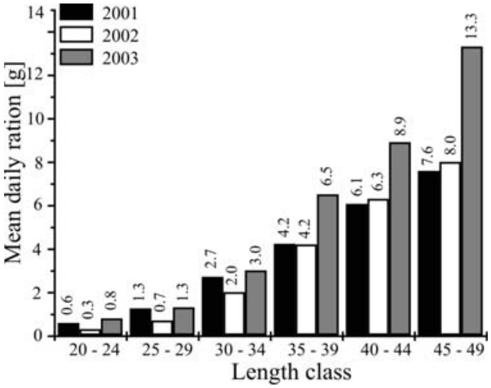
where W_{st} ist the median value of the stomach content weight at any given length, TL is the total length of fish and a and b are constants. Non-linear regression analysis was performed separately on each year's data. The results are shown in table 2. As an example, figure 3 illustrates the observed relationship and the distribution of data in 2002.



▲ **Figure 3.** *Champsocephalus gunnari* – Median values of stomach content wet weight against length of fish with regression line and equation. *Error bars* indicate 25% and 75% percentiles.

▼ **Table 2.** Results of non-linear regression analysis on the relationship of stomach content weight and length of *Champsocephalus gunnari* in 2001 – 2003. Regression function: $y = a \times e^{x \times b}$

Year	a	b	R2
2001	0.425	0.089	0.75
2002	0.133	0.106	0.74
2003	0.205	0.101	0.59



◀ **Figure 4.** *Champsocephalus gunnari* – Mean daily rations in grams per day in 5 cm length classes, 2001-2003.

▼ **Table 3.** Mean daily feeding rates (*r’*, in % body weight) in each length class of *Champsocephalus gunnari* from the South Shetland Islands 2001 to 2003. N = Number of stomachs with food per length group

Length	2001		2002		2003	
class	N	r’ [%]	N	r’ [%]	N	r’ [%]
20 - 24 cm	137	0.8	100	0.5	111	1.2
25 - 29 cm	179	1.0	30	0.6	104	1.1
30 - 34 cm	70	1.0	76	0.9	204	1.4
35 - 39 cm	147	1.0	93	1.2	121	1.7
40 - 44 cm	164	0.9	26	1.1	109	1.7
45 - 49 cm	66	0.9	12	1.0	11	1.5
Mean	-	1.0	-	1.2	-	1.5

▾ **Table 4.** Krill biomass consumed by standing stocks of *Champsocephalus gunnari* around Elephant Island and the South Shetland Islands in 2001 and 2002. 95% confidence limits are indicated in brackets

	2001	**2002**
Standing stock biomass [t]*	5121 (3402 – 9587)	3019 (1509 – 16787)
Krill consumption [t/month]	1149.0 (763.3 – 2149.1)	686.3 (343.1 – 3816.4)
*Source	Jones et al. 2001	Kock et al. 2002a

Feeding rates

Average daily rations and relative feeding rates per length class in all years are provided in Table 3 and Figure 4. Fish smaller than 20cm and larger than 49cm were not taken into consideration due to a limited number of individuals caught in these length classes. The mean daily ration increased with increasing body size. In 2001, it was 0.6g per day in the 20–24cm length class and 7.6g per day in the 45–49cm length class. In 2002 and 2003, the range was from 0.3g to 8.6g and 0.8g to 13.3g, respectively (Figure 4). Overall mean daily ration was 3.4g in 2001, 2.5g in 2002 and 4.1g in 2003. The relative feeding rate was constant over the observed length range in 2001, ranging from 0.8 to 1.0% body weight per day in each length group. In the following year, rates in fish smaller than 30 cm were considerably lower (0.5 - 0.6%) than in larger animals (0.9 - 1.2%). Mean rate of food intake in all fish was 1.0% body weight per day both in 2001 and 2002. Higher feeding rates were observed in 2003, when the average feeding rate was 1.5% body weight (Table 3).

The daily rations, together with the total sizes and length compositions of the stocks, enabled the calculation of the total krill consumption of the stock of *C. gunnari* around Elephant Island and the South Shetland Islands in 2001 and 2002. Using the estimated biomass of *C. gunnari* from 2001 (Jones et al. 2001) and 2002 (Kock et al. 2002), we calculated the monthly krill consumption of mackerel icefish stocks to approximately 1150 t in 2001 and 690 t in 2002 (Table 4).

Food composition

The diet of *C. gunnari* consisted of only a few species in all three years. The food composition is provided in Table 5. Krill was by far the most dominant prey item. In 2001, 99% of the stomachs with food contained krill, and 4% contained unidentifiable material, as well as algae and stones. Other food items, such as *Themisto gaudichaudii* (Hyperiidae; 1%), myctophids (1%) and unidentified crustaceans (< 1%) were encountered occasionally. Unidentified crustaceans were probably largely krill that were too fragmented by digestion to be identified to species level. *Euphausia superba* also dominated in terms of relative number and stomach content wet weight (each 99%). Samples collected in 2002 and 2003 exhibited a similar range of prey items. Krill was again the dominant prey species which was present in 92 % and 91 % of the stomachs, respectively. Of the stomachs collected in 2002, 5% contained *Themisto gaudichaudii*. Other prey items were unidentified fish (1%) and *Euphausia sp.* (1%).

Material in 6% of the stomachs was unidentifiable. In 2003, *Thysanoessa macrura* together with other euphausiids were found in some stomachs (8%). *T. gaudichaudii* and unidentified amphipods were found in 4% of the stomachs. Unidentified fish (2%) and myctophids (1%) occurred occasionally. Other food items were encountered in less than 1% of the stomachs. 1% of the prey objects were unidentifiable.

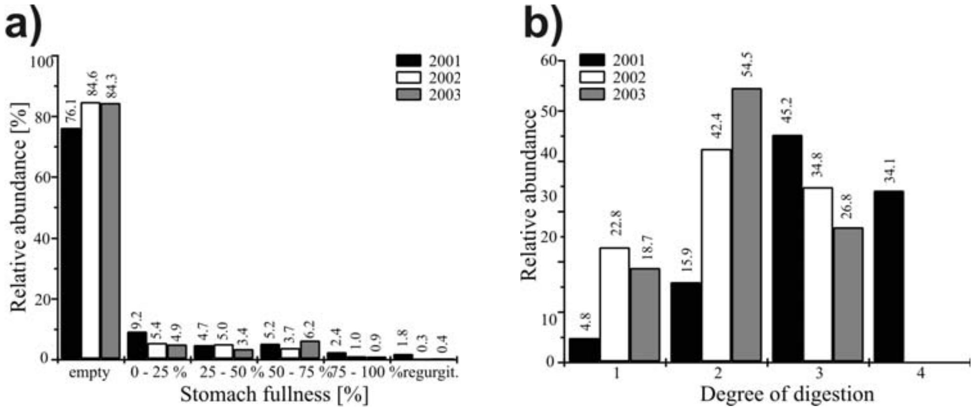
2.3.2 *Chaenocephalus aceratus*

Stomach fullness and degree of digestion

Most of the stomachs collected in 2001 (76%) were empty. The majority of the stomachs containing food (14%) were in filling degree 1 or 2. Few stomachs (2%) appeared to be regurgitated. In 2002 and 2003, the proportion of empty stomachs was even higher (85% and 84%, respectively). Most of the stomachs with food (9% and 8%, respectivelz) were in filling degree 1 or 2, and fewer than 1% showed signs of being regurgitated (Figure 5a).

▼ **Table 5.** Composition of the diet of *Champsocephalus gunnari* from the South Shetland Islands 2001-2003: percentage frequencies of occurence (F%), number (N%) and wet weight (W%); number of stomachs with food in each year in parentheses

	2001 (823)			2002 (309)	2003 (682)
	F %	**N %**	**W %**	**F %**	**F %**
Crustaceans (total)	100.1	99.9	99.3	97.1	102.2
Euphausiacea					
E. superba	98.7	99.3	98.7	91.6	91.2
E. frigida	-	-	-	-	0.3
Euphausia spec.	-	-	-	0.6	3.5
Thysanoessa macrura	-	-	-	-	3.5
Mysidacea					
Mysidacea indet.	-	-	-	-	0.1
Amphipoda					
T. gaudichaudii	0.7	0.6	0.0	4.9	2.1
Amphipoda indet.	-	-	-	-	1.5
Crustacea indet.	0.4	-	0.6	0.0	-
Fish (total)	1.2	0.1	0.1	1.0	2.9
Notothenioidei					
L. larseni	-	-	-	-	0.1
Myctophoidei					
Myctophidae indet.	1.1	0.1	0.1	0.0	0.6
Pisces indet.	< 0.1	-	-	1.0	2.2
Others (total)	4.3		0.6	6.5	1.5
Polychaeta					
Polychaeta indet.	-	-	-	-	0.1
Ophiuroida					
Ophiuridae indet.	-	-	-	-	0.1
Unidentified	4.3	-	0.6	6.5	1.3



▲ **Figure 5.** *Chaenocephalus aceratus* – distribution of stomach fullness (a) and degrees of digestion (b) in 2001 (dark columns), 2002 (white columns) and 2003 (grey columns). The percentages of abundance of stomachs in each category are indicated *above* the columns.

A large proportion of the stomach contents sampled in 2001 (79%) was heavily digested (DOD 3 or 4). In 2002 and 2003, the greater proportion of stomach contents (65%, 73%) was hardly digested at all (DOD 1 or 2), with the remaining portion (35%, 37%) being in an advanced stage of digestion (DOD 3) (Figure 5b).

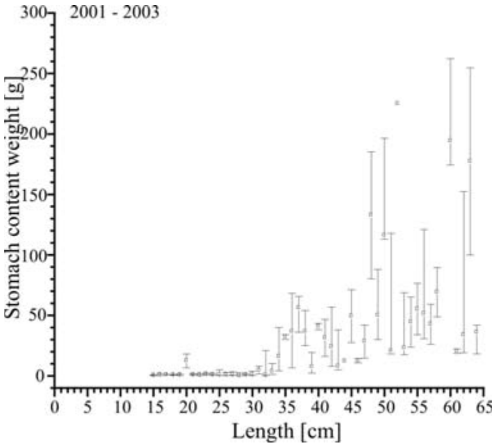
Stomach content weight

Stomach content wet weight ranged from < 1g to approximately 400g in 2001 and 2002, and up to approximatelz 160g in 2003. Mean weights were 20.4g (SD = 53.07) in 2001, 33.9g (SD = 72.20) in 2002 and 14.6g (SD = 30.04) in 2003.

Given the small number of stomachs with food in each year, we pooled data from all years in order to describe the relationship of stomach content weight with total length of fish. The results are illustrated in Figure 6. Stomach content weights of fish < 34cm were below 50g, increasing very slightly with increasing size of *C. aceratus*. In larger fish, stomach content weights fluctuated heavily, with largest values occurring in the largest fish (≥ 60cm). Due to these fluctuations, no appropriate function could be fitted to the data.

Food composition

In general, diet composition of *C. aceratus* consisted of a mix of small crustaceans, mostly krill and mysids, and demersal fish species. The Overall diet composition is shown in Table 6. The diet composition varied between stations in all three years of investigation. However, the number of stomachs with food per station was too low to conclude any geographic pattern of feeding preference.



◀ **Figure 6.** *Chaenocephalus aceratus* –Median values of stomach content wet weight against length of fish. *Error bars* indicate 25% and 75% percentiles.

▼ **Table 6.** Composition of the diet of *C. aceratus* from the South Shetland Islands in 2001 and 2002: percentage frequencies of occurence (F%), number (N%) and wet weight (W%); number of stomachs with food in parentheses

	2001 (128)			**2002 (90)**	**2003 (126)**
	F %	**N %**	**W %**	**F %**	**F %**
Crustaceans (total)	72.3	91.5	11.3	68.9	78.6
Euphausiacea					
E. superba	55.5	79.0	10.3	48.9	50.8
Mysidacea					
A. maxima					12.7
Mysidacea indet.	9.2	12.6	0.9	11.1	12.7
Amphipoda					
T. gaudichaudii	-	-	-	2.2	-
Amphipoda indet.	-	-	-	-	0.8
Crustacea indet.	7.6	-	0.1	6.7	1.6
Fish (total)	26.9	7.5	85.3	33.3	19.8
Notothenioidei					
G. gibberifrons	5.0	1.7	41.6	-	-
L. larseni	0.8	0.5	2.8	12.2	6.3
L. nudifrons	1.7	0.5	3.8	1.1	2.4
C. gunnari	3.4	1.0	6.7	7.8	2.4
C. aceratus	2.5	0.7	7.2	-	0.0
Channichthyidae indet.		-	-	1.1	-
Parachaenichthys charcoti	-	-	-	1.1	-
Harpagifer antarcticus	-	-	-	-	1.6
Myctophoidei					
Myctophidae indet.	1.7	-	-	-	-
Trichiuroidei					
Gempylidae indet.	-	-	-	1.1	-
Pisces indet.	11.8	3.1	23.1	8.9	7.1
Unidentified	4.2	-	1.5	1.1	4.8

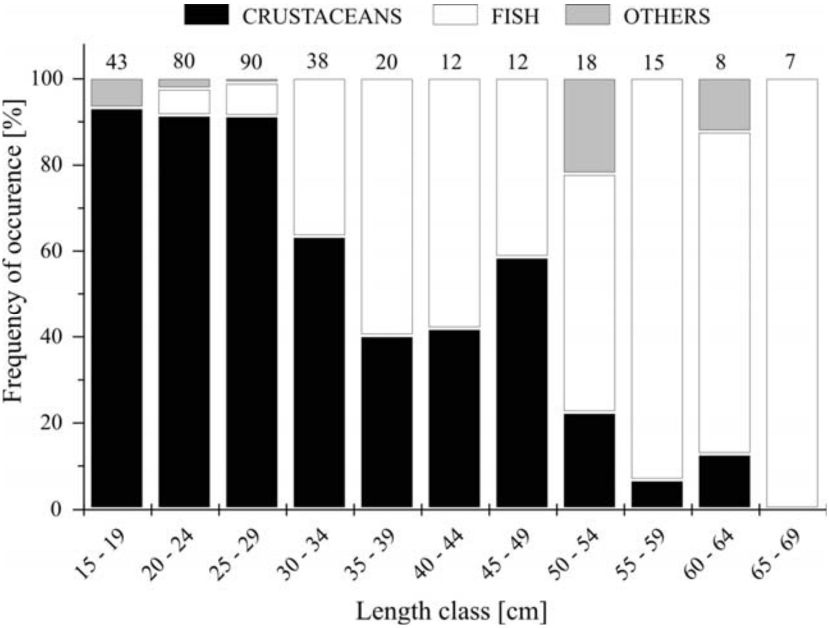
▾ **Table 7.** Dietary coefficient *Q* of different prey items of *Chaenocephalus aceratus* from the South Shetland Islands in 2001. *Q* was calculated separately for smaller (< 30 cm) and larger fish (≥ 30 cm), and for all specimens

	< 30 cm	**≥ 30 cm**	**all**
Crustaceans (total)	7811.0	441.6	1027.8
Euphausiacea			
E. superba	5545.8	369.1	814.5
Mysidacea			
A. maxima	84.3	-	2.0
Mysidacea indet.	22.1	1.9	3.8
Fish (total)	12.2	738.8	735.4
Notothenioidei			
G. gibberifrons	-	73.4	70.3
L. larseni	-	1.4	1.3
L. nudifrons	-	1.9	1.8
C. gunnari	12.2	4.5	6.5
C. aceratus	-	5.5	5.2
Myctophoidei			
Myctophidae inet.	-	1.7	1.6
Pisces indet.	-	75.9	72.7

In 2001, *Euphausis superba* was the most frequent prey species (56%). However, it accounted for only 10% of the total wet weight of the prey. *Gobionotothen gibberifrons* and unidentified fish were the most important prey items in terms of weight, accounting for 42% and 23% of the diet, respectively. With regard to the small number of filled stomachs obtained, it seemed reasonable to lump all prey species into the two categories ‘crustaceans’ (krill, mysids and others) and ‘fish’ when discussing the importance of different fractions of the diet in terms of the dietary coefficient *Q*. Accordingly, crustaceans (1028) and fish (735) could both be ranked as main prey (Table 7).

In 2002 and 2003, food items were registered by frequency of occurrence only. In 2002, Crustaceans (69%) and fish (33%) showed a distribution similar to 2001. Crustaceans were mostly krill (49%), mysids (11%) and unidentified crustaceans (7%). Among the fishes, *L. larseni* (12%), unidentified fish (9%) and *C. gunnari* (8%) were found most frequently. Other fish species only occurred sporadically.

In 2003, the proportion of crustaceans in the diet (79%) was significantly higher than in the two preceding years. *E. superba* was taken most often (51%), followed by *Antarctomysis maxima* (12.7%) and unidentified mysids (12.7%). Other crustaceans were of minor importance. Fish occurred in 20% of the stomachs with food. *L. larseni* (6%) and *L. nudifrons* (2%) were taken most often. *Harpagifer antarcticus* was encountered occasionally. Fish in 7% of the stomachs could not be identified to species level.



▲ **Figure 7.** *Chaenocephalus aceratus* – frequency of occurrence of prey items per 5 cm length class. *Columns* represent pooled data from three years of investigation (2001-2003). The number of stomachs with food in each length class is provided *above* the columns.

There was a significant change in the diet from smaller to larger *C. aceratus* (Figure 7). The overwhelming proportion stomach contents of fish shorter than 30 cm consisted of crustaceans, predominantly krill and mysids. A change in the composition of the diet was apparent when *C. aceratus* became larger than 30 cm. These older *C. aceratus* gradually relied more and more on fish diet, and in those larger than 50cm, only a few stomachs contained crustaceans in addition to prey fish. The fishes found in the stomachs were primarily those notothenioids that were also found to be abundant in trawl catches, such as *C. gunnari*, *Gobionotothen gibberifrons*, *C. aceratus*, *Lepidonotothen nudifrons* and *L. larseni*. In terms of the dietary coefficient *Q*, crustaceans were the only notable prey (7811) in *C. aceratus* shorter than 30 cm in 2001, and the importance of fish (12) was negligible. In animals ≥ 30 cm, fish was the most important prey item (739), and despite their low proportional weight, crustaceans could as well be classified as main prey (442) (Table 7).

2.4 Discussion

2.4.1 *Champsocephalus gunnari*

Food composition

Krill (*Euphausia superba*) seems to be more or less the exclusive prey species of *Champsocephalus gunnari* in the Elephant Island / South Shetland Islands region. While this has been demonstrated earlier by Taverdieva and Pinskaya 1980, Kock 1981, Kozlov 1988 and Takahashi and Iwami 1997), these studies were either confined to a small area of investigation or were limited in the number of samples investigated. Gröhsler (1992) reported a broader range of prey items at Elephant Island in May / June 1986. It is possible that *C. gunnari* switched to a more diverse prey in order to compensate for lower availability of krill since krill biomass in the area is usually substantially lower during the winter (Siegel 2000).

The availability of krill is quite variable in the area of distribution of mackerel icefish. High densities of *E. superba* are usually found in the southern part of the Scotia Arc, Elephant Island, the South Shetland Islands and the Antarctic Peninsula during austral summer, whereas krill abundance fluctuates significantly between years at South Georgia (Siegel 2000). In the latter area, the proportion of krill in the diet of *C. gunnari* varied considerably between different sampling years (Kozlov et al. 1988, McKenna 1991, Kock et al. 1994, Barrera-Oro et al. 1997, Kock and Everson 2003).

Obviously, mackerel icefish replace part of their diet with other prey, such as *Themisto gaudichaudii*, mysids or other crustaceans when krill is not sufficiently available (Kock et al. 1994). In the Elephant / South Shetland Islands region, the constant predominance of krill in the diet suggests that its availability for *C. gunnari* is not limited there during austral summer.

Feeding intensity

The high feeding intensities observed during the three years of investigation support the notion that *C. gunnari's* major food source was not limited. Most of the stomachs analysed were more than 25% full in all the three years. This suggests that the fish had fed the night prior to capture, based on an estomated digestion time of 36 – 48 hours (Kock 1992). The average time span between food intake and capture was probably smaller in 2002 and 2003 than in 2001, as indicated by the distribution of degrees of digestion.

Some variability in feeding intensity was indicated by a higher proportion of empty stomachs in 2002. Similarly high portions of empty stomachs were reported at South Georgia, in the years when the availability of krill was low (Kock et al. 1994), or at Elephant Island in the austral winter, when feeding intensity seemed to be low, and less krill was available (Gröhsler 1992). It is possible that the higher proportion of empty stomachs in 2002 reflected a reduced availability of *E. superba* on a local scale.

The feeding intensity of *C. gunnari* can vary extensively both on a temporal and a spatial scale (Kock et al. 1994). The overall biomass density of krill at Elephant Island was higher in 2001 than the long term average (Thomasson et al. 2002), which may have resulted in maximum feeding activity of mackerel icefish in that summer. Data on krill biomass from 2002 and 2003 were not available. The grid of the regular AMLR and "Polarstern" surveys in the region in summer (15 nm distance between sampling stations) appears to be too coarse to adequately reflect small scale differences in the abundance of krill for the purpose of a feeding study.

Quantitative food intake

In *C. gunnari*, there was a moderately exponential increase in stomach content weight with increasing body size in all three years. An exponential model could be fitted to the data of each year separately. However, the relationship of fish length with stomach content weight seemed to vary considerably between years, as indicated by the different model constants *a* and *b*.

The positive correlation of stomach content weight with the size of fish was reflected by a similar trend in the daily rations. Mean daily rations per individual in 2001 and 2002 were at the upper end of the range reported by other authors, which were from between 0.1 and 1.2g per day (Gröhsler 1992) to 3.0g per day (Duhamel and Hureau 1985). In 2003, they were significantly above these values. The mean daily ration is dependent on the size composition of the investigated fish. Thus, results from different investigations are hardly comparable if the size compositions of the sampled fish are not similar.

Daily feeding rates ranged from 1.0 to 1.5% body weight in the three years of investigation. They were well within the expected range for notothenioids which was 0.5% to 2.5% of total fish weight per day (Kock 1992), as well as close to previous approximations ranging between 0.5% (Gröhsler 1992) and 2.2% body weight per day (Duhamel and Hureau 1985). In 2002, the feeding rates in fish < 30 cm were significantly lower than in larger animals. Almost 50 % of these smaller *C. gunnari* were caught at three stations located close to each other north of Livingston Island. This observation probably reflects a local effect due to low availability of prey in that area.

Daily rations and feeding rates were derived from a general model on the course of feeding and digestion which can only provide a rough approximation. A number of mathematical models have been developed to describe gastric evacuation over time (Bajkov 1935; Windell 1966; Elliott and Persson 1978; Jobling et al. 1977; Persson 1986; Dos Santos and Jobling 1995; Andersen 1999, 2001). Almost all of these experimental studies were conducted on fish from temperate or warm waters. Only Hop and Tonn (1998) provided extensive experimental data on digestion rates in cold adapted arctic cod. Since channichthyids are difficult to keep under laboratory conditions, no data were yet available on their digestion rates based on feeding experiments. Experiments on other Notothenioids have been conducted by Crawford (1978), Montgomery et al. (1989) and Boyce et al. (2000). The latter two reports suggest that an exponential model of gastric evacuation can be helpful in realistically estimating feeding rates of *C. gunnari*.

Previous estimates of daily rations and feeding rates of mackerel icefish from field data were obtained with a variety of methods, ranging from the calculation of a mean daily stomach content weight to various gastric evacuation models (Taverdieva 1982, Naumov et al. 1983, Duhamel and Hureau 1985, Gröhsler 1992). Our results were within the range reported by these authors, with the exception of Taverdieva (1982) who reported much higher daily rations and feeding rates. However, these were far outside the usual range estimated for notothenioids (Crawford 1978; Naumov et al. 1983; Montgomery et al 1989; Pakhomov and Tseitlin 1992) and should be considered with caution.

The krill consumption by *C. gunnari* in the area of investigation was between 700 and 1200 t per month in 2001 - 2002, and probably considerably higher in 2003 because of higher feeding rates in that year. In all three years, krill consumption was significantly above the values calculated by Gröhsler (1992) for the Elephant Island area in early winter 1986. As mentioned above, seasonal effects can strongly influence diet composition and feeding intensity of *C. gunnari*. For this reason, we did not use the data to calculate the annual krill consumption because too little is known about the feeding of mackerel icefish throughout the rest of the year.

The importance of *C. gunnari* as a major predator on krill in the region has declined significantly since the depletion of the stock in the late 1970s. The stock was most likely an order of magnitude larger than today (Kock 1992), and so was its impact on krill in the area. Whether this decrease of the population of *C. gunnari* has had a positive effect on krill populations or concurring predators, would be an interesting question for future investigations.

2.4.2 *Chaenocephalus aceratus*

Diet composition

In *C. aceratus,* a change in feeding behaviour was apparent at a length of 30-35 cm. At this stage, the composition of the diet changed gradually from crustaceans (mostly krill and mysids) to demersal fish. This observation is also supported by earlier results of Siegel (1980) who found that the infestation rates of endoparasitic nematodes that have typically fish as intermediate hosts increased from less than 20% to 100% in *C. aceratus* of 30 – 35 cm length.

In the 2001 data, the ontogenetic shift in diet composition could be illustrated by the dietary coefficient *Q*, although *Q* values calculated separately for small and large fish suggested that crustaceans were still important in larger animals. The observed similarity of the species composition of fish found in stomachs and trawl catches in all three years suggests that large *C. aceratus* are opportunistic and take what they can get, including crustaceans.

Data on the diet of *C. aceratus* are scarce. Most previous studies were based on a limited number of samples since a large proportion of stomachs was usually empty. The results also varied in the manner thez were presented: numerical (Kock 1981, Kozlov et al. 1988), gravimetric (Takahashi and Iwami 1997) or both (Gröhsler 1992). However, our findings suggest that the exclusive application of either numerical or quantitative methods can be misleading with respect to the importance of different food items in *C. aceratus*. A dietary coefficient, such as *Q*, can enhance the comparability of different sets of data if the food composition is heterogeneous (Hyslop 1980).

On the basis of this coefficient, crustaceans and fish turned out to be almost equally important to the diet of Scotia Sea icefish on an overall view. Our results were within the range of the above mentioned investigations, if it were taken into account that the proportions of crustaceans and fish can fluctuate considerably between different years as well as different areas of investigation (Kock 1981, Kozlov et al. 1988, Takahashi and Iwami 1997). These fluctuations could either be due to changes in the availability of one or both prey types, or to differing size compositions of the *C. aceratus* investigated.

Feeding intensity

In *C. aceratus*, a high proportion of empty stomachs is a common phenomenon (Kock 1981, Gröhsler 1992, Casaux et al. 2003a). It has been suggested that a large proportion of Scotia Sea icefish regurgitate when they are caught (Kock 1981, Gröhsler 1992). In contrast, few stomachs with signs of regurgitation, such as reversed or expanded stomach walls, were found in this study, implying that *C. aceratus* fed very infrequently. However, this deduction should still be viewed with caution because it cannot be excluded that stomachs re-contract quickly after regurgitation.

Stomach content weight

The change in the diet from small crustaceans to demersal fish is accompanied by a remarkable rise in the stomach content weights of fish > 30 cm. Because of considerable variability in the sizes of the ingested fish, stomach content weight fluctuated considerably in larger Scotia Sea icefish in all three years. These fluctuations made it impossible to fit the data adequately to a model describing the relationship between stomach content weight and fish length, even if records from three years were pooled together

2.5 Conclusions

Champsocephalus gunnari and *Chaenocephalus aceratus* represent two different lifestyles within the family Channichthyidae which are clearly reflected both by diet composition and feeding intensity. Both species are known to take advantage of planktonic crustaceans, primarily *E. superba*. However, they differ significantly in the extent to which they use this resource.

In the course of evolution, *C. gunnari* developed adaptations supporting the exploitation of midwater resources, such as a more streamlined body shape and reduced buoyancy compared to other channichthyids of the seasonal pack-ice zone (Eastman and Sidell 2002). The early life stages of mackerel icefish are pelagic (Frolkina 2002). After attaining sexual maturity, they change to a more semi-pelagic mode of life. They undertake regular diurnal migrations into the water column, where they feed mainly on euphausiids, becoming more demersal the older they get (Duhamel and Hureau 1985, Trunov et al. 2000, Frolkina 2002). The Elephant / South Shetland Islands region provides unlimited availability of krill during the austral summer, thereby supporting high feeding intensities and a continuous mode of food intake.

Like their planktivorous sister species *C. gunnari*, *C. aceratus* up to a size of 30-35cm seem to take advantage of small crustaceans. They gradually feed more on demersal fish the larger they become. For young *C. aceratus*, there is nothing as abundant, as high in energy and as easy to catch as krill and mysids (Clarke and Prince 1980, Siegel 2000). A switch to a demersal, more piscivorous mode of life is probably advantageous for older animals: Although fish are less abundant, they can deliver a large amount of energy once they are caught. An energy saving, ambush feeding mode of life, as indicated by behavioural observations (Daniels 1982,) would be appropriate to perform such a feeding strategy.

Acknowledgements

We thank the crews of 'RV Yuzhmorgeologiya' and RV 'Polarstern' for their excellent support on board. Special thanks go to the US AMLR program for logistic help.

Key references

- Eastman JT, Clarke A (1998) A comparison of adaptive radiations of Antarctic fish with those of non Antarctic fish. In: Di Prisco G, Pisano E, Clarke A (eds) Fishes of Antarctica. A biological overview. Springer Press, Milan, pp 3-26
- Gröhsler T (1992) Nahrungsökologische Untersuchungen an antarktischen Fischen um Elephant Island unter besonderer Berücksichtigung des Südwinters. Mitteilungen des Instituts für Seefischerei 47:1 -296
- Kock K, Wilhelms S, Gröger J (1994) Variations in the diet composition and feeding intensity of mackerel icefish *Champsocephalus gunnari* at South Georgia (Antarctic). Marine Ecology Progress Series 108:43-57
- Hop H, Tonn WM (1998) Gastric evacuation rates and daily rations of Arctic cod (*Boreogadus saida*) at low temperatures. Polar Biology 19:293-301
- Kozlov AN, Pinskaya IA, Podrazhanskaya SG, Tarverdieva MI (1988) Feeding of glassfishes in different regions of the Atlantic sector of Antarctica. Journal of Ichthyology 28(6):137-145

Measuring the size of lanternfish.

CHAPTER 3

Energy content of Antarctic mesopelagic fishes: Implications for the marine food web

Anton P. Van de Putte, Hauke Flores, Filip A.M. Volckaert
& Jan A. van Franeker

Abstract. For a better understanding of the role of mesopelagic fish in the Southern Ocean food web, the energy and water content of Bathylagus antarcticus, *Electrona antarctica* and *Gymnoscopelus braueri* from the Lazarev Sea were investigated. Mean dry weight energy content of *B. antarcticus* (20.4 kJ g^{-1}) was significantly lower than in *E. antarctica* and *G. braueri* (both 29.4 kJ g^{-1}). In *E. antarctica*, an increase of dry weight energy density with age was evident from 26.9 kJ g^{-1} in juveniles of less than 1 year of age to 32.0 kJ g^{-1} in 3-year-old fish. Water content decreased with size in all three species. Abundant high-energy species such as *E. antarctica* are at a key position in the food web. Due to a marked influence of age on energy content, population structure can be an important variable in estimates of energy fluxes in the Southern Ocean ecosystem.

Polar Biology 29 (2006): 1045-1051

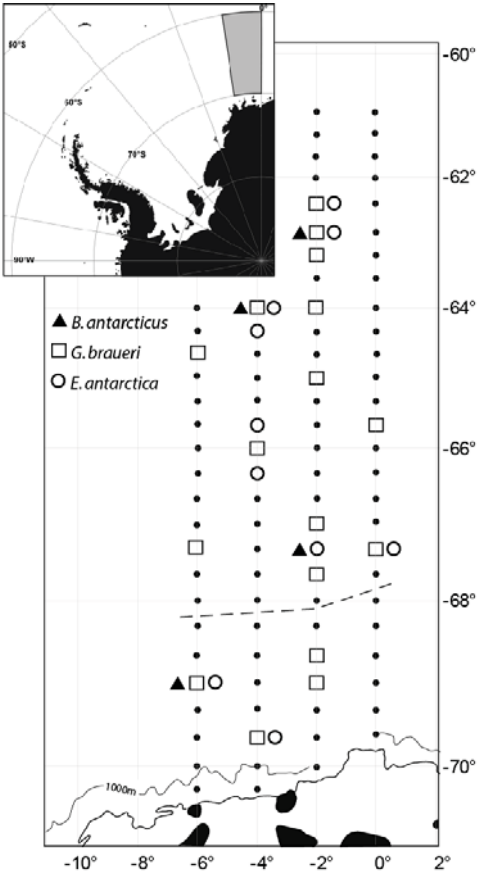
3.1 Introduction

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 flux from lower to higher trophic levels. As such, they are valuable for the development of ecosystem models and play an important role in ecosystem management. With increasing evidence that the classic diatom-krill-consumer model of 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 (Ainley et al. 1992, 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). They are major predators on mesozooplankton (Pakhomov et al. 1996; Pusch et al. 2004). Among them, *Electrona antarctica* (Günther, 1878) is considered a key species due to its high abundance and almost circumpolar distribution (Hulley 1990; Sabourenkov 1990; Hopkins et al. 1993; Barrera-Oro 2002). They display a diel migration between 300–650 m during the day and close to the surface layer at night. *E. antarctica* are an important prey for birds and seals (Lea et al. 2002a; Quillfeldt 2002; Casaux et al. 2003b). The myctophid *Gymnoscopelus braueri* (Lönnberg, 1905) exhibits a similar ubiquity, but appears to be less abundant than *E. antarctica* (Torres and Somero 1988; Lancraft et al. 1989; Sabourenkov 1990). Their role in the food web can be significant on a local scale (Ainley et al. 1991, 1994). *Bathylagus antarcticus* Günther, 1878 (family Bathylagidae) is widely distributed throughout the Antarctic Ocean. It is generally considered a deeper-dwelling midwater species mainly occurring between 950 and 170 m depth, with some vertical migration on a diel as well as seasonal basis (Lancraft et al. 1989;Gon 1990). Apart from sporadic occurrence in the diet of Antarctic fur seals (Casaux et al. 2004), *B. antarcticus* has not been reported to play a significant role in the diet of higher predators.

Energy content of Southern Ocean mesopelagic fish species has been estimated with respect to depth, season or region (Donnelly et al. 1990; Lea et al. 2002b; Tierney et al. 2002), or in the context of diet studies (Clarke and Prince 1980; Cherel and Ridoux 1992; Eder and Lewis 2005). Most studies were based on relatively small sample sizes.

This paper contributes a new dataset for a region so far not sampled in the context of energetic analyses for ecosystem-based energy budget models. We discuss the influence of population structure on the energy budget based on the species-specific evolution of energy content with size and age. The ecological role of the three species investigated is evaluated in the light of their nutritional value, distribution, biology and function in the food web.



◂ **Figure 1.** RMT sampling grid with geographic overview in upper left corner. Stations sampled for energy content are indicated with different markers for each species. Dashed line represents northern edge of the sea ice cover.

3.2 Materials and methods

3.2.1 Sampling procedure

Samples were collected during the autumn SO-GLOBEC cruise of RV ‘‘Polarstern’’ (ANT XXI/4) in the Lazarev Sea (CCAMLR statistical subarea 48.6), between March 3 and May 5, 2004 (Figure 1). The station grid consisted of four longitudinal transects between 0° and 6°W and 61°S–72°S, with a latitudinal spacing of 20 nautical miles between stations. Fish were caught using Rectangular midwater trawl nets (RMT 8 + 1), consisting 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 haul consisted of a standard double oblique tow from the surface down to 200 m and back to the surface. Towing speed was approximately 2.5 knots. Further details on the sampling procedure are outlined in Siegel et al. (2004).

Fish were sorted from the total catch of the RMT 8 and identified to species level. Dry mass and energetic content was determined for three species: *E. antarctica*, *B.*

antarcticus and *G. braueri*. Individuals were sampled from 21 stations distributed over the entire survey area where sufficient fish were caught to allow subsampling for energy measurements. From each of these stations, a subsample of up to 12 individuals per species covering the whole length range caught were stored at -20°C.

3.2.2 Water and energy content

To prevent errors due to the loss of body fluids during dissection, water and energy content were determined for whole individuals only. Frozen fish were thawed, blotted dry and their standard length (SL) was deter¬mined to the lower full mm. Total wet weight (WW) was determined to the nearest 0.1 mg. Fish were dried until complete desiccation (constant mass) in a drying oven at a constant temperature of 60°C. 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 (0.1–1.2 g) was used for calorimetry, depending on the size of the fish.

3.2.3 Data analysis

Mean energy and water content with standard deviations were calculated for each species. Fish were divided into three size classes: small, medium and large. We used the maximum lengths reported in Hulley (1990) and Gon (1990) for each species and divided them by three to obtain size groups comparable for future studies. Reliable size–age data were available for *E. antarctica* (Greely et al. 1999). In order to obtain biologically more relevant categories, we calculated age in years based on the pooled length–age regression provided by Greely et al. (1999):

$$a = \frac{SL - 8.869}{0.063 * 365}$$

a = age in years

Based on the results of equation (1), fish were divided in year groups 0 ($a < 1$), 1 ($1 \leq a < 2$), 2 ($2 \leq a < 3$) etc.. Analysis of variance (ANOVA) was applied to detect significant differences in energy and water content between species and their individual size classes and age groups. Tukey's Honestly Significant Difference test (Tukey's HSD) was used as a post-hoc test to discriminate species and single size classes and age groups from each other. Additionally, various regression analyses were performed in order to estimate the effect of size on energy and water content. Significance threshold α was 0.05 for all statistical tests.

Species	Known range [mm]	n	Size range [mm]	Mean size [mm]
B. antarcticus	0-170	12	36 – 123	71.6 (23.42)
E. antarctica	0-102	113	16 – 83	47.6 (15.90)
G. braueri	0-132	20	64 – 132	87.3 (18.05)

◂ **Table 1.** Known size ranges (Gon 1990; Hulley 1990), sampled size ranges and mean sizes of all three species investigated. Standard deviation in parentheses; *n* = sample size

3.3 Results

3.3.1 Species comparison

Electrona antarctica was abundant throughout the sampling area. A large and continuous part of the total size range was covered in this species. Both other species were caught infrequently. Only the upper portion of the natural size range was obtained for *G. braueri*. *B. antarcticus* was represented by a low number of samples spread over a wide size range, the bulk ranging from 36 to 95 mm, with only one larger specimen of 123 mm (Table 1).

While mean WW energy content of *B. antarcticus* (2.9 kJ g-1) was significantly lower than that of *E. antarctica* (9.4 kJ g-1) and *G. braueri* (8.9 kJ g-1), no significant difference could be detected between the two myctophids in either WW or DW energy density. Conversely, the bathylagid's mean water content (86%) was significantly higher compared to that of *E. antarctica* (68%) and *G. braueri* (70%). The two myctophids showed no statistically significant difference in water content from each other (Table 2).

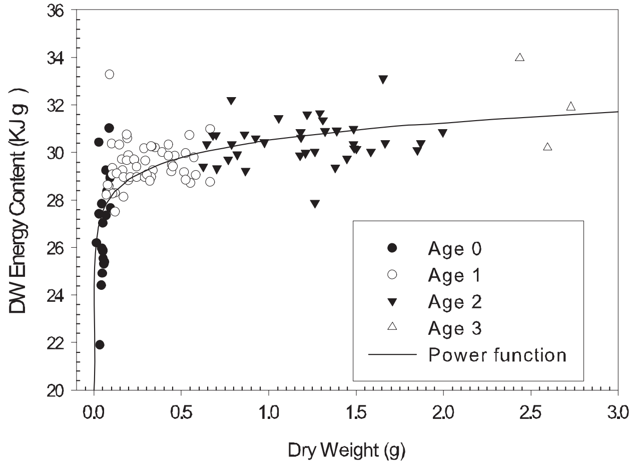
3.3.2 Size and age effects on energy content in *E. antarctica*

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.

Among the models tested, a linear regression of the ln-transformed data proved to deliver the statistically most robust results. The corresponding power function exhibits a steep increase of energy density with size, DW and WW in age group 0 and 1 fish, and a gradual increase in older fish (Figure 2). The model parameters for energy content as a function of size, DW and WW are listed in Table 3.

▾ **Table 2**. Mean water content, mean wet (WW) and dry weight (DW) energy density of all investigated species. Standard deviation in parentheses. Variation between species significant for all three variables (ANOVA: $p < 0.01$). (*)Values significantly different from all other values in the same column (Tukey's HSD: $p < 0.05$)

Species	Water content [%]	WW energy density [kJ g^{-1}]	DW energy density [kJ g^{-1}]
B. antarcticus	85.6 (2.46)	2.92 (0.421)*	20.36 (1.319)*
E. antarctica	68.4 (4.14)	9.35 (1.575)	29.40 (1.800)
G. braueri	69.5 (3.96)	8.86 (1.421)	29.37 (1.509)



▲ **Figure 2.** *Electrona antarctica*. Relationship between dry weight (DW) and dry weight energy density with indicated age groups. Regression parameters of power function provided in Table 3.

Mean WW energy density increased from 7.5 KJ g^{-1} in small fish to 10.3 KJ g^{-1} in large specimens (Table 4). Small fish were significantly lower in DW and WW energy content than medium and large fish, which could not be statistically discriminated from each other. The opposite trend was significant in water content which decreased from 73 % in small *E. antarctica* to 66-67 % in the two larger size classes (Table 4).

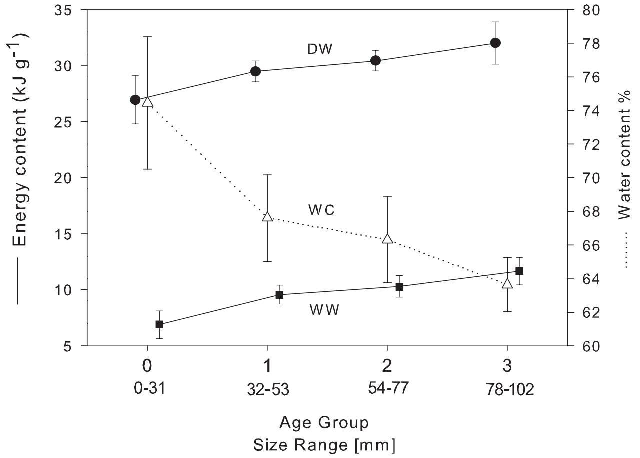
Water and energy content by age group are shown in Figure 3. An increase in energy content was apparent from age group 0 (6.9 KJ g^{-1} WW) to age group 3 fish (11.7 KJ g^{-1} WW). The difference in DW and WW energy density between age classes 0, 1 and 2 was statistically significant. Mean water content declined from 74 % in age class 0 to 64 % in age class 3. However, only age group 0 fish could be statistically discriminated from older fish (Table 4).

▼ **Table 3**. *Electrona antarctica*. Energy density (*y*) of dry weight (DW) and wet weight (WW) as a function of size, WW and DW (*x*). Regression parameters *a* and *b*, adjusted r^2 and *p*-value for linear regressions of ln-transformed data[1], and corresponding power function[2]

x	y [KJ g^{-1}]	a	b	p	r^2	e^a
Size	DW	2.9361	0.1164	< 0.01	0.40	18.8422
[mm]	WW	0.7942	0.3745	< 0.01	0.47	2.2127
WW	DW	3.3778	0.0367	< 0.01	0.44	29.3062
[g]	WW	2.2154	0.1165	< 0.01	0.50	9.16507
DW	DW	3.4181	0.0347	< 0.01	0.46	30.5114
[g]	WW	2.3500	0.1160	< 0.01	0.58	10.4856

[1] Form: $\ln(y) = a+ b \ln(x)$

[2] Form: $y = x^b e^a$



▲ **Figure 3.** *Electrona antarctica*. Mean water content (WC), dry weight (DW) and wet weight (WW) energy content by age group. Error bars indicate 95% confidence intervals.

3.4 Discussion

3.4.1 Inter-specific differences

Energy measurements on *E. antarctica* were at the higher end of the reported range, exceeded only by values reported by Lea et al. (2002b) (Table 5). Our values for *B. antarcticus* and *G. braueri* closely resemble autumn energy densities calculated from proximate composition by Donnelly et al. (1990) in specimens from the Weddell Sea.

Calorific values vary strongly among Southern Ocean fishes (Donnelly et al. 1990; Barrera-Oro 2002; Lea et al. 2002b; Tierney et al. 2002). Variation in energy content can be attributed to numerous factors, such as species, population, time of year, geographic location, sex and maturity stage, feeding condition, mode of life and size (Lawson et al. 1998; Saadettin et al. 1998; Eder and Lewis 2005).

The differences in energy/water content between the two myctophids compared to the bathylagid mirror the differences in life style and feeding regime. Both myctophids are strong diurnal migrators that feed mainly on euphausiids and copepods (Lancraft et al. 1991;Hopkins et al. 1993; Pakhomov et al. 1996; Pusch et al. 2004). In contrast,

▼ **Table 4**. *Electrona antarctica*. Mean energy and water content of size classes and age groups. Standard deviation in parentheses; *n* = sample size. Variation between species significant for all three variables (ANOVA: $p < 0.01$). (*)Values significantly different from all other values in the same column (Tukey's HSD: $p < 0.05$)

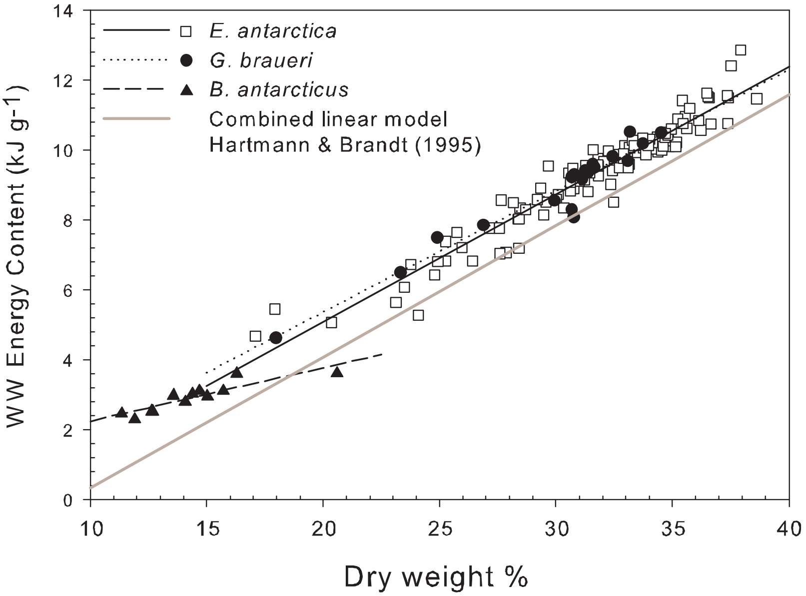
Class / Group	Size range [mm]	n	Water content [%]	DW energy content [kJ g^{-1}]	WW energy content [kJ g^{-1}]
Small	0-34	32	73.1 (3.84)*	27.76 (2.235)*	7.49 (1.36)*
Medium	35-68	68	66.4 (2.21)	29.92 (0.887)	10.05 (0.79)
Large	69-102	14	66.7 (3.25)	30.69 (1.541)	10.25 (1.42)
Age group 0	0-31	21	74.4 (3.92)*	26.94 (2.156)*	6.89 (1.231)*
Age group 1	32-53	52	67.6 (2.57)	29.49 (0.922)*	9.56 (0.826)*
Age group 2	54-77	37	66.3 (2.56)	30.45 (0.919)	10.27 (0.959)
Age group 3	78-102	3	63.6 (1.60)	32.01 (1.885)	11.66 (1.197)

▼**Table 5.** Review of mean water and energy contents of *B. antarcticus*, *E. antarctica* and *G. braueri* by season and region of the Southern Ocean. Standard deviation in parentheses; *n* = sample size

Year	Season	Region	Method[1]	*n*	Mean size [mm]	Size range [mm]	Water content [%]	DW energy content [kJ g^{-1}]	WW energy content [kJ g^{-1}]	Source[2]
Bathylagus antarcticus										
1983	Spring	Scotia Sea	PCA	8	99.4	44 - 145	85.1 (2.3)		3.12	**a**
1986	Autumn	Weddell Sea	PCA	32	77.2	32 - 143	85.9 (2.0)		2.94	**a**
1988	Winter	Scotia Sea	PCA	16	90.0	51 - 150	88.4 (1.4)		2.37	**a**
1999	Summer	Macquarie Ridge	BC	18	116.8	73 - 196	81.8 (1.8)	21.5 (5.0)		**b**
2004	Autumn	Lazarev Sea	BC	12	71.6	36 - 123	85.6 (2.5)	20.4 (1.32)	2.92 (0.42)	**d**
Electrona antarctica										
1983	Spring	Scotia Sea	PCA	16	66.1	33 - 98	69.0 (3.7)		7.93	**a**
1986	Autumn	Weddell Sea	PCA	27	61.9	29 - 101	68.7 (3.4)		8.02	**a**
1988	Winter	Scotia Sea	PCA	35	68.3	29 - 101	69.6 (3.7)		8.45	**a**
1998	Winter	Kerguelen Plateau	BC	5	64.5		60.8 (8.8)	34.3 (3.8)	13.3 (2.6)	**c**
1999	Summer	Macquarie Ridge	BC	20	50.4	30 - 73	69.9 (4.3)	30.8 (9.7)	9.04	**b**
2004	Autumn	Lazarev Sea	BC	113	47.0	16 - 83	68.4 (4.14)	29.4 (1.80)	9.35 (1.58)	**d**
Gymnoscopelus braueri										
1983	Spring	Scotia Sea	PCA	3	110.3	106 - 114	64.2 (2.5)		9.46	**a**
1986	Autumn	Weddell Sea	PCA	3	101.3	88 - 124	66.6 (2.2)		8.83	**a**
1988	Winter	Scotia Sea	PCA	23	81.2	45 - 123	67.2 (2.3)		8.88	**a**
1999	Summer	Macquarie Ridge	BC	18	78.2	37 - 133	70 (7.1)	39.0 (14.3)	10.91	**b**
2004	Autumn	Lazarev Sea	BC	20	87.3	64 - 132	69.9 (4.0)	29.4 (1.51)	8.86 (0.61)	**d**

[1] BC = bomb calorimetry; PCA = proximate composition analysis

[2] a = Donnelly et al. (1990); b = Tierney et al. (2002); c = Lea et al. (2002b); d = this study



▲ **Figure 4.** Correlation between percentage dry weight and energy content per gram wet weight. Individual data from this study were added to the combined linear model of Hartmann and Brandt (1995). *E. antarctica*: y = -2.2077 + 0.3650 × x (r^2 = 0.93; p < 0.01); *G. braueri*: y = -1.5583 + 0.3467 × x (r^2 = 0.94, p < 0.01); *B. antarcticus*: y = 0.7136 + 0.1532 × x (r^2 = 0.8003; p < 0.01).

B. antarcticus remain at greater depth. They have a prey spectrum which includes many low-energy species such as coelenterates, polychaetes and chaetognaths which can affect the energy composition of the fish (Donnelly et al. 1990; Geiger et al. 2000).

Hartmann and Brandt (1995) provided a comprehensive collection of data on the relationship of energy content with proportional dry weight of fishes. Our values fit the results for a number of fishes, both in the Antarctic Ocean (Tierney et al. 2002) and worldwide (Hartmann and Brandt 1995; Anthony et al. 2000; Pedersen and Hislop 2001). The slopes of the regression lines of *E. antarctica* and *G. braueri* closely resemble the combined model of Hartmann and Brandt (1995; Figure 4). The elevated intercepts of the two myctophids are probably related to the body tissue being generally energy dense, which concurs with reported high lipid values in almost all tissue fractions of *E. antarctica* (Reinhardt and Van Vleet 1986; Phleger et al. 1997b). A stable high proportion of lipids could explain the comparatively high energy density at low relative dry mass. The steady increase in energy density with decreasing water content could be explained by a replenishment of energy stores, replacing water with proteins and fat (Geiger et al. 2000).

In *B. antarcticus*, the relationship of energy density and proportional dry weight follows a different pattern. Its high intercept and small slope imply a comparatively high energy content in body tissues at high water content. Energy density only slowly rises when water content declines (Figure 4). This suggests that the tissue replacing water is relatively poor in energy, which agrees with low lipid contents reported by Reinhardt and Van Vleet (1986) and Donnelly et al. (1990).

Electrona antarctica has a lipid class composition which is very different from both *B. antarcticus* and *G. braueri* (Reinhardt and Van Vleet 1986; Lea et al. 2002b). Although differences in lipid class composition are often correlated to differences in biology, they have limited effects on energy content. It has been proposed that *E. antarctica* stores lipids to survive periods of low food supply, whereas *B. antarcticus* probably relies on a short-term use of energy reserves which implies the need to feed constantly (Reinhardt and Van Vleet 1986; Geiger et al. 2000).

3.4.2 Size and age effects on energy content in *E. antarctica*

An increase in energy content was significant with increasing size classes and age groups (Table 4). These trends correspond with the size effect found by Donnelly et al. (1990). In contrast, Tierney et al. (2002) found the highest energy content in the smallest size class. Within specimens of uniform species, geographic location, time of year and size, there can still be considerable variation in energy content due to undetermined random factors (Paul et al. 1998). For example, Tierney et al. (2002) used 6–7 specimens per size class. They could not exclude possible outliers which could have led to an overestimate of the reported mean value in small fish (M. Tierney, personal communication).

The energy content of *E. antarctica* strongly increases with size in age group 0. From the second year on, size-related increase in energy content slows down considerably, while variation increases. Part of this variation may be related to differences in gender and maturation condition. Another source of variation might be the time of spawning. Since *E. antarctica* is believed to be a batch spawner (Hulley 1990), different batches within the same year class may encounter very different food availability which can have a strong influence on the energetic composition of the fish.

Energy data in relation to age groups rather than to arbitrary size classes can be a practical tool to estimate ecosystem energy budgets. The results of this study indicate that using distinct energy contents for each age group in *E. antarctica* could significantly improve energy budget estimates: The total energy budget of a population would strongly be influenced by the proportion between age group 0 juveniles and older fish.

3.4.3 Ecological implications

The size–energy density relationship of *E. antarctica* suggests that the smallest fish invest proportionally more energy in growth and locomotion than older individuals. This view agrees with the common notion that there is a strong need for young fish to grow quickly in order to escape predation pressure (Anthony et al. 2000). The need of an abundant species such as *E. antarctica* to build up high energy reserves over a short period of 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).

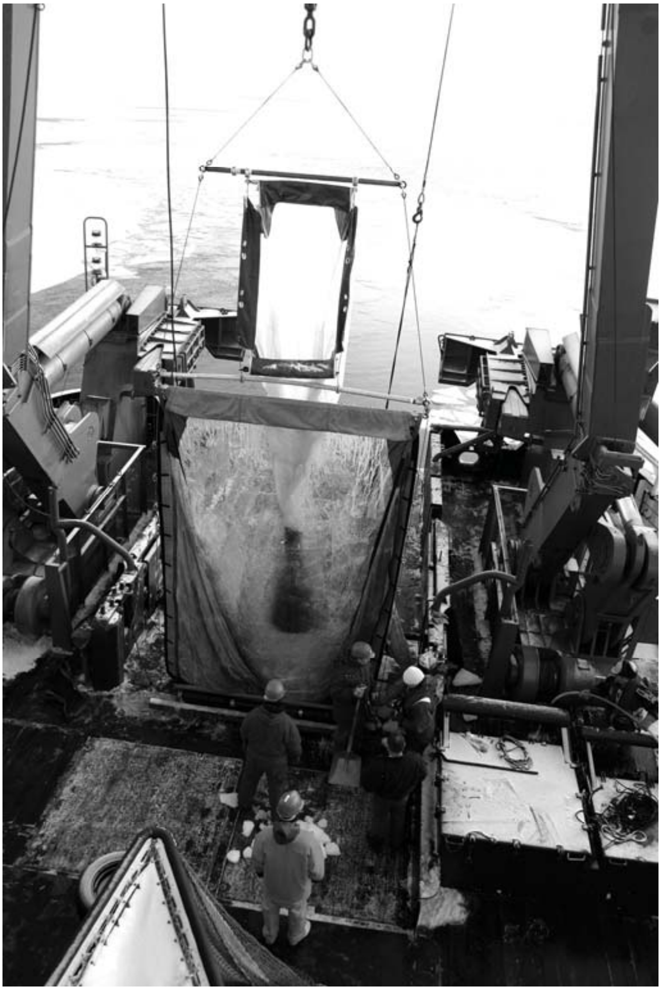
Through its pelagic mode of life, abundance and high lipid content, *E. antarctica* could be seen as the off-shelf counterpart of Antarctic silverfish *Pleuragramma antarcticum*, the primary prey of many top predators in High-Antarctic shelf waters (Hubold 1985; Arnould and Whitehead 1991; Creet et al. 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 an energy density more than twice that of Antarctic krill *Euphausia superba* (Clarke and Prince 1980; Torres et al. 1994). Although being usually much lower in biomass than krill (Lancraft et al. 1989), they represent 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 (e.g. van Franeker 2001; Bost et al. 2002; Quillfeldt 2002; Osman et al. 2004).

Acknowledgements

Special thanks go to V. Siegel (Federal Research Centre for Fisheries, Hamburg) who kindly provided the sampling material for this study. We thank the crew of RV "Polarstern" and J. Buyse for their support. M. Leopold and J. Maes contributed to the improvement of this paper. This work was funded by the Belgian Science Policy (project PELAGANT EV/01/30B), the Dutch Ministry for Agriculture, Nature and Food quality (LNV) and the Dutch Polar Programme (NPP).

Key References

- Donnelly J, Torres JJ, Hopkins TL, Lancraft TM (1990) Proximate composition of Antarctic mesopelagic fishes. Marine Biology 106:13-23
- Greely T, Gartner JVJ, Torres JJ (1999) Age and growth of *Electrona antarctica* (Pisces: Myctophidae), the dominant mesopelagic fish of the Southern Ocean. Marine Biology 133:145-158
- Hartmann KJ, Brandt SB (1995) Estimating energy density of fish. Transcripts of the American Fisheries Society 124:347-355
- Lea MA, Nichols PD, Wilson G (2002b) Fatty acid composition of lipid-rich myctophids and mackerel icefish (*Champsocephalus gunnari*) – Southern Ocean food-web implications. Polar Biology 25:843-854
- Tierney M, Hindell M, Goldsworthy S (2002) Energy content of mesopelagic fish from Macquarie Island. Antarctic Science 14:225-230



The Rectangular Midwater Trawl (RMT).

CHAPTER 4

Distribution, abundance and ecological relevance of pelagic fishes in the Lazarev Sea, Southern Ocean

Hauke Flores, Anton P. Van de Putte, Volker Siegel, Evgeny A. Pakhomov, Jan A. van Franeker, Erik (H.W.G.) Meesters & Filip A. M. Volckaert

Abstract. The distribution and abundance of larval and postlarval fishes was investigated in the Lazarev Sea, Southern Ocean, in March and April 2004. The upper 200 m of the water column were sampled with an 8 m^2 rectangular midwater trawl at 93 stations. The larval species community clustered in a diverse coastal community with high densities of Antarctic silverfish *Pleuragramma antarcticum* larvae and a less diverse offshore community dominated by Antarctic jonasfish *Notolepis coatsi* and the lanternfish *Electrona antarctica*. No postlarval fish were caught in coastal areas. The offshore community of postlarval fishes consisted of the deep-sea smelt *Bathylagus antarcticus*, and the lanternfishes *Gymnoscopelus braueri*, *G. nicholsi* and *E. antarctica*. The latter species clearly dominated, occurring at mean individual and wet mass densities of 0.17 individuals m^{-2} and 0.26 g m^{-2}, respectively. A Generalized Additive Model significantly related the density of postlarval *E. antarctica* to the abundance of Antarctic krill *Euphausia superba*, ocean depth and sea surface temperature. The diet of *E. antarctica* was dominated by copepods and euphausiid larvae. Mean energy density of *E. antarctica* in the upper 200 m was 2.8 kJ m^{-2}, which is equivalent to 36% of the energy stored in Antarctic krill stocks and probably would be considerably higher if a greater depth range were considered. This suggests that *E. antarctica* is a major energy transmitter in the food web of the Lazarev Sea, challenging the classical krill-dominated food web paradigm of the Southern Ocean.

Marine Ecology Progress Series 367 (2008): 271-282

4.1 Introduction

Pelagic offshore waters form the largest marine realm in the Antarctic, accounting for 89% of the marine primary production (Arrigo et al. 1998). In the early years of pelagic ecosystem research, studies focused on the role of Antarctic krill *Euphausia superba*, which forms a major food source of many species of fish, squid, birds and mammals (González & Rodhouse 1998, Wienecke et al. 2000, Casaux et al. 2004, Chapter 2). With time it has become increasingly clear that the Antarctic food web is more complex than the simplistic diatom–krill–top predator concept initially assumed. Especially the importance of pelagic fishes as energy transmitters may have been underestimated (Ainley & DeMaster 1990, Barrera-Oro 2002).

The mesopelagic ichthyofauna of the Southern Ocean comprises 73 species belonging to 24 families (Kock 1992). It is dominated, in species number as well as biomass, by the family Myctophidae or lanternfishes (Barrera-Oro 2002). Thirty-five species of myctophids are known from the Southern Ocean (Hulley 1990). Lanternfishes are major consumers of mesozooplankton (Pakhomov et al. 1996, Pusch et al. 2005) and an important, often dominating part of the diet of a number of bird and mammal species (Barrera-Oro 2002, Casaux et al. 2004). South of the Antarctic Polar Front (APF), the myctophid *Electrona antarctica* is the most abundant lanternfish (Sabourenkov 1990). With the exception of the Ross Sea, it exhibits an almost ubiquitous distribution between the APF and the continental shelf (Hulley 1990).

Other abundant non-myctophid, mesopelagic and epipelagic fishes in the Southern Ocean belong to the families Bathylagidae (deep-sea smelts) and Paralepididae (barracudinas). The deeper-dwelling bathylagid *Bathylagus antarcticus*,for example, is widely distributed in the Southern Ocean. It is found at depths down to 4000 m, but vertical migration extends up to the surface layer (Lancraft et al. 1989, Gon 1990). The paralepidid *Notolepis coatsi* (Antarctic jonasfish) is known to occur between the surface and 2000 m depth (Post 1990).

The early stages of most Antarctic fish species are usually epipelagic. Larvae of Bathylagidae, Myctophidae and Paralepididae are common in oceanic near-surface waters (Hoddell et al. 2000, Fisher et al. 2004). In high Antarctic shelf waters, the nototheniid *Pleuragramma antarcticum* (Antarctic silverfish) is the dominating pelagic species (White & Piatkowski 1993, Hoddell et al. 2000). Spatial separation has been hypothesized between the different life stages of *P. antarcticum*; larvae feed on zooplankton in the surface layer of the shelf waters and move into deeper layers farther offshore when they become juveniles. Mature adults return to the shelf for spawning (Hubold 1992, Maes et al. 2006).

The Lazarev Sea belongs to the less intensively investigated sectors of the Southern Ocean. Between the Antarctic Circumpolar Current in the north and the Coastal Current in the south, large areas are influenced by the eastern extension of the Weddell Gyre with an eastward flow in the north and branches turning south and west in the central Lazarev Sea (Klatt et al. 2005). The major part of the Lazarev Sea covers deep sea and a narrow shelf borders the Antarctic continent.

A scientific survey in austral autumn 2004 provided an opportunity to sample the pelagic ichthyofauna of the Lazarev Sea and to evaluate the results in the light of various abiotic and biological datasets collected in parallel. The objectives of this study are to (1) investigate the distribution of larval and postlarval fishes in the top 200 m layer of the Lazarev Sea, (2) assess the role of different biotic and abiotic factors in controlling the distribution of the most abundant species, *Electrona antarctica*, and (3) evaluate the ecological relevance of myctophid fishes to the pelagic ecosystem.

4.2 Material and methods

4.2.1 Sampling scheme

Larval and postlarval fish were collected between 7 and 26 April 2004 during an expedition with RV ‘Polarstern’ (ANT XXI-4). The cruise was mainly dedicated to surveying the distribution and abundance of Antarctic krill *Euphausia superba* on behalf of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The station grid in the Lazarev Sea (CCAMLR statistical Subarea 48.6) included 4 longitudinal transects along the 0°, 2°, 4° and 6° W meridian and extended from 61° S to the continental coast at approximately 71° S (Figure 1a). Latitudinal spacing between stations was 20 nautical miles (n miles) (37.0 km).

A rectangular midwater trawl (RMT 8+1) net was used as the routine sampling device. It consisted of an RMT 1 (mesh size = 0.33 mm) mounted above an RMT 8 with net opening areas of 1 and 8 m^2, respectively. The RMT 8 had a mesh size of 4.5 mm at the opening and a mesh size of 0.85 mm at the cod end. A calibrated mechanical impeller flow meter mounted outside the net opening allowed the volume of water passing through the net to be estimated. At each station, standard double oblique hauls were conducted, reaching to a depth of 200 m at a trawling speed of 2.5 knots (4.5 km h^{-1}).

4.2.2 Environmental data

Ocean depth, sea surface temperature and surface salinity were continuously recorded by the ship’s sensors. Based on RMT 8 and RMT 1 samples, euphausiid larval and postlarval abundance data (individuals [ind.] 1000 m^{-3}) were collected following the procedures described in Siegel et al. (2004). Surface water total chlorophyll concentration (mg m–3) at each sampling station was obtained from a public database based on the NASA Ocean Biogeochemical model (NOBM: NASA 2007, Gregg & Casey 2007).

The proportion of the sea surface covered by sea ice was monitored by an observer on board while the ship travelled between stations according to the method described in van Franeker et al. (1997). Total ice coverage was estimated for each station as a function of latitude using a linear model with a logit link function (explained deviance

= 67.4%, $p < 0.001$). The same method was applied to estimate the proportion of the sea surface covered by pack-ice floes excluding young ice (explained deviance = 34.2%, $p < 0.05$).

4.2.3 Fish data

All larval and postlarval fish were collected from the RMT 8 and identified to species level. Larvae were either frozen or preserved in 70% ethanol. We measured the standard length (SL) of each postlarval fish to the lower full millimeter immediately after capture. One-third of the postlarval fish were preserved on 4% hexamine-buffered formaldehyde solution in seawater; the rest were frozen at −20°C. In the home laboratory, the frozen fish were thawed and blotted dry with paper tissue. Wet weight (WW) was estimated to an accuracy of 0.01 g. The length–weight relationship obtained from these specimens was used to calculate the WW of the remaining fish (Table 1).

From the 14 stations where a sufficient number of fish were caught, the diet was analysed in 139 *Electrona antarctica*. Stomachs were collected from the fish immediately after thawing and fixed in 4% hexamine-buffered formaldehyde solution in seawater. After fixation, stomachs were dissected under a stereoscopic microscope. Food items were identified to species level and ontogenetic stage if possible. In the case of strongly digested crustaceans, the number of ingested individuals was assumed to be half the number of facet eyes. Calanoid copepods were grouped in the size classes of small (<3 mm) and large (≥3 mm). Reconstructed dry weight was calculated for major taxonomic groups of prey species using published data on mean individual dry mass (Donnelly et al. 1994, Torres et al. 1994, Hagen 2001).

4.2.4 Data analysis

Fish larvae

A hierarchical cluster analysis of sampling sites was performed to investigate the spatial structure of larval species communities. Unidentified larvae and stations where no larvae were caught were excluded from the analysis. A dissimilarity matrix based on the Bray–Curtis index was constructed using presence–absence data of species at each station. Clusters were fused by group-average linking. The density of fish larvae was estimated at each station based on the number of individuals per volume of water filtered and expressed as the number of individuals per surface area (ind. $m^{-3} \times 200$ m = ind. m^{-2}). Overall density per species was calculated as the average over all stations.

▾ **Table 1.** *Bathylagus antarcticus*, *Electrona antarctica* and *Gymnoscopelus braueri*. Parameters of the length–weight regressions. The wet weight (WW) in g was expressed as a function of the standard length (SL) in mm according to the equation: $\log_{10}(WW) = a + b \times \log_{10}(SL)$. N = sample size

Species	N	a	b	R^2	p
Bathylagus antarcticus	24	−5.5296	3.0949	0.90	<0.001
Electrona antarctica	649	−5.2708	3.2157	0.97	<0.001
Gymnoscopelus braueri	35	−5.2182	3.0709	0.91	<0.001

Postlarval fish

Daylight hauls (solar radiation > 10 W m^{-2}) were excluded from analysis of postlarval fish to avoid an underestimation of density and biomass due to vertical migration into deeper layers at daytime (Piatkowski et al. 1994, Pusch et al. 2005, Loots et al. 2007). Similar to density estimates of larvae, number of individuals, wet biomass and energy densities of postlarval fishes were calculated and expressed in ind. m^{-2}, g m^{-2} and kJ m^{-2}, respectively. Energy density was estimated based on the sum of the individual energy contents of adult *Bathylagus antarcticus*, *Electrona antarctica* and *Gymnoscopelus braueri*. Individual energy contents were calculated using the mean wet mass energy content in *B. antarcticus* and *G. braueri* and the relationship between SL and energy content estimated from a subsample of fish from the same survey in *E. antarctica* (Chapter 3).

Generalized Additive Models (GAMs, Hastie & Tibshirani 1995) were used to investigate the relationship of environmental variables with the individual density of *Electrona antarctica* using a suite of publicly available physical and biological datasets and euphausiid abundance data obtained simultaneously by RMT sampling. Data included: ocean depth, surface temperature, surface salinity, surface water total chlorophyll concentration, total ice coverage, abundance of postlarval *Euphausia superba*, abundance of larval *E. superba*, abundance of postlarval euphausiid *Thysanoessa macrura*, and abundance of larval *T. macrura*.

GAMs can be considered as an extension of Generalized Linear Models (GLM, McCullagh & Nelder 1989). They extend the implicit linear relationship between response and explanatory variables of GLMs by fitting higher order smoothing functions to explanatory variables. The flexibility of the smoothing function is determined by the degrees of freedom associated with the smoothing term. The flexibility of the smoother increases at higher degrees of freedom.

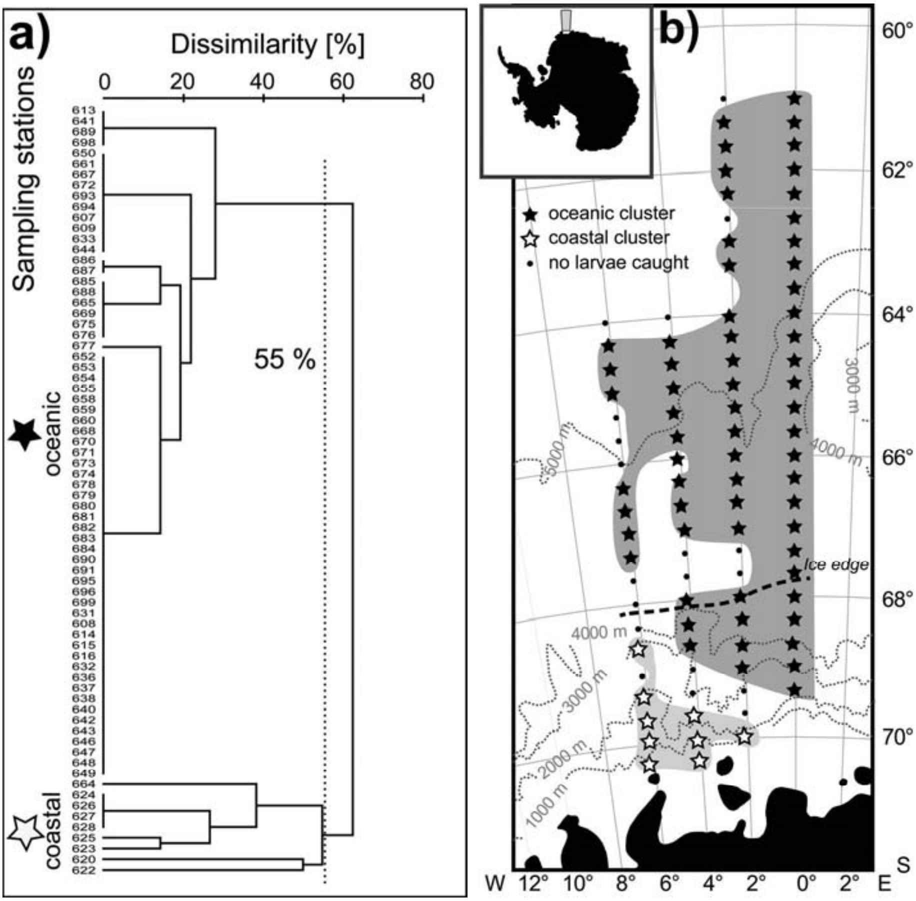
Fish density is comparable with count data, which are typically modeled using a Poisson error distribution (McCullagh & Nelder 1989). We used a Poisson error distribution with a correction for overdispersion (in R termed quasipoisson) combined with a log link function. The number of fish caught per station was used as the discrete response variable. To relate the number of fish to actual densities, the amount of filtered water was used as an offset variable.

The 2 shelf stations with depths less than 500 m were excluded. *Electrona antarctica* is an offshore species and was not caught at these localities. To obtain an equal spread over the entire range of the data, depth values were log-transformed, and a 4th-root transformation was applied to the euphausiid abundance data. Colinearity of variables was assessed by calculating correlation coefficients and variance inflation factors (VIF). The VIF values of all variables were <10, a value below which colinearity is usually not regarded as serious (Quinn and Keough 2004).

Models were fitted with smoothing splines using cross-validation to obtain the optimal degrees of freedom for each variable. The best model was estimated by stepwise forward selection based on the lowest deviance. Significance of decreasing deviance was confirmed with the *F*-test (Quinn and Keough 2004). Regression assumptions were assessed visually by plotting the response variable against fitted values and residuals against variables. The procedure was repeated using ice floe coverage instead of total ice coverage as a descriptor of sea ice conditions. Statistical calculations were performed with the R (R Development Core Team 2006) and Brodgar (Highland Statistics 2006) software packages.

Taxonomic group and species	**N**	**No. of stations**	**F_O (%)**	**F_R (%)**
Bathylagidae				
Bathylagus antarcticus	16	8	8.6	1.8
Myctophidae				
Electrona antarctica	262	55	59.1	29.0
Muraenolepidae				
Muraenolepis sp.	1	1	1.1	0.1
Paralepididae				
Notolepis coatsi	362	60	64.5	40.1
Bathydraconidae				
Akarotaxis nudiceps	1	1	1.1	0.1
Racovitza glacialis	1	1	1.1	0.1
Channichthyidae				
Channichthyidae spp.	4	3	3.2	0.4
Nototheniidae				
Notothenia kempi	2	2	2.2	0.2
Pleuragramma antarcticum	248	7	7.5	27.5
Nototheniidae sp.	1	1	1.1	0.1
Unidentified	5	3	3.2	0.5
No fish	-	20	21.5	-
Total	903	93	-	100.0

◄ **Table 2.** Species composition of larval fishes in the Lazarev Sea, March and April 2004. F_O = frequency of occurrence (percentage of stations where fish larvae were caught), F_R = relative frequency (percentage of the total number of fish sampled), N = number of fish larvae caught



▲ **Figure** 1. (a) Cluster dendrogram of stations according to the species composition of larval fishes and (b) geographic distribution of species clusters in polar stereographic projection. Stations where fish larvae were caught were grouped in a coastal and an oceanic cluster. Geographic overview of the Antarctic continent in inset shows the survey area shaded in grey

4.3 Results

4.3.1 Larval fish

Ninety-three stations were sampled for fish larvae. At 74 of these stations, 903 fish larvae 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 97% of the larvae caught (Table 2).

A hierarchical cluster analysis separated the stations into 2 groups at a dissimilarity level of 55% (Figure 1a). Most stations of one cluster were located in the southern shelf and slope region of the survey area, which is, therefore, referred to as the coastal cluster (Figure 1b). Sea ice was common in this region. At only one station was a single

▾ **Table 3.** Densities (ind. m–2) of dominant species of fish larvae in the spatial clusters shown in Figure 1

Cluster	**Coastal**		**Oceanic**		**Total**	
	Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
Bathylagus antarcticus	0.000	-	0.014	0.046	0.010	0.038
Electrona antarctica	0.000	-	0.221	0.258	0.152	0.237
Notolepis coatsi	0.000	-	0.307	0.241	0.211	0.246
Pleuragramma antarcticum	1.454	2.194	0.000	-	0.141	0.778
All species	1.526	2.215	0.546	0.372	0.523	0.825

specimen of *Notothenia kempi* caught, at a bottom depth of 4100 m. The species composition of the coastal cluster consisted exclusively of notothenioid larvae. It was dominated by *Pleuragramma antarcticum*, which was encountered at 7 of the 9 stations in this cluster. Due to the high numbers of *P. antarcticum* larvae, overall density of larvae in the coastal cluster was considerably higher than in the oceanic cluster (Table 3).

Stations deeper than 3000 m formed an oceanic cluster (Figure 1b). Larvae of *Electrona antarctica* and *Notolepis coatsi* were found throughout this region. *N. coatsi* were more abundant than *E. antarctica* larvae (Table 3). On the easternmost transect, larvae of *Bathylagus antarcticus* were encountered at 8 stations, and a single *Muraenolepis* sp. larvae was obtained.

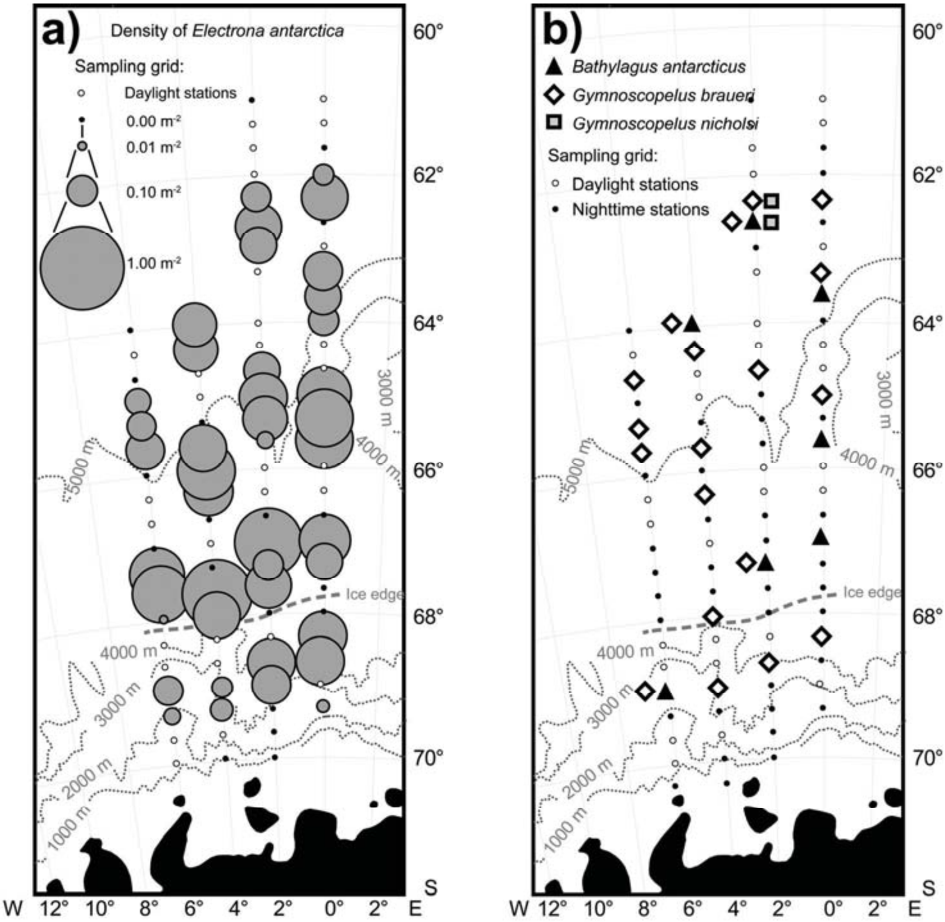
4.3.2 Postlarval fish

Species composition and distribution patterns

The analysis was limited to the 61 stations sampled in darkness because large parts of the populations of the species caught are known to dwell at depths below 200 m during daylight. In total, 1094 individuals of 4 species were caught. *Electrona antarctica* clearly dominated the species community. It was caught at most stations throughout the oceanic part of the area of investigation (Table 4, Figure 2a). The distribution of *Gymnoscopelus braueri* was similar to that of *E. antarctica*, but it occurred in much lower numbers. *Bathylagus antarcticus* was collected at 7 localities (Figure 2b). Twenty-nine of the 40 individuals sampled were caught at a single locality at 69° S, 6° W. Two *G. nicholsi* were caught at 2 stations in the northern part of the survey area (Table 4).

Taxonomic group and species	**N**	**No of stations**	**F_O (%)**	**F_R (%)**	**Length range (mm)**
Bathylagidae					
Bathylagus antarcticus	40	7	11.5	3.7	29–130
Myctophidae					
Electrona antarctica	987	42	68.9	90.2	21–102
Gymnoscopelus braueri	65	20	32.8	5.9	64–132
Gymnoscopelus nicholsi	2	2	3.3	0.2	158–180
No fish	-	19	31.1	-	-
Total	1094	61	-	100.0	-

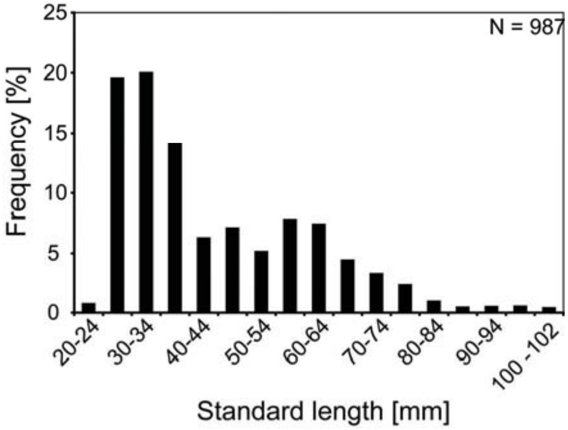
◂ **Table 4.** Species composition of postlarval fishes in the Lazarev Sea, March and April 2004. F_O = frequency of occurrence (percentage of stations where fish were caught), F_R = relative frequency (percentage of total number of fish sampled), N = number of fish caught



▲ **Figure 2**. Spatial distribution of postlarval fishes (polar stereographic projection). (a) Individual density of *Electrona antarctica* (daylight stations excluded from analysis) and (b) stations where *Bathylagus antarcticus*, *Gymnoscopelus braueri* and *Gymnoscopelus nicholsi* were caught (all stations included)

▼ **Table 5.** Individual, biomass and energy densities of the 3 most abundant species of postlarval fish

Species	**Density (ind. m^{-2})**		**Biomass (g m^{-2})**		**Energy (kJ m^{-2})**	
	Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
Bathylagus antarcticus	0.005	0.027	0.012	0.082	0.036	0.246
Electrona antarctica	0.170	0.172	0.261	0.255	2.827	2.723
Gymnoscopelus braueri	0.011	0.026	0.074	0.175	0.614	1.534



◂ **Figure 3.** *Electrona antarctica.* Length–frequency distribution of postlarvae. The percentage of the total number of fish is shown for each 5 mm length class

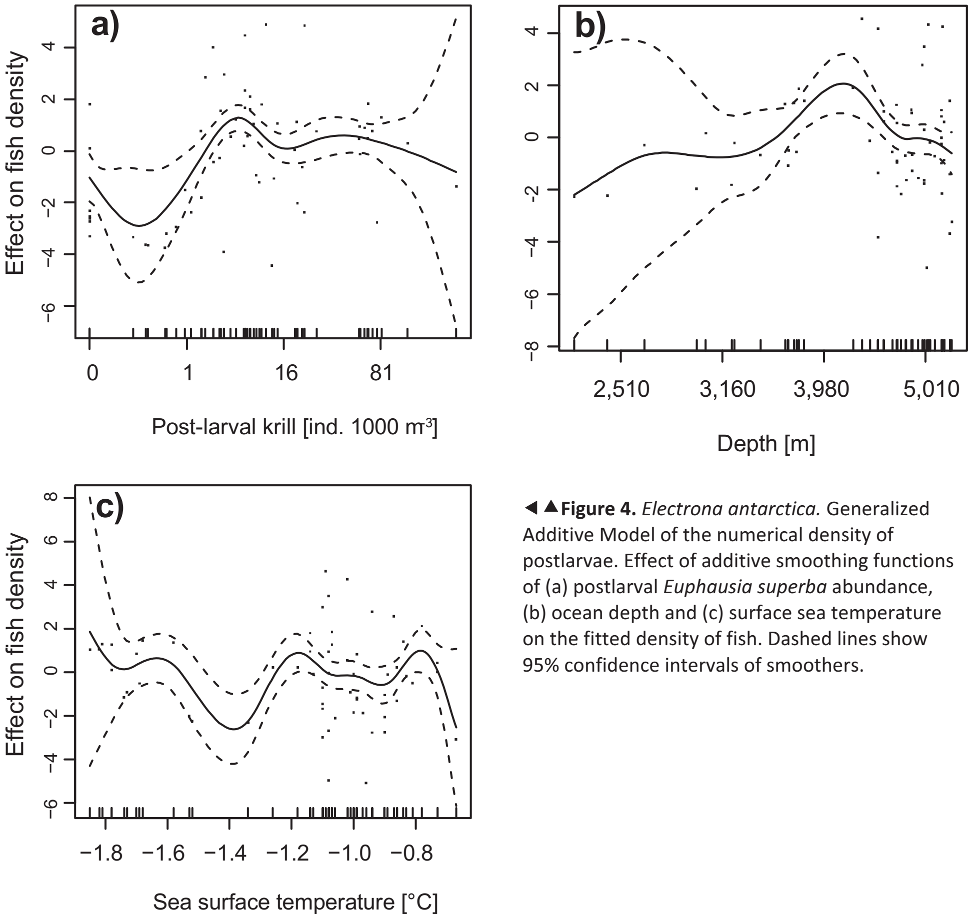
The overall average number of individuals, biomass and energy densities of postlarval *Bathylagus antarcticus*, *Electrona antarctica* and *Gymnoscopelus braueri* are shown in Table 5. Highest densities of *E. antarctica* were found between 66° and 68° S (Figure 2a). The length-frequency distribution of the postlarval E. antarctica covered almost the entire known size range (Hulley 1990) and was dominated by fish between 25 and 39 mm SL, averaging at 43.6 mm (Figure 3). The low numbers caught of *B. antarcticus* and *G. braueri* preclude a meaningful analysis of their distribution patterns and size distributions.

Density of postlarval Electrona antarctica in relation to environmental variables

The relationship of the density of postlarval *Electrona antarctica* with a number of environmental variables was explored using GAMs. The GAM with the lowest deviance included abundance of postlarval *Euphausia superba*, ocean depth, sea surface temperature and abundance of *Thysanoessa macrura* larvae. This model explained 78.3% of the deviance (Table 6). The smooth term of the latter variable, however, was insignificant (Table 7). Excluding the abundance of T. macrura larvae led to an increase in unexplained deviance of only 4%, suggesting that a combination of postlarval krill abundance, depth and sea surface temperature was the best predictor of the density of postlarval *E. antarctica* (Table 6);

▾ **Table 6.** *Electrona antarctica*. Comparison of Generalized Additive Models relating the density of fish to combinations of stepwise added environmental variables. p = *F*-test significance of change in deviance compared with the model in the preceding row. The model discussed in the text is highlighted in **bold** and shaded

Model no.	Variables	Deviance	Explained deviance	p
1	Postlarval krill abundance	624.1	42.1%	0.003
2	Model 1 + ocean depth	498.0	53.8%	0.008
3	Model 2 + sea surface temperature	247.6	74.5%	0.032
4	Model 3 + larval Thysanoessa macrura abundance	233.6	78.3%	0.041



◀ ▲**Figure 4.** *Electrona antarctica.* Generalized Additive Model of the numerical density of postlarvae. Effect of additive smoothing functions of (a) postlarval *Euphausia superba* abundance, (b) ocean depth and (c) surface sea temperature on the fitted density of fish. Dashed lines show 95% confidence intervals of smoothers.

▼**Table 7.** Model parameters of smoothing terms of the 2 most parsimonious models (from Table 6). df = degrees of freedom, p = significance of smoother. The model analyzed in the discussion is highlighted in bold and shaded

	Model 3		**Model 4**	
Smoother for variable	**df**	**p**	**df**	**p**
Postlarval krill abundance	6.6	<0.001	4.7	<0.001
Ocean depth	6.6	0.005	4.1	0.001
Sea surface temperature	9.0	0.041	2.7	0.019
Larval *Thysanoessa macrura* abundance	-	-	1.6	0.168

Postlarval krill abundances between 2 and 11 ind. m^{-3} and depths between 3800 and 4500 m positively affected the fitted density of *Electrona antarctica*. Low abundance of postlarval krill had a negative effect on the fitted density of this lanternfish (Figure 4a,b). The effect of sea surface temperature on modeled fish density was largely neutral, although it significantly improved the overall model fit in combination with the other variables (Figure 4c). Large confidence intervals indicate that model reliability was low at depths shallower than approximately 3200 m, postlarval krill abundances above 80 ind. m−2 and sea surface temperatures below −1.7°C (Figure 4).

Diet of Electrona antarctica

Stomachs of 139 postlarval fish were investigated for their content. The fish had a mean SL of 43.9 mm, ranging between 20 and 79 mm. Stomachs were not collected from the few larger fish obtained, which were sacrificed entirely for energy investigations (Chapter 3). Of the total examined, 120 stomachs contained food items. Most of the stomach contents, however, were at an advanced stage of digestion. At least 12 prey species were found. The majority of prey items were copepods (Table 8). Calanoid copepods ≥ 3 mm were the most numerous, accounting for 28% of the number of prey items. Among them, *Metridia gerlachei* was the most frequently identified species. The second most frequent large copepod species identified was *Pareuchaeta antarctica*. Among the copepods < 3 mm in size (16% of food items), *Aetidiopsis minor* and *Scolecithricella minor* were the only identifiable prey species. Euphausiids accounted for 28% of the food items. A small number of furcilia larvae and adult euphausiids could be identified as *Thysanoessa macrura*. Ostracods (6.6%) and amphipods (5.7%; e.g. *Hyperiella dilatata*) were less frequent (Table 8). *Limacina* spp. (1.9%) were found occasionally.

Prey item	N	Proportional N (%)	Mean ind. DW (mg)	Proportional DW (%)
Ostracods	21	6.6	0.54[a]	4.55
Copepods	166	52.6	0.68[a]	44.80
Postlarval euphausiid	8	2.5	3.94[b]	12.57
Euphausiid furcilia	13	4.1	0.85[c]	4.41
Euphausiid calyptotis	67	21.2	0.22[c]	5.87
Euphausiids total	88	27.8		22.85
Amphipods	18	5.7	3.87[b]	27.81
Others	23	7.3	-	-
Total	316	100.0	-	100.0

[a]from Donnelly et al. (1994)
[b]from Torres et al. (1994)
[c]from Hagen (2001)

◂ **Table 8.** *Electrona antarctica.* Diet composition from 139 fish sampled (20–79 mm SL); 19 stomachs were empty. Proportional dry weights were reconstructed based on published mean individual weights. DW = dry weight, N = number of diet items

4.4 Discussion

Only a few fish surveys have been conducted in the less intensively investigated sectors of the Southern Ocean (Hoddell et al. 2000, Granata 2002, Donnelly et al. 2004). Our study forms the first published record on the distribution of postlarval fishes in the pelagic waters of the Lazarev Sea and contributes new data on the distribution of fish larvae, 23 yr after the data collection of the most recent published record (Efremenko 1991). The restricted fishing depth (0–200 m) of the survey limited the chances of sampling the full range of deep-dwelling species. Because the natural depth distributions of the postlarval fishes caught exceed 200 m at night (Collins et al. 2008), and due to possible net avoidance by larger fish, their individual and biomass densities were probably underestimated. With few exceptions (Piatkowski et al. 1994, Duhamel et al. 2000, Collins et al. 2008), however, data collected with relatively small macrozooplankton nets present the best information on mesopelagic fish in the Southern Ocean available to date (Lancraft et al. 2004, Donnelly et al. 2006). In this sense, the standardized, spatially dense sampling scheme of the present study provided a dependable dataset for minimum abundance estimates of Antarctic mesopelagic fishes.

4.4.1 Larval fish

Ten species of larval fish belonging to 7 families were collected. The taxonomic richness was small compared with reports from nearby areas, such as Efremenko (1991) who found 25 species from 8 families in the Lazarev Sea in autumn, and White & Piatkowski (1993) who reported 18 species from 8 families from the adjacent Weddell Sea in summer. Comparability among studies is often complicated by the difference in depth ranges sampled and sampling gears used. More importantly, extensive sampling of the diverse shelf-associated species assemblage in these studies probably contributed to an elevated species richness compared with our more oceanic sampling scheme. In high Antarctic offshore waters, species numbers comparable with our findings are representative for a sampling depth between 100 and 300 m (Kaufmann et al. 1995, Morales-Nin et al. 1995, Fisher et al. 2004).

A distinct separation into coastal and oceanic species communities was apparent from the cluster analysis. This pattern reflects the contrast between the shelf-associated species community dominated by notothenioids and the offshore community of mesopelagic fishes in the Southern Ocean (DeWitt 1970, Hoddell et al. 2000, Granata 2002). The 6 notothenioid species encountered on the few shelf stations can be considered as a subsample of the coastal ichthyoplankton community of the Lazarev Sea (Efremenko 1991, White & Piatkowski 1993). Many species of this taxonomic group are endemic to high Antarctic waters (Loeb et al. 1993). Three of these, *Akarotaxis nudiceps*, *Rakovitza glacialis* and *Pleuragramma antarcticum*, were collected during the present survey. The dominance of *P. antarcticum* larvae often observed in Antarctic shelf and slope waters could be confirmed for the Lazarev Sea (Kaufmann et al. 1995, Hoddell et al. 2000, Granata 2002).

The ichthyoplankton composition was less diverse in offshore waters. *Electrona antarctica* and *Notolepis coatsi* larvae occurred widely in the offshore parts of the survey area. They are typically the dominant species of fish larvae in the oceanic part of the Southern Ocean south of the APF (Morales-Nin et al. 1995, Hoddell et al. 2000, Fisher et al. 2004). *Muraenolepis* sp. and *Bathylagus antarcticus* have been reported to be scarce in high Antarctic surface waters (Kaufmann et al. 1995, Morales-Nin et al. 1995). The elevated frequency of *B. antarcticus* larvae in the east of the survey area might be related to upwelling of deeper water layers close to the Maud Rise seamount (Holland 2001).

As a consequence of their planktonic mode of life, a pronounced role of bottom topography and prevailing currents in structuring the distribution of larval fish communities is typical (Koubbi et al. 1991, White & Piatkowski 1993, Hoddell et al. 2000). In the ocean around the Antarctic continent, separation of coastal and offshore waters is enhanced by a latitudinal succession of circumpolar current systems with longitudinal flow, such as the westward flowing Coastal Current. In the Lazarev Sea, the northern boundary of this current system largely coincides with the shelf break, forming an effective physical barrier between oceanic and coastal ichthyoplankton communities (Klatt et al. 2005).

4.4.2 Postlarval fish

Species composition and distribution patterns

Four species of postlarval fish were collected in offshore waters: *Bathylagus antarcticus* (Bathylagidae) and *Electrona antarctica*, *Gymnoscopelus braueri* and *G. nicholsi* (Myctophidae). The absence of these mesopelagic fishes from the coastal areas reflected the spatial separation observed in the larval community. Shelf-associated postlarval fish were probably not sampled representatively at the few shelf and slope stations of the survey, leaving no evidence of postlarval *Pleuragramma antarcticum*, the dominating pelagic species on the Antarctic shelf. A range of species similar to our findings with *E. antarctica* as the most common postlarval fish was reported from the upper 200 m of the water column in various areas of the Southern Ocean (Hoddell et al. 2000, Lancraft et al. 2004, Donnelly et al. 2006).

The density of *Electrona antarctica* individuals (0.170 ind. m^{-2}) was substantially higher compared with values reported for the upper 200 m, which range between 0.011 (Lancraft et al. 2004) and 0.099 ind. m–2 (Kaufmann et al. 1995). The majority of *E. antarctica* sampled in the Lazarev Sea were juveniles. The 2 major modes in the length-frequency distribution (30 to 34 mm and 55 to 59 mm) correspond to the length classes of 1 and 2 year old fish (Figure 3; Greely et al. 1999). Due to the dominance of juveniles, high individual densities were not reflected in biomass density (0.261 g WW m^{-2}), which was at the lower end of the range reported from the western Weddell Sea and adjacent waters (Lancraft et al. 1989, Donnelly et al. 2006), but considerably higher than values reported from the Ross Sea, the Scotia Sea and the

APF (Piatkowski et al. 1994, Donnelly et al. 2004, Collins et al. 2008). The low numerical and biomass densities of *Bathylagus antarcticus* and *Gymnoscopelus braueri* in the Lazarev Sea were in the range reported from the near-surface layer (Kaufmann et al. 1995, Donnelly et al. 2006).

Density of postlarval Electrona antarctica in relation to environmental variables

Postlarval *Electrona antarctica* density could best be modeled by a GAM including abundance of postlarval *Euphausia superba*, ocean depth and sea surface temperature. Ocean depths between about 3800 and 4500 m had a positive effect on the modeled density of *E. antarctica*, whereas low abundances of postlarval krill negatively affected the fitted fish density (Figure 4a,b).

A growing number of studies has exemplified the benefit of GAMs in ecological datasets, including marine and fisheries ecology (Maravelias et al. 2007, Zarauz et al. 2007). Loots et al. (2007) modeled the habitat use of *Electrona antarctica* as a function of bathymetry, sea surface temperature and chlorophyll *a* (chl *a*) concentration in the Kerguelen Archipelago. They argued that chl *a* concentration inversely reflected food availability. Unlike the findings of Loots et al. (2007), surface chlorophyll concentration did not significantly contribute to the predicted density of *E. antarctica* in our model. Chlorophyll concentration cannot always be correlated to food availability because it indicates algal standing stock rather than the primary production rate. Instead, abundance of postlarval krill was the most significant component. In less productive waters, postlarval krill can be expected to be scarce. The same holds true for copepods and euphausiid larvae, the primary prey of *E. antarctica* (Table 8). The negative effect of declining postlarval krill abundance on the modeled density of *E. antarctica* indicates that both species responded to similar environmental constraints. Despite differences in approach, hydrographical setting, zoogeographic zone and environmental variables, the investigations of Loots et al. (2007) and ours agree in relating the distribution of E. antarctica to hydrography and food availability. It can be assumed that the inclusion of a parameter more directly reflecting food availability, such as overall mesozooplankton biomass, would increase model performance, when available.

Ecological significance of fish: the case of Electrona antarctica

The environmental variables positively affecting the modeled density of *Electrona antarctica* in the Lazarev Sea occur widely in the Southern Ocean, indicating a huge potential of this species in the pelagic ecosystem. The diet of *E. antarctica* was dominated by copepods with respect to numerical and dry mass proportions (Table 8). The food composition of *E. antarctica* is known to vary with area and season and has been reported to shift towards a higher proportion of euphausiids in larger fish (Rowedder 1979, Williams 1985). The proportion of euphausiids in the diet might have been somewhat underestimated because the largest fish (SL ≥ 80 mm) were very scarce and not available for stomach analysis. This study confirms the dominance of copepods in the diet of postlarval *E. antarctica* <90 mm SL in the Lazarev Sea reported by Pakhomov et al. (1996).

The taxonomical range of the diet composition reflected a typical catholic diet, indicating that *Electrona antarctica* can rely on a diversity of resources (Sabourenkov 1990). A diverse prey spectrum in combination with diel vertical migration enables *E. antarctica* to exploit both mesopelagic and epipelagic resources. Through diel vertical migration, the fish acts as an effective energy store and carrier between the mesopelagic and epipelagic realms. Such a 'biological pump' (Radchenko 2007) could work both downwards and upwards. The myctophid's high energy storage capacity effectively binds resources in periods of elevated epipelagic secondary production, enhancing a fast transfer into deeper layers (Donnelly et al. 1990, Chapter 3). During times of poor epipelagic food availability, the myctophid can rely on these reserves as well as deeper living zooplankton, providing energy to the top predators at the surface by nocturnal upward migration.

The relative importance of myctophids for the Southern Oceanic ecosystem is often distorted by the omnipresence of Antarctic krill and the under-representation of pelagic fishes in many sampling schemes. The perceived limited ecological significance of myctophids contrasts with their common presence in the diets of a range of Antarctic marine bird and seal species (Ainley et al. 2003a, Connan et al. 2007, Luque et al. 2007). Ichii et al. (2007) recently demonstrated that non-breeding chinstrap penguins *Pygoscelis antarctica* and lactating Antarctic fur seals *Arctocephalus gazella* perform foraging trips to obtain energy-rich myctophids, even when krill is abundant close to their breeding colonies. While biomass density of *Electrona antarctica* (0.3 g m^{-2}) was low compared with the concurrently sampled Antarctic krill, which were in the order of 1.9 g m^{-2} (V. Siegel unpubl. data), energy density of the fish averaged 2.8 kJ m^{-2} (Table 5). For comparison, a tentative estimate of the energy density of Antarctic krill in the area of investigation, based on an average wet weight energy content of 4.1 kJ g^{-1} (Torres et al. 1994), calculates to 7.8 kJ m^{-2}. Thus, *E. antarctica* in the upper 200 m alone represented 36% of the energy density of Antarctic krill. This figure is probably an underestimate of the total population's energy content due to the shallow sampling depth. In high Antarctic oceanic waters, about 24 to 70% of the biomass of *E. antarctica* between the surface and 1000 m depth has been reported to occur in the upper 200 m at night (Lancraft et al. 1989, Donnelly et al. 2006). In contrast, krill biomass estimates are unlikely to change when a wider depth range is considered (Siegel 2005). Thus, *E. antarctica* may have formed an energy resource similar in magnitude to the more abundant krill.

Assuming 2 major trophic pathways in the high Antarctic (Hopkins et al. 1993), the energy flow starting with phytoplankton and protozoans will mainly flow either (1) via krill, or (2) via copepods and myctophids to the top predators, partly comprising intermediate trophic steps via cephalopods and large fishes. The latter food web contains an additional trophic level, which would be associated with about 90% energy loss. Interestingly, estimates of bulk biomass in the Southern Ocean were very similar for krill (67 to 297 × 10^6 t; Atkinson et al. 2004, Siegel 2005) and myctophids (70 to 275 × 10^6 t; Gjosaeter & Kawaguchi 1980, Naumov 1985, Lubimova et al. 1987). Currently, there is an accepted paradigm that total biomass of Antarctic krill and copepods in the Antarctic are equal (Voronina 1998). Yet, the annual krill production to biomass (P/B) ratio coefficient is about 1 (Pakhomov 2000, Siegel 2000), while for copepods it is at least 6 to 7 for large calanoid copepods and perhaps higher for small copepods (Voronina 1984). This leads to the conclusion that energy flow through the copepod community could be several (up to 10) times higher than through krill, largely accounting for an extra trophic level and explaining why the total biomass of myctophids and Antarctic krill in the Southern Ocean can be expected to be in the same order of magnitude.

By comparing krill and myctophid energy stocks sampled simultaneously, this study provided new evidence that the copepod–fish–top predator link is probably as important as the traditionally emphasized krill trajectory in the Southern Ocean food web. However, better knowledge of trophic interactions at all trophic levels is necessary to obtain an accurate picture of the role of fish in the pelagic food web, and more precise estimates of mesopelagic fish stocks and their distribution are needed that are based on sampling schemes specifically tailored for that purpose.

4.5 Conclusions

This study provided a novel baseline assessment of the pelagic ichthyofauna of the Lazarev Sea. A wide and abundant distribution of larval and postlarval fishes and a pronounced role of *Electrona antarctica* in the pelagic energy budget in autumn provided evidence that pelagic fishes play an important role in the ecosystem of the Southern Ocean, challenging the traditional krill-centered concept of the Southern Ocean food web. It was demonstrated that the distribution of an ecologically important species such as *E. antarctica* can be related to a limited set of environmental variables. On a larger scale, similar models may help to explain the distribution of *E. antarctica* and its response to a changing environment. In the context of ecosystem management, a closer look at mesopelagic fishes could add a new perspective relating to the ecological consequences of human activities in the Antarctic marine environment. This aspect might become more important in the future with respect to bycatch in the expanding krill fisheries and potentially developing fisheries directed at mesopelagic fish.

Acknowledgements.

Captain and crew of RV ‘Polarstern’ provided excellent support in a challenging environment. We kindly thank U. Bathmann and the Alfred Wegener Institute for Polar and Marine Research (AWI) for support. We express special thanks to M. Haraldsson, M. Vortkamp and S. Schöling for technical assistance during the cruise and to R. Johnson for grammatical corrections. Some data used in this study were acquired using the GES-DISC Interactive Online Visualization ANd aNalysis Infrastructure (Giovanni) as part of the NASA's Goddard Earth Sciences (GES) Data and Information Services Center (DISC). This study was supported by the Netherlands AntArctic Programme (NAAP project no. 851.20.011), the Dutch Ministry for Agriculture, Nature and Food Quality (LNV), the Belgian Science Policy (BELSPO project no. EV/01/30B, ‘PELAGANT’) and the German Federal Ministry for Food, Agriculture and Consumer Protection (BMVEL).

Key References

- Efremenko V (1991) Ichthyoplankton studies in the Lazarev Sea. Journal of Ichthyology 32:129-133
- Hopkins TL, Ainley DG, Torres JJ, Lancraft TM (1993) Trophic structure in open waters of the marginal ice zone in the Scotia-Weddell confluence region during spring (1983). Polar Biology 13:389-397
- Loeb V, Kellermann A, Koubbi P, North A, White M (1993) Antarctic larval fish assemblages: a review. Bulletin of Marine Science 53:416-449
- Loots C, Koubbi P, Duhamel G (2007) Habitat modelling of *Electrona antarctica* (Myctophidae, Pisces) in Kerguelen by Generalized Additive Models and Geographic Information Systems. Polar Biology 30:951-959
- Pakhomov EA, Perissinotto R, McQuaid C (1996) Prey composition and daily rations of myctophid fishes in the Southern Ocean. Marine Ecology Progress Series 134:1-14

The EM-Bird for measuring ice thickness being connected to the helicopter.

CHAPTER 5

Density of pack-ice seals and penguins in the western Weddell Sea in relation to ice thickness and ocean depth

Hauke Flores, Christian Haas, Jan A. van Franeker
& Erik (H.W.G.) Meesters

Abstract. Aerial band transect censuses were carried out parallel with ice thickness profiling surveys in the pack ice of the western Weddell Sea during the ISPOL (Ice Station POLarstern) expedition of R.V. Polarstern from November 2004 to January 2005. Three regions were surveyed: the deep sea of the Weddell Sea, a western continental shelf/slope region where R.V. Polarstern passively drifted with an ice floe (ISPOL), and a northern region (N). Animal densities were compared among regions and in relation to bathymetry and ice thickness distribution. Crabeater seals *Lobodon carcinophaga* were the most abundant species in all three regions. Their density was significantly lower in the deep sea (0.50 km^{-2}) than in the ISPOL (1.00 km^{-2}) and northern regions (1.21 km^{-2}). Weddell seals *Leptonychotes weddellii* were not sighted in the deep-sea region, their density elsewhere ranging from 0.03 (N) to 0.08 km^{-2} (ISPOL). Leopard seals *Hydrurga leptonyx* were observed in all three areas, but could only be quantified in the deep-sea (0.05 km^{-2}) and northern regions (0.06 km^{-2}). The abundance of emperor penguins *Aptenodytes forsteri* was markedly higher in the northern (0.75 km^{-2}) than in the ISPOL (0.13 km^{-2}) and the deep-sea region (not quantified). Crabeater seal density was significantly related to ocean depth and modal ice thickness.

Deep Sea Research II 55 (2008): 1068-1074

5.1 Introduction

In the Southern Ocean, sea ice is a major factor controlling the distribution of birds and mammals (Ainley et al. 1994, 1998; van Franeker et al. 1997; Southwell et al. 2005). For many top predators, ice provides a foraging ground, resting site and nursery platform. Changes in the extent of sea ice are thus bound to affect populations of those species (Croxall et al. 2002; Weimerskirch et al. 2003). In the Weddell Sea the distribution of pack ice is largely controlled by the Weddell Gyre (Orsi et al. 1993; Yaremchuk et al. 1998). Its clockwise transport of surface water enhances the retention of sea ice in the southern and western Weddell Sea, making it a region where significant amounts of oceanic multi-year ice persist through summer (Gill 1973; Harder and Fischer 1999).

Various characteristics of sea ice, including ice cover, floe size, age and structure, are closely related to ice thickness distribution. Satellite imagery does not provide sufficient small-scale detail on ice thickness, but a new method using airborne electromagnetic induction can provide highresolution data (Haas et al. 2007a, b).

A number of bird and mammal species have developed a mode of life entirely adapted to the Antarctic pack ice. Four ice-breeding seal species are found in the Antarctic. Among them, the crabeater seal *Lobodon carcinophaga* is the most abundant (Erickson and Hanson 1990). During the breeding period, which lasts from September to early November (Siniff 1991; Southwell et al. 2003), its distribution may be controlled by ocean depth and sea-ice distribution (Southwell et al. 2005). The leopard seal *Hydrurga leptonyx* is less abundant but disperses more widely (Bester et al. 1995 2002). Mother–pup pairs were observed on sea ice between early November and late December (Southwell et al. 2003). The Weddell seal *Leptonychotes weddellii* contrasts with the previous two species by being largely confined to coastal shelf areas (Siniff 1991), breeding on fast ice between October and December (Reijnders et al. 1990; Lake et al. 1997; Southwell et al. 2003). The Ross seal *Ommatophoca rossii* is the least abundant species of ice seals, breeding on sea ice in the period from late October to late November (Southwell et al. 2003).

Among the penguins, only two species are fully adapted to life in ice-covered waters. The emperor penguin *Aptenodytes forsteri* even breeds on coastal fast ice during the winter period (Woehler 1993; Kooyman 2002). The Adélie penguin *Pygoscelis adeliae* breeds during summer in colonies on ice-free parts of the continental coast or nearby islands (Woehler 1993; Kerry et al. 1995; Kirkwood and Robertson 1997). The Chinstrap Penguin *Pygoscelis antarctica* is an ice species to some extent, but is restricted to more northerly areas, barely reaching the outer edge of the pack ice (Kooyman 2002).

There is little recent information on top predator abundance in the inner Weddell Sea. A number of attempts were made to quantify seal abundance, dating from more than 20 years ago (Bonner and Laws 1964; Siniff et al. 1970; Erickson et al. 1983). The latest report gathers data mainly collected in the eastern Weddell Sea, where pack ice was virtually absent during the survey (Bester and Odendaal 2000). Other more recent top predator censuses concentrated on the more northern Weddell Sea pack ice and adjacent open water (Joiris 1991; van Franeker 1992), the Lazarev Sea (Bester et al. 1995, 2002), east Antarctica (McMahon et al. 2002; Southwell et al. 2005) and the Ross Sea (Ainley et al. 1984; Van Dam and Kooyman 2003).

Several publications have attempted to link top predator density to ice properties, mostly focusing on 'horizontal' properties, such as proportion of ice cover, floe size or ice type (van Franeker et al. 1997; Bester et al. 2002; Chapman et al. 2004; Southwell et al. 2005). Only McMahon et al. (2002) included ice thickness as a variable tested to predict the distribution of crabeater seals in winter.

During the ISPOL 2004/2005 expedition, aerial ice thickness profiling surveys offered the opportunity to combine top predator censuses with on-line ice thickness measurements. This paper provides new information on the distribution and abundance of penguins and seals in the pack ice of the western Weddell Sea and discusses potential correlations of crabeater seal density with ice thickness and bathymetry.

5.2 Methods

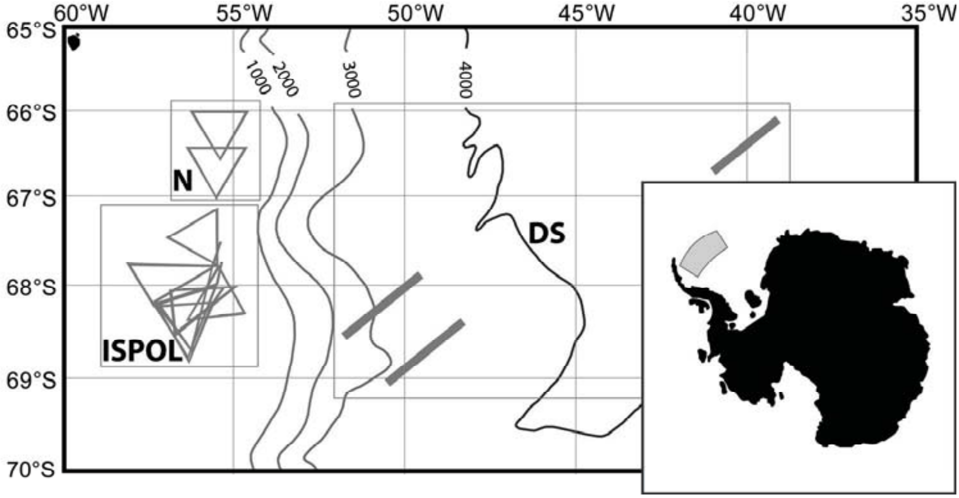
5.2.1 Data collection

Aerial surveys of top predators and ice thickness measurements were conducted simultaneously from a BO 105 helicopter between 20 November 2004 and 4 January 2005 during the Ice Station POLarstern (ISPOL) cruise of R.V. Polarstern (ANT XXII-2).

Ice thickness was measured with a helicopter-borne electro-magnetic induction sensor, the so-called EM-Bird. Ice thickness was obtained as an estimate of total ice (plus snow) thickness with an accuracy of 70.1 m over level ice and with a spacing of 3–4 m between measurements. For further details on the accuracy and processing of EM measurements, see Haas et al. (2007a, b) and Pfaffling et al. (2007).

Censuses of top predators were conducted by a single observer (H. Flores) during flights made for ice thickness distribution mapping. Some aspects of census methods were imposed by requirements for the ice study. Most importantly, flight altitude for ice measurements was generally fixed at 730 m, which is well below the altitude commonly used in aerial surveys of pack-ice seals (Bester and Odendaal 2000; Bester et al. 2002; Southwell 2005b). Standard flight speed during the surveys was 780 knots (7148 km h^{-1}).

Census methodology followed a band transect procedure (e.g., Wiig and Derocher 1999). Because of the low altitude and relatively high speed of the helicopter, a very narrow transect width had to be used to meet the prerequisite of detection of all animals present within the band. Reference points inside the cockpit were used to



▲ **Figure 1**. Distribution of census flights in the western Weddell Sea. Flight patterns in indicated survey regions drawn in grey. DS = deep sea region; ISPOL = ISPOL floe region; N = northern region. Solid lines represent 1000 m – isobaths. Geographic overview in lower right corner.

identify the borders of the transect band. The cockpit reference points were constructed using markings on the heli-deck viewed by the observer in a fixed position. Distances between markings on deck were extrapolated to bandwidth at ground level when flying at standard altitude. Depending on the actual flight altitude, the width of the transect band at ground level varied from 70 to 80 m. Correctness of the reference points in identifying band width at ground level was controlled by flying over an object of known length (the Polarstern) at survey altitude.

Flights were conducted in three different regions (Figure1; Table 1):

- The deep-sea part of the Weddell Sea with ocean depth exceeding 2000 m (DS);
- the region around ISPOL where *Polarstern* was anchored to an ice floe and drifted along the western shelf-slope of the Weddell Sea (ISPOL);
- a region along the ship’s northbound track after leaving the floe (N).

Flight tracks were designed as either two parallel transects (DS) or in a triangular pattern (ISPOL, N), in which case each side of the triangle was considered as a transect. Ice thickness measurements were made during all flights in the deep-sea and ISPOL areas, but not in the northern region. One northern flight was made exclusively for the predator survey, during which flight altitude was changed to 60 m, widening the transect band to 140 m. Ocean depth at the geographic centre point of each transect was estimated with bathymetric data based on combined depth soundings and satellite-based gravity measurements from a public database (Smith and Sandwell 1997; Scripps Oceanographic Institution 2006).

▼**Table 1.** List of census flights. Hour of day in approximate solar time. Flights without parallel ice thickness measurements in *italic*

Region	**Flight Date**	**Hour of day**	**Depth [m]**	**No of transects**	**Transect width [m]**	**Area [km^2]**
Deep sea (DS)	20 Nov 2004	12-14	4644	2	70	9.6
	22 Nov 2004	13-14	3378	2	70	11.0
	24 Nov 2004	10-12	3280	2	70	11.9
DS total				6		32.5
ISPOL	29 Nov 2004	8-9	1006	3	70	10.4
	9 Dec 2004	5-7	601	3	80	17.6
	14 Dec 2004	5-7	1328	3	75	14.7
	14 Dec 2004	8-9	629	3	75	15.7
	15 Dec 2004	10-12	458	3	75	17.8
	18 Dec 2004	6-8	539	3	70	18.4
	29 Dec 2004	10-12	492	4	70	20.1
ISPOL total				22		114.7
North (N)	*03 Jan 2005*	11-13	1211	3	140	31.7
	04 Jan 2005	8-9	698	3	70	12.1
N total				6		43.8
All regions				34		190.9

Seals and penguins were identified to species if possible, and counted. Animals sighted outside the transect band also were noted in order to collect qualitative distributional data on less common species. Each sighting was assigned a GPS waypoint to record time and position along the transect line. The census was continuous during the time the helicopter was moving along the transect at standard altitude and speed. Counting was paused when passing corner points of triangular flights to avoid repeated counts of the same animals.

5.2.2 Data analysis

For all ice thickness measurement flights, average, mode, minimum, maximum and coefficient of variance of ice thickness were calculated per transect. We computed the percentages of younger first-year (thickness 0.20–1.49 m), older first-year (1.50–2.19 m), second-year (2.20–3.49 m) and ridged ice (43.50 m). Newly formed ice was not observed during the surveys. Measurements of ice thickness < 0.20 m were considered open water.

The density of penguins and seals was calculated per species for each transect, and the average transect densities were calculated for each region.

The relationship of the density of crabeater seals with bathymetry and ice characteristics in the deep-sea and ISPOL regions was explored with Generalised Linear Models (GLM: McCullagh and Nelder 1989). We used a Poisson error distribution with a correction for over-dispersion (in R termed quasipoisson) combined with a log-link function. Seal densities were transformed to numbers per 10 km^2 in order to obtain discrete values necessary for the assumed Poisson distribution of the model. Depth data were log-transformed. Variables were tested for collinearity using variance inflation factors (VIF). A VIF value of 10 is often suggested as proof of

▼**Table 2.** Averages (± SE) of ice thickness characteristics in the deep sea and ISPOL regions. No measurements were obtained in the northern region. Marked values significantly different from other region (Mann-Whitney U-test: * *P* < 0.05; ** *P* < 0.01)

Area surveyed	**Deep Sea** **32.5 km^2**	**ISPOL** **114.7 km^2**
Modal thickness [m]	0.6* ± 0.4	1.9 ± 0.2
Average thickness [m]	2.1** ± 0.2	2.9 ± 0.1
Open water [%]	9.6** ± 2.0	3.1 ± 0.5
Young first-year [%] (20-149 cm)	27.9** ± 7.5	6.8 ± 0.7
Old first-year [%] (150-219 cm)	20.2 ± 2.2	22.1 ± 1.5
Second-year [%] (220-349 cm)	28.0* ± 4.7	40.2 ± 1.2
Ridged [%] (≥350 cm)	14.4** ± 3.0	27.8 ± 2.4

strong collinearity (Quinn and Keough 2004). In the selection procedure, the variable with the highest VIF value was removed and calculations repeated until all variables had VIF values below 10. After exclusion of variables with VIF410, high values remained for the variables percentage open water (9.9) and maximum ice thickness (9.2). Exclusion of these two variables lowered VIF values of the remaining set below 2.5. For the regression we selected this set of variables including log(depth), modal ice thickness, minimum ice thickness, coefficient of variance of ice thickness, percentage young first-year ice and percentage old first-year ice. During the model selection process variables were eliminated by a best subset regression using a stepwise forward and backward procedure, and the best model was estimated based on the lowest Akaike Information Criterion. Regression assumptions were assessed visually by plotting residuals against variables and fitted values. Statistical analyses were performed using the R (R Development Core Team 2006) and Brodgar (Highland Statistics 2006) software packages.

5.3 Results

Between 20 November 2004 and 4 January 2005, 34 transects were completed over a total linear distance of 2410.5 km, totalling to a surveyed area of 190.9 km2 (Figure 1; Table 1). All deep sea and ISPOL transects were over dense pack ice, with ice concentrations between 90% and 100% (Table 2). Ice thickness could not be measured in the northern region. The ice edge as estimated from shipboard observations was situated at a distance of 7110 km from the northern edge of the northernmost survey, at approximately 65°33’S.

The ice was significantly thicker and the proportion of open water was lower in the ISPOL than in the deep-sea region (Table 2). This observation was reflected by the thickness distribution with a significantly higher proportion of second-year ice, a lower percentage of young first-year ice and a larger amount of ridged ice in the ISPOL region (Haas et al. 2007a, b; Hellmer et al. 2006). First-year ice floes were covered with 0.2–0.4 m of snow, and second-year floes by 0.6–1.0 m. The snow layer is included in the ice thickness estimates in Table 2.

▾ **Table 3**. Mean densities (± SE) of seals and penguins on pack-ice in different regions of the Weddell Sea. **-** = Species not sighted; **+** = Species sighted but not present inside transect bands. *n*: number of sightings in transect band. Marked values significantly different from all other regions (Mann-Whitney U-test: * $P < 0.05$; ** $P < 0.01$)

Area surveyed	**Deep Sea** **32.5 km²**	**ISPOL** **114.7 km²**	**North** **43.8 km²**
Crabeater seal (n=194)	0.50* ± 0.14	1.00 ± 0.13	1.21 ± 0.16
Weddell seal (n=11)	-	0.08 ± 0.06	0.03 ± 0.02
Leopard seal (n=4)	0.05 ± 0.05	+	0.06 ± 0.04
Unid. Seal (n=2)	0.06 ± 0.04	+	+
Emperor penguin (n=44)	+	0.13** ± 0.05	0.75 ± 0.25
Adélie penguin	-	-	+
Unid. penguin	-	+	+

A total of 211 seals were counted within the band transects: 194 crabeater, 4 leopard, 11 Weddell, and 2 unidentified seals. Seals sighted outside the transect band included 390 crabeater, 7 leopard, 10 Weddell and 53 unidentified seals. No Ross seals were observed. A total of 44 emperor penguins was counted within the transect band. Penguins sighted outside the transect band included 86 emperor penguins, one Adélie penguin and eleven unidentified penguins.

Densities of seals and penguins are listed in Table 3. The density of crabeater seals in the deep-sea region was significantly lower than in the two shallower western areas. The density of emperor penguins in the northern region was almost an order of magnitude higher than in the ISPOL and deep-sea regions. Low sighting frequencies of Weddell and leopard seals prevent meaningful density comparisons. Weddell seals were not sighted at all (in or out of transect) in the deep-sea region.

Results of the GLM analysis applied to investigate the relationship of crabeater seal density with ice characteristics and ocean depth are provided in Table 4. The best model (model 1) included ocean depth, modal ice thickness and the coefficient of variance of ice thickness (CV). However, the regression coefficient for CV was not significant and model performance was not significantly better after removal of CV (F-test: $F_{24,25} = 2.69$, $P = 0.11$). Consequently, model 2, including depth and modal ice thickness was chosen as the most parsimonious model to describe crabeater seal density.

▾ **Table 4.** Coefficients for Generalised Linear Models on crabeater seal density and environmental variables. Model 1 is the best model with lowest AIC. Model 2 the most parsimonious model. AIC = Akaike Information Criterion; CV = coefficient of variation of ice thickness; D = depth; MTH = modal ice thickness; Rdev = residual deviance. Significance: * $P < 0.05$; ** $P < 0.01$

Model	**Rdev**	**Intercept**	**Log(D)**	**CV**	**MTH**	**AIC**
1	106.17	6.64**	-1.09*	0.95	-0.33*	241.02
2	115.48	6.44**	-1.26**	-	-0.31*	242.66

5.4 Discussion

5.4.1 Abundance and distribution

Among the 211 seals seen inside the transect band, 92% were crabeater, 2% leopard, 0% Ross, 5% Weddell and 1% unidentified seals. Bester and Odendaal (2000) found those proportions in the Weddell Sea to be 91% crabeater, 1% leopard, 0.3% Ross, 2% Weddell and 6% unidentified seals. Overall density estimates for Antarctic pack-ice seals reported by Erickson and Hanson (1990) work out to 89% crabeater, 4% Leopard, 2% Ross and 5% Weddell seals. Thus, the proportional abundance of seal species encountered on the ISPOL 2004/2005 helicopter surveys compares well with that of other studies. The limited survey area reduced detectability of low abundance species in some or all regions, such as Ross seals in general and Weddell seals in the deep-sea region (Table 3).

The overall density of crabeater seals in our study was 1.02 km^{-2} (194 seals in 190.9 km^2) with regional averages ranging from 0.50 to 1.21 km^{-2}. Such densities in the Weddell Sea pack-ice are within the range reported for the Weddell Sea in studies conducted farther to the north (Joiris 1991; van Franeker 1992) and to the east (Bester et al. 1995, 2002). Only Bester and Odendaal (2000) found a considerably higher crabeater seal density of 8.01 km^{-2}, which was considered an exceptional concentration in a small residual ice area in late summer. Observed densities of leopard and Weddell seals in our study were similar to those reported for nearby areas (Erickson and Hanson 1990; Joiris 1991; van Franeker 1992).

Densities of crabeater seals in the westerly ISPOL and northern regions were significantly higher than in the more eastern deep-sea area (Table 3). Erickson et al. (1983) made an analogous observation over a similar longitudinal range further north, observing a decline in crabeater seal density from 2.74 km^{-2} in shelf and slope areas to 0.41 km^{-2} over eastern deeper waters.

Van Franeker (1992) made north–south transects in the western Weddell Sea south to 62°S and indicated that seal densities remained high irrespective of distance from the ice edge. Our current observations confirm that statement for pack ice south to 69°S, further indicating that high food availability under ice is not limited to an enriched marginal ice zone, but persists throughout the closed pack ice.

Crabeater seals are known to have synchronized haulout patterns that vary with season and time of day. Southwell (2005a) found that a stable proportion of approximately 80% of crabeater seals hauled out on ice during most of the daylight period (from ±07:00 to 17:00 h) in the post-pupping season (after 30 November). Based on a smaller sample size, Bengtson and Cameron (2004) estimated the proportion of crabeater seals hauling out at maximum 65% in December, and for a shorter daylight period. A tentative correction for haulout behaviour of crabeater seals would increase the uncorrected overall density of 1.02 km^{-2} to a corrected density in the range of 1.28 (according to Southwell 2005a) to 1.57 km^{-2} (according to Bengtson and Cameron 2004).

Emperor penguins were significantly more abundant in the northern region than in the other two regions, also exceeding densities of emperor penguins found in the pack ice as reported by e.g. Ainley et al. (1984); Joiris (1991) and Woehler (1997). The locally elevated density of emperor penguins is consistent with the recent discovery of a nearby colony of this species on fast ice close to Snow Hill Island 64°32'S, 57°26'W(Coria and Montalti 2000).

Only one Adélie penguin was observed outside the transect band during the helicopter surveys. Also from the ship, at stations and during sailing, the species was only sighted infrequently. Apparently, Adélie penguins breeding around the tip of the Antarctic Peninsula and South Orkney Islands do not forage this far south during the breeding season. The closest breeding colonies reported by Woehler (1993) are situated at approximately 64°S 57°W, two to five degrees of latitude (220–560 km) north of the area surveyed in this study. Closer to those breeding locations, Joiris (1991) and van Franeker (1992) observed considerable densities of Adélie penguins. In the vicinity of these breeding areas, chinstrap penguins also can be seen in the pack ice, in spite of their preference for more open-water situations in the marginal ice zone and more northerly waters. No chinstrap penguins at all were encountered in our study area.

5.4.2 Crabeater seal density in relation to ice characteristics and ocean depth

A negative relation of crabeater seal distribution with both ice thickness and ocean depth was apparent from our model. Crabeater seal abundance has been reported to correlate with sea-ice concentration (van Franeker 1992; Bester et al. 2002). In our study, however, sea-ice concentration (inversely expressed as the percentage of open water) was excluded in the model selection process because of high variance inflation in combination with the other variables. Similar to McMahon et al. (2002), ocean depth and ice thickness were identified as the only two factors related to crabeater seal density. Our results show a slightly negative relationship between modal ice thickness and seal density, whereas McMahon et al. (2002) found the opposite trend. This disagreement most likely can be explained by the absence of new ice (<20 cm) from our dataset. In our model calculations, thin ice unsuitable for haulout would contribute to a positive relationship of seal density and ice thickness. The pattern observed in our study appears to be typical for the high end of the ice thickness range, where thick, ridged ice seems less attractive for seals.

The negative relationship of ocean depth with crabeater seal density from our model agrees with the model of McMahon et al. (2002). A similar correlation also was found by Chapman et al. (2004), who did not include ice thickness in their model. Concentrations of top predators are often associated with shelf and slope areas such as the ISPOL and northern regions, where local hydrographical patterns may enhance primary production, supporting an enriched food web up to the level of top predators (Ainley et al. 1998; Tynan 1998).

5.5 Conclusions

The present study adds new data on the summer density of pack-ice seals and penguins in the rarely surveyed inner pack ice of the western Weddell Sea. Results show that the inner pack ice is as important for crabeater seal populations as the marginal ice zone. This study is the first combining animal censuses with continuous ice thickness measurements, showing the relation between density of crabeater seals, ocean depth and ice thickness. In spite of limitations in spatial coverage and methodology, the applicability of this combined approach could be demonstrated.

Acknowledgements

We are grateful for the support received from the crew of the RV *Polarstern* ANT XXII-2 (ISPOL) expedition, Jürgen Büchner and Markus Federowitz from Heli Transair and Ismael Nunez-Riboni (AWI). We would like to thank the reviewers M.N. Bester and J. Plötz for their contribution to the improvement of this publication. This project was funded by the Netherlands Organisation for Scientific Research (NWO), the Netherlands Polar Programme (NPP) and the Netherlands Ministry for Agriculture, Nature and Food Quality (LNV).

Key References

- Chapman EW, Ribic CA, Fraser WR (2004) The distribution of seabirds and pinnipeds in Marguerite Bay and their relationship to physical features during austral winter 2001. Deep Sea Research II 51, 2261-2278
- McMahon C, Hindell M, Dorr T, Massom RA (2002) Winter distribution and abundance of crabeater seals off George V Land, East Antarctica. Antarctic Science 14, 128-133
- Siniff DB (1991) An overview of the ecology of Antarctic seals. American Zoologist 31, 143-149
- Southwell C (2005a) Optimising the timing of visual surveys of crabeater seal abundance: haulout behaviour as a consideration. Wildlife Research 32, 333-338
- Woehler EJ (1993) The distribution and abundance of Antarctic and subantarctic penguins. Scientific Committee on Antarctic Research (SCAR), Cambridge, England

Diving under the ice. Foto: C. Wancke.

CHAPTER 6

Sympagic occurrence of Eusirid and Lysianassoid amphipods under Antarctic pack ice

Rupert H. Krapp, Jørgen Berge, Hauke Flores, Bjørn Gulliksen
& Iris Werner

Abstract. During three Antarctic expeditions (2004, ANT XXI-4 and XXII-2; 2006, ANT XXIII-6) with the German research icebreaker R/V Polarstern, six different amphipod species were recorded under the pack ice of the Weddell Sea and the Lazarev Sea. These cruises covered Austral autumn (April), summer (December) and winter (August) situations, respectively. Five of the amphipod species recorded here belong to the family Eusiridae (*Eusirus antarcticus*, *E. laticarpus*, *E. microps*, *E. perdentatus* and *E. tridentatus*), while the last belongs to the Lysianassidea, genus *Cheirimedon* (cf. *femoratus*). Sampling was performed by a specially designed under-ice trawl in the Lazarev Sea, whereas in the Weddell Sea sampling was done by scuba divers and deployment of baited traps. In the Weddell Sea, individuals of *E. antarcticus* and *E. tridentatus* were repeatedly observed in situ during under-ice dives, and single individuals were even found in the infiltration layer. Also in aquarium observations, individuals of *E. antarcticus* and *E. tridentatus* attached themselves readily to sea ice. Feeding experiments on *E. antarcticus* and *E. tridentatus* indicated a carnivorous diet. Individuals of the Lysianassoid *Cheirimedon* were only collected in baited traps there. Repeated conventional zooplankton hauls performed in parallel to this study did not record any of these amphipods from the water column. In the Lazarev Sea, *E. microps*, *E. perdentatus* and *E. laticarpus* were regularly found in under-ice trawls. We discuss the origin and possible sympagic life style of these amphipods.

Deep Sea Research II 55 (2008): 1015-1023

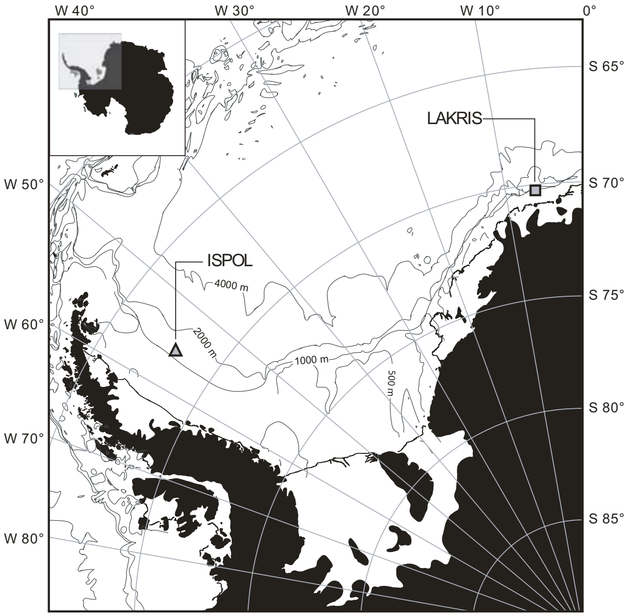
6.1 Introduction

The lower boundary layer of polar sea ice is inhabited by several allochthonous and autochthonous species, of which amphipods have been described as the most conspicuous macrofaunal elements in the Arctic, while euphausiids are the dominant group in the Antarctic (Lønne and Gulliksen, 1991; Gulliksen and Lønne, 1991). Copepods are common in the sea-ice habitats of both regions. Unlike in the Arctic sea-ice zone, where amphipods have been commonly recorded both under coastal fast ice as well as under offshore pack ice, Antarctic sympagic amphipods have mostly been described for the coastal fast-ice zone (Arndt and Swadling, 2006). In this habitat, species like Paramoera walkeri, *Cheirimedon fougneri* and *Pontogeneia antarctica* seem to originate from the benthos and occur under the sea ice only seasonally and in relatively shallow water depths (Sagar, 1980; Gulliksen and Lønne, 1991; Garrison, 1991). Comparatively little is known about the distribution of Antarctic amphipods in sea ice above greater water depths, although several reports of amphipods in the sub-ice or even under-ice habitat have been published recently (Kaufmann et al., 1993, 1995; Fisher et al., 2004). This could be due to the relative inaccessibility of these areas, as well as the higher frequency and greater feasibility of studies based on land stations. Also, the distribution of these highly motile under-ice organisms at the ice undersurface is often very patchy (Hop et al., 2000), and the effective observation and collection require the use of divers or ROVs (remotely operated vehicles), while core-hole based methods like under-ice pumping or video camera systems cover only a very limited sampling area surrounding the hole (Werner and Lindemann, 1997).

Ainley et al. (1986) discovered the amphipod *Eurythenes gryllus* along with the decapod *Pasiphaea longispina* and the ostracod *Gygantocypris mulleri* in seabird stomachs collected in pack ice of the Southern Ocean. All three species were otherwise believed to be mesopelagic, but since the sea bird species examined (Antarctic petrel, *Thalassoica antarctica*) was known to dive no deeper than 5 m, it was concluded that these crustacean plankton species must have migrated to the immediate sub-ice habitat. Another report by Kaufmann et al. (1995) mentions the Lysianassoid *Abyssorchomene rossi* in large numbers from baited traps deployed directly under pack ice of the northwestern Weddell Sea, while deeper traps did not catch any of these amphipods.

During the three Antarctic research cruises reported here, six amphipod taxa were sampled directly from the underside of sea ice floes by various methods, in what we believe to be the first recorded observation and collection of these species from Antarctic pack ice.

The aims of this paper are: (1) to present findings of new sympagic occurrences of Eusirid and Lysianassoid amphipods; (2) to record feeding behaviour observed in some of these taxa; (3) to compare these findings with other reports of Antarctic amphipods found in association with sea ice.



▲ **Figure 1.** Map of the study area indicating the sampling areas of the ISPOL drift station and the LAKRIS 2004 and 2006 cruises. For details on positions, ice cover and depth, refer to tables.

6.2 Material and methods

6.2.1. Study area

This study is based on three Antarctic cruises with the German research icebreaker R/V Polarstern. The two expeditions into the Lazarev Sea (ANT XXI-4, March– May 2004 and ANT XIII-6, June–August 2006) were part of the multiyear study LAzarev Sea KRill Survey (LAKRIS). The goal of the expedition into the Weddell Sea (ANT XXII-2, November 2004 to January 2005) was to carry out the Ice Station POLarstern experiment (ISPOL), see Hellmer et al. (2008). For the purpose of this paper, the three expeditions will be referred to by these acronyms: LAKRIS 2004, ISPOL and LAKRIS 2006 (see Figure. 1, Tables 1 and 2 for details).

6.2.2. ISPOL—sampling

The ISPOL drift station was set up in an area where sea-ice cover contained both first-year and multi-year ice, with ice cover of 8–9/10. The vessel was moored to a large ice floe and drifted with it for the period of November 29, 2004 to January 02, 2005, between positions 68°2.7’S 54°51.1’W and 67°21.2’S 55°24.3’W, while sounded depths ranged from 1030 to 2075 m. An introduction and overview of the ISPOL experiment is given by Hellmer et al. (2008).

▾ **Table 1.** Sampling stations during the ISPOL drift station

	Sampling method	Location		Date	Latitude	Longitude	Depth (m)	Ice thickness (m)
Weddell Sea								
ISPOL	SCUBA	2		December 01, 2004	68°10.4'S	54°53.4'W	1896	0.9
	SCUBA	3		December 03, 2004	68°7.9'S	55113.8'W	1576	0.9
	SCUBA	4		December 11, 2004	67°59.7'S	55°19.0'W	1471	0.9
	SCUBA	5		December 15, 2004	67°46.6'S	55°29.2'W	1274	0.9
	SCUBA	6		December 18, 2004	67°45.9'S	55°18.1'W	1504	0.9
	Baited traps	7	From	December 07, 2004	67°25.6'S	55°24.2'W	1494	0.8
			To	January 02, 2005	67°21.2'S	55°24.3'W	1382	1.0
	Slush sample	8		January 01, 2005	67°22.6'S	55°25.8'W	1398	1.0

During the course of the ISPOL experiment, ice underside and under-ice temperatures, salinity and chlorophyll a values were measured from ice cores as well as under-ice water samples at regular intervals. Ice-core salinity and chlorophyll a content were measured from sampled core segments, melted at 4°C in the dark. Chlorophyll *a* content also was determined from melted core segments that were filtered and extracted from a detailed time-series study of these parameters in the ISPOL floe (Steffens & Dieckmann, unpublished data). Under-ice water and zooplankton samples were obtained from an under-ice pumping system, deployed simultaneously to the time-series core sampling events, and results of this are presented in detail in Kiko et al. (2008b).

Under-ice fauna was sampled by scuba diving as well as by deployment of baited traps (see Table 1). Scuba divers used a hand-net with 25 x 25-cm frame opening and 500-mm mesh size, which was scraped along the underside of the ice. Sampling by scuba diving was done on five different dates and positions (see Table 1), while baited traps were checked every other day from initial deployment on December 07, 2004 until final retrieval on January 2, 2005.

Traps deployed along the floe edge as well as through core holes were plastic tubes with 102.5 mm inside diameter, 150 mm tube length, with a funnel opening to the inside on one end and a 100 mm aluminium mesh on the other end. The opening of the funnel was 12 mm wide, and traps were suspended in the water column in such a way that the two openings were aligned horizontally. Traps were deployed just off the floe edge and through core holes at 1, 5 and 10 m from the edge, and were positioned directly at the ice–water interface (ice depth), 5, 10, 15, 20 and 35 m below the ice. Bait consisted of fish and shrimp meat enriched with fish oil.

Sampling from the infiltration layer was performed either by picking up individuals from the slush with small hand-sieves of 500 mm mesh size, or by collecting slush with a bucket and pouring the content through a larger sieve of the same mesh size.

Parallel to these sampling efforts, zooplankton sampling was performed at regular intervals and with conventional zooplankton gear, i.e. multinet and bongo net hauls (see Table 5).

ISPOL—feeding experiments

Amphipods were separated by species and size and kept in aquaria at 0°C in a climate-controlled room. Every other day, a small piece of artificial sea ice was added to each aquarium to provide a substrate, and to ensure that the water temperature remained constant. Sea-ice blocks were produced using pre-filtered water which was frozen in zip-loc bags at -20°C.

A subsample (*n* = 15) of the species *Eusirus antarcticus* was fed with ice algal concentrates that were frozen into these artificial sea-ice blocks, while a control group (also *n* = 15) was provided with ''pure'' Sea-ice blocks, therefore regarded as unfed. All organisms were kept in aquaria for at least 10 days to allow evacuation of the digestive tract of the unfed animals, whereas the algal-fed group was regularly offered frozen algal concentrates during that period. Mortality was noted on a daily basis, and dead animals, animal parts and exuviae were removed and preserved in 70% ethanol for taxonomic analysis. After the end of the experiment, all remaining animals were immediately frozen in liquid nitrogen and stored at -80°C for later chlorophyll extraction. Extracts were then analyzed using spectrophotometry.

A second feeding experiment with both *E. tridentatus* (*n* = 2) as well as *E. antarcticus* (*n* = 3) was performed, using two known copepod species as live prey. Single amphipods of both species were kept in separate aquaria and were offered an abundance of prey items of either *Metridia gerlachei* or *Calanoides acutus*. Daily control counts yielded the number of consumed prey items (see Table 4).

6.2.3. LAKRIS—sampling

During the LAKRIS 2004 and 2006 cruises, the sea-ice undersurface was sampled using a ''Surface and Under Ice Trawl'' (SUIT) (see Table 2). In contrast to conventional trawls, the SUIT was towed sideways of the ship, allowing to sample under undisturbed ice, at a distance of approximately 50 m from the water channel produced by the towing vessel. The upper side of the net frame was equipped with drivers to provide permanent close contact of the net with the undersurface of the ice. The net had a frame with an opening of 2.25 x 2.25 m and was equipped with a 7-mm mesh shrimp net. Towing speed was 1.0–1.5 knots. During LAKRIS 2004 a plankton net with a 50-cm diameter (mesh size 0.3 mm) was attached inside the rear end of the shrimp net in a centered position. Towing speed was approximately 2.5 knots. In total,

Table 2. Sampling stations during the LAKRIS cruises

	Sampling method	**Location**	**Date**	**Latitude**	**Longitude**	**Depth (m)**	**Ice thickness (m)**
Lazarev Sea							
LAKRIS 2004	SUIT	1	April 10, 2004	70°18.5’S	6°1.1’W	240	n.a.
LAKRIS 2006	SUIT	9	July 05, 2006	67°26.1’S	2°53.2’E	4564	0.2–0.6
	SUIT	10	July 06, 2006	68°32.6’S	2°51.4’E	4130	0.4–0.6
	SUIT	11	July 07, 2006	69°31.1’S	3°12.7’E	3765	0.9–1.0
	SUIT	12	July 12, 2006	67°31.2’S	0°3.5’W	4499	0.3–0.5
	SUIT	13	July 19, 2006	66°8.0’S	0°11.0’W	3840	0.2–0.7
	SUIT	14	July 19, 2006	66°7.7’S	0°10.5’W	3840	0.4–0.6
	SUIT	15	July 29, 2006	69°22.8’S	2°43.7’W	3312	0.2–1.0
	SUIT	16	July 30, 2006	68°0.3’S	2°54.3’W	4090	0.2–0.8
	SUIT	17	August 03, 2006	66°3.5’S	3°3.8’W	4760	0.4
	SUIT	18	August 04, 2006	65°5.3’S	2°51.2’W	no data	0.2–0.6

24 stations were sampled covering an area between 0°W to 6°W in longitude and 61°S to 70°S in latitude. Further details on the LAKRIS 2006 expedition are provided in Smetacek et al. (2005). During LAKRIS 2006, the rear end of the net was entirely lined with 0.3 mm gaze. In total, 30 stations were sampled covering an area between 3°E to 3°W in longitude and 57°S to 70°S in latitude. On both expeditions, the catch was immediately sorted by taxon. The size of amphipods was measured as the length from the frontal edge of the eye to the tip of the telson. They were either preserved on 4% buffered formaldehyde–seawater solution or directly frozen at -20 or -80°C.

6.2.4. Species identification

Identification of all Eusirid species treated herein follows Andres et al. (2002), where a key to the *Eusirus* species from Antarctica is given.

6.3 Results

6.3.1. Environmental parameters—ISPOL station

Temperature values ranged from -2.2 to -1.4°C for the lowermost centimetres of the ice and -1.8 to -1.9 1C for the under-ice water down to 8 m below the ice. Salinity values ranged from 5 to 11.6 for the lowermost centimetres and 34.2 to 34.7 for the under-ice water down to 8 m below the ice, while chlorophyll a values ranged from 57.64 to 261:69 mg l-1 and from 0.07 to 0:35 mg l-1, respectively.

Table 3. Amphipod species observed under Antarctic pack ice

Expedition	Species	Location	Total number	Size range (mm)
LAKRIS 2004	*Eusirus perdentatus*	1	1	49
	Eusirus microps	1	1	42
ISPOL	*Eusirus antarcticus*	2, 3, 4, 6, 7, 8	60	9–15
	Eusirus tridentatus	2, 5, 8	3	18–24
	Cheirimeidon (cf. *femoratus*)	7	8	8–10
LAKRIS 2006	*Eusirus laticarpus*	9, 10, 12, 13, 14, 15, 16, 17, 18	24	6–19
	Eusirus microps	9, 12, 15, 16, 18	7	12–38

6.3.2. Under-ice amphipods of the ISPOL station

Two species of the five Eusirid amphipod species reported here, *E. tridentatus* and *E. antarcticus*, were found at several sampling sites at the underside of the pack ice, in the infiltration layer as well as in baited traps deployed at the ice–water interface (see Table 3). Another amphipod species, *Cheirimedon* cf. *femoratus*, was found exclusively in those baited traps deployed directly at the ice–water interface (see Table 3). No amphipods were collected by any of the baited traps deployed below the ice–water interface.

Lysianassoid amphipods

Material examined: Eight specimens, including one immature female and one immature male, both 10 mm in length. All specimens were collected with baited traps, from Weddell Sea.

Identification: The specimens collected during this study could not be identified to species level with certainty, as the studied specimens possess morphological affinities with both of the two species *C. femoratus* and *C. fougneri*. These are both very common shallow benthic species in the Southern Ocean. The main discrepancies between the sampled material and *C. femoratus* and *C. fougneri* are as follows:

- our material differs from *C. fougneri* in having two relatively short antennae, (*C. fougneri*: two long antennae), antenna 1 stout with broad peduncule 1;
- eyes longer and more droplet shaped;
- our material shows a rounded epimeral plate 3 (*C. femoratus* has a produced epimeral plate 3);
- our material: coxa 1 anteriorly expanded (as in *C. femoratus*).

Based upon these morphological discrepancies, and as we did not have any adult individuals at our disposal from the Weddell Sea, we will herein refer to the material as *C.* cf *femoratus*, as it shares the distinct shape of the coxa 1 with this species, although the shape of the epimeral plate 3 is different.

6.3.3. Under-ice amphipods of the LAKRIS cruises

Two individual amphipods were collected at one station of the LAKRIS 2004 autumn expedition. They were identified as *E. microps* and *E. perdentatus*. The sizes of both specimens were at the higher end of the size ranges of these species (Table 2). On the winter expedition LAKRIS 2006, another Eusirid species was obtained from SUIT catches. This was *E. laticarpus*, which occurred at 9 of the 30 stations sampled, covering a broad size range. *E. microps* was found only at 5 stations (Table 3). Specimens of this species kept in an aquarium with sea ice actively sought the ice and stayed attached to it. All amphipods collected on the LAKRIS 2006 expeditions occurred in the part of the sampling area south of 64°S.

6.3.4. Feeding experiments—ISPOL station

Selected individuals of *E. tridentatus* and *E. antarcticus* were observed repeatedly to predate both on smaller *E. antarcticus* as well as on copepods of the species *Metridia gerlachei* and *Calanoides acutus*, which were offered in controlled feeding experiments (Table 4).

The other feeding experiment performed with *E. antarcticus*, offering ice algae frozen into artificial ice blocks was analyzed for chl *a* content. Methanolic extracts of both fed and unfed amphipods did not show any significant difference in their chlorophyll signatures, which were both below the detection limit.

6.3.5. Collection of zooplankton samples under pack ice

Sampling of zooplankton with conventional net hauls did not yield any of the aforementioned amphipod species collected from the pack ice underside. Instead, other amphipod taxa, both Hyperiidae and Scinidae, as well as some isopods, were routinely sampled in multinet hauls, alongside with copepods, for which results will be presented in detail in Schnack-Schiel et al. (2008a). A single Eusirid amphipod was recorded from a bongo net haul (December 23, 2004, 200–0 m) but was determined to belong to a different genus than *Eusirus*.

▾ **Table 4.** Feeding experiment of *Eusirus tridentatus* and *Eusirus antarcticus* with calanoid copepods

	Day 1	**Day 2**	**Day 3**	**Day 4**	**Day 5**	**Day 6**	**Day 7**
E. tridentatus	3 M.g.	3 M.g.	1 M.g.	0 C.a.	1 C.a.	0 C.a.	0 C.a.
E. antarcticus	1 C.a.	1 C.a.	1 C.a.	0 C.a.	0 C.a.	1 C.a.	0 C.a.

Numbers indicate individual prey items devoured by one amphipod d-1.
E. = *Eusirus*, M.g: = *Metridia gerlachei*, C.a: = *Calanoides acutus*.

6.4 Discussion

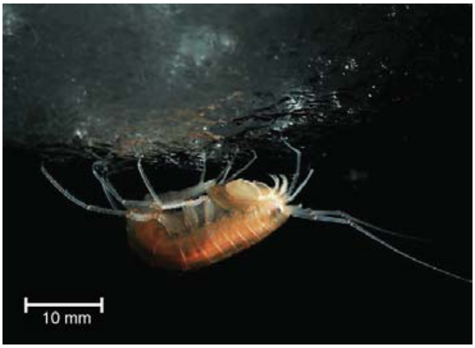
This paper presents data from under-ice amphipods found in the pack ice of the Weddell Sea and the Lazarev Sea. While many authors have previously described amphipods living attached to sea ice close to shore and over relatively shallow water depths, such recordings so far have only been reported occasionally from sea ice over deep water and further offshore in the Antarctic (Gulliksen and Lønne, 1991; Kaufmann et al., 1995). We discuss the possible origin and the degree of sympagic adaptation in these species, based on direct observations and feeding experiments.

6.4.1. Origin of Eusirid species found under Antarctic pack ice

Our samples of the species *E. antarcticus*, *E. laticarpus*, *E. microps*, *E. perdentatus* and *E. tridentatus* reported here fit well with previous records of these species from ice-covered Antarctic waters, although in most cases methodological constraints prohibit a statement about their exact origin. For example, Foster (1987) reports the Eusirid *E. antarcticus* for his zooplankton collections done through holes in the land-fast ice of the McMurdo Sound, but his study sampled integrated depth intervals of 100–0 and 300–0 m. In another study of the zooplankton of McMurdo Sound, Hopkins (1987) also reports the Eusirids *E. tridentatus* and *E. propeperdentatus* among his plankton net samples, as well as the Lysianassoid amphipods *Abyssorchomene plebs* and *A. rossi*. The samples described in this study were performed by oblique sweeps of the upper 800 m with a Tucker trawl. The Eusirid species *E. antarcticus* and *E. microps* also have been recorded from epipelagic (0–50, 50–100 m) MOCNESS trawl samples in the NW Weddell Sea performed at pack-ice covered stations (Fisher et al., 2004). A switch from a pelagic to a sympagic mode of life as soon as ice becomes available is supported by low pelagic catches of *E. microps* and *E. antarcticus* when sea ice was present compared to significantly higher catches in ice-free waters reported by Fisher et al. (2004). Reports on *E. laticarpus* are scarcer and further complicated by the fact that this species was often included in *E. antarcticus* in the past, before the species was re-established by De Broyer and Jazdzewski (1993).

E. perdentatus was caught only once at a shelf station of the LAKRIS 2004 expedition and due to its relatively shallow depth (see Table 2) it is conceivable that it had actively sought the under-ice habitat, because potential prey, especially euphausiid larvae, were abundant under the ice at that time (Flores, unpublished data). However, it is possible but unlikely that the specimen originated from a shallower area and subsequently drifted to the location of capture with the sea ice. Klages (1993) and Klages and Gutt (1990) cover the distribution and feeding patterns of *E. perdentatus*, which had been sampled from meso-and epiplagic stations by various gear. However, recent re-analysis of the material used for the former publication by Andres et al. (2002) revealed a new species, *E. giganteus*, which had mistakenly been regarded as *E. perdentatus*, so these results should be treated with caution. It also should be noted

▲ **Figure2.** *Eusirus antarcticus* attached to artificial sea ice, image © IngoArndt.



▲ **Figure3.** *Eusirus tridentatus* attached to artificial sea ice, image © IngoArndt.

that *E. tridentatus* Bellan-Santini and Ledoyer (1974), and *E. microps* Walker (1906) have been described as separate species by Barnard and Karaman (1991), but were synonymized by De Broyer and Jazdzewski (1993). Therefore, reports of *E. microps* will also have to be treated with some caution, depending on whose species definition they were based on. The same is also true about the other Eusirids found by this study: De Broyer (1983) treated *E. antarcticus* and *E. laticarpus* as separate species, while Barnard and Karaman (1991) treated them as synonyms. We follow the most recent key to Antarctic Eusirids by Andres et al. (2002) who clearly distinguishes and maintains all above mentioned species and names.

Due to the range of gears and depths, we regard all these above mentioned records as epipelagic to mesopelagic. To our knowledge, direct under-ice observation and sampling of any of the above mentioned species has not been reported from the Antarctic pack ice zone (Arndt and Swadling, 2006). Based on these reports and our own observations and samples, we conclude that the pelagic realm is the most likely origin for these Eusirids. Since our samples also cover a considerable temporal and spatial range, it seems safe to say that there is evidence for a pelago-sympagic coupling, i.e. Eusirid amphipods seem to be able to utilize the under-ice habitat during their life cycle.

This hypothesis is supported by our *in situ* observations as well as aquarium observations. Both *E. tridentatus* and *E. antarcticus* were observed by divers to swim very close to the underside of the ice and attach themselves for periods of time to it, as well as sometimes to enter cracks and holes in the ice. Single individuals were even found in slush sampled from the infiltration layer (see Table 3). Also, whenever a small piece of artificially produced sea ice was put in their aquarium, individuals of *E. antarcticus*, *E. microps* and *E. tridentatus* immediately started to swim towards it and then attached themselves to its surfaces (see Figs. 2 and 3).

▾ **Table 5.** Amphipods and isopods caught by multinet hauls during ISPOL station, see Schnack-Schiel et al. (2008a)

Date	Depth range (m)	Scinidae	Hyperiidae	Isopoda
December 01, 2004	1000–500	1		
December 06, 2004	100–50	1		
December 06, 2004	500–200	1	3	
December 06, 2004	1000–500	1		
December 09, 2004	500–200	3		
December 09, 2004	1000–500	4		
December 13, 2004	500–200		1	
December 13, 2004	1000–500	1		1
December 17, 2004	200–100		1	
December 17, 2004	500–200	1	3	
December 21, 2004	1000–500	2		
December 21, 2004	500–200	1		
December 21, 2004	1000–500	3		1
December 26, 2004	500–200	2		
December 26, 2004	1000–500	2		
December 29, 2004	500–200	2		
December 29, 2004	1000–500	1	1	
January 02, 2005	100–50		1	
January 02, 2005	200–100			1
January 02, 2005	500–200		4	
January 02, 2005	1000–500	3		

However, although the water column had been sampled extensively and regularly during the month-long ISPOL drift station, not one Eusirid amphipod of the species recorded under the ice was found in those zooplankton net samples (see Table 5). As mentioned above, all of these species have otherwise been reported from zooplankton samples with various gear and depth ranges, so it seems strange that none were collected by our zooplankton sampling efforts. This seems even more surprising given the fact that those samples regularly recorded Hyperiidae and Scinidae of similar size ranges, proving that animals of such size and shape could be found in our samples after all.

6.4.2. Origin of Lysianassoid species found under Antarctic pack-ice

We were not able to directly observe any specimen of *Cheirimedon* in or around the ice, but only recorded them in two neighbouring traps immediately after their first retrieval (see Table 3). The animals showed limited swimming activities in holding tanks, and were not observed to seek contact with sea ice when offered.

Lysianassoids have previously been reported by Kaufmann et al. (1993) who found hundreds of large specimens of *A. rossi* from baited traps deployed just under the pack ice, while similarly deployed traps in open water remained empty. The authors argued that this observation suggests that these amphipods may be present in large numbers just beneath the ice surface, and established this as the first record of these scavenging amphipods in the microhabitat of the Antarctic pack ice, where water depths in excess of 1000 m were recorded. This was confirmed by Tucker trawl hauls from the same cruise, published by the same authors in Kaufmann et al. (1995), where *A. rossi* also was found in shallow trawl samples (10–35, 50–85 m) taken at night in partly ice-covered waters. Fisher et al. (2004) also list *A. rossi* from MOCNESS trawls at depth intervals 100–50 and 50–0 m in that area. Stockton (1982) collected what probably was the same species (using its previous genus name, Orchomene rossi) also in baited trap samples taken from under the Ross Ice Shelf, 400 km from the shelf edge at a depth of 600 m, so one must assume that this species is flexible in its habitat use.

Although we were not able to determine the species of the Lysianassoids found on the ISPOL drift station, a very different picture can be gained from the literature for the most similar to those found in this study. No source known to us has listed either *C. femoratus* or *C. fougneri* from a pelagic sampling station. Instead, Bregazzi (1972a,b, 1973) described *C. femoratus* to be bottom-dwelling types with limited swimming capabilities which inhabit the top layer of sandy-gravelly subtidal zones around Antarctica (Jazdzewski et al., 2000).

Gulliksen and Lønne (1991) describe *C. fougneri* from sampling efforts in McMurdo Station, where amphipods were only recorded in significant amounts under sea ice above relatively shallow water, i.e. in the tens of metres. Interestingly, they also noticed a broodcast event of *C. fougneri* for the period November–December, based on observations of a rapid increase of free-swimming juveniles between two sampling dates, while adults were still observed with unreleased juveniles in their marsupia on the first sampling event (Gulliksen, pers. comm.). From that, one can assume that this species annually utilizes the sea ice underside both as adult and juvenile stages for part of their life span.

In other cases where shallow benthic Lysianassoid amphipods were unexpectedly found under pack ice, Werner et al. (2004) and Nygård (2005) described *Anonyx sarsi* under Arctic pack-ice, but their stations were also at much shallower water depths than in the present study. Therefore, the authors argued that their findings could be explained by benthic–sympagic coupling. In our case, it seems safe to say that any benthic–sympagic coupling based on active migration is unlikely, since water depths exceeded 1000 m.

Also, since our findings are exclusively of small and juvenile specimens which we estimate to be no older than one year, one has to assume that they have either been advected to the ice since their hatching, or that they indeed were hatched in the vicinity of the ice. Still, the basic question remains as to how they got to the ice station where we found it in our baited traps. If active migration is ruled out, then advection or other passive transport seems to be the only possible alternative. The most likely transport medium would be the ice itself, as it cannot be ruled out that some of the ice present in the area of our ISPOL study had originally formed over shallower depths. Since the ISPOL drift station was set up in an area with a variety of ice types and probably ages and origins, it seems futile to speculate about when and where the colonization or advection of benthic amphipods might have taken place. Still, the relatively small size and inferred young age of the *C.* cf *femoratus* points to the hypothesis that these animals had been hatched under the ice and had been developing there since.

Aerial transport could be mentioned as another—though rather improbable—possibility for advection. There are a few published reports, p.e. Segerstråle (1946, 1954), where the author proves experimentally how the freshwater amphipod *Gammarus lacustris* was able to cling to bird feathers and even showed tolerance exposure of up to 2 h. One could alternatively also speculate that penguins might have acted as vectors, but we regard both possibilities as highly unlikely in this case.

6.4.3. Feeding types in Antarctic sympagic amphipods

The feeding experiments indicate that *E. antarcticus* and *E. tridentatus* are predatory and carnivorous species. The initially observed cannibalism cannot be excluded to be an artificially induced behaviour in captivity.

Since investigations covering the ice-algal biomass found within the ice as well as the under-ice water had shown ice algae to be there, and the succession of these concentrations even indicated some melting out of ice algae into the underlying water (see Kiko et al., 2008b), one could have assumed that this would serve as a food source for the amphipods found under the ice, in a similar fashion as it had been established for krill earlier (Marschall, 1988). However, we were not able to prove ice algal uptake by means of methanolic extractions. Preferably, the feeding experiment should have been performed following the procedure described in Werner (1997), where algal concentrations before and after introduction of grazers were determined.

In a paper by Klages and Gutt (1990), a macropredatory carnivorous feeding type is documented for *E. perdentatus* from aquaria observations. This has been confirmed by Graeve et al. (2001), who present lipid, fatty acid and digestive tract content analyses, and by Dauby et al. (2001), who describe the relative proportions (in %) of food items for various amphipods and found that *E. perdentatus* contained a broader range of food items, all of which could well originate from predation as well as scavenging. Unfortunately, due to the sampling gear used, we cannot report any observed feeding behaviour for this species, but concurrent sampling of zooplankton yielded an abundance of copepods and krill larvae under the ice.

We did not directly record any feeding behaviour for *C.* cf *femoratus*. Richardson and Whitaker (1979) describe the closest species, i.e. *C. femoratus* as predator and *Pontogeneia antarctica* as algal grazer in a scuba-based observational and sampling study off Signy Island. Both species were recorded in the immediate vicinity of sea ice by them, where *C. femoratus* was observed actively preying on the newly released young of *Pontogeneia antarctica*. Bregazzi (1972b) reports algal material for juveniles of *C. femoratus*, while adult specimens contained a large variety of food items ranging from algae to copepods and euphausiid larvae. In the same study, trap experiments recorded a strong response from these amphipods as well. These reports fit well with our results from baited trap samples, which suggest a possible scavenging behaviour for *C.* cf *femoratus*. However, due caution should be applied when comparing these results, since our material very likely belongs to another species than either *C. femoratus* or *C. fougneri*.

6.5 Conclusion

The results from this study suggest that the underside of Antarctic pack ice serves at least temporarily as a habitat for Eusirid amphipods. Although this could not be determined with certainty, we believe that their origin for the reported oceanic occurrences is most probably the pelagic habitat, from which they can colonize the sea ice during favorable conditions. It is thus puzzling that none of these amphipods were found in any of the extensive concurrent zooplankton sampling efforts, which did record a number of isopods, as well as Scinid and Hyperiid amphipods of similar size classes. One explanation might be that the transition to a sympagic life style had been initiated prior to our sampling period.

For the Lysianassoid *Cheirimedon* cf. *femoratus*, which also were found by this study, such a pelagic origin seems less likely, but since the species determination is still uncertain for the sampled material, it cannot be completely ruled out.

In conclusion, we recommend that further studies of the under-ice fauna of Antarctic pack ice should be undertaken to gain more insight into the biology, distribution and significance of amphipods in this habitat. One aspect that should deserve special attention is the possible interaction of amphipods with other under-ice and zooplankton organisms like krill and copepods, where possible predatory interaction can be assumed. Also, their potential role and availability as food for higher trophic levels like fish and sea birds should be investigated.

Acknowledgements

We thank the captain and crew of the R/V Polarstern for excellent support during ANT XXI-4 (LAKRIS 2004), ANT XXII-2 (ISPOL) and ANT XXIII-6 (LAKRIS 2006) cruises. Also, we would like to express our deepest gratitude to the cruise leader and the organizers of the "Ice Station POLarstern" (ISPOL) field experiment, which provided a unique opportunity to work in the Antarctic pack ice environment for such an extended period. Ingo Arndt, the expedition photographer of ANT XXII-2, skillfully produced the excellent images of live amphipods. Sigi Schiel generously shared both the multinet amphipod samples as well as live copepods for the predation experiments with us, and both Angelika Brandt and Wim Vader provided insightful and constructive comments as reviewers.

Key References

- Andres H, Lörz A, Brandt A (2002) A common, but undescribed huge species of *Eusirus* KRØYER, 1845 (Crustacea, Amphipoda, Eusiridae) from Antarctica. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 99, 109–126
- Arndt C, Swadling K (2006) Crustacea in Arctic and Antarctic sea ice: distribution, diet and life history strategies. Advances in Marine Biology 51, 197–315
- De Broyer C, Jazdzewski K (1993) A checklist of the Amphipoda (Crustacea) of the Southern Ocean. In: Studiedocumenten van het Koninklijk Belgisch Institut voor Natuurwetenschappen, vol. 73. Royal Belgian Institute for Natural Sciences, Brussels
- Foster B (1987) Composition and abundance of zooplankton under the spring sea-ice of spring sea-ice of McMurdo Sound, Antarctica. Polar Biology 8, 41–48
- Kaufmann R, Smith Jr K, Baldwin R, Glatts R, Robison B, Reisenbichler K,(1993) Epipelagic communities in the northwestern Weddell Sea: results from acoustic, trawl, and trapping surveys. Antarctic Journal of the United States 28, 138–141

Deploying SUIT in a stormy night.

CHAPTER 7

Epipelagic macrofauna under sea ice and in open waters of the Lazarev Sea, Southern Ocean

Hauke Flores, Jan A. van Franeker, Boris Cisewski, Harry Leach, Anton P. Van de Putte, Erik (H.W.G). Meesters, Ulrich Bathmann & Wim J. Wolff

Abstract. A new fishing gear was used to sample the macrozooplankton and nekton community in the surface layer (0 – 2 m) under ice and in open water, the Surface and Under Ice Trawl (SUIT). In total, 71 hauls were conducted in the Lazarev Sea (Southern Ocean) during three different seasons (autumn 2004, winter 2006, summer 2007 / 2008). At least 47 species from eight phyla were caught in all three seasons combined. The community composition differed significantly between seasons. The species composition responded significantly to the presence of sea ice in autumn and summer, although there was not sufficient evidence for a separation into distinct communities. In winter, the species community under the closed pack-ice cover changed along gradients of hydrography and chlorophyll concentration. The response of the community composition to the presence of sea ice was illustrated by species that were significantly more abundant at the open surface than under ice (*Cyllopus lucasi*, *Hyperiella dilatata*), significantly associated with ice (*Eusirus laticarpus*), or were only seasonally abundant under ice (*Clione antarctica*). Distinct diurnal patterns were apparent in the surface occurrence of abundant species in winter and summer. These results emphasize the potential of a number of zooplankton and nekton species to act as energy transmitters between the production in the sea ice and the pelagic system. The significant influence of ice properties on the species composition adds new and direct evidence to the perception that the ice is a major factor shaping the ecosystem structure of the Antarctic seasonal sea ice zone.

7.1 Introduction

Large parts of the rich top predator community typical for the Southern Ocean directly or indirectly depend on resources from the surface layer (Ainley et al. 1991). For example, surface swarms of Antarctic krill Euphausia superba have been reported since the early days of Antarctic research, and whales have frequently been observed feeding at the surface (Hardy & Gunther 1935, Hamner 1982, Nemoto 1983). The high biological potential of the surface layer is prominent in the Antarctic marginal sea ice zone in spring and summer, when the decay of the ice creates a shallow mixed layer by means of a layer of less dense melt water, significantly enhancing primary production (Eicken 1992, Arrigo et al. 1997). This primary production is heavily grazed by a diverse zooplankton community including Antarctic krill, salps, copepods, amphipods and a range of jelly fish and comb jelly fish, which in turn nourish fish, squid and the warm-blooded top predators (Hopkins et al. 1993, Ross et al. 1998, Froneman et al. 2000).

At least during parts of the year, the surface carries an additional substrate in the form of sea ice. Besides providing a haul-out and nursery platform for the penguins and seals of the seasonal sea ice zone, the ice forms a habitat for a variety of sympagic ("ice-associated") lifeforms. The sympagic meiofauna community existing in the seasonally vanishing sea ice, illustrates the potential of this environment as a diverse and ecologically relevant habitat (Schnack-Schiel 2003, Kiko et al. 2008b, Schnack-Schiel et al. 2008b). A rich sympagic macrofauna community is known from Arctic multi-year sea ice. Sympagic macrofauna in association with Antarctic sea ice was reported mainly from shelf waters and fast ice (Gulliksen & Lonne 1991, Arndt & Swadling 2006). Recent reports on new ice-associated species in Arctic fast ice, Antarctic sea ice and at Antarctic shelf ice suggest that ice habitats may be more diverse than assumed to date (Watanabe et al. 2006, Bluhm et al. 2007, Kiko et al. 2008a).

Sea ice primary and secondary production are assumed to play a key role in the seasonal sea ice zone. Most of the primary production occurs not in the water column but in the pack-ice during large parts of the year (Lizotte 2001, Arrigo & Thomas 2004). The productivity of the sea ice system has been proposed to play a key role in supporting the typically high wildlife stocks of the Antarctic pack-ice zone (Ainley et al. 1986, van Franeker et al. 1997). It has been shown that copepods, larval and postlarval krill aggregate under sea ice and feed on ice algae and sympagic meiofauna (Marschall 1988, Daly 2004, Tanimura et al. 2008). The extent to which non-euphausiid macrofauna use the ice-water interface, however, is largely unknown to date. If the food web of the Southern Ocean seasonal sea ice zone depends in large parts on the production of ice algae, a quantitative description of the species community in the ice-water interface layer is an important prerequisite for unraveling the trophic pathways connecting the sea ice and the pelagic systems that ultimately lead to the warm-blooded top predators.

Direct quantitative evidence of macrofauna species closely associated with seasonal sea ice in Antarctic offshore waters is largely missing to date due to the difficulties imposed by the ice on conventional sampling techniques. The need to obtain a better assessment of the temporal and spatial distribution of Antarctic krill and other macrofauna has long been recognized (Stretch et al. 1988, Siegel et al. 1990). In the past decade autonomous underwater vehicles (AUV) provided the first large-scale data on the distribution of krill under ice (Brierley et al. 2002). However, the echosounding technology used could not resolve the upper few meters of the water column, where the interaction of the pelagic and the sympagic communities is mainly expected. Although it is theoretically possible, in practice this technology is not capable of differentiating species and record their size compositions with sufficient reliability to date.

To assess the importance of the Antarctic open surface and ice-water interface layer for macrozooplankton and nekton, a new quantitative sampling device was developed, the Surface and Under Ice Trawl (SUIT). Three expeditions in the Lazarev Sea provided the opportunity to investigate the macrofauna species composition in the surface layer of the seasonal sea ice zone both under ice and in open water in autumn, winter and summer. This study aims to:

- describe and analyze the community structure of macrozooplankton and nekton in the open surface layer and under ice during three seasons;
- estimate the role of sea ice and other environmental factors that potentially drive the community composition;
- identify species that are potentially important for the trophic interaction of the sea ice with the pelagic food web;
- discuss the ecological relevance of the ice-water interface layer and its importance for biodiversity.

7.2 Material and methods

7.2.1 Data collection

Sampling area

Data were collected during three research cruises of RV "Polarstern" in the Lazarev Sea in austral autumn 2004 (ANT XXI-4, 27th March to 6th May 2004), winter 2006 (ANT XXIII-6, 17th June to 21st August 2006) and summer 2007 / 2008 (ANT XXIV-2, 28th November 2007 to 4th February 2008). The expeditions were part of a multi-year field experiment embedded in the largely German funded LAzarev Sea KRIll Study (LAKRIS) dedicated to the investigation of the distribution, population dynamics and physiology of Antarctic krill Euphausia superba. The LAKRIS surveys sampled a regular station grid with 3 - 4 meridional transects with a spacing of 2 – 3 degrees longitude and a latitudinal station spacing of 20 – 30 nm, ranging from 6°W to 3°E and from 60°S to the continental coast at approximately 71°S (Figure 1).

Surface layer sampling

Surface and Under Ice Trawls (SUIT) were used to sample macrozooplankton and nekton in the upper two meters of the water column. The net systems consisted of a steel frame with an approximately 2 x 2 m net opening with a 15 m long 7 mm half-mesh commercial shrimp net attached to it. Large floaters at the top the frame keep the net at the surface. To enable sampling under undisturbed ice, an asymmetric bridle forces the net to shear at an angle of approximately 60° starboard from the ship's track at a cable length of 120 m. Wheels on top of the frame allow the net to roll along the underside of ice floes. In summer 2004, a circular plankton net (diameter 50 cm, 0.3 mm mesh) was mounted inside the shrimp net to sample mesozooplankton. In winter 2006 and summer 2007 / 2008, the rear three meters of the net were lined with 0.3 mm plankton gauze. A strobe light and a video camera were attached to the frame. Technical details of the SUIT systems used are provided in Table 1.

An acoustic Doppler Current Profiler (ADCP) was used in winter 2006 and summer 2007 / 2008 to estimate the amount of water entering the net and to analyze its flow properties. The device, an Nortek EasyV river velocity monitor, operates with two 2 MHz measuring beams situated at an angle of 50° against each other. The ADCP is capable of measuring current speed at an accuracy of 1% of the measured value at three different positions horizontally across the net opening. The central measuring cell was used to estimate the effective water distance passed (eD) as the sum of the products of the duration [s] and the current speed [m s^{-1}] of each measuring interval (5 - 20 s).

For SUIT hauls conducted in autumn 2004, eD was estimated a posteriori by means of a linear regression of ADCP-estimated eD versus the ship's track distance during trawling from the 2006 and 2007 / 2008 current speed measurements (eD = 0.8 * Ship track distance + 148 m; $R^2 = 0.88$; $p < 0.05$). The amount of filtered water [m^3] and the surface area sampled [m^2] were calculated for each haul by multiplying eD with the net's opening area and the opening width, respectively. Corresponding figures were calculated for the separate plankton net used during autumn 2004 using the circular opening area and the diameter. A detailed description of the SUIT and its fishing properties is provided in Chapter 9. Standard hauls lasted 25 minutes, with a minimum of 15 and a maximum of 49 minutes and an average towing speed of 1.5 – 2.5 kn (0.8 – 1.3 m s^{-1}). During each trawl, changes in ship speed, ice coverage [%], ice thickness [cm] and irregularities were recorded by an observer watching the net from the ship.

Of the total 75 SUIT hauls, 24 hauls were conducted in autumn 2004, 30 hauls in winter 2006 and 21 hauls in summer2007 / 2008. Four locations were sampled outside the regular LAKRIS grid on the three expeditions. For the purpose of this

▼**Table 1**. Technical details of SUIT systems used during LAKRIS expeditions

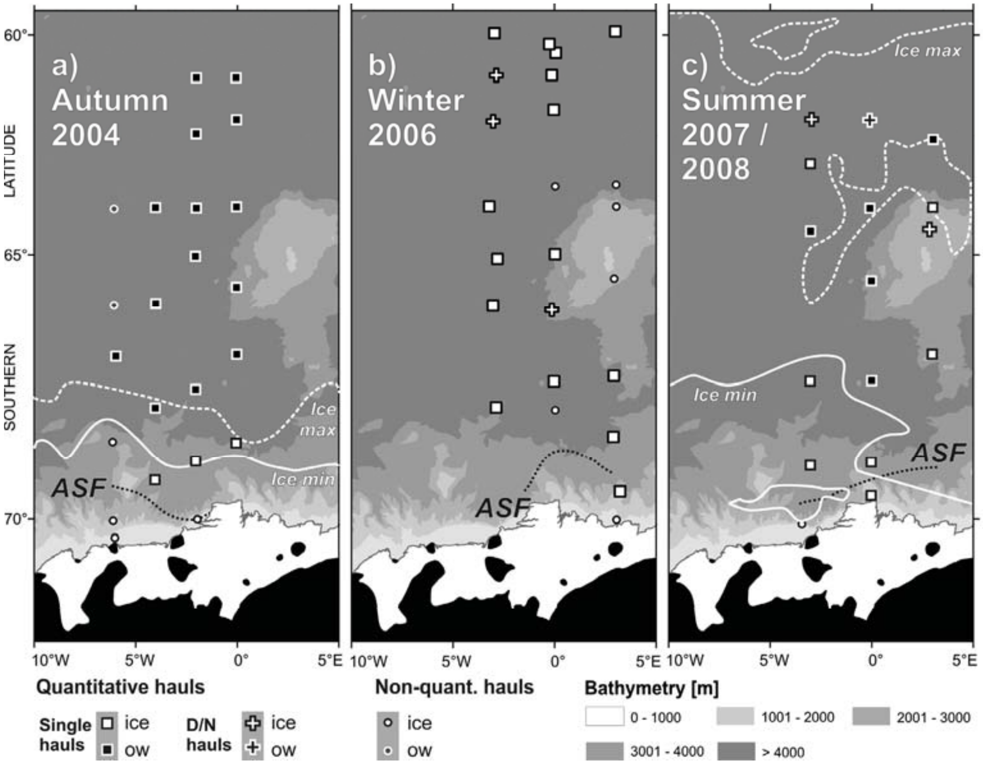
Expedition	**Mouth height**	**Mouth opening**	**Main net mesh size**	**Plankton net diameter**	**Plankton net mesh size**	**Additional equipment**
Autumn 2004	225 cm	5.06 m^2	7 mm	50 cm$^{(1)}$	0.3 mm	Strobe light, video
Winter 2006	225 cm	5.06 m^2	7 mm	ca. 100 cm$^{(2)}$	0.3 mm	Strobe light, ADCP
Summer 2007 / 2008	231 cm	4.53 m^2	7 mm	ca. 100 cm$^{(2)}$	0.3 mm	Strobe light, ADCP, video

(1) Separate plankton net centred in main net

(2) Flexible plankton net sewn into main net

study, data were restricted to the 71 hauls conducted on the LAKRIS grid (south of 59°S). Fourteen of them were used in qualitative analysis (species occurrence), but excluded from quantitative analysis because of irregularities during the tow. The majority (46) of the remaining 57 quantitative hauls were conducted at night. Six hauls at three locations were dedicated to day / night comparisons in winter 2006 and in summer 2007 / 2008, respectively (Figure 1). The catch was immediately sorted on board. After the collection of all macrofauna > 0.5 cm from either the entire sample or a representative subsample, the mesozooplankton fraction was preserved on 4% hexamine-buffered formaldehyde-seawater solution. In autumn 2004, the mesozooplankton fraction was obtained from the separate plankton net. Other animals > 0.5 cm collected from this net were combined with the shrimp net catch in subsequent analyses. Because of limited comparability of small animals only quantitatively caught by the plankton nets with macrofauna that is also caught by the shrimp nets, copepods were not included in the present analysis.

Macrozooplankton and nekton were separated by species. Displacement volume and number of individuals of each species were noted. For details on euphausiid sampling see Chapter 8. Euphausiid furcilia larvae from the mesozooplankton fraction were identified to species level and counted. In each species, the number of animals caught was expressed as the density of individuals per surface area sampled [N 1,000 m^{-2}].



▲**Figure 1**. SUIT sampling locations on the LAKRIS grid and ice coverage in autumn 2004 (a), winter 2006 (b) and summer 2007 / 2008 (c). Hauls excluded from quantitative analyses are marked separately (see legend). Minimum (Ice min) and maximum (Ice max) ice extent during the sampling period are indicated by approximate 15 % ice cover derived from satellite data. The entire survey area was covered by pack-ice in winter 2006. ASF = Antarctic slope front; D/N = day/night comparative hauls; ice = SUIT hauls under ice; ow = SUIT hauls in open water.

Hydrography and environmental data

Vertical profiles of temperature, salinity and density were derived from measurements made by lowering a CTD (Conductivity, Temperature, Depth) probe to depths varying between 1,000 m and the sea floor at LAKRIS grid stations (49 stations in autumn 2004, 59 in winter 2006 and 50 in summer 2007 / 2008). The CTD used was a Sea-Bird Electronics SBE 911*plus*, supplemented by an altimeter to measure the distance to the sea floor, a transmissometer type Wet Labs C-Star to measure the attenuation of light, which in the open ocean is indicative of the concentration of particulate organic carbon. A chlorophyll-sensitive fluorometer (Dr. Haardt BackScat) was used in autumn 2006 and summer 2007 / 2008 to estimate the chlorophyll *a* concentration [mg l^{-1}] in the water column. The temperature and conductivity sensors (two pairs of sensors) were calibrated prior to the cruise to an accuracy of better than 0.001°C and 0.001 S^{-1}, respectively. A difference criterion was applied to predict the mixed layer depth (MLD) from the density field alone. The MLD was defined as the depth at which the calculated *in situ* density increased by $\Delta\sigma_T = 0.02$ compared to the surface value (Cisewski et al. 2005, Cisewski et al. 2008).

Solar radiation [W m^{-2}] was measured by the ship's meteorological system. Bottom depth [m] was estimated for each station position using modeled global bathymetry from a publicly available database (Smith & Sandwell 1997, Scripps 2006).

The proportion of the effective towing distance (eD) when the SUIT was towed under sea ice was used to estimate the percentage of sea ice coverage for each SUIT haul. SUIT hauls with a proportional ice coverage > 10 % were considered under-ice hauls. The proportional ice coverage among these hauls ranged from 18 % to 100 %, averaging at 68 %. The average ice thickness during each under-ice haul was estimated by calculating the products of different ice thicknesses and the corresponding towing distances and dividing the sum of these products by the total towing distance under ice.

7.2.2 Data analysis

Data from the 57 quantitative hauls were used to calculate the arithmetic mean density of individuals of each species [N 1,000 m^{-2}] for different sampling seasons and for hauls conducted under ice and in open water, respectively. Mean wet masses [g 1,000 m^{-2}] were computed by multiplication of the abundance of each species with the replacement volume per individual in each season, assuming 1 ml = 1 g. When ice occasionally accumulated in the net, jellyfish (Cnidaria) and comb jellyfish (Ctenophora) could be damaged to varying degrees and were therefore excluded from quantitative analysis. Data were log (x + 1) transformed for comparative ANOVA analysis to obtain similar variances in the residuals.

Patterns in species composition were explored for all samples combined and separately for each sampling season by cluster analysis using complete linkage and by non-metric multi dimensional scaling (NMDS, Kruskal 1964). These analyses were based on a Bray-Curtis dissimilarity matrix produced from the Wisconsin double standardized abundance data. In Wisconsin double standardization species are first standardized by maxima and then sites by site totals (Bray & Curtis 1957, Oksanen et al. 2008). Taxa not determined to species level that possibly represented more than one species were excluded from community analysis.

The influence of environmental variables on species composition was investigated separately for each sampling year using two techniques:

The correlations of the environmental variables with the NMDS ordination were projected as vectors on the ordination to visualize their relationship with the sample ordination. The vectors point into the direction of the most rapid change in the environmental variable, and their length is proportional to the correlation between ordination and environmental variable. The significance of correlations was tested with a randomized permutation test using 10,000 permutations.

To also detect non-linear dependencies, for each environmental variable a smooth surface was fitted to the two ordination axes using thinplate splines (Wood 2003). Fitted values were then calculated for a regular grid which was used to draw contour lines on the ordination plot.

The following environmental variables were included in the analyses:

- MLD;
- water temperature (0 m – MLD);
- water temperature (0 – 200 m);
- salinity (0 m – MLD);
- salinity (0 – 200 m);
- attenuation (0 m – MLD);
- attenuation (0 – 200 m);
- potential temperature at depth of temperature maximum;
- chlorophyll a conc. (0 – 200 m; only 2006 and 2007 / 2008);
- ocean depth;
- solar radiation;
- proportional ice coverage during SUIT hauls;
- mean ice thickness during SUIT hauls.

Because collinear variables may cause problems in these analyses (Quinn and Keough 2004), we first assessed collinearity using correlation and variance inflation factors (VIF). VIF values were calculated for the full set of variables in order to reduce the data to a set of non-collinear predictors. Because VIF values above 10 are often considered indicative of high collinearity (Quinn and Keough 2004), we applied a stepwise procedure, in which the variable with the highest VIF value was removed before re-calculating VIF values for the remaining set of variables, until all variables had VIF values below 10. Analyses were performed with the selection of variables resulting from this procedure.

We identified indicator species for groups recognized in cluster analysis and NMDS analysis using the indicator species index introduced by Dufrene & Legendre (1997):

$\text{IndVal} = A_{ij} \times B_{ij} \times 100$;

where A_{ij} in our study is the mean density of individuals of species *i* in the samples of group *j* divided by the sum of the mean densities of individuals of species *i* over all groups, and B_{ij} is the number of samples in group *j* where species *i* is present divided by the number of samples in group *j*. This index reaches its maximum (100 %) for species that are present at all samples in one group and absent from all other groups.

All statistical analyses were performed with the statistical program R (R Development Core Team 2008) version 2.7.1 using additional packages ‘car’ (Fox 2008), ‘labdsv’ (Roberts 2007), ‘MASS’ (Venables & Ripley 2002), ‘mgcv’ (Wood 2006) and ‘vegan’ (Oksanen et al. 2008).

7.3 Results

7.3.1 Hydrography and ice coverage

The largest part of the LAKRIS survey area was characterized by the inflow of Warm Deep Water (WDW) of circumpolar origin with the southern, westward setting branch of the Weddell Gyre. It formed a layer of maximum potential temperature at a depth of 200 - 400 m. The Coastal Current south of the Antarctic Slope Front (ASF) was limited to few stations in the very south of the area of investigation in each sampling season (Figure 1). An influence of the Maud Rise seamount on the local hydrography was indicated by a persistent current jet on its northern slope. Our results are in general agreement with previously reported hydrographical studies showing a quasi-stationary pool of relatively warm WDW immediately west of this seamount which entered this region along its northern slope (Bersch et al. 1992; Gordon & Huber 1995). Mesoscale eddies forming in the lee of the sea mount propagated in a south-south-easterly direction. The most prominent seasonal hydrographical pattern was apparent from the mixed layer depth, which never exceeded 50 m in summer 2007 / 2008, whereas it ranged between 12 and 200 m in autumn 2004 and between 30 and 450 m in winter 2006.

Significant amounts of sea ice only occurred south of 68°S in autumn 2004 (Figure 1 a). Most parts of the predominantly young ice cover in that season had formed only days to weeks before the sampling. A substantial pack-ice cover was present throughout the entire area of investigation in winter 2006 (Figure 1 b). The ice edge during the 2006 sampling period was situated north of the LAKRIS grid at approximately 57°S. A very dynamic sea ice situation was characteristic of summer 2007 / 2008. Large parts of the survey area were ice-covered at the beginning of the sampling campaign in early December 2007. A polynia north of Maud Rise expanded during the investigation period, resulting in an intermediate situation with an open area between 63°S and 67°S. When the area was left in late January 2008, only a residual ice cover persisted south of 67°S (Figure 1 c).

▼**Table 2.** Frequency of occurrence [%] of macrofauna encountered in the surface layer (0 - 2 m) on the LAKRIS grid south of 59°S. All hauls included.

	Autumn 2004	**Winter 2006**	**Summer 2007 / 2008**
Number of hauls	23	29	19
CNIDARIA			
Peryphylla peryphylla	0	3.4	0
Calycopsis borchgrevinki	8.7	20.7	0
Diphyes antarctica	43.5	89.7	5.3
CTENOPHORA			
Beroe cucumis	1)	1)	36.8
Beroe forskalii	1)	1)	31.6
Callianira antarctica	1)	1)	57.9
Unidentified ctenophore	35.8	31.0	10.5
MOLLUSCA			
Pteropoda			
Clione antarctica	13.0	75.9	68.4
Clio piatkowskii	0	0	10.5
C. pyramidata	21.7	20.7	84.2
Spongiobranchaea australis	8.7	13.8	5.3
Cephalopoda			
Paralarvae			
Mesonychoteuthis hamiltoni	4.3	0	0
Psychrotheutis glacialis	0	0	21.1
Unidentified squid	0	3.4	0
Adults			
Kondakovia longimana	0	3.4	0
ANNELIDA			
Polychaeta			
Tomopteris carpentieri	13.1	13.8	57.9
T. planctonis	0	0	15.8
T. septentrionalis	8.7	3.4	15.8
Vanadis antarctica	20.7	13.8	5.3
ARTHROPODA			
Crustacea			
Amphipoda			
Eusirus laticarpus	0	31.0	89.5
E. microps	4.3	17.2	47.4
E. perdentatus	4.3	0	0
Eusirus spp.	0	3.4	10.5
Ischerocerus sp.	0	3.4	0
Scina sp.	0	6.9	0
Cyllopus lucasi	47.8	20.7	26.3
Hyperia macrocephala	17.4	3.8	26.3
Hyperiella dilatata	52.2	13.3	21.1

▼**Table 2 (**continued)

Hyperoche medusarum	52.2	24.1	36.8
Primno macropa	0	17.2	52.6
Unidentified amphipod	0	6.9	0
Euphausiacea			
Furcilia larvae			
Euphausia crystallorophias	4.3	0	0
E. superba	43.5	72.4	0
Thysanoessa macrura	56.5	17.2	5.3
Postlarval krill			
E. crystallorophias	0	0	10.5
E frigida	17.4	0	0
E. superba	69.6	75.9	100.0
Thysanoessa macrura	0	0	84.2
Decapoda			
Decapod larvae	0	0	21.1
CHAETOGNATHA			
Eukronia hamata	52.2	62.1	5.3
Pseudosagitta gazellae	69.6	69.0	94.7
CHORDATA			
Salpida			
Ilhea racovitzae	17.4	0	10.5
Salpa thompsoni	13.0	20.7	10.5
Vertebrata			
Fish larvae			
Dissostichus sp.	0	0	5.3
Lepidonotothen squamifrons	8.7	0	0
Pagothenia borchgrevinki	0	6.9	0
Trematomus loennbergii	0	13.8	10.5
T. scottii	4.3	0	0
Artedidraco sp.	0	0	5.3
Gymnodraco acuticeps	4.3	0	0
Unidentified channichthyid	0	0	5.3
Unidentified notothenioid	8.7	3.4	5.3
Unidentified fish	4.3	6.9	0
Postlarval fish			
Notolepis sp. (juveniles)	0	0	15.7
Electrona antarctica	21.7	3.4	0
Aethotaxis mitopteryx	0	3.4	0
Total number of species	27	28	34

[1] Condition of ctenophores precluded species identification in 2004 and 2006.

▼**Table 3.** Mean density of macrofauna [N 1,000 m^{-2}] on the LAKRIS sampling grid at the open surface and under ice (0 – 2 m). Only quantitative hauls were included. **ice** = SUIT hauls under ice; **ow** = SUIT hauls in open water

	Autumn 2004			**Winter 2006**	**Summer 2007/2008**		
	ow	**ice**	**total**	**total (ice)**	**ow**	**ice**	**total**
Number of hauls	14	3	17	21	7	11	18
MOLLUSCA							
Pteropoda							
Clione antarctica	0.09	0	0.08	4.01	2.95	0.70	1.58
Clio piatkowskii	0	0	0	0	0.12	0	0.05
C. pyramidata	2.08	0.46	1.80	0.74	53.10	10.47	27.05
Spongiobranchaea australis	0.01	0.18	0.04	0.08	0.04	0	0.02
Cephalopoda							
Paralarvae							
Psychrotheutis glacialis	0	0	0	0	0.16	0.05	0.09
Adults							
Kondakovia longimana	0	0	0	0.01	0	0	0
ANNELIDA							
Polychaeta							
Tomopteris carpentieri	0.08	0	0.07	0.07	1.60	0.73	1.07
T. planctonis	0	0	0	0	0.23	0.69	0.51
T. septentrionalis	0.16	0	0.13	0.03	0.41	0.02	0.17
Vanadis antarctica	0.16	0	0.13	0.04	0	0.02	0.01
ARTHROPODA							
Crustacea							
Amphipoda							
Eusirus laticarpus	0	0	0	0.31	0.82	11.04	7.07
E. microps	0	0	0	0.12	0.31	0.54	0.45
Ischerocerus sp.	0	0	0	0.05	0	0	0
Scina sp.	0	0	0	0.015	0	0	0
Cyllopus lucasi	6.42	0	5.29	0.13	2.32	0	0.90
Hyperia macrocephala	0.05	0	0.04	0.03	0.04	0.15	0.11
Hyperiella dilatata	2.57	0	2.12	0.09	4.05	0.05	1.60
Hyperoche medusarum	1.10	0.27	0.95	0.24	0.24	0.09	0.15
Primno macropa	0	0	0	0.18	0.98	0.99	0.99
Euphausiacea							
Furcilia larvae							
Euphausia crystallorophias	0	0.36	0.06	0	0	0	0
E. superba	3.94	81.97	17.71	62.09	0	0	0
Thysanoessa macrura	0.86	2.07	1.08	1.71	0.08	0	0.03
Postlarval krill							
E frigida	0.93	0	0.76	0	0	0	0
E. crystallorophias	0	0	0	0	< 0.01	0	< 0.01
E. superba	932.73	6.03	769.20	2490.13	105.97	1224.93	789.78
T. macrura	0	0	0	0	184.78	275.16	240.01

▼**Table 3** (continued)

Decapoda (larvae)							
Unidentified decapod	0	0	0	0	0.15	0.15	0.15
CHAETOGNATHA							
Eukronia hamata	5.38	1.40	4.68	3.29	0.15	0	0.06
Pseudosagitta gazellae	1.50	1.29	1.46	2.67	47.18	26.82	34.74
CHORDATA							
Salpida							
Ilhea racovitzae	0.07	0.18	0.09	0	0	0.06	0.03
Salpa thompsoni	0.06	0	0.05	0.86	0.67	0.36	0.48
Vertebrata							
Fish larvae							
Dissostichus sp.	0	0	0	0	0.04	0	0.02
Lepidonotothen squamifrons	0.03	0	0.02	0	0	0	0
Pagothenia borchgrevinki	0	0	0	0.03	0	0	0
Trematomus loennbergii	0.02	0	0.02	0.25	0	0.05	0.03
T. scottii	0.01	0	0.01	0	0	0	0
Gymnodraco acuticeps	0	0.08	0.01	0	0	0	0
Unidentified channichthyid	0	0	0	0	0.12	0	0.02
Postlarval fish							
Notolepis sp. (juveniles)	0	0	0	0	0.15	0.02	0.07
Electrona antarctica	0.06	0	0.05	0	0	0	0
Aethotaxis mitopteryx	0	0	0	0.01	0	0	0
Overall abundance	958.31	94.29	805.85	2567.19	418.89	1562.69	1117.88

▼**Table 4.** Mean wet biomass of macrofauna [g WW 1,000 m^{-2}] on the LAKRIS sampling grid at the open surface and under ice (0 – 2 m). Only quantitative hauls were included. **ice** = SUIT hauls under ice; **ow** = SUIT hauls in open water

	Autumn 2004			**Winter 2006**	**Summer 2007/2008**		
	ow	**ice**	**total**	**total (ice)**	**ow**	**ice**	**total**
Number of hauls	14	3	17	21	7	11	18
MOLLUSCA							
Pteropoda							
Clione antarctica	0.04	0	0.03	0.86	0.64	0.15	0.34
Clio piatkowskii	0	0	0	0	0.20	0	0.08
C. pyramidata	0.76	0.17	0.66	0.04	14.29	2.82	7.28
Spongiobranchaea australis	< 0.01	0.027	0.01	0.01	0.01	0	< 0.01
Cephalopoda							
Paralarvae	0	0					
Psychrotheutis glacialis	0	0	0	0	0.11	0.03	0.06
Adults							
Kondakovia longimana	0	0	0	2.50	0	0	0
ANNELIDA							
Polychaeta							
Tomopteris carpentieri	0.08	0	0.07	0.07	1.59	0.72	1.06
T. planctonis	0	0	0		< 0.01	0.01	0.01
T. septentrionalis	0.21	0	0.17	0.01	0.17	0.01	0.07
Vanadis antarctica	0.16	0	0.13	0.04	0	0.02	0.01
ARTHROPODA							
Crustacea							
Amphipoda							
Eusirus laticarpus	0	0	0	0.03	0.08	1.09	0.70
E. microps	0	0	0	0.10	0.13	0.23	0.19
Ischerocerus sp.	0	0	0	< 0.01	0	0	0
Scina sp.	0	0	0	< 0.01	0	0	0
Cyllopus lucasi	1.69	0	1.39	0.03	0.58	0	0.23
Hyperia macrocephala	0.05	0	0.04	0.03	0.03	0.13	0.09
Hyperiella dilatata	0.16	0	0.13	0.01	0.25	< 0.01	0.10
Hyperoche medusarum	0.20	0.09	0.24	0.08	0.06	0.02	0.04
Primno macropa	0	0	0	0.02	0.10	0.10	0.10
Euphausiacea							
Furcilia larvae							
Euphausia crystallorophias	0	0.01	< 0.01	0	0	0	0
E. superba	0.07	1.43	0.31	1.09	0	0	0
Thysanoessa macrura	0.02	0.04	0.02	0.03	< 0.01	0	< 0.01
Postlarval krill							
E. crystallorophias	0	0	0	0	< 0.01	0	< 0.01
E frigida	0.04	0	0.03	0	0	0	0
E. superba	335.29	1.38	120.35	568.13	16.58	191.65	123.57
T. macrura	0	0	0	0	8.89	13.24	11.55

Table 4 (continued)

Decapoda (larvae)							
Unidentified decapod	0	0	0	0	0.02	0.02	0.02
CHAETOGNATHA							
Eukronia hamata	0.09	0.02	0.08	0.06	< 0.01	0	< 0.01
Pseudosagitta gazellae	0.24	0.21	0.24	0.62	25.12	14.28	18.50
CHORDATA							
Salpida							
Ilhea racovitzae	0.11	0.27	0.14	0	0	0.09	0.05
Salpa thompsoni	0.06	0	0.08	1.12	1.06	0.57	0.76
Vertebrata							
Fish larvae							
Dissostichus sp.	0	0	0	0	0.04	0	0.02
Lepidonotothen squamifrons	0.03	0	0.02	0	0	0	0
Pagothenia borchgrevinki	0	0	0	0.020	0	0	0
Trematomus loennbergii	0.01	0	0.01	0.10	0	0.03	0.02
T. scottii	0.01	0	0.01	0	0	0	0
Gymnodraco acuticeps	0	0.08	0.01	0	0	0	0
Unidentified channichthyid	0	0	0	0	0.02	0	< 0.01
Postlarval fish							
Notolepis sp. (juveniles)	0	0	0	0	0.14	0.02	0.06
Electrona antarctica	0.13	0	0.11	0	0	0	0
Aethotaxis mitopteryx	0	0	0	0.25	0	0	0
Total biomass	339.44	3.72	124.26	575.24431	70.12	225.23	164.90

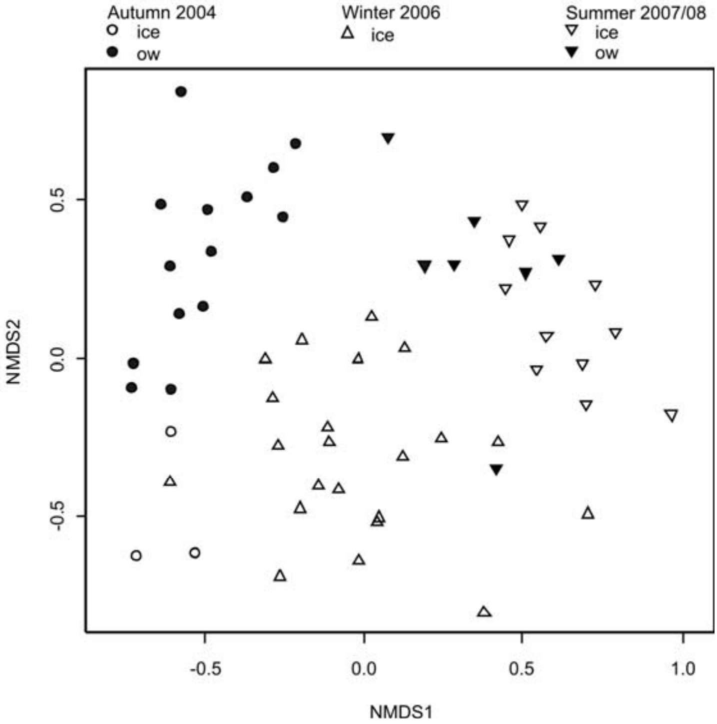
7.3.2 Species composition, abundance and biomass

At least 47 macrofauna species were encountered in the upper two meters of the Lazarev Sea, of which 16 were common to all three sampling seasons. The majority of species were crustaceans (14 species) and vertebrates (11 species). Overall species richness was slightly higher in summer 2008 (34 species) compared to autumn 2004 (26 species) and winter 2006 (28 species) (Table 2). With the highest species richness in the sampling season with the lowest number of hauls (summer 2007 / 2008: Table 2), san effect of sample size on the differences in species numbers between seasons was not evident. Postlarval Antarctic krill *Euphausia superba* clearly dominated the species community in terms of both abundance and biomass in each year (Table 3, Table 4). In terms of frequency of occurrence, however, it was outranked by the siphonophore *Diphyes antarctica* in winter 2006, demonstrating that cnidarians and probably also ctenophores were significant constituents of the species community (Table 2). Next to *E. superba*, the pteropods *Clione antarctica* and *Clio pyramidata*, the amphipods *Cyllopus lucasi*,*Hyperiella dilatata* and the arrow worm *Pseudosagitta gazellae* were important in all three seasons (Table 3, Table 4).

Mean bulk biomass of macrofauna excluding cnidarians and ctenophores was highest in winter 2006, followed by autumn 2004 and summer 2007 / 2008. These differences were largely due to variations in the biomass density of Antarctic krill in each sampling season (Table 4). When data were split by ice-covered and open water stations, a seasonally divergent pattern was apparent between autumn 2004 and summer 2007 / 2008. In autumn, mean biomass of all species including postlarval Antarctic krill was very low under ice, whereas it was dominated by about two orders of magnitude higher values in postlarval *E. superba* in open waters (Table 4). The dominance of postlarval Antarctic krill was less pronounced in summer, when *Thysanoessa macrura* and *P. gazellae* accounted for about 30% of the mean abundance and 20 % of the mean biomass of postlarval *E. superba*. In contrast to the autumn situation, postlarval Antarctic krill concentrated under ice in summer, where it clearly dominated in both abundance and biomass. In open waters, mean bulk biomass was almost threefold lower. Here, *T. macrura* dominated in abundance and *P. gazellae* in biomass (Table 3, Table 4).

7.3.3 Community structure in relation of environmental variables

A strong influence of the sampling season on the species composition was apparent from the ordination plot (Figure 2) and a high correlation of the horizontal ordination axis 1 with the sampling season (Pearson correlation coefficient: 0.97; $p \ll 0.001$). An influence of the presence of sea ice during SUIT hauls on the ordination of samples along NMDS ordination axis 2 (Pearson correlation coefficient: 0.91; $p \ll 0.001$) was also apparent to a lesser degree (Figure 2). In order to exclude the interference of seasonal divergence in the influence of ice coverage and other environmental variables on the community structure, we investigated these relationships separately for each sampling season.



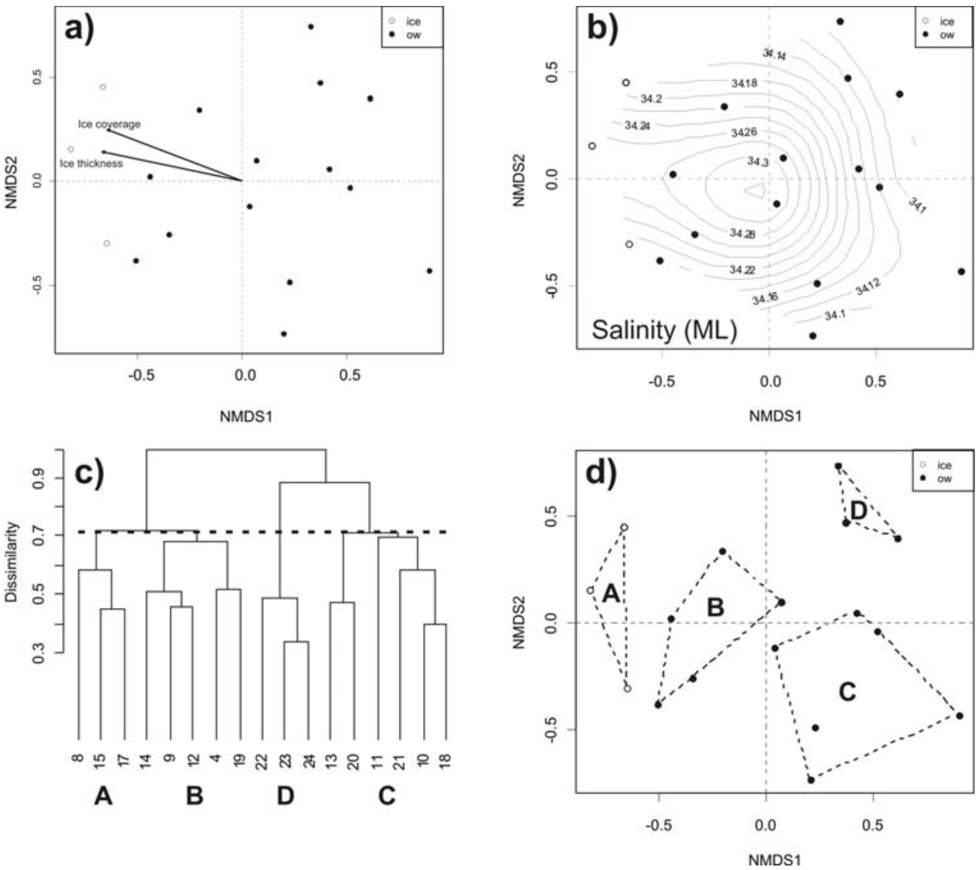
▲**Figure 2.** NMDS plot of SUIT samples. Samples were marked according to sampling season and under-ice / open water hauls. **ice** = SUIT hauls under ice; **ow** = SUIT hauls in open water; **NMDS 1, 2** = ordination axes.

Autumn 2004

In autumn 2004 ordination was significantly correlated to the proportional ice coverage during SUIT hauls and the corresponding ice thickness (Figure 3 a). A non-linear influence of mixed layer salinity was also present, reflecting the latitudinal transition in the survey area from ice covered and relatively saline surface waters in the south to open, less saline waters in the north (Figure 3 b; Table 5). The samples were not clearly separated into distinct groups in the NMDS ordination. In combination with cluster analysis, however, a change in species composition was evident following the gradients of the three significant environmental variables (Figure 3). Samples from autumn 2004 were separated into four major clusters (Group A – D) at a dissimilarity level of 0.72 (Figure 3 c). Group A and B were associated with a generally more saline mixed layer than group C and D. Group A comprised the only three hauls conducted under ice in combination with relatively high salinities. Group D was associated with the lowest salinities in the mixed layer. The neritic / ice-covered and the oceanic / ice-free extremes of the community composition in the LAKRIS survey area in autumn 2004 were reflected by different indicator species of group A (*Euphausia crystallorophias* furciliae, *E. superba* furciliae, *Gymnodraco acuticeps* larvae) and D (*Clione antarctica*, *Euphausia frigida*, *Tomopteris carpenteri*), respectively. No significant indicator species could be determined for groups B and C, indicating that their species community was largely also part of one or more other groups (Table 6).

▼**Table 5.** Autumn 2004. Summary statistics for the correlation of environmental vectors and of smooth functions of modeled surfaces with the NMDS ordination. Only significant relationships of either method are shown ($P < 0.05$). **ML** = mixed layer; **NMDS1, 2** = ordination axes; **r** = correlation coefficient

	Linear correlation				**Smooth function**	
Env. Variable	**r(NMDS1)**	**r(NMDS2)**	**r^2**	**P**	**Expl. Deviance**	**p**
Ice coverage	-0.948	0.317	0.465	0.004	86.3 %	0.003
Ice thickness	-0.986	0.169	0.461	0.009	75.1 %	0.010
Salinity (ML)	-0.984	-0.176	0.287	0.094	73.1 %	0.042



▲**Figure 3.** Autumn 2004. Relationship of environmental variables with NMDS ordination of SUIT samples. Vectors of environmental variables ($p < 0.05$) (a), contour lines for mixed layer salinity (b), cluster dendrogram (c) and resulting sample groups (A-D) projected on NMDS ordination (d). Hatched line in (c) indicates dissimilarity threshold used for sample grouping. Numbers below dendrogram refer to sample identifiers. Summary statistics of correlations and smooth function are shown in Table 5. Marker legend as in Figure 2. **ML** = mixed layer.

◄**Table 6.** Autumn 2004. Indicator values of species of different sample groups. Only values with a significance of $p < 0.10$ are shown. Values with $p < 0.05$ are underlined

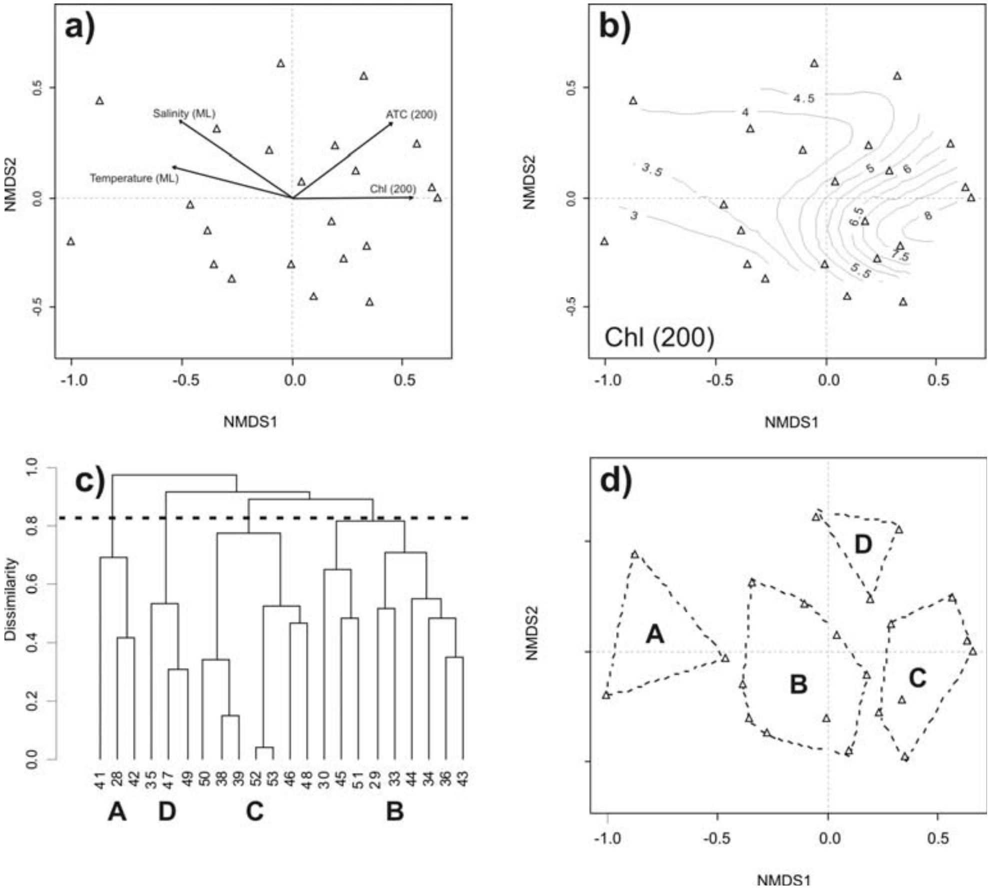
	Sample group			
Indicator Species	**A**	**B**	**C**	**D**
E. superba furc.	89.8			
E. crystallorophias furc.	33.3			
Gymnodraco acuticeps larv.	33.3			
Clione antarctica				100.0
Tomopteris carpenteri				66.7
Euphausia frigida				77.4
Tomopteris septentrionalis				66.7

Winter 2006

In winter 2006 the ordination of samples was significantly related to the chlorophyll *a* concentration in the upper 200 m and water temperature, salinity and attenuation in the mixed layer (Figure 4 a). In the case of chlorophyll *a* and attenuation, ordination was best explained by a smooth function (Figure 4 b, Table 7). The fitted contour lines were very similar for these two variables. Like in autumn 2004, a separation into distinct communities was not clear, but gradual changes in the species composition were evident when clustering and NMDS ordination were combined. The change in community composition along environmental gradients was most evident when samples were divided into four groups at a dissimilarity level of 0.85 (Figure 4 c, d). Group A, B and C marked the transition from a relatively warmer and more saline mixed layer and lower chlorophyll *a* concentrations (group A) to a colder and less saline mixed layer with high chlorophyll *a* concentrations (group C). The three daytime hauls in winter 2006 clustered together in group D. Distinct indicator species in each of the four groups highlighted the change in the species composition along environmental gradients and the influence of daylight (Table 8).

▼**Table 7.** Winter 2006. Summary statistics for the correlation of environmental vectors and of smooth functions of modeled surfaces with the NMDS ordination. Only significant relationships of either method are shown ($p < 0.05$). **ATC (200)** = attenuation in the upper 200 m; **chl (200)** = chlorophyll *a* concentration in the upper 200 m; **ML** = mixed layer; **NMDS1, 2** = ordination axes; **r** = correlation coefficient; **T** = water temperature

	Linear correlation				**Smooth function**	
Env. Variable	**r(NMDS1)**	**r(NMDS2)**	**r^2**	**P**	**Expl. Deviance**	**p**
ATC (200)	0.804	0.594	0.428	0.005	92.1 %	< 0.001
Chl (200)	1.000	0.001	0.391	0.008	78.0 %	0.007
Salinity (ML)	-0.828	0.560	0.510	0.001	61.5 %	0.001
T (ML)	-0.968	0.250	0.415	0.006	51.4 %	0.027



▲**Figure 4.** Winter 2006. Relationship of environmental variables with NMDS ordination of SUIT samples. Vectors of environmental variables ($p < 0.05$) (a)**,** contour lines for chlorophyll *a* concentration in the upper 200 m (b), cluster dendrogram (c) and resulting sample groups (A-D) projected on NMDS ordination (d). Hatched line in (c) indicates dissimilarity threshold used for sample grouping. Numbers below dendrogram refer to sample identifiers. Summary statistics of correlations and smooth function are shown in Table 7. Marker legend as in Figure 2. **ATC (200)** = attenuation in upper 200 m; **Chl (200)** = Chlorophyll *a* concentration in upper 200 m; **ML** = mixed layer.

◄**Table 8.** Winter 2006. Indicator values of species of different sample groups. Only values with a significance of $p < 0.10$ are shown. Values with $p < 0.05$ are <u>underlined</u>

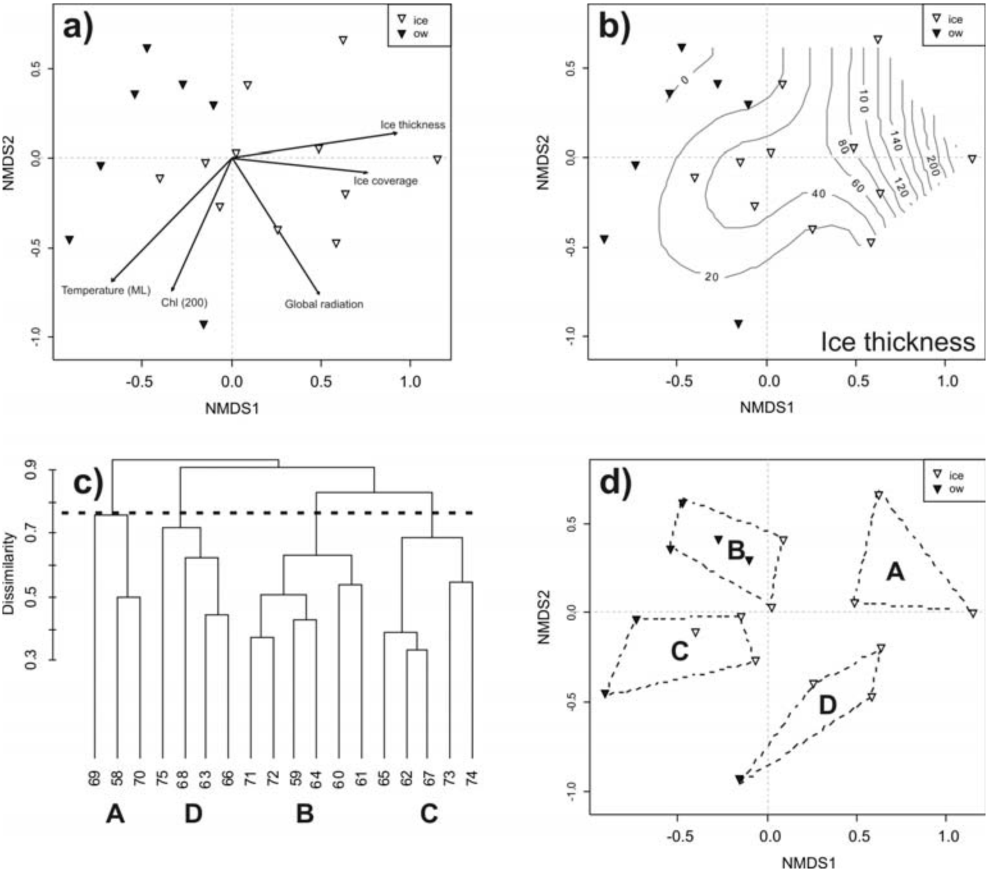
	Sample group			
Indicator Species	**A**	**B**	**C**	**D**
Eusirus microps	<u>90.8</u>			
Eusirus laticarpus	<u>54.4</u>			
E. superba furc.		<u>71.3</u>		
Trematomus loennbergi larv.		44.4		
Clione antarctica			<u>65.6</u>	
Euphausia superba			81.0	
Hyperiella dilatata			42.9	
Primno macropa				<u>97.6</u>
Thysanoessa macrura furc.				<u>94.1</u>
Scina sp.				<u>33.3</u>

Summer 2007 / 2008

In summer 2007 / 2008 the presence or absence of sea ice during SUIT hauls had a high impact on the ordination. The only exception to this pattern was the single daytime haul conducted in open waters (Figure 5 a). A distinct separation of ice and open water hauls, however, was not supported by the cluster analysis, indicating a more complex interaction of the five significant environmental variables in summer 2007 / 2008 (Figure 5 a). Besides the linear relation with global radiation, water temperature in the mixed layer and chlorophyll *a* concentration in the upper 200 m, smooth functions for proportional ice coverage and corresponding ice thickness during SUIT hauls explained a large part of the variation (Table 9). Their influence on the community composition was illustrated when samples were separated into four groups at a dissimilarity level of 0.76 in the cluster analysis (Figure 5 c). The well supported separation of group A from group B and C reflected the gradient from SUIT hauls conducted under very thick ice (group A) to hauls under thin ice and in open water (group B, C; Figure 5b, d). The less well supported distinction of group B and C corresponded to a trend towards a warmer mixed layer and higher chlorophyll *a* concentrations in the upper 200 m (Figure 5 c, d). Group D consisted of the only four hauls conducted in bright sunlight (global radiation > 100 W m^{-2}) and was thus strongly related to the gradient of global radiation. Groups A – C could be characterized by significant indicator species (Table 10). Only few species occurred at the bright-light stations of group D, where *E. superba* was the only indicator species with marginal significance ($p = 0.105$; Table 10).

▼**Table 9.** Summer 2007 / 2008. Summary statistics for the correlation of environmental vectors and of smooth functions of modeled surfaces with the NMDS ordination. Only significant relationships of either method are shown ($p < 0.05$). **chl (200)** = chlorophyll *a* concentration in the upper 200 m; **ML** = mixed layer; **NMDS1, 2** = ordination axes; **r** = correlation coefficient; **T** = water temperature

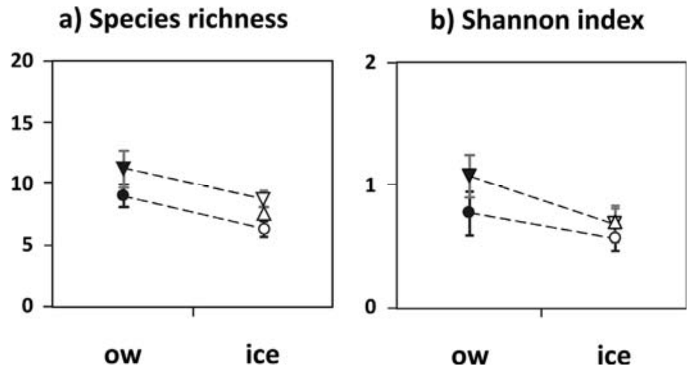
	Linear correlation				**Smooth function**	
Env. Variable	**r(NMDS1)**	**r(NMDS2)**	**r^2**	**p**	**Expl. Deviance**	**p**
Chl (200)	-0.411	-0.911	0.425	0.016	42.4 %	0.025
Global radiation	0.541	-0.841	0.530	0.002	84.0 %	0.003
Ice coverage	0.995	-0.104	0.358	0.036	84.0 %	0.006
Ice thickness	0.989	0.147	0.559	< 0.001	97.1 %	< 0.001
T (ML)	-0.698	-0.716	0.597	< 0.001	76.3 %	0.001



▲**Figure 5.** Summer 2007 / 2008. Relationship of environmental variables with NMDS ordination of SUIT samples. Vectors of environmental variables ($p < 0.05$) (a)**,** contour lines for ice thickness (b), cluster dendrogram (c) and resulting sample groups (A-D) projected on NMDS ordination (d). Hatched line in (c) indicates dissimilarity threshold used for sample grouping. Numbers below dendrogram refer to sample identifiers. Summary statistics of correlations and smooth function are shown in Table 9. Marker legend as in Figure 2. **chl (200)** = chlorophyll *a* concentration in upper 200 m; **ML** = mixed layer.

	Sample group			
Indicator Species	**A**	**B**	**C**	**D**
Trematomus loennbergi larv.	66.7			
Channichthyidae larv.	33.3			
Ilhea racovitzae	33.3			
Tomopteris carpenteri		57.4		
Primno macropa		54.2		
Tomopteris septentrionalis		50.0		
Hyperoche medusarum		46.6		
Decapod larvae			80.0	
Clio pyramidata			78.2	
Pseudosagitta gazellae			60.9	
Hyperiella dilatata			59.5	

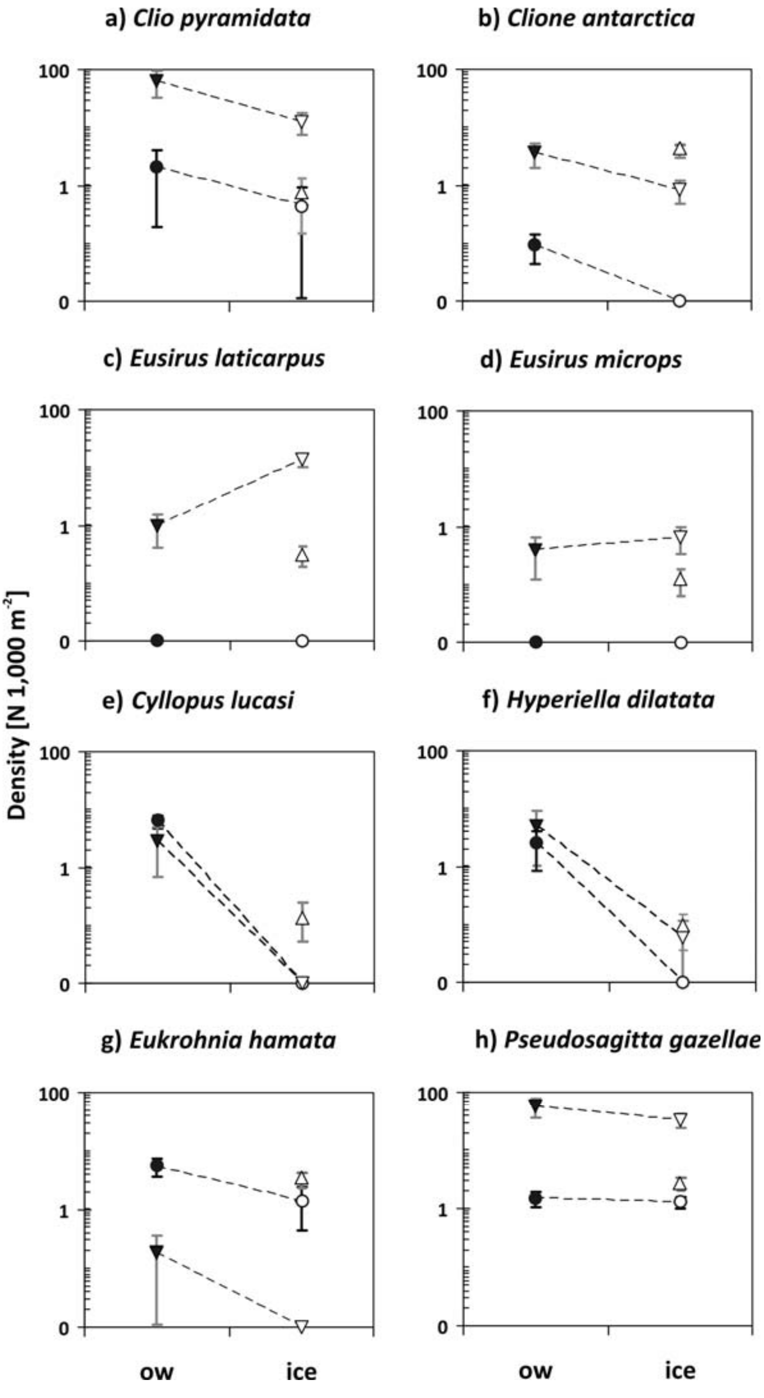
◄**Table 10.** Summer 2007 / 2008. Indicator values of species of different sample groups. Only values with a significance of $p < 0.10$ are shown. Values with $p < 0.05$ are underlined



◀ **Figure 6.** Average species richness (a) and Shannon diversity index (b) of sampling stations in relation to sampling season and under-ice / open water SUIT hauls. Error bars denote standard errors. Marker legend as in Figure 2.

Effect of ice and season on diversity indices and single species

The impact of sampling season and sea ice on species composition was investigated more closely at the level of diversity indices and a selection of dominant species. Mean species richness significantly responded to both factors and was highest in summer 2007 / 2008, lowest in autumn 2004, and was generally higher in open water than at sea ice stations. This pattern of elevated diversity in summer and in open water, however, was not significantly reflected in the Shannon index (Figure 6 a, b; Table 11). A detailed analysis of the abundance, distribution and population structure of surface layer euphausiids from the present data collection including a description of their relationship with the presence of sea ice at different seasons was provided in Chapter 8 (ibidem Figure 2, Figure 10). Among non-euphausiid species, *Clio pyramidata*, *Eusirus microps* and *Pseudosagitta gazellae* were significantly more abundant in summer than in autumn and winter (Figure7 a, d, h). The opposite trend was apparent in *Eukrohnia hamata* (Figure 7 g). In addition to the seasonal factor, the presence of sea ice had a significant negative effect on the abundance of *Cyllopus lucasi* (Figure 7 e). A preference for open water was also significant in *Hyperiella dilatata*, independent of the sampling season (Figure 7 f). It was not possible to separate the effects of season and the presence of sea ice from each other in *Clione antarctica* and *Eusirus laticarpus* due to a significant interaction of the two factors (Table 11). While the highest mean abundance of *C. antarctica* was under the 2006 winter pack-ice, the pteropod was more abundant in open water than under ice in autumn 2004 and summer 2007 / 2008 (Figure 7 b). *E. laticarpus* was not encountered in autumn 2004. It was clearly more abundant under ice than in open waters in summer 2007 / 2008. The mean open water abundance in summer, however, was still above under-ice abundances in winter 2006, when no open water stations were sampled for comparison.



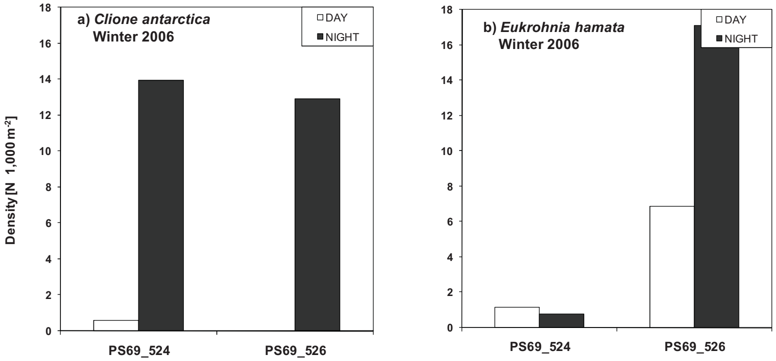
▲**Figure 7.** Mean density of selected non-euphausiid macrofauna species in relation to sampling season and under-ice / open water SUIT hauls. Error bars denote standard errors. Euphausiid data were shown in Chapter 8, Figure 2 and Figure 10. Y-axes in logarithmic scale. Marker legend as in Figure 2.

	Presence of sea ice	Season	Interaction (ice:season)
Clio pyramidata	ns	***	ns
Clione antarctica	*	ns	***
Eusirus laticarpus	***	***	***
E. microps	ns	**	ns
Cyllopus lucasi	***	*	ns
Hyperiella dilatata	***	ns	ns
Eukrohnia hamata	ns	***	ns
Pseudosagitta gazellae	ns	***	ns
Species richness	**	*	ns
Shannon index	ns	ns	ns

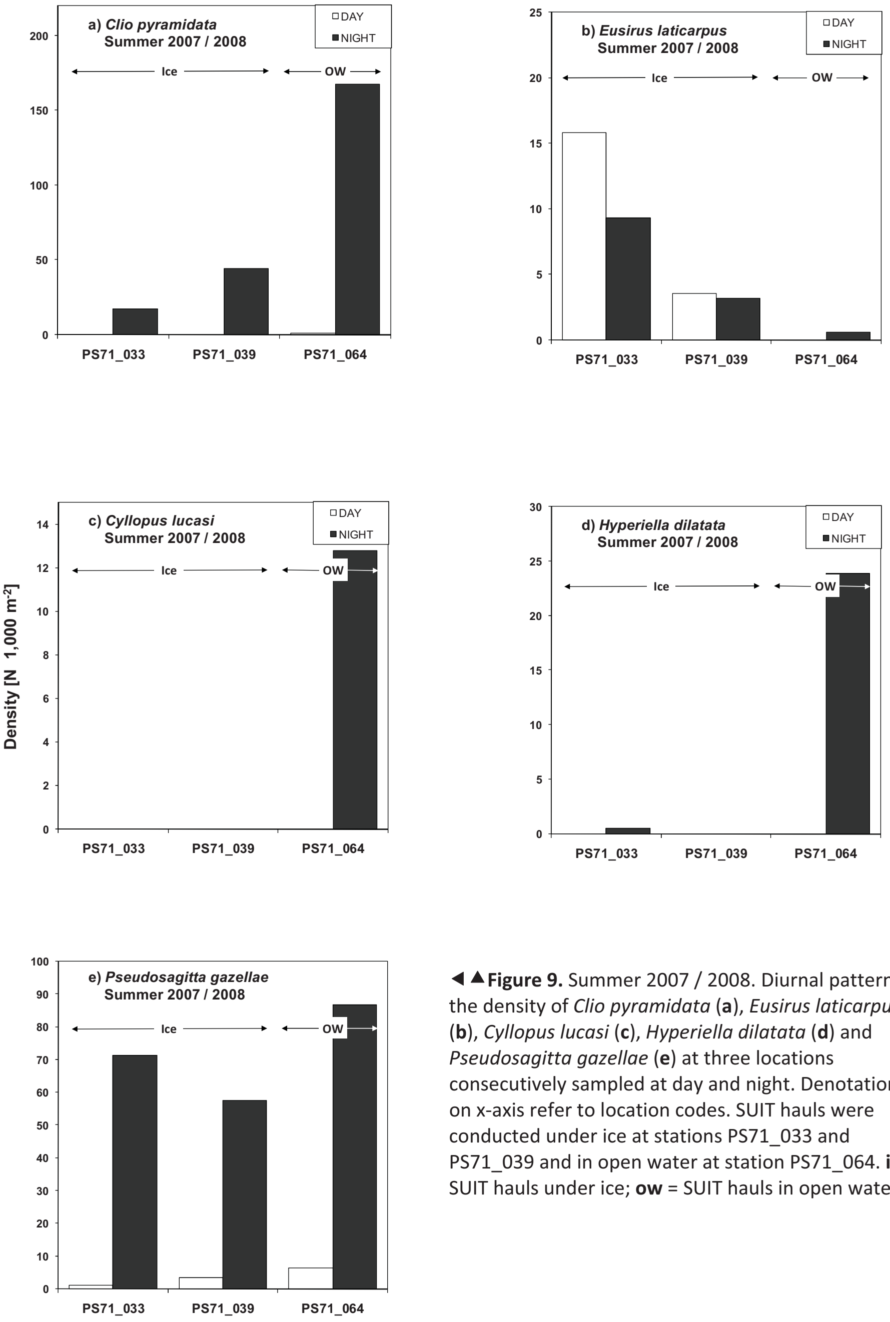
◀**Table 11.** Relationship of a selection of non-euphausiid zooplankton species, species richness and Shannon diversity index from the surface layer (0 – 2 m) with the presence of sea ice, sampling season and the interaction of the two. Significance (ANOVA): ***** $p < 0.05$; ****** $p < 0.01$; ******* $P < 0.001$; ns = not significant. Corresponding euphausiid data are presented in Chapter 8

Effect of daylight

The significant influence of light conditions on the species composition in winter 2006 and summer 2007 / 2008 apparent from the multivariate analyses was verified for a number of species at the five stations repeatedly sampled at day and night that yielded sufficient numbers of animals. In winter 2006, *Clione antarctica* was clearly abundant in the ice-water interface layer at night and largely absent from this environment at day (Figure 8 a). A similar, but less pronounced pattern was apparent in *Eukrohnia hamata* at the only station where enough animals were caught (Figure 8b). These two species were not sufficiently abundant to allow meaningful diurnal comparisons at the three stations sampled in summer 2007 / 2008. In this season, *Clio pyramidata* (Figure 9 a), *Cyllopus lucasi* (Figure 9 c), *Hyperiella dilatata* (Figure 9 d) and *Pseudosagitta gazellae* (Figure 9 e) were abundant at night, but largely absent from SUIT catches during daytime. This pattern was independent of the presence of sea ice in *C. pyramidata* and *P. gazellae*. The other two species were not (*C. lucasi*) or barely (*H. dilatata*) encountered under ice. A pronounced diurnal pattern was not apparent in *Eusirus laticarpus*, of which only a few specimens were caught at night at the open water station (Figure 9 b).



▲**Figure 8.** Winter 2006. Diurnal patterns of the abundance of Clione antarctica (**a**) and Eukrohnia hamata (**b**) at two locations consecutively sampled at day and night. Denotations on x-axis refer to location codes. All SUIT hauls were conducted under ice.



◀ ▲**Figure 9.** Summer 2007 / 2008. Diurnal patterns of the density of *Clio pyramidata* (**a**), *Eusirus laticarpus* (**b**), *Cyllopus lucasi* (**c**), *Hyperiella dilatata* (**d**) and *Pseudosagitta gazellae* (**e**) at three locations consecutively sampled at day and night. Denotations on x-axis refer to location codes. SUIT hauls were conducted under ice at stations PS71_033 and PS71_039 and in open water at station PS71_064. **ice** = SUIT hauls under ice; **ow** = SUIT hauls in open water.

7.4 Discussion

7.4.1 Taxonomic composition and community structure

Species richness and diversity

The 47 macrofauna species caught covered eight phyla ranging from hydrozoans to vertebrates, included free drifting, actively swimming and potentially sympagic species ranging in size order from millimeters (larval krill) to decimeters (squid, fish). Although equal or higher in sample size than the present investigation, offshore studies in the Southern Ocean with a sampling depth of 50 to 300 m did not find higher species numbers in the size range considered in our study than the approximately 30 species per season found in the upper two meters alone (Lancraft et al. 1989, Fisher et al. 2004, Donnelly et al. 2006, Hunt et al. 2007). This tentative comparison indicates that depth intervals that are orders of magnitudes greater may not yield higher species numbers than the mere upper two meters of the water column. Higher species numbers were reported from typically more diverse areas, such as the Weddell-Scotia Confluence (Lancraft et al. 1991, Siegel et al. 1992) and the Polar Frontal Zone (Pakhomov and Froneman 2000), or where substantial parts of the sampling area were on the shelf (Boysen-Ennen & Piatkowski 1988, Piatkowski 1989).

Next to a significant seasonal pattern, the mean species richness was significantly higher at the open surface than under ice (Figure 6, Table 11). A general trend of decreasing species richness from open water into the closed pack-ice was also observed by Siegel et al. (1992) in the upper 60 m and, to a lesser extent, by Donnelly et al. 2006 in the 0 – 200 m stratum. In contrast to the pattern observed in species richness, Shannon diversity under ice was not significantly lower than at the open surface in our data from the Lazarev Sea (Figure 6, Table 11). This index increases with greater evenness and increasing number of rare species, emphasizing the importance of the ice-water interface layer for less abundant species, of which some might be closely associated with the sea ice habitat.

Comparisons between studies, however, should be considered with caution due to the variability in sampling methodology and effort, sampling depth, seasonal and geographical coverage. Certainty about the comparability of the new field sampling technique introduced with SUIT can only slowly be obtained when more comparative datasets become available. Like in all fishing nets, the selectivity of the SUIT depends on the towing speed, the size of the net opening, the mesh size, the size and the body shape of the targeted species and their ability to detect and actively avoid the net. ADCP flow measurements during the hauls included in quantitative analysis indicated that the net was directed forward, both in open water and under ice, and towing speed was in the range commonly used in macrozooplankton studies (Chapter 9; Fisher et al. 2004, Donnelly et al. 2006). Based on the mesh size of the nets used (7 mm), it can be assumed that hard-bodied zooplankton was captured quantitatively down to a minimum size of 10 mm, and only minor losses can be expected in 5 to 10 mm sized species. A comparison of the size composition of Antarctic krill *Euphausia superba* between catches of SUIT and the well-established rectangular midwater trawl (RMT) at identical sampling stations indicated that the size selectivity of the SUIT did not differ significantly from the RMT at least up to the size of large euphausiids (Chapter 8, Table 4). To date, SUIT probably provides the most quantitative way possible to directly sample macrozooplankton and micronekton in the ice-water interface layer and at the open surface with the same gear. This approach overcomes the spatial limitation of observations by divers and autonomous camera systems and the problems with surface reflections and accurate determination of species and their size compositions associated with hydro-acoustic methods (Marschall 1988, Zhou et al. 1994, Kaufmann et al. 1995, Brierley et al. 2002).

Effect of environmental parameters on community structure

A pronounced seasonal variation is typical for the community composition of Southern Ocean zooplankton and was also observed in our study (Figure 2; Fisher et al. 2004, Hunt et al. 2007). There was not sufficient evidence, however, to identify distinct communities based on the number of hauls conducted per sampling season in this investigation. Variations in the dissimilarity threshold determining the separation of samples in different groups shown in Figure 3 – 5 may be equally meaningful. A change of the species composition along major environmental gradients was nonetheless evident and illustrated by significant indicator species at least at the extremes of the gradients.

Our results from the two seasons when the transition from open water to closed pack-ice was sampled implied a strong response of the species community to sea ice. In autumn 2004 and summer 2007 / 2008, the distribution of sea ice and of remaining heavy winter and multi-year ice, respectively, largely coincided with the continental shelf and slope (Figure 1). Consequently, shelf-associated species were indicative of the sample groups of under-ice hauls in autumn 2004 (Group A, Figure 3) and of hauls associated with thick ice in summer 2007 / 2008 (Group A; Figure 5). When the entire survey area was covered by ice in winter 2006, the community structure most significantly responded to the closely related concentrations of chlorophyll *a* and attenuation, a proxy for particulate organic carbon (POC). The species assemblage associated with high chlorophyll *a* concentrations (and high POC) could have been attracted by relatively high biological activity in the water column (Figure 4, group C). A high indicator value of the planktivorous sea slug *Clione antarctica* supports this impression. The possibly sympagic amphipods *Eusirus laticarpus* and *E. microps* (Chapter 6) and Antarctic krill larvae were indicative of species assemblages associated with low concentrations of chlorophyll *a* and POC in the water column, emphasizing a high relevance of the ice-water interface for these species assemblages (Figure 4, group A, B).

Effect of daytime

The pronounced diurnal pattern in the occurrence of many species in the surface layer (Figure 8, 9) reflected the diel vertical migration described for a number of these species and generally for zooplankton (Lancraft et al. 1989, Nordhausen 1994a, Donnelly et al. 2006). Vertical migration behaviour may have introduced a minor negative bias to abundance and biomass estimates of our study because the eleven daytime hauls were included in the analysis. The vertical migration behaviour is often considered as the consequence of diurnal changes in the balance of benefits (e.g. better food availability) and risks (e.g. visual predators) to stay in a certain depth layer and has a cost, the energy invested in vertical movement (Gabriel & Thomas 1988, De Robertis 2002). In that sense, the diurnal patterns observed in the present study indicate that both the open surface and the ice-water interface layer are an attractive environment for Antarctic macrofauna, supplying sufficient benefits to compensate for the cost of vertical migration in spite of their exposure to ice, atmosphere, airborne and ice-based predators.

7.4.2 Ecological significance of macrofauna in the ice-water interface and open surface layer

The higher trophic levels of the Antarctic seasonal sea ice zone may depend considerably on energy ultimately derived from algae growing in sea ice (Ainley et al. 1991, van Franeker et al. 1997, Ainley et al. 2003b). Energy can be transferred from the sea ice system to the pelagic food web through vertical migration, food chains and sinking detritus (reviewed in Brierley & Thomas 2002). Thus, potentially all biota directly or indirectly depending on sea ice production may act as energy vectors between the ice and the water column. Among macrofauna, Antarctic krill dominated the biomass composition in each sampling season, undoubtedly playing an important role in this context. A separate chapter was therefore dedicated to the euphausiids, allowing a closer look on their distribution, population structure and ecological significance (Chapter 8).

Other macrofauna species, however, may also be locally, regionally or temporarily important. Indications for an association with the ice-water interface layer were present in three species: *Eusirus laticarpus*, *E. microps* and *Clione antarctica*. In the latter species, the highest abundances in all three seasons were encountered under the sea ice in winter 2006. However, abundances at the open surface were generally above values under ice in autumn and summer, causing a significant interaction of the factors season and presence of ice in relation to the abundance of *C. antarctica* (Table 11, Figure 7). Because no stations were sampled in open water in 2006, we cannot exclude that the high abundances under the winter ice reflected inter-annual variation with possibly even higher abundances in open waters to the north. Yet the relatively high density of *C. antarctica* under ice and its vertical migration into the ice-water interface layer indicates a certain relevance of this environment for the sea slug in winter. The following tentative rationale could explain the seasonally divergent abundance pattern with respect to the presence of sea ice: *C. antarctica* is a monophagus predator on another pteropod, *Limacina helicina* (Lalli & Gilmer 1989). *Limacina* spp. were abundant in SUIT catches from all three sampling seasons but were excluded from the present analysis due to their small size. *L. helicina* mainly feed on phytoplankton in summer, but little is known how they survive the winter in Antarctic ice-covered waters (Lalli & Gilmer 1989). In the Arctic, juvenile *L. helicina* have been proposed to rely on particulate organic matter originating from the sea ice in winter (Kobayashi 1974, Gannefors et al. 2005). If that is also the case in the Southern Ocean, *L. helicina* is likely to concentrate under ice in winter and prefer the phytoplankton-rich open waters in summer. Its predator *C. antarctica* can be expected to follow this behaviour. *C. antarctica* and its prey *L. helicina* have a high lipid content and are thus rich in energy, making them potentially significant vectors in the energy transfer between the sea ice community and the pelagic food web in winter (Phleger et al. 1997a, Gannefors et al. 2005).

A much closer association with sea ice was evident from the amphipod *Eusirus laticarpus*. There was no evidence of the amphipod in the largely open surface layer in autumn, frequent occurrence under ice in winter at moderate abundances and a wide distribution and significantly higher abundances under ice than in open water in summer (Table 2, Table 3, Figure 7 c). Such a seasonal pattern would agree with the pelago-sympagic mode of life proposed in Chapter 6 based on a subsample of the data presented here: Being absent from the surface layer in autumn, the amphipods raise to the maturing sea ice in winter, reaching the highest spatial coverage and abundances under ice before the onset of melting in summer. Female *E. laticarpus* with brood sacs were caught under summer pack-ice (H.F., unpublished data), indicating that the reproductive cycle was completed at the end of the sea ice period. A similar seasonal pattern was observed in *E. microps* (Table 2, Table 3), which was also suggested to be a potentially sympagic species (Chapter 6). However, its under-ice abundances were not significantly above open water values in summer (Figure 7 d, Table 11), indicating either a generally more pelagic mode of life or an earlier switch to the pelagic phase in this species. *E. laticarpus* was often not distinguished from the morphologically similar *E. antarcticus* in early taxonomic studies (De Broyer & Jazdzewski 1993). A direct trophic link of *E. laticarpus* with sea ice biota could thus be indicated by reports of *E. antarcticus* grazing on the underside of ice floes (Hopkins & Torres 1988). As foragers at the ice-water interface, *E. laticarpus* and *E. microps* could form a trophic link from the sea ice to the pelagic species community as well as directly to the air-breathing top predators.

Species that were abundant both under ice and in the open surface layer, such as *Clio pyramidata* and *Pseudosagitta gazellae* may also contribute to the exchange between the sea ice system and the water column (Figure 7 a, h,). A high potential with respect to energy transfer from both the ice-water interface layer and the open surface to the water column may be expected from *P. gazellae*, which was second in biomass after *E.*

superba under ice and the biomass dominant in open waters in summer 2007 / 2008 (Table 4). This predator forages on zooplankton that can be assumed to rely on surface layer and under-ice resources.

An accurate assessment of the importance of macrofauna dwelling under ice and at the open surface for the pelagic food web, however, is beyond the possibilities of this baseline investigation. Complete answers to the underlying ecological processes are only possible with a better knowledge on the biology, diet composition and spatio-temporal distribution of relevant species in the water column, at the open surface and under ice, including mesozooplankton and nekton. Squid and fish for example mostly feed on copepods and other zooplankton, potentially allocating much of the energy from the open surface and the ice-water interface into the mesopelagic realm and ultimately to the air-breathing top predators (Hopkins et al. 1993). Our study accounts for occasional catches of three species of postlarval fish (*Aethotaxis mitopteryx*, *Electrona antarctica*, *Notolepis* sp.) and one species of adult squid (*Kondakovia longimana*) in the LAKRIS grid, as well as an additional species of squid (*Slosarczykovia circumantarctica*) at a station excluded from this study in the marginal ice zone north of 60°S in winter 2006 (H.F., unpublished data). The true abundances of surface-dwelling nekton may have been higher due to net avoidance. Yet, the evidence of fish and squid in the 0 – 2 m stratum supports the high importance of the open surface and ice-water interface layer as a foraging ground for pelagic nekton and air-breathing top predators suggested by Ainley et al. (1986).

7.4.4 Conclusions

Plasticity in terms of taxonomic composition, mode of life and size range characterized the species community of the 0 – 2 m surface layer in the Lazarev Sea. Rather than being a depleted border region of the pelagic realm, the surface layer probably attracts most species also found over much greater depth ranges. Especially the ice-water interface layer appears to be important for the biodiversity of the Southern Ocean as a temporary habitat for a variety of less abundant species.

Several species associated with the ice-water interface may be important in the energy transfer from sea ice biota into the pelagic food web besides the often dominant Antarctic krill. Together with the observed significant effect of ice properties on the community composition, these findings strongly support the perception that the ice is a major factor shaping the ecosystem structure of the Antarctic seasonal sea ice zone.

A concise investigation of the trophic interactions between the sea ice system, near-surface plankton and nekton and the pelagic food web including deeper layers is the next logical step to gain a more accurate picture of the ecological importance of the ice-water interface and the open surface layer in the Southern Ocean.

Acknowledgements

This study was made possible by extraordinary support by the crews of the *Polarstern* expeditions ANT XXI-4, ANT XXIII-6 and ANT XXIV-2, Captain Uwe Pahl, Captain Stefan Schwarze and the Alfred Wegener Institute for Polar and Marine Research (AWI). The following people contributed greatly to the successful completion of our research: A. Meijboom, M. van Dorssen, R. Fijn, B. Fey, D. Martynova, H. Verdaat, I. Nunez-Riboni, U. Piatkowski and M. Scheidat. This study was supported by the Netherlands AntArctic Programme (NAAP Project nr. 851.20.011) and the Dutch Ministry for Agriculture, Nature and Food Quality (LNV).

Key references

- Brierley AS, Thomas DN (2002) Ecology of Southern Ocean pack ice. Advances in Marine Biology, Vol 43 43:171-276
- Kaufmann R, Smith KJ, Baldwin R, Glatts R, Robinson B, Reisenbichler K (1995) Effects of seasonal pack ice on the distribution of macrozooplankton and micronecton in the northwestern Weddell Sea. Marine Biology 124:387-397
- Lalli CM, Gilmer RW (1989) Pelagic snails. The biology of holoplanktonic gastropod mollusks. Stanford University Press, Stanford, California
- Piatkowski U (1989) Macroplankton communities in Antarctic surface waters - spatial changes related to hydrography. Marine Ecology-Progress Series 55:251-259
- Siegel V, Skibowski A, Harm U (1992) Community structure of the epipelagic zooplankton community under the sea-ice of the northern Weddell Sea. Polar Biology 12:15-24

Preparing a large sample for sorting. The is a lot of of krill in the catch.

CHAPTER 8

Antarctic krill species (Crustacea: Euphausiidae) under sea ice and in the open surface layer

Hauke Flores, Jan A. van Franeker, Volker Siegel, Matilda Haraldsson, Volker Strass, Erik (H.W.G.) Meesters, Ulrich Bathmann & Wim J. Wolff

Abstract. The distribution, density and population structure of Antarctic euphausiids in the surface layer (0 – 2 m) under ice and in open waters was investigated with Surface and Under Ice Trawls (SUIT) during three expeditions in the Lazarev Sea (Southern Ocean) in autumn 2004, winter 2006 and summer 2007 / 2008. Data were compared to the density and size distributions of euphausiids from the upper 200 m collected with concurrently deployed Rectangular Midwater Trawls (RMT). *Euphausia superba* and *Thysanoessa macrura* were the most abundant among the four krill species collected. The highest mean density of *E. superba* in the surface layer occurred under sea ice in winter (2.7 N m^{-2}). In summer, they were significantly more abundant under ice (1.2 N m^{-2}) than at the open surface (0.1 N m^{-2}). Overall mean surface density was low in autumn (0.8 N m^{-2}). Mean densities in the 0 – 200 m stratum were below surface densities under ice in winter and summer, higher in open water in summer and generally higher in autumn. *T. macrura* was only caught at the surface in summer. The overall mean surface density (0.2 N m^{-2}) was generally much lower than in the 0 - 200 m stratum and not related to the presence of sea ice. These results indicate that pelagic nets may significantly underestimate the density of Antarctic krill in ice-covered waters. High densities of *E. superba* under ice hundreds of kilometres south of the ice edge demonstrated that krill were abundant under the ice throughout the pack-ice area rather than being associated with the marginal ice zone, implying that changes in sea ice structure and extent may affect Antarctic krill and the Southern Ocean ecosystem far more seriously than assumed to date.

8.1 Introduction

Antarctic krill *Euphausia superba* is the most abundant krill species (family Euphausiidae) occurring in the Southern Ocean south of the Antarctic Polar Front (APF) (Everson 2000). It often dominates the zooplankton community in numbers and biomass (Fisher et al. 2004; Lancraft et al. 2004), and the total stock biomass has been estimated at 169 * 10^6 metric tons (Siegel 2005). *E. superba* has adapted to almost the entire range of marine habitats in the Southern Ocean, including the abyssal plains (Clarke & Tyler 2008) and the underside of pack-ice (Marschall 1988; Siegel et al. 1992). Its potential distribution covers large parts of the Southern Ocean, with the exception of the inner shelf areas of the Ross and Weddell Seas (Everson 2000; Atkinson et al. 2008). In high-abundance regions, such as near the Antarctic Peninsula, in the Scotia Sea and the Scotia Arc archipelagos, *E. superba* is a highly influential factor in the ecosystem, capable of grazing as much as 55% of the net primary production (Ross et al. 1998) and forming the dominant prey item of many higher predators (Chapter 2; Lynnes et al. 2004; Osman et al. 2004).

Four more euphausiids are widely distributed and often abundant species in the Southern Ocean south of the APF, but have gained less scientific attention: *Euphausia frigida*, *E. crystallorophias*, *E. triacantha* and *Thysanoessa macrura*. The geographic distribution of the smaller *T. macrura* widely overlaps with that of Antarctic krill, and it can be locally more abundant in numbers, although not in biomass (Fisher et al. 2004). It is more omnivorous than *E. superba* and is an important diet item of mesopelagic fishes (Chapter 4; Pakhomov et al. 1996; Phleger et al. 2002; Pusch et al. 2005). *E. frigida* occurs mostly outside the seasonal sea ice zone and mainly dwells at greater depths, only approaching the surface at day (John 1936; Piatkowski 1985). It has been reported to be an important diet component of Antarctic fishes (Vacchi et al. 1994). *E. triacantha* is another mesopelagic species, and little is known about its role in the food web (Baker 1959). *E. crystallorophias* occurs mainly in the shelf areas of the Southern Ocean (Everson 2000). Being a major prey of various penguin and seal species, its importance in the Ross Sea ecosystem is comparable to the pronounced ecological role of Antarctic krill in the Scotia Arc / Antarctic Peninsula region (Smith et al. 2007).

An environment largely neglected in the past is the surface layer, i.e. the upper few meters of the water column in open waters and under ice. Both in sea ice and open water, surface swarms of Antarctic krill have been reported repeatedly (Hardy & Gunther 1935; Nemoto 1983; Miller & Hampton 1989). Yet the extent to which Antarctic euphausiids and their larvae use the surface layer as a habitat is poorly investigated, because most quantitative sampling techniques integrate krill abundance over a depth range of at least 50 m from the surface (Pakhomov et al. 1998; Fisher et al. 2004; Lancraft et al. 2004; Donnelly et al. 2006), and the hydro-acoustic technology used to date has not been capable to resolve the upper few meters of the water column (Nordhausen 1994b; Kaufmann et al. 1995; Brierley et al. 2002).

Until today, common knowledge on krill aggregations at the underside of sea ice has been limited to semi-quantitative observations on small spatial scales provided by divers and submersible camera systems (Hamner 1982; O'Brien 1987; Marschall 1988; Siegel et al. 1990).

The life cycle and winter survival of *E. superba* is closely linked with sea ice (Siegel & Loeb 1995). In winter, ice algae growing at the underside of ice floes constitute an important resource for euphausiid furcilia larvae (Daly 2004) as well as post-larvae (Marschall 1988; Stretch et al. 1988). However, data on *E. superba* from the areas covered by pack-ice are scarce due to the logistic constraints to sampling in the ice-covered ocean (Nicol 2006). To which extent *E. superba* survives the dark months in close association with the underside of ice is therefore still unclear, and alternative hypotheses, e.g. benthic feeding and starvation combined with shrinkage are also being discussed (Gutt & Siegel 1994; Lawson et al. 2004).

An analysis of historical abundance data from the entire Southern Ocean further emphasized the significance of sea ice for the survival of Antarctic krill by showing that krill density in summer is positively correlated with the sea ice extent in the preceding winter (Atkinson et al. 2004). Under-ice data collected with upward-looking echosounders provided first evidence of elevated krill concentrations under pack-ice several kilometres away from the ice margin (Brierley et al. 2002). Also *E. crystallorophias*, which occurs in Antarctic shelf areas often ice-covered throughout the year, has been reported to dwell at the underside of sea ice (O'Brien 1987) and under shelf ice (Craven et al. 2006). Interactions of other krill species with sea ice are largely unknown to date.

An assessment of the importance of sea ice for the different krill species is complicated by their diel vertical migration patterns. The vertical migration behaviour of Antarctic krill can vary considerably between seasons. They stay largely within the upper 100 m in summer. In winter, their diurnal vertical migration is assumed to range between 100 m depth at night and more than 300 m at day (Siegel 2005). Especially the hibernal vertical migration behaviour of *E. superba*, however, is still under debate due to the general scarcity of winter data from the sea ice zone.

Seasonal differences in depth distribution are also apparent from *T. macrura*. Being abundant in the upper 200 m in summer (Piatkowski 1985), *T. macrura* was reported to be largely absent from the upper 200 m in autumn and winter (Lancraft et al. 1991; Nordhausen 1994b; Lancraft et al. 2004). *E. frigida* has been reported to be largely avoiding the upper 200 m at day and to perform a nocturnal migration to the surface in summer (Piatkowski 1985). *E. crystallorophias* has been described as a diurnal vertical migrator in summer, with dense swarms aggregating close to the surface at night (Pakhomov et al. 1998).

In order to investigate the importance of the surface layer for Antarctic euphausiids and other macrofauna both under ice and in open water, a new sampling device was developed for the quantitative sampling of macrofauna in this environment, the

Surface and Under Ice Trawl (SUIT). Three expeditions conducted in the same area in the Lazarev Sea provided the opportunity to investigate the occurrence of euphausiids in the surface layer during different seasons. This study aims to

- Investigate the population structure and quantify the density of euphausiids and their larvae in the immediate surface layer both under sea ice and in open waters;
- analyze these data in the context of environmental parameters, such as seasonality, sea ice properties, light regime and hydrography;
- assess the importance of the ice-water interface layer for the encountered Antarctic euphausiids.

8.2 Material and methods

8.2.1 Data collection

Surface layer sampling

Sampling was performed during three research missions of RV "*Polarstern*" in the Lazarev Sea (Southern Ocean) in austral autumn 2004 (ANT XXI-4, March 27th to May 6th 2004, winter 2006 (ANT XXIII-6, June 17th to August 21st 2006) and summer 2007 / 2008 (ANT XXIV-2, November 28th 2007 to February 4th 2008) (Figure 1). The expeditions were part of a multi-year field experiment embedded in the largely German funded LAzarev Sea KRIll Study (LAKRIS) dedicated to the investigation of the distribution, population dynamics and physiology of Antarctic krill *Euphausia superba*. The LAKRIS surveys sampled a regular station grid with 3 - 4 meridional transects with a spacing of 2 – 3 degrees longitude and a latitudinal station spacing of 20 – 30 nm, ranging from 6°W to 3°E and from 60°S to the continental coast at approximately 71°S (Figure 1). A detailed description of the area of investigation and the sampling scheme was provided in Chapter 7.

Surface and Under Ice Trawls (SUIT) were used to sample macrozooplankton and micronekton in the upper two metres of the water column. The net systems consisted of a steel frame with an approximately 2 x 2 m net opening with a 15 m long 7 mm half-mesh commercial shrimp net attached to it. In autumn 2004, a circular plankton net (diameter 50 cm, 0.3 mm mesh) was mounted inside the shrimp net to sample mesozooplankton and krill larvae. In winter 2006 and summer 2007 / 2008, the rear three meters of the net were lined with 0.3 mm plankton gauze. An Acoustic Doppler Current Profiler (ADCP) was used in winter 2006 and summer 2007 / 2008 to estimate the amount of water entering the net mouth and to analyze its flow properties. A detailed description of the SUIT and its fishing properties was provided in Chapter 9. During each trawl, changes in ship speed, proportional ice coverage [%], ice thickness [cm] and irregularities were recorded by an observer on deck.

Of the total 75 SUIT hauls, 24 hauls were conducted in autumn 2004, 30 hauls in winter 2006 and 21 hauls in summer 2007 / 2008. One SUIT station was sampled outside the regular LAKRIS grid during each expedition. These stations were positioned at 54°S 0 °W (autumn 2004), 58°S 3°E (winter 2006) and 52°S 0° (summer 2007 / 2008). The latter station was sampled during two consecutive nights. In order to assess diurnal patterns in the density of macrofauna in the surface layer, three locations on the LAKRIS grid were sampled at day as well as at night in winter 2006 and in summer 2007 / 2008, respectively.

The catch was immediately sorted on board. After the collection of all macrofauna > 0.5 cm from either the entire sample or a representative subsample, the mesozooplankton fraction was preserved on 4% hexamine-buffered formaldehyde-seawater solution. In autumn 2004, the mesozooplankton fraction was obtained from the separate plankton net. Animals > 0.5 cm collected from this net were combined with the shrimp net catch in subsequent analyses.

Euphausiids were separated by species. Displacement volume and number of individuals of each species were noted. Euphausiids for length-frequency analysis were fixed in formaldehyde solution for 48 to 96 hours before sex determination and length measurement. *E. superba* were measured from the front edge of the eye to tip of telson (the "*Discovery*" method). All other euphausiids were measured from the tip of the rostrum to the tip of the telson. Euphausiid furcilia larvae from the mesozooplankton fraction were identified to species level and counted. For each krill species and their furcilia larvae, the number of animals caught was standardized to the surface area sampled and expressed as the density of individuals per square metre [N m^{-2}].

Midwater sampling

Standardized double-oblique hauls to a depth of 200 m and back to the surface were conducted with a Rectangular Midwater Trawl (RMT) on all LAKRIS grid stations during the three expeditions. The sampling device consisted of an RMT 1 (mesh size = 0.33 mm) mounted above an RMT 8 with net openings of 1 and 8 m^2, respectively. The RMT 8 has a mesh size of 4.5 mm at the opening and a codend mesh size of 0.85 mm. A calibrated mechanical impeller flow meter mounted outside the net opening allowed the volume of water passing through the net to be estimated. The mean trawling speed was 2.5 knots (1.3 m s^{-1}).

Immediately after catch retrieval, the volume of the RMT sample was measured and euphausiids were removed from the RMT 8 sample. Euphausiids were sorted quantitatively from the RMT 8. If the sample size was larger than 1 liter, a representative subsample was analyzed. Euphausiids were stored in 4 % formalin-seawater solution for length measurements and maturity stage analyses.

RMT 1 samples were immediately preserved in a 4 % formaldehyde-seawater solution. Using a Folsom plankton splitter, one to two fractions of between 1/2 to

1/32 of the preserved amount were counted to ascertain the numbers of euphausiid larvae. Data were finally standardized to the surface area sampled [N m^{-2}]. A detailed description of the RMT sampling procedure was provided in Chapter 4 and by Siegel et al. (2004).

Hydrography and environmental data

Vertical profiles of temperature, salinity and density were obtained by lowering a CTD (Conductivity, Temperature, Depth) probe to depths varying between 1,000 m and the sea floor. The CTD was supplemented by an altimeter to measure the distance to the sea floor, a transmissometer to measure the attenuation of light and a chlorophyll-sensitive fluorometer (only in winter 2006 and summer 2007 / 2008). The temperature-salinity profiles were used to calculate the mixed layer depth (MLD [m]) for each station (Cisewski et al. 2005; Cisewski et al. 2008). Solar radiation [W m^{-2}] was measured by the ship's meteorological system. Bottom depth [m] was estimated for each station position using modeled global bathymetry from a publicly available database (Smith & Sandwell 1997; Scripps 2006).

The proportion of the distance the SUIT was towed under sea ice was used to estimate the percentage of sea ice coverage for each SUIT haul. SUIT hauls with a proportional ice coverage > 10 % were considered under-ice hauls. We also estimated the mean thickness [cm] of the ice at under-ice hauls. The full procedure of environmental data collection was explained in Chapter 7.

8.2.2 Data analysis

The arithmetic mean density of individuals per surface area [N m^{-2}] in the surface layer (SUIT: 0 – 2 m) at different years and ice conditions was calculated for each species based on the hauls conducted on the LAKRIS grid (south of 59°S). Hauls conducted at daytime (surface radiation > 10 W m^{-2}) were excluded from the autumn 2004 and winter 2006 datasets due to the diurnal vertical migration behaviour of Antarctic euphausiids in these seasons (Nordhausen 1994b; Siegel 2005). The remaining 53 quantitative hauls were submitted to statistical analysis. RMT hauls fulfilling the same criteria were selected from stations where quantitative SUIT hauls were conducted to compare surface densities and size compositions of euphausiids with established midwater sampling methodology. Data were log(x + 0.001) transformed for variance analyses (ANOVA) on the effect of season and the presence of sea ice during SUIT hauls to obtain similar variances in the residuals.

Initial exploration showed non-linear relationships between environmental variables and densities of postlarval *E. superba*. Therefore, the relationship of the surface density (0 – 2m) of postlarval *Euphausia superba* with environmental variables was investigated with Generalized Additive Models (GAM, Hastie & Tibshirani 1995). The following environmental variables were included in the analysis:

- MLD;
- water temperature (0 m – MLD);
- water temperature (0 – 200 m);
- salinity (0 m – MLD);
- salinity (0 – 200 m);
- attenuation (0 m – MLD);
- attenuation (0 – 200 m);
- potential temperature at depth of temperature maximum;
- chlorophyll a conc. (0 – 200 m; only 2006 and 2007 / 2008);
- ocean depth;
- solar radiation;
- proportional ice coverage during SUIT hauls;
- mean ice thickness during SUIT hauls.

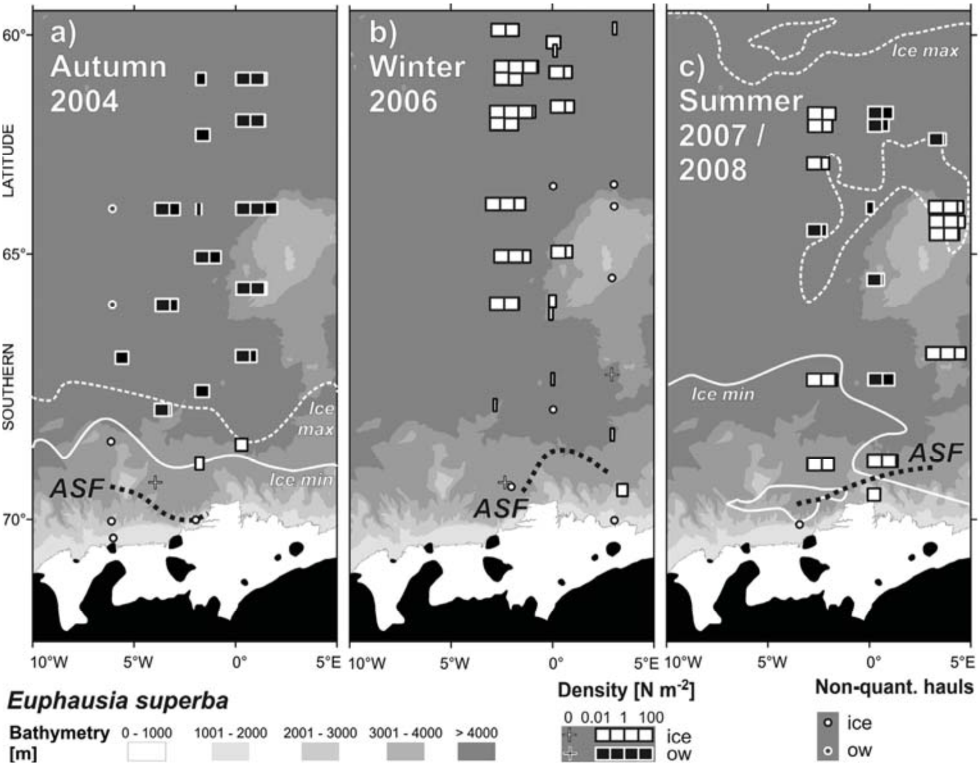
Krill densities were log(x + 0.001) transformed. Due to multiple interactions of environmental variables with sampling season, separate models were computed for each season. Collinearity of variables was assessed by calculating correlation coefficients and variance inflation factors (VIF: e.g. Quinn & Keough 2004). VIF values above 10 are generally considered indicative of high collinearity (Quinn & Keough 2004). Using a stepwise procedure, the variable with the highest VIF value was repeatedly removed until the VIF values of all remaining variables were below 10. Gaussian additive models were fitted using cubic splines and cross-validation to obtain the optimal degrees of freedom for each variable (Wood 2006). The optimal model was estimated by stepwise backward exclusion of insignificant model terms with the highest p-value until the Akaike information criterion (AIC) reached a minimum. Sometimes the estimated degrees of freedom of smooth terms were so low that a linear relationship may have been sufficient. In that case the model was tested with parametric terms, and preferred if these were significant and the AIC was lower. Regression assumptions were assessed visually by plotting the response variable against fitted values and residuals against variables.

Spatial patterns in the size composition of postlarval *E. superba* were assessed with hierarchical agglomerative cluster analysis using unweighted pair-group average linking. This analysis was based on a Bray-Curtis similarity matrix derived from length-frequency data of hauls with ≥ 150 animals scaled to the percentage of animals in each mm size class. The size composition of postlarval *T. macrura* was analysed in an analogue way with a minimum number of 50 animals per station.

8.3 Results

8.3.1 Hydrographical setting and ice coverage

The Weddell Gyre fed Warm Deep Water of circumpolar origin into the LAKRIS survey area during all three sampling seasons. This water mass reached as far south as approximately 69°S, where the Antarctic Slope Front (ASF) was situated (Figure 1). Much colder and more saline waters of the Antarctic Coastal Current prevailed south of the ASF. The hydrography of the area was further influenced by current jets and eddies forming around the Maud Rise seamount (Chapter 7). In autumn 2004 the young pack-ice was largely confined to waters south of 68°S (Figure 1 a). Heavy pack-ice was present throughout the entire area of investigation in winter 2006 (Figure 1 b). In summer 2007 / 2008, sea ice extended north up to 60°S in December 2007, but retreated to a residual area south of 67°S in late January 2008 (Figure 1 c). A detailed description of the hydrography and the ice situation in the LAKRIS survey area was provided in Chapter 7.



▲**Figure 1.** *Euphausia superba*. Spatial distribution of the surface layer density of postlarval krill in autumn 2004 (a), winter 2006 (b) and summer 2007 / 2008 (c). Minimum (**Ice min**) and maximum (**Ice max**) pack-ice extent during the sampling period is indicated by approximate 15 % ice coverage derived from satellite data. The entire survey area was covered by sea ice in winter 2006. **ASF**: Antarctic Slope Front; **ice** = under-ice SUIT hauls; **ow** = open water SUIT hauls.

8.3.2 *Euphausia superba*

Density and distribution

Four species of larval and postlarval euphausiids and their furcilia larvae were caught in the surface layer: *Euphausia superba, Thysanoessa macrura, E. frigida* and *E. crystallorophias*. The same species were present in the 0 – 200 m stratum. *Euphausia superba* was clearly the most abundant krill species and the only euphausiid caught at the surface in all three seasons (Table 1; Table 2). With a density of 3.40 N m^{-2}, it was also the dominant euphausiid of the station sampled outside the LAKRIS grid in winter 2006 (58°S 3°E). The mean surface density within the LAKRIS sampling grid was highest in winter 2006 (2.70 N m^{-2}), followed by autumn 2004 (0.82 N m^{-2}) and summer 2007 / 2008 (0.79 N m^{-2}) (Table 2).

Elevated densities were concentrated north of 66°S along the 0° meridian in autumn 2004 and at 3°W in winter 2006. In summer 2007 / 2008, densities were highest at the north and the south slopes of the Maud Rise seamount, between 64°S and 67°S 3°E (Figure 1). A few exceptionally high catches were obtained in these areas. These were one haul in autumn 2004 (9.60 N m^{-2}), two hauls in winter 2006 (17.86 and 23.11 N m^{-2}) and one haul in summer 2007 / 2008 (6.33 N m^{-2}).

▼**Table 1.** Number of hauls with krill species and their larvae in the surface layer of the Lazarev Sea. All hauls included

	Autumn 2004	**Winter 2006**	**Summer 2007/2008**
Total no of hauls	24	30	21
Postlarval krill			
Euphausia crystallorophias	-	-	2
Euphausia frigida	4	-	2
Euphausia superba	16	20	21
Thysanoessa macrura	-	-	18
Furcilia larvae			
E. crystallorophias furciliae	1	-	-
E. frigida furciliae	-	-	2
E. superba furciliae	9	21	-
T. macrura furciliae	12	4	2
Unidentified furciliae	1	6	2

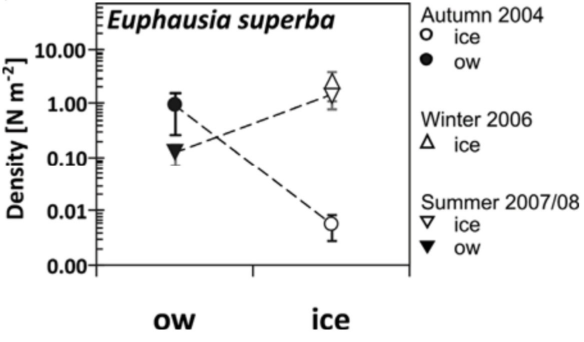
▼**Table 2.** *Euphausia superba*. Density of postlarval krill [N m^{-2}] at the open surface and under ice (0 – 2 m) on the LAKRIS grid. **ice** = under-ice SUIT hauls; **ow** = open water SUIT hauls; **p**: ANOVA significance

	Autumn 2004			Winter 2006	Summer 2007/2008		
	ow	ice	total	total (ice)	ow	ice	total
Number of hauls	13	3	16	19	7	11	18
Mean	1.0	0.01	0.82	2.70	0.11	1.22	0.79
St. Dev.	2.61	0.01	2.36	6.49	0.11	1.83	1.51
Min	0.01	0	0	0	< 0.01	0.01	< 0.01
Max	9.60	0.01	9.60	23.11	0.21	6.33	6.33
p	0.01		-	-	0.01		-

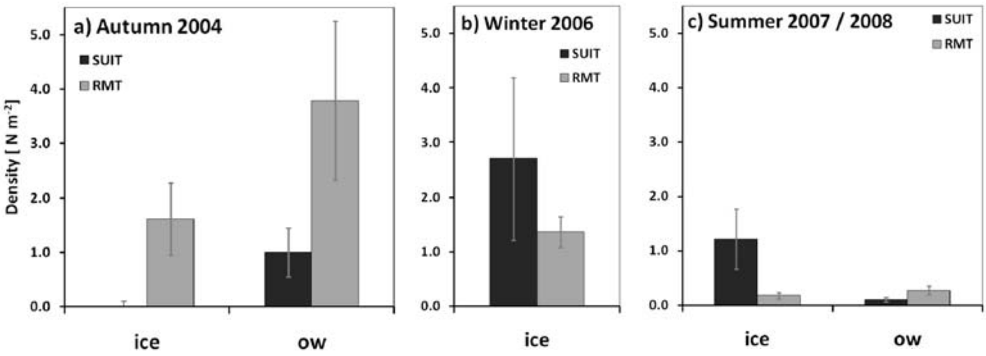
The relation between the under-ice and open water surface layer densities of postlarval Antarctic krill significantly differed among sampling seasons (ANOVA: $p < 0.01$; Figure 2). The highest overall and local densities of postlarval *E. superba* were recorded under the winter sea ice in 2006. Antarctic krill density at the surface was significantly higher under ice than in open water in summer 2007 / 2008 (Table 2). In autumn 2004, the density of postlarval Antarctic krill was significantly lower under ice than in open waters. The mean under-ice density, however, was based on only three of the 16 quantitative stations sampled on the LAKRIS grid in that year (Table 2).

In RMT hauls conducted at the SUIT sampling locations, the density of postlarval *E. superba* in the 0 – 200 m stratum significantly differed among the sampling seasons (ANOVA: $p < 0.01$), but was not significantly related to the presence of sea ice during SUIT hauls (ANOVA: $p > 0.1$). In autumn 2004, the integrated mean density per m^2 was considerably higher over the 0 – 200 m depth range than only at the surface in both open water and under ice (Figure 3 a). In contrast, in winter 2006, mean krill density in the 0 – 200 m stratum was below the mean density from the ice-water interface layer mainly due to a few exceptionally high SUIT catches (Figure 3 b). In summer 2007 / 2008, the mean density in the 0 – 200 m stratum was considerably lower than in the ice-water interface layer and above the mean density at the open surface (Figure 3 c). These patterns were significant in pairwise comparison for open water stations in autumn 2004 and stations where SUIT sampled under ice in summer 2007 / 2008 (paired Mann-Whitney U-test: $P < 0.05$, respectively).

5



◄**Figure 2.** *Euphausia superba*. Mean density of postlarval krill in the surface layer in relation to sampling season and presence of sea ice during SUIT hauls on the LAKRIS grid. Error bars denote standard errors. **ice** = under-ice SUIT hauls; **ow** = open water SUIT hauls.



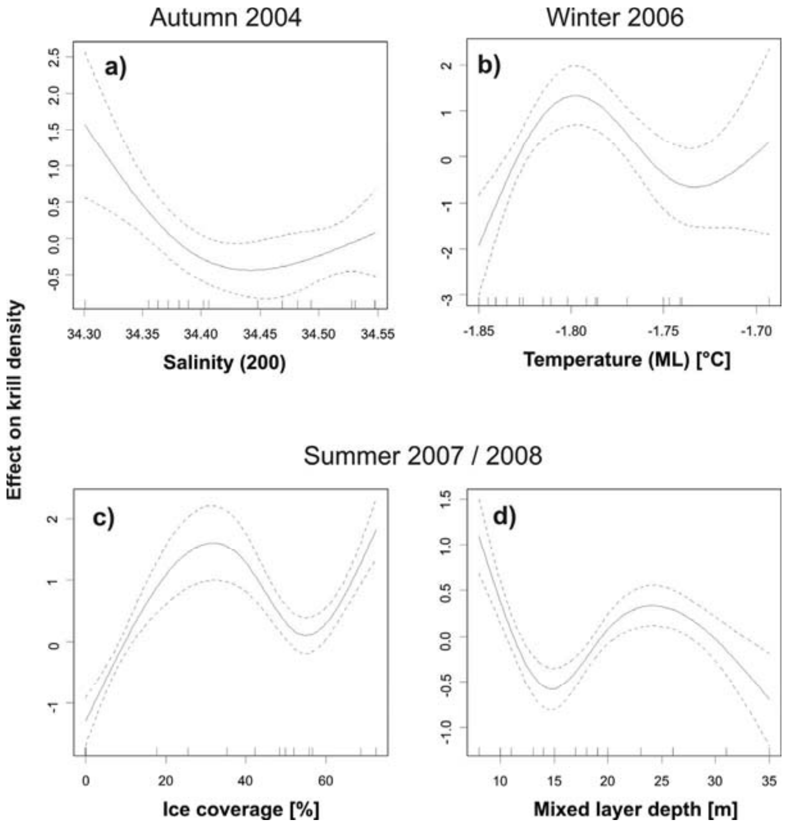
▲**Figure 3.** *Euphausia superba.* Comparison of the integrated mean densities per m^2 of postlarval krill at stations sampled by SUIT (0 – 2 m) and RMT (0 – 200 m). Error bars denote standard errors. **ice** = under-ice SUIT hauls; **ow** = open water SUIT hauls.

Relationship of postlarval krill density with environmental parameters

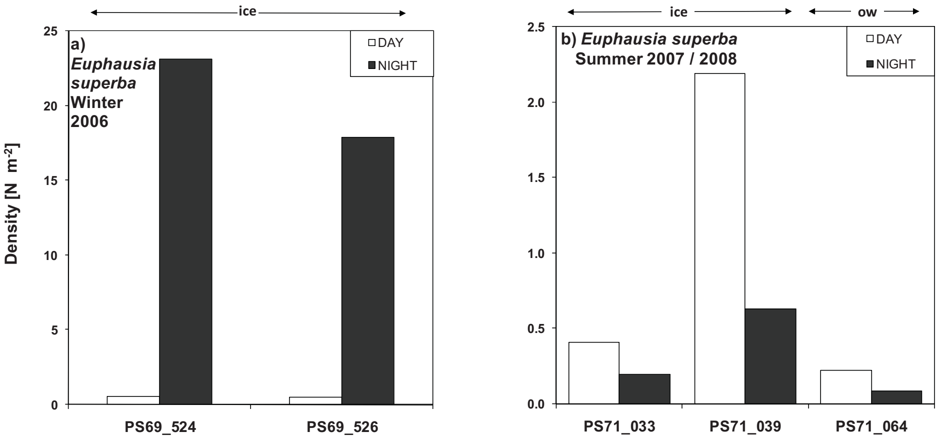
The density of postlarval Antarctic krill in the surface layer was significantly related to different combinations of environmental variables in each sampling season. The most parsimonious model in autumn 2004 related krill density to the parametric term of water temperature in the mixed layer and a smooth function for salinity in the upper 200 m. Modeled density was highest at a combination of high water temperatures in the mixed layer and low salinities (Table 3; Figure 4 a). In winter 2006, the best model included the parametric predictors ocean depth and MLD and a smooth function for the water temperature in the mixed layer. The modeled krill density was positively affected by both increasing depth and MLD and water temperatures in the mixed layer between approximately -1.83°C and -1.76°C (Table 3, Figure 4 b). In summer 2007 / 2008, parametric terms for mean ice thickness and attenuation in the mixed layer combined with smooth functions of proportional ice coverage during SUIT hauls and MLD obtained a very good model fit, explaining 94.6 % of the deviance. The modeled krill density was positively affected by both decreasing ice thickness and attenuation in the mixed layer, and approximate proportional ice coverage > 12 % and a MLD < 12 m or between 20 and 30 m (Table 3; Figure 4 c, d).

▼**Table 3.** *Euphausia superba*. Parameters for optimal models relating the density of postlarval krill to environmental variables on the LAKRIS grid. **ATC** = attenuation; **df** = estimated degrees of freedom of smoother; **MLD** = mixed layer depth; **s** = cubic spline smoother

Sampling season	Overall model statistics		Model terms			
			Environmental variables	Linear estimate	df	p
Autumn 2004	AIC	35.7	Temperature (MLD)	2.0715		< 0.01
	Expl. deviance	70.8 %	s(salinity 0 - 200 m)		2.2	0.03
Winter 2006	AIC	59.2	Depth	0.0007		0.01
	Expl. deviance	72.2 %	MLD	0.0261		0.01
			s(temperature (MLD))		2.9	0.01
Summer 2007 / 2008	AIC	9.6	Ice thickness	-0.2096		< 0.01
	Expl. deviance	94.6 %	ATC(MLD)	-2.2845		< 0.01
			s(Ice coverage)		3.0	< 0.01
			s(MLD)		3.0	< 0.01



▲**Figure 4.** *Euphausia superba*. Generalized Additive Models of the density of postlarval krill. Effect of additive smoothing functions of salinity in the upper 200 m in autumn 2004 (a), temperature in the mixed layer in winter 2006 (b), proportional ice coverage during SUIT hauls (c) and mixed layer depth (d) in summer 2007 / 2008 on the fitted density of krill. Dashed lines show 95 % confidence intervals of smoothers. **ML** = mixed layer.



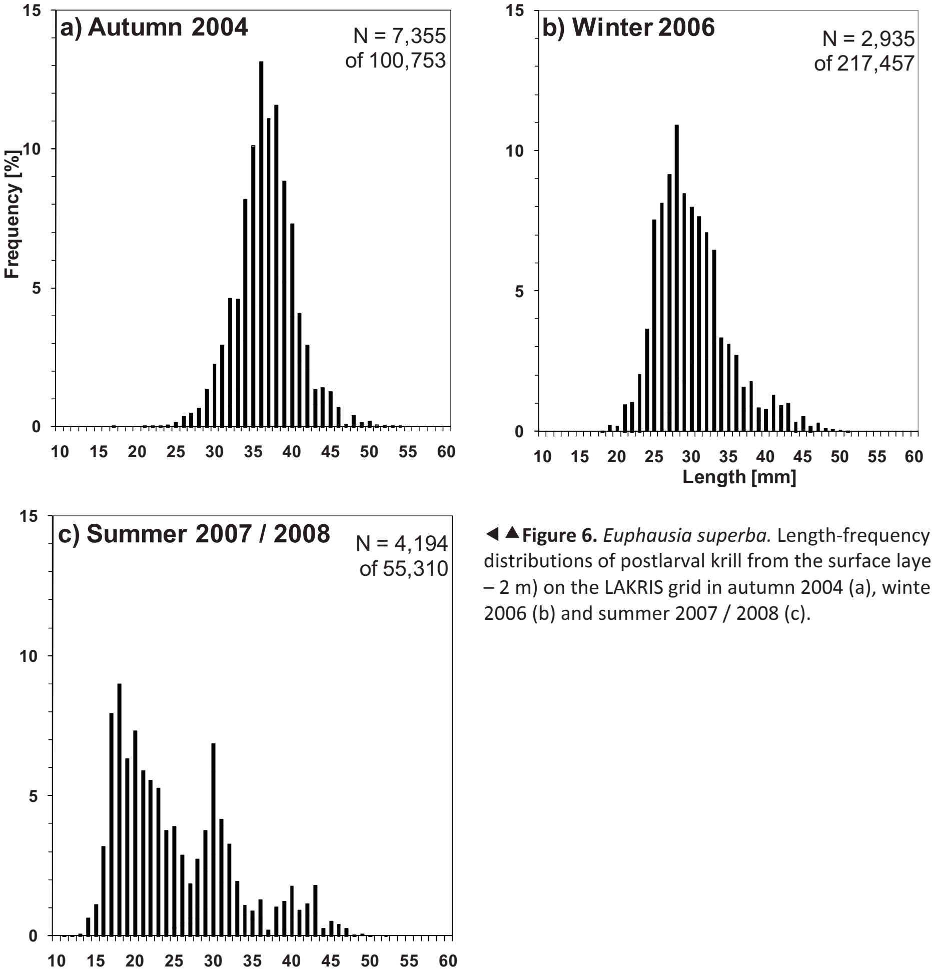
▲**Figure 5.** *Euphausia superba*. Day/night comparisons of the surface layer density of postlarval krill at two stations in winter 2006 (a) and at three stations in summer 2007 / 2008 (b). Scaling of y-axis differs. Denotations on x-axis are location codes. **ice** = under-ice SUIT hauls; **ow** = open water SUIT hauls.

Diurnal patterns

A pronounced diurnal pattern in the surface density of postlarval Antarctic krill was apparent from the five day/night comparative locations that yielded a sufficient number of animals in winter 2006 and summer 2007 / 2008. In winter 2006 the under-ice density at night was up to two orders of magnitude above daytime values (Figure 5 a). In summer 2007 / 2008, densities of postlarval *E. superba* were higher at day than at night, both under ice and in open water. This difference, however, was less pronounced than the opposite pattern observed in winter 2006 (Figure 5 b).

Size composition

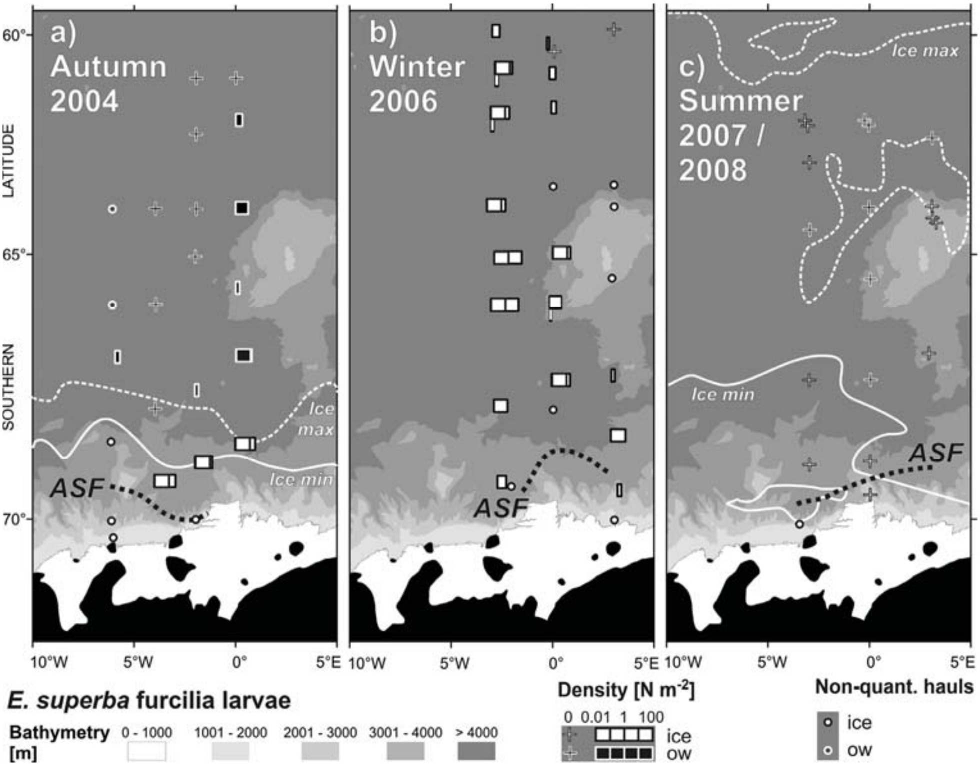
The overall size range (13 – 54 mm) was largely similar in all three sampling seasons (Figure 6). Modes, however, occurred at different lengths in each season. A single mode at 36 mm was observed in autumn 2004 (Figure 6a). The mode in winter 2006 (28 mm) was considerably lower (Figure 6b). In summer 2007 / 2008, the dominating fraction was juveniles, peaking at 18 mm. A second mode appeared at 30 mm (Figure 6c). Segregation in two clusters was apparent from the cluster analysis in all three seasons. The differences in the size distributions among the groupings, however, were not significant (Kolmogorov-Smirnov test, $P > 0.05$). Thus, a meaningful spatial separation of size clusters was not possible based on the sample size of this investigation. No significant difference was apparent in any sampling season, when size distributions of postlarval *E. superba* sampled by SUIT were compared with RMT length-frequency data (Table 4).



◄▲**Figure 6.** *Euphausia superba.* Length-frequency distributions of postlarval krill from the surface layer (0 – 2 m) on the LAKRIS grid in autumn 2004 (a), winter 2006 (b) and summer 2007 / 2008 (c).

▼**Table 4.** *Euphausia superba*. Comparison of the size distributions of postlarval krill in the surface layer and the 0 – 200 m layer on the LAKRIS grid. **p**: Kolmogorov-Smirnov test significance

	Autumn 2004		Winter 2006		Summer 2007 / 2008	
	Surface	0 – 200 m	Surface	0 – 200 m	Surface	0 – 200 m
Mean length [mm]	36.7	35.2	30.1	33.7	25.2	26.7
Range [mm]	17 - 54	21 - 58	18 - 52	20 - 54	13 – 52	13 – 52
p	0.45		0.06		0.98	



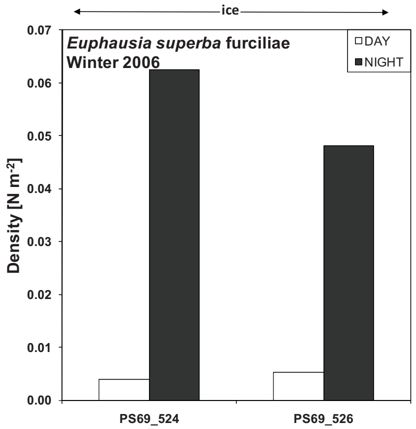
▲**Figure 7.** *Euphausia superba*. Spatial distribution of the surface layer density of furcilia larvae in autumn 2004 (a), winter 2006 (b) and summer 2007 / 2008 (c). Legend for hydrography and ice coverage as in Figure 1.

Furcilia larvae

Furciliae of *E. superba* were the dominant euphausiid larvae at the surface in autumn 2004 (0.02 N m^{-2}) and winter 2006 (0.08 N m^{-2}), but absent from SUIT catches in summer 2007 / 2008 due to sampling very early in the spawning season. In contrast to postlarval Antarctic krill, they were significantly more abundant under ice than in open water in autumn 2004 (Figure 7, Table 5). A diel pattern similar to postlarval Antarctic krill was observed in larvae in winter 2006 (Figure 8).

▼**Table 5.** *Euphausia superba*. Density furcilia larvae [N m^{-2}] at the open surface and under ice (0 – 2 m) on the LAKRIS grid. **ice** = under-ice SUIT hauls; **ow** = open water SUIT hauls; **p**: ANOVA significance

	Autumn 2004			Winter 2006	Summer 2007/08
	ow	ice	total	total (ice)	total
Number of hauls	14	3	17	19	18
Mean	< 0.01	0.08	0.02	0.08	0
St. Dev.	0.01	0.03	0.04	0.15	-
Min	0	0.05	0	0	-
Max	0.03	0.11	0.11	0.48	
p	< 0.01		-	-	-



◀ **Figure 8.** *Euphausia superba*. Day/night comparisons of the surface layer density of furcilia larvae at two stations in winter 2006. Denotations on x-axis are station codes. **ice** = under-ice SUIT hauls.

8.3.3 Other krill species

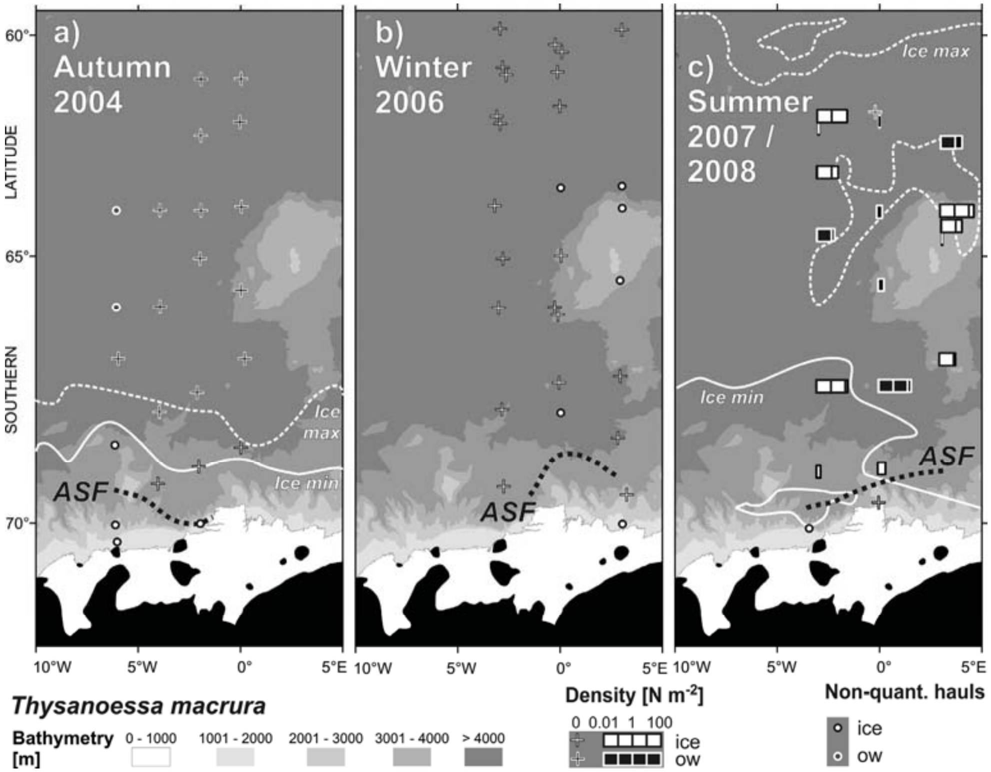
Thysanoessa macrura

Postlarval *T. macrura* were only caught at the surface in summer 2007 / 2008. Occurring at 18 of the 20 quantitative hauls, they locally reached higher densities than *E. superba* (Figure 1; Figure 9). Overall mean surface density on the LAKRIS grid (0.24 N m^{-2}), however, was below that of Antarctic krill (0.79 N m^{-2}). The surface layer density was not significantly related to the presence of sea ice during SUIT hauls (Figure 10; Table 6).

At RMT stations corresponding to SUIT sampling locations, postlarval *T. macrura* were caught in all three seasons. They were considerably (> 10 times) more abundant in the 0 – 200 m stratum than at the surface in summer 2007 / 2008. When *T. macrura* were absent from the surface layer in autumn 2004 and winter 2006, very low densities compared to summer values were recorded in the 0 – 200 m stratum (Figure 11). This pattern was not related to the presence of sea ice at corresponding SUIT stations (ANOVA: $p > 0.1$).

	Autumn 2004 total	Winter 2006 total (ice)	Summer 2007/2008		
			ow	ice	total
Number of hauls	17	19	7	11	18
Mean	0	0	0.18	0.28	0.24
St. Dev.	-	-	0.43	0.46	0.43
Min	-	-	0	0	0
Max			1.15	1.36	1.36
p			0.52		

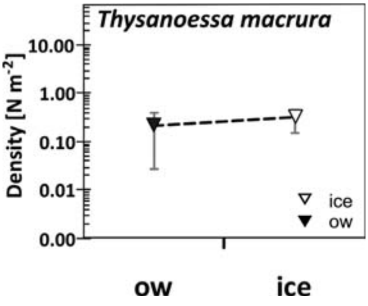
◀ **Table 6.** *Thysanoessa macrura*. Density of postlarval krill [N m^{-2}] at the open surface and under ice (0 – 2) m on the LAKRIS grid. **ice** = under-ice SUIT hauls; **ow** = open water SUIT hauls; **p** = ANOVA significance

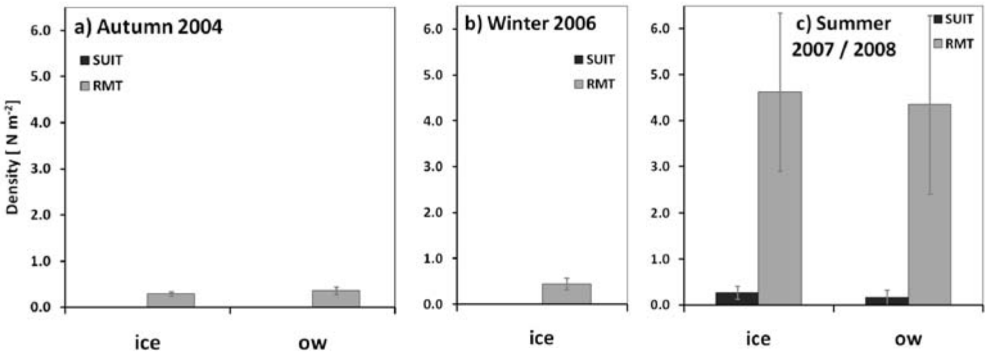


▲**Figure 9.** *Thysanoessa macrura*. Spatial distribution of the surface layer density of postlarval krill in autumn 2004 (a), winter 2006 (b) and summer 2007 / 2008 (c). Legend for hydrography and ice coverage as in Figure 1.

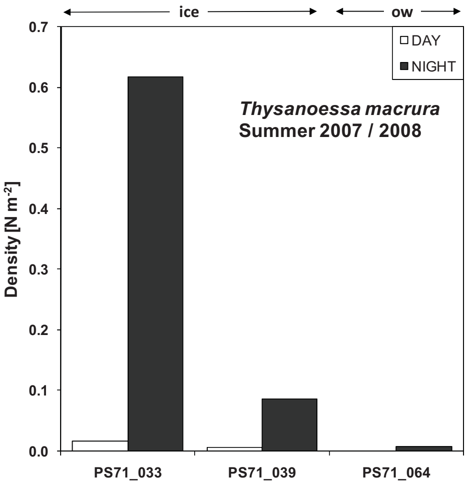
In the surface layer, they were only abundant at night and almost absent from this environment at day in summer 2007 / 2008 (Figure 12). The length of postlarval *T. macrura* caught in summer 2007 / 2008 ranged between 8 and 30 mm. They exhibited a unimodal overall size distribution, peaking at 16 mm (Figure 13). The station at 64.5°S 3°W (Figure 9) was grouped apart by the cluster analysis. Its size composition differed significantly from all other stations in being heavily dominated by very small animals < 12 mm (Kolmogorov-Smirnov test, $p < 0.01$). The overall size distributions of the surface and 0 – 200 m stratum were not significantly different from each other (Kolmogorov-Smirnov test, $p > 0.05$).

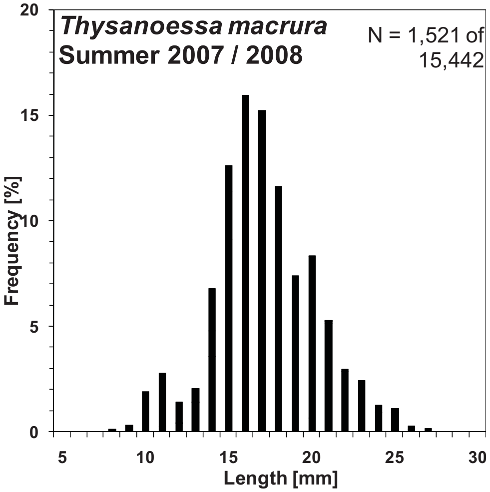
▶**Figure 10.** *Thysanoessa macrura*. Mean density of postlarval krill in the surface layer on the LAKRIS grid in relation to the presence of sea ice during SUIT hauls in summer 2007 / 2008. Error bars denote standard errors. **ice** = under-ice SUIT hauls; **ow** = open water SUIT hauls.





▲**Figure 11.** *Thysanoessa macrura.* Comparison of the integrated mean densities per m^2 of postlarval krill at stations sampled by SUIT (0 – 2 m) and RMT (0 – 200 m) nets. Error bars denote standard errors. **ice** = under-ice SUIT hauls; **ow** = open water SUIT hauls.





▲**Figure 12.** *Thysanoessa macrura*. Day/night comparisons of the surface layer density of postlarval krill at three stations in summer 2007 / 2008. Denotations on x-axis are station codes. **ice** = under-ice SUIT hauls; **ow** = open water SUIT hauls.

▲**Figure 13.** *Thysanoessa macrura.* Length-frequency distributions of postlarval krill from the surface layer (0 – 2 m) in summer 2007 / 2008.

Thysanoessa macrura furciliae were caught at 9 of the 24 SUIT hauls in autumn 2004, but their overall density was low in the LAKRIS grid (< 0.01 N m^{-2}). The highest local density (0.03 N m^{-2}) was encountered in winter 2006. However, they only occurred at four of 30 hauls, resulting in a mean density of < 0.01 N m^{-2} within the LAKRIS grid (Table 1). Only 24 specimens were caught at 3 locations in summer 2008.

Euphausia frigida

Postlarval *E. frigida* were restricted to stations north of 62°S in autumn 2004, reaching a maximum density of 0.01 N m^{-2} at the surface. In summer 2007 / 2008, they were the dominating krill species at the two hauls conducted at the station north of the LAKRIS grid (52°S 0°), reaching a local density of 0.12 - 0.13 N m^{-2}. Their furciliae were also encountered at this station (0.02 N m^{-2}) (Table 1).

Euphausia crystallorophias

Postlarval *Euphausia crystallorophias* were only caught in the ice-water interface layer at two stations in the southern shelf area in summer 2007 / 2008, yielding 4 and 55 animals, respectively. The latter catch had to be excluded from quantitative analysis because the ship got stuck in heavy multi-year ice during trawling. Evidence of *E. crystallorophias* furciliae in the surface layer was limited to two specimens caught at a shelf station in autumn 2004 (Table 1).

8.4 Discussion

8.4.1 *Euphausia superba*

Association with the ice-water interface layer

Independently of the distance from the ice edge, high densities of postlarval Antarctic krill at the ice-water interface were encountered in two out of three seasons (Figure 1). This is in contrast to earlier findings suggesting that krill aggregations under ice are limited to a narrow band in the marginal ice zone in summer (Brierley et al. 2002). Our results indicate that concentrations of postlarval Antarctic krill under ice are common in the entire seasonal pack-ice zone both in summer and winter.

The ice-water interface layer has been identified early as an important site of krill aggregations (O'Brien 1987; Marschall 1988; Siegel et al. 1990). It is known that sea ice constitutes the substrate of a rich ice-associated community, of which ice algae are the trophic base and an important resource for Antarctic krill (Marschall 1988; Stretch et al. 1988; Brierley & Thomas 2002). This floating substrate constantly exposes the algae to light at day, allowing photosynthetic production even in winter (Lizotte 2001). The size spectra in the surface layer indicate that the association with the ice-water interface layer was common in Antarctic krill throughout their ontogenetic development, from furcilia larvae to at least two-year old animals (Figure 6). There was no direct evidence for an ontogenetic segregation with respect to the use of the ice-water interface layer based on the comparison with the corresponding size distribution from the 0 – 200 m stratum (Table 4; Nordhausen 1994b; Zhou et al. 1994).

In summer 2007 / 2008 postlarval *E. superba* were significantly more abundant in the surface layer under ice than in open waters (Figure 2; Table 2). The positive effects of increasing ice coverage during SUIT hauls and a shallow mixed layer on modeled krill density suggested that the density of postlarval *E. superba* was highest under sea ice and / or where a meltwater lens stabilized a shallow mixed layer (Figure 4 c,d; Table 3). These conditions enhance ice algal and phytoplankton production, respectively, and thus characterize attractive foraging grounds. Especially where both effects were combined in the melting pack-ice, krill could be expected to concentrate near the surface. The tendency to concentrate in the ice-water interface layer was demonstrated by a significantly higher mean krill density under ice in the upper 2 m alone than integrated over the 0 – 200 m depth range. In open water resources were not concentrated at the surface and krill were dispersed over a wider depth range, resulting in a higher mean density in the 0 - 200 m stratum compared to the surface layer (Figure 3 c).

A comparison between the ice-covered and the open water surface layer was not possible in winter 2006 because the entire survey area was covered by pack-ice. Nevertheless, a high relevance of the ice-water interface layer was demonstrated by a higher mean density under ice compared to the entire upper 200 m (Figure 3 b), as well as by a pronounced diurnal migration into the ice-water interface layer (Figure 5 a). Only in autumn 2004 were postlarval Antarctic krill more abundant at the open surface than under ice (Figure 2). In young ice the bacterial activity is suppressed (Grossmann & Dieckmann 1994). The ice at the three stations successfully sampled in the ice-covered part of the survey area in this season was young and unlikely to host a microbial community providing sufficient resources for postlarval *E. superba*. The low attractiveness of the young sea ice as a foraging ground was reflected in a dispersal of krill over a wider depth range apparent from the consistently higher densities in the 0 - 200 m stratum (Figure 3 a). The horizontal distribution of postlarval Antarctic krill in the surface layer reflected broad-scale hydrographical patterns when biologically mature pack-ice was merely absent (autumn 2004), or the entire survey was covered by ice (winter 2006) (Figure 4 a, b; Table 3).

Remarkably, the sums of the mean densities of the surface layer and the 0 – 200 m stratum were similar both in autumn 2004 and winter 2006 (4.2 and 4.1 N m^{-2}, respectively), possibly indicating that the two sampling methods combined reflected the dispersal behaviour of the total stock in the upper 200 m at night. In summer 2007 / 2008, the combined mean density of both strata was much lower (1.0 N m^{-2}). Assuming that krill did not migrate to greater depths (Siegel 2005), such an apparent reduction might be related to various causes, including low recruitment, swarming behaviour and differing patterns of water advection.

Our study agrees with a number of investigations highlighting the tendency of postlarval Antarctic krill to concentrate in ice-covered rather than open waters at least during certain times of the year (Siegel et al. 1992; Kaufmann et al. 1995). A discrepancy with midwater sampling efforts finding the opposite pattern (Fisher et al. 2004; Donnelly et al. 2006) may be attributed to an under-estimate of postlarval Antarctic krill density in the pack-ice by water column sampling. The lower mean density of postlarval Antarctic krill in the pack-ice estimated from RMT sampling in the 0 – 200 m stratum in winter 2006 and summer 2007 / 2008 compared to the upper 1 % of this depth range sampled by the SUIT (Figure 3 b, c) indicates that large parts of the krill population dwelling in the ice-water interface layer may not be sufficiently sampled by pelagic nets. A low probability of midwater sampling to detect the close association of postlarval Antarctic krill with sea ice could explain why the significant difference in krill density between ice-covered and open waters in the surface layer in summer 2007 / 2008 was not observed in the 0 – 200 m stratum (Table 2; Figure 3 c).

Sea ice has been proposed repeatedly to play a crucial role for the overwintering of Antarctic krill (Marschall 1988; Siegel & Loeb 1995; Atkinson et al. 2004). Our study supports this notion with the first large-scale quantitative evidence of postlarval *E. superba* dwelling under ice in winter. However, other winter investigations could not find any indication of krill aggregations under ice (Nordhausen 1994b; Zhou et al. 1994). Feeding on ice biota may be only one among a variety of overwintering strategies, including starvation and benthic feeding, depending on the availability of ice biota and other resources (reviewed in Nicol 2006). Larval *E. superba* cannot afford starvation during periods of low food availability. Their survival highly depends on sea ice resources during winter (Daly 2004). This dependence was illustrated by their elevated density even under the young ice of autumn 2004, supporting the hypothesis that the distribution patterns of adult and larval Antarctic krill differ most when food availability is lowest (Nicol 2006).

Diurnal patterns

Seasonal differences were apparent in the diurnal presence of postlarval Antarctic krill in the surface layer (Figure 5). The mere absence from the surface at day and high densities at night in winter contrasting with the lack of a clear diurnal pattern in summer partly reflects the seasonal shift between high diel vertical migration amplitudes in winter and low amplitudes close to the surface in summer proposed by Siegel (2005). Our results add new evidence to this concept that the vertical migration includes the surface layer at all seasons rather than being largely limited to deeper layers in autumn and winter. Moreover, diurnal migration close to the surface may even be inversed in summer.

The observed differences in the diurnal surface layer presence of postlarval Antarctic krill in winter and summer corresponded to the scenarios of equal risk in all depth strata with no or weak vertical migration (summer) and high risk in surface and shallow depths with strong vertical migration (winter) (Alonzo & Mangel 2001). A tentative explanation of such a seasonally divergent vertical migration behaviour would be that high food availability in the shallow mixed layer compensates for the elevated risk of being detected by visual predators at day in summer, whereas the risk of being caught by a predator seems to outweigh the benefit of foraging on the poor food sources in shallow depths at day in winter. The diel vertical migration behaviour of *E. superba*, however, is far from understood. Hernandez-Leon et al. (2001) demonstrated that nocturnal downward migration in summer could be explained by a shift in the feeding behaviour of Antarctic krill rather than predator avoidance. A similar 'inverse' diel migration in summer was also observed in copepods and has been suggested to reflect a response to an increased availability of ice algae washed out of the melting sea ice during the day (Tanimura et al. 2008).

8.4.2 Other krill species

Surface and Under Ice Trawls (SUIT: Chapter 9) allowed to quantify for the first time the distribution and density of Antarctic euphausiids in the upper two meters under sea ice and at the open surface with the identical sampling gear. Our study shows that the surface layer is frequented by all four krill species present in the area of investigation, although to a different degree. The ability of the SUIT to represent euphausiid species and their size spectra depends on the technical performance and catch efficiency of this new sampling device, which were discussed in Chapter 7 and Chapter 9. Based on the similarity in euphausiid species composition and size distribution it can be assumed that the size selectivity of the SUIT did not differ significantly from the well-established RMT (Table 4). Because net-avoidance cannot be entirely excluded, a precautious approach to krill density estimates obtained with SUIT would be to consider them rather conservative.

Thysanoessa macrura

The presence of the second most abundant krill species *Thysanoessa macrura* in the surface layer was limited to the summer months. In the 0 – 200 m stratum, however, it was found at all seasons sampled. These results agree with other studies finding that *T. macrura* largely avoids surface waters in the dark period of the year (Siegel et al. 1992; Nordhausen 1994b; Zhou et al. 1994; Fisher et al. 2004). A generally deeper distribution of this species in autumn and winter explains the lower densities in the 0 – 200 m stratum compared to summer (Lancraft et al. 1989; Lancraft et al. 1991; Lancraft et al. 2004; Donnelly et al. 2006). With few exceptions (e.g. Siegel et al. 1992), *T. macrura* shows neither a positive nor a negative relationship with sea ice (Fisher et al. 2004; Donnelly et al. 2006). This perception is supported by our results from the 0 – 200 m stratum and extended to the open surface and the ice-water interface layer in summer. Postlarval *T. macrura* only reached the surface layer at night in summer 2007 / 2008. This result agrees with the perception that *T. macrura* is a vertically migrating species within shallow depths in summer (Nordhausen 1994a). The divergent diel patterns of *T. macrura* and *E. superba* imply that the vertical migration reflects different benefit-risk balances for the two euphausiids probably related to their different food spectra.

Euphausia crystallorophias

Only a small number of stations sampled in the present study were situated on the Antarctic shelf. Consequently, the shelf-bound *E. crystallorophias* was scarcely encountered both in the surface layer and in the 0 – 200 m stratum. The ice-water interface is believed to be less important for *E. crystallorophias* since they are considered to be unable to consume ice algae (Pakhomov et al. 1998) and seem not to rely on sea ice resources during winter as inferred from their lipid composition and vertical distribution (Nordhausen 1994b; Nicol 2004). This study's evidence of the presence of *E. crystallorophias* under sea ice, however, confirms earlier reports that this species dwells under sea ice and under shelf ice (O'Brien 1987; Craven et al. 2006). Sea ice hosts more valuable food than just ice algae for an omnivorous species such as *E. crystallorophias* (Pakhomov et al. 1998; Brierley & Thomas 2002). This may suggest that appropriate studies in its area of distribution may reward with new insights on the interaction of *E. crystallorophias* with sea ice in the future.

Euphausia frigida

As with *E. crystallorophias* in the south, the LAKRIS sampling grid had little overlap with the distribution range of *E. frigida* in the north. Yet the density range of *E. frigida* in the surface layer on the repeatedly sampled location at 52°S 0° in summer 2007 / 2008 was high compared to reported densities integrated over a greater depth range (Piatkowski 1985; Lancraft et al. 1991). This indicates a potentially higher relevance of the surface layer for this species than previously realized.

8.4.3 Ecological implications

Food demand of the top predator community has been shown to persist or even increase hundreds of kilometres deep into the pack ice, although pelagic primary production there indicated low availability of resources (van Franeker et al. 1997). This pattern was also observed during the sampling campaigns of the present study, supporting the hypothesis that the surface layer, and especially the ice-water interface, might play a crucial role in sustaining the top predator populations of the Antarctic seasonal sea ice zone (Ainley et al. 1986, 1992; van Franeker et al. 1997).

An under-estimate by pelagic sampling in the past may have caused ice-covered areas to appear poorer in biological resources than they are in reality. The pronounced presence of postlarval *E. superba* under the ice highlights its potential as an energy transmitter between the production of ice algae and the pelagic food web. The trophic relationships among sea ice algae, *E. superba* and higher predators, however, are complex. A range of abundant Antarctic homoiotherms rely on fish or squid rather than krill (van Franeker et al. 2001; Ainley et al. 2003a; Connan et al. 2007; Luque et al. 2007). The potential relevance of nekton in the food web has been demonstrated for the Lazarev Sea, where mesopelagic fish may constitute an energy source comparable to Antarctic krill (Chapter 3; Chapter 4). To date, it is unclear in which way the pelagic nekton and its ontogenetic stages interact with the sea ice system, and to which extent it is involved in the energy transmission from the ice to the top predators. In this context, the concentration of postlarval Antarctic krill under sea ice should be considered more as an indicator of the ecological potential of the sea ice system than as the sole pathway of energy transmission. Antarctic krill shares this role with a wide spectrum of other species, including ice-associated copepods, pteropods, chaetognaths and amphipods (Chapter 7, Schnack-Schiel 2003).

Our results indicate that concentrations of Antarctic krill under ice are common throughout the entire seasonal pack-ice zone when the ice offers sufficient resources. In a warming climate, however, ice thickness distribution, ice structure, and with it the potential to support a complex biological community, might change long before a significant reduction in total seasonal ice cover is apparent (Siegel 2005; Smetacek & Nicol 2005; Clarke et al. 2007). If krill aggregations are not predominantly restricted to a narrow band associated with the ice margin, their ice habitat would shrink rather with the surface area, suggesting that the impact of diminishing sea ice on Antarctic krill stocks might be far more serious than estimated before (Loeb et al. 1997; Atkinson et al. 2004).

8.4.4 Conclusions

The presence of Antarctic krill under ice throughout the entire seasonal sea ice zone both in summer and winter exemplifies a high ecological relevance of the sea ice system throughout most parts of the year. The importance of the ice-water interface layer may have been underestimated in the past due to limitations of pelagic sampling and acoustic methods. Our findings obtained with a new sampling device emphasize the need to better understand the interactions between the sea ice, the pelagic food web and the air-breathing top predators. A better view of the relevance of the sea ice system in terms of ecology and biodiversity can be expected from closer investigations on the physical-biological processes in this understudied environment.

Due to the apparent high importance of sea ice for Antarctic krill and the ecosystem of which it is part, a profound understanding of the habitat use of E. superba is crucial to predict the long-term development of krill populations under such scenarios as decadal climate oscillations or anthropogenic global warming. It is thus an important prerequisite of the ecosystem-based management approach envisaged by CCAMLR (Hewitt and Linen Low 2000; Croxall 2004).

Acknowledgements

This study was made possible by extraordinary support of the crews of the POLARSTERN expeditions ANT XXI-4, ANT XXIII-6 and ANT XXIV-2, Captain Uwe Pahl, Captain Stefan Schwarze and the Alfred Wegener Institute for Polar and Marine Research (AWI). The following people contributed greatly to the successful completion of our research: André Meijboom, Michiel van Dorssen, Ruben Fijn, Bram Fey, Anton van de Putte, Martina Vortkamp, Susanne Schöling, Daria Martynova, Hans Verdaat, Ismael Nunez-Riboni, Sarah Hermann and Bettina Meyer. This study was supported by the Netherlands AntArctic Programme (NAAP Project nr. 851.20.011), the Dutch Ministry for Agriculture, Nature and Food Quality (LNV) and the German LAKRIS project (BMBF MGS 03F046A).

Key references

- Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432:100-103
- Brierley AS, Fernandes PG, Brandon MA, Armstromg F, Millard NW, McPhail SD, Stevenson P, Pebody M, Perrett J, Squires M, Bone DG, Griffiths G (2002) Antarctic krill under sea ice: Elevated abundance in a narrow band just south of ice edge. Science 295:1890-1892
- Everson I (2000) The distribution of standing stock - the Southern Ocean. In: Everson I (ed) Krill - biology, ecology and fisheries. Blackwell Science Ltd., London, p 63-79
- Marschall HP (1988) The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. Polar Biology 9:129-135
- Siegel V (2005) Distribution and population dynamics of *Euphausia superba*: summary of recent findings. Polar Biology 29:1-22

The SUIT ready to go on the working deck of *Polarstern.*

CHAPTER 9

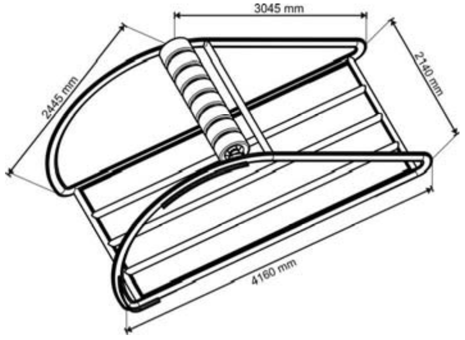
The Surface and Under-Ice Trawl (SUIT)

Jan A. van Franeker, Hauke Flores & Michiel van Dorssen

9.1 Background

The birds, seals and whales of the Antarctic seasonal sea ice zone ultimately depend to a large extent on primary production from algae growing in the pack-ice (Brierley and Thomas 2002). However, how biomass and energy assimilated within the sea ice are transferred into the pelagic food web that connects producers (ice algae) and final consumers (birds and mammals), is not well understood. Animals dwelling in the ice-water interface can naturally be assumed to form an important trophic link between the ice and the pelagic food web. However, this harsh environment is difficult to access with conventional sampling methods. As a first approach to quantitatively collect animals dwelling close under the ice canopy, a new sampling gear was developed, the Surface and Under Ice Trawl (SUIT). SUIT systems were successfully deployed on four cruises with the icebreakers *Polarstern* and *Aurora Australis* so far.

▲ **Figure 1.** SUIT in ice during deployment, Lazarev Sea 2006.



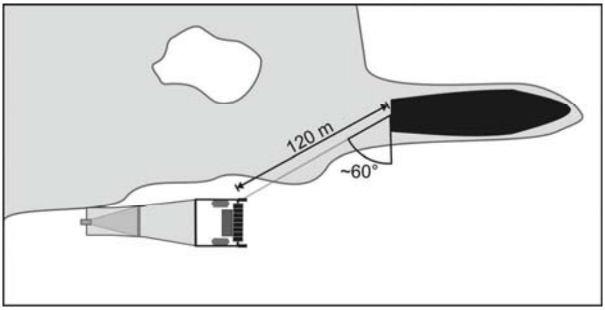
▲ **Figure 2.** Technical drawing with major dimensions of the SUIT frame used with RV *Polarstern* in austral summer 2007 / 2008.

▲ **Figure 3.** SUIT frame with floaters and side nets during a test deployment in the harbour of Texel (NL).

9.2 Construction

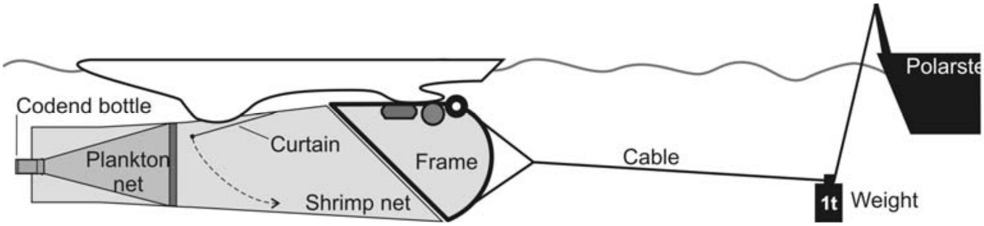
The frame consists of 3-inch pipes enclosing an opening of approximately 2*2 m. The front pipes are rounded like the gliding bars of a sledge to allow smooth gliding under ice. Gliding is further facilitated by a closed row of wheels above the frontal opening. At the rear side of the frame, oblique slide bars conduct big ice chunks out of the frame through the open top. Floaters attached at the top ensure the upper edge of the SUIT to be in contact with the underside of the ice or at surface level in open water, respectively. The starboard side plane of the frame is filled out with 7 mm half-mesh shrimp nets. Canvas fitted into the portside side plane enhances sideward shearing.

The bridle is attached only to the portside of the SUIT frame, causing the net to shear out to the starboard side of the ship (Figure 4). To avoid interference of the towing cable with ice floes, a 900 kg weight hung on the cable ensures it to stay several meters under water directly behind the vessel (Figure 5, Figure 6). The position of the weight on the cable is adjustable. SUIT can be deployed without the weight in open water.



▲ **Figure 4.** Sketch of shearing SUIT in bird-eye view.

▲ **Figure 5.** Deployment of the weight on the towing cable

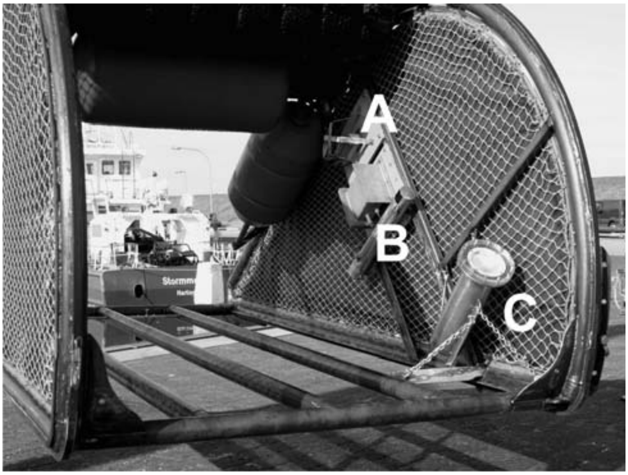


▲ **Figure 6.** Side view sketch of SUIT with cable and weight.

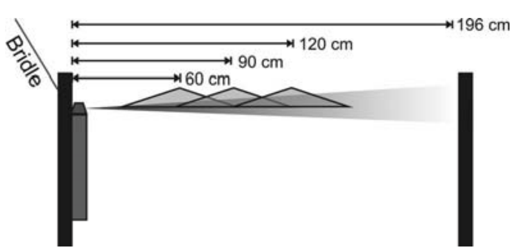
A 7 mm half-mesh shrimp net of approximately 15 m length was used during standard deployments. In the frontal part, a net curtain with a lead line at the bottom closes the net at slow towing speed, impeding animals caught to escape from the net. The rear 3 meters of the net are lined with 0.3 mm plankton gauze connectedto the shrimp net with zippers (Figure 6). The catch is collected in a 70 cm long codend bottle attached to the end of the plankton net. The approximately 20 cm inner diameter of this bottle creates a still water space during the trawl, protecting the catch from mechanical disruption (Figure 7).

Rails in the SUIT frame allow the attachment of various additional devices. To date, a strobe light, a video system and an acoustic Doppler current profiler (ADCP) have been used with SUIT (Figure 8). The latter device served as a standard tool to estimate the amount of water passing through the net.

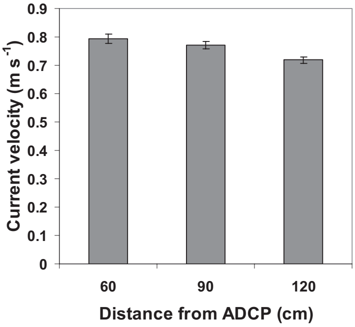
▲ **Figure 7.** Codend bottle attached to plankton net.



▲ **Figure 8.** View from the front into the net mouth of the SUIT frame. A camera cage (A), an ADCP housing (B) and a strobe light (C) are mounted at the portside.



▲ **Figure 9.** Position of ADCP measurement cells viewed from top. Triangles show overlapping ranges.

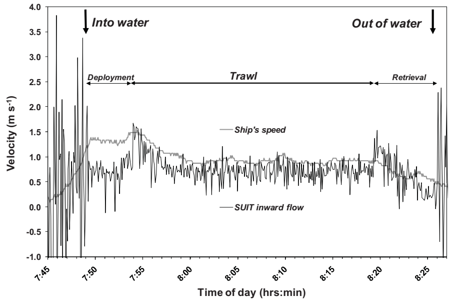


▲ **Figure 10.** Example of mean (± s.e.) current velocities in SUIT mouth.

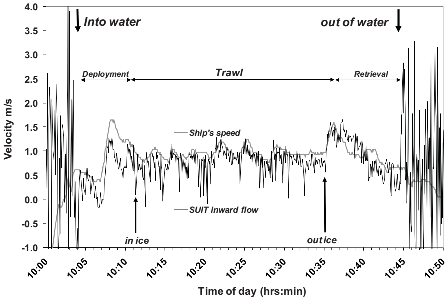
9.3 Towing performance

In winter 2006 and summer 2007 / 2008 an ADCP was installed in the SUIT frame to allow a detailed analysis of the water flow into the net. The ADCP is able to measure current speed continuously at three different positions across the net opening (Figure 9). By standard, the central measurement cell was used to estimate inward directed current velocity.

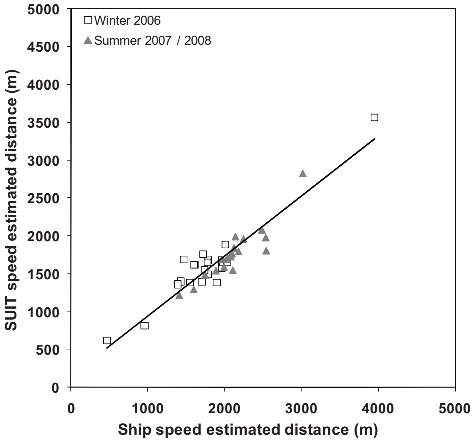
During deployment the towing cable length is increasing, causing SUIT to move considerably slower than the ship. During the phase of steady trawling, fluctuations in shearing slow down the average current velocity inside the frame to about 90 % of the ship's speed in water. Wave action causes moderate oscillations in current speed. During retrieval, the towing cable is taken in, causing SUIT to move faster than the decelerating ship as long as shearing continues (Figure 11). Using real-time current speed measurements directly in the net opening as a basis for quantitative calculations inherently accounts for the difference between the water distance sampled compared to the distance covered by the ship.



▲ **Figure 11.** Current velocity in the SUIT mouth during an open water haul. The ADCP cannot measure outside water.



▲ **Figure 12.** Current velocity in the SUIT mouth during a haul under sea ice.



◂ **Figure 13**. Relationship of the distance passed through water estimated from the ship's speed in water with distance estimated from current speed in the SUIT.

During ice-breaking the ship's speed is more variable than in open water because it needs permanent adjustment to maintain the standard range of trawling speed (1.5 – 2.0 knots = 0.8 – 1.1 m s^{-1}). Impacts of floe edges and under-ice topography cause sudden extreme but short-lasting negative oscillations of inward directed water current (Figure 12).

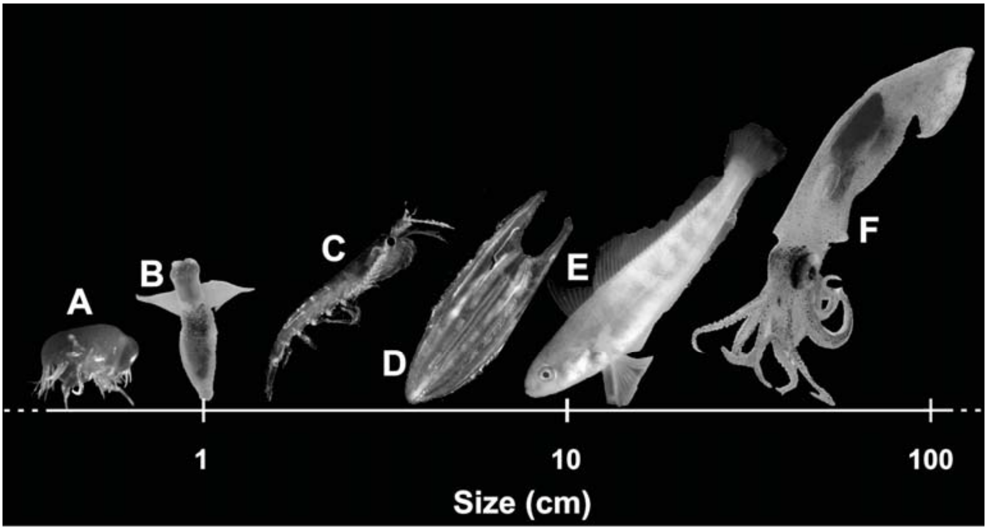
The ADCP flow measurements were used to calculate the distance of water filtered by SUIT according to the procedure described in chapters 7 and 8. The reliable relationship with the sampled distance estimated from the ship's speed in water allowed the reconstruction of the distance of water sampled by SUIT for autumn 2004, when no ADCP was used (Figure 13).

9.4 Catch composition

A wide spectrum of plankton and nekton species was caught with SUIT ranging in size from ostracods (< 1 mm) to adult squid (420 mm) (Figure 14; Chapter 7). The biggest fish caught with SUIT was a snake pipefish *Entelurus aequoreus* (390 mm) collected during a test haul in the Dutch Wadden Sea (Van Franeker & Flores 2007). The most frequently caught macrofauna species was Antarctic krill *Euphausia superba*.

There was no significant difference between the size compositions of krill caught by SUIT and krill caught by the well-established rectangular midwater trawl (RMT) in three sampling seasons (Figure 15; Chapter 8). This similarity indicates that there was no significant difference in the size selectivity of the two nets.

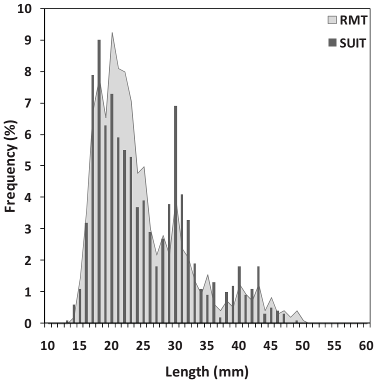
SUIT catches from summer 2007 / 2008 yielded higher densities at day than at night, indicating that krill could not avoid the net even at optimum visibility. Although direct evidence is still lacking, these results strongly support the assumption that SUIT is able to sample Antarctic krill and other micronekton species quantitatively.



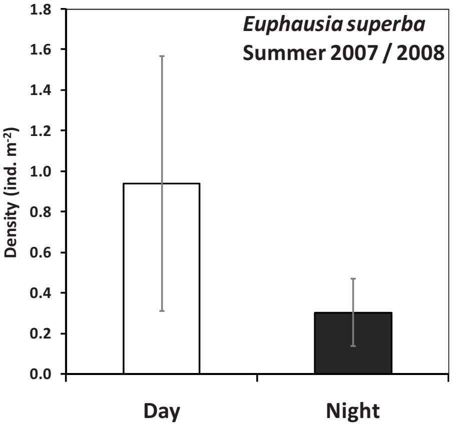
▲ **Figure 14.** Examples of macrofauna caught with SUIT. **A:** amphipod *Hyperiella dilatata*; **B:** sea angel *Clione antarctica*; **C**:Antarctic krill *Euphausia superba*; **D:** comb jellyfish *Callianira antarctica*; **E**: threadfin pithead *Aethotaxis mitopteryx*; **F:** squid *Slosarcszykovia circumantarctica*.

Uncertainty, however, remains for the catch efficiency for true nekton (adult fish and squid). For example, the density of the lanternfish *Electrona antarctica* was much higher in RMT than in SUIT catches in autumn 2004 (Chapter 4, Chapter 7), leaving unclear whether only a small proportion of the population reached the surface layer or most fish could avoid the net. Although more clarity is needed with regard to these limitations, SUIT provides a new opportunity of direct quantitative sampling in the ice-water interface layer and at the open surface with the same gear at least for zooplankton and micronekton.

SUIT was designed by Jan Andries van Franeker and built by M van Dorssen Metaalbewerking (Texel, The Netherlands). Detailed information about SUIT is available on request from J.A. van Franeker, Wageningen IMARES.



◀ **Figure 15.** Length-frequency distributions of Antarctic krill *Euphausia superba* caught with SUIT and RMT at identical locations in the Lazarev Sea in austral summer 20s07 / 2008.



◄ **Figure 16.** Mean (± s.e.) density of day / night comparisons of postlarval Antarctic krill at three Locations sampled by SUIT in the Lazarev sea, austral summer 2007 / 2008.

Acknowledgements

The following people and companies supported Wageningen IMARES and van Dorssen Metaalbewerking in the development and application of SUIT:

A. Meijboom, R. Fijn, B. Fey, J. Zegers, U. Bathmann, *Polarstern* crews of ANT XXI/4, ANT XXIII/6 and ANT XXIV/2 (particularly U. Grundmann, B. Clasen, D. Beth, K. Hoppe), V. Siegel , crew of RV *Navicula*, D. de Haan, J. Betsema, A. Boon, R. Wilzewski, the Alfred Wegener Institute for Polar and Marine Research (AWI), C.I.V. Texel b.v., Zeilmakerij Texel, Schat Harding GmbH, Qmetrix b.v.. SUIT development and application was funded by the Netherlands AntArctic Programme (NAAP Project nr. 851.20.011) and the Dutch Ministry for Agriculture, Nature and Food Quality (LNV) through its Statuary Research Tasks Programme (WOT project 04-003).

Key references

- Brierley AS, Thomas DN (2002) Ecology of Southern Ocean pack ice. Advances in Marine Biology, 43:171-276
- van Franeker JA, Flores H (2007) Zuidpool en zeenaalden? Nederlandse Zeevogelgroep Nieuwsbrief 8:4

Pinguin-art in the pack-ice.

CHAPTER 10

Synthesis:
Untangling the Antarctic sea ice food web

10.1 Two classic paradigms of the food web in the Antarctic pack-ice zone

During the last quarter of the 20th century the widely accepted model of the food web of the Antarctic seasonal sea ice zone was based on two paradigms. The first one may be called the concept of the pivotal role of krill. According to this paradigm, the food web of the Southern Ocean has a simple structure, in which the assimilation products of planktonic algae are transmitted from primary producers to top predators primarily via Antarctic krill as the single intermediate trophic level. Top predators in most other marine ecosystems usually depend on resources derived from multiple pathways of energy transmission comprising a higher number of trophic levels. Because 80 – 90 % of energy are lost at each trophic step, the quantities of birds, seals and whales in the Southern Ocean were in large parts attributed to the energetic efficiency of the krill-centered food web (e.g. Hempel 1985).

The second paradigm relates to the decisive function of the productivity of the marginal ice zone for the Antarctic seasonal sea ice zone ecosystem. When sea ice melts during summer, it leaves a lens of less dense water at the surface. This process creates a shallow mixed layer providing optimal growth conditions for phytoplankton. Nutrients and ice algae released from the ice further enhance the productivity of the marginal ice zone system. The apparent concentration of life in the vicinity of the ice edge often witnessed by visitors of Antarctic waters has been attributed to this effect. The stocks of Antarctic krill in the pack-ice have long been thought to rely chiefly on the fecundity of the marginal ice zone, because primary production was considered negligible in waters covered by a canopy of ice (reviewed in Marchant & Murphy 1994).

Until today the productivity of the marginal ice zone in combination with the energy-efficient, krill-dominated food web have been considered the most important drivers of the ecosystem of the Antarctic seasonal sea ice zone (e.g. Smetacek & Nicol 2005; Gross 2007). In the course of this synthesis I will discuss whether the research compiled in this thesis challenges the paradigm of the pivotal role of krill. Furthermore, I will illustrate how a novel sampling technique helps to understand why the entire pack-ice area rather than the marginal ice zone alone provides significant amounts of biological resources, and which role the ice plays as an important habitat sustaining the biodiversity of the Southern Ocean.

10.2 The pivotal role of krill

Euphausia superba is among the most abundant macrofauna species in the world with an estimated biomass of $169 * 10^6$ t (Siegel 2005). Its stocks, however, are not homogenously distributed over the Southern Ocean. The highest concentrations of Antarctic krill typically occur along the islands of the Scotia Arc (South Shetlands, South Orkneys and South Georgia archipelagos) and in the confluence zone of the Weddell and Scotia seas (Atkinson et al. 2008). In this region, the eastward-flowing

Antarctic Circumpolar Current is deflected northwards by the Antarctic Peninsula, transporting krill from the Bellingshausen Sea in the west over the productive shelf of the Scotia Arc. The concentration of *E. superba* in this area is further enhanced by the advection of krill from the Weddell Sea in the east with the northward limb of the Weddell Gyre that meets the Antarctic Circumpolar Current in the Weddell-Scotia confluence zone. The extensive research programmes in the 1980s and early 1990s that largely shaped our understanding of the Southern Ocean ecosystem focused on these economically important areas (e.g. El-Sayed 1994).

A typical example from this region of high krill availability was provided in Chapter 2. The summer diet of the planktivorous mackerel icefish *Champsocephalus gunnari* consisted almost exclusively of Antarctic krill, probably because it was the most abundant food source available. On the shelf of the South Shetland Islands, the pelagic resource *E. superba* was even consumed in significant amounts by juveniles of the demersal Scotia Sea icefish *Chaenocephalus aceratus*. Adults, however, were piscivorous. Hydrographic conditions enhancing high concentrations of krill and other pelagic resources, as are present in the Scotia Arc region, may have supported the evolution of the semi-pelagic mode of life exhibited by *C. gunnari* in the primarily demersal icefishes (Channichthyidae; reviewed in Kock 2005a; Kock 2005b). Icefishes are important diet components of a range of abundant top predators (Barrera-Oro 2002). The almost exclusive dependence of a major prey species of birds and mammals on Antarctic krill can be considered as an example of a krill-dominated food chain, although the trophic relevance of *E. superba* for the warm-blooded top predators is indirect in this case.

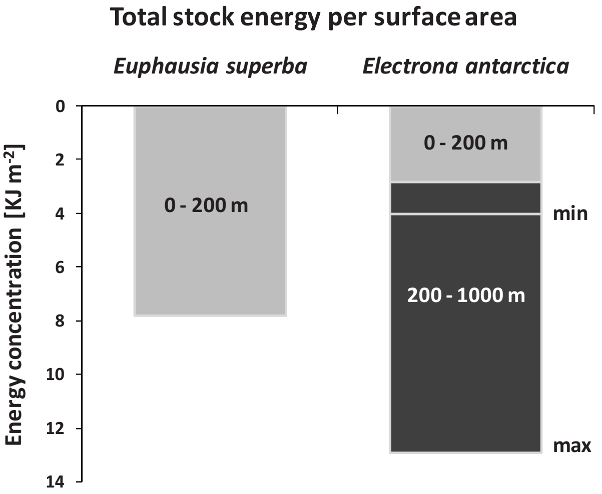
In the South Shetland Islands and Elephant Island region, mackerel icefish were estimated to consume about 700 – 1200 metric tons of Antarctic krill per month (Chapter 2). The impact of *C. gunnari* on krill was probably much more pronounced before the collapse of mackerel icefish stocks caused by over-exploitation in the early 1980s (Kock 1992). It has been argued that krill-eating fish benefited from a surplus of *E. superba* after seals and whales had been depleted in the 19th and 20th century (Laws 1977a). However, such simple reasoning must be considered with caution in the complex ecosystem of the Southern Ocean. Antarctic fur seals in the Scotia Arc region, for example, seem to cover only a limited proportion of their food demand with local krill, even when it is abundant, and rather travel large distances to forage on mesopelagic fish (Ichii et al. 2007). In fact, many of the abundant top predators of the Antarctic seasonal sea ice zone depend on Antarctic krill only to a limited degree (Laws 1977b; Ainley et al. 2003; Connan et al. 2007; Luque et al. 2007). Although not as abundant as Antarctic krill, pelagic fish and squid are virtually ubiquitous in the Southern Ocean. Their adults are usually bigger and have a higher energy density than krill, providing a much higher amount of energy per prey item. The energy density of the lanternfish *Electrona antarctica*, for example, is twice as high as that of *E. superba* (Chapter 3). For top predators such as Antarctic fur seals, this surplus is apparently sufficient to compensate for the energetic costs of foraging trips far away from coastal breeding areas (Ichii et al. 2007).

The oceanographic conditions of the Scotia Arc / Antarctic Peninsula region that favour the enrichment of Antarctic krill represent only a small part of the Southern Ocean. By far the largest proportion of the area covered by the Southern Ocean consists of deep sea (Davey 2007). Only the Ross Sea comprises a wide shelf that hosts a unique ecosystem (Smith et al. 2007). The Weddell and Lazarev seas, where the investigations presented in Chapters 3 – 9 were conducted, may serve as examples of a more typical Antarctic marine environment characterized by large and deep offshore areas with a narrow shelf.

Chapter 3 and 4 concentrate on the role of mesopelagic fishes in the offshore food web of the Lazarev Sea. A pronounced ecological relevance was shown for *E. antarctica*, the most abundant mesopelagic fish in the Southern Ocean south of the Antarctic Polar Front (Sabourenkov 1990). The quick increase of energy content in growing first-year *E. antarctica* shown in Chapter 3 indicates a high efficiency in the accumulation of energy reserves that implies intense feeding. As mesozooplankton feeders, *E. antarctica* are likely to transfer a significant proportion of the pelagic secondary production to the upper trophic levels of the food web (Pakhomov et al. 1996). Krill only accounted for a limited proportion of the diet of *E. antarctica* in the Lazarev Sea (Chapter 4). Instead, this lanternfish predominantly fed on copepods, implying that they were part of a trophic pathway alternative to the classic paradigm of the pivotal role of krill. In this pathway, the assimilation products of phytoplankton are transmitted via mesozooplankton (mainly copepods) and nekton (adult fish and squid) to the top predators (birds and mammals; Hopkins 1993). Assuming that between 24 and 70 % of the population of *E. antarctica* dwell in the upper 200 m (Lancraft et al. 1989; Donnelly et al. 2006), *E. antarctica* appears to be at least as important as Antarctic krill in the pelagic food web of the Lazarev Sea in terms of energy (Figure 1).

As in other oceans, the species composition on the Antarctic shelf significantly differs from that of offshore communities. The distinct separation of shelf and offshore species compositions was demonstrated at the example of the ichthyoplankton community of the Lazarev Sea (Chapter 4). *E. antarctica* and other lanternfishes are usually absent from the continental shelf. This association with offshore waters was reflected in the negative effect of shallow depths on the density of *E. antarctica* apparent from the model on the effect of environmental parameters on the density of *E. antarctica* applied in Chapter 4.

Also on the continental and island shelves, the traditionally assumed key role of euphausiids is challenged by a dominance of fish in the diet of many top predator species (e.g. Van Franeker et al. 2001; Casaux et al. 2006). Similar to the role of *E. antarctica* in Antarctic offshore waters, the Antarctic silverfish *Pleuragramma*



▲ **Figure 1.** Total energy concentration per surface area [KJ m^{-2}] represented by the stocks of Antarctic krill *Euphausia superba* and *Electrona antarctica* in the Lazarev Sea in autumn 2004. Values estimated for the sampling depth of 200 m shown in light grey. Minimum (**min**) and maximum (**max**) stock energy of *E. antarctica* expected to dwell below 200 m shown in dark grey, assuming that between 24 and 70 % of the population were distributed in the upper 200 m. Total stock energy was calculated based on nighttime abundances of both species. Values of y-axis increase downwards.

antarcticum was proposed early as an ecological key species on the shelf (Hubold 1985). The energy density of adult Antarctic silverfish is similar to that of the lanternfish (Van de Putte et al. in press). In high-Antarctic shelf waters, the ecological function of Antarctic krill is in large parts taken by its neritic sister species *Euphausia crystallorophias* (Everson 2000). *E. crystallorophias* and Antarctic silverfish share the key position in the food web of the shelf-dominated ecosystem of the Ross Sea (Smith et al. 2007).

These considerations strongly suggest that, next to euphausiids, fish play a major role in both the offshore and inshore food webs of the Antarctic sea ice zone. Nonetheless, it is difficult to quantify the predation impact of fish on mesozooplankton as well as their significance as prey items on a larger scale. Accurate population estimates of pelagic fishes in the Southern Ocean have been hampered by a lack of dedicated sampling campaigns and the overall scarcity of abundance data in space and time (Kock et al. in press). The ecological importance of Antarctic krill may further be put into proportion if other nekton is considered as well. Cephalopods for example are major predators on zooplankton and fish and an important diet item of many birds and mammals (Van Franeker et al. 2001; Piatkowski et al. 2002; Libertelli et al. 2004; Zimmer et al. 2007). Rodhouse & White (1995) found that squid can replace the trophic function of fish in some areas of the Southern Ocean, indicating that cephalopods are a third important vector of energy transmission through the pelagic food web.

10.3 The function of sea ice

In the large offshore areas of the Antarctic seasonal sea ice zone not influenced by frontal systems, the wealth of life in the Antarctic pack-ice has mainly been attributed to the extraordinary productivity of the marginal ice zone (Marchant & Murphy 1994). At the onset of spring, this belt of productive waters propagates from north to south, until it reaches either the continental coast or the areas of residual multi-year ice in the Weddell and Ross seas. Like in the Scotia Arc region, the trophic role of krill in this system may have been over-estimated under the impression of krill swarms and predators foraging on them in these areas (Laws 1977b; Fraser & Ainley 1986; Ribic et al. 1991).

The occurrence of local concentrations of life along the northern margin of the pack-ice is unquestionable, as are the processes that lead to an enhanced primary production and subsequent enrichment of intermediate consumers and top predators (reviewed in Knox 2007). At any given place, however, this phenomenon only persists for a restricted period. Systematic investigations in the seasonal sea ice zone demonstrated that the food demand of the top predator community persists on a high level throughout the entire pack-ice area, rather than being temporarily concentrated in the marginal ice zone (van Franeker 1992; van Franeker et al. 1997). Since phytoplankton stocks are obviously small in waters shaded by an ice canopy, the pack-ice food web must rely on other sources of primary production. Instead, ice algae probably provide much of the assimilation needed to suit the high food demand of the top predator stocks present throughout the pack-ice areas. In contrast to the short-lasting phytoplankton blooms in the marginal ice zone, ice algal production occurs almost year-round (Arrigo et al. 1997). Over the past decades, sea ice primary production has become increasingly acknowledged as a key foundation of the food web in the seasonal sea ice zone (Brierley & Thomas 2002).

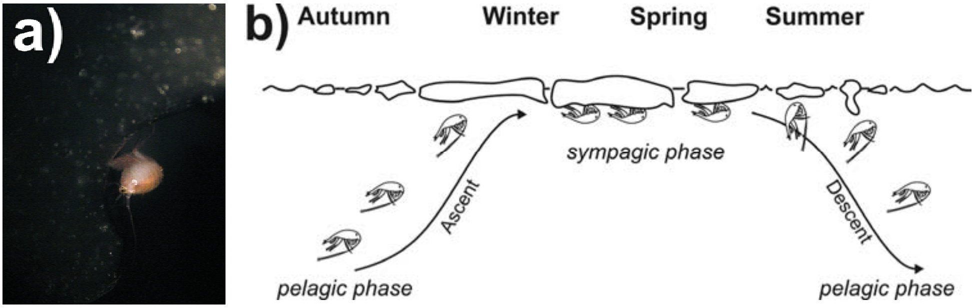
The perception that the entire seasonal sea ice zone can sustain large populations of top predators was supported by the results of Chapter 5. This study focused on a rarely visited area in the ice-covered western Weddell Sea. Densities of pack-ice seals were found to be similar to values reported from the marginal ice zone to the north of the study area. A novel approach in Chapter 5 was the measurement of ice thickness concurrent to the top predator censuses using real-time data collected by an electromagnetic device. The high resolution of sea ice data allowed an analysis of the correlation of various ice properties in combination with bathymetry with the observed densities of crabeater seals. Since much of the area of investigation was situated close to the eastern shelf slope of the Antarctic Peninsula, crabeater seal distribution was observed to respond to the transition from a deep-sea to a shelf environment. In addition to changes in bathymetry, ice thickness had a significant effect on the density of crabeater seals. In the heavy ice of the surveys analyzed in Chapter 5, crabeater seals preferred the thinner ice more suitable for haul-out.

The effect of sea ice properties on the distribution of crabeater seals exemplifies the significant influence of the ice on the structure of the seasonal sea ice zone ecosystem. The sea ice is known to form its own micro-habitat, supporting an ice-associated (i.e. sympagic) species community. The recent discovery of a new sympagic gastropod species (Kiko et al. 2008a) illustrates that the ice habitat is not yet fully described and can be expected to be more diverse than known to date.

If ice algae constitute the trophic basis of the food web in the Antarctic seasonal sea ice zone, their assimilates must be exported out of the ice into the water column, where they can be transferred through the pelagic food web to the top predators. Outside the melting season, export of biomass and energy from the sea ice into the pelagic realm can occur by means of three major processes closely interacting with each other: migration, predation and the passive export of organic matter such as feces, exuviae and decomposing material (Brierley & Thomas 2002). Both the migratory and the predatory pathway of energy transmission demand the existence of species that act as energy vectors between the sea ice and the water column. They can be expected to dwell at the ice-water interface at least during certain times. Macrozooplankton and nekton that feed (and are fed on) in the ice-water interface layer would constitute the most direct energy transmitters from the sea ice to the top predators.

In the Arctic Ocean, amphipods often dominate the sympagic macrofauna community of the ice-water interface layer (Arndt & Swadling 2006). In the Southern Ocean, amphipods have adapted to a multitude of habitats, but sympagic amphipods have been documented only on the shelf so far (Arndt & Swadling 2006). The results of Chapter 6 and 7 suggest that also in offshore waters at least two amphipod species are very likely to conduct a sympagic mode of life as a part of their life cycle. *Eusirus laticarpus* and *E. microps* were encountered frequently under sea ice in the Lazarev Sea. The observations reported in Chapter 6 and 7 suggest a pelago-sympagic life cycle that is described using the example of *E. laticarpus* (Figure 2):

- In autumn, *E. laticarpus* were not caught in both the open and ice-covered surface layer, indicating that they arrive at the ice-water interface layer not before early winter.
- In winter, they were more abundant under the older sea ice in the south and absent from this habitat in northerly areas. The results from early summer show that the distribution of *E. laticarpus* covers the entire sea ice area at the beginning of the melting season. This suggests that the amphipods subsequently occupy the ice habitat from south to north.
- In summer, the occurrence of female *E. laticarpus* with brood sacs under sea ice indicated that reproduction takes place at the end of the sea ice season. Juveniles are released into the water, and the amphipods can be assumed to return to the pelagic phase of their life cycle.



▲ **Figure 2.** *Eusirus laticarpus* attached to sea ice in an aquarium on board Polarstern (a). Proposed pelago-sympagic life strategy (b). In early winter, the sympagic phase begins when amphipods occupy the underside of ice floes with increasing suitability of the sea ice habitat from south to north. They stay there until the ice breaks up in summer. During the melting season, the juveniles are released, and the amphipods return to the pelagic phase of their life cycle.

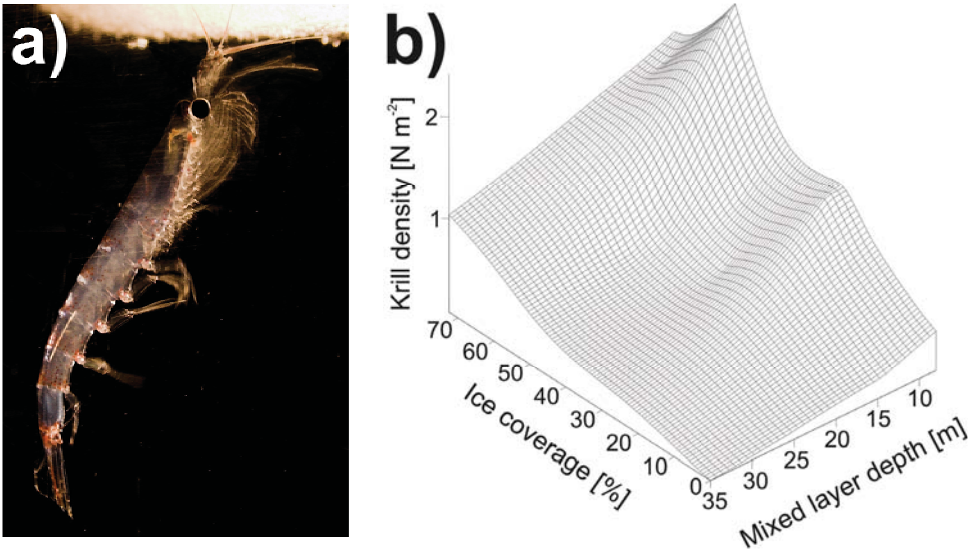
The life strategy proposed here for *E. laticarpus*, however, leaves many questions open. For example, diet investigations are urgently needed in order to assess this species' trophic interaction with sea-ice biota. It is further still unclear, how the amphipod survives the summer months. Only a few potential records were reported from pelagic sampling, dating from times before the species was separated from *E. antarcticus* (Boysen-Ennen & Piatkowski 1988; Hopkins & Torres 1988; De Broyer & Jazdzewski 1993). Thus, it is also possible that they stay in bathypelagic layers during summer, or even switch to a benthic mode of life.

Similar to these at least partially sympagic amphipods, several macrofauna species depend strongly on sea ice to complete their life cycle. Antarctic krill belongs to this group. Particularly its furcilia larvae need to feed on ice algae during the winter (Daly 2004). A temporarily limited form of ice association may be represented by the sea angel *Clione antarctica*. This pelagic sea slug (pteropod) preferred open waters in summer and autumn, but was abundant under ice in winter. Such a seasonally divergent pattern in sea ice use may represent a type of plankton that is abundant and widespread in the open Southern Ocean, but within the seasonal sea ice zone depends on sea ice resources to survive the dark period of the year. Certain other species that are abundant at the surface in open water, such as the amphipods *Cyllopus lucasi* and *Hyperiella dilatata*, seem to avoid the ice-water interface layer (Chapter 7). These species are apparently not adapted to the sea ice environment.

By attracting certain species that have adapted to benefit from the ice environment (e.g. sympagic amphipods, euphausiids and their larvae) and repelling others (e.g. pelagic amphipods), the ice-water interface layer shapes its own species community. The effect of sea ice on the community composition in the surface layer was demonstrated in Chapter 7 (ibidem, Figure 2). Change of ice properties was significantly correlated with the change in community composition in two out of three seasons. At the same time the species composition also responded to water column properties. During the summer 2007 / 2008 sampling campaign, both the open and ice-covered surface layer were sampled with similar effort, illustrating the interaction of environmental parameters of the water column and sea ice properties. During this season, a species community associated with heavy ice was separated from less distinct communities exhibiting a subtle transition from ice-covered and colder waters poor in phytoplankton to open and warmer waters with high chlorophyll concentrations (Chapter 7, Figure 5).

The macrofauna community dwelling in the surface layer of the Lazarev Sea was dominated by Antarctic krill in numbers and biomass. Chapter 8 presents the first quantitative multi-seasonal record of *E. superba* from the under-ice habitat that covers the entire pack-ice zone from the marginal ice zone to the continental shelf. The highest local concentrations of *E. superba* were found under the pack-ice in winter, adding strong evidence to an early suggestion by Marschall (1988) that Antarctic krill may depend on the sea ice habitat to survive the dark months of the year. During the winter investigation, the mean krill density per surface area integrated over the 0 – 200 m stratum was considerably lower than that observed in the only 1 % of this depth range represented by the ice-water interface layer. It also never reached the local maxima observed under the ice. This pattern of high concentrations of krill under ice at moderate abundances in the underlying water column was even more pronounced in summer. Only in autumn, when the ice was young and biologically immature, krill were scarce directly under the ice. In open waters, the integrated density of *E. superba* in the 0 – 200 m layer was generally higher than at the surface. Thus, the general pattern in the Lazarev Sea seems to be that Antarctic krill concentrate under pack-ice as soon as it offers sufficient resources, and disperse in the water column when ice is absent or biologically poor.

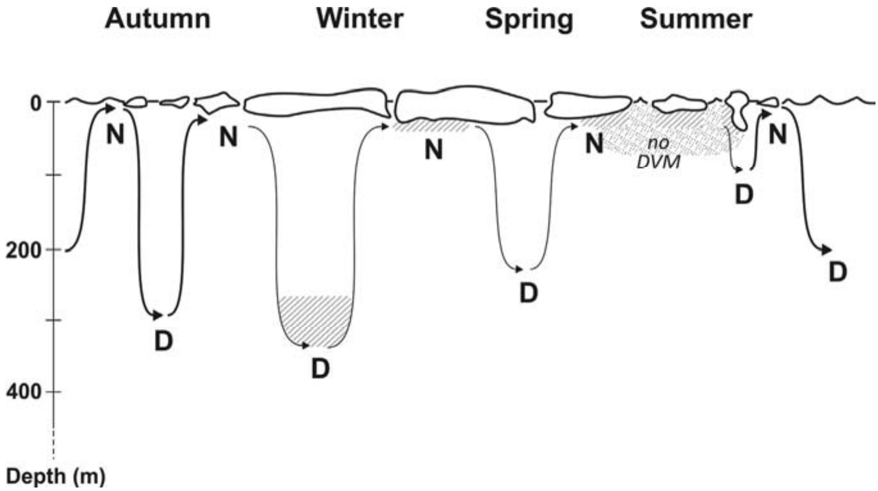
The trade-off between dispersal in the water column and concentration in the ice-water interface layer was illustrated by the modeled relationship of the surface layer density of Antarctic krill with environmental parameters in summer 2007 / 2008. In this season, krill density in the upper 2 m significantly responded to both water column (attenuation, mixed layer depth) and sea ice (ice coverage, ice thickness) properties. The projection of the modeled density of *E. superba* on the two non-linear factors ice coverage and mixed layer depth in Figure 3 shows clearly that high krill densities were associated with high proportional ice coverage. Assuming that in open water krill disperses mainly within the mixed layer where phytoplankton production is high, density at the surface can be expected to increase when this layer becomes thinner. Thus, at low ice coverage, the model predicted elevated krill densities at the surface only when the mixed layer was very shallow.



▲ **Figure 3.** Antarctic krill *Euphausia superba*. Animal dwelling under sea ice in an aquarium on board Polarstern (a). Surface layer density [N m^{-2}] of Antarctic krill in the Lazarev Sea in summer 2007 / 2008 in relation to proportional ice coverage [%] and mixed layer depth [m] predicted by the Generalized Additive Model applied in Chapter 8 (b).

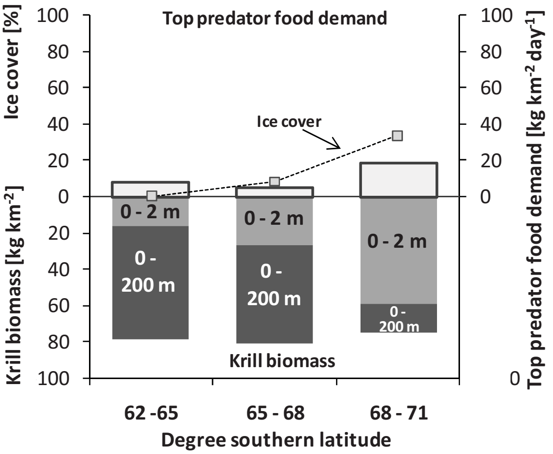
The ability to directly sample the surface layer added new evidence that the diurnal vertical migration of Antarctic krill includes the surface layer virtually year-round (Chapter 8, Figure 5). Summarizing the diurnal and seasonal patterns and the association with sea ice apparent from combined surface layer and midwater sampling and assuming a general seasonal pattern of diurnal vertical migration described in Siegel (2005), Figure 4 shows a tentative scheme of the vertical distribution of *E. superba* in the Lazarev Sea over the course of the year:

- During the open water season, the vertical distribution of Antarctic krill comprises the euphotic zone, the depth range of diurnal vertical migration increasing towards the end of the season;
- as soon as a biologically mature pack-ice cover has developed, a large proportion of the population concentrates in the ice-water interface layer at night and migrates down to depths of several hundred meters at day;
- in the melting season, krill continue to concentrate under ice floes, but as this habitat vanishes subsequently forage on the rich phytoplankton bloom of the shallow mixed layer in the marginal ice zone. At this time, diurnal vertical migration ceases or may be inverted within a shallow depth range.



▲ **Figure 4.** Tentative course of the seasonal and diurnal change in vertical dispersal of Antarctic krill in the Lazarev Sea. During diurnal vertical migration (**DVM**) krill are near the surface at night (**N**) and migrate to greater depth at day (**D**). Hatched areas indicate concentrations of major parts of the population. **Bold arrows** indicate more dispersed distribution. **Dotted area** indicates absence of DVM.

Although the data presented in Chapter 8 provide some evidence for this proposed annual course of vertical dispersal, important questions in this context remain to be considered. For example, the true extent of the diurnal vertical migration in autumn and winter could not be resolved with the 200 m depth limit of the standard CCAMLR midwater sampling protocol we applied. Partly based on data collected in the Lazarev Sea (Siegel et al. 2004), Siegel (2005) assumed that diurnal vertical migration would reach below the standard sampling depth of 200 m in autumn, down to a maximum depth of 350 m in winter. Furthermore, the spatial resolution of the sampling scheme and the applied net sampling approach were unlikely to detect the effect of swarming behaviour. In summer 2007 / 2008 surface swarms of Antarctic krill were seen in the marginal ice zone and in the open ocean to the north. Swarming is an important and utterly complex component of the life strategy of *E. superba* (e.g. Watkins 2000). For a profound understanding of the distribution of krill in relation to depth, sea ice and other environmental factors, observations of the spatial distribution, density and size of krill swarms are essential. This could be achieved by using e.g. sonar technology, autonomous underwater vehicles equipped with optical or acoustic sensors, or aerial surveys of surface swarms.

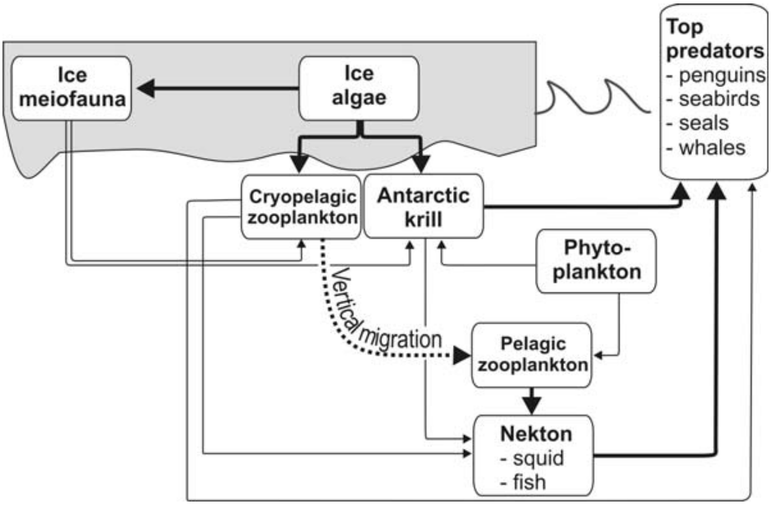


▲ **Figure 5.** Mean integrated biomass of Antarctic krill [kg km^{-2}] and mean food demand [kg m^{-2} day^{-1}] of the top predator community within the seasonal sea ice zone along the 0° meridian between 62°S and 71°S in the Lazarev Sea in summer 2007 / 2008. Krill were sampled with surface nets (SUIT: **0 – 2 m**; in light grey) and midwater nets (RMT: **0 – 200 m**; in dark grey). Values of krill biomass increase downwards.

10.4 Challenging the dominant role of krill in the pack-ice food web?

The results of Chapter 7 and 8 demonstrate that aggregations of krill and other species under ice are not limited to the marginal ice zone, but are common throughout the seasonal sea ice zone. These findings confirm the assumption with quantitative evidence that in the pack-ice pelagic life concentrates at the underside of the ice (Ainley et al. 1986; Marchant & Murphy 1994). Possibly due to this wide distribution of under-ice resources, the abundance and total food demand of top predators in the Lazarev Sea remained high throughout the seasonal sea ice zone, as exemplified for the summer situation in the Lazarev Sea in Figure 5 (van Franeker, unpublished data). Conversely, food availability in the form of Antarctic krill was at a similar level in closed pack-ice and open water areas. Notably, only the combination of surface layer- plus midwater data could reveal the persistence of high krill biomass in the closed pack-ice (Figure 5). This zone would have appeared deprived of Antarctic krill based on the standard water column sampling used for scientific stock estimates by CCAMLR.

Does the dominance of Antarctic krill under ice add new support for the pivotal role of krill in the food web of the Antarctic seasonal sea ice zone? In order to address this question, a closer look must be taken at the trophic processes connecting the sea ice, the pelagic system and the top predators. Two trophic pathways are considered to play a major role in the energy transmission from the primary producers to the top predators: 1) via Antarctic krill (the 'classic' krill-dominated food chain); 2) via mesozooplankton (mainly copepods), fish and squid (reviewed in Knox 2007). Both



▲ **Figure 6.** Energy flow through a simplified food web in the Antarctic seasonal sea ice zone. Bold arrows indicate major trajectories of energy transmission. Energy is transmitted from sea ice biota to Antarctic krill and cryopelagic zooplankton, such as the temporarily sympagic copepods and amphipods. These animals become a part of the pelagic zooplankton by means of vertical migration. Pelagic zooplankton is consumed by fish and squid. From the nekton, energy is transmitted to the warm-blooded top predators. Alternatively, energy can flow to the top predators through Antarctic krill, either by means of direct consumption or through fish and squid.

food chains interact at various trophic levels and are probably equally productive in energetic terms (Chapter 4). With the ability to directly sample the ice-water interface layer, a link between the ice and the krill-centered pathway was demonstrated in Chapter 8. However, a disproportionately low overall biomass of *E. superba* compared to the concomitant top predator food demand for example shown in Figure 5 may imply that Antarctic krill only accounts for a limited proportion of the food necessary to support the top predators of the Lazarev Sea. Many birds and mammals of the Lazarev Sea rely predominantly on fish and squid (van Franeker et al. 2001; Ainley et al. 2003; Luque et al. 2007). We found some of the most typical nektonic prey species of these top predators under the pack-ice. However, their quantities were too low to indicate a meaningful trophic link between the sea ice system and warm-blooded predators. The true abundance of fast-swimming nekton, however, may have been underestimated due to net avoidance (Chapter 7). Furthermore, the total amount of energy bound in fish can be assumed to be in a range similar to that of krill in the Lazarev Sea (Chapter 3, Chapter 4).

Alternatively, the trophic relationship between the sea ice community and nekton species might be indirect. Many prey species of *E. antarctica* are known to occur also under sea ice and can allocate energy into the pelagic food web by means of diurnal vertical migration (Chapter 4). Especially copepods that shift between a pelagic and a sympagic mode of life, such as *Stephos longipes* and *Paralabidocera antarctica*, may act as trophic vectors between the sea ice and the mesopelagic fishes feeding on them (Schnack-Schiel 2003). Such a vertical energy transmission may be further enhanced by the vertical migration of the fishes themselves. In addition to such a function as a vertical energy vector, their high energy storage capacity enables lanternfishes to allocate energy over time, supplying energy accumulated during more productive periods of the year at times when resources are scarce (Chapter 4).

In conclusion, the relevance of fish in the energy budget of the Lazarev Sea and in the diet composition of many bird and mammal species suggests that the importance of fish and squid for Antarctic top predators is at least equal to that of Antarctic krill (Chapter 4). At the same time, the concentration of krill under ice illustrates the importance of the ice-water interface layer as a site of energy transmission from the sea ice into the pelagic food web. Figure 6 visualizes these processes in a simplified way. Appropriate investigations of both mesozooplankton and nekton in the ice-water interface layer are necessary to shed further light on the relevance of the ice for the copepod – fish / squid – top predator pathway.

10.5 Lessons for the future

Over the past decade the conceptual view of the ecosystem of the Antarctic seasonal sea ice zone has changed from the idea of a simple trophic structure with spatially and temporary very limited peaks of production to a system that is comparable in complexity with other high-latitude marine ecosystems and that is productive over large areas virtually year-round (Knox 2007). The work compiled in this thesis adds further evidence for a complex and productive Antarctic seasonal sea ice zone. In particular, new insights were gained on the role of the ice-water interface layer as a functional node between the sea ice and the pelagic food web.

If significant parts of the Southern Ocean ecosystem depend on the sea ice habitat, major changes in the structure, spatial and temporal extent of the annual ice cover in the Southern Ocean will considerably affect its unique composition of biota and its biological capacity. In order to predict the reaction of life in the Antarctic seasonal sea ice zone to a warming climate, however, a concise understanding of the mechanisms driving the sea ice ecosystem is urgently needed. In spite of the progress made in recent years, the role of several important components of the Antarctic pack-ice ecosystem is still not understood with sufficient accuracy. These include, for example, the quantification of fish and squid and their relationship with the sea ice community, and the role of the microbial loop.

In a deep-water environment such as the Lazarev Sea, various processes can be expected to link the near-surface waters and the extensive deep-sea habitat underneath, including the benthic community. These include vertical and horizontal migration patterns, seasonal patterns in the life strategies and the ontogeny of species at various trophic levels, the recycling of organic matter through the microbial loop and the advection of nutrients and organisms by ocean currents. It is necessary to better understand these processes in order to assess the biological capacity of the Antarctic seasonal sea ice zone in a scientifically profound way. For example, biogeochemical tracers may be used to follow the signal of sea ice production through the pelagic food web. If successful, such an approach would be a decisive step towards a well-founded estimate of the overall importance of ice algal primary production in the food web of the Antarctic seasonal sea ice zone.

Evidently, major advances with respect to functional processes in the food web can only be expected from multidisciplinary research. In this context, the multidisciplinary approach of the LAKRIS programme can be considered a successful example of integrated research initiatives. Several studies of this thesis demonstrate that statistical models can help to link the distribution of ecological key species to a limited set of environmental predictors. This illustrates how the inclusion of datasets from different research disciplines helps to understand patterns in the distribution of species which would otherwise have been left to speculation (Chapter 5, 7, 8). Modeling techniques can be a useful tool to assess the reaction of the ecosystem to a changing environment when they are applied to large-scale datasets. Due to the intrinsic limitations of statistical models, however, field data remain the key to our understanding of the seasonal sea ice zone ecosystem.

The Arctic Ocean is experiencing the most dramatic decline in sea ice extent today (Serreze et al. 2007). It is one of the fundamental differences between the Arctic and the Antarctic sea ice habitats, that the Arctic pack-ice has been dominated by thick, multi-year ice, whereas most of the Antarctic ice cover melts away in summer (Parkinson 2006). With the predicted disappearance of summer ice, the Arctic sea ice ecosystem is likely to become more similar to the Antarctic system in the future. Thus, a profound analysis of the relevance of the annual sea ice for the biological capacity of the Antarctic seasonal sea ice zone ecosystem may also allow estimating future change in the biological performance of the Arctic Ocean.

Currently, the region of the Antarctic Peninsula is experiencing one of the highest temperature rises on earth caused by global warming. As a consequence, the distribution ranges of species begin to alter, and serious changes in the marine ecosystems are starting to become visible. Much of the ecological change has been attributed to the decline of sea ice (Clarke et al. 2007). The region hosts the largest stocks of Antarctic krill and is also the key area of commercial fishing and touristic activities. With a further shrinking of the annual sea ice cover, krill and other sea ice dependent biological resources can be expected to decline (Atkinson et al. 2004). The consequences of anthropogenic climate change will thus not only alter the ecosystem but also affect its economic potential. In contrast, the vast areas of the seasonal sea ice zone off the eastern part of the Antarctic continent show no sign of a decline in sea ice until now (Zwally et al. 2002). But with a predicted temperature rise of 2 - 4°C in the course of this century, global warming will inevitably also distress these areas (IPCC 2007). The ability to anticipate the expected changes of the ecosystem under changing sea ice conditions will be fundamentally important, both from a conservation and resource management point of view.

In the Southern Ocean, unique climatic conditions and an effective ecological isolation promoted the evolution of a species community that has no match elsewhere on the planet. Its remote position and a harsh climate protected this environment to some extent from an occupation for human needs that has by now severely distressed at least 41 % of the marine ecosystems on earth (Halpern et al. 2008). The peculiarity of Antarctic life is closely linked with the widespread presence of sea ice. The ice symbolizes not only the harshness, but also the distinctive beauty and the fragility of Antarctic nature. Its esthetic charisma in combination with a relative pristine state of nature have been impressing and inspiring visitors from the early explorers to today's tourists, fishermen and scientists. The high prevalence of Antarctic nature in literature and popular media as well as a growing tourism in the South Polar Region support the notion that the relatively untouched nature, as it appears in Antarctica, has an intrinsic value to people.

Such intrinsic value of nature is stated as a guiding principle by the United Nations Convention on Biodiversity (UNCED 1992). However, it has been under-represented in the scientific discussion related to biodiversity and conservation management over the past decades. Instead, scientists have increasingly endorsed the concept of "ecosystem services" to justify the need for research in this field. This concept defines the benefit of nature conservation in economic terms, such as nutritional, pharmaceutical and genetic resource availability or recreational value (Rozzi 2007). This utilitarian approach to ecological problems has proved to be a successful tool in the socio-economic context of contemporary science funding. However, disregarding the underlying ethical concern has led to an underdeveloped ethical consensus with respect to marine conservation by both scientists and decision makers. Such indecision underlies many justification conflicts, for example with respect to the designation of Marine Protected Areas (Sloan 2002). It therefore appears timely to increase the role of ethical considerations in the context of research and conservation (Rozzi 2007).

In spite of their pristine appearance, Antarctic ecosystems have experienced almost two centuries of human exploitation and are suffering from the global effects of anthropogenic pollution and climate change. The ecosystem-based fisheries management applied by CCAMLR addresses this issue with a precautionary approach. The underlying principle implies that the exploitation of a natural resource is minimized to a precautionary limit as long as the role of the resource in the ecosystem is not fully understood (Constable et al. 2000; Kock et al. 2007). Given that the Antarctic pack-ice ecosystem is even less well understood than most other marine ecosystems, continuous moderation in the use of its natural resources seems highly warranted. Such ongoing restraint can only be pursued with success if it roots in a broad social recognition of the intrinsic value of Antarctic nature.

Key refererences

- Arndt CE, Swadling KM (2006) Crustacea in Arctic and Antarctic sea ice: Distribution, diet and life history strategies. Advances in Marine Biology 51:197-315
- Clarke A, Murphy EJ, Meredith MP, King JC, Peck LS, Barnes DKA, Smith RC (2007) Climate change and the marine ecosystem of the western Antarctic Peninsula. Philosophical Transactions of the Royal Society B-Biological Sciences 362:149-166
- IPCC (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, IPCC, Geneva
- Marchant HJ, Murphy EJ (1994) Interactions at the base of the Antarctic food web. In: El-Sayed SZ (ed) Southern Ocean Ecology. Cambridge University Press, Cambridge, p 267-285
- Sloan NA (2002) History and application of the wilderness concept in marine conservation. Conservation Biology 16:294-305

References

Ainley DG, Jacobs SS (1981) Sea-bird affinities for ocean and ice boundaries in the Antarctic. Deep Sea Research Part a 28 (10):1173-1185

Ainley DG, O'Connor EF, Boekelheide RJ (1984) The marine ecology of birds in the Ross Sea, Antarctica. Ornithological Monographs 32:1-97

Ainley DG, Fraser WR, Sullivan CW, Torres JJ, Hopkins TL, Smith WO (1986) Antarctic mesopelagic micronekton: Evidence from seabirds that pack ice affects community structure. Science 232:847-849

Ainley DG, DeMaster DP (1990) The upper trophic levels in polar marine ecosystems. In: Smith I, Walker O (eds) Polar oceanography. Academic Press, London, p 599-630

Ainley DG, Fraser WR, Smith WOJ, Hopkins TL, Torres JJ (1991) The structure of upper level pelagic food webs in the Antarctic: effect of phytoplankton distribution. Journal of Marine Systems 2:111-122

Ainley DG, Ribic CA, Fraser WR (1992) Does prey preference affect habitat choice in Antarctic seabirds? Marine Ecology Progress Series 90:207-221

Ainley DG, Ribic CA, Fraser WR (1994) Ecological structure among migrant and resident seabirds of the Scotia-Weddell Confluence region. Journal of Animal Ecology 63:247-364

Ainley DG, Jacobs SS, Ribic CA, Gaffney I (1998) Seabird distribution and oceanic features of the Amundsen and southern Bellingshausen seas. Antarctic Science 10 (2):111-123

Ainley DG, Ballard G, Barton KJ, Karl BJ, Rau GH, Ribic CA, Wilson PR (2003a) Spatial and temporal variation of diet within a presumed metapopulation of Adelie Penguins. Condor 105 (1):95-106

Ainley DG, Tynan CT, Stirling I (2003b) Sea ice: a critical habitat for polar marine mammals and birds. In: Thomas DN, Dieckmann G (eds) Sea ice - an introduction to its physics, chemistry, biology and geology. Blackwell Science, Oxford, p 240-266

Ainley DG, Ballard G, Karl BJ, Dugger KM (2005) Leopard seal predation rates at penguin colonies of different size. Antarctic Science 17 (3):335-340

Alonzo SH, Mangel M (2001) Survival strategies and growth of krill: avoiding predators in space and time. Marine Ecology Progress Series 209:203-217

Andersen NG (1999) The effects of predator size, temperature, and prey characteristics on gastric evacuation in whiting. Journal of Fish Biology 54:287-301

Andersen NG (2001) A gastric evacuation model for three predatory gadoids and implications of using pooled field data of stomach contents to estimate food rations. Journal of Fish Biology 59:1198-1217

Andres H, Lörz A, Brandt A (2002) A common, but undescribed huge species of *Eusirus* Krøyer, 1845 (Crustacea, Amphipoda, Eusiridae) from Antarctica. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 99:109–126

Anthony JA, Roby DD, Turco KR (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Journal of Experimental Marine Biology and Ecology 248 (1):53-78

Arndt CE, Swadling KM (2006) Crustacea in Arctic and Antarctic sea ice: distribution, diet and life history strategies. Advances in Marine Biology 51:197-315

Arndt I, Lieckfeld CP (2005) Logbuch Polarstern. Friedeking & Thaler, Munich

Arnould JPY, Whitehead MD (1991) The diet of Antarctic Petrels, Cape Petrels and Southern Fulmars rearing chicks in Prydz Bay. Antarctic Science 3 (1):19-27

Arntz WE, Gutt J, Klages M, Battaglia B, Valencia J, Walton DWH (1997) Antarctic marine biodiversity: an overview. In: Antarctic communities, species structure and survival. Cambridge University Press, Cambridge, p 3-14

Arrigo KR, Robinson DH, Sullivan CW (1993) A high resolution study of the platelet ice ecosystem in McMurdo Sound, Antarctica: photosynthetic and bio-optical characteristics of a dense microalgal bloom. Marine Ecology Progress Series 98:173-185

Arrigo KR, Dieckmann G, Gosselin M, Robinson DH, Fritsen CH, Sullivan CW (1995) High resolution study of the platelet ice ecosystem in McMurdo Sound, Antarctica: biomass, nutrient and production profiles within a dense microalgal bloom. Marine Ecology Progress Series 127:255-268

Arrigo KR, Worthen DL, Lizotte MP, Dixon P, Dieckmann G (1997) Primary production in Antarctic sea ice. Science 276:394-397

Arrigo KR, Worthen D, Schnell A, Lizotte MP (1998) Primary production in Southern Ocean waters. Journal of Geophysical Research-Oceans 103 (C8):15587-15600

Arrigo KR, Thomas DN (2004) Large scale importance of sea ice biology in the Southern Ocean. Antarctic Science 16:471-486

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432 (7013):100-103

Atkinson A, Siegel V, Pakhomov EA, Rothery P, Loeb V, Ross RM, Quetin LB, Schmidt K, Fretwell P, Murphy EJ, Tarling GA, Fleming AH (2008) Oceanic circumpolar habitats of Antarctic krill. Marine Ecology Progress Series 362:1-23

Bajkov AD (1935) How to estimate the daily food consumption of fish under natural conditions. Transcripts of the American Fisheries Society 65:288-289

Baker AdC (1959) The distribution and life history of *Euphausia triacantha* Holt and Tattersall. Discovery Reports 29:309-340

Barnard J, Karaman G (1991) The families and genera of marine gammaridean Amphipoda (except marine gammaroids), Part 1,2. Records of the Australian Museum Supplement 13:1–866

Barnes DKA, Kaiser S, Griffiths HJ, Linse K (2008) Marine, intertidal, freshwater and terrestrial biodiversity of an isolated polar archipelago. Journal of Biogeography DOI: 10.1111/j.1365-2699.2008.02030.x

Barrera-Oro, E., Casaux, R. y Roux, A. (1997) Diet composition of *Champsocephalus gunnari* in the Subarea 48.3, Dr. Eduardo Holmberg Survey, February/March 1994. Boletín del Instituto de Investigaciones y Desarrollo Pesquero (INIDEP) 11: 53-62

Barrera-Oro E (2002) The role of fish in the Antarctic marine food web: differences between inshore and offshore waters in the southern Scotia Arc and west Antarctic Peninsula. Antarctic Science 14 (4):293-309

Bengston JL, Cameron MF (2004) Seasonal haulout patterns of crabeater seals (*Lobodon carcinophaga*). Polar Biology 27:344-349

Bersch M, Becker GA, Frey H, Kolterman KP (1992) Topographic effects of the Maud Rise on the stratification of the Weddell Gyre. Deep Sea Research I 39:303-331

Bester MN, Erickson AW, Ferguson JWH (1995) Seasonal change in the distribution and density of seals in the pack ice off Princess-Martha-Coast, Antarctica. Antarctic Science 7 (4):357-364

Bester MN, Odendaal PN (2000) Abundance and distribution of Antarctic pack ice seals in the Weddell Sea. In: Davison W, Howard-Williams C (eds) Antarctic ecosystems: models for wider ecological understanding. Caxton Press, Christchurch, p 51-55

Bester MN, Ferguson JWH, Jonker FC (2002) Population densities of pack ice seals in the Lazarev Sea, Antarctica. Antarctic Science 14 (2):123-127

Bluhm BA, Gradinger R, Piraino S (2007) First record of sympagic hydroids (Hydrozoa, Cnidaria) in Arctic coastal fast ice. Polar Biology 30 (12):1557-1563

Bonner WN, Laws RM (1964) Seals and sealing. In: Priestley R, Adie JR, Robin GdQ (eds) Antarctic research. Butterworths, London, p 163-190

Bost CA, Zorn T, LeMaho Y, Duhamel G (2002) Feeding of diving predators and diel vertical migration of prey: King penguins' diet versus trawl sampling at Kerguelen Islands. Marine Ecology Progress Series 227:51-61

Boyce SJ, Murray AWA., Peck LS (2000) Digestion rate, gut passage time and absorption efficiency in the Antarctic spiny plunderfish. Journal of Fish Biology 57(4): 908-929

Boysen-Ennen E, Piatkowski U (1988) Meso- and macrozooplankton communities in the Weddell Sea, Antarctica. Polar Biology 9:17-35

Brandt A (2005) Evolution of Antarctic biodiversity in the context of the past: the importance of the Southern Ocean deep sea. Antarctic Science 17 (4):509-521

Brandt A, Brix S, Brokeland W, Choudhury M, Kaiser S, Malyutina M (2007) Deep-sea isopod biodiversity, abundance, and endemism in the Atlantic sector of the Southern Ocean-Results from the ANDEEP I-III expeditions. Deep Sea Research II 54:1760-1775

Bregazzi P (1972a) Habitat selection by *Cheirimedon femoratus* (Pfeffer) and *Tryphosella kergueleni* (Miers) (Crustacea: Amphipoda). British Antarctic Survey Bulletin 31:21–31

Bregazzi P (1972b) Life cycle and seasonal movements of *Cheirimedon femoratus* (Pfeffer) and *Tryphosella kergueleni* (Miers) (Crustacea: Amphipoda). British Antarctic Survey Bulletin 30:1–34

Bregazzi P (1973) Locomotor activity rhythms in *Tryphosella kergueleni* (Miers) and *Cheirimedon femoratus* (Pfeffer) (Crustacea: Amphipoda). British Antarctic Survey Bulletin 33–34:17–32

Bray JR, Curtis JT (1957) An ordination of upland forest communities of southern Wisconsin. Ecological Monographs 27:325-349

Brierley AS, Fernandes PG, Brandon MA, Armstromg F, Millard NW, McPhail SD, Stevenson P, Pebody M, Perrett J, Squires M, Bone DG, Griffiths G (2002) Antarctic krill under sea ice: elevated abundance in a narrow band just south of ice edge. Science 295 (5561):1890-1892

Brierley AS, Thomas DN (2002) Ecology of Southern Ocean pack ice. Advances in Marine Biology 43:171-276

Calow P, Townsend CR (1981) Resource utilization in growth. In: Townsend CR, Calow P (eds) Physiological ecology: an evolutionary approach to resource use. Sinauer Associates, Sunderland, MA, p 220-244

Casaux R, Barrera-Oro E, Baroni A, Ramón A (2003a) Ecology of inshore notothenioid fish from the Danco Coast, Antarctic Peninsula. Polar Biology 26:157-165

Casaux R, Baroni A, Ramon A (2003b) Diet of Antarctic fur seals *Arctocephalus gazella* at the Danco Coast, Antarctic Peninsula. Polar Biology 26:49-54

Casaux R, Bellizia L, Baroni A (2004) The diet of the Antarctic fur seal *Arctocephalus gazella* at Harmony Point, South Shetland Islands: evidence of opportunistic foraging on penguins? Polar Biology 27:59-65

Casaux R, Baroni A, Ramon A (2006) The diet of the weddell seal *Leptonychotes weddellii* at the Danco Coast, Antarctic Peninsula. Polar Biology 29 (4):257-262

CCAMLR (1982) Convention on the Conservation of Antarctic Marine Living Resources. CCAMLR, Hobart

CCAMLR (2008) Estimates of IUU toothfish catches (tonnes) in the CCAMLR Convention Area from the 1996/97 to the 2005/06 fishing seasons. http://www.ccamlr.org/pu/E/sc/fish-monit/iuu-est-table.pdf, Accessed 2008/12/16

Chapman EW, Ribic CA, Fraser WR (2004) The distribution of seabirds and pinnipeds in Marguerite Bay and their relationship to physical features during austral winter 2001. Deep Sea Research II 51:2261-2278

Chen LB, DeVries AL, Cheng CHC (1997) Convergent evolution of antifreeze glycoproteins in Antarctic notothenioid fish and Arctic cod. Proceedings of the National Academy of Sciences of the United States of America 94 (8):3817-3822

Cherel Y, Ridoux V (1992) Prey species and nutritive value of food fed during summer to king penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. Ibis 134:118-127

Cherel Y, Kooyman GL (1998) Food of emperor penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctica. Marine Biology 130 (3):335-344

Cisewski B, Strass VH, Prandke H (2005) Upper-ocean vertical mixing in the Antarctic Polar Front Zone. Deep Sea Research II 52 (9-10):1087-1108

Cisewski B, Strass VH, Losch M, Prandke H (2008) Mixed layer analysis of a mesoscale eddy in the Antarctic Polar Front Zone. Journal of Geophysical Research - Oceans 113 (C05017) DOI: 10.1029/2007JC004372

Clarke A, Prince PA (1980) Chemical composition and calorific value of food fed to Mollymauk chicks *Diomedea melanophris* and *Diomedea Chrysostoma* at Bird-Island, South Georgia. Ibis 122 (4):488-494

Clarke A, Murphy EJ, Meredith MP, King JC, Peck LS, Barnes DKA, Smith RC (2007) Climate change and the marine ecosystem of the western Antarctic Peninsula. Philosophical Transactions of the Royal Society B-Biological Sciences 362 (1477):149-166

Clarke A, Tyler PA (2008) Adult Antarctic krill feeding at abyssal depths. Current Biology 18 (4):282-285

Collins MA, Rodhouse PGK (2006) Southern Ocean Cephalopods. Advances in Marine Biology 50:191-265

Collins MA, Xavier JC, Johnston NM, North AW, Enderlein P, Tarling GA, Waluda CM, Hawker EJ, Cunningham NJ (2008) Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. Polar Biology 31:837-851

Connan M, Cherel Y, Mabille G, Mayzaud P (2007) Trophic relationships of white-chinned petrels from Crozet Islands: combined stomach oil and conventional dietary analyses. Marine Biology 152:95-107

Constable AJ, de la Mare WK, Agnew DJ, Everson I, Miller D (2000) Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). ICES Journal of Marine Science 57 (3):778-791

Coria, NR, Montalti D (2000) A newly discovered breeding colony of Emperor Penguins *Aptenodytes forsteri*. Marine Ornithology 28, 119–120.

Craven M, Carsey F, Nicol S (2006) Short note - Ice krill under the Amery Ice Shelf, East Antarctica. Antarctic Science 18 (1):81-82

Crawford RE (1978) Digestive system morphology, gastric evacuation rates and energetics in Antarctic Notothenia. University of Maine, USA

Creet S, Van Franeker JA, Van Spanje TM, Wolff WJ (1994) Diet of the Pintado Petrel *Daption capense* at King George Island, Antarctica, 1990/91. Marine Ornithology 22:221-229

Croxall JP, Prince A, Rickets C (1985) Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. In: Siegfried W, Condy P, Laws R (eds) Antarctic nurient cycles and food webs. Springer Verlag, Berlin

Croxall JP, Trathan PN, Murphy EJ (2002) Environmental change and Antarctic seabird populations. Science 297 (5586):1510-1514

Croxall JP (2004) Management of Southern Ocean fisheries: global forces and future sustainability. Antarctic Science 16 (4):569-584

Cruz M, Gabor N, Mora E, Jimenez R, J. M (2003) The known and unknown about marine biodiversity in Ecuador (Continental and Insular) Gayana 67 (2):232-260

Daly KL (2004) Overwintering growth and development of larval *Euphausia superba*: an interannual comparison under varying environmental conditions west of the Antarctic Peninsula. Deep Sea Research II 51:2139-2168

Daniels RA (1982) Feeding ecology of some fishes of the Antarctic Peninsula. Fisheries Bulletin 80(3):575-588

Dauby P, Scailteur Y, Chapelle G, De Broyer C (2001) Potential impact of the main benthic amphipods on the eastern Weddell Sea shelf ecosystem (Antarctica). Polar Biology 24:657–662

Davey F (2007) Southern Ocean: Bathymetry. In: Riffenburgh B, Cruwys L (eds) Encyclopedia of the Antarctic. Taylor & Francis Group, New York, p 938-942

De Broyer C (1983) Recherches sur la systématique et l’evolution des crustacés amphipodes gammarides antarctiques et subantarctiques. Universite´ Catholique de Louvain, Faculte´ des Sciences, Louvain-la-Neuve.

De Broyer C, Jazdzewski K (1993) Contribution to the marine biodiversity inventory: a checklist of the Amphipoda (Crustacea) of the Southern Ocean. Studiedocumenten van het KBIN (73):1-154

De Robertis A (2002) Size-dependent visual predation risk and the timing of vertical migration: an optimization model. Limnology and Oceanography 47 (4):925-933

Dell RK (1972) Antarctic benthos. Advances in Marine Biology 10:1-216

DeWitt HH (1970) The character of the midwater fish fauna of the Ross Sea, Antarctica. In: Holdgate MW (ed) Antarctic Ecology, Vol 1. Academic Press, London

di Prisco G, Cocca E, Parker SK, Detrich HW (2002) Tracking the evolutionary loss of hemoglobin expression by the white-blooded Antarctic icefishes. Gene 295 (2):185-191

Donnelly J, Torres JJ, Hopkins TL, Lancraft TM (1990) Proximate composition of Antarctic mesopelagic fishes. Marine Biology 106:13-23

Donnelly J, Torres JJ, Hopkins TL, Lancraft TM (1994) Chemical composition of Antarctic zooplankton during austral fall and winter. Polar Biology 14 (3):171-183

Donnelly J, Torres JJ, Sutton TT, Simoniello C (2004) Fishes of the eastern Ross Sea, Antarctica. Polar Biology 27 (11):637-650

Donnelly JJ, Sutton TT, Torres JJ (2006) Distribution and abundance of micronekton and macrozooplankton in the NW Weddell Sea: relation to a spring ice-edge bloom. Polar Biology 29 (4):280-293

Dos Santos J, Jobling M (1995) Test of a food consumption model for the Atlantic cod. ICES Journal of Marine Science 52:209-219

Dufrene M, Legendre P (1997) Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67 (3):345-366

Duhamel G, Hureau JC (1985) The role of zooplankton in the diets of certain sub-Antarctic marine fish. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer Press, Berlin, Heidelberg, pp 421-436

Duhamel G, Koubbi P, Ravier C (2000) Day and night mesopelagic fish assemblages off the Kerguelen Islands (Southern Ocean). Polar Biology 23:106-112

Eastman JT, Clarke A (1998) A comparison of adaptive radiations of Antarctic fish with those of non-Antarctic fish. In: DiPrisco G, Pisano E, Clarke A (eds) Fishes of Antarctica: a biological overview. Springer Verlag Italia, Milan, p 3-26

Eastman JT, Eakin RR (2000) An updated species list for notothenioid fish (Perciformes: Notothenioidei), with comments on Antarctic species. Archive of Fisheries and Marine Research 48:11-20

Eastman JT, Sidell BD (2002) Measurements of buoyancy for 13 species of Antarctic notothenioid fishes from the South Shetland Islands. Polar Biology 25:753-760

Eastman JT (2005) The nature of the diversity of Antarctic fishes. Polar Biology 28:93-107

Eder EB, Lewis MN (2005) Proximate composition and energetic value of demersal and pelagic prey species from the SW Atlantic Ocean. Marine Ecology Progress Series 291:43-52

Efremenko V (1991) Ichthyoplankton studies in the Lazarev Sea. Journal of Ichthyology 32 (3):129-133

Eicken H (1992) The role of sea ice in structuring Antarctic ecosystems. Polar Biology 12:3-13

Eicken H (2007) Sea ice: crystal texture and microstructure. In: Riffenburgh B, Cruwys L (eds) Encyclopedia of the Antarctic. Taylor & Francis Group, New York, p 840-845

Elliott JM, Persson L (1978) The estimation of daily rates of food consumption for fish. Journal of Animal Ecology 47:977-991

El-Sayed SZ (1994) History, organization and accomplishments of the BIOMASS programme. In: El-Sayed S (ed) Southern Ocean ecology. Cambridge University Press, Cambridge, p 1-10

Erickson AW, Hanson MB, Kehoe DM (1983) Population densities of seals and whales observed during the 1983 circumnavigation of Antarctica by the USCGC POLAR STAR. Antarctic Journal of the US 18:163-166

Erickson AW, Bledsoe LJ, Hanson MB (1989) Bootsrap correction for diurnal activity cycle in census data for Antarctic seals. Marine Mammal Science 51 (1):29-56

Erickson AW, Hanson MB (1990) Continental estimates and population trends of Antarctic ice seals. In: Kerry KR, Hempel G (eds) Antarctic ecosystems Ecological change and conservation. Springer-Verlag, Berlin Heidelberg New York, p 253-264

Erickson AW, Siniff DB, Harwood J (1993) Estimation of population sizes. In: Laws RM (ed) Antarctic seal research methods and techniques. Cambridge University Press, Cambridge, NY, p 29-45

Everson I (1977) The living resources of the Southern Ocean. GLO/S0/77/1, Food and Agriculture Organization, Rome

Everson I (2000) The distribution of standing stock - the Southern Ocean. In: Everson I (ed) Krill - biology, ecology and fisheries. Blackwell Science Ltd., London, p 63-79

Fisher EC, Kaufmann RS, Smith KLJ (2004) Variability of epipelagic macrozooplankton/micronekton community structure in the NW Weddell Sea, Antarctica (1995-1996). Marine Biology 144 (2):345-360

Foster B (1987) Composition and abundance of zooplankton under the spring sea-ice of McMurdo Sound, Antarctica. Polar Biology 8:41–48

Fox J (2008) car: Companion to Applied Regression. R package version 1.2-8

Fraser WR, Ainley DG (1986) Ice edges and seabird occurrence in Antarctica. Bioscience 36 (4):258-263

Frolkina ZA (2002) Distribution of mackerel icefish (*Champsocephalus gunnari*) (Channichthyidae) around South Georgia at various stages of its life cycle. Commission for the Conservation of Antarctic Marine Living Resources CCAMLR Science 9:49-69

Froneman PW, Pakhomov EA, Perissinotto R, McQuaid CD (2000) Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer 1993 - Part 2. Biochemical zonation. Deep Sea Research I 47 (9):1687-1702

Gabriel W, Thomas B (1988) Vertical migration of zooplankton as an evolutionarily stable strategy. American Naturalist 132 (2):199-216

Gannefors C, Boer M, Kattner G, Graeve M, Eiane K, Gulliksen B, Hop H, Falk-Petersen S (2005) The Arctic sea butterfly *Limacina helicina*: lipids and life strategy. Marine Biology 147 (1):169-177

Garrison D (1991) Antarctic sea ice biota. American Zoologist 31:17–33

Geiger SP, Donnelly J, Torres JJ (2000) Effect of the receding ice-edge on the condition of mid-water fishes in the northwestern Weddell Sea: results from biochemical assays with notes on diet. Marine Biology 137:1091-1104

Gill AE (1973) Circulation and bottom water production in Weddell Sea. Deep Sea Research 20 (2):111-140

Gjosaeter J, Kawaguchi K (1980) A review of the world resources of mesopelagic fish. FAO Fisheries Technical Papers 193:1-151

Gon O (1990) Bathylagidae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahamstown, p 107-110

Gonzalez AF, Rodhouse PG (1998) Fishery biology of the seven star flying squid *Martialia hyadesi* at South Georgia during winter. Polar Biology 19 (4):231-236

Gordon AL, Huber BA (1995) Warm Weddell deep water west of Maud Rise. Journal of Geophysical Research - Oceans 100 (C7):13747-13753

Graeve M, Dauby P, Scailteur Y (2001) Combined lipid, fatty acid and digestive tract content analyses: a penetrating approach to estimate feeding modes of Antarctic amphipods. Polar Biology 24:853–862

Granata A (2002) Ichthyoplankton abundance and distribution in the Ross Sea during 1987-1996. Polar Biology 25 (3):187-202

Grant S, Constable A, Raymond B, Doust S (2006) Bioregionalisation of the Southern Ocean: Report of Experts Workshop, WWF-Australia and ACR CRC, Hobart, September 2006

Greely T, Gartner JVJ, Torres JJ (1999) Age and growth of *Electrona antarctica* (Pisces: Myctophidae), the dominant mesopelagic fish of the Southern Ocean. Marine Biology 133:145-158

Green K, Williams R (1986) Observations on food remains in faeces of elephant, leopard and crabeater seals. Polar Biology 6 (1):43-45

Gregg W, Casey N (2007) Modeling Coccolithophores in the Global Oceans. Deep Sea Research II 54:447-477

Griffiths HJ, Linse K, Barnes DKA (2008) Distribution of macrobenthic taxa across the Scotia Arc, Southern Ocean. Antarctic Science 20 (3):213-226

Gröhsler T (1992) Nahrungsökologische Untersuchungen an antarktischen Fischen um Elephant Island unter besonderer Berücksichtigung des Südwinters. Mitteilungen des Instituts für Seefischerei 47:1 -296

Gross L (2007) As the Antarctic ice pack recedes, a fragile ecosystem hangs in the balance. PLoS Biology 3 (4):0557-0561

Grossmann S, Dieckmann GS (1994) Bacterial standing stock, activity, and carbon production during formation and growth of sea-ice in the Weddell Sea, Antarctica. Applied and Environmental Microbiology 60 (8):2746-2753

Gulliksen G, Lønne OJ (1991) Sea ice macrofauna in the Antarctic and the Arctic. Journal of Marine Systems 2:53-61

Gutt J, Siegel V (1994) Benthopelagic aggregations of krill (*Euphausia superba*) on the deeper shelf of the Weddell Sea (Antarctic). Deep Sea Research I 41 (1):169-178

Haas C, Hendricks S, Doble M (2007a) Comparison of the sea ice thickness distribution in the Lincoln Sea and adjacent Arctic Ocean in 2004 and 2005. Annals of Glaciology 44, 247-252

Haas C, Nikolaus M, Batzke A, Willmes S, Lobach J (2007b) Changes in sea ice physical properties during the onset of melt. In: El Naggar, S., Dieckmann, G., Haas, C., Schröder, M., Spindler, M. (Eds.), The Expeditions ANTARKTIS-XXII/1 and XXII/2 of the Research Vessel “Polarstern” in 2004/2005. Reports on Polar and Marine Research 551 p 71–102

Hagen W (2001) Lipid metabolism of the Antarctic krill *Euphausia superba* and its ecological implications. Marine Biology 139 (1):95-104

Hahn S (1998) The food and chick feeding of blackbellied stormpetrel (*Fregatta tropica*) at King George Island, South Shetlands. Polar Biology 19:354-357

Hall-Aspland SA, Rogers TL (2004) Summer diet of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. Polar Biology 27 (12):729-734

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. Science 319 (5865):948-952

Hamner W (1982) Procedures for in situ observations of krill schools in the Southern Ocean. Antarctic Journal of the US 8:165

Harder M, Fischer H (1999) Sea ice dynamics in the Weddell Sea simulated with an optimized model. Journal of Geophysical Research-Oceans 104 (C5):11151-11162

Hardy A, Günther E (1935) The plankton of the South Georgia whaling grounds and adjacent waters, 1926-1927. Discovery Reports No 1

Hartmann KJ, Brandt SB (1995) Estimating energy density of fish. Transactions of the American Fisheries Society 124:347-355

Hastie T, Tibshirani R (1995) Generalized additive models. Standford University

Hellmer H, Haas C, Dieckmann G, Schröder M (2006) Sea ice feedbacks observed in western Weddell Sea. EOS Transactions 87 (18):173-179

Hellmer H, Schröder M, Haas C, Dieckmann G, Spindler M (2008) The ISPOL drift experiment. Deep Sea Research II 55 (8-9):913-917

Hempel G (1985) Antarctic marine food webs. In: Siegfried W, Condy P, Laws R (eds) Antarctic nutrient cycles and food webs. Springer Press, Berlin, p 267-270

Hernandez-Leon S, Portillo-Hahnefeld A, Almeida C, Becognee P, Moreno I (2001) Diel feeding behaviour of krill in the Gerlache Strait, Antarctica. Marine Ecology Progress Series 223:235-242

Hewitt RP, Linen Low EH (2000) The fishery on Antarctic krill: defining an ecosystem approach to management. Reviews in fisheries science 8 (3):235-298

Highland Statistics (2006) Brodgar. Software Package for Data Exploration, Univariate Analysis, Multivariate Analysis and Time Series Analysis, Vers. 2.5.2. Newburgh, UK

Hoddell RJ, Crossley AC, Williams R, Hosie GW (2000) The distribution of Antarctic pelagic fish and larvae (CCAMLR division 58.4.1). Deep Sea Research II 47:2519-2541

Holland DM (2001) Explaining the Weddell Polynya - a large ocean eddy shed at Maud Rise. Science 292 (5522):1697-1700

Hop H, Tonn WM (1998) Gastric evacuation rates and daily rations of Arctic cod (*Boreogadus saida*) at low temperatures. Polar Biol 19:293-301

Hop H, Poltermann M, Lønne O, Falk-Petersen S, Korsnes R, Budgell W (2000) Ice amphipod distribution relative to ice density and under-ice topography in the northern Barents Sea. Polar Biology 23:357–367

Hopkins T (1987) Midwater food web in McMurdo Sound, Ross Sea, Antarctica. Marine Biology 96:93–106

Hopkins TL, Torres JJ (1988) The zooplankton community in the vicinity of the ice edge, western Weddell Sea, March 1986. Polar Biology 9:79-87

Hopkins TL, Torres JJ (1989) Midwater food web in the vicinity of a marginal ice-zone in the western Weddell Sea. Deep Sea Research Part a - Oceanographic Research Papers 36 (4):543-560

Hopkins TL (1993) Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1988). Deep Sea Research I 40 (1):81-105

Hopkins TL, Ainley DG, Torres JJ, Lancraft TM (1993) Trophic structure in open waters of the marginal ice zone in the Scotia-Weddell confluence region during spring (1983). Polar Biology 13:389-397

Hubold G (1985) The early life-history of the high-Antarctic silverfish, *Pleuragramma antarcticum*. In: Siegfried W, Condy P, Laws R (eds) Antarctic nutrient cycles and food webs. Springer Press, Berlin, Heidelberg, p 445-451

Hubold G (1992) Zur Ökologie der Fische im Weddelmeer. Berichte zur Polarforschung 103:1-157

Hulley PA (1990) Myctophidae. In: Gon O, Heemstra P (eds) Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahamstown, p 146-178

Hunt BPV, Pakhomov EA, Trotsenko BG (2007) The macrozooplankton of the Cosmonaut Sea, east Antarctica (30ºE to 60ºE), 1987-1990. Deep Sea Research I 54:1042-1069

Hureau JC (1969) Biologie comparée de quelques poissons antarctiques (Nototheniidae). Bulletin de l'Institut Océanographique de Monaco 68:1-44

Hyslop EJ (1980) Stomach contents analyses - a review of methods and their application. Journal of Fish Biology 17:411-429

IAATO (2008) Overview of Antarctic tourism 2007-2008 Antarctic season and preliminary estimates for 2008-2009 Antarctic season. Antarctic Treaty Consultative Meeting. Kyiv, Ukraine, 2-13 June 2008

Ichii T, Bengston JL, Boveng PL, Takao Y, Jansen JK, Hiruki-Raring LM, Cameron MF, Okamura H, Hayashi T, Naganbu M (2007) Provisioning strategies of Antarctic fur seals and chinstrap penguins produce different responses to distribution of common prey and habitat. Marine Ecology Progress Series 344:277-297

IPCC (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, IPCC, Geneva

Jazdzewski K, De Broyer C, Pudlarz M, Dauby P (2000) Amphipods of a stony beach in the maritime Antarctic. Polskie Archiwum Hydrobiologii/Polish Archives of Hydrobiology 47:569–577

Jarman SN, Elliott NG, Nicol S, McMinn A (2000) Molecular phylogenetics of circumglobal *Euphausia* species (Euphausiacea : Crustacea). Canadian Journal of Fisheries and Aquatic Sciences 57:51-58

Jobling M, Gwyther D, Grove DJ (1977) Some effects of temperature, meal size and body weight on gastric evacuation time in dab *Limanda limanda* (L). Journal of Fish Biology 10:291-298

John DD (1936) The southern species of the genus *Euphausia*. Discovery Reports 14:193-324

Joiris (1991) Spring distribution and ecological role of seabirds and marine mammals in the Weddell Sea, Antarctica. Polar Biology 11:415-424

Jones CD, Kock K, Ramm D, Ashford J, Wilhelms S, Near TJ, Gong N., Flores H (2001) Results and standing stock biomass estimation of finfish from the 2001 U.S. AMLR bottom trawl survey of the South Shetland Islands (Subarea 48.1). Commisson for the Conservation of Antarctic Marine Living Resources, WG-FSA-01/33, Rev.1. 44 pp, Hobart, Australia

Jones CD, Kock KH, Wilhelms S, Near TJ a.o. (2003) Results and standing stock biomass estimation of finfish from the 2001 U.S. AMLR bottom trawl survey of the South Shetland Islands (Subarea 48.1). Commisson for the Conservation of Antarctic Marine Living Resources, WG-FSA, Hobart, Australia

Kaufmann RS, Smith JR, Baldwin RJ, Glatts RC (1993) Epipelagic communities in the northwestern Wedell Sea: results from acoustic, trawl and trapping surveys. Antarctic Journal of the United States 28:99-102

Kaufmann R, Smith KJ, Baldwin R, Glatts R, Robinson B, Reisenbichler K (1995) Effects of seasonal pack ice on the distribution of macrozooplankton and micronecton in the northwestern Weddell Sea. Marine Biology 124:387-397

Kerry KR, Clarke JR, Else GD (1995) The foraging range of Adélie Penguins at Bechervaise Island Mac. Robertson Land Antarctica as determined by satellite telemetry. In: Dann P, Norman I, Reilly R (eds) The penguins: Ecology and management Second international Penguin conference, Cowes, Victoria, Australia, Aug 1992, Beatty, Chipping Norton, NSW, Australia, p 216-243

Kiko R, Kramer M, Spindler M, Wägele H (2008a) *Tergipes antarcticus* (Gastropoda, Nudibranchia): distribution, life cycle, morphology, anatomy and adaptation of the first mollusc known to live in Antarctic sea ice. Polar Biology 31 (11):1383-1395

Kiko R, Michels J, Mizdalski E, Schnack-Schiel SB, Werner I (2008b) Living conditions, abundance and composition of the metazoan fauna in surface and sub-ice layers in pack ice of the western Weddell Sea during late spring. Deep Sea Research II 55 (8-9):1000-1014

Kirkwood R, Robertson G (1997) Seasonal change in the foraging ecology of emperor penguins on the Mawson Coast, Antarctica. Marine Ecology Progress Series 156:205-223

Klages M, Gutt J (1990) Observations on the feeding behaviour of the Antarctic gammarid *Eusirus perdentatus* Chevreux, 1912 (Crustacea: Amphipoda) in aquaria. Polar Biology 10:359–364

Klages M (1993) Distribution, reproduction and population dynamics of the Antarctic gammaridean Amphipod *Eusirus perdentatus* Chevreux, 1912 (Crustacea). Antarctic Science 5:349–359

Klatt O, Fahrbach E, Hoppema M, Rohardt G (2005) The transport of the Weddell Gyre across the Prime Meridian. Deep Sea Research II 52 (3-4):513-528

Klingenberg CP, Ekau W (1996) A combined morphometric and phylogenetic analysis of an ecomorphological trend: pelagization in Antarctic fishes (Perciformes: Nototheniidae). Biological Journal of the Linnean Society 59 (2):143-177

Knox GA (2007) Biology of the Southern Ocean. Taylor & Francis Group, New York

Kobayashi HA (1974) Growth cycle and related vertical distribution of thecosomatous pteropod *Spiratells (Limacina) helicina* in central Arctic ocean. Marine Biology 26 (4):295-301

Kock K-H (1981) Fischereibiologische Untersuchungen an drei Fischarten: *Champsocephalus gunnari* Lönnberg 1905, *Chaenocephalus aceratus* Lönnberg, 1906 und *Pseudochaenichthys georgianus* Norman 1937 (Notothenioidei, Channichthyidae). Mitteilungen des Instituts für Seefischerei 32:1–226

Kock K-H (1982) Fischereibiologische Untersuchungen bei Elephant Island im März 1981. Archiv für Fischereiwissenschaften 33 (Suppl 1):127–142

Kock K-H, Kellermann A (1991) Reproduction in Antarctic notothenioid fish – a review. Antarctic Science 3(2):125-150

Kock K-H (1992) Antarctic fish and fisheries. Cambridge University Press, Cambridge

Kock K-H, Wilhelms S, Gröger J (1994) Variations in the diet composition and feeding intensity of mackerel icefish *Champsocephalus gunnari* at South Georgia (Antarctic). Marine Ecology Progress Series 108:43-57

Kock K-H (1998) Changes in the fish biomass around Elephant Island (Subarea 48.1) from 1976 to 1998. CCAMLR Science 5:165-190

Kock K-H, Stransky C (2000) The composition of the coastal fish fauna around Elephant Island (South Shetland Islands, Antarctica). Polar Biology 23:825-832

Kock K-H, Jones CD, Wilhelms S (2001) Biological characteristics of Antarctic fish stocks in the southern Scotia Arc. CCAMLR Science 7:1–41

Kock K-H, Jones CD, v Bertouch G , Doolittle DF, la Mesa M, Pshenichnov L, Riehl R, Romeo T, Schöling S, Zane L (2002) Standing stock estimates of finfish biomass from the 2002 ‚Polarstern' bottom trawl survey around Elephant Island and the South Shetland Islands (Subarea 48.1). Commission for the Conservation of Antarctic Marine Living Resources, WG-FSA-02, 44 pp, Hobart, Australia

Kock, K-H, Everson, I (2003) Shedding new light on the life cycle of mackerel icefish in the Southern Ocean. Journal of Fish Biology 63: 1-21

Kock K-H, Jones CD (2005) Fish stocks in the southern Scotia Arc region – a review and prospects of future research. Reviews in Fisheries Science 13 (2): 75-108

Kock K-H (2005a) Antarctic icefishes (Channichthyidae): a unique family of fishes. A review, Part II. Polar Biology 28 (12):897-909

Kock K-H (2005b) Antarctic icefishes (Channichthyidae): a unique family of fishes. A review, Part I. Polar Biology 28 (11):862-895

Kock K-H, Reid K, Croxall J, Nicol S (2007) Fisheries in the Southern Ocean: an ecosystem approach. Philosophical Transactions of the Royal Society B: Biological Sciences 362 (1488):2333-2349

Kock K-H, Agnew DJ, Barrera-Oro E, Belchier M, Collins MA, Hanchet S, Pshenichnov L, Shust KV, Welsford D, Williams R (in press) The role of fish as predators of krill (*Euphausia superba*) and other pelagic resources in the Southern Ocean. CCAMLR-XXVII and SC-CAMLR-XXVII. Hobart, 10/27/2008 - 07/11/2008

Kooyman GL (2002) Evolutionary and ecological aspects of some Antarctic and sub-Antarctic penguin distributions. Oecologia 130 (4):485-495

Koubbi P, Ibanez F, Duhamel G (1991) Environmental influences on spatio-temporal oceanic distribution of ichthyoplankton around the Kerguelen Islands (Southern-Ocean). Marine Ecology Progress Series 72 (3):225-238

Kruskal JB (1964) Nonmetric Multidimensional Scaling - a numerical method. Psychometrika 29 (2):115-129

Kozlov AN, Pinskaya IA, Podrazhanskaya SG, Tarverdieva MI (1988) Feeding of glassfishes in different regions of the Atlantic sector of Antarctica. Journal of Ichthyology 28(6):137-145

Lake SE, Burton HR, Hindell MA (1997) Influence of time of day and month on Weddell seal haul-out patterns at the Vestfold Hills, Antarctica. Polar Biology 18 (5):319-324

Lalli CM, Gilmer RW (1989) Pelagic snails. The biology of holoplanktonic gastropod mollusks. Stanford University Press, Stanford, California

Lancraft TM, Torres JJ, Hopkins TL (1989) Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). Polar Biology 9:225-233

Lancraft TM, Hopkins TL, Torres JJ, Donnelly J (1991) Oceanic micronektonic / macrozooplanktonic community structure and feeding in ice-covered Antarctic waters during the winter (AMERIEZ 1988). Polar Biology 11:157-167

Lancraft TM, Reisenbichler KR, Robinson BH, Hopkins TL, Torres JJ (2004) A krill-dominated micronekton and macrozooplankton community in Croker Passage, Antarctica with an estimate of fish predation. Deep Sea Research II 51:2247-2260

Laws RM (1977a) Seals and whales of Southern Ocean. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 279 (963):81-96

Laws RM (1977b) The significance of vertebrates in the Antarctic marine ecosystem. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Smithsonian Institution, Washington, DC, p 411-438

Lawson JW, Magalhaes AM, Miller EH (1998) Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. Marine Ecology Progress Series 164:13-20

Lawson GL, Wiebe PH, Ashjian CJ, Gallager SM, Davis CS, Warren JD (2004) Acoustically-inferred zooplankton distribution in relation to hydrography west of the Antarctic Peninsula. Deep Sea Research II 51 (17-19):2041-2072

Lea M, Cherel Y, Guinet C, Nichols P (2002a) Antarctic fur seals foraging in the polar frontal zone: inter-annual shifts in diet as shown from fecal and fatty acid analysis. Marine Ecology Progress Series 245:281-297

Lea MA, Nichols PD, Wilson G (2002b) Fatty acid composition of lipid-rich myctophids and mackerel icefish (*Champsocephalus gunnari*) – Southern Ocean food-web implications. Polar Biology 25:843-854

Libertelli MM, Daneri GA, Piatkowski U, Coria NR, Carlini AR (2004) Predation on cephalopods by *Pygoscelis papua* and *Arctocephalus gazella* at South Orkney Islands. Polish Polar Research 25 (3-4):267-274

Linse K, Griffiths HJ, Barnes DKA, Clarke A (2006) Biodiversity and biogeography of Antarctic and sub-Antarctic mollusca. Deep Sea Research II 53 (8-10):985-1008

Lizotte M (2001) The contribution of sea ice algae to Antarctic marine primary production. American zoologist 41:57-73

Loeb VJ (1991) Distribution and abundance of larval fishes collected in the western Bransfield Strait region, 1986-87. Deep Sea Research I 38 (8-9):1251-1260

Loeb VJ, Kellermann A, Koubbi P, North A, White M (1993) Antarctic larval fish assemblages: a review. Bulletin of Marine Science 53 (2):416-449

Loeb VJ, Siegel V, Holm-Hansen O, Hewitt R, Fraser W, Trivelpiece W, Trivelpiece S (1997) Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. Nature 387 (6636):897-900

Longhurst AR (1998) Ecological geography of the sea. Academic Press, Florida

Lønne O, Gulliksen B (1991) Sympagic macro-fauna from multiyear sea-ice near Svalbard. Polar Biology 11:471–477

Loots C, Koubbi P, Duhamel G (2007) Habitat modelling of *Electrona antarctica* (Myctophidae, Pisces) in Kerguelen by Generalized Additive Models and Geographic Information Systems. Polar Biology 30 (8):951-959

Lubimova TG, Shust KV, Popkov VV (1987) Specific features of the ecology of Southern Ocean mesopelagic fish of the family Myctophidae. In: Biological resources of the Arctic and Antarctic (collected papers). Nauka Press, Moscow, p 320-337

Luque S, Arnould JPY, Miller EH, Cherel Y, Guinet C (2007) Foraging behaviour of sympatric Antarctic and subantarctic fur seals: does their contrasting duration of lactation make a difference? Marine Biology 152:213-224

Lutjeharms JRE (1990) The oceanography and fish distribution of the Southern Ocean. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahamstown, RSA, p 6-27

Lynnes AS, Reid K, Croxall JP (2004) Diet and reproductive success of Adélie and chinstrap penguins: linking response of predators to prey population dynamics. Polar Biology 27 (9):544-554

Maes J, Van de Putte A, Hecq J, Volckaert FAM (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

Maravelias C, Tsitsika E, Papaconstantinou C (2007) Evidence of Morocco dentex (*Dentex maroccanus*) distribution in the NE mediterranean and relationship with environmental factors determined by Generalized Additive Modelling. Fisheries Oceanography 16 (3):294-302

Marchant HJ, Murphy EJ (1994) Interactions at the base of the Antarctic food web. In: El-Sayed SZ (ed) Southern Ocean Ecology. Cambridge University Press, Cambridge, p 267-285

Marschall HP (1988) The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. Polar Biology 9 (2):129-135

McCullagh P, Nelder JA (1989) Generalized Linear Models, 2nd edition. Chapman & Hall, New York

McKenna JE Jr (1991) Trophic relationships within the Antarctic demersal fish community off South Georgia Island. Fisheries Bulletin 89:643-653

McMahon C, Hindell M, Dorr T, Massom RA (2002) Winter distribution and abundance of crabeater seals off George V Land, East Antarctica. Antarctic Science 14 (2):128-133

Miller DGM, Hampton I (1989) Biology and ecology of the Antarctic krill (*Euphausia superba* Dana): A review. BIOMASS Scientific Series 9

Montgomery JC, Foster BA, Cargill JM (1989) Stomach evacuation rate in the planktivorous Antarctic fish *Pagothenia borchgrevinki*. Polar Biology 9:405-408

Morales-Nin B, Palomera I, Schadwinkel S (1995) Larval fish distribution and abundance in the Antarctic Peninsula region and adjacent waters. Polar Biology 15 (2):143-154

NASA (2007) Giovanni. http://reason.gsfc.nasa.gov/OPS/Giovanni/ocean.modelDay.shtml. Accessed 01 May 2007

Naumov AG, Svetlov MF, Kozlov AN, Pinskaya IA (1983) Some peculiarities of distribution and feeding of *Notothenia guentheri* (Nototttheniidae). Journal of Ichthyology 23(1):149-156

Naumov AG (1985) System analysis of the structure of the Antarctic waters community. In: Vinogradov ME, Flint MV (eds) Biological basis of the commercial utilization of the open regions of the ocean. Nauka Press (in Russian), Moscow, p 57-80

Nemoto T (1983) Net sampling and abundance estimates of euphausiids. Biological Oceanography 2:211-226

Nicol S (2004) Condition of *Euphausia crystallorophias* off East Antarctica in winter in comparison to other seasons. Deep Sea Research II 51 (17-19):2215-2224

Nicol S (2006) Krill, currents, and sea ice: *Euphausia superba* and its changing environment. Bioscience 56 (2):111-120

Nordhausen W (1994a) Distribution and diel vertical migration of the euphausiid *Thysanoessa macrura* in Gerlache Strait, Antarctica. Polar Biology 14 (4):219-229

Nordhausen W (1994b) Winter abundance and distribution of *Euphausia superba*, *E. crystallorophias*, and *Thysanoessa macrura* in Gerlache Strait and Crystal Sound, Antarctica. Marine Ecology Progress Series 109 (2-3):131-142

Nygård H (2005) Couplings between bottom and ice fauna in a shallow area in Svalbard, Norway. Master’s Thesis, åbo Akademi, åbo, Finland

O'Brien D (1987) Direct observations of the behavior of *Euphausia superba* and *Euphausia crystallorophias* (Crustacea: Euphausiacea) under pack ice during the Antarctic spring of 1985. Journal of Crustacean Biology 7:437-448

Oksanen J, Kindt R, Legendre P, O'Hara RB, Simpson GL, Stevens MHH (2008) Vegan: Community ecology package version 1.8.3. http://cran.r-project.org/. Accessed August 01 2008

Orsi AH, Nowlin WD, Whitworth T (1993) On the circulation and stratification of the Weddell Gyre. Deep Sea Research I-Oceanographic Research Papers 40 (1):169-203

Orsi AH, Whitworth T, Nowlin WD (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. Deep Sea Research I 42 (5):641-673

Osman LP, Hucke-Gaete R, Moreno CA, Torres D (2004) Feeding ecology of Antarctic fur seals at Cape Shirreff, South Shetlands, Antarctica. Polar Biology 27:92-98

Pakhomov EA, Tsejtlin VB (1992) The feeding of seven Antarctic fish species and estimation of their daily rations. Journal of Ichthyology 32(1):138-146

Pakhomov EA, Perissinotto R, McQuaid C (1996) Prey composition and daily rations of myctophid fishes in the Southern Ocean. Marine Ecology Progress Series 134:1-14

Pakhomov EA, Perissinotto R, Froneman PW (1998) Abundance and trophodynamics of *Euphausia crystallorophias* in the shelf region of the Lazarev Sea during austral spring and summer. Journal of Marine Systems 17 (1-4):313-324

Pakhomov EA (2000) Demography and life cycle of Antarctic krill, *Euphausia superba*, in the Indian sector of the Southern Ocean: long-term comparison between coastal and open ocean regions. Canadian Journal of Fisheries and Aquatic Sciences 57:68-90

Pakhomov EA, Froneman PW (2000) Composition and spatial variability of macroplankton and micronekton within the Antarctic Polar Frontal Zone of the Indian Ocean during austral autumn 1997. Polar Biology 23:410-419

Pakhomov EA, Perissinotto R, McQuaid CD, Froneman PW (2000) Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer 1993 - Part 1. Ecological zonation. Deep Sea Research I 47 (9):1663-1686

Parkinson CL (2004) Southern Ocean sea ice and its wider linkages: Insights revealed from models and observations. Antarctic Science 16 (4):387-400

Parkinson CL (2006) Earth's cryosphere: Current state and recent changes. Annual Review of Environment and Resources 31:33-60

Paul AJ, Paul JM, Smith RL (1998) Seasonal changes in whole-body energy content and estimated consumption rates of age 0 walleye pollock from Prince William Sound, Alaska. Estuarine Coastal and Shelf Science 47 (3):251-259

Pedersen J, Hislop JRG (2001) Seasonal variations in the energy density of fishes in the North Sea. Journal of Fish Biology 59 (2):380-389

Persson L (1986) Patterns of food evacuation in fishes: a critical review. Environmental Biology of Fishes 16:51-58

Pfaffling A, Haas C, Dieckmann G, Reid JE (2007) A direct helicopter EM - sea ice thickness inversion, assessed with synthetic and field data. Geophysics 72:F127-F137

Phleger CF, Nichols PD, Virtue P (1997a) Lipids and buoyancy in southern ocean pteropods. Lipids 32 (10):1093-1100

Phleger CF, Nichols PD, Virtue P (1997b) The lipid, fatty acid and fatty alcohol composition of the myctophid fish *Electrona antarctica*: high levels of wax esters and food chain implications. Antarctic Science 9:258–265

Phleger CF, Nelson MM, Mooney BD, Nichols PD (2002) Interannual and between species comparison of the lipids, fatty acids and sterols of Antarctic krill from the US AMLR Elephant Island survey area. Comparative Biochemistry and Physiology B-Biochemistry & Molecular Biology 131 (4):733-747

Piatkowski U (1985) Distribution, abundance and diurnal migration of macrozooplankton in Antarctic surface waters. Meeresforschung 30:262-279

Piatkowski U (1989) Macroplankton communities in Antarctic surface waters - spatial changes related to hydrography. Marine Ecology Progress Series 55 (2-3):251-259

Piatkowski U, Rodhouse PG, White MG, Bone DG, Symon C (1994) Nekton community of the Scotia Sea as sampled by RMT 25 during austral summer. Marine Ecology Progress Series 112 (1-2):13-28

Piatkowski U, Vergani DF, Stanganelli ZB (2002) Changes in the cephalopod diet of southern elephant seal females at King George Island, during El Nino-La Nina events. Journal of the Marine Biological Association of the United Kingdom 82 (5):913-916

Plötz J, Bornemann H, Knust R, Schröder A, Bester M (2001) Foraging behaviour of Weddell seals, and its ecological implications. Polar Biology 24:901-909

Post A (1990) Paralepididae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahamstown, p 138-141

Pusch C, Hulley PA, Kock KH (2005) Community structure and feeding ecology of mesopelagic fishes in the slope waters of King George Island (South Shetland Islands, Antarctica). Deep Sea Research I 51 (11):1685-1708

Quillfeldt P (2002) Seasonal and annual variation in the diet of breeding and non-breeding Wilson's storm-petrels on King George Island, South Shetland Islands. Polar Biology 25 (3):216-221

Quinn G, Keough M (2004) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

R-Development-Core-Team (2006) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Raclot T, Groscolas R, Cherel Y (1998) Fatty acid evidence for the importance of myctophid fishes in the diet of king penguins, *Aptenodytes patagonicus*. Marine Biology 132:523-533

Radchenko VI (2007) Mesopelagic fish community supplies "biological pump". The Raffles Bulletin of Zoology Suupl. 14:265-271

Reijnders PJH, Plötz J, Zegers J, Grafe M (1990) Breeding biology of Weddell seals (*Leptonychotes weddellii*) at Drescher Inlet, Riiser Larsen Ice Shelf, Antarctica. Polar Biology 10 (4):301-306

Reinhardt SB, Van Vleet ES (1986) Lipid-composition of 22 species of Antarctic midwater zooplankton and fish. Marine Biology 91 (2):149-159

Ribic CA, Ainley DG, Fraser WR (1991) Habitat selection by marine mammals in the marginal ice-zone. Antarctic Science 3 (2):181-186

Rice DW (1998) Marine mammals of the world: systematics and distribution. Society of Marine Mammalogy, Special Publication 4

Richardson M, Whitaker T, (1979) An Antarctic fast-ice food chain: observations on the interaction of the amphipod *Pontogeneia antarctica* Chevreux with ice-associated micro-algae. British Antarctic Survey Bulletin 47:107–115

Roberts DW (2007) labdsv: Ordination and mulitivariate analysis for ecology. R package version 1.3-1.

Rodhouse PG, White MG (1995) Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic Polar Frontal Zone. Biological Bulletin 189 (2):77-80

Rogers TL, Byrden MM (1997) Density and haul-out behavior of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. Marine Mammal Science 13 (2):293-302

Ross RM, Quetin LB, Haberman KL (1998) Interannual and seasonal variability in short-term grazing impact of *Euphausia superba* in nearshore and offshore waters west of the Antarctic Peninsula. Journal of Marine Systems 17 (1-4):261-273

Rowedder U (1979) Feeding ecology of the myctophid *Electrona antarctica* (Günther, 1878) (Teleostei). Meeresforschung 27:252-263

Rozzi R (2007) Future environmental philosophies and their biocultural conservation interfaces. Ethics & The Environment 12 (2):142-145

Ruud JT (1954) Vertebrates without erythrocytes and blood pigment. Nature 173: 848-850

Saadettin G, Dincer B, Alemdag N, Colak A, Turfekci M (1998) Proximate composition and selected mineral content of commercially important fish species from the Black Sea. Journal of the Science of Food and Agriculture (78):337-342

Sabourenkov E (1990) Mesopelagic fish of the Southern Ocean - summary results of recent Soviet studies. WG-FSA-90/23, CCAMLR, Hobart

Sagar P (1980) Life cycle and growth of the Antarctic gammarid amphipod *Paramoera walkeri* (Stebbing, 1906). Journal of the Royal Society of New Zealand 10:259–270

Schnack-Schiel SB (2003) The macrobiology of sea ice. In: Thomas DN, Dieckmann G (eds) Sea ice - an introduction to its physics, chemistry, biology and geology. Blackwell Science, Oxford, p 211-239

Schnack-Schiel SB, Michels J, Mizdalski E, Schodlok M, Schröder M, (2008a) Composition and community structure of zooplankton in the sea ice covered western Weddell Sea in spring 2004—with emphasis on calanoid copepods. Deep Sea Research II 55 (8-9):1040-1055

Schnack-Schiel SB, Haas C, Michels J, Mizdalski E, Schunemann H, Steffens M, Thomas DN (2008b) Copepods in sea ice of the western Weddell Sea during austral spring 2004. Deep Sea Research II 55 (8-9):1056-1067

Scripps Oceanographic Institution, 2006. Http://topex. ucsd.edu/marine_topo/mar_topo.htmls

Segerstråle S (1946) On the occurrence of the amphipod, *Gammarus duebeni* Lillj. in Finland, with notes on the ecology of the species. Societas Scientiarum Fennica: Commentationes Biologicae 9:1–22

Segerstråle S (1954) The freshwater amphipods, *Gammarus pulex* (l.) and *Gammarus lacustris* G. O. Sars, in Denmark and Fennoscandia—a contribution to the late- and post-glacial immigration history of the aquatic fauna of northern Europe. Societas Scientiarum Fennica: Commentationes Biologicae 15:1–91

Serreze MC, Holland MM, Stroeve J (2007) Perspectives on the Arctic's shrinking sea-ice cover. Science 315 (5818):1533-1536

Siegel V (1980) Quantitative investigations on parasites of Antarctic channichthyid and nototheniid fishes. Reports on Marine Research 28(2):146-156

Siegel V, Bergström B, Stromberg JO, Schalk PH (1990) Distribution, size frequencies and maturity stages of Krill, *Euphausia superba*, in relation to sea ice in the northern Weddell Sea. Polar Biology 10 (7):549-557

Siegel V, Skibowski A, Harm U (1992) Community structure of the epipelagic zooplankton community under the sea-ice of the northern Weddell Sea. Polar Biology 12:15-24

Siegel V, Loeb V (1995) Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. Marine Ecology Progress Series 123 (1-3):45-56

Siegel V (2000) Krill (Euphausiacea) demography and variability in abundance and distribution. Canadian Journal of Fisheries and Aquatic Sciences 57:151-167

Siegel V, Loeb V, Bergström B, Schöling S, Haraldsson M, Kitchener J, Vortkamp M (2004) Demography of Antarctic Krill in the Lazarev Sea (Subarea 48.6) and the Elephant Island area (Subarea 48.1) in 2004. WG-EMM-04/23, CCAMLR, Hobart

Siegel V (2005) Distribution and population dynamics of *Euphausia superba*: summary of recent findings. Polar Biology 29 (1):1-22

Siniff DB, Cline DR, Erickson AW (1970) Population densities of seals in the Weddell Sea, Antarctica in 1968. In: Holdgate, MW (ed.) Antarctic Ecology, vol. 1. Academic Press, London, New York, p 377–397

Siniff DB (1991) An overview of the ecology of Antarctic seals. American Zoologist 31 (1):143-149

Sloan NA (2002) History and application of the wilderness concept in marine conservation. Conservation Biology 16 (2):294-305

Smetacek V, Bathmann U, Helmke E (2005) The expeditions ANTARKTIS XXI/3-4-5 of the research vessel ''Polarstern'' in 2004. Reports on Polar and Marine Research 500. Alfred-Wegener-Institute for Polar and Marine Research, Bremerhaven

Smetacek V, Nicol S (2005) Polar ocean ecosystems in a changing world. Nature 437 (7057):362-368

Smith WHF, Sandwell DT (1997) Global sea floor topography from satellite altimetry and ship depth soundings. Science 277 (5334):1956-1962

Smith WO, Nelson DM (1986) Importance of ice edge phytoplankton production in the Southern Ocean. Bioscience 36:51–257

Smith WO, Ainley DG, Cattaneo-Vietti R (2007) Trophic interactions within the Ross Sea continental shelf ecosystem. Philosophical Transactions of the Royal Society B-Biological Sciences 362 (1477):95-111

Sosinski J (1985) Some data on the taxonomy and biology of Antarctic icefish *Champsocephalus gunnari* Lönnberg 1905. Acta Ichthyolgica et Pisca 15:3–54

Southwell C, Kerry K, Ensor P, Woehler EJ, Rogers T (2003) The timing of pupping by pack-ice seals in East Antarctica. Polar Biology 26 (10):648-652

Southwell C (2005a) Optimising the timing of visual surveys of crabeater seal abundance: haulout behaviour as a consideration. Wildlife Research 32 (4):333-338

Southwell C (2005b) Response behaviour of seals and penguins to helicopter surveys over the pack ice off East Antarctica. Antarctic Science 17 (3):328-334

Southwell CJ, Kerry KR, Ensor PH (2005) Predicting the distribution of crabeater seals *Lobodon carcinophaga* off east Antarctica during the breeding season. Marine Ecology Progress Series 299:297-309

Stockton W (1982) Scavenging amphipods from under the Ross ice shelf, Antarctica. Deep Sea Research 29:819–835

Stretch JJ, Hamner PP, Hamner WM, Michel WC, Cook J, Sullivan CW (1988) Foraging behavior of Antarctic krill *Euphausia superba* on sea ice microalgae. Marine Ecology Progress Series 44 (2):131-139

Takahashi M, Iwami T (1997) The summer diet of demersal fish at the South Shetland Islands. Antarctic Science 9(4):407–413

Tanimura A, Hattori H, Miyamoto Y, Hoshiai T, Fukuchi M (2008) Diel changes in vertical distribution of *Oithona similis* (Cyclopoida) and *Oncaea curvata* (Poecilostomatoida) under sea ice in mid-summer near Syowa Station, Antarctica. Polar Biology 31 (5):561-567

Taverdieva MI, Pinskaya IA (1980) The feeding of fishes of the family Nototheniidae and Channichthyidae on the shelves of the Antarctic Peninsula and the South Shetlands. Voprosy Ikthiologij 20(4):644–655

Taverdieva MI (1982) The food composition, daily ration and feeding habits of the icefish *Champsocephalus gunnari* Lönnberg off the South Orkneys. Trudy VRNO, Characteristics of the pelagic community from the sea of Scotia and adjacent waters: 69-76

Thomas JA, DeMaster DP (1982) An acoustic technique for determining diurnal activities in leopard (*Hydrurga leptonyx*) and crabeater (*Lobodon carcinophagus*) seal. Canadian Journal of Zoology 60:2029-2031

Thomas JA, DeMaster DP (1983) Diel haul-out patterns of Weddell seal (*Leptonychotes weddellii*) females and their pups. Canadian Journal of Zoology 61:2084-2096

Thomasson MA, Emery JH, Rademann J, Hewitt RP, Bergström BI (2002) Results of an acoustic investigation of Antarctic krill, *Euphausia superba* biomass-density in the Elephant Island area in January/February 2001. Commission for the Conservation of Antarctic Marine Living Resources, WG-EMM-02/30, 14 pp, Hobart, Australia

Thorpe SE, Murphy EJ, Watkins JL (2007) Circumpolar connections between Antarctic krill (*Euphausia superba* Dana) populations: Investigating the roles of ocean and sea ice transport. Deep Sea Research I 54 (5):792-810

Tierney M, Hindell M, Goldsworthy S (2002) Energy content of mesopelagic fish from Macquarie Island. Antarctic Science 14 (3):225-230

Torres J, Somero G (1988) Vertical distribution and metabolism in Antarctic mesopelagic fishes. Comparative Biochemistry and Physiology 90B:521-528

Torres J, Donnelly J, Hopkins T, Lancraft T, Aarset A, Ainley D (1994) Proximate composition and overwintering strategies of Antarctic micronektonic crustacea. Marine Ecology Progress Series 113:221-232

Tréguer P, Jacques G (1992) Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. Polar Biology 12 (2):149-162

Trunov IA, Frolkina ZA, Konstantinova MP (2000) Vertical distribution of the Antarctic icefish *Champsocephalus gunnari* and *Nototheniops larseni* on the shelf of South Georgia (Antarctic). Journal of Ichthyology 40(2):150-154

Tynan CT (1998) Ecological importance of the southern boundary of the Antarctic Circumpolar Current. Nature 392 (6677):708-710

UNCED (1992) The Rio United Nations Conference on Environment and Development: the Biodiversity Convention; Agenda 21 and the Rio Declaration. UNCED, Gland, Switzerland

Vacchi M, Lamesa M, Castelli A (1994) Diet of two coastal nototheniid fish from Terra-Nova Bay, Ross Sea. Antarctic Science 6 (1):61-65

van Dam RP, Kooyman GL (2003) Latitudinal distribution of penguins, seals and whales observed during a late autumn transect through the Ross Sea. Antarctic Science 16 (3):313-318

Van de Putte AP (2008) Ecology and evolution of fishes in the Southern Ocean, with special focus on the myctophid *Electrona antarctica*. PhD thesis, Catholic University of Leuven

Van de Putte AP, Jackson GD, Pakhomov EA, Flores H, Volckaert FAM (in press) Distribution of squid and fish in the pelagic zone of the Cosmonaut Sea and Prydz Bay region during the BROKE-west expedition, January-March 2006. Deep Sea Research II van Franeker JA (1992) Top predators as indicators for ecosystem events in the confluence zone and marginal ice zone of the Weddell and Scotia seas, Antarctica, November 1988 to January 1989 (EPOS Leg 2). Polar Biology 12:93-102

van Franeker JA, Bathmann UV, Mathot S (1997) Carbon fluxes to Antarctic top predators. Deep Sea Research II 44 (1-2):435-455

van Franeker JA (2001) Mirrors in ice. PhD Thesis, Rijksuniversiteit Groningen

van Franeker JA, Williams R, Imber MJ, Wolff WJ (2001) Diet and foraging ecology of the Southern Fulmar *Fulmarus glacialoides*, Antarctic Petrel *Thalassoica antarctica*, Cape Petrel *Daption capense* and Snow Petrels *Pagodroma nivea* ssp. on Ardery Island, Wilkes Land, Antarctica. In: van Franeker JA (ed) Mirrors in ice. PhD thesis. University of Groningen, Groningen

van Franeker JA, Flores H (2007) Zuidpool en zeenaalden? Nederlandse Zeevogelgroep Nieuwsbrief 8:4

Venables WN, Ripley BD (2002) Modern applied statistics with S. Fourth edition. Springer, New York

Verity PG, Smetacek V (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. Marine Ecology Progress Series 130:277-293

Voronina NM (1984) Pelagic ecosystems of the Southern Ocean. Nauka Press (in Russian), Moscow

Voronina NM (1998) Comparative abundance and distribution of major filter-feeders in the Antarctic pelagic zone. Journal of Marine Systems 17 (1-4):375-390

Watanabe Y, Bornemann H, Liebsch N, Plotz J, Sato K, Naito Y, Miyazaki N (2006) Seal-mounted cameras detect invertebrate fauna on the underside of an Antarctic ice shelf. Marine Ecology Progress Series 309:297-300

Watkins JL (2000) Aggregation and vertical migration. In: Everson I (ed) Krill - biology, ecology and fisheries. Blackwell Science Ltd., London, p 80-102

Weatherly JW, Zhang Y (2001) The response of the polar regions to increased CO2 in a global climate model with elastic-viscous-plastic sea ice. Journal of Climate 14 (3):268-283

Weimerskirch H, Inchausti P, Guinet C, Barbraud C (2003) Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. Antarctic Science 15 (2):249-256

Werner I (1997) Grazing of Arctic under-ice amphipods on sea-ice algae. Marine Ecology Progress Series 160:93–99

Werner I, Lindemann F (1997) Video observations of the underside of Arctic sea ice—features and morphology on medium and small scales. Polar Research 16:27–36

Werner I, Auel H, Kiko R (2004) Occurrence of *Anonyx sarsi* (Amphipoda: Lysianassidae) below Arctic pack ice—an example for cryo-benthic coupling? Polar Biology 27:474–481

White MG, Piatkowski U (1993) Abundance, horizontal and vertical distribution of fish in eastern Weddell Sea micronekton. Polar Biology 13:41-53

Wienecke BC, Lawless R, Rodary D, Bost CA, Thomson R, Pauly T, Robertson G, Kerry KR, LeMaho Y (2000) Adelie penguin foraging behaviour and krill abundance along the Wilkes and Adelie land coasts, Antarctica. Deep Sea Research II 47 (12-13):2573-2587

Wiig O, Derocher AE (1999) Application of aerial survey methods to polar bears in the Barents Sea. In: Garner GW, Amstrup SC, Laake JL, Manly BFJ, McDonald LL, Robertson DG (eds) Marine mammal survey and assessment methods. Balkema, Rotterdam Brookfield, p 27-36

Williams R (1985) Trophic relationships between pelagic fish and euphausiids in Antarctic waters. In: Siegfried W, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer Press, Berlin, Heidelberg, p 453-459

Wilson DL, Smith WO, Nelson DM (1986) Phytoplankton bloom dynamics of the western Ross Sea ice edge.1. Primary productivity and species-specific production. Deep Sea Research Part a 33 (10):1375-1387

Wilson GDF (1998) Historical influences on deep-sea isopod diversity in the Atlantic Ocean. Deep Sea Research II 45 (1-3):279-301

Windell JT (1966) Rate of digestion in bluegill sunfish. Invest Indiana Lakes Streams 7:185-214

Woehler EJ (1993) The distribution and abundance of Antarctic and subantarctic penguins, Scientific Committee on Antarctic Research (SCAR), Cambridge, England

Woehler EJ (1997) Seabird abundance, biomass and prey consumption within Prydz Bay, Antarctica, 1980/1981-1992/1993. Polar Biology 17 (4):371-383

Wood SN (2003) Thin plate regression splines. Journal of the Royal Statistical Society Series B-Statistical Methodology 65:95-114

Wood SN (2006) Generalized Additive Models: An introduction with R. Taylor & Francis Group, New York

Yaremchuk M, Nechaev D, Schroter J, Fahrbach E (1998) A dynamically consistent analysis of circulation and transports in the southwestern Weddell Sea. Annales Geophysicae-Atmospheres Hydrospheres and Space Sciences 16 (8):1024-1038

Zarauz L, Irigoien X, Urtizberea A, Gonzalez M (2007) Mapping plankton distribution in the Bay of Biscay during three consecutive spring surveys. Marine Ecology Progress Series 345:27-39

Zhou M, Nordhausen W, Huntley M (1994) ADCP Measurements of the distribution and abundance of Euphausiids near the Antarctic Peninsula in winter. Deep Sea Research I 41 (9):1425-1445

Zimmer I,Piatkowski U, Brey T (2007) The trophic link between squid and the emperor penguin *Aptenodytes forsteri* at Pointe Geologie, Antarctica. Marine Biology 152 (5):1187-1195

Zwally HJ, Comiso JC, Parkinson CL, Cavalieri DJ, Gloersen P (2002) Variability of Antarctic sea ice 1979-1998. Journal of Geophysical Research - Oceans 107 (C5) DOI: 10.1029/2000JC000733

Acknowledgements

The lonesome scientific genius, driven by boundless curiosity and ambition, enlightened by his genuine bright ideas, is a myth. In reality, scientific work is a team effort relying on the expertise of many people and the accomplishments of countless predecessors.

I would like to thank my promotor Wim Wolff and my co-promotor Jan Andries van Franeker for excellent academic courtesy. From the moment of signing my contract at the Rijksuniversiteit Groningen, Wim smoothly guided my scientific development and, finally, the preparation of this thesis with the wisdom of the experienced top-scientist and the routine of a long-time academic fellow. Jan Andries was both a committed 24/7 supervisor and an inspiring scientific sparring partner to me.

Wageningen IMARES, formerly Alterra, provided laboratory and office facilities. I would like to thank the former director of Alterra Texel, Han Lindeboom, and the directors of the department of ecology at Wageningen IMARES, Floris Groenendijk and Jacob Asjes, for letting me work in an exceptionally professional environment.

The crews of RV *Yuzhmorgeologiya* and RV *Polarstern* provided excellent support during the field work. In particular, I would like to thank the cruise leaders Christopher Jones, Uli Bathmann and Michael Spindler as well as Captain Uwe Pahl, Captain Stefan Schwarze, Steffen Spielke, Dethlef Beth, Kurt Hoppe and Siegfried Moser of the *Polarstern* crew for their outstanding engagement.

Field work in Antarctica is doomed to failure without an excellent team handling excellent gear. Both were present in the *Flying Dutchmen* teams of the *Polarstern* expeditions ANT 21-4, ANT 23-6 and ANT 24-2. The success of SUIT was based on just the right mixture of the different personalities of Jan Andries van Franeker, André Meijboom, Michiel van Dorssen, Ruben Fijn, Bram Fey and Koos Zegers. In addition, Anton Van de Putte has significantly contributed to the success of SUIT, which earned him the membership of honour in the *Flying Dutchmen* team. I would especially like to thank Uli Bathmann for his extra-ordinary engagement for SUIT, both as an expedition leader and as a hands-on decksman.

The *Flying Dutchmen*, Jan Betsema and Dick de Haan twisted their brains over the seemingly impossible task to design a net that can fish under ice. During the building and testing of the gear, they were supported by the crew of RV *Navicula* and the staff of CIV Texel and Zijlmakerij Texel. Uwe Grundmann and Burkhard Clasen of the *Polarstern* crew contributed significantly to the improvement of the '*Kampfwagen*'. René Wilzewski provided excellent technical drawings.

Whether on board or in the lab, Hans Verdaat, Martina Vortkamp, Daria Martynova, Susanne Schöling, Rainer Kiko, Matilda Haraldsson and Piet-Wim van Leeuwen helped working up the samples. Sigi Schiel, Jan Michels, A.V. Balushkin, Uwe Piatkowski and Henk van Hoving helped with the identification of species.

During diving under ice, my life hung on a thin line held by my dive partners Carsten Wancke, Saskia Brandt, Markus Eßer and Rupert Krapp during the ISPOL expedition (2004/2005), and Uli Freier, Carsten Pape, Said Yasseri and Susanne Spahic during ANT 23-6 (2006). Frank Donat , Antje Klawon and the fabulous scientific diver class of 2004 in Oldenburg taught me to dive safely under extreme conditions.

Carsten Wancke did a great job in the merciless pack-ice of the Weddell Sea. The crew of Heli Transair, in particular Jürgen Büchner and Markus Federowitz, flew the most beautiful triangles. Christian Haas gave me a seat and pleasant company during helicopter surveys.

I would like to thank Ismael Nunez-Riboni and Sahra Hermann for making datasets available, Viola Kimmel for GIS design and Peter-Roy Alkema and Bert Aggenbach for logistic help. Ingrid de Raad, Michaela Scholl, Joukje de Vries-Veldkamp and Gezien Roon-ter-Horst helped with a mountain of administrative work.

I am grateful for the extensive contributions of the co-authors and reviewers of this thesis. I really enjoyed the struggle of minds. Evgeny Pakhomov, Mardik Leopold and Karl-Hermann Kock readily reviewed manuscripts before submission. Science came alive during discussions with Volker Siegel, Bettina Meyer, Matilda Haraldsson, Jacqueline Stefels, Boris Cisewski, Volker Strass, Harry Leach and Peter Reijnders. In particular, I would like to thank the members of the Manuscript Commission, Uli Bathmann, Hein de Baar and Filip Volckaert, for carefully reading the thesis draft and providing useful comments at the last minute.

I would especially like to thank all my colleagues at IMARES Texel for the interesting conversations and the uncomplicated and warm-hearted working atmosphere.

There is no accomplishment without a proper last-minute task force. My wife Julia, Liesbeth van der Vlies, Kati Flores, Oscar Bos, Robert Johnson, Karoline Stürmer and the IMARES Journal Club did not hesitate to sacrifice their valuable time when it was needed the most.

My parents Sabine and Klaus Flores, Sophie Brasseur, Eric Hercules, Konrad Gorsky, Geno Gonzales-Mireles and my friends Tim Schlegel and Michael Faden have kept my mind in balance over the past five years. In Anton I found a new friend and scientific partner, with whom I am glad to have shared lots of science, lots of fun, lots of whisky and a cabin.

The research of this thesis was co-funded by the Netherlands AntArctic Programme (NAAP) under project number ALW 851.20.011 of the Netherlands Organisation for Scientific Research (NWO), and by the Netherlands Ministry of Agriculture, Nature and Food Quality (LNV) under its Statutory Research Tasks Nature & Environment projects WOT-04-003-002 and KB-01-012-002. Parts of the scientific work were supported by the German Federal Ministry of Education and Research (BMBF) and the Belgian PELAGANT project.

The Alfred Wegener Institute for Polar and Marine Research (AWI) generously took care of logistics during preparation and execution of the field work and provided working space and berths on *Polarstern*.

I would also like to thank CIV Texel, CIV Den Oever, Schat Harding GmbH, Qmetrix b.v and the Zijlmakerij Texel for advice and support.

Above all, I would like to thank my wife Julia for enduring my absence during expeditions, nerdy discussions with nerdy friends and carrying a great share of the burden in finishing this thesis.

Contributing authors

Ulrich Bathmann
Alfred Wegener Institute for Polar and Marine Research
Am Handelshafen 12
27570 Bremerhaven
Germany

Jørgen Berge
University Center in Svalbard
P.O. Box 156
9171 Longyearbyen
Norway

Boris Cisewski
Alfred Wegener Institute for Polar and Marine Research
Bussestrasse 24
27570 Bremerhaven
Germany

Bjørn Gulliksen
University Center in Svalbard
P.O. Box 156
9171 Longyearbyen
Norway

Christian Haas
Department of Earth and Atmospheric Sciences
University of Alberta
Edmonton T6G 2E3
Canada

Matilda Haraldsson
Sven Lovén Centr. Kristineberg
Göteborgs universitet
Marin ekologi
Kristineberg 566
450 34 Fiskebäckskil
Sweden

Christopher D. Jones
Southwest Fisheries Science Center
National Oceanic and Atmospheric Administration
8604 La Jolla Shore Dr
CA 92037
La Jolla
USA

Karl-Hermann Kock
Johann Heinrich von Thünen-Institut
Institute for Sea Fisheries
Palmaille 9
22767 Hamburg
Germany

Rupert H. Krapp
University Center in Svalbard
P.O. Box 156
9171 Longyearbyen
Norway

Harry Leach
Department of Earth and Ocean Sciences
University of Liverpool
4 Brownlow Street
Liverpool
L69 3GP
United Kingdom

Erik (H.W.G.) Meesters
Wageningen IMARES
P.O. Box 167
1790 AD Den Burg
The Netherlands

Evgeny A. Pakhomov
Department of Earth and Ocean Sciences
University of British Columbia
6339 Stores Road
Vancouver
British Columbia V6T 1Z4
Canada

Volker Siegel
Johann Heinrich von Thünen-Institut
Institute for Sea Fisheries
Palmaille 9
22767 Hamburg
Germany

Volker Strass
Alfred Wegener Institute for Polar and Marine Research
Bussestrasse 24
27570 Bremerhaven
Germany

Anton P. Van de Putte
Laboratory of Aquatic Ecology
Catholic University Leuven
Ch. Deberiotstraat 32
3000 Leuven
Belgium

Michiel van Dorssen
Van Dorssen Metaalbewerking
Stoompoort 7 I
1792 CT Oudeschild
The Netherlands

Jan A. van Franeker
Wageningen IMARES
P.O. Box 167
1790 AD Den Burg
The Netherlands

Filip A.M. Volckaert
Laboratory of Aquatic Ecology
Catholic University Leuven
Ch. Deberiotstraat 32
3000 Leuven
Belgium

Iris Werner
Institute for Polar Ecology
University of Kiel
Wischhofstrasse 1-3
24148 Kiel
Germany

Sunhild Wilhelms
Helenenstrasse 16
22765 Hamburg
Germany

Wim J. Wolff
Center for Ecological and Evolutionary Studies
University of Groningen
P.O.Box 14
9750 AA Haren (Gn)
The Netherlands

Stellingen behorende bij het proefschrift

Frozen Desert Alive

The role of sea ice for pelagic macrofauna and its predators: implications for the Antarctic pack-ice food web

van **Hauke Flores**

1. **The classic assumption that Antarctic krill is the key organism of the Antarctic food web is biased, because a large number of studies it is based on were conducted in economically interesting regions where krill is superabundant.**

   Atkinson A, Siegel V, Pakhomov EA, Rothery P, Loeb V, Ross RM, Quetin LB, Schmidt K, Fretwell P, Murphy EJ, Tarling GA, Fleming AH (2008) Oceanic circumpolar habitats of Antarctic krill. Marine Ecology Progress Series 362: 1-23

   CCAMLR (2008) Statistical Bulletin 20 (1998–2007) CCAMLR, Hobart, Australia

   This thesis

2. **When in the Antarctic Ocean the ice cover shrinks, the increasing accessibility of fisheries resources is outweighed by decreasing biological productivity.**

   Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432 (7013):100-103

   Lizotte M (2001) The contribution of sea ice algae to Antarctic marine primary production. American zoologist 41:57-73

   This thesis

3. **Scratching the surface can be more rewarding than ploughing the deep.**

   This thesis

4. **A shift of scientific attention towards pelagic ecosystems in the open ocean will significantly improve estimates of the global marine carbon budget.**

   Collins MA, Rodhouse PGK (2006) Southern Ocean Cephalopods. Advances in Marine Biology 50: 191-265

   Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423: 280-283

   Wilson RW, Millero FJ, Taylor JR, Walsh PJ, Christensen V, Jennings S, Grosell M (2009) Contribution of Fish to the Marine Inorganic Carbon Cycle. Science 323, 359-362

   Sutton TT, Porteiro FM, Heino M, Byrkjedal I, Langhelle G, Anderson CIH, Horne J, Søiland H, Falkenhaug T, Godø OR, Bergstad OA (2008) Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. Deep-Sea Research II 55: 161-184

   This thesis

5. **The number of diving resorts in the North Sea will surpass that of the Seychelles in 2040.**

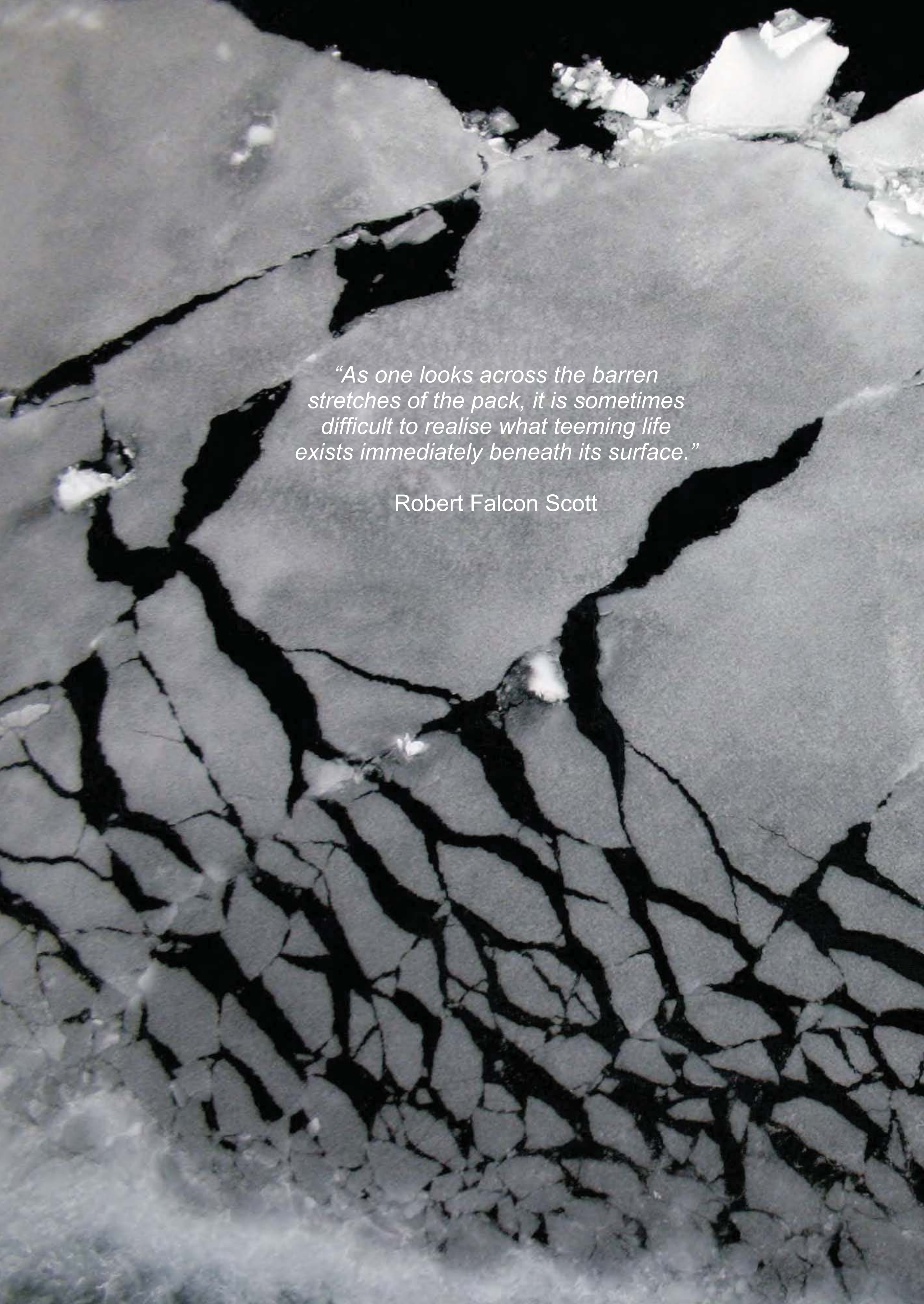
   IPCC (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, IPCC, Geneva

   Anonymous (2004) Connect 6000 MW – Eindrapportage. Ministerie voor Economische Zaken, Den Haag

6. **Whales and dolphins are beneficiaries of the financial crisis.**

   Van der Have (2008) Crisis treft scheepvaart hard. Financiel Dagblad, 10/27/2008. http://www.fd.nl/artikel/10382615/crisis-treft-scheepvaart-hard#

   Laist DW, Knowlton AR, Mead JG, Collet AS, Podesta M (2001) Collisions between ships and whales. Marine Mammal Science 17(1): 35-75



> *"As one looks across the barren stretches of the pack, it is sometimes difficult to realise what teeming life exists immediately beneath its surface."*
>
> Robert Falcon Scott