TROPHIC INTERACTIONS WITHIN HIGH ANTARCTIC SHELF COMMUNITIES -

FOOD WEB STRUCTURE AND THE SIGNIFICANCE OF FISH

TROPHISCHE INTERAKTIONEN IN LEBENSGEMEINSCHAFTEN AUF DEM HOCHANTARKTISCHEN SCHELF –

STRUKTUR DES NAHRUNGSNETZES UND DIE BEDEUTUNG VON FISCHEN

KATJA MINTENBECK

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von

Katja Mintenbeck

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1. Gutachter: Prof. Dr. W.E. Arntz

Stiftung Alfred-Wegener-Institut für Polar- und Meeresforschung in der Helmholtz-Gemeinschaft (AWI), Bremerhaven, Germany

2. Gutachter: Prof. Dr. U. Saint-Paul

Zentrum für Marine Tropenökologie (ZMT), Bremen, Germany

Cover Picture (Fish Photo): *Pagetopsis macropterus* (Channichthyidae, Notothenioidei)

Courtesy of the photographers: J. Gutt (AWI, Bremerhaven) & W. Dimmler (Fielax, Bremerhaven)

Dedicated to my parents

“Till my soul is full of longing

For the secret of the sea,

And the heart of the great ocean

Sends a thrilling pulse through me.”

H.W. Longfellow (1807-1882), The Secret of the Sea

SUMMARY

The marine high Antarctic is increasingly threatened by environmental alterations due to climate change, and there is no doubt that environmental changes will affect structure and functioning of this unique ecosystem. Trophic connections are the major biological key interaction that determine ecosystem structure and function by linking all organisms within an ecosystem to each other. Knowledge about food web structure and trophic relationships is therefore essential for the identification of bottlenecks and vulnerable compartments to estimate ecosystem response to alterations and its impact on overall ecosystem functioning. The aim of this thesis was (i) to investigate use and limitations of methods usually applied to study trophic relationships (in particular stable isotope analysis), and (ii) to illuminate structure and stability of the high Antarctic Weddell Sea shelf food web with particular emphasis on the functional role of fish.

Analysis of organisms' stable isotope composition proved to be a useful tool in studies on trophic relationships, in particular in combination with direct dietary analyses. However, sample treatment and data analysis techniques needs to be carefully chosen to avoid strongly biased estimates. Lipid extraction from sample tissue (alone and in combination with sample acidification), for example, significantly affects not only δ^{13}C but also δ^{15}N. Mathematical δ^{13}C lipid normalization/correction models were found not to provide a reliable alternative to chemical lipid extraction. The natural variability of primary food sources needs to be taken into account, too. In benthic consumers of POM a depth related, trophic-guild specific increase of δ^{15}N was observed, reflecting feeding preferences, POM dynamics and degradation.

Fish take a central position in the Southern Ocean food web: they are characterized by high functional (trophic) diversity and provide an important food source for a multitude of warm-blooded apex predators, including seals and penguins. The benthic fish community seems to be rather resistant to species extinctions and resource fluctuations due to high functional redundancy and a high degree of species' trophic generalism. The pelagic fish community on the shelf, in contrast, seems to be highly vulnerable to changes. The whole pelagic community is almost exclusively composed of a single species, the Antarctic silverfish *Pleuragramma antarcticum*. This species obviously occurs in shoals and was found to undertake diel vertical migrations between the sea floor and the upper water column, thereby providing an easy accessible food source and a major trophic link to demersal and pelagic piscivores, as well as to warm-blooded apex predators foraging in surface waters. *P. antarcticum* obviously occupies a similar ecological role in the high Antarctic zone as krill, *Euphausia superba*, does in the seasonal sea ice zone. However, *P. antarcticum* is rather a specialist consumer and thus highly sensitive to alterations at lower trophic levels. In case this species gets extinct, it is likely that no other species will be able to provide full functional compensation. *P. antarcticum* represents an Achilles' heel in the high Antarctic marine ecosystem and any kind of alterations affecting this species (directly or indirectly) will have severe consequences for overall ecosystem functioning.

ZUSAMMENFASSUNG

Wie viele andere Meeresgebiete ist auch das Südpolarmeer zunehmend von Veränderungen der Umwelt durch den globalen Klimawandel bedroht, und Umweltveränderungen jeglicher Art werden zweifellos Auswirkungen auf Struktur und Funktion dieses einmaligen Ökosystems haben. Struktur und Funktion eines Ökosystems werden durch verschiedene Parameter bestimmt, einer der wichtigsten biologischen Schlüsselmechanismen aber sind trophische Interaktionen, über die alle Organismen innerhalb eines Systems direkt oder indirekt miteinander verknüpft sind. Kenntnisse über Nahrungsnetzstruktur und Nahrungsbeziehungen zwischen Organismen sind also grundlegende Voraussetzung, um Schwachstellen im System zu identifizieren und um abschätzen zu können, wie ein System auf Veränderungen reagieren wird und welche Auswirkungen auf die Ökosystemfunktionen zu erwarten sind. Ziel dieser Arbeit war (i) die Untersuchung der Nützlichkeit verschiedener in der Analyse von Nahrungsbeziehungen angewandter Methoden (inbesondere die Analyse der stabilen Isotopenzusammensetzung) sowie die Identifikation potentieller Fehlerquellen, und (ii) die Untersuchung der Struktur und Stabilität des Nahrungsnetzes auf dem hochantarktischen Weddellmeerschelf mit besonderem Augenmerk auf der funktionalen Bedeutung von Fischen.

Die Analyse der stabilen Isotopenzusammensetzung von Organismen hat sich bei der Untersuchung von Nahrungsbeziehungen und trophischen Hierarchien als sehr nützlich erwiesen, insbesondere wenn diese Methode mit direkten Nahrungsanalysen kombiniert wird. Um erhebliche Verfälschungen und Missinterpretationen der Ergebnisse zu vermeiden, sind allerdings korrekte Probenbehandlung und Datenaufbereitung von großer Wichtigkeit. Die Extraktion von Lipiden (allein

angewandt ebenso wie in Kombination mit Ansäuerung) aus dem Probengewebe, zum Beispiel, verändert nicht nur die δ^{13}C Werte sondern auch δ^{15}N. Verschiedene, häufig verwendete, mathematische δ^{13}C Normalisierungs-/Korrektur-Modelle haben sich als keine verlässliche Alternative zur chemischen Lipid-Entfernung erwiesen. Auch die natürliche Variabilität und Dynamik primärer Nahrungsquellen im System muss berücksichtigt werden. In benthischen POM-Konsumenten wurde ein tiefenabhängiger, Ernährungstyp-spezifischer Anstieg der δ^{15}N Werte gefunden. Der Anstieg in δ^{15}N und die Unterschiede zwischen den Ernährungstypen sind auf unterschiedliche Nahrungs-Präferenzen sowie Dynamik und mikrobiellen Abbau von POM Partikeln zurückzuführen.

Fische nehmen eine bedeutende Rolle im Nahrungsnetz der Hochantarktis ein. Zum einen findet sich unter den Arten eine hohe funktionale (trophische) Diversität, zum anderen stellen Fische eine der Hauptnahrungsquellen für eine Vielzahl warmblütiger Tiere, wie z.B. Pinguine und Robben. Bodenfischgemeinschaften scheinen relativ resistent gegenüber Artverlust und Schwankungen der Nahrungsquellen zu sein, da diese Arten eine hohe funktionale Redundanz aufweisen und überwiegend Generalisten mit einem sehr breiten Nahrungsspektrum sind. Die pelagische Fischgemeinschaft auf dem Schelf scheint hingegen sehr empfindlich gegenüber Veränderungen zu sein. Die pelagische Fischfauna wird deutlich von einer einzigen Art dominiert: dem Antarktischen Silberfisch, *Pleuragramma antarcticum*. Diese Art zeigt eine Art von Schwarmverhalten und unternimmt tägliche Vertikalwanderungen zwischen dem Meeresboden und oberen Wasserschichten. Hierdurch stellt *P. antarcticum* eine effizient nutzbare Nahrungsquelle und eine der wichtigsten trophischen Verbindungen zwischen kleinen pelagischen Invertebraten, benthischen und pelagischen Piscivoren und warmblütigen Top-Prädatoren dar. Diese Fischart nimmt in der Hochantarktis offensichtlich eine ähnliche ökologische Rolle ein wie Krill, *Euphausia superba*, in der saisonalen Meereis-Zone. *P. antarcticum* hat ein sehr enges Nahrungsspektrum und wird somit sehr empfindlich auf Schwankungen der Nahrungsressourcen reagieren. Der Verlust dieser Art wird vermutlich durch keine andere Art auf dem Schelf vollständig kompensiert werden können. *P. antarcticum* stellt demnach eine Achillesferse im marinen Ökosystem der Hochantarktis dar, und jegliche Art von Veränderungen im System, die diese Art direkt oder indirekt beeinträchtigen, kann fatale Auswirkungen auf die Funktion des gesamten Ökosystems haben.

B. OVERVIEW

C. PUBLICATIONS

D. SYNTHESIS

A. PREFACE

One of the most prominent features of the Antarctic ecosystem is the uniqueness of its fauna, above as well as below the ice and water surface. At the end of the 19th century knowledge about the Antarctic regions was still limited (see e.g. Fig. A1) and based on just a few expeditions (Anonymous 1887). Within the last 100 years our knowledge has improved considerably, but in fact we are just starting to comprehend structure, dynamics and functioning of the Antarctic marine ecosystem. The list of properly described species continues to grow for various taxonomic groups (e.g. Brandt et al. 2007, Eakin & Balushkin 2000, Chernova & Eastman 2001, Allcock et al. 2001), and the complex interactions among and within abiotic and biotic components of the system are not yet understood. While scientists are therefore still busy to unravel its mysteries, the Antarctic marine ecosystem is threatened by drastic environmental alterations due to climate change (Gille 2002, Curran et al. 2003, Murphy et al. 2007, Rignot et al. 2008). Alterations due to increasing water temperature are most evident off the Antarctic Peninsula, where significant spatio-temporal shifts in primary

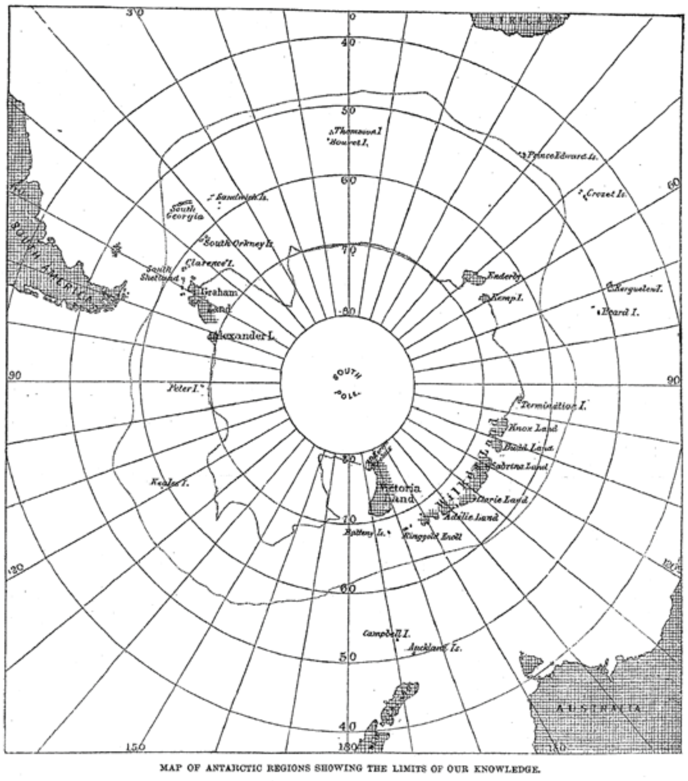

Fig. A1 Map of the Antarctic region published in "Science" in 1887 (Anonymous 1887) production and zooplankton composition due to reduced surface water salinity and a reduction in duration and extent of sea ice have been observed (Nicol et al. 2000, Loeb et al. 1997, Atkinson et al. 2004, Moline et al. 2004). So far, there is no significant increase in water temperature detectable in the high Antarctic, but indirect evidence from historical whaling records suggests that a major sea ice retreat occurred in the Weddell Sea during the 1960s (Cotté & Guinet 2007). In light of the continuing global warming trend, high Antarctic communities will most likely be affected by significant environmental alterations in the near future, as well.

As all organisms within an ecosystem are linked to each other directly or indirectly through feeding interactions, environmental changes not only affect physiological performance and survival of particular species but might also entail secondary effects. To evaluate ecosystem response to environmental change and its impact on overall ecosystem functioning, it is therefore essential to know about food web structure (“who eats whom”) within the system.

Fish are an integral part in marine ecosystems, including the Southern Ocean. Fish species often occupy a central position within the food web and are known to be affected by environmental alterations not only directly at the physiological level (e.g. McFarlane et al. 2000, Pörtner 2002) but also indirectly at the trophic level (Beaugrand et al. 2003, Benson & Trites 2002). Fish might thus (i) serve as a leading indicator of systemic changes, and (ii) changes affecting fish might cause dramatic alterations in overall food web structure. Deeper understanding of the functional role of fish in the Antarctic marine food web and species’ sensitivity to changes in other biotic compartments of the system will provide an important step towards the evaluation of food web stability and ecosystem resilience in the light of forthcoming climate change.

B. OVERVIEW

1. HOW TO STUDY TROPHIC RELATIONSHIPS

Different approaches are used to study trophic relationships among organisms. The most traditional methods are observations of feeding habits, experimental feeding studies in captive animals, and analyses of scats and stomach contents. Direct observations on feeding habits might be useful in terrestrial animals but are rather difficult if not impossible in aquatic ecosystems. Experimental studies provide insight into feeding behaviour and prey preferences, but give no information about prey composition in a consumer's natural environment. Diet analyses based on scats are (1) difficult to apply in aquatic animals, and (2) might result in underestimation of particular prey items, as in scats mainly hard remains (e.g., fish otoliths, squid beaks) persist digestion during gut passage. Modern methods which become increasingly relevant to marine ecologists include the analysis of organisms' fatty acid composition (see, e.g., Iverson et al. 2004, Nyssen et al. 2005) and tissue stable isotope composition.

This thesis is largely based on results of analyses of stomach contents and stable isotope composition, and therefore, these two methods are illuminated in more detail below.

1.1 Stomach Content Analyses

The analysis of stomach content provides detailed insight into an organism's food composition. This method often allows precise identification of prey species, as well as estimates of body-size, abundance, biomass and frequency of occurrence of particular prey in a consumer's diet (e.g., Hyslop 1980, Publication III). Estimates of stomach fullness (either gravimetric or using indices) and state of prey digestion (see, e.g., Dalpado & Gjøsæter 1988) make stomach content analyses a valuable tool to evaluate daily rations and evacuation rates (Olaso et al. 2004, Montgomery et al. 1989, Boyce et al 2000), and to trace diel feeding patterns (e.g., Carpentieri et al. 2006; Publication III). Usually, the consumers of interest are killed and stomachs or whole gastrointestinal tracts are removed and investigated, but non-lethal removal of stomach content, e.g. by stomach flushing, is also possible and often applied in vertebrates (Hyslop 1980, Light et al. 1983, Arnould & Whitehead 1991, Piatkowski & Vergani 2002).

Data obtained by means of stomach content analyses provide a multitude of useful information. Knowledge on detailed food composition helps to identify ultimate food sources (benthic *vs*. pelagic, inshore *vs*. offshore, autochthonous *vs*. allochthonous, etc.). A species' feeding strategy (specialist *vs.* generalist consumer) can be inferred from prey diversity (Publication IV) and prey evenness (e.g., according to Pielou 1966). The importance of particular prey items in a consumer's diet can be estimated either graphically (Cortés 1997; see Fig. B1) or arithmetically, for example by calculating main food indices (Publication XIII). Calculations of diet overlap between co-existing species (e.g., Colwell & Futuyama 1971) allow the assessment of food competition. Detailed information on "who eats whom", moreover, provides the essential base for comprehensive studies on community characteristics, such as consumer-resource body-size relationships (Publication VIII & X), and for models on food web structure, dynamics and stability (e.g., Jarre-Teichmann et al. 1995, Dunne et al. 2005).

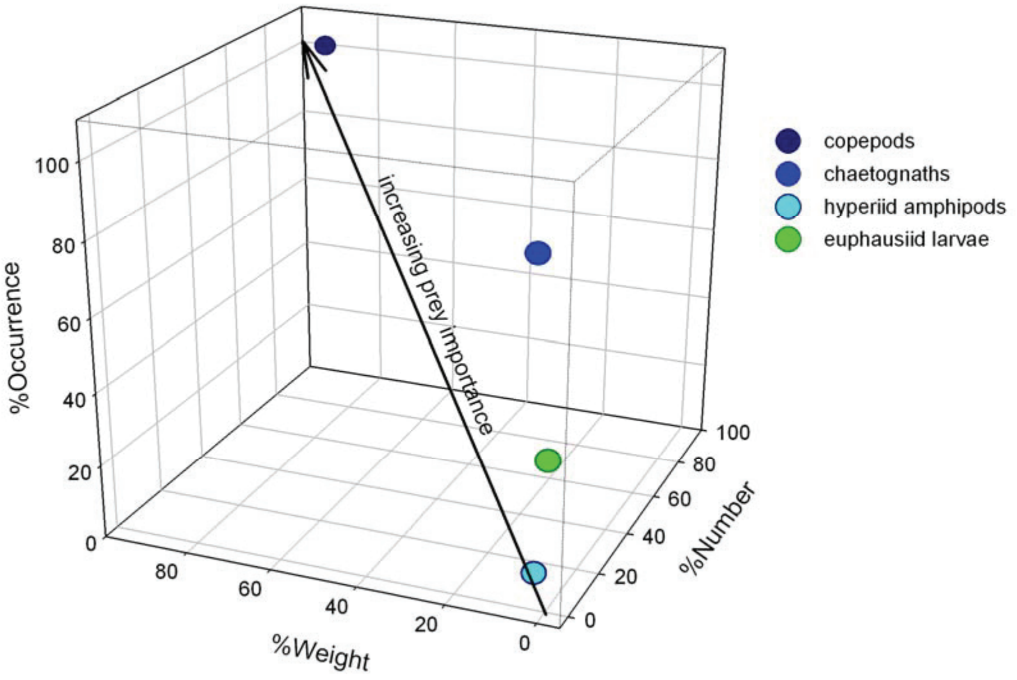

Fig. B1 Three-dimensional graphical representation of stomach content data according to Cortés (1997). This example shows food composition of the fish species *Pleuragramma antarcticum* (N = 10).

However, this method also involves some drawbacks: The investigation of stomach contents can be easily performed in larger animals such as fish but becomes increasingly complicated with decreasing organism size (e.g., in zooplankton). The detailed analysis of food composition is very time-consuming and the results often represent only a snapshot of an organism’s diet in time and space. Moreover, stomach content data reflect what was ingested but do not provide information about what is really assimilated. Last but not least digestion rates differ strongly between prey types, which might result in considerable underestimation of, for example, the contribution of gelatinous prey to bulk diet (Montgomery et al. 1989, Arai et al. 2003).

1.2 Stable Isotope Analyses

During the past 20 years the analysis of naturally-occurring stable isotopes of carbon (^{12}C and ^{13}C) and nitrogen (^{14}N and ^{15}N) has become a widespread tool in studies on trophic patterns within communities and energy transfer along food chains (e.g., Fry 1988, Harvey & Kitchell 2000, Polunin et al. 2001). Stable isotopes are atoms of an element that differ in atomic mass and do not decay with time (in contrast to their radioactive counterparts). The abundance of the heavy and the light stable isotope in a sample and the isotope ratio ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) are determined by means of an isotope ratio mass spectrometer (IRMS). Because differences between absolute isotope abundances are typically small and subject to natural fluctuation (e.g. within the mass spectrometer), the isotope ratio of the sample (R_{sample}) is compared relative to a standard ($R_{standard}$) (see, e.g., Lajtha & Michener 1994):

$$\delta = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000 \ [‰] \tag{1}$$

The conventional standards are a marine limestone fossil, Pee Dee Belemnite (PDB), for carbon and atmospheric air (N_2) for nitrogen. The deviation from this standard is given in delta (δ) notation ($\delta^{13}C$, $\delta^{15}N$) and expressed in per mill (‰, parts per thousand). The mass spectrometer is typically coupled to an elemental analyzer that provides additional data on sample bulk carbon and nitrogen content and C/N ratio (molar or by mass).

Stable isotope analysis is a useful technique in food web research because the isotopes of an element differ in their reaction rates (due to different atomic masses), and consequently, many physical and chemical processes result in isotope fractionation.

During photosynthetic carbon assimilation in photoautotrophic primary producers processes involved in carbon fixation discriminate against the heavier isotope (^{13}C), plants are consequently isotopically "lighter" than their inorganic carbon source (e.g., Park & Epstein 1961). During heterotrophic food assimilation, in contrast, enzymatic reactions discriminate against the lighter isotopes (^{12}C and ^{14}N) and consumers thus tend to be isotopically "heavier" than their food source. The per-trophic-step increase in $\delta^{13}C$ and $\delta^{15}N$ along a food chain is supposed to be rather consistent (though this applies to $\delta^{13}C$ to a limited extent only, see below), and $\delta^{13}C$ and $\delta^{15}N$ values of a consumer therefore reflect isotopic composition of its diet plus a few per mill ("You are what you eat", see Fig. B2). $\delta^{13}C$ and $\delta^{15}N$ values of a consumer integrate the isotopic signatures of the assimilated food (not only ingested prey as do stomach content analyses, see above), which with the time scale is proportional to tissue turnover time (Hobson & Clark 1992).

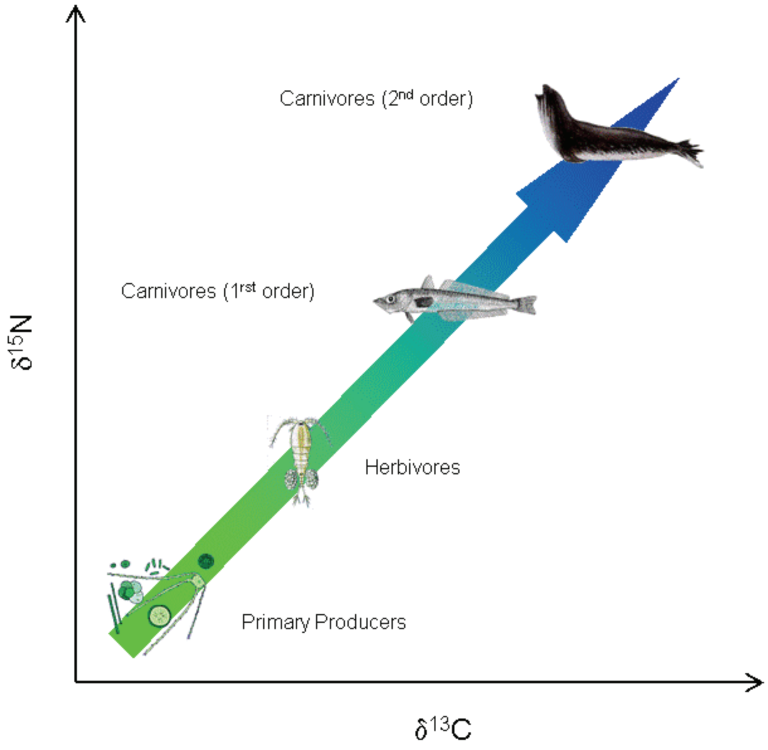

Fig. B2 Illustration of a simple theoretical food chain based on $\delta^{13}C$ and $\delta^{15}N$ measurements

$\delta^{13}C$ increase per trophic transfer is small and usually accounts for less than 1 ‰ (Fry & Sherr 1984, McConnaughey & McRoy 1979, Rau et al. 1983). As there are pronounced differences in primary producer $\delta^{13}C$ depending on location (e.g., latitude or altitude, Rau et al. 1982, Hobson et al. 2003), taxonomical affiliation (e.g. phytoplankton *vs.* macroalgae), and photosynthetic pathway (C_3 *vs.* C_4 *vs.* CAM) (Fry & Sherr 1984, O'Leary 1981), $\delta^{13}C$ provides a useful tracer of primary carbon sources. The increase in $\delta^{15}N$ is more pronounced and averages about 3.3 ‰ per trophic step, making $\delta^{15}N$ a valuable indicator of an organism's trophic position within a food web (DeNiro & Epstein 1981, Minagawa & Wada 1984, Wada et al. 1987, Vander Zanden & Rasmussen 2001). Accordingly, a consumer's trophic level ($TL_{consumer}$) can be approximated by

$$TL_{consumer} = \frac{(\delta^{15}N_{consumer} - \delta^{15}N_{base})}{3.3} + \lambda \tag{2}$$

where $\delta^{15}N_{consumer}$ is the isotope ratio measured in the consumer of interest, $\delta^{15}N_{base}$ is the ratio of the chosen base, and λ is the trophic position of the organism used to estimate $\delta^{15}N_{base}$ ($\lambda = 1$ for primary producers, $\lambda = 2$ for primary consumers) (see Post 2002a). Because of high temporal within-system as well as between-system variability in $\delta^{15}N$ of primary producers such as phytoplankton, primary consumers are usually the most suitable isotopic base of choice for trophic level estimates (e.g., Vander Zanden & Rasmussen 1997). By integrating the assimilation from all trophic pathways leading to the consumer, $\delta^{15}N$ provides a continuous measure of an organism's trophic position in a particular food web. When these different trophic pathways (e.g., from feeding observations or stomach content analyses) and isotopic signatures of sources are known, the partitioning of sources that contribute to the mixed isotopic signature in a consumer can be calculated by mixing models based on mass balance (Phillips & Gregg 2003).

Stable isotope signatures are used to study trophic structure and food web dynamics of ecological communities (e.g., Post 2002a, Rau et al. 1991a, 1992, Hansson & Tranvik 2003, Kaehler et al. 2000, Nyssen et al. 2002, PUBLICATION IX), to trace species origin and migrations (Cherel et al. 2000, Hobson 1999, Hobson et al. 1999, 2003, Hansson et al. 1997, Kline et al. 1998), and to assess the impact of environmental disturbance (Chasar et al. 2005) and human activities such as fishery on living communities (Jennings et al. 2001, PUBLICATION VII). Stable isotope measurements (particularly δ^{15}N) are an integral part in studies on general food web paradigms such as the potential relation between trophic position and body size (Jennings et al. 2002a,b, Layman et al. 2005), and have proved to be also a valuable tool to trace accumulation and magnification of contaminants along food chains (Hansson et al. 1997, Atwell et al. 1998, Ruus et al. 2002). Moreover, within-population variability in stable isotope ratios was recently proposed as a descriptor of omnivory (Sweeting et al. 2005) and even as a measure of trophic niche width (Bearhop et al. 2004).

However, though the use of stable isotopes in trophic ecology is widely accepted there are still some potential sources of error and uncertainties that have to be taken into account. Isotopic fractionation of both carbon and nitrogen and thus per-trophic-step enrichment differs between tissue types (Hobson et al. 1996, Pinnegar & Polunin 1999). ^{15}N enrichment seems to vary depending on an organism's biochemical form of nitrogen excretion (Vanderklift & Ponsard 2003). δ^{13}C is known to vary depending on tissue $CaCO_3$ content (PUBLICATION XI) and on tissue lipid content, as lipids are depleted in ^{13}C isotope compared to protein and carbohydrate fractions (Parker 1964, Smith &

Epstein 1970, DeNiro & Epstein 1978). Whether or not starvation affects tissue stable isotope ratios is still not clear (compare Olive et al. 2003, Hobson et al. 1993 versus Gorokhova & Hansson 1999, Frazer et al. 1997, Tamelander et al. 2006). To some extent, this variability may be kept at minimum by sampling of uniform tissue type (e.g., muscle tissue) and the removal of inorganic carbonates and lipids from samples prior to analyses. However, sample treatment itself might introduce large bias into stable isotope estimates. For example, chemical sample preservation in ethanol or formalin alters tissue isotope signatures (Kelly et al 2006, Kaehler & Pakhomov 2001, Bosley & Wainright 1999, Sarakinos et al. 2002) with the magnitude of isotopic change obviously depending on tissue biochemical composition (Sweeting et al. 2004). The most appropriate preservation method of samples for stable isotope analysis seems to be immediate freezing (Bosley & Wainright 1999, Ponsard & Amlou 1999, Sweeting et al. 2004). Samples have to be lyophilized and ground to powder prior to analysis without interruption of the cooling chain before freeze-drying, because defrosting and tissue rotting significantly alter both δ^{13}C and δ^{15}N (Dannheim et al. 2007, Ponsard & Amlou 1999). To remove inorganic carbonate samples are often acidified with HCl, but the technique applied should be carefully chosen to avoid effects on δ^{15}N (Bunn et al 1995, Bosley & Wainright 1999, PUBLICATION XI). Extraction of lipids from sample tissue using polar organic solvents is also commonly applied to reduce δ^{13}C variability due to differing fat content (e.g., Gu et al. 1997, Carseldine & Tibbets 2005). Lipid extraction, however, might affect δ^{15}N as well but the magnitude of isotopic shift, potential causes for effect variability, and the mechanisms involved are still not clear (Pinnegar & Polunin 1999, Sotiropoulos 2004, Sweeting et al. 2006, Bodin et al. 2007). To avoid the bias introduced by chemical lipid extraction, various mathematical δ^{13}C lipid normalization and correction models have been developed (McConnaughey & McRoy 1979, Kiljunen et al 2006, Sweeting et al. 2006, Post et al 2007), most of which are based on empirical relationships between lipid content and C/N ratio and C/N ratio and δ^{13}C. The general suitability of these models, however, remains questionable.

Despite intense research on stable isotope biochemistry and ecology since decades, there is still a multitude of open questions. Many treatment induced effects and their causes are not yet fully understood and a uniform treatment procedure is still lacking.

SUMMARY - HOW TO STUDY TROPHIC RELATIONSHIPS

In this thesis trophic relationships are investigated based on stomach content analyses and stable isotope analyses (δ^{13}C and δ^{15}N).

- ***stomach content analysis* provides detailed information on ingested prey but the method is time-consuming and represents only a snapshot of an organism's diet;**
- ***stable isotope analysis* provides a useful and simple tool to estimate an organism's trophic position within a particular food web and to trace primary carbon sources; isotopic signatures of assimilated food are integrated over relatively long time scales; however, there are potential sources of error introduced by sample preparation and treatment, as well as natural variability in δ^{13}C and δ^{15}N that needs to be taken into account!**

2. THE ANTARCTIC MARINE ECOSYSTEM

The Southern Ocean surrounding the Antarctic continent represents one of the most unique marine environments on earth. Long evolutionary history and geographic as well as oceanographic particularities of the Southern Ocean ecosystem have resulted in modern biota that differ from those found elsewhere in the world’s oceans (see, e.g., Knox 1994). In contrast to sub-Antarctic regions, the high Antarctic is, except for the removal of large baleen whales in the 1950-60s, one of the last regions on earth almost free from human impact such as fishery or habitat destruction. Based on current knowledge, the most important characteristics, processes and interaction of the Southern Ocean marine ecosystem and particularities of Antarctic marine living communities are described below.

2.1 Geographical & Physical Characteristics

The Antarctic is geographically isolated from other continents by great distances (>1000 km to South America, >3000 km to South Africa and Australia) and large abyssal basins of more than 4000 m depth surrounding the continent. The only connection to other continents with in general less than 2000 m water depth is the Scotia Ridge composed of numerous islands which link South America to the Antarctic Peninsula (Tomczak & Godfrey 1994, Arntz et al. 2005). The Atlantic, Indian and Pacific basins are connected by the Antarctic Circumpolar Current (ACC) flowing eastward. The ACC, driven by strong westerly winds, encircles the whole continent and includes the Antarctic Polar Front, a region of downwelling and sharp temperature change of 3-4°C (Knox 1970). The ACC thus acts as a thermal barrier by keeping warm ocean water

away (see, e.g., Orsi et al. 1995). As a result, water temperatures in the Southern Ocean are consistently low (about -1.86°C close to the continent) with little seasonal variation (Deacon 1984). Close to the continent, the Antarctic Coastal Current (East Wind Drift) flows in the opposite direction and forms clockwise gyres in the Weddell Sea, Ross Sea and Bellingshausen Sea (Gordon & Goldberg 1970). The region between both current systems is an area of wind and density driven upwelling of nutrient rich circumpolar deep water (Antarctic Divergence), overlaid by Antarctic surface water in the upper layers (see, e.g., Eastman 1993).

Beside the unique current system the most important physical feature structuring the Antarctic marine ecosystem is the ice. The whole Antarctic shelf is narrow and depressed by the large continental ice sheet to depths of about 200-600m. The continental ice sheet extends far beyond the coastline and is a major source of calving icebergs (Nicol & Allison 1997), which significantly affect vast areas of the shelf by grounding and seabed scouring (e.g., Gutt 2001).

Sea ice is present all year round but overall coverage varies strongly with season, ranging from 4×10^6 km^2 in austral summer to up to 20×10^6 km^2 in winter (Zwally et al. 1983, Nicol & Allison 1997). Most areas of the high Antarctic (e.g., vast parts of the Weddell Sea), close to the continent, are almost permanently covered by ice and belong to the so-called *high-Antarctic zone* or *perennial pack ice zone* (Fig. B3). The adjacent *seasonal sea ice zone* is characterized by open water in summer and ice coverage in winter. The transition zone from sea ice to the ice free open ocean, the *marginal ice zone*, is a region of enhanced ice drift, fragmentation and deformation, and ice-ocean interaction (see Eicken 1992). Dynamics of sea ice significantly affect stratification of the underlying water column. During autumn the depth of the mixed layer in the ice-free zone is mainly determined by the wind regime. During ice formation and growth cold and highly saline (and thereby highly dense) sea water is ejected from the ice into the water below, resulting in thermo-haline convection and a deepening of the mixed layer (and the pycnocline) to a depth of 50-200m. In spring during sea ice melt, the entry of freshwater with low density lowers and stabilizes the pycnocline (Eicken 1995, Gordon et al. 1984). Light conditions in the Antarctic and in the upper layer of the Southern Ocean also undergo strong seasonal variations ranging from 24 hours of light in summer to complete darkness during the winter months.

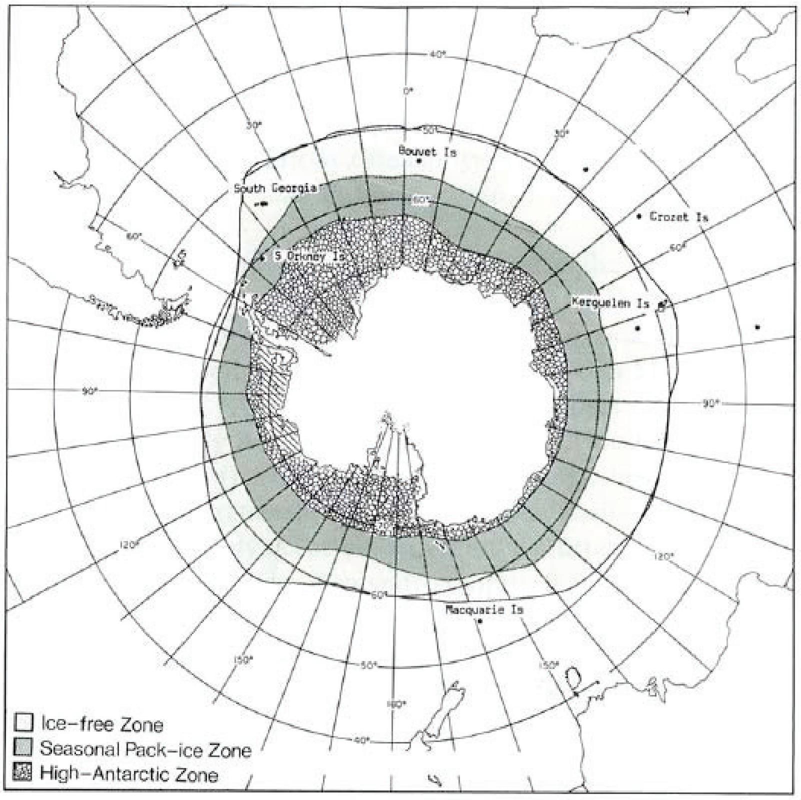

Fig. B3 Zonation of the Southern Ocean marine environment and approximate position of the Antarctic Convergence (indicated by the line; source: Kock 1992)

However, despite these strong seasonal fluctuations in ice coverage and light regime, general geographical and physical conditions in the Antarctic marine environment (isolation, low water temperatures, seasonal ice coverage) have been quite stable since more than 20 million years (see, e.g., Dayton 1990, and citations herein).

2.2 Biological Characteristics

The enduring existence of a permanently cold and isolated environment over long time scales allowed for the evolution of unique and well adapted Antarctic marine biota characterized by a high degree of endemism and eco-physiological adaptations to life in cold water conditions. Particularly in the high Antarctic primary production as well as organisms' life cycles and strategies are closely coupled to the seasonal sea ice dynamics described above.

During winter autotrophic primary production is low and mostly restricted to the sea ice (Arrigo et al. 1997, Lizotte 2001). During spring and summer, when the sea ice is melting, the released ice algae fuel subsequent phytoplankton blooms in the shallow and stable mixed layer of the marginal ice edge (Lizotte 2001, Smith & Nelson 1986). In autumn sea ice extends again and remaining algae are incorporated into newly formed ice (e.g. Melnikov 1998). Phytoplankton blooms, mainly composed of large diatoms and *Phaeocystis* (Nöthig et al. 1991, Estrada & Delgado 1990), account for most of the annual primary production in the Southern Ocean but their occurrence is temporarily and spatially restricted (e.g., Smith & Sakshaug 1990, Scharek & Nöthig 1995). Small-sized pico- and nanoplankton, in contrast, is present in the water column throughout the whole year. Though this component achieves much lower biomass and productivity than the bloom system, the pico- and nanoplankton fraction builds a constant and persistent component of Antarctic phytoplankton communities throughout the whole year (Detmer & Bathmann 1997, Scharek & Nöthig 1995).

The pelagic fauna of the Southern Ocean is mainly composed of copepods, salps, fish larvae, chaetognaths and euphausiids, larger pelagic predators include squid and fish (Siegel et al. 1992, Hempel 1985). Antarctic krill, *Euphausia superba*, is distinctly dominating the community in the seasonal sea ice zone and life history pattern of this species is closely linked to the seasonal sea ice cycle (Smetacek et al. 1990). In the permanent pack ice zone, *E. superba* is replaced by the smaller euphausiid species *E. crystallorophias* (e.g., Hempel 1985). Most pelagic grazers (*E. superba*, *E. crystallorophias*, herbivorous copepods) and predators (chaetognaths, carnivorous copepods) are present and feeding in the upper water column or at the ice underside the whole year round (Bathmann et al. 1991, Marshall 1988, Smetacek et al. 1990, Øresland 1995).

The benthic community on the continental shelf and upper slope is characterized by extraordinarily high biomass and diversity (Dayton et al. 1994, Brey & Gerdes 1997, Gutt et al. 2004). Most benthic invertebrates are slow growing and reproduction rates are in general low (Brey & Clarke 1993, Arntz et al. 1994). Benthic shelf communities are distinctly dominated by suspension-feeding species such as sponges, and in some regions also by deposit feeders (e.g., echinoderms; Gutt & Starmans 1998, Voss 1988, Dayton et al. 1974). In particular large sponges form a typical 3-dimensional habitat for a diverse invertebrate community in vast areas (Arntz et al. 1994, Gutt & Starmans 1998). Regionally, benthic community structure is shaped by physical disturbance due to iceberg scouring (e.g., in Austasen, northeastern Weddell Sea shelf). Local disturbance of the seafloor by icebergs results in a patchy distribution of various successional stages and increased between-habitat diversity (e.g., Gutt 2000, 2001, PUBLICATION V & XII). Below the depth zone of macroalgal presence benthic consumers depend on pelagic production (e.g., Mincks et al. in press, PUBLICATION IX). On the high Antarctic continental shelf, where benthic macroalgae are completely absent, tight bentho-pelagic coupling therefore plays an important role. The high benthic biomass found on the shelf indicates a highly efficient transfer of organic matter from surface waters towards the seafloor (e.g., Smith et al. 2006). The vertical export of energy is driven either passively, via sinking particulate organic matter (POM), or actively by organisms carrying out vertical migrations within the water column.

POM provides the major food source for suspension and deposit feeders. The vertical export flux and POM composition at any water depth are a function of particle sinking velocity, aggregate coagulation and fragmentation, and consumption by zooplankton and microorganisms (Kiørboe 2000, 2001; Lee et al. 2004), which result in the rapid decrease of bulk POM and the alteration of biochemical POM composition with increasing water depth (Suess 1980, Wakeham & Lee 1993, Boyd & Stevens 2002, Lam & Bishop 2007). Microbial degradation is evident in a depth related increase of POM C/N ratio (Yamaguchi et al. 2005, Gordon 1971, 1977, Wefer et al. 1982, Smith et al. 1992, Tanoue & Handa 1979) and stable isotope ratio δ^{15}N (Altabet & Francois 2001, Altabet & McCarty 1986, Biggs et al. 1987, Guo et al. 2004, Rau et al. 1991b, Saino & Hattori 1980, 1985, 1987, Wu et al. 1999).

Sinking velocity ν [cm d^{-1}], and thus residence time in the water column, are a function of particle size and density and can be calculated using Stoke's law (see, e.g., Vogel 1995):

$$\nu = d^2 (\rho_p - \rho_s) g / (18 \eta) \qquad (3)$$

where d is the particle diameter [cm], ρ_p is the particle density [g cm^{-3}], ρ_s is the seawater density [g cm^{-3}], η is the seawater viscosity [g cm^{-1} s^{-1}] and g is the acceleration due to gravity (g = 981 cm s^{-1}). Faecal material such as krill faecal strings is most rapidly sinking out of the euphotic zone due to high density and large size (see Fig. B4). The significance of faecal material in vertical organic matter transport is widely recognized (Dilling & Alldredge 1993, Iseki 1981, Le Fèvre et al. 1998, Fortier et al. 1994) and these particles presumably make up the major part of organic matter that is deposited in the sediment. Diatoms aggregated to large chains might exhibit sinking velocities of up to 50m day^{-1}. Sinking velocities of small-sized pico- and nano-phytoplankton cells (0.1 – 20µm) are very low.

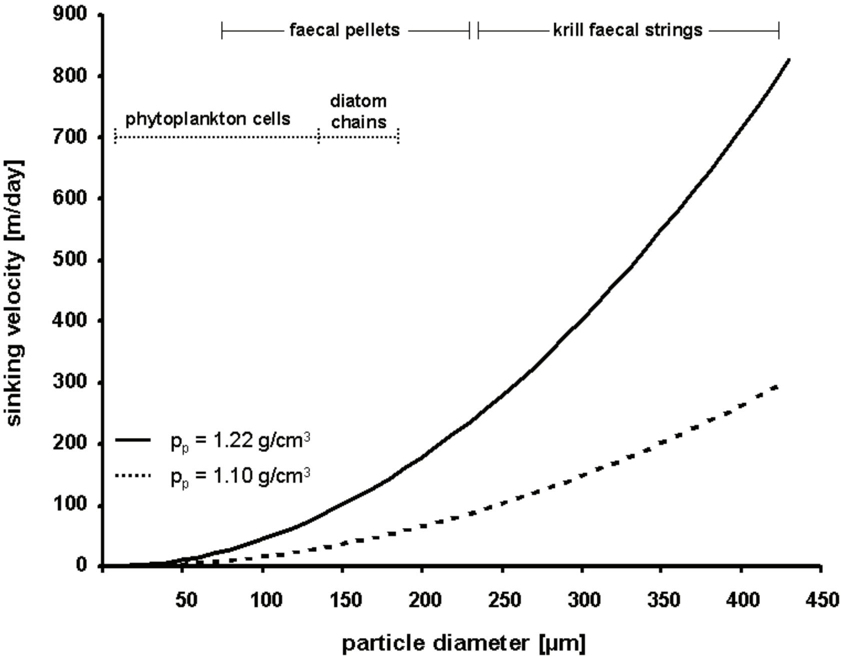

Fig. B4 Sinking velocity v [m d^{-1}] of various particles as a function of diameter d [µm] and density p_p [g cm^{-3}]. p_p = 1.1g cm^{-3} for phytoplankton particles (van Ierland & Peperzak 1984; dotted line), and p_p = 1.22g cm^{-3} for faecal pellets and faecal strings (Komar et al. 1981; solid line). The indicated size ranges of faecal material and diatom chains are taken from Bathmann et al. (1991) and Peperzak et al. (2003). Seawater density and viscosity are assumed to be constant along the water column, with ρ_s = 1.03g cm^{-3} and η = 0.02g cm^{-1} s^{-1} (35‰ salinity, -1.8°C)

Accordingly, POM flux in deeper water layers of the Weddell Sea is dominated by faecal pellets, krill faecal strings and large diatoms (Nöthig & von Bodungen 1989; Bathmann et al. 1991, Fischer 1989, von Bodungen et al. 1988). Mass sedimentations of ice-algae, *Phaeocystis* or diatoms after ice melt and termination of blooms are seasonally important (see, e.g., Riebesell et al. 1991, Scharek et al. 1999, DiTullio et al. 2000) but short-term events, whereas faecal pellets are produced the whole year round.

However, zooplankton organisms not only contribute to vertical energy export by faecal pellet production, but also by active diel vertical migration (e.g., Morales 1999, Steinberg et al. 2000). Many organisms, including krill (*Euphausia superba*), copepods and salps ingest large amounts of particles in the euphotic zone during night and spend the rest of the day in deeper water layers (Casareto & Nemoto 1986, Hernández-Léon et al. 2001, Wiebe et al. 1979, Gili et al. 2006, Zhou & Dorland 2004, Tarling et al 2002, Atkinson et al. 1992) where they provide an important food source for epibenthic predators (e.g., fish, Mintenbeck 2001) and even for some suspension feeders (Orejas et al. 2001). The linkage between pelagic and benthic communities by migrating animals is a common phenomenon in aquatic ecosystems worldwide, but driving forces for vertical migration, their potential interaction and flexibility are under discussion (predator-avoidance hypothesis, Hays 2003, Lampert 1993; hunger-satiation hypothesis, Pearre 2003; adaptive decision making, Lima & Dill 1990).

The marine living communities of the Southern Ocean are exploited by a multitude of warm-blooded animals. Whales and seabirds are seasonal guests foraging in the seasonal sea ice zone and under the pack ice during summer (van Franeker et al. 1997, Murase et al. 2002, Boyd 2002). Penguins (mainly Emperor penguin, *Aptenodytes* *forsteri*, and Adélie penguin, *Pygoscelis adeliae*) and seals (Weddell seal, Ross seal, Crabeater seal, Fur seal, Elephant seal) are permanent inhabitants of Antarctic coastal areas. In particular extensive cracks in the ice shelf covered by sea ice, such as the Drescher Inlet in the Riiser-Larsen Shelf ice (eastern Weddell Sea) are important breeding and foraging grounds for Weddell seals and large Emperor penguin colonies (Plötz et al. 1987).

For a long time, scientists kept hold of the concept of a typical short and simple Antarctic food chain from diatoms to krill to consumers. Krill, *Euphausia superba*, was regarded as inexhaustible resource and the base of the whole Antarctic food web, supporting fish, penguins, seabirds, seals and whales (see, e.g., Murphy 1962). However, this paradigm is apparently too simple: Krill not only feeds on diatoms (Hewes et al. 1985, Scharek & Nöthig 1995, Hérnandez-Léon et al. 2001) and vertebrate consumers do not feed exclusively on krill (e.g. Boyd 2002, Ridoux & Offredo 1989, Schwarzbach 1988). Krill indeed seems to be a key species in the marine high Antarctic (particularly in the seasonal sea-ice zone), but high benthic species diversity and tight bentho-pelagic coupling point towards a more complex system where the diatom-krill-consumer chain is only one component of a highly complex food web (*c.f.* Clarke 1985, Jarre-Teichmann et al. 1995).

2.3 Southern Ocean Fish Communities

The fish fauna of the Southern Ocean is distinctly dominated by a single taxonomic group, the perciform suborder Notothenioidei, which accounts for about 35% of species (Eastman 1993). In shelf areas, e.g. on the northeastern Weddell Sea shelf, dominance of notothenioids increases to up to 98% of fish abundance and biomass

(Knust, Schröder, Mintenbeck; unpublished data). All in all 96 notothenioid fish species have been described in the Southern Ocean (Eastman & Eakin 2000) but still new species are discovered (see, e.g., Eakin & Balushkin 1998, 2000; Eakin & Eastman 1998). About 97% of notothenioid species are endemic (Andriashev 1987) and are mainly represented by 5 families (Nototheniidae, Channichthyidae, Artedidraconidae, Bathydraconidae, Harpagiferidae). Typical members of boreal and upwelling fish communities, such as clupeids, are absent. Non-notothenioid fish species inhabiting the Southern Ocean for the most part belong to typical deep sea groups such as zoarcids, liparids, macrourids and myctophids. Occurrence of these groups is largely restricted to the lower slope and the deep-sea where notothenioid fish are almost absent (Boysen-Ennen & Piatkowski 1988; Donnelly et al. 2004, Gon & Heemstra 1990, Kock 1992).

The composition of shelf and upper slope fish communities differs regionally (see Hureau 1994, Kock 1992). In the seasonal sea ice zone, including sub-Antarctic island shelves and at the northern tip of the Antarctic Peninsula, the fish fauna is dominated by the notothenioid species *Notothenia* spp., *Lepidonotothen* spp. *Gobionotothen* spp., *Champsocephalus gunnari*, *Chaenocephalus aceratus* and harpagiferids (Everson 1969, Kock 1982, Kock & Stransky 2000, Duhamel 1987, Mintenbeck et al. 2003). Pelagic fish communities are composed of the few Antarctic myctophid species and early life history stages of notothenioids (Hureau 1994, Kellermann 1986). High Antarctic shelf communities in the Weddell and Ross Seas are dominated by several *Trematomus* species, *Dolloidraco longedorsalis* and *Chionodraco myersi* (Schwarzbach 1988, Eastman & Hubold 1999, Hubold 1992). These communities are also characterized by high proportions of artedidraconid and bathydraconid species. Harpagiferids and

Lepidonotothen species are almost absent. The pelagic fish fauna above the high Antarctic shelf is mainly composed of the species *Pleuragramma antarcticum* (Nototheniidae) and notothenioid larvae and juveniles (Hubold & Ekau 1987, Granata et al. 2002). Despite limited space on the narrow shelf and sponges with low nutritive value (Barthel 1995) dominating benthic communities (see above) high Antarctic fish assemblages are characterized by high species diversity (Hubold 1992, Eastman & Hubold 1999, Schwarzbach 1988). This high biodiversity is supposed to be (at least in part) the result of small scale horizontal and vertical niche separation (Schwarzbach 1988, PUBLICATION XIII).

The uniqueness of the Southern Ocean fish fauna with a single group dominating the whole community is the result of a long evolutionary history of adaptive radiation in isolation at sub-zero temperatures. Physiological adaptations, in particular antifreeze glycopeptides and reduced blood viscosity, enabled notothenioid species to survive under cold water conditions (e.g., Clarke & Johnston 1996). Due to the lack of competition from other fish groups, morphological and ecological diversification allowed for the occupation of numerous niches (e.g., Ekau 1988, Eastman & McCune 2000). Despite the lack of a swim bladder in all notothenioids, a few species even gained neutral buoyancy (e.g., the nototheniid *Pleuragramma antarcticum*) by anatomical modifications such as reduction in skeletal mineralization and lipid storages (Eastman & DeVries 1982, Eastman 1985a). Accordingly, notothenioid fish species occupy benthic, bentho-pelagic, pelagic as well as cryopelagic habitats. The majority of species, however, is more or less closely associated to the sea floor.

Eastman (2005) refers to the high Antarctic shelf as being an evolutionary hot spot and notothenioid fish can be regarded as a marine species flock (*sensu* Ribbink 1984), thereby resembling fish assemblages in some ancient African lakes (Eastman & Clarke 1998, Eastman & McCune 2000). However, physiological adaptation to sub-zero temperatures also involves some impairment, such as cold-stenothermy (Somero & DeVries 1967, Somero et al. 1998) and limited aerobic capacity, e.g., in haemoglobin-less icefishes (reviewed in Kock 2005). As in most invertebrates inhabiting the Southern Ocean (see above) life history traits of notothenioid fish are characterized by slow growth (reviewed in La Mesa & Vacchi 2001), advanced age at first maturity (Kock 1992), and low fecundity (Duhamel et al. 1993) compared to many boreal and temperate fish species. Life cycles of most fish species also involve a prolonged pelagic larval stage (Kock & Kellermann 1991, Kock 1992).

Notothenioid fish play a central role in the high Antarctic food web. On the one hand, adaptive radiation also included trophic diversification (*c.f.* Ekau 1988, Schwarzbach 1988) and notothenioid fish occupy a multitude of trophic niches. Kock (1992) distinguished between five main feeding types according to their principal prey: benthos feeders, fish and benthos feeders, plankton and fish feeders, plankton and benthos feeders, and plankton feeders. As some species such as the channichthyid *Dacodraco hunteri* rely almost exclusively on fish (Schwarzbach 1988, Eastman 1999) a sixth group of pure “fish feeders” does also exist. On the other hand, notothenioid fish are preyed upon by all high-level predators inhabiting the Southern Ocean, including piscivorous fish, cephalopods, penguins, sea birds, seals, and whales (for review see Kock 1992, Hureau 1994, La Mesa et al. 2004). Notothenioids thus provide an important link between small sized invertebrates and the top predators of the Antarctic marine ecosystem. Moreover, recent evidence indicates vertical migrations of the species *Pleuragramma antarcticum* within the water column (Plötz et al. 2001, Fuiman et al. 2002); i.e. notothenioid fish might also play a significant role in bentho-pelagic coupling (see also above).

SUMMARY - THE ANTARCTIC MARINE ECOSYSTEM

The Southern Ocean represents one of the most unique environments on earth. General geographical and physical conditions have been more or less stable since >20 million years, and allowed for the evolution of exceptional living communities. The most important characteristics of this system are:

- **a narrow and depressed shelf of about 200-600m depths, geographical and thermal *isolation* of the fauna;**
- **sub-zero water temperatures, strong *seasonal variability* in light regime, sea ice cover and primary production;**
- **high *endemism*, most organisms are physiologically adapted to cold water conditions;**
- **tight *bentho-pelagic coupling* via POM (passive) and organisms that undertake diel vertical migrations (active);**
- **Antarctic krill, *Euphausia superba*, is a major component of the *zooplankton community*, particularly in the seasonal sea ice zone;**
- **high benthic biomass and diversity, the *benthic community* is dominated by suspension and deposit feeders;**
- **fish play an important role in the food web, *fish communities* are distinctly dominated by one group, the perciform suborder Notothenioidei, and this group is characterized by extraordinarily high diversity both in terms of species and trophic function.**

3. FOOD WEB STABILITY AND COMMUNITY RESILIENCE

Alteration of environmental parameters induced by climate change, particularly increasing temperature, may result in species extinctions (e.g., Thomas et al. 2004), species invasion (Stachowicz et al. 2002), changes in local community composition (Alheit et al. 2005, Attrill et al. 2007), and shifts in species' phenology (Edwards & Richardson 2004). Such direct, physiologically mediated effects on particular species might entail trophically mediated secondary effects and species extinctions owing to inappropriate resources, trophic mismatch, competitive exclusion (by invasive species) or trophic cascades. The risk of a particular species to be negatively affected by such indirect effects depends on its ability to cope with bottom up and top down effects and is, therefore, determined by (i) the species' plasticity to respond to resource fluctuations (consumer dietary generalism) and (ii) the species' exploitation or predator induced mortality. This "trophic vulnerability" (as opposed to "physiological vulnerability") can be inferred from the number of trophic linkages to prey species and predator species (Fig. B5; e.g., Memmot et al. 2000).

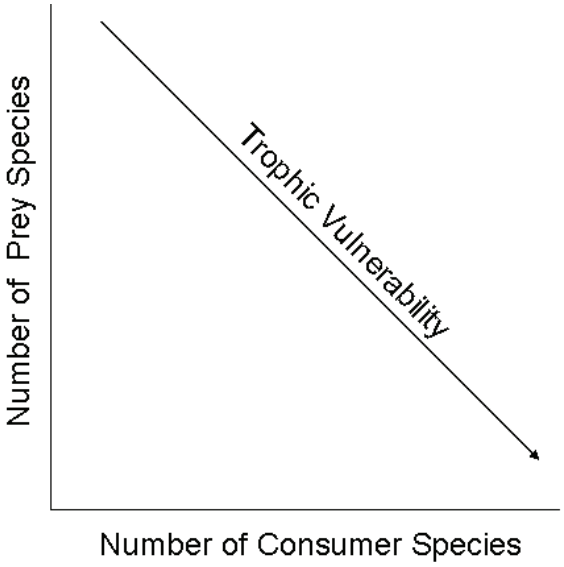

Fig. B5 Species trophic vulnerability as determined by dietary generalism and number of predators

The fundamental question regarding overall ecosystem functioning, however, is how community and ecosystem respond to (primary and/or secondary) species loss. Food web stability and community persistence seem to be ultimately determined by functional diversity and thus by trophic complexity (MacArthur 1955, Cardinale et al. 2006, Thébault & Loreau 2006, Duffy et al. 2007, McCann 2000). High diversity within trophic levels (horizontal diversity) and across trophic levels (vertical diversity, food chain length; see Duffy et al. 2007) indicates an increased number of trophic interactions and stabilizing weak trophic linkages in natural food webs (McCann et al. 1998, McCann 2000, Bascompte et al. 2005). High within-trophic level diversity further indicates niche overlap and thus high functional redundancy and trophic compensability (Fig. B6; Johnson 2000, Naeem & Li 1997, Naeem 1998). The effect of species loss on community persistence and ecosystem functioning therefore depends on the species' functional role within the food web and the communities' capacity for functional compensability.

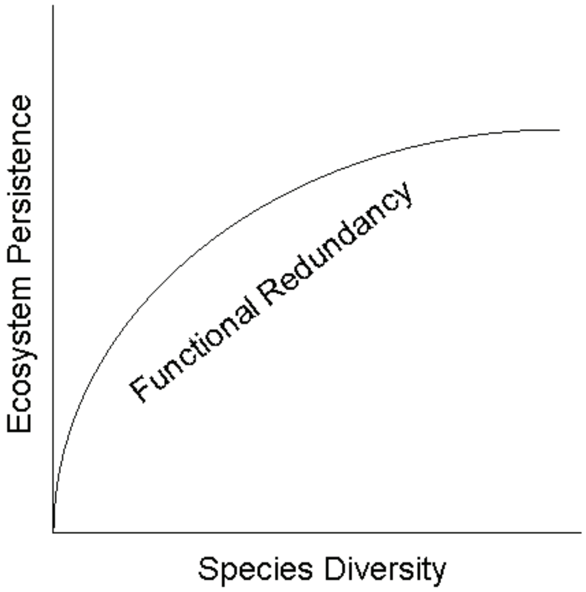

Fig. B6 Relationship between functional diversity and ecosystem persistence

SUMMARY – FOOD WEB STABILITY AND COMMUNITY RESILIENCE

Species are affected by environmental changes not only directly at the physiological level but also indirectly at the trophic level.

- **a species *trophic vulnerability* to changes in food web structure is determined by its trophic flexibility and generalism, and predator exploitation;**
- **consequences of species loss for overall food web structure depend on a species' *functional redundancy* and the communities' capacity for trophic compensability.**

4. THESIS OUTLINE

This thesis deals with the structure and complexity of the high Antarctic Weddell Sea food web and the identification of its functional components. As fish are an important component of the marine high Antarctic, the study mainly focuses on the functional role of fish in the food web, their trophic interaction with other organisms and their vulnerability to changes in food web structure in the light of forthcoming climate change. This thesis consists of four core publications (I-IV; see also PUBLICATIONS Chapter 1); other publications closely related to this thesis are listed as well (PUBLICATIONS Chapter 2).

Trophic relationships are investigated based on data of stomach contents and organisms' stable isotope signature of carbon and nitrogen (own analyses and published sources). The first, essential step towards a reliable stable isotope database is the analysis of potential sources of error and variability. Therefore, we investigated the potential bias introduced by different sample treatment techniques and data correction models (PUBLICATION I). Additionally, the advantage of the combination of stomach content data and stable isotope analysis is discussed in the synthesis. The high Antarctic shelf is a system of substantial water depth, dominated by suspension and deposit feeders. These organisms primarily rely on POM from the euphotic zone, and thus, on a highly dynamic and spatially variable food source. We investigated whether and how the natural variability in POM isotopic composition is reflected in POM consumers and discuss the potential consequences for stable isotope based food web studies (PUBLICATION II).

General structure and complexity of the Weddell Sea food web are elucidated in the synthesis. The majority of notothenioid fish species inhabiting the high Antarctic shelf are closely associated to the sea floor; one of the few exceptions is the Antarctic silverfish, *Pleuragramma antarcticum*, which is an important food source for warm-blooded animals such as seals and penguins. Recent evidence suggests that this species undertakes vertical migrations within the water column, and thereby possibly also contributes to bentho-pelagic coupling. We investigated the vertical migration behaviour of *P. antarcticum* in the Drescher Inlet, the potential driving forces and implications for other compartments of the food web (Publication III).

We are living at an age of rapid climate change and alterations in community composition are already evident in the Antarctic marine environment. But which organisms will be (most likely) affected and what are the consequences for the overall ecosystem functioning? Traditionally, krill, *Euphausia superba*, is regarded as the key species and the bottleneck in the Antarctic food web. But is krill really the only species occupying such a central position? On the high Antarctic shelf *E. superba* is scarce and fish take a central position within the food web. We investigated the functional redundancy of notothenioid fish species, their potential sensitivity to changes in food web structure, and whether this trophic vulnerability is related to a species' functional role within the food web (Publication IV). The insights concerning trophic vulnerability and functional compensability gained from notothenioid fishes are expanded in the synthesis to the whole system to evaluate stability of the entire food web and resilience of the high Antarctic shelf community.

C. PUBLICATIONS

1. PUBLICATIONS CONTRIBUTING TO THIS THESIS

PUBLICATION I

Mintenbeck, K., Brey, T., Jacob, U., Knust, R., Struck, U. (2008). How to account for the lipid effect on carbon stable isotope ratio ($\delta^{13}C$) – sample treatment and model bias. *Journal of Fish Biology* 72: 815-830.

I developed the idea, the conceptual approach and the experimental design. Sample preparation and treatment was done by me, the mass spectrometric analyses by the fifth author. Data analysis, interpretation and manuscript preparation was done by me in cooperation with the second author and discussed with all co-authors.

PUBLICATION II

Mintenbeck, K., Jacob, U., Knust, R., Arntz, W.E., Brey, T. (2007). Depth-dependence in stable isotope ratio $\delta^{15}N$ of benthic POM consumers: The role of particle dynamics and organism trophic guild. *Deep-Sea Research I* 54: 1015-1023.

Idea and basic concept originated from me. Data analysis and interpretation are the result of discussions between me, the third and the fifth author. The manuscript was written by me and the fifth author and improved by discussions with all co-authors.

PUBLICATION III

Mintenbeck, K., Knust, R., Schiel, S., Arntz, W.E. (manuscript draft). Eat and be eaten: behavioural trade-offs in the Antarctic silverfish, *Pleuragramma antarcticum*, and its implications for the food web.

I and the second author developed the conceptual approach and carried out the sampling. Sample and data analyses were done by me. The manuscript concept was developed and written by me.

PUBLICATION IV

Mintenbeck, K., Jacob, U., Knust, R., Arntz, W.E., Brey, T. (submitted). Trophic vulnerability of fish – the search for Achilles' heel in the high Antarctic food web. *Marine Ecology Progress Series*.

The initial idea originated from me, the functional approach is the result from discussions with the second and the fifth author. I wrote the manuscript in cooperation with the fifth author, the final version was improved by discussions with all co-authors.

2. FURTHER PUBLICATIONS RELATED TO THIS THESIS (in chronological order)

PUBLICATION V

Gerdes, D., Isla, E., Knust, R., **Mintenbeck, K.**, Rossi, S. (submitted). Response of benthic communities to disturbance: the artificial disturbance experiment BENDEX on the eastern Weddell Sea shelf, Antarctica. *Polar Biology*.

PUBLICATION VI

Jacob, U., Brose, U., Jonsson, T., **Mintenbeck, K..**, Brey, T. (submitted). Trophic uniqueness and flexibility characterize consumer trophic niches and function. *Ecology*.

PUBLICATION VII

Dannheim, J., Brey, T., Schröder, A., **Mintenbeck, K.**, Knust, R., Arntz, W.E. (submitted). Trophic look at soft-bottom communities – the long way of recovery from trawling. *Marine Ecology Progress Series*.

PUBLICATION VIII

Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J.L., Brey, T., Carpenter, S.R., Cattin Blandenier, M.-F., Cushing, L., Dawah, H.A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M.E., Martinez, N., Memmott, J., **Mintenbeck, K**., Pinnegar, J.K., Rall, B.C., Rayner, T.S., Reuman, D.C., Ruess, L., Ulrich, W., Williams, R.J., Woodward, G., Cohen, J.E. (2006). Consumer-resource body-size relationships in natural food webs. *Ecology* 87: 2411-2417

PUBLICATION IX

Jacob, U., Brey, T., Fetzer, I., Kaehler, S., **Mintenbeck, K**., Dunton, K., Beyer, K., Struck, U., Arntz, W. E. (2006). Towards the trophic structure of the Bouvet Island marine ecosystem. *Polar Biology* 29: 106-113.

PUBLICATION X

Brose, U., Cushing, L., Berlow, E.L., Jonsson, T., Banasek-Richter, C., Bersier, L.F., Blanchard, J.L., Brey, T., Carpenter, S.R., Cattin Blandenier, M.F., Cohen, J.E., Dawah, H.A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Knapp, R. A., Ledger, M. E., Memmott, J., **Mintenbeck, K**., Pinnegar, J.K., Rall, B.J., Rayner, T., Ruess, L., Ulrich, W., Warren, P., Williams, R. J., Woodward, G., Yodzis, P., Martinez, N.D. (2005). Empirical body sizes of consumers and their resources. *Ecology* 86: 2545.

PUBLICATION XI

Jacob, U., **Mintenbeck, K**., Brey, T., Knust, R., Beyer, K. (2005). Stable isotope food web studies: a case for standardized sample treatment, *Marine Ecology Progress Series* 287: 251-253.

PUBLICATION XII

Knust, R., Arntz, W. E., Boche, M., Brey, T., Gerdes, D., **Mintenbeck, K**., Schröder, A., Starmans, A., Teixidó, N. (2003). Iceberg scouring on the eastern Weddell Sea shelf (Antarctica): a benthic system shaped by physical disturbances? In: Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J. (eds): Antarctic biology in a global context. Backhuys Publishers, Leiden: 96-101.

PUBLICATION XIII

Brenner, M., Buck, B. H., Cordes, S., Dietrich, L., Jacob, U., **Mintenbeck, K**., Schröder, A., Brey, T., Knust, R., Arntz, W. (2001). The role of iceberg scours in niche separation within the Antarctic fish genus *Trematomus*. *Polar Biology* 24, 502-507.

PUBLICATION I

Mintenbeck, K., Brey, T., Jacob, U., Knust, R., Struck, U.

How to account for the lipid effect on carbon stable isotope ratio (δ^{13}C) – sample treatment and model bias.

Journal of Fish Biology

2008

Volume 72, pages 815-830

$$L = \frac{93}{1 + (0.246 * (C/N) - 0.775)^{-1}}$$

$$\delta^{13}C' = \delta^{13}C - 3.32 + 0.99 * C/N$$

$$\delta^{13}C' = \delta^{13}C + D * \left(I + \frac{3.90}{1 + (287/L)} \right)$$

$$\delta^{13}C'_{protein} = \frac{(\delta^{13}C * C/N) + (7 * (C/N - C/N_{protein}))}{C/N}$$

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How to account for the lipid effect on carbon stable isotope ratio ($\delta^{13}C$) – sample treatment and model bias

K. Mintenbeck[1], T. Brey[1], U. Jacob[2,3], R. Knust[1], U. Struck[4]

[1]Alfred Wegener Institute for Polar and Marine Research, PO Box 120161, 27515, Bremerhaven, Germany, [2]Department of Zoology, Ecology and Plant Science, Distillery Fields, University College Cork, Ireland, [3]Environmental Research Institute, Lee Road, University College Cork, Ireland and [4]Museum of Natural History Berlin, Humboldt University, Invalidenstrasse 43, D-10115 Berlin, Germany

ABSTRACT

Stable carbon isotope ratios, $\delta^{13}C$, are known to depend on tissue lipid and $CaCO_3$ content, hence samples are often treated prior to mass spectrometric analysis to remove lipids and inorganic carbonates. This study investigates the impact of lipid extraction, $CaCO_3$ removal and of both treatments combined on fish tissue $\delta^{13}C$, $\delta^{15}N$, and C/N ratio. Furthermore, the suitability of empirical $\delta^{13}C$ lipid normalisation and correction models is examined.

$\delta^{15}N$ is affected by lipid extraction (increase of up to 1.65 ‰) and by the combination of both treatments, while acidification alone shows no effect. The observed shift in $\delta^{15}N$ represents a significant bias in trophic level estimates, i.e. lipid extracted samples are not suitable for $\delta^{15}N$ analysis. C/N and $\delta^{13}C$ are significantly affected by lipid extraction, proportional to initial tissue lipid content. For both parameters, rates of change with lipid content (ΔC/N and $\Delta\delta^{13}C$) are species-specific.

All tested lipid normalisation and correction models produce biased estimates of fish tissue $\delta^{13}C$, probably due to a non-representative data base and/or incorrect assumptions and generalisations the models are based on. Improved models need *a priori* more extensive and detailed studies of the relationships between lipid content, C/N and $\delta^{13}C$, as well as of the underlying biochemical processes.

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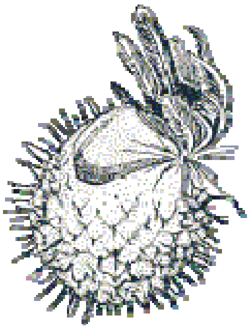

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Depth-dependence in stable isotope ratio $\delta^{15}N$ of benthic POM consumers: The role of particle dynamics and organism trophic guild

K. Mintenbeck[a,*], U. Jacob[b,c], R. Knust[a], W.E. Arntz[a], T. Brey[a]

[a] *Alfred Wegener Institute for Polar and Marine Research, P.O. Box 120161, 27515 Bremerhaven, Germany*
[b] *Department of Zoology, Ecology and Plant Science, Distillery Fields, University College Cork, Ireland*
[c] *Environmental Research Institute, Lee Road, University College Cork, Ireland*

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Abstract

The stable nitrogen isotope ratio ($\delta^{15}N$) is an established indicator of trophic hierarchy in marine food-web studies. Most of these studies presume that spatial variation in the primary food source is negligible, although a water-depth-related increase in $\delta^{15}N$ of particulate organic matter (POM) has been found in many systems. We used the high-Antarctic Weddell Sea shelf and slope ecosystem to test whether such a depth-related change in $\delta^{15}N$ is reflected at higher trophic levels, i.e., benthic consumers of POM. In suspension feeders (SF) we found a significant increase in $\delta^{15}N$ with water depth of up to 9.8‰, whereas in deposit feeders (DF) a depth effect was barely detectable. Particle-size preferences of the two feeding guilds combined with particle-size-dependent sinking velocities and biogeochemical reworking of POM are discussed as the major causes of these differences. It is essential to marine food-web studies to take into account the general depth effect on POM $\delta^{15}N$ as well as potential feeding-guild-specific differences in the response of POM consumer tissue $\delta^{15}N$ to avoid serious bias and misinterpretation of stable-isotope-based trophic information.

Keywords: $\delta^{15}N$ variability; Suspension feeders; Water depth; Particulate organic matter; POM dynamics; Particle settling; Antarctica; Weddell Sea

1. Introduction

Analyses of trophic hierarchy based on stable nitrogen isotope ratio ($^{15}N/^{14}N = \delta^{15}N$) are an integral part of state-of-the-art food-web studies in marine ecosystems. The underlying principle is the enzymatic selection for the heavier isotope ^{15}N with each assimilation step in the food chain. Fractionation of ^{15}N is variable but averages a $\delta^{15}N$ increase of 3.3‰ per trophic level (e.g., Minagawa and Wada, 1984). Recently, within-population variability in $\delta^{15}N$ was additionally proposed as a descriptor of omnivory (Sweeting et al., 2005). Most studies of metazoan consumers rely on one important *a priori* presumption, namely that within-system spatial variation in $\delta^{15}N$ of the primary food source is negligible. This, however, may not necessarily hold true in systems of substantial water depth, where particulate organic

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*Corresponding author.
E-mail address: Katja.Mintenbeck@awi.de (K. Mintenbeck).

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matter (POM) originating from the euphotic-zone food web is considered to be the primary food source.

Composition and production of the euphotic-zone community are the principal determinants of formation and fate of POM. The origin of particles contributing to bulk POM in this water layer is obviously reflected in a δ^{15}N signature that tends to increase with particle size (3 to $>150\,\mu$m; Wada et al., 1987; Altabet, 1988; Rau et al., 1990; Wu et al., 1997). The POM particle-size spectrum at any water depth is a function of various interacting processes (see model in Stemmann et al., 2004), in particular (i) sinking velocity as determined by particle size and density (Stokes's law), (ii) coagulation and fragmentation, and (iii) consumption by zooplankton and by microorganisms (Kiørboe, 2000, 2001; Lee et al., 2004). These processes result in the rapid decrease of bulk POM and the alteration of biochemical POM composition (Suess, 1980; Wakeham and Lee, 1993; Boyd and Stevens, 2002).

In particular, biological and biochemical processes discriminate against individual organic components, as is evident in the increase of the C/N ratio of POM with depth (Tanoue and Handa, 1979; Wefer et al., 1982; Smith et al., 1992). The rapid loss of nitrogen compared to carbon is attributed mainly to hydrolytic enzymatic activity and microbial consumption, since bacteria primarily degrade nitrogen-rich compounds (Smith et al., 1992; Lee et al., 2004). However, microbial activity alters not only the general organic composition of POM, but also its isotopic composition. Biochemical processes during bacterial degradation result in the release of nitrogen depleted in ^{15}N and a corresponding enrichment in ^{15}N of the residual material (Saino and Hattori, 1980; Wada, 1980; Macko and Estep, 1984; Macko et al., 1986). Microbial consumption is thus reflected in an increase of POM δ^{15}N with depth, as observed in several oceanic areas. The overall increase in δ^{15}N may amount to 5 to >10‰ between 0 and 1000 m depth (Saino and Hattori, 1980; Biggs et al., 1987; Rau et al., 1991; Altabet and Francois, 2001).

The central question for any food-web study is whether this depth-related change will cause a detectable depth trend in δ^{15}N of consumer species. The first indication for such a depth-related δ^{15}N increase owing to degeneration of the basal food source was found in higher trophic level consumers (fish and crustaceans) on the western Mediterranean slope (Polunin et al., 2001) and in the northeast Atlantic Ocean (Rau et al., 1989). The effect of depth on δ^{15}N might, moreover, differ between small particles suspended in the water column and large, fast sinking particles depositing on the sea floor. The smaller the particle, the longer the residence time in the water column and the higher the rate of microbial alteration and the corresponding increase in δ^{15}N. Since benthic suspension feeders (SF) depend on small suspended food particles, preferably well below 100 μm in diameter (Reiswig, 1971; Ribes et al., 1998; Orejas et al., 2003), the depth-related increase in δ^{15}N of POM should be reflected within this trophic guild. In contrast, deposit-feeding organisms (DF) rely on material deposited on the sea floor and can handle particles across the whole size range of POM (see e.g., Massin, 1982). Since organic matter in the sediment mainly originates from larger and faster sinking particles which are supposed to be less exposed to microbial alteration during vertical transport, δ^{15}N increase with depth should be less pronounced within this trophic guild. We therefore hypothesize that:

(i) δ^{15}N of benthic POM consumers will increase with water depth, and
(ii) SF will show this effect more clearly than DF.

On the basis of a large dataset of δ^{15}N values referring to benthic species from the Weddell Sea shelf and slope, we present the first attempt to demonstrate a depth-related increase in δ^{15}N of primary POM consumers. The results are discussed in respect of known POM dynamics. If our hypotheses prove true, sampling and analysis strategies would have to be adjusted accordingly in order to avoid serious bias in estimates of organisms' trophic level or the degree of omnivory within populations.

2. Methods

Samples considered in this study were taken by means of trawls and grabs during three RV "Polarstern" expeditions into the northeastern Weddell Sea (expeditions ANT XIII/3 in 1996, ANT XV/3 in 1998, ANT XXI/2 in 2003). All samples were collected between December and February in the ice-free zone ranging from 70°30′S to 75°00′S and from 010°00′W to 027°20′W (Fig. 1). Benthic SF and DF were collected from the shelf and slope between 50 and 1600 m water depth.

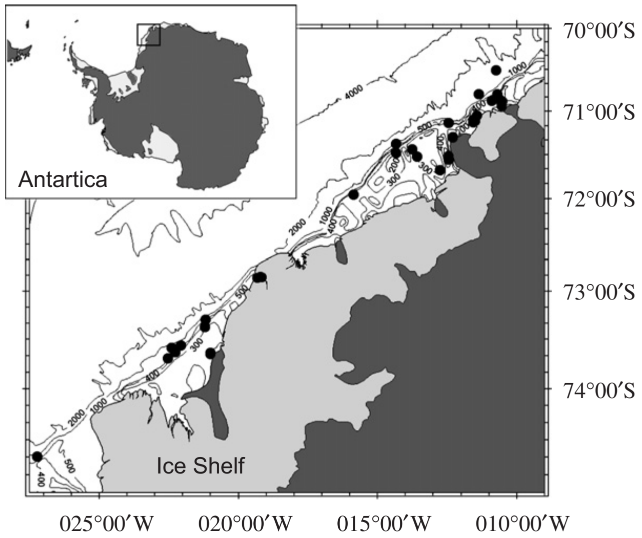

Fig. 1. Study area on the northeastern Weddell Sea shelf with sampling locations (●). Depth contours are in meters.

Sampled taxa include amphipods, anthozoans, ascidians, bivalves, bryozoans, crinoids, pterobranchs, hydrozoans, sponges (Porifera), holothurians, irregular echinoids, sipunculan worms and echiuroid worms. Body tissue samples were thoroughly cleaned with seawater and stored deep-frozen at −30 °C until further preparation.

Back in the laboratory, the frozen samples were lyophilised for 24 h, ground to fine powder, and treated with $1\,\text{mol}\,\text{l}^{-1}$ hydrochloric acid to remove inorganic carbon. Afterwards, samples were dried in an oven at 60 °C and ground again. Mass-spectrometric analysis of stable isotope composition was carried out in the GeoBioCenter in Munich (Thermo/Finnigan Delta plus, precision $\leqslant 0.15‰$), with stable isotope ratio of $^{15}N/^{14}N$ expressed as $\delta^{15}N$ in ‰ (for details on stable isotope terminology and measurement see, e.g., Peterson and Fry, 1987).

Analysis of covariance (ANCOVA) was applied to identify the effect of (log transformed) water depth, of feeding guild, and of taxon on individual $\delta^{15}N$. Finally, the relation of $\delta^{15}N$ to water depth within feeding guilds was described by regression models.

3. Results

Our data set of POM consumers includes 42 data points of DF and 140 data points of SF. Body tissue $\delta^{15}N$ and log(depth) are significantly related ($p<0.001$), but this relationship differs in slope between SF and DF, as indicated by the significant interaction term ($p = 0.009$, Table 1).

Table 1
Analysis of covariance (ANCOVA) of the effect of feeding guild (DF vs. SF) and covariate log(depth) on $\delta^{15}N$

Source	df	Sum of squares	Mean square	*p*
Analysis of variance				
Model	3	315.640	105.213	<0.001
Error	178	681.894	3.831	
Total	181	997.534		
Effect tests				
log(depth)	1	86.081	22.470	<0.001
Feeding guild	1	4.946	1.291	0.257
log(depth)∗feeding guild	1	56.832	7.004	0.009

df = degrees of freedom.

The DF data set comprises $\delta^{15}N$ values referring to seven species and four major taxa and covers the depth range 165–1600 m. $\delta^{15}N$ values range from about 6‰ to 9‰, except the two shallowest (165 m) data points, which have distinctly lower values (3.89‰ and 4.78‰, Fig. 2A). Taxon effects on $\delta^{15}N$ are not detectable. The fit of the regression model

$$\delta^{15}N_{\text{DF}} = 3.510 + 1.462 \times \log(\text{depth});$$
$$N = 42, \quad r^2 = 0.090, \quad p = 0.049$$

is poor, and becomes insignificant ($p = 0.504$) if the two data points at 165 m water depth are excluded.

The SF data refer to 26 species and 10 major taxa, which were sampled in water depths between 65 and 880 m (Fig. 2B). $\delta^{15}N$ in SF increases significantly with log(depth). The relationship differs significantly in intercept between sponges and the remaining taxa, i.e., sponge $\delta^{15}N$ signatures are generally higher:

$$\delta^{15}N_{\text{SF}} = -8.580 + 6.506 \times \log(\text{depth}) + 1.552 \times \text{Taxon};$$
$$N = 140, \quad r^2 = 0.530, \quad p<0.001;$$
$$\text{Taxon} = [1, -1] \quad \text{for} \quad [\text{Porifera, Others}].$$

4. Discussion

All samples considered in this study were taken during the same season (austral summer) to avoid potential effects of seasonality in POM composition on consumer $\delta^{15}N$. In order to ensure a clear

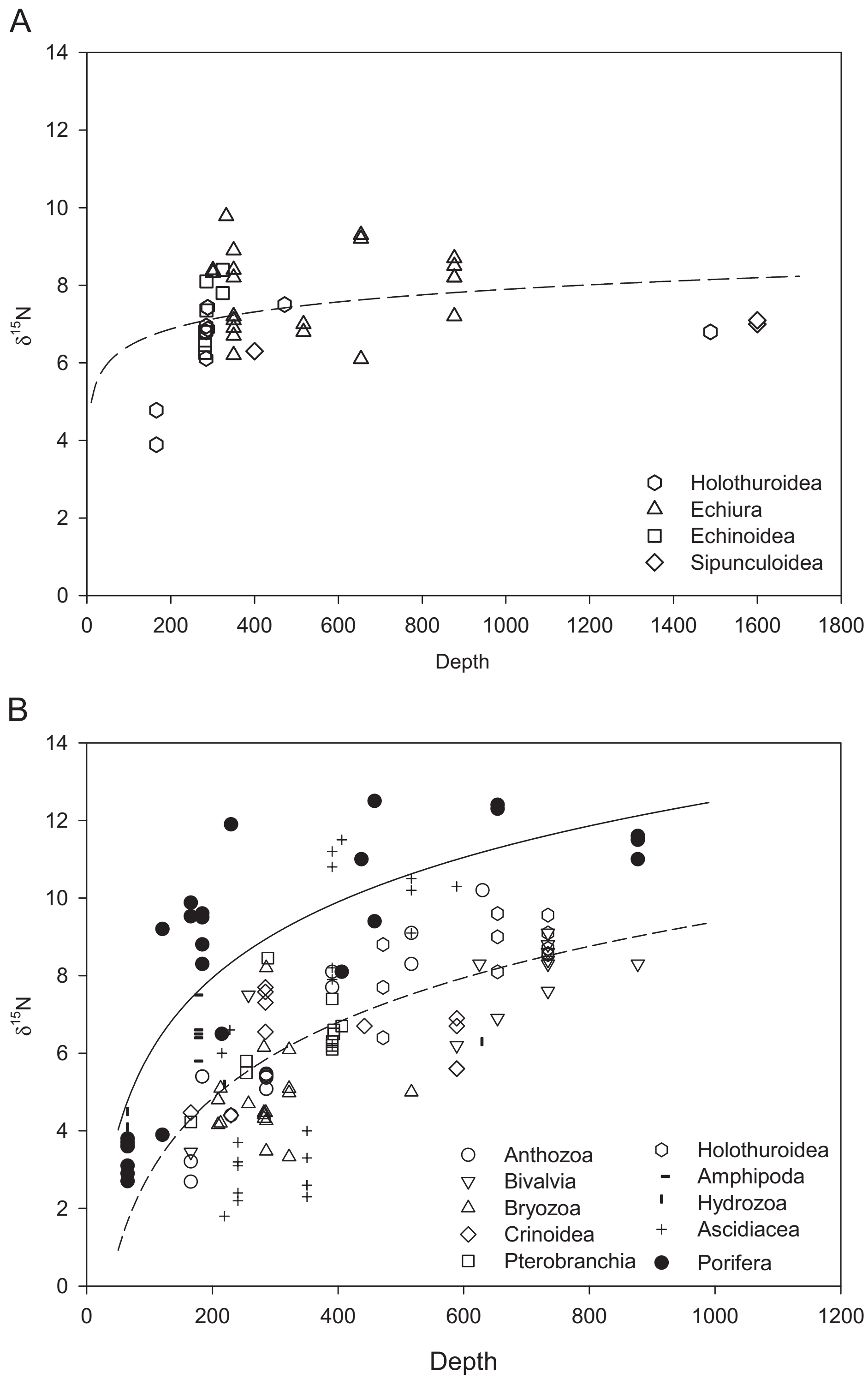

Fig. 2. Relationship between $\delta^{15}N$ [‰] and water depth [m] in (A) deposit feeders, DF, and (B) suspension feeders, SF, and adapted logarithmic regression models. Particular taxa are marked by different symbols. (A) DF: $\delta^{15}N = 3.510 + 1.462 \times \log(\text{depth})$ ($N = 42$, $r^2 = 0.09$, $p = 0.049$); (B) SF: $\delta^{15}N = -8.580 + 6.506 \times \log(\text{depth}) + 1.552 \times \text{Taxon}$; Taxon = 1 for Porifera (filled cycles, solid line), −1 for pooled remaining taxa (open symbols, dashed line) ($N = 140$, $r^2 = 0.53$, $p < 0.001$). Note different depth ranges in A and B.

separation of the two feeding guilds, SF and DF, we restricted our analysis to obligate DF (subsurface feeders and those that are morphologically constrained to feeding from the sediment surface) and to obligate SF (taxa that are morphologically constrained to feeding from the water column), i.e., we excluded taxa capable of both suspension-feeding and deposit-feeding (e.g., spionid polychaetes; Taghon and Greene, 1992), as well as facultative predators of zooplankton, such as some suspension-feeding hydroids and octocoralls (Orejas et al., 2001).

These data clearly support our initial hypotheses: the increase of δ^{15}N in POM with depth is reflected in POM consumer tissue, in particular in suspension-feeding taxa. However, variability in δ^{15}N remains high, particularly in SF, even if effects of depth and of major taxon (Porifera versus remaining taxa) are taken into account. Most likely this variability is taxon related, as the SF data set contains at least 26 species that may differ in δ^{15}N enrichment rates (Minagawa and Wada, 1984; Lovvorn et al., 2005) or in feeding preferences such as selection for specific items (e.g., cnidarians; Orejas et al., 2003) or for a narrow particle-size range (e.g., sponges; Reiswig, 1971). Unfortunately, the limited number of data/species does not allow for a thorough statistical analysis.

The generally higher δ^{15}N values of sponges may be related to either (i) the restriction of sponge diet to the smallest particles (e.g., Gili et al., 2001), which are the most degraded (see Section 1), or (ii) the heavy colonization of sponge surfaces and interstices by bacteria (e.g., Webster et al., 2004), which are most likely included in the analysed tissue samples.

Our data indicate that in suspension-feeding POM consumers δ^{15}N increases with water depth in a non-linear way; i.e., the rate of change decreases with depth, with the major shift in δ^{15}N of up to 9.8‰ (sponges) occurring apparently in the upper 500 m. It remains questionable, however, whether such a depth effect exists in deposit-feeding POM consumers (Fig. 2A, B).

This consumer δ^{15}N distribution reflects what has been observed previously for particulate nitrogen (PN) δ^{15}N and may be linked to the dynamics of POM production and sedimentation. Overall POM dynamics in the Southern Ocean are comparable to those in other marine systems: bulk POM decreases with depth (Biggs et al., 1987; Bathmann et al., 1997; Carlson et al., 2000), and POM δ^{15}N increases simultaneously (Biggs et al., 1987; Rau et al., 1991). In Fig. 3 δ^{15}N values of small suspended and large sinking particles from the Sargasso Sea (Altabet, 1988) and the northeastern Indian Ocean (Saino and Hattori, 1980) are shown as an example. Depth-related changes in δ^{15}N of fast sinking PN that will be deposited on the sea floor are minor. δ^{15}N of suspended PN consumed by SF, in contrast, distinctly increases with depth, mainly within the upper 100–500 m of the water column.

This pattern is attributed to rapid POM turnover and degradation in the upper mesopelagial, especially

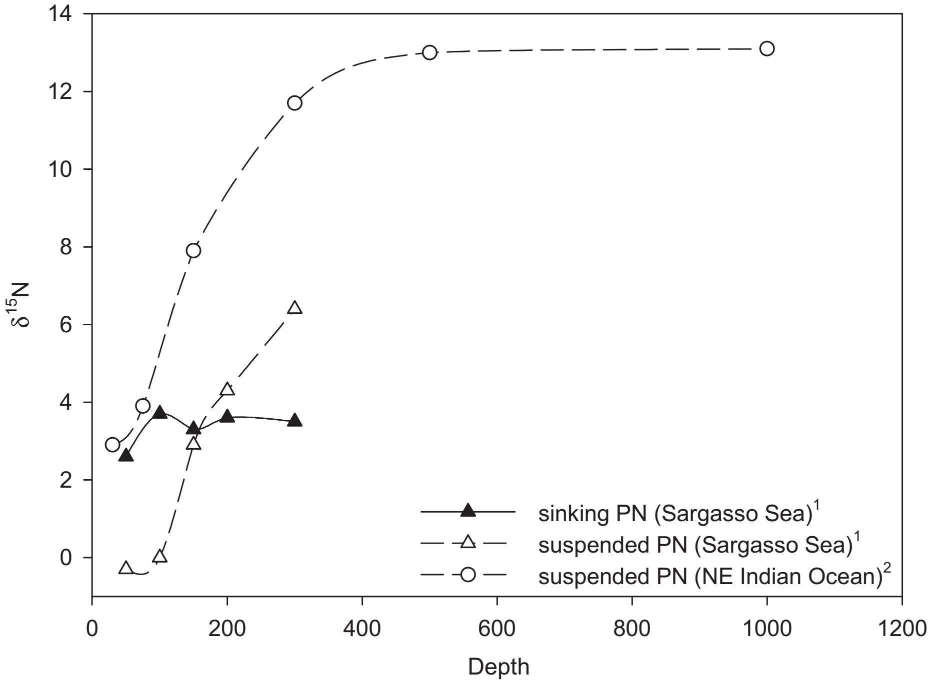

Fig. 3. Relationship between δ^{15}N [‰] and water depth [m] in suspended PN and sinking PN in the Sargasso Sea (^{1}redrawn from Altabet, 1988, pp. 545–546, Tables 2 and 3, with permission from Elsevier Ltd.), and the northeastern Indian Ocean (^{2}redrawn from Saino and Hattori, 1980, p. 753, Fig. 1, with permission from Macmillan Publishers Ltd.).

by mesozooplankton (Kiørboe, 2000, 2001) and by microorganisms that show highest abundance and activity in this zone of enhanced POM alteration (e.g., Lochte et al., 1997; Aristegui et al., 2002). δ^{15}N of SF from <100 m water depth was on average 3.6‰ (see Fig. 2B), which is about one trophic step above δ^{15}N of bulk POM observed in Southern Ocean surface waters during austral summer (0.4–1.6‰ between November and February; Biggs et al., 1987; Wada et al., 1987).

Large diatoms are not considered a principal food for benthic SF because of their large size and short period of availability (short-term blooms and rapid sedimentation; e.g., Scharek et al., 1999). Instead organisms of this trophic guild preferably consume particles from the pico- to nanoplankton fraction that are present year round, albeit in low concentrations during winter (Barnes and Clarke, 1995; Detmer and Bathmann, 1997).

If lost from the mixed layer, POM of this size exhibits extremely low sinking velocities (in general $<1\,\mathrm{m\,d^{-1}}$; Wakeham and Lee, 1993), owing to small size and low density ($\sim 1.1\,\mathrm{g\,cm^{-3}}$; van Ierland and Peperzak, 1984). The rate of microbial alteration of these particles will be correspondingly high, which results in rapid loss of ^{14}N and the distinct changes in δ^{15}N observed in POM and its suspension-feeding consumers above 500 m water depth. The aggregation to marine snow can increase the sinking velocity of small particles but simultaneously accelerate degradation because of intensive colonization by bacteria and sometimes even by protozoans (see review in Kiørboe, 2001). Accordingly, the POM size spectrum will shift towards larger, rapidly sinking particles with increasing depth. Faecal material of zooplankton origin, for example, exhibits sinking velocities of up to $800\,\mathrm{m\,d^{-1}}$ (Cadée et al., 1992) due to large particle size and high particle density ($1.22\,\mathrm{g\,cm^{-3}}$; Komar et al., 1981) and thus provides an important food source for benthic consumers at greater depth (see e.g., Iseki, 1981; Fortier et al., 1994). In fact, Weddell Sea POM flux is dominated by krill faecal strings, faecal pellets and large diatom cells at depth greater than 250 m (Nöthig and von Bodungen, 1989; Bathmann et al., 1991). These particles make up the major part of organic matter that is deposited in the sediment.

Large OM particles originating from surface waters have *a priori* higher δ^{15}N values and experience less enrichment in ^{15}N by microbial decomposition during sinking (see Section 1 and Sargasso Sea data in Fig. 3). Once settled on the sea floor, this fresh material is rapidly mixed into sediments by active bioturbation, and degraded slowly (Mincks et al., 2005), thus providing a "long-term" storage of high nutritive organic matter (Isla et al., 2006; Mincks et al., in press). Combined with sediment associated microorganisms, particle accumulation adds up to the rather consistent δ^{15}N of 4–6‰ measured in bulk surface sediment from various sites and depths in the Southern Ocean south of 60°S (e.g., Wada et al., 1987; Altabet and Francois, 1994; Mincks et al., in press). Accordingly, deposit-feeding consumers of this material exhibit about 3‰ higher δ^{15}N values (6–9‰) at all depths within the range considered here. Depth-independent δ^{15}N variability within this trophic guild is most likely caused by differences in the degree of particle selectivity or due to feeding in different sediment layers (Mincks et al., in press). Moreover, the probability of small, low δ^{15}N particles reaching the sea floor decreases exponentially with depth. Therefore, shallow water (above ~200 m) DF may show lower δ^{15}N values, as indicated by the two data points at 165 m (Fig. 2A).

In contrast to DF, SF are restricted mostly to the fine POM fraction (see above). At greater depth, SF therefore depend on small particles originating from fragmentation of large particles either in the water column or on the sediment surface (made available by resuspension). δ^{15}N of SF changes little at greater depth but is up to one trophic level higher than δ^{15}N of DF (see Fig. 2A, B). This indicates that the proposed particle fragmentation process involves a distinct increase in δ^{15}N, possibly due to the intense microbial activity in the benthic boundary layer (e.g., Lee et al., 2004).

δ^{15}N of suspended and sinking POM in the surface layer might vary depending on season: Lourey et al. (2003) observed a decrease in PN δ^{15}N during summer due to the uptake of recycled ^{15}N-depleted ammonium. During winter and spring (after sea-ice melting), mean POM δ^{15}N might significantly increase as ice-associated POM exhibits values much higher than POM originating from the free water column (Rau et al., 1991). Hence, surface water POM δ^{15}N values ranging from -5‰ to $+6$‰ were found in the Weddell Sea (Rau et al., 1991). However, such "short-term" variability in ephemeral water column POM δ^{15}N is integrated in tissues of long-living consumers, and obviously buffered in the sediment (Lovvorn et al., 2005; Mincks et al., in press).

The observed depth effects on $\delta^{15}N$ of benthic POM consumers are unlikely to be restricted to the Weddell Sea, as POM is subject to comparable physical, biological and biogeochemical processes in all marine systems. $\delta^{15}N$ signatures might vary between oceanic regions; the general pattern of $\delta^{15}N$ depth dependence, however, should remain the same (see e.g., Fig. 3). Indirect evidence from higher trophic level consumers in bathyal communities (Polunin et al., 2001; Rau et al., 1989; see Section 1), moreover, points towards the propagation of the depth-related increase in $\delta^{15}N$ along the food chain.

5. Conclusion

Our data confirm previous observations of depth-related changes in PN $\delta^{15}N$ and provide strong evidence for a trophic-guild-specific depth-dependence of $\delta^{15}N$ in benthic POM consumers. The depth-related change in $\delta^{15}N$ of POM causes a distinct bias in range and average of $\delta^{15}N$ in benthic SF and their consumers, and thus has serious implications for marine food-web studies that integrate data over a wider depth range: (i) The observed $\delta^{15}N$ range of up to 9.8‰ in certain SF taxa is well above the average enrichment per trophic step, 3.3‰ (Minagawa and Wada, 1984), and this bias would shift affected taxa one or more levels up in the trophic hierarchy, thus affecting the whole trophic structure. (ii) Depth-dependent shifts in $\delta^{15}N$ strongly affect estimates of consumer omnivory based on $\delta^{15}N$ variability (see Sweeting et al., 2005). There are two possible methods of compensating for the depth effect on $\delta^{15}N$: If both the $\delta^{15}N$-to-depth relationship for all SF taxa as well as all trophic links originating from these taxa are known, then a numerical correction could be applied to the affected $\delta^{15}N$ values. This, however, seems to be quite a complex and costly method. Therefore, we propose a depth-stratified approach towards systems with a wide vertical extension, in order to minimise depth effects on consumer $\delta^{15}N$.

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PUBLICATION III

Mintenbeck, K., Knust, R., Schiel, S., Arntz, W.E.

Eat and be eaten: behavioural trade-offs in the Antarctic silverfish, *Pleuragramma antarcticum*, and its implications for the food web.

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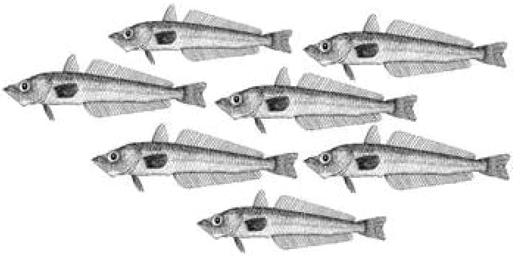

Eat and be eaten: behavioural trade-offs in the Antarctic silverfish, *Pleuragramma antarcticum*, and its implications for the food web

K. Mintenbeck, R. Knust, S. Schiel, W.E. Arntz

Alfred Wegener Institute for Polar and Marine Research, PO Box 120161, 27515, Bremerhaven, Germany

Key words: *Pleuragramma antarcticum*, vertical migration, predator-avoidance, feeding behaviour, trade-off, Weddell Sea, Antarctica

Abstract

The Antarctic silverfish, *Pleuragramma antarcticum*, is one of the few truly pelagic fish species in high Antarctic shelf areas and takes a central position within the food web, in particular as prey for warm-blooded animals such as Emperor penguins and Weddell seals. Recent evidence from seal foraging behaviour suggests that *P. antarcticum* undertakes vertical migrations within the water column. In this study we investigate the migration pattern of *P. antarcticum* in different depths of the water column in the Drescher Inlet at different times of the day, its driving forces and potential consequences for other compartments of the food web.

P. antarcticum is the dominating fish species in the Drescher Inlet and undertakes synchronous nocturnal migrations into the pycnocline. During the rest of the day *P. antarcticum* is found close above the sea floor. *P. antarcticum* preys exclusively upon zooplankton (copepods and chaetognaths) and despite the presence of potential food in the entire water column during the day, feeding of *P. antarcticum* is restricted to the short period during the night spent in the upper water column. Vertical migration of this species is thus not driven by vertically migrating prey but represents predator-avoidance behaviour. During the day above the sea floor, *P. antarcticum* provides a food source for demersal piscivorous fish without competing for food. During the night dense aggregations in the pycnocline provide an easily accessible and efficiently exploitable food source for warm-blooded predators such as Emperor penguins and Weddell seals.

Introduction

In the marine Antarctic ecosystem fish take a central position in the food web (Hureau 1994). The fish fauna in the high Antarctic is distinctly dominated by a single taxonomic group, the perciform suborder Notothenioidei. Notothenioid species are highly adapted to environmental conditions in the Southern Ocean and underwent extensive adaptive radiation in physiology and body structure to fill diverse niches within this ecosystem (Ekau 1988, Clarke & Johnston 1996, Eastman & McCune 2000). However, due to the lack of a swim bladder, most notothenioids are closely associated to the sea floor. Only few species are adapted to a pelagic life style by modifications in body structure, such as lipid deposits. One of the few truly pelagic notothenioid species that gained neutral buoyancy is the Antarctic silverfish, *Pleuragramma antarcticum*. This endemic species dominates the pelagic fish biomass in coastal waters of the Southern Ocean by > 90% (Hubold & Ekau 1987, DeWitt 1970, Donnelly et al. 2004). *P. antarcticum* is a typical zooplankton feeder (Daniels 1982, Hubold 1984a) and provides an important food source for warm-blooded animals (e.g. Hureau 1994, La Mesa et al. 2004). In particular Emperor penguins (*Aptenodytes forsteri*) and Weddell Seals (*Leptonychotes weddellii*), the two southernmost occurring warm-blooded animals living year round on the fast ice in the high Antarctic (e.g. Burns & Kooyman 2001), seem to feed extensively on *P. antarcticum* (Plötz 1986, Burns et al. 1998, Castellini et al. 1984, Klages 1989, Green 1986). In the marine high Antarctic *P. antarcticum* is thus supposed to be a key link in a relatively short and simple food chain connecting zooplankton and warm-blooded top predators (Cherel & Kooyman 1998). Moreover, *P. antarcticum* constitutes an important part of the diet of demersal piscivorous fish

(Eastman 1985, 1999, Schwarzbach 1988) and might thus also represent an important trophic link between the pelagic and the benthic part of the food web.

In the high Antarctic Weddell Sea and west off the Antarctic Peninsula, *P. antarcticum* has been described to show a characteristic vertical separation of age and size classes, respectively, with early developmental stages being distributed in upper water layers and adults occurring in deeper waters, close to the sea floor (Hubold 1984b, 1985, Kellermann 1986, Hubold & Ekau 1987). Avoidance of intraspecific competition and cannibalism were proposed to be the main causes for this vertical segregation (Hubold & Ekau 1987). Recent studies on seal foraging strategy and prey distribution, however, indicated that *P. antarcticum* undertakes nocturnal vertical migrations towards surface waters, which is reflected in the seals' diving behaviour (Plötz et al. 2001, Fuiman et al. 2002). Similar vertical migration of fish species, with individuals aggregating close to the bottom during the day and disperse in the upper water column at night, is known from lower latitudes, as well (e.g., herring and sprat, Nilsson et al. 2003; Atlantic redfishes, Gauthier & Rose 2002).

There are two main causes usually acting as driving force for vertical migration in organisms: In prey organisms, vertical migration often represents a predator avoidance behaviour (avoidance of visual predation), i.e. a top-down effect (see e.g. Lampert 1993). In predators, vertical migration reflects an adaptive foraging strategy by which the predator follows the migration of its prey, i.e. a bottom-up effect (e.g. Gaulthier & Rose 2002). However, most predatory organisms occupying intermediate trophic levels are at the same time potential prey for other predators. Vertical migration of a particular organism might consequently influence behaviour and foraging strategies of lower as well as of higher trophic level consumers (i.e. behavioural predator-prey interaction, e.g., Lima 2002).

Therefore, it is essential to know about an organism's feeding behaviour, its prey and predators, to understand causes for migration and their consequences for the entire food web.

To investigate the migration behaviour of *P. antarcticum*, its driving forces and potential consequences for predators, we studied (i) distribution and migration pattern of *P. antarcticum* within the water column, (ii) diet composition and feeding behaviour of *P. antarcticum*, and (iii) the role of *P. antarcticum* in the food web as prey for piscivorous fish and warm-blooded predators. These studies were carried out in the high Antarctic Drescher Inlet in the Weddell Sea. This ice-covered inlet is an important breeding and foraging ground for Emperor penguins and Weddell seals (Klages & Gerdes 1988, Klages 1989, Plötz 1986).

Methods

Study area

The Drescher Inlet is a crack of about 25 km in length and up to 2 km in width in the Rijser Larsen Ice shelf, eastern Weddell Sea (72°52'S, 19°25'W; Fig. 1). Water depth inside the Inlet ranges from 380 – 520m. The majority of samples were taken during the *RV Polarstern* expedition ANT XXI-2 in the beginning of January 2004. On our arrival we found typical summer light conditions with 24h light, and the inlet was still covered by a thick layer of fast ice. Water temperature was ranging from –1.5°C to –1.85°C, with a small but clear shift of 0.1 to 0.3°C in the pycnocline (D. Gerdes, AWI Bremerhaven, unpublished data).

Fish sampling

Samples for the study of fish community composition of the Drescher Inlet and distribution of *Pleuragramma antarcticum* within the water column were taken in the entrance of the inlet. The water column was sampled at different times of the day by means of a bentho-pelagic trawl (BPN, cod-end mesh size 10mm). The vertical position of the net was monitored by a net sensor system. 4 BPN hauls were carried out in the depth of the pycnocline the position of which was determined by CTD profile prior to each haul. The pycnocline was usually located between ~40 and 120m water depth, hence, the net was hauled at constant ship's velocity for 20min each at 120m, 80m and 40m. 2 BPN hauls were carried out close to the sea floor, 10-20 m above ground (at ~ 450-460m water depth). In addition to the samples taken in 2004, data from hauls taken at the same location during January/February 1998 (ANT XV) are considered in this study (data in part published in Plötz et al. 2001). These catches include 7

BPN hauls in the pycnocline (same procedure as in 2004; for details see also Knust et al. 1999), and 4 bottom trawls (BT, cod-end mesh size 20mm) carried out between 385 and 410m water depth. Details to all sampling stations are listed in Table 1.

Composition, abundance and biomass of species were determined for each haul (BPN and BT). To investigate the relationship between time of the day and vertical distribution of *Pleuragramma antarcticum* (pycnocline *vs* ground), data were converted into abundance and biomass per 1 hour trawling time ($N*1h^{-1}$ and $g*1h^{-1}$). Postlarvae of *P. antarcticum* were represented in most hauls carried out in the pycnocline, but were not considered in abundance and biomass estimates as the cod-end mesh-size of the used sampling gear (see above) was not appropriate for sampling of small sized larvae. Distribution of size classes of *P. antarcticum* in the pycnocline and above/on the ground were compared by means of length frequency distribution (in %). Total length (TL) and/or standard length (SL) of *P. antarcticum* (from most catches) were measured in cm. SL was used for the comparison of length distribution. In case only data on TL were available, SL was calculated from the relationship $SL = 0.8717*TL^{1.0063}$ ($R^2 = 0.99$; based on N=319).

Diet composition and feeding periodicity of Pleuragramma antarcticum

Samples for stomach content analyses were taken from 2 hauls in the pyncocline (St. 65-299, 16:30; St. 65-322, 00:10) and 2 hauls above the ground (St. 65-314, 15:32; St. 65-329, 11:57) in 2004. In each case 10 stomachs were removed from adult individuals (size range: 13.5-18.5cm SL) and immediately stored in 10% formaldehyde until further analysis. Back in the home lab, stomach contents were removed and rinsed on a 250µm sieve. Composition of stomach contents was analysed, and number, wet weight [g] and frequency of occurrence (percentage of stomachs in which an item is found; empty stomachs were not considered) of prey groups were determined.

Stomach fullness and state of prey digestion were used to estimate the time of the last feeding event. Degree of stomach filling was assessed using the classification of Dalpado & Gjøsæter (1988): 0 = empty, I = little contents (up to 30% filling), II = half full (30 to 70 % filling), III = full (70 to 100% filling, stomach wall retains its normal thickness), IV = distended (stomach expanded, stomach wall appears thin and smooth). State of prey digestion was visually assessed.

The role of Pleuragramma antarcticum in the Drescher Inlet food web

The importance of *P. antarcticum* as prey for higher trophic level predators that are typical members of the Drescher Inlet food web is investigated based on stable isotope analyses and current knowledge on predators' food composition from published sources. The stable isotope ratios of carbon and nitrogen ($^{13}C/^{12}C$, $^{15}N/^{14}N$) both increase along a food chain owing to isotope fractionation during the assimilation process, resulting in the enrichment of the heavier isotopes in consumer tissues. With each trophic transfer $^{15}N/^{14}N$ increases by about 3.3‰ and serves as an indicator of an organisms' trophic position within a particular food web (Minagawa & Wada 1984, Post 2002). The trophic fractionation of $^{15}N/^{14}N$ between diet and muscle tissue, and diet and metabolically inactive tissue such as fur and feathers seems to be similar (e.g. Hobson et al. 1996). The increase in $^{13}C/^{12}C$ is usually less (>1‰, Rau et al. 1983), but varies strongly depending on tissue lipid content (e.g. DeNiro & Epstein 1978, Mintenbeck et al. 2008). Samples for stable isotope analyses were taken from warm-blooded animals and fishes. Fur samples of 11 adult

Weddell seals (*Leptonychotes weddellii)*, down feathers of 11 Emperor penguin chicks (*Aptenodytes forsteri*), and the feather of one Giant petrel (*Macronectes giganteus*) were collected in December 2003 from individuals on the ice in the Inlet. Fur and feather samples were thoroughly cleaned in an ultrasonic bath and minced with a scalpel over full length. Fish samples include tissue samples from 10 adult *P. antarcticum* (muscle tissue; 15.0 – 18.5 cm SL), 10 *P. antarcticum* postlarvae (whole animals, in each case 2 individuals pooled to one sample), and 5 juvenile *Trematomus* sp. (gutted and decapitated) caught in the pycnocline of the Drescher Inlet. Additional tissue samples from two piscivorous demersal fish species (*Chionodraco myersi*, N = 10 and *Cryodraco antarcticus*, N = 9; Channichthyidae, Notothenioidei) that are abundant in the Drescher Inlet were taken there and in adjacent areas of the north-eastern Weddell Sea (off Kapp Norvegia). All fish tissue samples were freeze-dried and treated with 1 N hydrochloric acid (HCl) to remove inorganic carbonates.

Ultimate stable isotope analysis was carried out in the GeoBioCenter in Munich using a Thermo-Finnigan Delta Plus isotope-ratio mass spectrometer (precision ≤ 0.15‰). Stable isotope ratios are expressed in permill [‰] deviation from the international standard (PeeDee Belemnite for carbon and atmospheric N_2 for nitrogen) using conventional delta notation ($\delta^{13}C$ and $\delta^{15}N$).

Results

Composition of the Drescher Inlet fish fauna

The fish fauna in the pycnocline of the water column was composed of few species only. In terms of numbers and biomass most BPN catches were dominated by *Pleuragramma antarcticum* (Table 1, BPN 1-11). Notothenioid juveniles (mainly *Trematomus* spp.) and postlarvae (not shown, see Methods) were also highly abundant. The daggertooth *Anotopterus pharao* and channichthyids such as *Chionodraco hamatus* occurred only occasionally but in some cases largely contributed to fish biomass due to large body size. Some metres above the ground *P. antarcticum* was almost the only fish species present (Table 1, BPN 12-13). The demersal fish community on the seafloor (Table 1, BT 1-4) was characterized by high species diversity. Together with several *Trematomus* species and large icefishes (Channichthyidae) such as *Chionodraco* spp. and *Cryodraco antarcticum*, *P. antarcticum* significantly contributed to overall fish abundance and biomass on the sea floor, as well.

Vertical distribution of Pleuragramma antarcticum

Though distinctly dominating the fish community in the pycnocline, abundance and biomass of *P. antarcticum* varied strongly with time of the day, with a peak abundance of up to 1580 individuals and biomass of up to 31340 g (* $1h^{-1}$ trawling time) around midnight (Fig. 2 A,B). During the rest of the day *P. antarcticum* was highly abundant above/on the sea floor but rarely present in the pycnocline (ranging from 1 to a maximum of 70 individuals * $1h^{-1}$ trawling time).

In Fig. 3 the distribution of *P. antarcticum* length frequency during peak abundance in the pycnocline is compared with length frequencies in the pycnocline during the rest of the day and individuals caught above/on the ground. In 1998 as well as in 2004 two cohorts were found in the pycnocline. During peak abundance large individuals of *P. antarcticum* were distinctly predominating (Fig. 3 A). During the rest of the day small individuals <8cm largely contributed to the *P. antarcticum* community in the pycnocline (Fig. 3 B). Above/on the ground individuals < 8 cm were rarely found (Fig. 3 C). Except the absence of small individuals, composition of *P. antarcticum* length frequencies in the pycnocline and above/on the ground were similar, with a peak in occurrence of individuals between 13-14 cm in 2004 and a peak at 16 cm in 1998.

Diet composition and feeding periodicity of Pleuragramma antarcticum

Prey composition of *P. antarcticum* individuals caught in the pycnocline and above the ground was identical and the overall prey spectrum was restricted to five taxa (Table 2). Chaetognaths were frequently ingested, in particular by individuals caught in the pycnocline. Crustacean mysis larvae were occasional prey but did hardly account for biomass ingested. Ostracods and hyperiid amphipods were rarely fed on. Copepods were by far the most important prey item in terms of abundance, biomass and occurrence. In all food-containing stomachs, *Calanus propinquus*, *Metridia gerlachei*, and *Rhincalanus gigas* could be identified.

Stomachs of individuals from the pycnocline were filled with food (degree of filling III and IV), no matter if caught in the late afternoon or around midnight (Fig. 4). In individuals sampled above the ground around mid-day 40% of the stomachs contained no or little food, whereas the remaining 60% were full with the stomach wall distended. Samples taken from specimens close to the ground in the afternoon contained a high percentage of empty stomachs (60%), the rest of the investigated stomachs were half full (degree of filling II) to full (degree of filling III).

In all food-containing stomachs, from the pycnocline as well as from the ground, at least 2-3 different digestion states were found. One part of ingested prey was more or less fresh, and one part was heavily digested (composed of copepod exoskeletons and loose fleshy parts). In individuals caught in the pycnocline in the late afternoon the less digested part was composed of a large proportion of freshly ingested prey items (mainly fresh copepods) and a minor proportion of slightly digested items. Stomachs taken from individuals in the pycnocline at midnight contained a larger fraction of slightly digested prey and some freshly ingested items. Stomachs of *P. antarcticum* sampled above the ground contained slightly digested prey, but almost no freshly ingested organisms.

The role of Pleuragramma antarcticum in the Drescher Inlet food web

Stable isotope composition of abundant components of the Drescher Inlet community is shown in Fig. 5. To complete the picture data on isotopic composition of *P. antarcticum*'s main zooplankton prey were added (from Rau et al. 1991). $\delta^{13}C$ and $\delta^{15}N$ both increases from zooplankton (1-3 Copepods, 4 Chaetognaths) to pelagic fish (5 postlarval fish, 6 juvenile fish, 7 adult *P. antarcticum*), to piscivorous fish (9-10) and warm-blooded predators (8, 11-12).
Within the upper water column fish community $\delta^{15}N$ was lowest in juvenile *Trematomus* spp. (mean: 7.48 ‰) and *Pleuragramma* larvae (mean: 7.29 ‰), and about 1.5 ‰ higher in adult *P. antarcticum* (mean: 8.93 ‰). $\delta^{15}N$ values of demersal piscivorous channichthyids were increased compared to *P. antarcticum* by 2.47 ‰ (*Chionodraco myersi*) and 3.29 ‰ (*Cryodraco*

antarcticum), respectively. Emperor penguin chicks (*Aptenodytes forsteri*) had a mean $\delta^{15}N$ of 10.28 ‰ and are thus enriched in ^{15}N compared to juvenile fish by about 2.8 ‰ and compared to *P. antarcticum* by only 1.35 ‰. $\delta^{15}N$ of Weddell seals (*Leptonychotes weddellii*) averaged 13.92 ‰, which is 4.99 ‰ higher than mean $\delta^{15}N$ of *P. antarcticum*. Distinctly highest $\delta^{15}N$ of 15.55 ‰ was found in the Giant petrel *Macronectes giganteus*.

Discussion

The Antarctic silverfish, *Pleuragramma antarcticum*, contributed the major component of the fish fauna in the high Antarctic Drescher Inlet, both in terms of numbers and of biomass. *P. antarcticum* distinctly dominated the fish fauna in the pycnocline and some metres above the ground and contributed also largely to individuals and biomass directly on the ground. Juvenile notothenioids and postlarvae (not shown in Table 1, see Methods) were highly abundant in the pycnocline, as well, and are obviously restricted in their distribution to the upper water column. On the ground several *Trematomus* species and large channichthyids, in particular *Chionodraco myersi* and *Cryodraco antarcticum*, accounted for most of individuals and biomass beside *P. antarcticum*. A similar composition of the fish fauna is found in vast areas of the Weddell Sea shelf (see e.g. Hubold & Ekau 1987, Schwarzbach 1988, Ekau 1990).

Combined data on *P. antarcticum* abundance and biomass distribution during different times of the day clearly indicated a short but concentrated ascent of *P. antarcticum* into the pycnocline around midnight. During the rest of the day *P. antarcticum* was found in high numbers and biomass above/on the ground, while abundance of *P. antarcticum* in the pycnocline was low and a large proportion was composed of small individuals that obviously did not migrate into deeper water layers (similar to other notothenioid juveniles and postlarvae). Larger individuals in the pycnocline (> 8cm) were of the same sizes as those found above/on the ground. Moreover, diet composition was identical. The extreme temporal variability in abundance and biomass, as well as the similarity in length frequency distribution and diet composition between pycnocline and sea floor provided a strong evidence for a more or less synchronous vertical movement of adult *P. antarcticum*. The strict vertical separation of age/size classes as described by Hubold (1984b, 1985) and Hubold & Ekau (1987), thus, did not hold true in this part of the Weddell Sea. Separation between early developmental stages and adults is suspended, at least occasionally, by vertical migration of adult *P. antarcticum* into upper water layers.

What drives the short-term nocturnal, synchronous movement of *P. antarcticum*? Plötz et al. (2001) suggested that *P. antarcticum* might follow its migrating euphausiacean prey, i.e. a vertical migration driven by hunger. However, during our sampling period individuals did not feed on krill, even though krill was highly abundant in *P. antarcticum* rich hauls taken above the sea floor (personal observation). Diet was composed of pelagic prey items in all specimens caught in the pycnocline and above the sea floor, with the copepod species *Metridia gerlachei*, *Calanus propinquus* and *Rhincalanus gigas* building the major part. Though these copepod species have been described to undertake diel vertical migrations (nocturnal ascent; e.g. Atkinson et al. 1992, 1996, Lopez & Huntley 1995), all copepod species were most abundant in the upper water layers (50-200m) of the Drescher Inlet during the day. *M. gerlachei* was highly abundant in the entire water column down to 470m water depth (> 3000 Individuals / 1000m^3; S. Schiel & J. Michels, AWI Bremerhaven, unpublished data). Despite sufficient prey availability close to the sea floor, feeding of *P. antarcticum* seemed to be largely restricted to periods spent in the upper water column, as indicated by the differences in stomach fullness and stages of prey digestion of individuals sampled in the pycnocline (high proportion of filled stomachs containing freshly ingested prey) and above the ground (high proportion of empty stomachs, no freshly ingested prey).

Though there is some evidence that non-visual senses (e.g., lateral line) gain importance in adult *P. antarcticum* compared to larvae and juveniles

(Montgomery & Sutherland 1997, Eastman & Lannoo 1995), our study indicates that vision is important for, or at least distinctly facilitates, efficient prey detection in adult *P. antarcticum*. Similarly, the closely related cryopelagic species *Pagothenia borchgrevincki* is supposed to require photopic (= cone mediated) vision for efficient prey detection (Montgomery et al. 1989b, though the mechanosensory lateral line system seems to be well suited for this task, as well (Montgomery & Macdonald 1987). The eyes of *P. antarcticum* are not adapted for vision at greater water depth, as the retina is dominated by cones, which are less light sensitive but enhance visual contrast (Eastman 1988). *P. antarcticum* consequently undertakes feeding migrations into prey-rich surface waters where light conditions are more appropriate (even during darkest hours of the day) for visual detection and capture of small mobile prey. The timing of ascent and descent in migrating animals seems to be triggered by light intensity (Ringelberg 1995), and Fuiman et al. (2002) found the depth distribution of *P. antarcticum* in McMurdo Sound to be related to ambient light intensity even in the absence of a sunset (e.g. Fuiman et al. 2002). During feeding migrations into surface waters *P. antarcticum* itself provides an easy accessible food source for visually hunting warm-blooded animals, time spent in the pycnocline is thus largely restricted to a short period during the night (see Fig. 2) when predation risk is lowest. Vertical migration of *P. antarcticum* in the Drescher Inlet is thus obviously a behavioural trade-off between energy intake and predator avoidance. The length of near-surface residence time of *P. antarcticum* will most likely vary seasonally in line with the strong seasonal changes in day and night length found at high latitudes (see e.g. Hays 2003).

Whether the feeding migration of *P. antarcticum* occurs in a regular diel cycle or not is not absolutely clear, but digestion stages of stomach contents indicate a daily migration. Montgomery et al. (1989a) investigated prey decay in the closely related *Pagothenia borchgrevinki* and measured a half life of 37-49h for crustaceans and a half life of about 16h for ingested chaetognaths. As copepods were found in at least 2 different digestion stages and chaetognaths were identifiable in specimens from both catches above the ground (see Table 2), a daily feeding migration into upper water layers is likely. However, it should be noted that vertical migration is not a fixed, but a flexible behaviour, which might vary in timing and degree depending on predator presence (Lampert 1993, Lima & Dill 1990, Dawidowicz et al. 1990, Bollens & Stearns 1992, Jensen et al. 2006). Individual variability in vertical migration seems to be, moreover, influenced by body condition (Hays et al. 2001) and/or nutritional state (hunger/satiation hypothesis; Pearre 2003), which might explain the asynchronous migration behaviour of some isolated large individuals that were caught in the pycnocline during the day.

The lack of larvae and juveniles in deeper water layers and the vertical separation of ontogenetic stages of *P. antarcticum* were hitherto attributed to the avoidance of intraspecific competition and cannibalism (Hubold & Ekau 1987). Based on the fact that vertical migration in *P. antarcticum* is driven by predator avoidance, we propose an alternative explanation: According to the predator evasion hypothesis vertical migration is more pronounced in species/individuals that are most susceptible to visually orientating predators, and visibility (and thus susceptibility) increases with increasing size and pigmentation (reviewed in Hays 2003). Vertical migration is energetically disadvantageous (Lampert 1989) and small, larval and juvenile fish usually have higher metabolic rates than adults. Consequently, the smaller and the less pigmented a particular developmental stage, the higher the costs compared to the benefit of migration. Some indication exists that notothenioid postlarvae and juveniles undertake diel vertical migrations, as well (Kellermann 1986), but obviously to a lesser degree compared to adults, as cost and benefit of migration needs to be balanced. The maximum depth range of vertical migration and thus the vertical separation of different developmental stages of *P. antarcticum* during most of the day are thus most likely the result of differences in predation risk and energy requirements.

The vertical migration and feeding behaviour of adult *P. antarcticum* affect other parts of the food web. By feeding in the pycnocline but resting close to the sea floor for most of the day, *P. antarcticum* represents an important link in bentho-pelagic coupling. As known from previous stomach content analysis and supported by our stable isotope data (assuming a 3‰ ^{15}N enrichment per trophic step), *P. antarcticum* significantly contributes to the diet of demersal, piscivorous channichthyids, such as the abundant *Chionodraco myersi* and *Cryodraco antarcticum* (Takahashi & Nemoto 1984, Eastman 1985, Olaso 1999). As feeding of *P. antarcticum* is obviously restricted to the upper water layers, there is no interspecific competition for food between epibenthic zooplankton feeding fish species, such as *Trematomus eulepidotus* and *T. lepidorhinus* (Schwarzbach 1988, Mintenbeck 2001), and *P. antarcticum* during the time spent close to the sea floor.

For warm-blooded predators dense aggregations of *P. antarcticum* in the pycnocline are only available for short periods. Though Weddell seals and Emperor penguins are both excellent divers and capable to follow *P. antarcticum* to depth (Wienecke et al. 2007, Burns & Kooyman 2001), previous diet studies as well as stable isotope signatures indicate that these apex predators have additional food sources beside *P. antarcticum*. Adult Emperor penguins feed mainly on *P. antarcticum*, and to a lesser extent on squid and euphausiaceans (Cherel & Kooyman 1998, Green 1986, Gales et al. 1990, Pütz 1995). Chicks seem to be fed with the same diet (Zimmer et al. 2007). The δ^{15}N value, however, indicates that either the proportion of lower trophic level prey (such as euphausiaceans) is comparatively high or the major part of the chick diet is composed of small juvenile notothenioid fish (e.g. *Trematomus* spp., *P. antarcticum* postlarvae) as recently suggested by Burns & Kooyman (2001). The Southern Giant petrel, *Macronectes giganteus*, in contrast, seems to be largely independent from pelagic prey in the Drescher Inlet. The high δ^{15}N value measured in the feather confirms observations on hunting behaviour and stomach content analysis, according to which the bird mainly preys upon penguin chicks and scavenges on carcasses of seals (Hunter 1991, Hunter & Brooke 1992). However, Forero et al. (2005) observed sex-specific differences in the diet of *M. giganteus*, with males feeding mainly on penguin chicks and seals, while females additionally consumed marine prey, such as pelagic fish.

Though *P. antarcticum* was often found to be the main prey of the Weddell seal (e.g. Plötz 1986, Burns et al. 1998), fur was enriched in ^{15}N compared to *P. antarcticum* by about 5‰ (i.e. more than one trophic level). Plötz and co-authors found strong interannual variations in the Weddell seals' diet in the Drescher Inlet, with *P. antarcticum* being the major prey in one year (Plötz 1986), and large channichthyids such as *Ch. myersi* and *C. antarcticus* and other demersal notothenioids dominating the diet in another year (Plötz et al. 1991). Casaux et al. (2006), in contrast, reported Weddell seals at the Antarctic Peninsula to feed on a mixed diet composed of *P. antarcticum* and demersal fish. Fur (as well as feather) samples that were taken in the Drescher Inlet integrate isotopic signatures of prey assimilated during the growth period. Weddell seals, for example, moult once a year, mainly in February (H. Bornemann, AWI Bremerhaven, pers. comm.). The analysed fur thus incorporated dietary information of nearly a whole year. Isotopic signatures might, consequently, reflect a permanent mixed diet as well as a temporal shift in prey composition depending on local food supply. However, even if *P. antarcticum* (juveniles as well as adults) is not the only prey of warm-blooded animals, it is most likely the major prey.

The obviously synchronous migration behaviour of *P. antarcticum* provides further evidence (see e.g. Fuiman et al. 2002) that *P. antarcticum* is a shoaling fish species (after Pitcher 1983), thus, a patchy distribution of particular shoals as well as horizontal migrations of fish aggregates are most likely (see e.g. Makris et al. 2006). *P. antarcticum* shoals might migrate into and out of the inlet, seeking for food richest places. *P. antarcticum*, consequently, might be totally absent from the inlet for longer periods, during which seals and penguins are forced to shift to alternative prey, such as benthic and bentho-pelagic fishes in the case of the Weddell seal.

Similarly to vertical migration, shoaling behaviour of fishes can be considered as a trade-off between safety and energy intake, as shoaling goes along with increased competition for food (Lima & Dill 1990). Migration behaviour of *P. antarcticum* aggregations, vertically as well as horizontally, influences diving behaviour and foraging success of the air-breathing apex predators, as deep diving is required temporarily to exploit *P. antarcticum* shoals during the day or benthic feeding grounds. Diving into deeper water layers involves (i) increased swimming effort, (ii) shorter times at feeding depth, and/or (iii) longer diving durations followed by longer recovery phases (e.g. Kooyman 1989, Kooyman &

Kooyman 1995, Wilson & Quintana 2004). Moreover, feeding efficiency seems to be higher in shallow dives (e.g. Croxall et al. 1985), while encounter rates are probably lower in light depleted deep waters, as indicated by a lower number of feeding events at depth (see Plötz et al. 2005). *P. antarcticum* shoals in the pycnocline of the Drescher Inlet therefore represent an aggregated and easily accessible food source for warm-blooded predators and might be of particular importance during rearing of chicks and pups. Weddell seal cows do not feed during lactation and need to refill their energy storages after weaning of the pups (Reijnders et al. 1990), Emperor penguins need to forage for their own demands and additionally to nourish chicks until fledging.

Vertical migration within the water column and feeding behaviour makes *P. antarcticum* an important trophic link in the Drescher Inlet food web: (i) during the day *P. antarcticum* provides food for piscivorous demersal channichtyids without competing for food with benthic or epi-benthic fish species, and (ii) temporarily available dense aggregations in the pycnocline provide an easily accessible and efficiently exploitable food source for warm-blooded animals, which might positively affect population dynamics of these apex predators (see e.g. Barbraud & Weimerskirch 2001, Forcada et al. 2005).

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Tables

Table 1: List of trawls including date, average time and depth of sampling, and percentage composition of the fish fauna (upper row: %individuals; lower row: %biomass). Notothenioid fish species are sorted by families (Nototheniidae, Channichthyidae, Artedidraconidae, Bathydraconidae). The fish fauna was sampled in the pycnocline (**P**) and above/on the ground (**G**) of the Drescher Inlet by means of a bentho-pelagic net (**BPN**) and a bottom trawl (**BT**) in January and February 1998 and 2004. For details on cruises and stations see Arntz & Gutt (1999, ANT XV-3) and Arntz & Brey (2005, ANT XXI-2).

Gear (No.):	BPN	BPN	BPN	BPN	BPN	BPN	BPN	BPN	BPN	BPN	BPN	BPN	BPN	BT	BT	BT	BT
	1	2	3	4	5	6	7	8	9	10	11	12	13	1	2	3	4
Year:	1998	1998	1998	1998	1998	1998	1998	2004	2004	2004	2004	2004	2004	1998	1998	1998	1998
Cruise Code:	ANT XV-3	ANT XV-3	ANT XV-3	ANT XV-3	ANT XV-3	ANT XV-3	ANT XV-3	ANT XXI-2	ANT XXI-2	ANT XXI-2	ANT XXI-2	ANT XXI-2	ANT XXI-2	ANT XV-3	ANT XV-3	ANT XV-3	ANT XV-3
Station No.:	48-013	48-014	48-015	48-023	48-024	48-026	48-247	65-299	65-310	65-312	65-322	65-314	65-329	48-078	48-082	48-084	48-263
Date:	01/26	01/27	01/27	01/27	01/28	01/28	02/22	01/01	01/02	01/02	01/03	01/02	01/03	02/03	02/03	02/03	02/25
Time:	23:41	02:46	05:43	20:58	00:21	04:07	14:56	16:30	08:18	11:44	00:10	15:32	11:57	07:03	11:58	16:25	01:39
Trawling Depth:	P	P	P	P	P	P	P	P	P	P	P	G	G	G	G	G	G
	Catch Composition Pycnocline											**Catch Composition Ground**					
Nototheniidae																	
Pleuragramma antarcticum	**77.9**	**46.2**	**68.8**	**7.7**	**41.2**	**52.9**	**84.6**	**57.3**	**-**	**-**	**94.5**	**100**	**94.7**	**31.1**	**6.8**	**32.3**	**52.0**
	59.2	**50.2**	**63.5**	**26.0**	**4.8**	**5.2**	**47.7**	**96.4**			**99.4**	**100**	**97.0**	**8.2**	**4.3**	**14.1**	**21.9**
Trematomus eulepidotus	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	2.6	4.5	6.0
														0.5	8.8	5.4	9.6
Trematomus hansoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.3
																	6.8
Trematomus lepidorhinus	-	-	-	-	-	-	-	-	-	-	-	-	-	7.1	6.0	4.5	0.9
														5.7	6.1	1.8	0.4

Table 1 continued…	BPN 1	BPN 2	BPN 3	BPN 4	BPN 5	BPN 6	BPN 7	BPN 8	BPN 9	BPN 10	BPN 11	BPN 12	BPN 13	BT 1	BT 2	BT 3	BT 4
Trematomus loennbergii	-	-	-	-	-	-	-	-	-	-	-	-	-	1.2	0.9	1.5	0.4
														1.7	3.1	4.1	1.1
Trematomus nicolai	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2
																	1.2
Trematomus pennellii	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	3.4	-	0.2
														<0.1	0.2		<0.1
Trematomus scotti	-	-	-	-	-	-	-	-	-	-	-	-	-	12.9	36.8	27.1	4.0
														1.3	4.4	3.9	0.9
Aethotaxis mitopteryx	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7
																	2.3
Pagothenia borchgrevincki	-	-	-	-	-	-	7.7	-	-	-	-	-	-	-	-	-	-
							49.7										
Channichthyidae																	
Chaenodraco wilsoni	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-
														0.1			
Chionodraco hamatus	-	1.9	-	-	-	5.9	7.7	-	-	-	-	-	-	8.3	-	3.0	4.5
		14.4				25.0	2.7							19.7		9.6	15.5
Chionodraco myersi	-	-	-	-	-	-	-	-	-	-	-	-	-	13.3	13.7	12.0	4.7
														26.0	43.4	32.8	13.0
Cryodraco antarcticum	-	-	-	-	-	-	-	-	-	-	-	-	-	11.0	5.1	5.3	5.4
														19.9	21.6	22.7	16.6
Dacodraco hunteri	-	1.9	-	-	-	-	-	-	-	-	0.1	-	0.4	-	1.7	-	6.7
		1.0									0.1		2.2		2.7		4.7

Table 1 continued…	BPN 1	BPN 2	BPN 3	BPN 4	BPN 5	BPN 6	BPN 7	BPN 8	BPN 9	BPN 10	BPN 11	BPN 12	BPN 13	BT 1	BT 2	BT 3	BT 4
Neopagetopsis ionah	-	-	-	-	-	5.9	-	-	-	-	-	-	-	-	-	-	-
						0.4											
Pagetopsis maculatus	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	2.6	2.3	-
														0.1	2.0	1.2	
Artedidraconidae																	
Artedidraco loennbergi	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	6.0	0.8	-
														<0.1	0.4	0.1	
Artedidraco orianae	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	-	-	-
														<0.1			
Dolloidraco longedorsalis	-	-	-	-	-	-	-	-	-	-	-	-	-	3.5	1.7	1.5	0.9
														0.3	0.2	0.3	0.1
Pogonophryne lanceobarbata	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	0.9	-	0.2
														<0,1	0.1		<0.1
Pogonophryne marmorata	-	-	-	-	-	-	-	-	-	-	-	-	-	1.5	4.3	1.5	-
														0.3	0.3	0.1	
Pogonophryne scotti	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-
														0.1			
Bathydraconidae																	
Akarotaxis nudiceps	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	0.9	0.8	-
														<0.1	0.1	0.1	
Bathydraco macrolepis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2
																	<0.1
Cygnodraco mawsoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	0.2
																3.4	0.9

Table 1 continued…	BPN 1	BPN 2	BPN 3	BPN 4	BPN 5	BPN 6	BPN 7	BPN 8	BPN 9	BPN 10	BPN 11	BPN 12	BPN 13	BT 1	BT 2	BT 3	BT 4
Gerlachea australis	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	2.6	0.8	10.3
														0.4	1.3	0.2	4.7
Gymnodraco acuticeps	-	-	-	-	-	-	-	-	1.4	-	-	-	-	-	-	-	-
									8.3								
Notothenioidei juveniles	20.7	48.1	25.0	84.6	29.4	23.5	-	42.7	98.6	100	5.4	-	4.4	-	-	-	0.4
	0.7	2.9	0.8	55.6	0.4	0.5		3.6	91.7	100	0.5		0.7				<0.1
Others																	
Anotopterus pharao	1.4	1.9	6.3	-	29.4	5.9	-	-	-	-	0.1	-	-	-	-	-	-
	40.1	31.5	35.7		94.8	68.6					<0.1						
Notolepis coatsi	-	-	-	7.7	-	-	-	-	-	-	-	-	-	-	-	-	-
				18.2													
Bathyraja maccaini	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-	-
														15.5			
Macrouridae	-	-	-	5.9	-	-	-	-	-	-	-	-	-	-	-	-	-
				0.2													
Myctophidae	-	-	-	-	-	-	-	-	-	-	-	-	0.4	-	-	-	-
													0.1				
Liparidae	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	4.3	1.5	0.4
														0.1	0.9	0.2	<0.1
Zoarcidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2
																	0.1

Table 2: Prey composition of *Pleuragramma antarcticum* caught in the pycnocline (St. 65-299 & St. 65-322) and above the ground (St. 65-329 & 65-314) at different times of the day in 2004. Prey abundance [N], biomass [g] (means ± SD), and frequency of occurrence [%] are given (empty stomachs are excluded, number N of filled stomachs given in parentheses).

	Copepoda	Chaetognatha	Mysis larvae	Ostracoda	Hyperiidae
PYCNOCLINE					
16:30 (N=10)					
Abundance [N]	525.5 ± 295.38	5.9 ± 5.88	0.7 ± 1.06		0.1 ± 0.32
Biomass [g]	1.06 ± 0.4	0.04 ± 0.04	<0.01 ± <0.01	-	0.03 ± 0.09
Occurrence [%]	100	90	40		10
00:10 (N=10)					
Abundance [N]	440 ± 127.97	2.67 ± 2.34	1 ± 1.05	0.1 ± 0.32	
Biomass [g]	0.97 ± 0.29	0.03 ± 0.03	<0.01 ± <0.01	<0.01 ± <0.01	-
Occurrence [%]	100	90	60	10	
GROUND					
12:00 (N=8)					
Abundance [N]	338 ± 305.07	0.86 ± 1.46	0.63 ± 1.06	0.14 ± 0.38	
Biomass [g]	0.91 ± 0.59	0.02 ± 0.05	<0.01 ± <0.01	<0.01 ± <0.01	-
Occurrence [%]	100	50	37,5	12,5	
15:30 (N=4)					
Abundance [N]	307.25 ± 147.82	4.5 ± 3.7			
Biomass [g]	0.6 ± 0.34	0.02 ± 0.02	-	-	-
Occurrence [%]	100	75			

Figures

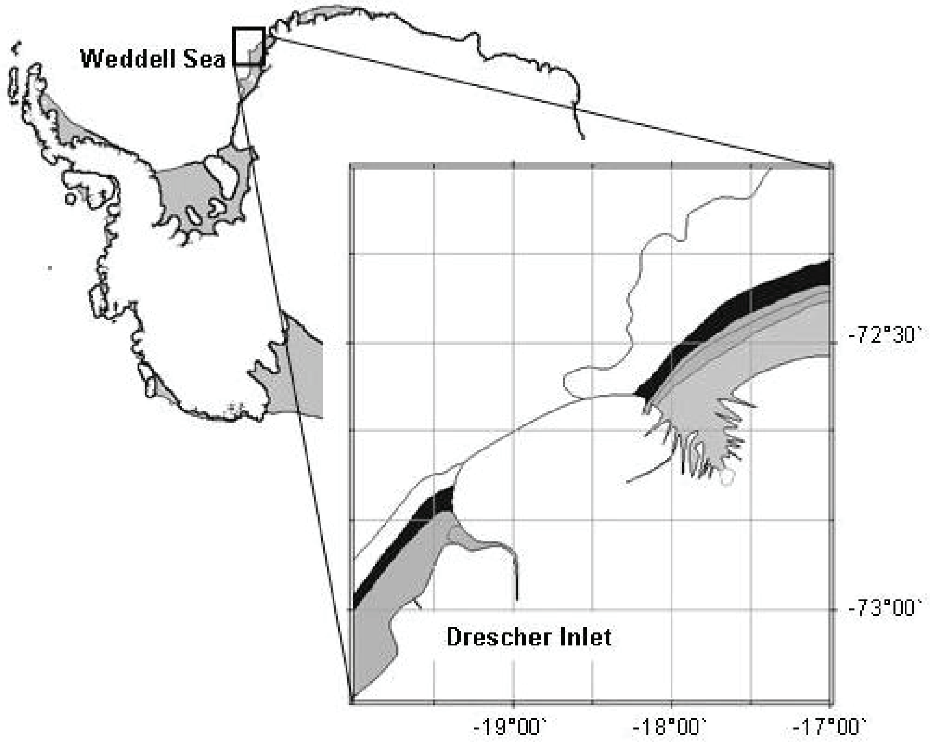

Fig. 1: General map of the study area in the south eastern Weddell Sea and enlarged map of the Drescher Inlet located in the Rijser Larsen Ice shelf.

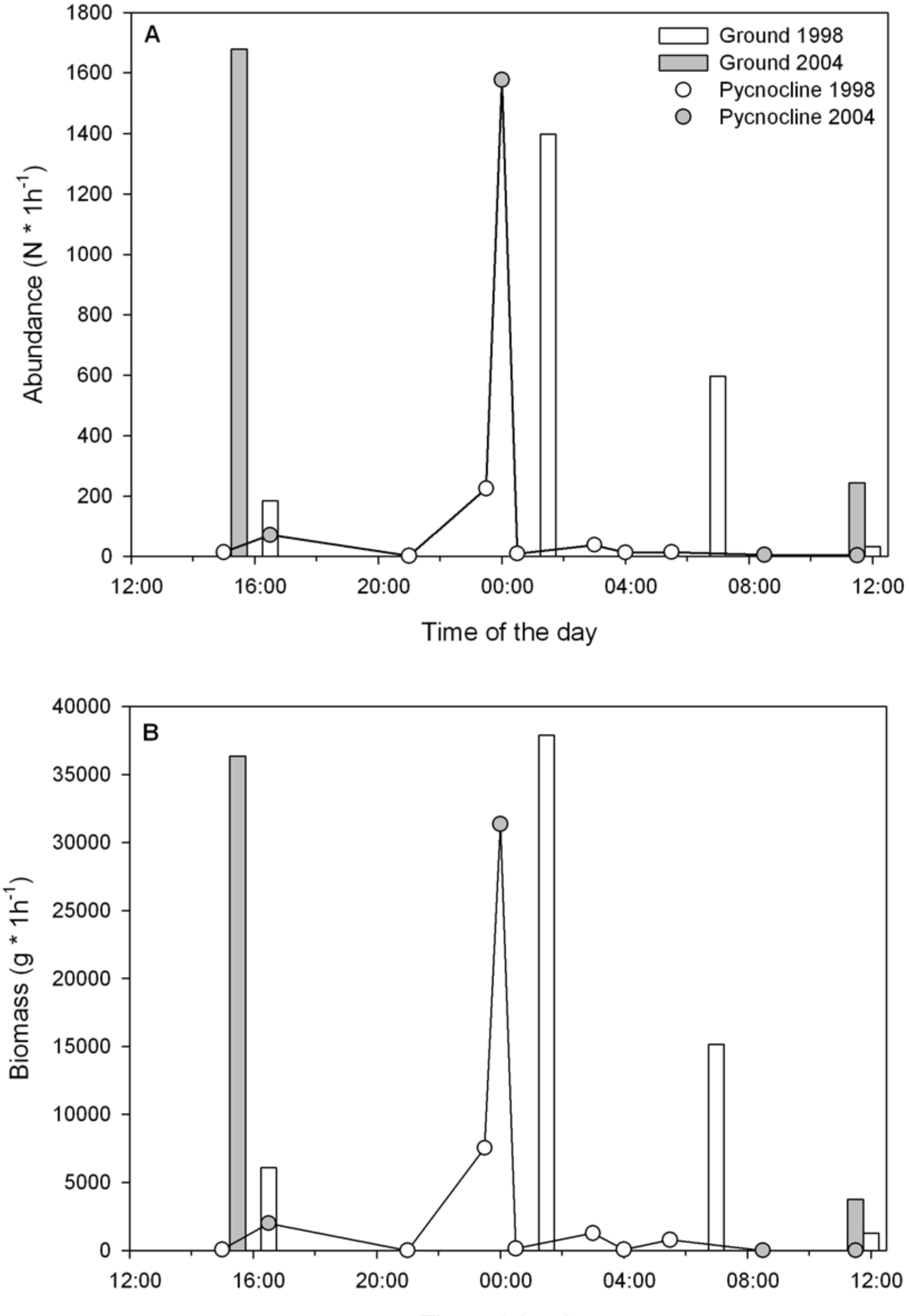

Fig. 2: Abundance (**A**) and biomass (**B**) (per 1 hour trawling time) of *Pleuragramma antarcticum* in the pycnocline (line/scatter plot) and above/on the ground (bar charts) at different times of the day (UTC). For details on sampling dates and gear see Table 1.

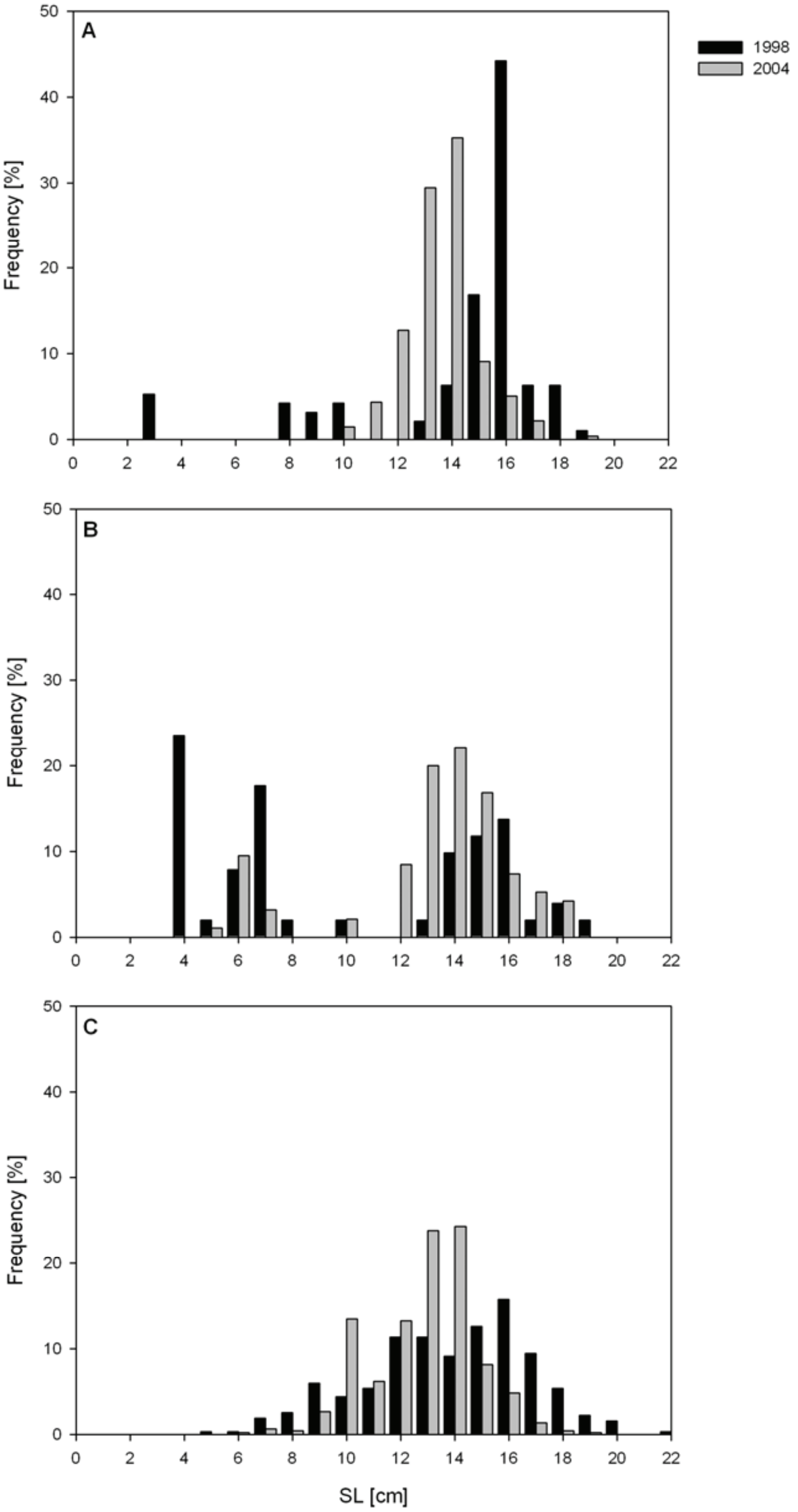

Fig. 3: Length frequency distribution [%] of *Pleuragramma antarcticum* (**A**) at peak abundance during the night (23:30-00:30; 1998: BPN St. 48-013, N=95; 2004: BPN St. 65-322, N=275), (**B**) in the pycnocline during the rest of the day (1998: 4 BPN, N=51; 2004: 3 BPN, N=95), and (**C**) above/on the ground (1998: 3 BT, N=317; 2004: 2 BPN, N=453). Length is given in standard length, SL [cm].

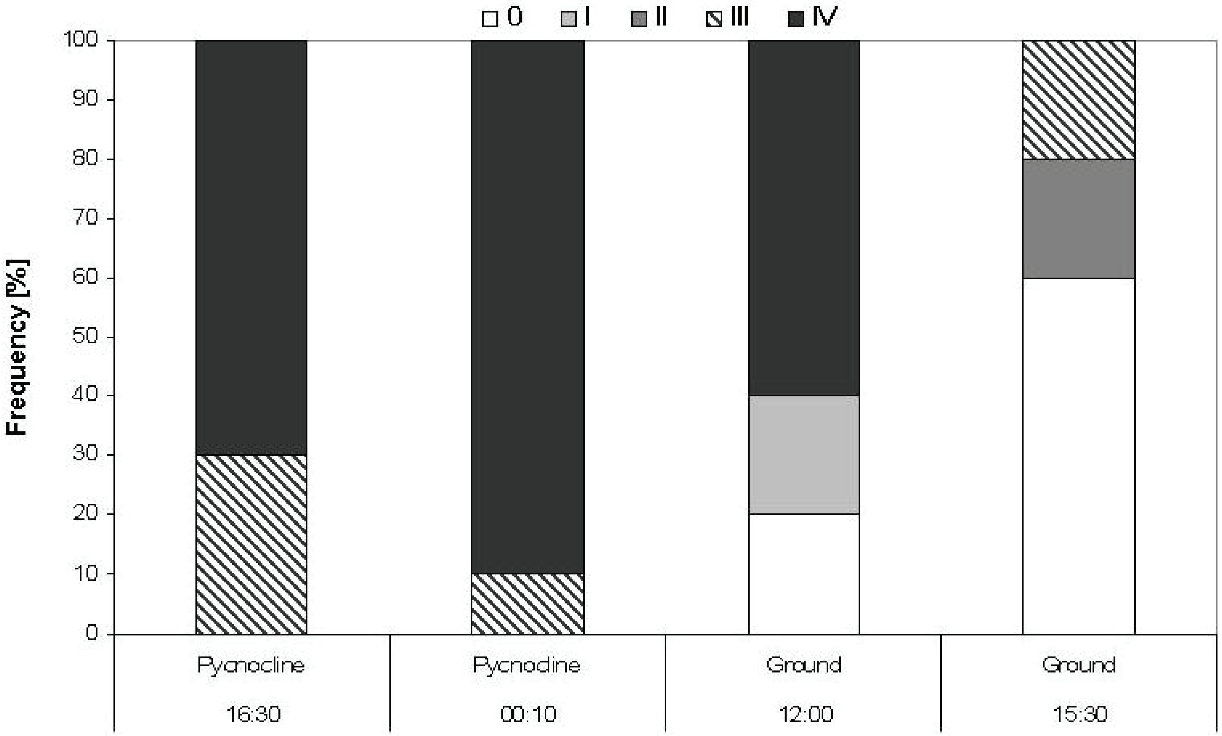

Fig. 4: Frequency of occurrence [%] of the degree of stomach filling in *P. antarcticum* caught in the pycnocline (St. 65-299, N=10; St. 65-322, N=10) and above the ground (St. 65-329, N=10; St. 65-314, N=10). 0 = empty, I = little contents, II = half full, III = full, IV = distended (see Methods for details).

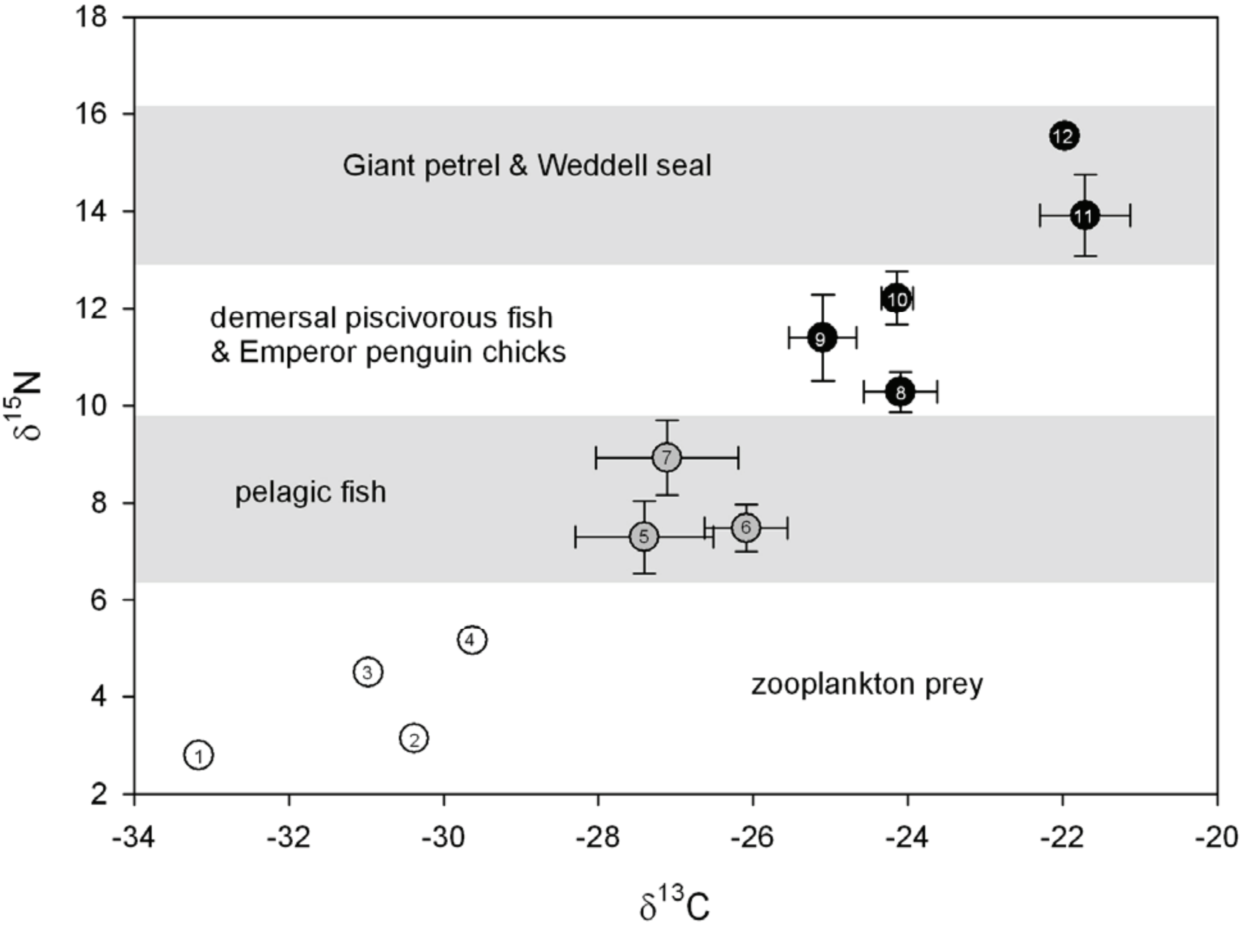

Fig. 5: Trophic hierarchy within the food web of the Drescher Inlet. Stable isotope composition ($\delta^{15}N$ and $\delta^{13}C$ in ‰, mean ± SD) of selected invertebrates, fish species and warm-blooded animals are shown. For details see text. 1 *Rhincalanus gigas* (Copepoda), 2 *Metridia gerlachei* (Copepoda), 3 *Calanus propinquus* (Copepoda), 4 *Sagitta marri* (Chaetognatha), 5 *Pleuragramma antarcticum* larvae, 6 *Trematomus* sp. juveniles, 7 *Pleuragramma antarcticum*, 8 Emperor penguin chicks (*Aptenodytes forsteri*), 9 *Chionodraco myersi*, 10 *Cryodraco antarcticus*, 11 Weddell seal (*Leptonychotes weddellii*),12 Giant petrel (*Macronectes giganteus*). Data on isotopic composition of *P. antarcticum*'s main zooplankton prey (copepods and chaetognaths) were taken from Rau et al. (1991).

PUBLICATION IV

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Trophic vulnerability of fish – the search for Achilles' heel in the high Antarctic food web.

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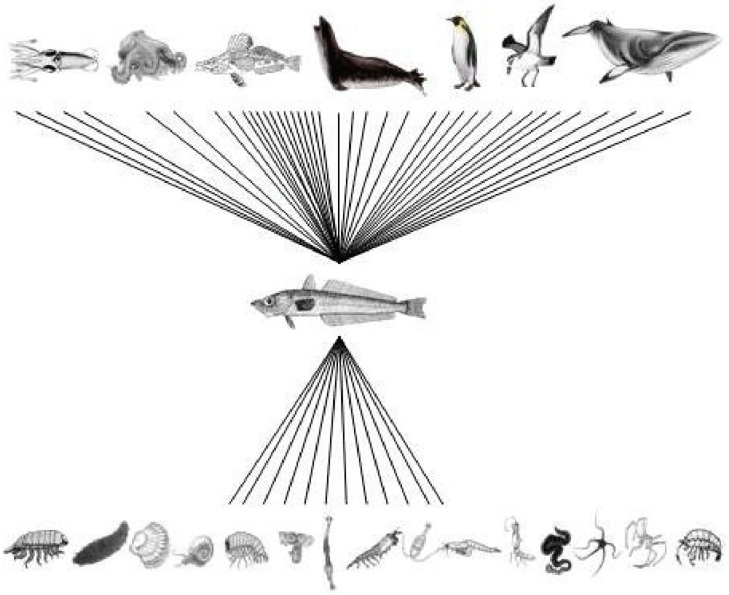

TROPHIC VULNERABILITY OF FISH – THE SEARCH FOR ACHILLES' HEEL IN THE HIGH ANTARCTIC FOOD WEB

K. Mintenbeck[1*], U. Jacob[2,3], R. Knust[1], W.E. Arntz[1], T. Brey[1]

[1]Alfred Wegener Institute for Polar and Marine Research, PO Box 120161, 27515,
Bremerhaven, Germany
[2]Department of Zoology, Ecology and Plant Science, Distillery Fields, University College Cork,
Ireland
[3]Environmental Research Institute, Lee Road, University College Cork, Ireland

RUNNING HEAD Trophic vulnerability of Antarctic fish

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[*] Email: Katja.Mintenbeck@awi.de

ABSTRACT

Climate change driven alterations of the environment take effect not only directly at the organism level but also indirectly at the system level, primarily mediated through the trophic interactions web. The significance of alterations in food web structure and dynamics for overall ecosystem functioning depends on consumer species vulnerability and functional redundancy. We evaluate the relative trophic vulnerability and functional redundancy of fish inhabiting the high Antarctic Weddell Sea based on trophic linkages to prey and predator species. Species vulnerability is mainly determined by the number of prey items, i.e. the degree of generalism. Among benthos feeders trophic vulnerability is low and functional redundancy is high. Plankton consumers, in contrast, show high vulnerability and low functional redundancy. The plankton feeding *Pleuragramma antarcticum* holds a central position in the pelagic food web, resembling schooling clupeid fish species such as sardine and anchovy in upwelling systems. It is not only the dominant species in terms of abundance and biomass, but also the one with the highest vulnerability. Hence, *P. antarcticum* can be seen as the “Achilles’ heel” in the high Antarctic food web. Extinction of this species will result in strong alterations of food web structure with severe consequences for ecosystem functioning, particularly concerning system top predators.

KEY WORDS trophic vulnerability, functional redundancy, food web, climate change, notothenioid fish, Weddell Sea, Antarctic

INTRODUCTION

Antarctic marine ecosystems are increasingly threatened by alterations of the abiotic and biotic environment induced by climate change (Gille 2002, Curran et al. 2003, Shindell & Schmidt 2004). These systems are particularly sensitive to environmental change because of (1) the adaptation of most poikilothermic Antarctic organisms to a narrow and cold temperature window (Clarke 1990), and (2) the close coupling of life strategies to the seasonal sea ice cycle, especially through direct or indirect trophic linkage to pelagic primary production (Loeb et al. 1997, Nicol et al. 2000, Atkinson et al. 2004).

The vulnerability of a particular species to changes in food web structure and dynamics depends on its ability to cope with both “bottom-up” and “top-down” effects: Trophic plasticity, i.e. the capability to cope with fluctuations in resource availability, is positively related to prey diversity (specialist vs. generalist consumers; Mihuc & Minshall 1995, Johnson 2000). Predator induced mortality is the principal “top-down” effect and thus resilience capability is related to predator diversity (e.g. Memmot et al. 2000). Accordingly, species vulnerability is expected to decrease with prey diversity and to increase with predator diversity. Whether and how the complete loss of one species will affect overall food web structure and ecosystem functioning depends on the communities’ capacity for functional compensability, i.e. species trophic redundancy (Naeem 1998, Johnson 2000).

Fish are known to be highly sensitive to environmental change through mechanisms operating directly at the ecophysiological level (fitness and survival) but also indirectly at the trophic level (through feeding relationships) (McFarlane et al. 2000, Benson & Trites 2002, Beaugrand et al. 2003). In the Antarctic, teleost fish play a central role, particularly on the continental shelf

(Hureau 1994). The perciform suborder Notothenioidei dominates both pelagic and benthic fish assemblages (e.g. Kock 1992). Notothenioid fish occupy a multitude of trophic niches with differing proportions of benthic, planktonic and fish prey, and they are preyed upon by piscivorous fish, cephalopods, and a variety of warm-blooded animals, including seasonal guests such as whales and seabirds (for review, see e.g. Kock 1992, Hureau 1994, La Mesa et al. 2004). Due to their role as a major trophic link between small-sized invertebrates and apex predators, fish might serve as a leading indicator of change in Antarctic ecosystems, making its potential vulnerability to systemic shifts of outstanding interest.

In this study we introduce a quantitative measure of relative (trophic) vulnerability based on the number of feeding links to prey and predator species, respectively. We evaluate patterns of vulnerability in the notothenioid fish fauna of the high Antarctic Weddell Sea shelf and relate vulnerability to life style. Finally we discuss the implications of our findings for overall Antarctic food web stability in the light of forthcoming climate change.

MATERIALS AND METHODS

Fish was sampled in 200-600 m water depth during four *RV Polarstern* expeditions (1996-2004, December-May) on the north-eastern Weddell Sea shelf (Antarctic) between 70°50'S 010°35'W and 75°03'S 027°20'W. 26 hauls were taken by an otter trawl (OT, opening width 22 m, cod-end mesh size 20 mm) and 10 hauls by a bentho-pelagic net (BPN, opening width 25 m, cod-end mesh size 10 mm). Trawling distance varied between 500 m and 4000 m (0.3 - 2.2 nm) in OT hauls and between 5600 m and 11800 m (3.0 - 6.5 nm) in BPN hauls.

Fish were identified to the species, and numbers and wet mass per species *i* and haul *j* were determined and converted into abundance $N_{i,j}$ [ind km^{-2}] and biomass $B_{i,j}$ [g km^{-2}] (post-larvae and small juveniles were excluded). To account for different numbers of OT and BPN hauls, weighted $N_{mean,i}$ and $B_{mean,i}$ were computed for each species *i*, i.e.

$$N_{mean,i} = \left(\sum_{j=1}^{m} N_{i,j} \bullet w_j) \right) / \sum_{j=1}^{m} w_j \tag{1}$$

where *m* is total number of hauls (*m* = 36) and weight w_j is 10 for each OT haul and 26 for each BPN haul. Standard deviation SD_i of $N_{mean,i}$ was computed by

$$SD_i = \left[\left(\sum_{j=1}^{m} SD_{i,j}^{\,2} \bullet w_j^{\,2}) \right) / \left(\sum_{j=1}^{m} w_j \right)^2 \right]^{0.5} \tag{2}$$

where $SD_{i,j}$ is the standard deviation of $N_{mean,i}$ within the corresponding sample type (OT or BPN). Biomass was treated accordingly. Additionally, relative dominance of individuals (*%N*) and biomass (*%B*) as well as frequency of occurrence (*%F*) were calculated. Non-notothenioid fish species were pooled into a one-taxon category.

For each taxon *i*, the total number of prey species NP_i, the number of prey species belonging to the functional groups "Benthos", "Plankton" and "Fish", $NP_{B,i}$, $NP_{P,i}$, $NP_{F,i}$, and the number of predators NC_i were taken from the trophic data base published by Brose et al. (2005) that includes information on feeding relations of 497 species from the Antarctic Weddell Sea. *NC* was taken as a measure of vulnerability to top-down effects, and *NP* as an (inverse) measure of vulnerability to bottom-up effects (see e.g. Memmot et al. 2000). The index of relative vulnerability VI_i of fish species *i* was computed by:

$$VI_i = NC_i / (NP_i + NC_i) \quad (3)$$

with $NP_i + NC_i \geq 1$ and $0 \leq VI_i \leq 1$. The dependence of relative vulnerability *VI* on the number of prey species from the functional groups "Benthos", "Plankton", "Fish" and from the number of predators was examined by multiple linear regression. All parameters were log(x+1) transformed to achieve linearity. Outliers in the sample space [$\log(NP_B+1)$, $\log(NP_P+1)$, $\log(NP_F+1)$, $\log(NC+1)$, $\log(VI+1)$] were identified by Mahalanobis Jackknife distances (Barnett & Lewis 1994) and excluded from the subsequent fit of a predictive model for $\log(VI+1)$. Finally, we used an effect screening (Haaland 1989) to visualize the relative effect size of each independent variable on $\log(VI+1)$ by means of a Pareto effects plot.

RESULTS

A total of 50 fish species were found on the north-eastern Weddell Sea shelf, among these 42 notothenioids. Rays (*Bathyraja* sp.), eelpouts (Zoarcidae), liparids, the grenadier fish *Macrourus whitsoni*, the daggertooth *Anotopterus pharao* and one myctophid constituted the eight non-notothenioid species. Notothenioids accounted for 99.4% of all individuals and 97.6% of biomass. *Pleuragramma antarcticum* (No. 24 in Table 1) was the most frequent species (*%F* = 72%) and dominated the fish community in terms of both abundance (*%N* = 54.6%) and biomass (*%B* = 30.9%) (Table 1).

Information on prey composition and links to predators was available for 37 of the 42 notothenioid species. The number of prey items *NP* ranged from 5 in some planktivorous fish to >100 in benthos feeders. The number of predators *NP* ranged from 13 to 46 (Table 1). The majority of notothenioid fish are benthos feeders and mixed feeders, consuming varying proportions of benthos and plankton (Fig. 1).

Relative vulnerability *VI* is related to the distribution of prey species among the functional groups “Benthos”, “Plankton” and “Fish”. *VI* is lowest in benthos feeders and benthos and fish feeders (*VI* 0.1 – 0.2), intermediate in fish feeders and mixed feeders of benthos and plankton (*VI* < 0.4), and highest in species feeding almost exclusively on planktonic prey or on a mixture of plankton and fish (*VI* > 0.7).

Three species were identified as multivariate outliers, reducing the data set for multivariate analysis to 34 species. The relationship between relative vulnerability, prey functional groups and predator numbers is described best by

$\log(VI+1) = 0.014 - 0.069 * \log(NP_B+1) - 0.053 * \log(NP_P+1) - 0.019 * \log(NP_F+1) + 0.204 * \log(NC+1)$; $r^2 = 0.97$, $p < 0.001$ for all independent variables except for $\log(NC+1)$ with $p = 0.005$.

The Pareto effects plot (Fig. 2) illustrates that $\log(NP_B+1)$ is the dominant factor, contributing 72 % to the total effect of all independent variables on $\log(VI+1)$, followed by $\log(NP_P+1)$ with 13 %, and $\log(NP_F+1)$ and $\log(NC+1)$, both with <8 %.

DISCUSSION

The Southern Ocean is warming since the 1950s (Gille 2002) and a reduction in duration and extent of sea ice was observed in vast areas, including the Weddell Sea (e.g. Curran et al. 2003, Cotté & Guinet 2007). The decline in sea ice already resulted in significant spatio-temporal shifts in water column primary production and zooplankton composition in parts of the Southern Ocean (Nicol et al. 2000, Loeb et al. 1997, Atkinson et al. 2004). Nevertheless, so far, our limited models of forthcoming climate change in the Antarctic (e.g. Shindell & Schmidt 2004, Overpeck et al. 2006) do not allow to anticipate with confidence through which cause-and-effect chains and in which direction Antarctic biota will be affected at the species level. Thus, we may hypothesize that both shifts and increased variability in abiotic and biotic parameters will cause quasi-random elimination of species from the system. Our measure of relative vulnerability VI is an indicator of consumer species risk to be negatively affected by such changes. The ecologically most interesting question is now, whether there is a "correlation risk" in any particular compartment of the high Antarctic ecosystem.

In notothenioid fish, relative vulnerability VI is mainly determined by the number of prey items ($NP_B + NP_P + NP_F$), i.e by the degree of generalism (see Fig. 2). The effect of predator diversity is of minor significance, as most fish species share the same number of potential predators that feed non-selectively on fish.

On the high Antarctic shelf, species numbers and biodiversity are much higher in the benthic compartment compared to the pelagic and fish communities (Gutt et al. 2004). This pattern is obviously reflected in notothenioid prey diversity and thus in trophic vulnerability: The number of benthic prey species NP_B is the principal determinant of VI (Fig. 2); the higher the share of benthic species in the diet, the lower is VI (Fig. 1). The resilience of the entire system, i.e., to what extent the extinction of particular consumer species from the system impacts overall food web stability and ecosystem functioning, strongly depends on the systems' ability to compensate for the loss by co-occurring species (Naeem 1998, Johnson 2000). As the majority of species include a certain proportion of benthic prey in their diet, functional redundancy seems to be high among benthos feeders (see Fig. 1). Obviously, feeding on benthos goes along with a high degree of trophic generalism and functional redundancy and hence with a certain capability to adapt food choice to prey availability and to dampen bottom-up effects. Plankton consumers show a distinctly higher vulnerability (Fig. 1). These species tend to specialize on a comparatively narrow prey spectrum, which makes them more sensitive to changes in prey availability. As there are less plankton feeding species in the system, the potential for functional compensability is lower, too. Thus, there exists a certain "correlation risk" in the plankton feeder compartment, making it particularly sensitive to change. Moreover, the whole fish community is distinctly dominated by only one species, the plankton feeding Antarctic silverfish, *Pleuragramma antarcticum*, which has the highest vulnerability of all species (Table 1). *P. antarcticum* is one of the few notothenioids with a truly pelagic live style, occurring in loose shoals or swarms (Eastman 1985, Fuiman et al. 2002). No other species, neither fish (e.g. myctophids or other pelagic notothenioids), nor invertebrates (e.g. squid or krill), may be able to provide full functional compensation in the event of extinction of *P. antarcticum*, in particular because none combines a pelagic shoaling life style with a *P. antarcticum* like size spectrum and energy content (e.g. Ainley et al. 2003).

P. antarcticum thus play a key role within the high Antarctic food web (see also Hureau 1994, La Mesa et al. 2004). It is the principal consumer of zooplankton and, besides krill, is the most important food source for a multitude of predators, in particular for warm-blooded animals inhabiting Antarctic shelf areas (e.g. Plötz 1986, La Mesa et al. 2004). In its central role in a relatively simply structured and highly productive pelagic system, *P. antarcticum* resembles schooling clupeid fishes in upwelling systems such as off Peru/Chile or off Namibia (e.g. Cury et al. 2000). Driven by global climate oscillations, such systems undergo dramatic changes at semi-regular intervals. In the eastern South Pacific, for example, El Niño events involve strong reductions in stocks of anchovy and sardine owing to bottom-up effects, causing starvation and mortality in the very top predators, birds and seals (e.g. Arntz 1986). These clupeid fishes, however, are evolutionarily adapted to strong environmental fluctuations, mainly by fast growth (growth constant K = 0.5 - 0.8, e.g. Cubillos et al. 2002) and comparatively high relative fecundity (550-600 eggs g^{-1} female, e.g. Alheit 1986), both facilitating population recovery. Moreover, shoals can emigrate into waters with more favourable environmental and food conditions (Arntz 1986). The Antarctic *P. antarcticum*, in contrast, has much lower recovery potential: emigration is limited by stenothermy (Somero & DeVries 1967), growth is comparatively slow (K = 0.05 - 0.16, Hubold & Tomo 1989), and relative fecundity is low (70-160 eggs g^{-1} female, Gerasimchuk 1988).

Its central position, high vulnerability and lack of functional redundancy, combined with low resilience, make *P. antarcticum* the “Achilles’ heel” of the high Antarctic food web. Systemic shifts affecting *P. antarcticum* will cause strong alterations of food web structure with severe consequences for system top predators in particular and overall ecosystem functioning in general.

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TABLE

Table 1. Composition of the fish community on the north-eastern Weddell Sea shelf (species are listed in alphabetical order). For each notothenioid species weighted mean abundance (N_{mean}, ind km^{-2}) and biomass (B_{mean}, g km^{-2}) with corresponding standard deviations (*SD*), relative contribution of individuals (*%N*) and mass (*%B*) to entire fish community, and frequency of occurrence (*%F*) in hauls (N=36) are given. Non-notothenioid fish species are pooled. The index of relative vulnerability *VI* was calculated from the total number of prey species (*NP*) and total number of predator species (*NC*) (see equation 3). Trophic groups (*TG*) were assigned according to main food components as shown in Fig. 1, with B = benthos, P = plankton, F = fish. na = no information on trophic linkages available

		N_{mean}	*SD*	B_{mean}	*SD*	*%N*	*%B*	*%F*	*NP*	*NC*	*VI*	*TG*
1	*Aethotaxis mitopteryx*	0.01	0.01	2.68	1.65	0.08	0.35	11	53	14	0.21	BP
2	*Akarotaxis nudiceps*	<0.01	<0.01	0.03	0.01	0.02	<0.01	14	79	13	0.14	B
3	*Artedidraco loennbergi*	0.07	0.03	0.39	0.16	0.56	0.05	42	108	14	0.11	B
4	*A. orianae*	0.07	0.02	1.70	0.41	0.64	0.22	44	27	14	0.34	BP
5	*A. shackletoni*	0.02	0.01	0.41	0.14	0.21	0.05	33	110	14	0.11	B
6	*A. skottsbergi*	0.07	0.02	0.38	0.13	0.61	0.05	36	86	13	0.13	B
	Bathydraco macrolepis	<0.01	<0.01	0.01	<0.01	0.01	<0.01	3		- na -		
7	*B. marri*	0.01	0.01	0.11	0.09	0.07	0.01	8	47	13	0.22	B
8	*Chaenodraco wilsoni*	0.12	0.06	10.34	4.87	1.01	1.35	47	16	15	0.48	PF
9	*Chionobathyscus dewitti*	<0.01	<0.01	0.84	0.60	0.30	0.11	6	10	14	0.58	PF
10	*Chionodraco hamatus*	0.09	0.02	25.73	6.42	0.82	3.35	64	15	15	0.50	PF
11	*C. myersi*	1.25	0.58	227.67	119.09	10.85	29.66	64	10	15	0.60	PF
12	*Cryodraco antarcticus*	0.20	0.05	41.46	7.09	1.70	5.40	67	5	15	0.75	P
13	*Cygnodraco mawsoni*	0.04	0.01	6.32	2.45	0.33	0.82	44	57	14	0.20	BP
14	*Dacodraco hunteri*	0.09	0.04	6.53	3.76	0.81	0.85	28	43	15	0.26	F
15	*Dissostichus mawsoni*	<0.01	<0.01	0.75	0.69	0.04	0.10	8	52	21	0.29	BP
16	*Dolloidraco longedorsalis*	0.37	0.12	3.99	1.44	3.20	0.52	44	142	14	0.09	B
17	*Gerlachea australis*	0.13	0.04	4.27	1.35	1.12	0.56	33	14	14	0.50	P
18	*Gymnodraco acuticeps*	0.02	0.01	4.02	1.52	0.18	0.52	44	35	14	0.29	P
19	*Histiodraco velifer*	0.02	0.01	1.85	0.56	0.20	0.24	25	90	13	0.13	BF
20	*Neopagetopsis ionah*	<0.01	<0.01	2.51	1.37	0.03	0.33	14	5	14	0.74	P
21	*Pagetopsis macropterus*	0.02	0.01	1.81	0.92	0.18	0.24	22	52	15	0.22	F
22	*P. maculatus*	0.03	0.01	1.68	0.42	0.26	0.22	44	10	15	0.60	PF

23	*Pagothenia borchgrevincki*	<0.01	<0.01	0.09	0.07	0.01	0.01	6	18	13	0.42	P
24	*Pleuragramma antarcticum*	6.28	4.47	237.461	190.98	54.60	30.93	72	12	46	0.79	P
	Pogonophryne barsukovi	0.01	<0.01	1.00	0.46	0.09	0.13	17	- na -			
	P. lanceobarbata	0.01	0.01	0.34	0.29	0.12	0.04	14	- na -			
	P. macropogon	<0.01	<0.01	0.23	0.21	0.02	0.03	8	- na -			
25	*P. marmorata*	0.03	0.01	1.09	0.31	0.27	0.14	39	45	14	0.24	BP
26	*P. permittini*	0.01	<0.01	0.35	0.24	0.05	0.05	8	79	14	0.15	B
27	*P. phyllopogon*	0.01	<0.01	0.17	0.10	0.04	0.02	11	78	14	0.15	B
	P. scotti	0.02	0.01	2.52	1.31	0.14	0.33	22	- na -			
28	*Prionodraco evansii*	0.19	0.12	1.00	0.45	1.67	0.13	31	89	14	0.14	BP
29	*Racovitzia glacialis*	0.04	0.02	2.40	1.05	0.37	0.31	33	90	14	0.13	BP
30	*Trematomus bernacchii*	0.01	<0.01	0.74	0.39	0.05	0.10	14	93	14	0.13	B
31	*T. eulepidotus*	0.54	0.16	64.56	23.57	4.72	8.40	64	46	14	0.23	BP
32	*T. hansoni*	0.04	0.01	13.65	3.63	0.38	1.78	39	86	14	0.14	BF
33	*T. lepidorhinus*	0.60	0.19	30.13	11.10	5.25	3.92	69	71	14	0.16	BP
34	*T. loennbergi*	0.04	0.01	6.12	1.86	0.31	0.80	31	110	14	0.11	BF
35	*T. nicolai*	0.06	0.03	9.76	3.97	0.56	1.27	31	88	14	0.14	B
36	*T. pennellii*	0.38	0.15	24.40	10.31	3.28	3.18	42	169	14	0.08	BF
37	*T. scotti*	0.52	0.16	8.30	2.99	4.51	1.08	67	121	14	0.10	B
	Non-notothenioid species					0.58	2.42	61				

FIGURES

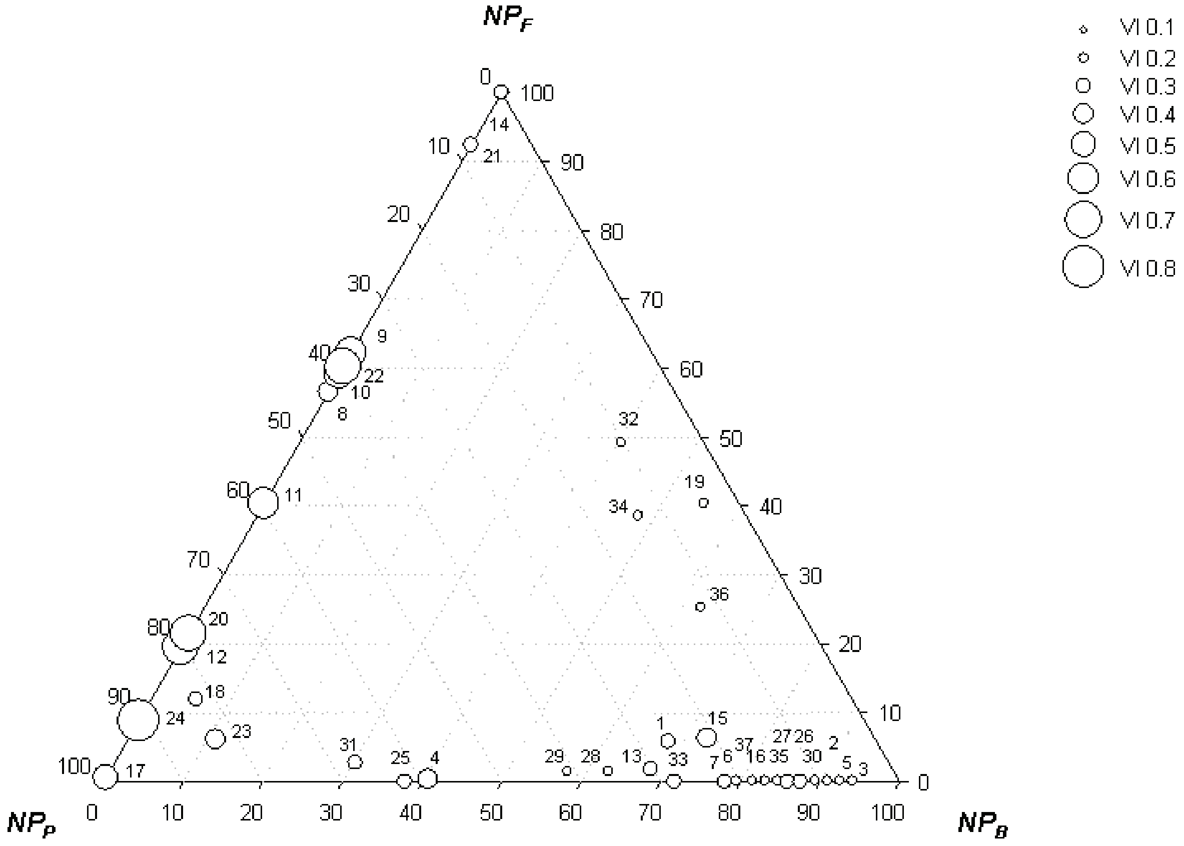

Fig. 1. Relative proportions [%] of benthos (NP_B), plankton (NP_P) and fish (NP_F) in the diet of notothenioid fish species. Each circle represents one species; circle diameter indicates relative vulnerability (*VI*). For species code numbers see Table 1

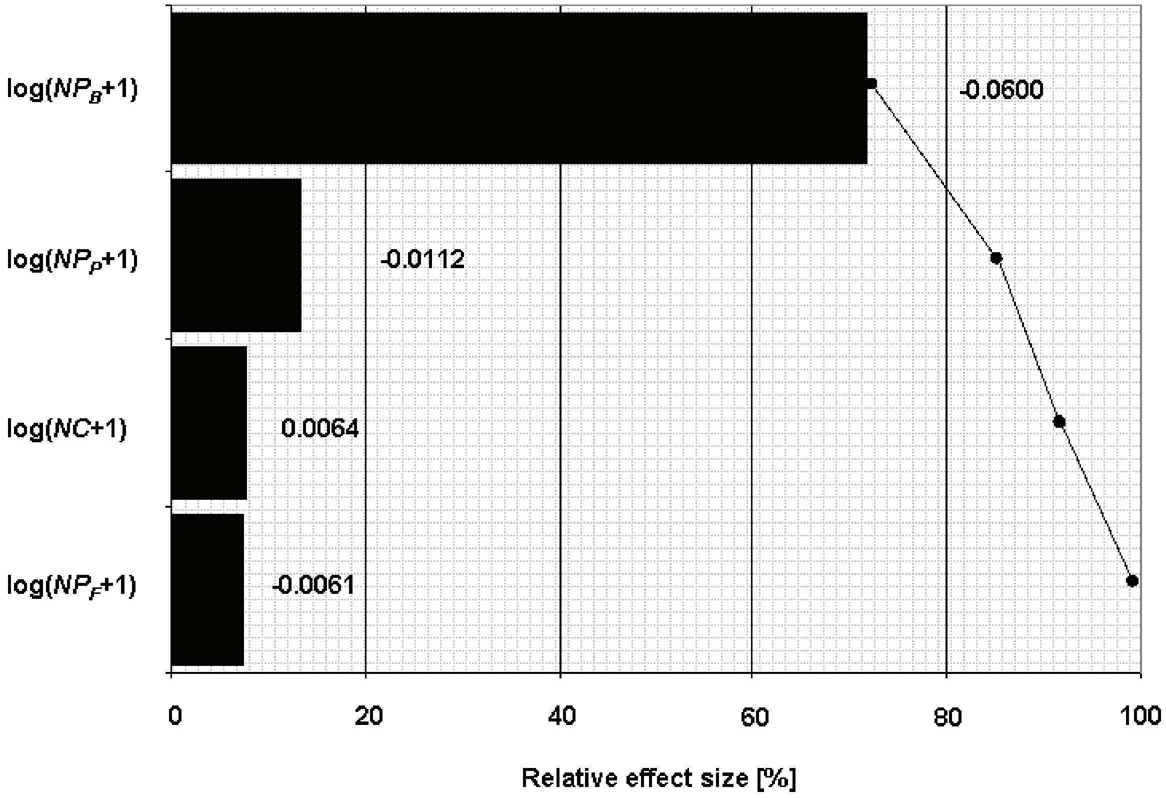

Fig. 2. Pareto plot illustrating the relative effect magnitude [%] of scaled parameter estimates (centered by the mean and scaled by range/2, standardized and orthogonalized to be uncorrelated) on vulnerability *VI* regarding the multiple model $\log(VI+1) = 0.014 - 0.069 * \log(NP_B+1) - 0.053 * \log(NP_P+1) - 0.019 * \log(NP_F+1) + 0.204 * \log(NC+1)$. Bar charts show percentage composition, curve shows cumulative percentages. Numbers to the right of the bars indicate absolute values of scaled estimates, with +/- indicating the direction of the effect

D. SYNTHESIS

1. USE & LIMITATIONS OF STABLE ISOTOPE BASED TROPHIC INFORMATION

1.1 Sample Treatment and Isotope Correction Models

The first essential step towards a useful and reliable stable isotope based trophic database is a correct and uniform sample preparation and treatment. Sample acidification and lipid extraction are commonly applied prior to isotope analysis to remove inorganic carbonates and tissue lipids, both known to alter δ^{13}C values. The dimension and direction of potential side effects of these treatments on δ^{15}N, however, were inconclusive so far (*c.f.* Bunn et al. 1995, Bosley & Wainright 1999, Pinnergar & Polunin 1999, Sotiropoulos et al. 2004, Sweeting et al. 2006).

We tested the effects of sample acidification and lipid extraction as well as a combination of both treatments on fish muscle tissue stable isotope signatures (PUBLICATION I). The results of our study clearly show that sample treatment, in particular chemical lipid extraction and treatment combination, not only affects C/N ratio and δ^{13}C but also introduces an ecologically relevant bias of up to 1.65 ‰ in δ^{15}N (Fig D1.1). Only sample acidification applied alone did not significantly affect δ^{15}N (but see PUBLICATION XI, Kennedy et al. 2005). The positive relationship between sample lipid content and amount of change in δ^{15}N ($\Delta\delta^{15}$N) suggest a leaching of lipid associated proteins enriched in ^{14}N induced by lipid extraction (see also Sotiropoulos et al. 2004, Sweeting et al. 2006) and an additional, apparently lipid independent, loss of ^{15}N enriched nitrogen compounds (e.g., non-essential amino-acids such as cysteine) in the combined treatment (see PUBLICATION I). Comparison of our results with previous studies (e.g. Pinnegar & Polunin 1999, Sotiropoulos et al. 2004, Sweeting et al. 2006) strongly suggest that the amount of change $\Delta\delta^{15}N$ induced by chemical lipid extraction depends on biochemical tissue composition (concerning nitrogen-containing compounds such as ammonia or trimethylamides), making the effect of treatment on $\delta^{15}N$ hard to predict. Any kind of treatment that involves lipid extraction thus should be avoided in samples intended for $\delta^{15}N$ analysis. Whenever chemical lipid correction of $\delta^{13}C$ values is required in multiple isotope studies, samples have to be treated and analysed separately.

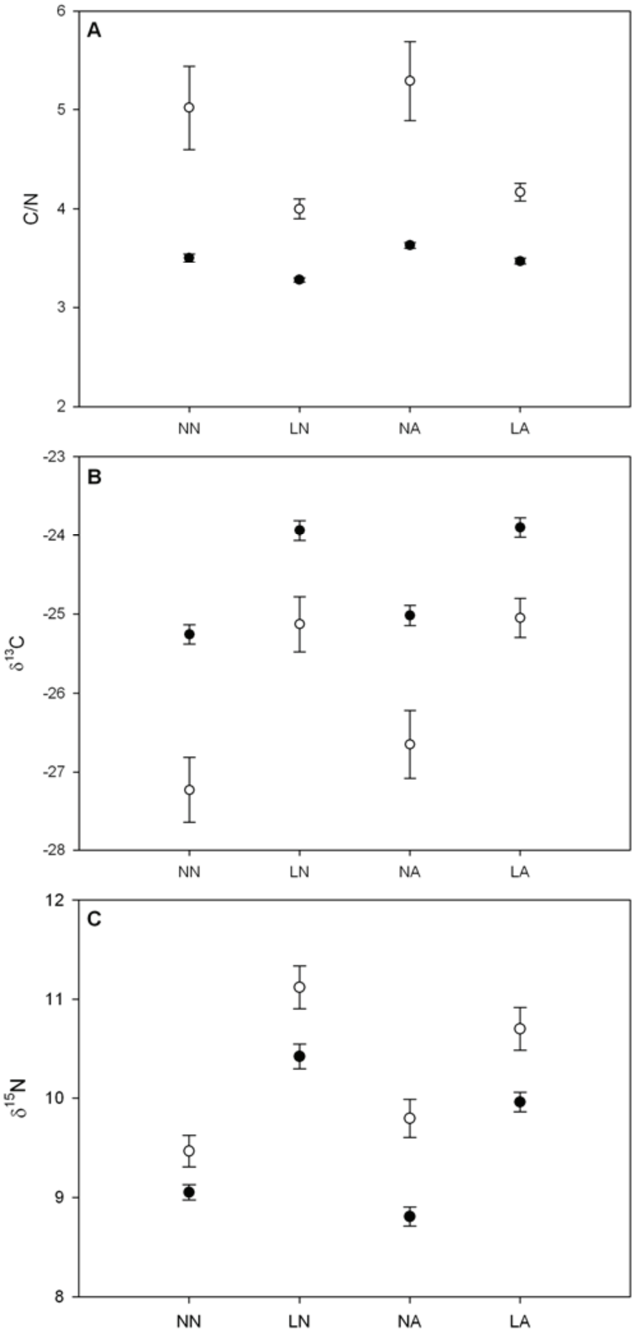

Fig. D1.1 Impact of sample treatment on means (± standard error) in tissue samples of the nototheniid fish species *Trematomus pennellii* (●) and *Pleuragramma antarcticum* (○). (**A**) C/N [by mass], (**B**) $\delta^{13}C$ [‰], and (**C**) $\delta^{15}N$ [‰]. NN: no treatment, LN: lipid removal, NA: acidification, LA: lipid removal + acidification.

To avoid additional costs and efforts caused by separate sample treatment and analysis, mathematical lipid correction might provide an alternative to account for the lipid effect on $\delta^{13}C$. Mathematical approaches include empirically derived lipid normalisation models (McConnaughey & McRoy 1979, Kiljunen et al. 2006, Post et al. 2007) and correction by mass balance (Sweeting et al. 2006). Lipid normalisation models attempt to correct $\delta^{13}C$ measurements of lipid containing samples according to C/N ratio by making use of the empirical relationships between (i) tissue lipid content and C/N ratio, and (ii) C/N ratio and lipid-induced differences in $\delta^{13}C$. The mass balance approach relies on the assumption that the sample tissue is exclusively composed of proteins and lipids and on the knowledge of C/N of pure protein. We examined some of the underlying assumptions lipid normalisation models are based on, and tested the suitability of normalisation and mass balance correction models to muscle tissue samples of two notothenioid fish species by comparing model output with $\delta^{13}C$ values measured in lipid extracted tissue (PUBLICATION I).

All tested models failed to predict correct $\delta^{13}C$ of lipid free tissue, primarily due to highly questionable assumptions most models are based on. The normalisation models of McConnaughey & McRoy (1979) and Kiljunen et al. (2006) rely on (i) the existence of a common, non-linear relationship between tissue lipid content and C/N, and (ii) a constant 6 ‰ difference in $\delta^{13}C$ between lipid and protein. In the two fish species used in our study this relationship turned out to be linear and moreover species-specific, making the first assumption invalid (Fig D1.2). The second assumption is questionable, as well, because ^{13}C depletion in lipids compared to other biochemical fractions or whole organisms is highly variable, and apparently also species-dependent (Park & Epstein 1961, Parker 1964, Thompson et al. 2000).

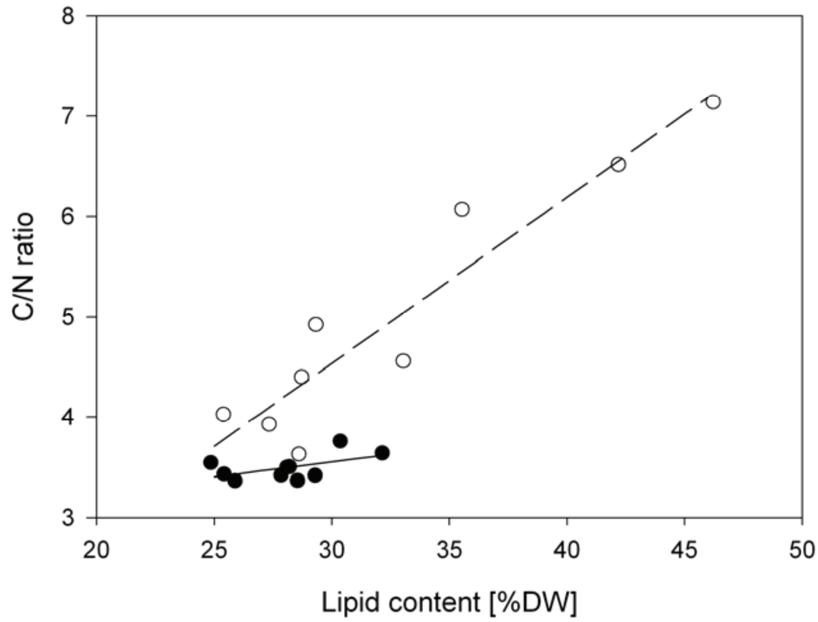

Fig. D1.2 Relationship between lipid content [%DW] and C/N ratio in untreated tissue samples of *T. pennellii* (●, —) and *P. antarcticum* (○, - - -).

The mass balance model of Sweeting et al. (2006) also relies on a constant difference in δ^{13}C between lipids and protein. This approach, moreover, assumes that tissues are composed of lipids and protein only, and that the C/N value of protein is constant (though it might be species or taxon-specific). Both assumptions are doubtful: First, fish muscle tissue is not exclusively composed of lipids and protein but contains also carbohydrates (Oehlenschläger & Rehbein 1982, Donnelly et al. 1990) that might contribute to C/N and δ^{13}C of bulk tissue. Second, even after lipid extraction we observed a variance in fish muscle C/N of about 1.5 %. The normalisation model of Post et al. (2007) is exclusively based on the assumption of a linear, species-independent relationship between C/N and lipid induced change in δ^{13}C ($\Delta\delta^{13}$C). Basically, this approach seems to be valid as our data confirm this linear and species-independent relationship. Nevertheless, accuracy of the model output was poor. All mathematical δ^{13}C lipid normalisation/correction models are highly sensitive to variation in basic parameters and deviation from model assumptions. There are still many gaps in our knowledge and inconsistent results concerning the basic relationships (see above). Until determinants and underlying biochemistry of these relationships are not fully understood, mathematical $\delta^{13}C$ correction does not provide a reliable alternative to chemical lipid extraction, unless a models' accuracy has been verified specifically for the organism of interest.

To avoid any treatment induced bias in stable isotope signatures all our samples analysed for studies on trophic relationships were only acidified with HCl using the drop-by-drop technique recommended by Jacob et al. (PUBLICATION XI). Neither chemical nor mathematical $\delta^{13}C$ lipid correction was applied.

SUMMARY – SAMPLE TREATMENT AND ISOTOPE CORRECTION MODELS

This chapter deals with the effect of lipid extraction and sample acidification on tissue C/N, $\delta^{13}C$ and $\delta^{15}N$:

- **chemical *lipid extraction* from sample tissue alone and in combination with *sample acidification* significantly affects $\delta^{15}N$ in an ecologically relevant dimension; the rate of change obviously depends on biochemical tissue composition;**
- **C/N and $\delta^{13}C$ changes following lipid extraction proportional to sample lipid content, but the rates of change are species-specific!**
- **mathematical *$\delta^{13}C$ lipid correction models* produce strongly biased estimates of $\delta^{13}C$ of lipid free tissue, all models are based on highly questionable and/or incorrect assumptions.**

1.2 Within-System Variability of the Primary Food Source

When interpreting stable isotope based trophic information it is essential to take the potential within-system variability of the primary food source into account. This is of particular importance in systems of substantial water depth, such as the Weddell Sea shelf, where particulate organic matter (POM) originating from the euphotic zone food web is the major food source for a rich suspension and deposit feeder community (see OVERVIEW, Chapter 2.2). $\delta^{15}N$ of POM might vary strongly: (i) $\delta^{15}N$ of particles contributing to bulk POM in surface waters tends to increase with particle size, most likely reflecting particles' origin (Wada et al. 1987, Altabet 1988, Rau et al. 1990, Wu et al. 1997); (ii) in several oceanic areas including the Southern Ocean $\delta^{15}N$ of bulk POM has been observed to increase with increasing water depth (Saino & Hattori 1980, Biggs et al. 1987, Rau et al. 1991b, Altabet & Francois 2001) due to the release of ^{15}N depleted nitrogen during microbial degradation (Wada 1980, Macko & Estep 1984, Macko et al. 1986); (iii) this depth-related increase in $\delta^{15}N$ is apparently pronounced in suspended particles but less evident in sinking particles (Altabet 1988).

Suspension and deposit feeders are usually assumed to belong to one functional group as both rely on material from the euphotic zone. However, particle preferences differ between these two feeding guilds: Deposit-feeding organisms rely on particles deposed on the sea-floor and can handle particles across the whole size range of POM (e.g., Massin 1982). Many benthic suspension feeders, in contrast, depend on particles of the pico- and nano-plankton size fraction suspended in the water column (Reiswig 1971, Ribes et al. 1999, Orejas et al. 2003).

We investigated whether the depth-related change in POM isotopic signature is reflected in these two groups of primary benthic POM consumers and found a pronounced δ^{15}N increase in suspension feeders but not in deposit feeders (PUBLICATION II). In suspension-feeding species tissue δ^{15}N increased in a non-linear way by up to 9.8 ‰ with the major shift occurring in the upper 500 m. Assuming a per trophic step enrichment in ^{15}N of 3.3 ‰ this difference corresponds to about 3 trophic levels. In deposit feeders, in contrast, such a depth effect on δ^{15}N was barely visible. The differences between trophic guilds and the pattern observed in suspension feeder δ^{15}N are supposed to be the result of the feeding guild specific particle preferences and dynamics of POM composition, turnover and sedimentation (see Fig D1.3).

Particles residence time in the water column and thus degradation are determined by sinking velocity that changes strongly with particle size and density (see OVERVIEW, Chapter 2.2). Small suspended particles ingested by suspension feeders exhibit extremely low sinking velocities. Microbial remineralisation and thus increase in particle δ^{15}N is accordingly high, particularly in the upper mesopelagial where bacterial abundance and activity is high (Lochte et al. 1997, Aristegui et al. 2002). Large particles such as faecal pellets and strings which make up the major part of sedimenting material that is ingested by deposit feeders, in contrast, pass this zone of enhanced POM turnover and alteration rapidly. This fresh material is rapidly mixed into the sediment by active bioturbation, and degraded slowly (Mincks et al. 2005), thus providing a ‘‘longterm’’ storage of high nutritive organic matter (*so called* ‘food bank’; Isla et al. 2006, Mincks et al. in press). Owing to differences in sinking velocities POM size spectrum shifts towards larger particles with increasing water depth. At greater depth suspension feeding organisms therefore depend on small particles originating from fragmentation of large particles made available by resuspension. Due to intense microbial activity at the benthic boundary layer (e.g., Lee et al. 2004), fragmentation and resuspension of large particles obviously involves a distinct increase in $\delta^{15}N$, as well. Accordingly, suspension feeder $\delta^{15}N$ changes little below 500 m water depth but is up to one trophic level higher than $\delta^{15}N$ of deposit feeders.

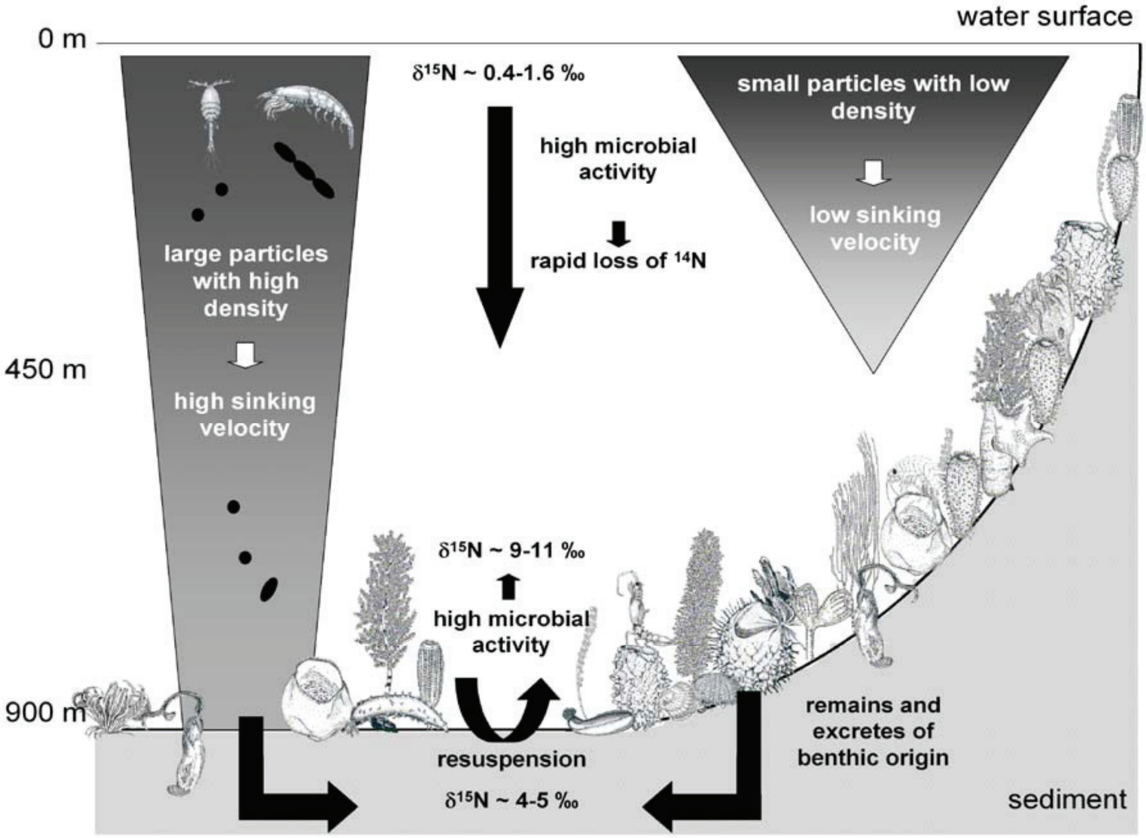

Fig. D1.3 Schematic overview of vertical particle distribution and processes at work in the water column and on the sediment that are supposed to result in the $\delta^{15}N$ patterns observed in benthic suspension- and deposit feeders (animal drawings from Sieg & Wägele 1990). $\delta^{15}N$ range of Southern Ocean surface water bulk POM (0.4-1.6 ‰) taken from Biggs et al. (1987) and Wada et al. (1987), sediment $\delta^{15}N$ according to Altabet & Francois (1994), Sigman et al. (1999), Wada et al. (1987). For further details see text.

The observed trophic-guild-specific depth dependence of $\delta^{15}N$ in benthic POM consumers might introduce a serious bias in marine isotope based food web studies that integrate data over a wide depth range. The depth related increase in suspension feeders δ^{15}N shifts affected taxa up in the trophic hierarchy, and this effect will propagate along the food chain via consumers such as sponge feeding asteroids (*Acondontaster* spp.; Dayton et al. 1974, Dearborn & Edwards 1985) towards higher trophic levels, thereby affecting the whole trophic structure. Depth-dependence in δ^{15}N of POM therefore has to be taken into account to avoid bias and misinterpretation of stable isotope based trophic information.

We tested our stable isotope database for a depth effect on higher trophic levels but found no indication for such a bias in benthic consumers from other trophic guilds. The majority of benthic consumers (except suspension and deposit feeders) were sampled on the shelf and upper slope between 350 and 600 m water depth.

SUMMARY – WITHIN-SYSTEM VARIABILITY OF THE PRIMARY FOOD SOURCE

In this chapter the relationship between depth dependent variability in δ^{15}N, POM dynamics, and trophic-guild specific feeding preferences is discussed:

- **POM δ^{15}N increases with water depth owing to *microbial degradation*; the rate of change depends on particle size and thus on sinking velocity, with small particles showing a strong increase in δ^{15}N, while changes in large rapidly sinking particles are negligible;**
- **particle dynamics and isotopic signature are clearly reflected in POM consumers, δ^{15}N of *suspension feeders* relying on smallest suspended particles increases with water depth by up to 10‰, while in *deposit feeders*, feeding on larger particles deposed on the sea floor, a depth effect was barely visible.**

1.3 Combination with Dietary Analyses

Stable carbon and nitrogen isotope signatures are useful to trace primary carbon sources and to estimate consumers' trophic levels within a particular system (see OVERVIEW, Chapter 1.2); however, the level of resolution is low. To illuminate trophic interactions in complex ecosystems stable isotope analyses need to be combined with information about detailed food composition from traditional methods such as direct diet studies (see also Post 2002a). In particular mixing models do only make sense when potential sources that might contribute to a consumer's overall diet are known. Each method on its own just tells part of the story, but in combination with traditional methods time-integrating stable isotope analysis provides additional information that might be missed by snapshot diet analyses.

In Fig. D1.4 mean stable isotope signatures δ^{13}C and δ^{15}N of 42 fish species inhabiting the Weddell Sea shelf and slope are compared with trophic group assignment based on major food composition (for sources on diet composition see ANNEX, Table G1). Stable isotope signatures reflect the pattern of trophic group positions expected from dietary studies very well. δ^{13}C of fish muscle tissue tends to increase from plankton consumers towards benthos and benthos and fish feeders. However, in some species such as *Aethotaxis mitopteryx* (24) and myctophid fish (42) δ^{13}C values are extremely low due to high tissue lipid content. δ^{15}N and thus trophic position is lowest in pure plankton feeders, e.g. nototheniid larvae (36) and juveniles (34), and highest in benthos feeders, benthos and fish feeders and pure fish predators. Highest trophic position among fish species is occupied by the artedidraconid *Dolloidraco longedorsalis* (5).

In the Antarctic toothfish *Dissostichus mawsoni* (25), which is usually supposed to be a piscivorous top predator (Pakhomov & Tseytlin 1992), δ^{15}N value is surprisingly low. The sampled individual, however, was a juvenile of only 20 cm total length and 40 g weight (adults attain up to 175 cm total length and 80 kg). Low δ^{15}N indicate a high proportion of planktonic low trophic level prey at earlier life stages, while large specimens will exhibit accordingly higher values. In consumers of a mixed diet interspecific δ^{15}N variability allows estimating the relative proportions of food components. δ^{15}N of the channichthyid *Chaenodraco wilsoni* (17), for example, is low compared to other plankton and fish feeders, reflecting the high proportion of *Euphausia crystallorophias* and the minor amount of fish in the diet of this species (see Takahashi & Nemoto 1984). In the benthos and plankton feeding species *Artedidraco orianae* (2), *Bathydraco marri* (12), and *Aethotaxis mitopteryx* (24) the proportion of high trophic level benthos seems to be high, while *Trematomus eulepidotus* (27), *T. lepidorhinus* (29) and *T. nicolai* (31) include a higher proportion of plankton in their diet (see also Schwarzbach 1988, Mintenbeck 2001). No or little dietary information is available for the notothenioid species *Pogonophryne macropogon* (7), *P. scotti* (10), *Bathydraco macrolepis* (11), and the rays *Bathyraja maccaini* (37) and *B. murrayi* (38). High δ^{15}N values in *P. macropogon* and *P. scotti* support the assumption that both most likely include a high proportion of benthos and/or fish in their diet as do most *Pogonophryne* species (Schwarzbach 1988, Olaso et al. 2000). *B. macrolepis* feeds on higher trophic level food compared to its congener *B. marri* (12). *Bathyraja murrayi* occupies an intermediate trophic position and might feed on a mixed diet of benthos and plankton or plankton and fish as do most of its non-Antarctic relatives (Ebert &

Bizzarro 2007, Scenna et al. 2006). The diet of *B. maccaini* obviously includes a higher proportion of high trophic level prey.

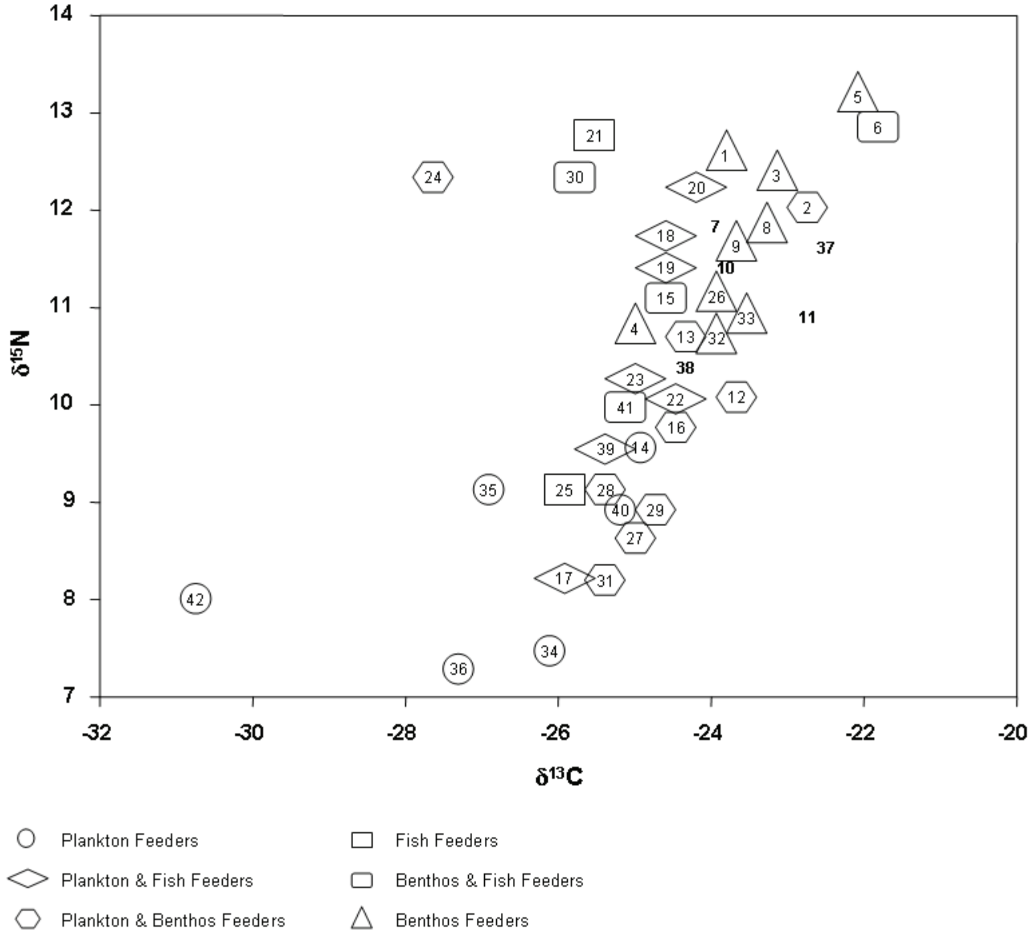

Fig. D1.4 Mean stable carbon and nitrogen isotope signatures (δ^{13}C, δ^{15}N) of fish species inhabiting the Weddell Sea shelf and slope (own data). Symbols indicate trophic group as assigned based on stomach content analyses (bold numbers without symbol represent species with unknown diet). Each number represents one species. For species code numbers and sources of dietary information see ANNEX, Table G1.

Even though analysis of stable isotope composition is not a true substitute for high-resolution dietary studies, isotope signatures may serve as an approximation to determine consumers' general food composition. In particular ^{15}N is a useful and reasonable enhancement that helps to complete trophic information and provides an easy accessible measure to estimate a species trophic position within a particular food web. The combination of both methods enables ecologists to characterize consumers' trophic niches and function in a much more detailed way (PUBLICATION VI) than one method alone (see, e.g., Bearhop et al. 2004).

SUMMARY – COMBINATION WITH DIETARY ANALYSES

This chapter elucidates the advantage of the combination of stable isotope analysis with traditional stomach content analysis:

- ***stable isotope analysis* provide low resolution but time-integrating diet information, *stomach content analyses* provide detailed high resolution but information but are often only a snapshot;**
- **each method on its own thus just tells half of the story, in combination the methods complement one another (e.g., to estimate relative proportions of planktonic and benthic prey in a consumer's diet and to characterize consumers' trophic niches).**

2. STRUCTURE AND COMPLEXITY OF THE WEDDELL SEA FOOD WEB

2.1 General Food Web Structure and Complexity

Based on stable isotope composition and dietary information multiple functional groups can be distinguished among species inhabiting the Weddell Sea shelf and slope. The pelagic part of the food web is composed of pelagic primary food sources (phytoplankton and POM), herbivorous and omnivorous zooplankton and pelagic invertebrate and vertebrate predators such as fish and squid (Fig. D2.1 A). The benthic part of the food web includes suspension and deposit feeders, benthic and bentho-pelagic omnivores, predators and opportunistic scavengers (Fig. D2.1 B). Warm-blooded animals include predatory seals, penguins and seabirds and few opportunistic scavenging seabirds (Fig. D2.1 C).

Definition of the ultimate base of the Weddell Sea food web (i.e. trophic level 1) is a nontrivial task, as primary consumers (herbivores and omnivores) utilize different autotrophic sources (diatoms, *Phaeocystis*, ice-algae, pico- and nano-phytoplankton) or a mixture of sources (e.g. Haberman et al. 2003) that differ in isotopic composition (Hobson et al. 1995, Rau et al. 1991b). Differences in particle preference are clearly reflected in variability of mean δ^{15}N values in herbivorous consumers (Fig. D2.1 A). For trophic level (TL) calculation in Fig. D2.1 the mean δ^{15}N value of diatoms and surface water POM was used as base (TL 1). For most herbivorous and omnivorous consumers this base seems to be appropriate as calculated TL of these species ranges between 2 and 2.5 (see Fig. D2.1 A). For salps (*Salpa thompsoni* and *Salpa* sp.) and their ectocommensal *Vibilia stebbingi* (Amphipoda, Hyperiidae; Madin & Harbison 1977, Harbison et al. 1977) this base is, however, overestimated. Salps are known to feed efficiently on smallest pico- and nanoplankton particles (Madin 1974, Kremer & Madin 1992, Fortier et al. 1994, Dubischar & Bathmann 1997). There are no data available but $\delta^{15}N$ value of this phytoplankton size fraction should be distinctly below 0 ‰.

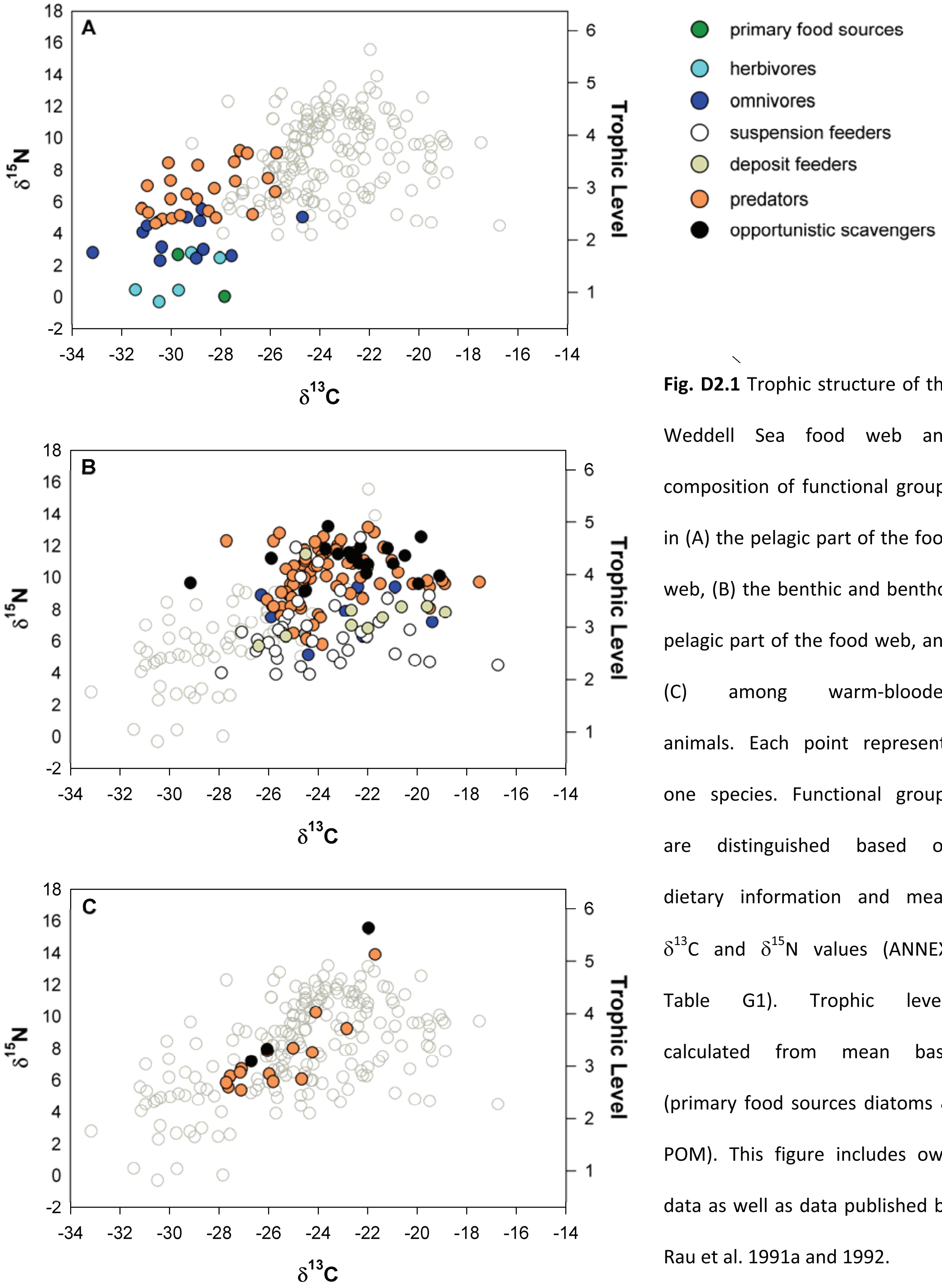

Fig. D2.1 Trophic structure of the Weddell Sea food web and composition of functional groups in (A) the pelagic part of the food web, (B) the benthic and bentho-pelagic part of the food web, and (C) among warm-blooded animals. Each point represents one species. Functional groups are distinguished based on dietary information and mean $\delta^{13}C$ and $\delta^{15}N$ values (ANNEX, Table G1). Trophic levels calculated from mean base (primary food sources diatoms & POM). This figure includes own data as well as data published by Rau et al. 1991a and 1992.

Pelagic predators include primary and secondary consumers and therefore cover a range of about 2 trophic levels (TL; Fig. D2.1 A). Benthic suspension feeders are scattered across some trophic levels (Fig. D2.1 B). Most species occupy trophic levels between 2 and 3, however, some species are located at trophic positions comparable to benthic predators due to the depth effect on POM δ^{15}N (see above, Chapter 1.2), differences in particle preference and facultative predation in some suspension feeder species (see, e.g., Orejas et al. 2001, 2003). Benthic and epibenthic predators occupy about 3 TLs (TL 3 – 5). Some of the benthic predators at lower trophic position feed on low TL suspension or deposit feeders such as ascidians or sponges (e.g., the gastropods *Marseniopsis* spp., TL 2.9 and 3.3; Numanami & Okutani 1991), but most of them rely additionally on pelagic food sources such as krill and copepods (e.g., demersal fish *Trematomus* spp.; Mintenbeck 2001). The high number of benthic predators at comparatively low trophic position distinctly emphasizes the importance of bentho-pelagic coupling via organisms that undertake vertical migrations within the water column.

Except for the Giant petrel *Macronectes giganteus* and the Weddell seal *Leptonychotes weddellii*, seals and birds occupy intermediate trophic position only. Though usually supposed to be top predators, these warm-blooded animals are located distinctly below most benthic predators and scavengers in the trophic hierarchy of the Weddell Sea food web (see Fig D2.1). Most seabirds, penguins and seals thus rely on prey from the pelagic part of the food web. Predatory as well as scavenging seabirds, such as Southern fulmar (*Fulmarus glacialoides*, TL 2.95), Cape petrel (*Daption capense*, TL 2.87), Antarctic petrel (*Thalassoica antarctica*, TL 2.60), Snow petrel (*Pagodroma nivea*, TL 3.06), and Wilson's storm petrel (*Oceanites oceanicus*, TL 3.32) seem to feed mainly on euphausiaceans (*Euphausia superba* and *E. crystallorophias*), hyperiid amphipods and pelagic fish (myctophid fish and *Pleuragramma antarcticum*) (Arnould & Whitehead 1991, Ridoux & Offredo 1989). The amount of carrion in the diet of opportunistic scavengers such as Wilson's storm petrel is obviously low. The Giant petrel *Macronectes giganteus* (TL 5.62), in contrast, seems to rely largely on birds (including penguins) and seal carcasses (*c.f.* Hunter 1983). Adélie penguin (*Pygoscelis adéliae*) and Emperor penguin (*Aptenodytes forsteri*) both prey mainly on euphausiaceans, squid and pelagic fish (*P. antarcticum*) (Cherel & Kooyman 1998, Zimmer et al. 2007, Ridoux & Offredo 1989, Ainley et al. 2003, Kent et al. 1998). Fish and squid, however, are obviously more important for the Emperor penguin (TL 4.03) while krill is the major food for Adélie penguins (TL 2.71). Among seals the Crabeater seal (*Lobodon carcinophagus*, TL 2.76) occupies the lowest trophic position, followed by Fur seal (*Arctocephalus gazelle*, TL 3.34) and Ross seal (*Ommatophoca rossii*, TL 3.72). This sequence reflects a shift in the contribution of euphausiaceans (and mysidaceans), and pelagic fish and squid in the diet (Boyd 2002, Green & Williams 1986, Daneri & Carlini 1999, Caseaux et al. 1998, Skinner & Klages 1994, Laws 1984). The Leopard seal (*Hydrurga leptonyx*) is known to prey upon pelagic fish, krill, penguins and seals (Green & Williams 1986, Walker et al. 1998); nevertheless, its comparatively low trophic position of 3.26 indicates that euphausiaceans or other low trophic level zooplankton might contribute significantly to overall diet. The highest trophic position among seals is occupied by the Weddell seal (*Leptonychotes weddellii*, TL 5.13). Besides pelagic fish and squid, demersal fish species constitute, at least seasonally, an important part of the Weddell seals' diet (Burns et al 1998, Plötz 1986, Plötz et al. 1991).

One important group missing in our stable isotope database due to evident difficulties in sampling are whales. About fifteen different species have been reported from the Southern Ocean most of which are seasonal guests during austral summer (see, e.g., Boyd 2002). Baleen whales such as the Minke whale (*Balaenoptera acutorostrata*) feed mainly on krill and copepods and will accordingly occupy low trophic positions. Beaked whales and sperm whales preying upon fish and squid, as well as Killer whales (*Orcinus orca*) hunting additionally on penguins and seals (Boyd 2002) are comparatively high in the trophic hierarchy of the Weddell Sea food web.

General food web complexity and vertical functional diversity can be inferred from maximum food-chain length (FCL), i.e. TL_{max} -1, with TL_{max} as the highest trophic position encountered within the food web (Post 2002b). In the pelagic part of the food web highest trophic positions are occupied by 3 fish species: the bathypelagic *Bathylagus antarcticus* (Bathylagidae), a species that occurs in deeper water layers above the slope, and the nototheniids *Dissostichus mawsoni* and *Pleuragramma antarcticum*, with the latter one being a typical member of the shelf fish fauna (Table D2.1). Benthic/demersal top predators are represented by the scavenging pycnogonid *Colossendeis* sp. and the fish species *Dolloidrao longedorsalis* (Nototheniidae). The food chain leading to benthic top predators is distinctly longer (by 1.2 TLs) compared to the maximum food chain leading to pelagic top predators, reflecting the high number of species and ecological niches (see OVERVIEW, Chapter 3), and an increased number of trophic interactions in the benthic compartment. Overall highest trophic position in the Weddell Sea food web of 5.6 is occupied by the scavenging Giant petrel *Macronectes giganteus*, accordingly, maximum FCL of the entire system is 4.6 TLs.

Table D2.1 Maximum trophic position (TL) occupied by pelagic, benthic/demersal and warm-blooded animals, and corresponding maximum food chain length (FCL_{max}).

Subsystem	**Top Predator**	**TL**	**FCL_{max}**
Pelagic	*Bathylagus antarcticus* *Dissostichus mawsoni (juv)* *Pleuragramma antarcticum*	**3.7**	**2.7**
Benthic/demersal	*Colossendeis* sp. *Dolloidraco longedorsalis*	**4.9**	**3.9**
Warm-blooded animals	*Macronectes giganteus*	**5.6**	**4.6**

The pattern of maximum TL and FCL in the Weddell Sea food web conforms with the general pattern observed in a variety of aquatic ecosystems: excluding warm-blooded animals, fish are the top predators in the majority of systems, and including warm-blooded animals increases FCL by on average 0.64 trophic levels compared to estimates using the fish top predator (Vander Zanden & Fetzer 2007). FCL_{max} in the Weddell Sea, however, is well above (~1 TL) the mean value for marine ecosystems (see Vander Zanden & Fetzer 2007[*]), most likely due to the presence of scavengers and species feeding on high trophic level benthos such as *Dolloidraco longedorsalis*.

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[*] Note that in Vander Zanden & Fetzer (2007) $FCL = TL_{max}$ is used, while our estimates are based on $FCL = TL_{max} - 1$ (following Post 2002b).

SUMMARY – GENERAL FOOD WEB STRUCTURE AND COMPLEXITY

In this chapter general structure and complexity of the Weddell Sea food web are discussed. The most important findings characterizing this ecosystem are:

- **based on species' lifestyle, dietary information and stable isotope signatures multiple functional groups can be distinguished;**
- **many benthic predators rely additionally on pelagic prey, thus, *bentho-pelagic coupling* via migrating zooplankton plays an important role;**
- **except for the Weddell seal and the Giant petrel most *warm-blooded animals* (seals, seabirds, penguins) depend on prey from the pelagic part of the food web;**
- **together with scavengers *fish* occupy highest trophic positions within the pelagic and the benthic food web; the scavenging Giant petrel is the top predator of the entire system;**
- **differences in number of species and ecological niches between pelagic and benthic system are reflected in differences in maximum food chain length, with an increased food chain length indicating increased *trophic complexity* in the benthic system.**

2.2 Role of Fish in the Food Web

Fish take a central position in the Antarctic marine food web. On the one hand fish species occupy a multitude of trophic niches and positions (see OVERVIEW, Chapter 2.3 and Fig. D1.4 in Chapter 1.3 above) and are among the top predators in the pelagic as well as in the benthic part of the Weddell Sea food web. On the other hand fish, particularly pelagic species, provide a food source for almost all warm-blooded vertebrates inhabiting high southern latitudes (see above, Chapter 2.1). Moreover, compared to other taxonomical groups such as squid, euphausiaceans and gelatinous zooplankton, finfish are the food source of highest energetic value (Fig. D2.2). Fish thus represent an important trophic link between small-sized, energetically less valuable invertebrates and apex predators. In particular myctophids but also nototheniids are characterized by high energy content (ANNEX, Table G2).

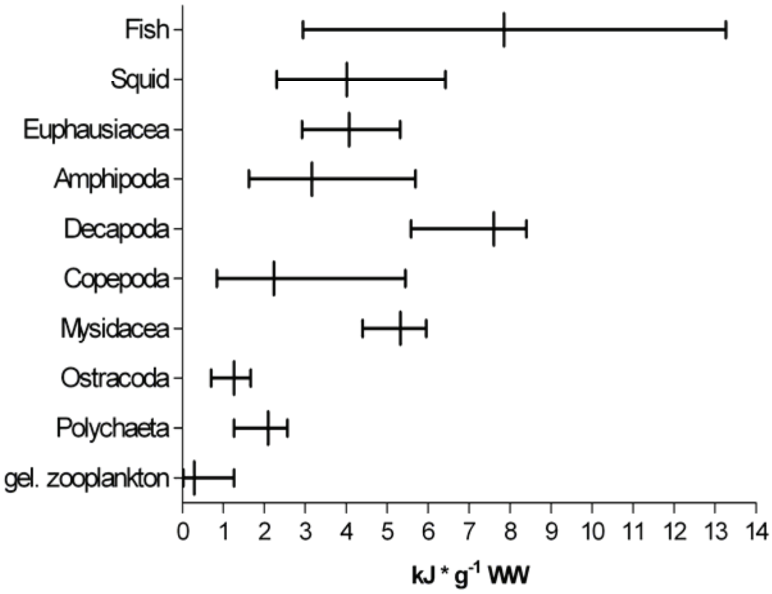

Fig. D2.2 Energetic value (kJ*g^{-1} wet weight) of Antarctic and sub-Antarctic species belonging to several taxonomic groups. Overall range and median are given (for details and data sources see ANNEX Table G2).

Myctophids are, however, bathypelagic fish and are almost absent on the high Antarctic shelf (see also Boysen-Ennen & Piatkowski 1988; Donnelly et al. 2004). On the north-eastern Weddell Sea shelf between 200-600 m water depth the fish fauna is composed of 50 species, with 42 species of notothenioids distinctly dominating both in terms of abundance and biomass (Fig. D2.3; ANNEX, Table G3).

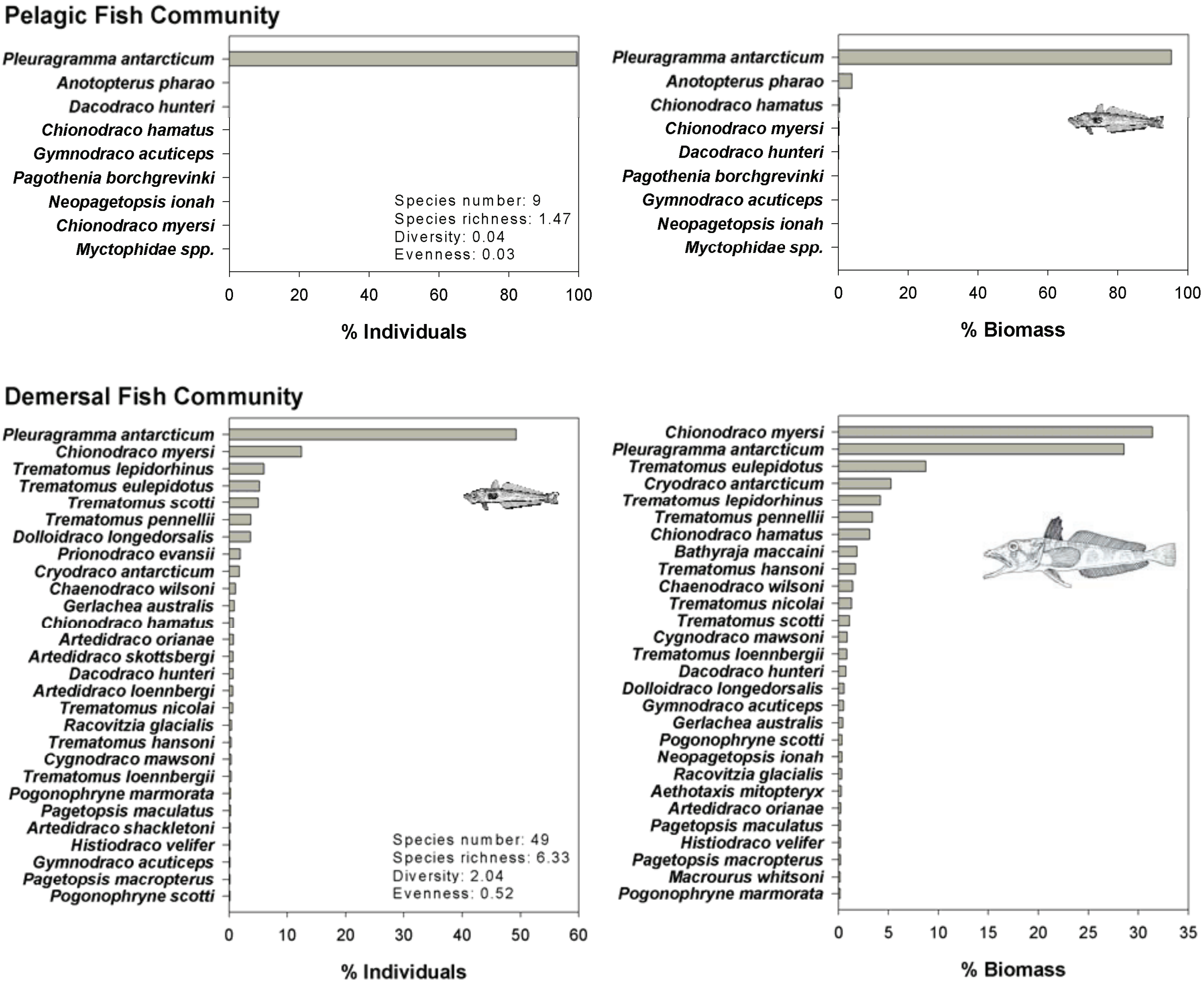

Fig. D2.3 Composition of the pelagic and demersal fish communities on the northeastern Weddell Sea shelf between 200 and 600 m water depth (see also ANNEX Table G3; only those 28 out of 49 species that contribute >0.15% to overall individuals and biomass are shown for the demersal community). Note different scales.

The demersal fish community is characterized by high species richness and diversity and includes 49 species (42 notothenioids). The pelagic fish community above the shelf is species-poor. Most species such as the channichthyids *Chionodraco* spp., *Dacodraco hunteri*, *Neopagetopsis ionah* and the bathydraconid *Gymnodraco acuticeps* are in fact demersal fish and are only occasional guests in the water column. The cryopelagic nototheniid *Pagothenia borchgrevinki* is closely associated to the underside of ice (e.g. Janssen et al. 1991) and is rarely found in the free water column. Both, the demersal community and the pelagic fish community in particular, are distinctly dominated by a single species: the Antarctic silverfish *Pleuragramma antarcticum*. The only species that attains higher biomass in the demersal community is the large icefish *Chionodraco myersi* (Fig. D2.3).

P. antarcticum is one of the few truly pelagic, neutrally buoyant notothenioids (see Overview). Trawling in different depth strata of the water column during the day and during the night confirms daily vertical migration (DVM) of adults (PUBLICATION III). During the day adult *P. antarcticum* are found close above the sea floor, during the night *P. antarcticum* migrates upwards into the pycnocline to feed on copepods and chaetognaths. The movement of individuals within the water column seems to be synchronous, providing further evidence for a shoaling behaviour of this fish species (see also Fuiman et al. 2002), which is unique among notothenioids. Despite sufficient prey availability at depth, feeding of *P. antarcticum* seems to be restricted to the time spent in the upper water column. *P. antarcticum* seems to rely largely on visual prey detection and the eyes of this species are not well adapted for vision at greater depth as was also indicated by studies on ocular morphology (Eastman 1988). During nocturnal feeding migrations into surface waters, the dense aggregations of *P.*

antarcticum provide an easily accessible food source for visually hunting warm-blooded animals (e.g. Plötz et al. 2001). To minimize the risk of predation, time spent in the pycnocline seems to be restricted to a short period. DVM of *P. antarcticum* is thus obviously a behavioural trade-off between food intake and predator avoidance rather than a following of migrating prey (as proposed by Plötz et al. 2001).

By feeding in the pycnocline but resting close to the sea floor for most of the day, *P. antarcticum* represents an important link in bentho-pelagic coupling: it significantly contributes to the diet of demersal, piscivorous fish species, such as the abundant *Chionodraco myersi*, *Cryodraco antarcticum* and many others (Takahashi & Nemoto 1984, Eastman 1985b, Olaso 1999). As feeding is obviously restricted to the upper water layers, *P. antarcticum* does not compete for vertical migrating prey with epibenthic zooplankton-feeding fish species, such as *Trematomus eulepidotus* and *T. lepidorhinus* (Schwarzbach 1988, Mintenbeck 2001). *P. antarcticum* is not only preyed upon by warm-blooded animals and fish but provides also an important food source for squid, such as *Psychroteuthis glacialis*, in different depth strata of the water column (Lu & Williams 1994).

However, *P. antarcticum* is not only an occasional prey; this pelagic notothenioid fish species is often, together with krill, the major food source for most of these predators (Eastman 1985b, Lu & Williams 1994, Arnould & Whitehead 1991, Green & Williams 1986, Skinner & Klages 1994, Daneri & Carlini 2002, Burns et al. 1998, Cherel & Kooyman 1998, Kent et al. 1998). Though some warm-blooded predators such as Weddell seal and Emperor penguin are excellent divers and capable to exploit demersal fish as well, diving into deeper water layers involves an increased swimming effort, shorter times at feeding depth, and/or longer diving duration followed by longer recovery phases (e.g. Kooyman 1989, Kooyman & Kooyman 1995, Wilson & Quintana 2004). Moreover, feeding efficiency seems to be higher in shallow dives (e.g. Croxall et al. 1985), whereas encounter rates are probably lower in light depleted deep waters, as indicated by a lower number of feeding events at depth (see Plötz et al. 2005).

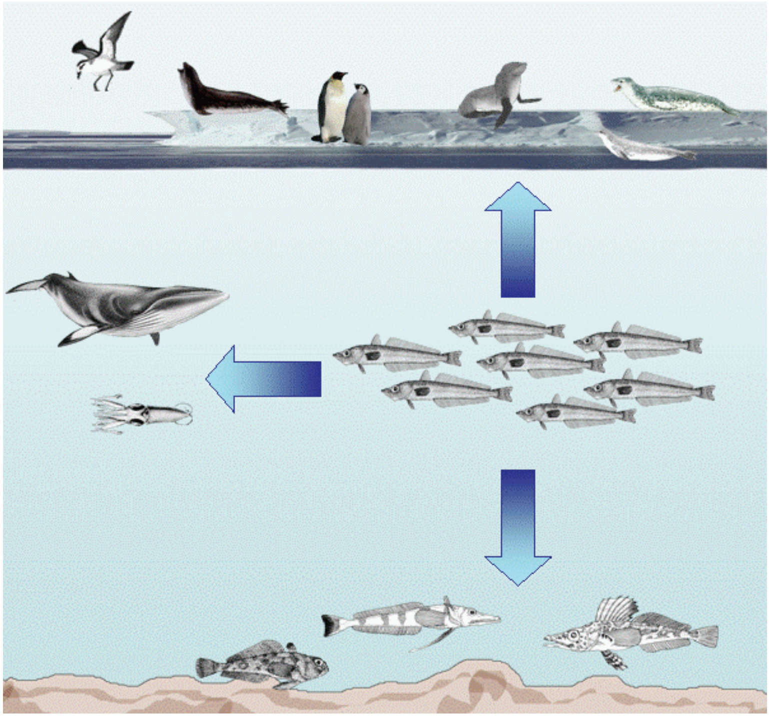

Fig. D2.4 The nototheniid fish species *Pleuragramma antarcticum* takes a central position in the high Antarctic food web and represents an essential trophic link within the pelagic part of the food web as well as between the pelagic and benthic compartments and seals and birds.

P. antarcticum is thus an essential trophic link (i) within the pelagic system, (ii) between the pelagic part of the food web and the benthic compartment, and (iii) between pelagial and warm-blooded vertebrates (Fig. D2.4). On the high Antarctic shelf *P. antarcticum* seems to occupy a similar ecological role in the food web as Antarctic krill, *E. superba*, does in the seasonal sea ice zone (see also Takahashi & Nemoto 1984, Hureau 1994, La Mesa et al. 2004, Kooyman et al. 2004).

SUMMARY – ROLE OF FISH IN THE FOOD WEB

Notothenioid fish take a central position in the Antarctic marine food web:

- fish are a food source with highest *energetic value* compared to other taxonomical groups (including krill);
- fish are a *major trophic link* between small-sized invertebrates and large warm-blooded predators;
- the shelf fish fauna is characterized by a species-poor *pelagic community* and high species richness within the *demersal fish community*;
- pelagic and demersal fish communities are distinctly dominated by a single species: the Antarctic silverfish, *Pleuragramma antarcticum*;
- *P. antarcticum* seems to occur in shoals, spends the day resting close above the sea floor and undertakes nocturnal *feeding migrations* into the upper water column;
- *P. antarcticum* provides food for pelagic predators such as squid, it is an important prey for demersal piscivorous fish thereby contributing to *bentho-pelagic coupling*, and the shoals provide the major food source for warm-blooded predators ⇒ *P. antarcticum* is an essential trophic link in the Weddell Sea food web and occupies a similar ecological role as krill does!

3. FOOD WEB STABILITY

Due to their significance in the food web, particularly their role as a major and energy-rich trophic link between small-sized invertebrates and apex predators, notothenioid fish might serve as a leading indicator of change in Antarctic ecosystems. The potential vulnerability of fish species to systemic shifts and alterations in food web structure is therefore of outstanding interest.

The risk of a particular species to be negatively affected by trophically mediated secondary effects (relative trophic vulnerability, *VI*) depends on the species' trophic plasticity and predator exploitation (see OVERVIEW, Chapter 3). In notothenioid fish, however, differences in *VI* are mainly determined by the number of trophic links to prey species and, therefore, by a species' trophic generalism (PUBLICATION IV). *VI* is significantly related to prey composition; most fish species inhabiting the Weddell Sea shelf include a high proportion of benthos in their diet, both in terms of prey species composition (PUBLICATION IV) and major abundance and biomass contribution (see Fig. D1.4 in Chapter 1.3 above). *VI* of these fish species is low. Feeding on benthos, therefore, goes along with a high degree of trophic generalism and functional redundancy and hence with a certain capability to adapt food choice to prey availability and to dampen bottom-up effects. More or less pure plankton consumers are rare among notothenioid fish and these few species are rather specialists with a narrow food spectrum and a high *VI*. Consequently, plankton feeders are most likely highly sensitive to alterations in prey composition and availability. Moreover, functional redundancy is extremely low within this compartment characterized by an increased risk of species loss, in particular because the dominating species (see above, Chapter 2.2), the plankton-feeding *P. antarcticum*, is the most vulnerable species of all nototheniods.

In case of extinction of *P. antarcticum*, no other species may be able to provide full functional compensation, neither in its role as a major zooplankton consumer nor as prey for warm-blooded predators: myctophid fish are almost absent on the shelf (see above), the only other truly pelagic notothenioid on the shelf beside *P. antarcticum*, the cryopelagic *Pagothenia borchgrevincki*, hides in cracks under the ice and is rarely available in the free water column (e.g. Janssen et al. 1991), squid is apparently rare in abundance on the shelf (Lubimova 1985, Kubodera 1989, Piatkowski 1987), and euphausiaceans are small in size compared to *P. antarcticum*. None of these combine a pelagic shoaling lifestyle including vertical migration with a *P. antarcticum* like size spectrum and energy content (see Chapter 2.2 above, ANNEX Table G2, and Ainley et al. 2003). In its functional role within the food web, *P. antarcticum* resembles shoaling clupeoid fish (e.g., anchovy and sardine) in upwelling systems such as off Peru/Chile (e.g. Cury et al. 2000), where El Niño events regularly involve strong reductions in stocks of small clupeoids owing to bottom-up effects, causing starvation and mortality in the very top predators, birds and seals (e.g. Arntz 1986). These clupeid fish, however, are evolutionarily adapted to strong environmental fluctuations by fast growth and high fecundity and can emigrate into waters with more favourable environmental and food conditions (see PUBLICATION IV, Arntz 1986). Resilience capability of *P. antarcticum* populations, in contrast, is low due to slow growth (Hubold & Tomo 1989), low fecundity (Gerasimchuk 1988) and limited emigration possibilities (Somero & DeVries 1967). The Antarctic silverfish *P. antarcticum* thus not only holds a key position but represents also a weak point in the high Antarctic food web.

The pattern of trophic vulnerability and functional redundancy among plankton and benthos consumers observed in notothenioid fish species most likely applies to the whole system, as indicated by differences in food chain length between the pelagic and the benthic part of the food web (see above, Chapter 2.1). Complex trophic structures support the persistence of long food chains, therefore, increased FCL in the benthic compartment indicates an increased number of trophic interactions and stabilizing weak trophic linkages (see OVERVIEW, Chapter 3). 3-dimensionality of the benthic habitat and small-scale habitat heterogeneity allow for niche separation, reduced competition and co-existence of functionally similar species (see OVERVIEW, Chapters 2.2 & 2.3, and Publication XIII), thereby promoting high species diversity and functional redundancy. The pelagic part of the food web is comparatively simply structured, with lower species number, low trophic complexity and limited number of niches occupied by few dominating species. The majority of warm-blooded animals rely on this low redundancy system (see above, Chapter 2.1).

Until recently, the largest non-natural disturbance of the high Antarctic ecosystem was the drastic reduction of large, krill-eating baleen whales (see OVERVIEW, Chapter 2) and this loss was obviously compensated by other krill consuming species (Trites et al. 2004). However, if the pattern that trophic vulnerability is mainly determined by the number of linkages to prey items (as observed in fish, Publication IV) applies to all or most consumers in the system, pelagic food web structure might be affected stronger by bottom-up effects than by top-down effects.

And that's the crux of the matter. During the last years climate change-related increases in temperature have become more and more evident in coastal waters of the Southern Ocean and these environmental alterations seem to affect primarily

organisms at the base of the food web. Off the Antarctic Peninsula, reduced surface water salinity due to increased glacial meltwater runoff as well as a reduction in duration and extent of sea ice has resulted in alterations of phytoplankton and zooplankton composition, with a significant shift towards a salp dominated community (Loeb et al. 1997, Atkinson et al. 2004, Moline et al. 2004, Nicol et al. 2000). Environmental alterations due to climate change are, however, not restricted to the Antarctic Peninsula (Jacobs et al. 2002, Curran et al. 2003, Rignot et al. 2008). If the warming trend continues and extents to the high Antarctic zone, salps may become increasingly prominent in vast areas of the marine Antarctic ecosystem (e.g., Pakhomov et al. 2002). An increase in gelatinous zooplankton related to climate change is observed in many marine systems (e.g., Brodeur et al. 1999, Attrill et al. 2007), but the effect of such alteration in community structure on systems' trophic structure and energy flow is widely unknown.

Salps are microphagous filter feeders, feeding highly efficiently on a wide range of particles even when phytoplankton concentrations are low (Hopkins 1985, Kremer & Madin 1992, Madin 1974). Salps significantly contribute to vertical flux of organic matter and thus to bentho-pelagic coupling: (i) salps undertake vertical migrations thereby providing surface food for benthic consumers (Wiebe et al. 1979, Gili et al. 2006); (ii) salps repack small non-sinking particles into rapidly sinking faecal pellets (Iseki 1981, Le Fèvre et al. 1998) that might significantly contribute to the formation of persistent sediment 'food banks' (see Chapter 1.2 above). The effects of a shift in the zooplankton community on the benthic system are, consequently, most likely minor. But what about pelagic predators such as *P. antarcticum*, that rely exclusively on zooplankton resources? Salps are able to develop large populations and biomass quickly (e.g., Mianzan et al. 2001) and their efficient grazing and high ingestion rates (Perissinotto & Pakhomov 1998a,b) might result in the competitive exclusion of other grazers, such as euphauseaceans and copepods. Fish, including some notothenioid species, are known to feed on salps occasionally but salps and other gelatinous zooplankton seem to be rather some kind of "survival food" when concentrations of alternative zooplankton are low (Kashkina 1986, Mianzan et al. 2001). Compared to crustacean zooplankton such as euphausiaceans and copepods, energy density and thus nutritive value of gelatinous zooplankton is extremely low (see above, Chapter 2.2). Low energy food will affect survival, growth, body condition and reproductive output of consumers such as *P. antarcticum* and their predators. Moreover, salps often occur in colonial chains and these aggregated forms are too large to be ingested by pelagic predators that are rather specialized to feed on copepods and small euphausiaceans.

On the high Antarctic shelf, where the majority of warm-blooded animals depend on the pelagic system that is characterized by high trophic vulnerability and low functional redundancy, shifts in pelagic community structure as observed off the Antarctic Peninsula pose an enormous threat. The risk that changes in zooplankton composition will affect *P. antarcticum* is high and this in turn will cause strong alterations of food web structure with severe consequences for system top predators in particular and overall ecosystem functioning in general.

If water temperatures are going to increase above a certain level, cold-stenothermal notothenioid fish will be affected at the physiological level as well, whereas fish species from temperate zones and upwelling systems might invade into Antarctic waters. Therefore, in the long run the functional role of small, zooplankton-feeding

pelagic shoal fish in the high Antarctic marine ecosystem might be taken over by clupeoid species.

SUMMARY – FOOD WEB STABILITY

This chapter deals with species' risk to be negatively affected by trophically mediated secondary effects, species' functional redundancy, and consequences for overall ecosystem functioning:

- **among notothenioid fish *trophic vulnerability* is mainly determined by trophic generalism and related to food composition, with low trophic vulnerability in benthos consumers and high trophic vulnerability in plankton feeders; *P. antarcticum* is the most vulnerable fish species;**
- ***functional redundancy* is high among demersal fish species and low among plankton consumers;**

⇒ its central position within the food web together with high trophic vulnerability and low functional redundancy makes *P. antarcticum* an Achilles' heel in the Weddell Sea shelf food web!

- **the pattern of high trophic vulnerability and low functional redundancy in case of species loss most likely applies to the entire system, with the benthic part of the food web being comparatively stable while the pelagic part of the food web seems to be highly sensitive to changes;**

⇒ as most warm-blooded predators depend on the pelagic part of the food web, any kind of change affecting pelagic community structure will have severe consequences for overall ecosystem functioning and might lead to a distinctly different ecosystem in the long run!

4. FUTURE RESEARCH

One of the major insights into the high Antarctic ecosystem functioning of this thesis is the identification of *Pleuragramma antarcticum* as one key species that is highly sensitive to changes in food web structure, particularly to alterations at lower trophic levels. To validate the trophic vulnerability of *P. antarcticum* (and other notothenioid fish species) and to investigate its physiological vulnerability (e.g., temperature sensitivity), experimental studies are urgently required. So far, experimental studies on *P. antarcticum* are extremely rare due to its fragile body structure that makes it rather impossible to sample this species alive by means of traditional sampling gear such as trawls. However, fishing rods or purse seines might provide a useful alternative. Experimental approaches will (i) provide insight into *P. antarcticum*'s physiological response to changes in abiotic parameters (temperature, CO_2, etc.), and (ii) help to analyse prey preference, prey size-spectrum handling capability, as well as the relationship between prey composition and fish body condition, energy content, growth and fecundity. To elaborate on the role of *P. antarcticum* (or fish in general) as prey, in particular for warm-blooded animals, future studies should also involve analyses of predator population dynamics (*c.f.* Forcada et al. 2005) depending on prey composition (e.g., fish *vs.* zooplankton) and investigation of horizontal migration patterns of *P. antarcticum* shoals (e.g., by remote sensing technique, Makris et al. 2006; see Discussion in PUBLICATION III).

E. ACKNOWLEDGEMENTS

The American novelist William Faulkner (1897-1961) once said: “My own experience has been that the tools I need for my trade are paper, tobacco, food, and a little whisky.” Though nowadays sheets of paper are replaced by notebooks, my experience was similar writing this thesis except for the fact that these were not the only tools I *needed* - these tools were *essential* to finish this thesis. I consumed tons of chocolate, at least a container full of cigarettes, and, yes, one or the other whiskey was occasionally involved as well (sometimes helpful to disentangle the cerebral muddle and to arrange one’s ideas). However, one, in fact the most important, tool ignored by Mr. Faulkner is the presence of people in the background supporting one. This chapter is dedicated to those “background people” that contributed to this thesis in multiple ways.

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G. ANNEX

Table G1 Trophic positions and functional role of species inhabiting the Weddell Sea shelf and slope. Trophic levels are inferred from stable nitrogen isotope signatures (δ^{15}N). Samples for stable isotope analyses (unpublished data compiled by T. Brey, U. Jacob, K. Beyer and K. Mintenbeck) were collected using various gears during four *RV Polarstern* expeditions between 1996 and 2004 (ANT XIII/3, XV/3, XVII/3, XXI/2). Additionally, data published in Rau et al. 1991a (*) and 1992 (**) are used. Mean δ^{15}N of POM and diatoms is used as base for trophic level calculation (i.e., trophic level 1; see OVERVIEW Chapter 2.1). Functional groups are distinguished based on calculated trophic level and dietary/feeding type information from various published sources (main references for each taxonomic group indicated by numbers in italics and itemized at the end of the table). P pelagic, B benthic, BP epibenthic/bentho-pelagic, W warm-blooded animal; PRIM primary food source, SF suspension feeder, DF deposit feeder, HERB herbivore, OMNI omnivore, PRED predator, SCAV opportunistic scavenger. For fish species included in Fig. D1.4 (own data only) trophic group and code number (bold) are given additionally.

Species	Trophic Level	Functional Group
Base		
POM		P PRIM
Diatoms		P PRIM
Mean Base:	1	
Radiolaria *(6, 83)*		
*Phaeodarian radiolaria**	2.37	P OMNI
Porifera *(6, 8)*		
Rosella sp.	4.52	B SF
Cinachyra antarctica	4.70	B SF
Cinachyra barbata	3.70	B SF
Iophon sp.	3.50	B SF
Kirkpatrickia variolosa	4.25	B SF
Stylocordyla borealis	2.09	B SF
Isodyctium sp.	3.76	B SF
Desmospongiae spp.	3.02	B SF
Anthozoa (Hexacorallia) *(6, 83)*		
Isosicyonis alba	3.92	B PRED
Hormosoma sp.	3.22	B PRED
Hexacorallia spp.	3.53	B PRED

Anthozoa (Octocorallia) *(66, 67)*		
Armadillogorgia cyathella	2.49	B SF
Alcyonaria sp.	2.94	B SF
Umbellula pallida	3.13	B SF
Primnoella sp.	2.12	B SF
Primnoisis sp.	2.28	B SF
Thouarella sp.	2.82	B SF
Ascolepsis splendens	3.55	B SF
Ainigmaptilon antarcticus	2.55	B SF
Primnoidae spp.	2.90	B SF
Scyphozoa *(6, 83)*		
*Atolla wyvillei**	2.92	P PRED
*Periphylla periphylla**	2.40	P PRED
Hydrozoa *(6, 31)*		
*Calycopora borchgrevinki**	3.13	P PRED
*Dimophyes arctica**	1.70	P OMNI
*Diphyes antartica**	2.44	P OMNI
Hydrozoa sp.	1.82	P OMNI
Symplectoscyphus sp.	2.79	B SF
Staurotheca sp.	2.46	B SF
Hydrozoa sp.	2.40	B SF
Ctenophora *(37, 49)*		
*Callianara antarctica**	2.49	P PRED
Plathelminthes *(6, 83)*		
Plathelminthes sp.	3.37	B PRED
Nemertini *(48, 75)*		
Baseodiscus antarcticus	4.72	B SCAV
Lineus longifissus	4.37	B SCAV
Nemertini sp.	4.20	B SCAV
Polyplacophora (76)		
Tonicina zschaui	3.37	B PRED
Nuttallochiton mirandus	3.44	B PRED
Gastropoda *(4, 22, 52)*		
*Limacina helicina**	1.66	P HERB
Marseniopsis mollis	3.25	B PRED
Marseniopsis conica	2.88	B PRED
Trichoconcha mirabilis	2.77	B PRED
Aforia magnifica	2.67	B PRED
Parmaphorella mawsoni	3.82	B PRED

Harpovoluta charcoti	4.52	B SCAV
Cephalopoda *(16, 57)*		
Psychroteuthis glacialis	2.98	P PRED
Pareledone charcoti	3.73	B PRED
Octopodidae spp.	4.21	B PRED
Bivalvia *(6, 83)*		
Limopsis marionensis	3.41	B SF
Cyclocardia astartoides	2.99	B SF
Sipuncula *(62)*		
Golfingia sp.	2.97	B DF
Echiurida *(43, 46, 63)*		
Echiurus antarcticus	3.03	B DF
Alomasoma belyaevi	3.39	B DF
Maxmuelleria faex	3.40	B DF
Hamingia sp.	3.29	B DF
Polychaeta *(27, 30, 38, 78)*		
*Vanadis antartica**	2.42	P PRED
Laetmonice producta	4.28	B PRED
Aglaophamus sp.	3.76	B PRED
Harmothoe spinosa	4.04	B PRED
Barrukia cristata	3.82	B PRED
Eulagisca gigantea	4.52	B PRED
Polynoidae sp.	4.13	B PRED
Eunoe sp.	4.28	B PRED
Terebellidae sp.	2.64	B DF
Maldane sp.	3.33	B DF
Pycnogonida *(22, 48)*		
Pentanymphon antarcticum	3.18	B PRED
Colossendeis sp.	4.91	B SCAV
Ostracoda *(39, 40)*		
*Conchoecia antipoda**	2.35	P OMNI
*Conchoecia hettarca**	2.44	P OMNI
Copepoda *(39, 40, 68)*		
*Calanoides acutus**	2.14	P OMNI
*Calanus propinquus**	2.28	P OMNI
*Euchaeta antartica**	3.03	P PRED
*Gaetanus intermedius**	2.88	P OMNI
*Gaetanus tenuispinus**	2.78	P OMNI
*Haloptilus ocellatus**	2.56	P PRED
*Metridia gerlachei**	1.86	P OMNI

*Rhincalanus gigas**	1.76	P OMNI
Euphausiacea *(28, 40)*		
*Thysanoessa macrura**	2.59	P OMNI
Euphausia crystallorophias	1.75	P HERB
*Euphausia superba**	1.61	P OMNI
Euphausia spp.*	1.66	-
Decapoda *(33)*		
Notocrangon antarcticus	3.76	B OMNI
Chorismus antarcticus	3.09	B PRED
Nematocarcinus lanceopes	2.82	B OMNI
Nematocarcinus longirostris	3.31	B OMNI
Mysidacea *(39)*		
Antarctomysis maxima	2.86	BP OMNI
Amphipoda (20, 39, 64)		
*Hyperiella dilatata**	2.32	P PRED
*Cyllophus lucasii**	2.60	P PRED
*Primno macropa**	2.78	P PRED
*Vibilia stebbingi**	1.05	P HERB
Ampelisca richardsoni	2.90	B SF
Eusirus perdentatus	3.69	B SCAV
Waldeckia obesa	4.43	B SCAV
Tryphosella sp.	4.36	B SCAV
Parschisturella ceruviata	4.50	B SCAV
Orchomenella sp.	4.21	B SCAV
Epimeria similis	3.40	B PRED
Abyssorchomene rossi	3.84	B SCAV
Iphimediella sp.	4.31	B SCAV
Isopoda *(9, 10, 81)*		
Glyptonotus antarcticus	3.91	B PRED
Ceratoserolis meridionalis	4.02	B SCAV
Frontoserolis bouvieri	4.49	B SCAV
Natatolana obtusata	4.40	B SCAV
Natatolana oculata	4.33	B SCAV
Arcturidae sp.	2.56	B SF
Priapulida *(6, 83)*		
Priapulida sp.	3.64	B PRED
Bryozoa *(7, 83)*		
Isoscyphoporella tricuspis	2.34	B SF
Camptoplites tricornis	2.37	B SF
Melicerita obliqua	2.18	B SF
Alcyonidium sp.	2.43	B SF

Bryozoa sp.	3.32	B SF
Chaetognatha *(6, 39, 40)*		
*Eukrohnia hamata**	2.53	P PRED
*Sagitta gazellae**	2.43	P PRED
*Sagitta marri**	2.48	P PRED
Pterobranchia *(6, 83)*		
Cephalodiscus sp.	2.89	B SF
Pterobranchia sp.	2.73	B SF
Crinoidea *(6, 69, 83)*		
Promachocrinus sp.	2.25	B SF
Anthometra adriani	2.75	B SF
Crinoidea sp.	2.94	B SF
Asteroidea *(3, 21, 22, 23)*		
Cuenotaster involutus	1.38	B SCAV
Cuenotaster sp.	3.82	B SCAV
Acodontaster spp.	3.82	B PRED
Bathybiaster loripes	3.88	B OMNI
Macroptychaster accrescens	3.40	B PRED
Labidiaster annulatus	3.97	B SCAV
Diplasterias sp.	3.85	B PRED
Solaster sp.	3.94	B PRED
Lophaster sp.	3.88	B PRED
Asteroidea spp.	4.32	-
Ophiuroidea *(17, 24)*		
Ophiosparte gigas	3.03	B PRED
Ophioceres incipiens	3.76	B OMNI
Ophionotus victoriae	2.73	B OMNI
Astronoma agassizii	3.70	B OMNI
Ophiurolepis brevirima	3.18	B OMNI
Echinoidea *(47, 69)*		
Sterechinus neumayeri	2.47	B OMNI
Sterechinus antarcticus	3.61	B OMNI
Abatus curvidens	3.77	B DF
Abatus cavernosus	3.09	B DF
Ctenocidaris sp.	4.18	B PRED
Holothuroidea *(7, 35, 36, 59)*		
Echinopsolus acanthocola	3.25	B SF
Bathyplotes fuscivinculum	3.18	B DF
Achlyonice violaecuspidata	2.82	B DF
Ekmocucumis sp.	3.09	B SF
Ypsilocucumis turricata	4.40	B DF

Psolidium incertum	3.60	B SF	
Psolus dubiosus	2.70	B SF	
Holothuroidea spp.	3.50		
Ascidiacea *(6, 80)*			
Synoicium sp.	2.09	B SF	
Cnemidocarpa sp.	3.95	B SF	
Ascidiacea spp.	2.55	B SF	
Thaliacea/Salps *(39, 54, 58)*			
*Salpa thompsoni**	1.04	P HERB	
Salpa spp.*	0.82	P HERB	
FISHES			**Trophic Group**
Artedidraconidae *(53, 65, 74, 85)*			
1 *Artedidraco loennbergi*	4.72	B PRED	Benthos Feeder
2 *Artedidraco orianae*	4.55	B PRED	Plankton & Benthos Feeder
3 *Artedidraco shackletoni*	4.66	B PRED	Benthos Feeder
4 *Artedidraco skottsbergi*	4.17	B PRED	Benthos Feeder
5 *Dolloidraco longedorsalis*	4.90	B PRED	Benthos Feeder
6 *Histiodraco velifer*	4.80	B PRED	Benthos & Fish Feeder
7 *Pogonophryne macropogon*	4.50	B PRED	Diet unknown
8 *Pogonophryne marmorata*	4.47	B PRED	Benthos Feeder
9 *Pogonophryne phyllopogon*	4.44	B PRED	Benthos Feeder
10 *Pogonophryne scotti*	4.37	B PRED	Diet unknown
Pogonophryne sp.	4.11	B PRED	-
Bathydraconidae *(25, 53, 74)*			
11 *Bathydraco macrolepis*	4.22	B PRED	Diet unknown
12 *Bathydraco marri*	3.97	B PRED	Plankton & Benthos Feeder
13 *Cygnodraco mawsoni*	4.16	B PRED	Plankton & Benthos Feeder
14 *Gerlachea australis*	3.81	BP PRED	Plankton Feeder
15 *Gymnodraco acuticeps*	4.27	B PRED	Benthos & Fish Feeder
16 *Prionodraco evansii*	3.89	B PRED	Plankton & Benthos Feeder
Channichthyidae *(18, 26, 74, 79)*			
17 *Chaenodraco wilsoni*	3.41	BP PRED	Plankton & Fish Feeder
18 *Chionodraco hamatus*	4.47	B PRED	Plankton & Fish Feeder
19 *Chionodraco myersi*	4.31	B PRED	Plankton & Fish Feeder
20 *Cryodraco antarcticus*	4.62	B PRED	Plankton & Fish Feeder
21 *Dacodraco hunteri*	4.79	B PRED	Fish Feeder
22 *Pagetopsis macropterus*	3.94	B PRED	Plankton & Fish Feeder
23 *Pagetopsis maculates*	3.98	B PRED	Plankton & Fish Feeder
Nototheniidae *(29, 41, 42, 51, 61, 74, PUBLICATION III, XIII)*			
24 *Aethotaxis mitopteryx*	4.64	BP PRED	Plankton & Benthos Feeder
25 *Dissostichus mawsoni*	3.66	P PRED	Fish Feeder

26 *Trematomus bernacchii*	4.28	B PRED	Benthos Feeder
27 *Trematomus eulepidotus*	3.56	BP PRED	Plankton & Benthos Feeder
28 *Trematomus hansoni*	3.66	BP PRED	Plankton & Benthos Feeder
29 *Trematomus lepidorhinus*	3.66	BP PRED	Plankton & Benthos Feeder
30 *Trematomus loennbergii*	4.65	BP PRED	Benthos & Fish Feeder
31 *Trematomus nicolai*	3.39	BP PRED	Plankton & Benthos Feeder
32 *Trematomus pennellii*	4.16	B PRED	Benthos Feeder
33 *Trematomus scotti*	4.20	B PRED	Benthos Feeder
34 *Trematomus* spp. juveniles	3.18	P PRED	Plankton Feeder
35 *Pleuragramma antarcticum*	3.65	P PRED	Plankton Feeder
36 *P. antarcticum* postlarvae	3.12	P PRED	Plankton Feeder
Rajiidae			
37 *Bathyraja maccaini*	4.43	B PRED	Diet unknown
38 *Bathyraja murrayi*	4.06	B PRED	Diet unknown
Macrouridae *(45)*			
39 *Macrourus whitsoni*	3.81	BP PRED	Plankton & Fish Feeder
Macrourus sp.	4.32	BP PRED	-
Muraenolepididae *(15, 60)*			
40 *Muraenolepis marmoratus*	3.60	BP PRED	Plankton & Fish Feeder
41 *Muraenolepis microps*	3.95	BP PRED	Benthos & Fish Feeder
Myctophidae *(40, 84)*			
42 *Myctophidae* sp.	3.35	P PRED	Plankton Feeder
*Electrona antarctica***	3.48	P PRED	
*Gymnoscopelus braueri***	3.43	P PRED	
Bathylagidae *(32, 40, 55)*			
*Bathylagus antarcticus***	3.70	P PRED	
Paralepididae *(32, 40, 55)*			
*Notolepis coatsi***	3.49	P PRED	
Birds *(1, 2, 5, 13, 14, 44, 50, 56, 72, 73, 86)*			
*Fulmares glacialoides***	2.95	W PRED	
Macronectes giganteus	5.62	W SCAV	
*Thalassoica antartica***	2.60	W PRED	
*Halobaena cerulean***	2.81	W PRED	
*Daption capense***	2.87	W PRED	
*Pagodroma nivea***	3.09	W SCAV	
*Pterodroma brevirostris***	3.29	W PRED	
*Oceanites oceanicus***	3.32	W SCAV	
*Sterna vittata***	2.55	W PRED	
*Sterna paradisea***	2.68	W PRED	
*Pachyptila desolata***	2.85	W PRED	

*Pygoscelis adeliae***	2.71	W PRED
Aptenodytes forsteri (chicks)	4.03	W PRED
Seals *(11, 12, 19, 34, 70, 71, 77, 82)*		
Lobodon carcinophagus **	2.76	W PRED
*Hydrurga leptonyx***	3.26	W PRED
*Arctocephalus gazella***	3.34	W PRED
Ommatophoca rossii **	3.72	W PRED
Leptonychotes weddellii	5.13	W PRED

Sources : (1) Abrams & Underhill 1986, (2) Ainley et al. 1991, (3) Arnaud 1970, (4) Arnaud 1978, (5) Arnould & Whitehead 1991, (6) Barnes 1980, (7) Barnes & Clarke 1995, (8) Barthel 1990, (9) Brandt 1988, (10) Brandt 1990, (11) Burns et al 1998, (12) Cherel et al. 1996, (13) Cherel et al. 2002, (14) Cherel & Kooymann 1998, (15) Cohan et al. 1990, (16) Collins & Rodhouse 2006, (17) Dahm 1996, (18) Daniels 1982, (19) Daneri 1996, (20) Dauby et al. 2001, (21) Dayton 1989, (22) Dayton et al. 1974, (23) Dearborn 1977, (24) Dearborn et al. 1996, (25) Eastman 1985b, (26) Eastman 1999, (27) Fachauld & Jumars 1979, (28) Falk-Petersen et al. 2000, (29) Fischer & Hureau 1985, (30) Gaston 1989, (31) Gili & Hughes 1995, (32) Gorelova & Kobyliansky 1985, (33) Gorny & Bruns 1995, (34) Green & Willimans 1986, (35) Gutt 1991, (36) Gutt *pers comm*., (37) Hamner & Hamner 2000, (38) Hartmann-Schröder 1996, (39) Hopkins 1985, (40) Hopkins & Torres 1989, (41) Hubold & Ekau 1989, (42) Hubold & Ekau 1990, (43) Hughes et al. 1993, (44) Hunter 1983, (45) Iwamoto 1990, (46) Jaccarini & Schembri 1977, (47) Jacob et al. 2003, (48) Jacob *pers comm.*, (49) Ju et al. 2004, (50) Klages & Cooper 1997, (51) Kunzmann & Zimmermann 1992, (52) Lalli & Gilmer 1989, (53) La Mesa et al. 2004, (54) Li et al. 2001, (55) Lipskaya et al. 1992, (56) Lorentsen et al. 1998, (57) Lu & Williams 1994, (58) Madin 1974, (59) Massin 1982, (60) McKenna 1991, (61) Mintenbeck 2001, (62) Murina 1984, (63) Nickel & Atkinson 1994, (64) Nyssen et al. 2002, (65) Olaso et al. 2000, (66) Orejas et al. 2001, (67) Orejas et al. 2003, (68) Pasternak & Schnack-Schiel 2001, (69) Pearse & McClintock unpublished in McClintock 1994, (70) Plötz 1986, (71) Plötz et al 1991, (72) Reid et al. 1997, (73) Ridoux & Offredo 1989, (74) Schwarzbach 1988, (75) Sieg 1990, (76) Sirenko 1997, (77) Skinner & Klages 1994, (78) Stiller 1996, (79) Takahashi & Nemoto 1984, (80) Tatian et al. 2004, (81) Wägele 1991, (82) Walker et al. 1998, (83) Westheide & Rieger 1996, (84) Williams 1985, (85) Wyanski & Targett 1981, (86) Zimmer et al. 2007

Table G2 Energy content of species from several taxonomic groups from published sources (sources itemized at the end of the table). Energetic values are given in kcal and kJ * g^{-1} wet weight (WW) and dry weight (DW), with kJ = kcal * 4.1868 and kcal = kJ * 0.2388 (original values in bold). Conversion factors (CF) DW-WW for notothenioid fish based on own (unpublished) data, CF for other taxonomical groups taken from Brey (2001).

Species	**Kcal * g^{-1} WW**	**KJ * g^{-1} WW**	**Kcal * g^{-1} DW**	**KJ * g^{-1} DW**	**Source**	**CF (DW/WW)**
Fish - Notothenioidei						
Pleuragramma antarcticum	1.095	4.583	**5.200**	21.771	(1)	0.211
	1.156	**4.840**	5.490	22.991	(2)	
Dissostichus eleginoides	2.498	**10.460**	11.865	49.688	(7)	0.211
Patagonotothen ramsay	1.643	**6.880**	7.804	32.682	(7)	0.211
Notothenia coriiceps	0.943	**3.950**	4.481	18.764	(2)	0.211
Gobionotothen gibberifrons	0.821	**3.440**	3.902	16.341	(2)	0.211
Chaenocephalus aceratus	0.781	**3.270**	3.709	15.533	(2)	0.211
Champsocephalus gunnari	0.824	**3.450**	3.914	16.388	(2)	0.211
	1.290	**5.400**	6.126	25.651	(8)	
Fish - Myctophidae						
Electrona antarctica	1.888	7.905	7.345	**30.760**	(9)	0.257
	3.169	**13.270**	12.330	51.634	(8)	
	1.915	**8.020**	7.452	31.206	(5)	
Electrona carlsbergi	1.402	**5.870**	5.454	22.840	(2)	0.257
	2.054	**8.600**	7.991	33.463	(8)	
Gymnoscopelus nicholsi	2.395	10.031	9.320	**39.030**	(9)	0.257
	2.013	**8.430**	7.833	32.802	(2)	
	2.340	**9.800**	9.106	38.132	(8)	
	2.949	**12.350**	11.475	48.054	(5)	
Gymnoscopelus braueri	2.121	**8.880**	8.251	34.553	(5), (8)	0.257
Krefftichthys andersoni	1.690	5.798	6.577	**27.540**	(9)	0.257
	1.863	**7.800**	7.248	30.350	(8)	
Fish - Others						
Bathylagus antarcticus	0.702	**2.940**	2.764	11.575	(5)	0.254
Notolepis coatsi	1.051	**4.400**	4.088	17.121	(5)	0.257
Paradiplospinus gracilis	2.030	**8.500**	7.898	33.074	(5)	0.257
Squid						
Illex argentinus	1.533	**6.420**	8.517	35.667	(7)	0.180
Moroteuthis ingens	1.347	**5.640**	7.482	31.333	(7)	0.180

	0.549	**2.300**	3.051	12.778	(8)	
Martialia hyadesi	1.015	**4.250**	5.638	23.611	(8)	0.180
Gonatus antarcticus	0.903	**3.780**	5.015	21.000	(8)	0.180
Loligo vulgaris	0.864	**3.620**	4.803	20.111	(4)	0.180
Euphausiacea						
Euphausia crystallorophias	1.021	4.275	**4.620**	19.343	(1)	0.221
Euphausia superba	1.268	**5.310**	5.738	24.027	(2)	0.221
E. superba (fall)	**0.971**	**4.070**	4.394	18.416	(10)	
E. superba (winter)	**0.907**	**3.802**	4.104	17.204	(10)	
Euphausia triacantha	**0.696**	**2.915**	3.149	13.190	(10)	0.221
Tysanoessa macura (fall)	**1.203**	**5.038**	5.443	22.796	(10)	0.221
T. macura (winter)	**0.887**	**3.717**	4.014	16.819	(10)	
Decapoda						
Pasiphaea scotiae (fall)	**2.004**	**8.397**	7.828	32.801	(10)	0.256
P. scotiae (winter)	**1.664**	**6.974**	6.500	27.242	(10)	
Petalidium foliacium (fall)	**1.331**	**5.575**	5.455	22.848	(10)	0.244
P. foliacium (winter)	**1.966**	**8.237**	8.057	33.758	(10)	
Amphipoda - Gammaridea						
Cyphocaris faueri	**0.577**	**2.420**	2.194	9.202	(10)	0.263
Cyphocaris richardi (fall)	**0.696**	**2.915**	2.646	11.084	(10)	0.263
C. richardi (winter)	**0.916**	**3.839**	3.483	14.597	(10)	
Parandania boecki	**0.387**	**1.623**	1.471	6.171	(10)	0.263
Amphipoda - Hyperiidea						
Cyllopus lucasii (fall)	**1.358**	**5.689**	6.657	27.887	(10)	0.204
C. lucasii (winter)	**0.684**	**2.867**	3.353	14.054	(10)	
Hyperia macrocephala	**0.899**	**3.769**	4.407	18.475	(10)	0.204
Hyperiella antarctica	**0.408**	**1.708**	2.000	8.373	(10)	0.204
Primno macropa (fall)	**1.175**	**4.921**	5.760	24.123	(10)	0.204
P. macropa (winter)	**0.771**	**3.231**	3.779	15.838	(10)	
Themiso gaudichaudi	**0.687**	**2.880**	3.368	14.118	(10)	0.204
Vibilia stebbingi (fall)	**0.981**	**4.112**	4.809	20.157	(10)	0.204
V. stebbingi (winter)	**0.914**	**3.828**	4.480	18.765	(10)	
Copepoda						
Calanoides acutus (fall)	**0.600**	2.512	**4.200**	17.585	(6)	
C. acutus (winter)	**0.600**	2.512	**3.700**	15.491	(6)	
Calanus propinquus (fall)	**1.300**	5.443	**5.100**	21.353	(6)	
C. propinquus (winter)	**0.500**	2.093	**3.200**	13.398	(6)	
Euchaeta antarctica (fall)	**1.100**	4.605	**5.200**	21.771	(6)	
E. antarctica (winter)	**0.800**	3.349	**4.800**	20.097	(6)	

Gaetanus tenuispinus (fall)	**0.400**	1.675	**2.900**	12.142	(6)	
G. tenuispinus (winter)	**0.500**	2.093	**2.900**	12.142	(6)	
Metridia gerlachei (fall)	**0.300**	1.256	**2.600**	10.886	(6)	
M. gerlachei (winter)	**0.200**	0.837	**2.300**	9.630	(6)	
Rhincalanus gigas (fall)	0.567	2.374	**3.000**	12.560	(6)	0.189
R. gigas (winter)	**0.300**	1.256	**3.300**	13.816	(6)	
Mysidacea						
Boreomysis rostrata	**1.050**	**4.398**	5.024	21.043	(10)	0.209
Eucopia australis	**1.270**	**5.320**	6.077	25.455	(10)	0.209
Gnathophausia gigas	**1.419**	**5.945**	6.789	28.445	(10)	0.209
Ostracoda						
Conchoecia antipoda	**0.400**	1.675	**2.800**	11.723	(6)	
Conchoecia belgicae	**0.300**	1.256	**1.900**	7.955	(6)	
Conchoecia hettacra	**0.300**	1.256	**1.700**	7.118	(6)	
Polychaeta						
Vanadis antarctica	**0.500**	2.093	**3.400**	14.235	(6)	
Tomopteris carpenteri	**0.300**	1.256	**2.200**	9.211	(6)	
	0.612	2.564	3.900	**16.330**	(3)	0.157
Chaetognatha						
Eukronia hamata (fall)	**0.100**	0.419	**1.800**	7.536	(6)	
E. hamata (winter)	**0.200**	0.837	**2.800**	11.723	(6)	
Sagitta gazellae (fall)	**0.100**	0.419	**1.200**	5.024	(6)	
S. gazellae (winter)	**0.100**	0.419	**1.800**	7.536	(6)	
Sagitta marri	**0.300**	1.256	**2.700**	11.304	(6)	
Cnidaria - Scyphozoa						
Atolla wyvillei	0.075	0.315	1.421	**5.950**	(3)	0.053
Cnidaria - Hydrozoa						
Calycopsis borchgrevinki	0.059	0.249	1.144	**4.790**	(3)	0.052
Botrynema brucei	0.024	0.102	0.468	**1.960**	(3)	0.052
Diphyes antarctica	0.037	0.155	0.712	**2.980**	(3)	0.052
Ctenophora						
Beroe sp.	0.036	0.152	1.034	**4.330**	(3)	0.035
Pleurobranchia sp.	0.004	0.017	0.112	**0.470**	(3)	0.036
Tunicata						
Salpa fusiformes	0.051	0.213	1.301	**5.450**	(3)	0.039

Sources: (1) Ainley et al. 2003, (2) Barrera-Oro 2002, (3) Clarke et al. 1992, (4) Croxall & Prince 1982, (5) Donnelly et al. 1990, (6) Donnelly et al. 1994, (7) Eder & Lewis 2005, (8) Lea et al. 2002, (9) Tierney et al. 2002, (10) Torres et al. 1994.

Table G3 Species composition of the demersal (26 Otter trawl hauls) and the pelagic fish community (10 hauls using a bentho-pelagic net) on the north eastern Weddell Sea shelf (200-600m water depth). Samples were taken by R. Knust, A. Schröder, E. Brodte and K. Mintenbeck during four *RV Polarstern* expeditions between 1996 and 2004 (December-May; ANT XIII/3, XV/3, XVII/3, XXI/2). N = mean abundance [%], W = mean biomass [%]; F = Frequency of occurrence [%]; small juveniles and larvae are excluded due to inappropriate sampling gear (cod-end mesh size of both gears ≥ 10mm). Species number, species richness, diversity and evenness are given for the entire communities (bold numbers) and for notothenioid species only (numbers in parentheses).

	Demersal			**Pelagic**		
	N [%]	**W [%]**	**F [%]**	**N [%]**	**W [%]**	**F [%]**
Notothenioidei:						
Nototheniidae						
Pleuragramma antarcticum	49.31	28.55	61.54	99.54	95.22	100
Pagothenia borchgrevincki	0.01	0.01	3.85	0.03	0.07	10
Trematomus eulepidotus	5.26	8.73	88.46	-	-	-
Trematomus lepidorhinus	4.19	6.02	96.15	-	-	-
Trematomus nicolai	0.64	1.33	42.31	-	-	-
Trematomus bernacchii	0.05	0.10	19.23	-	-	-
Trematomus scotti	5.07	1.13	92.31	-	-	-
Trematomus loennbergi	0.34	0.82	42.31	-	-	-
Trematomus hansoni	0.40	1.70	53.85	-	-	-
Trematomus pennellii	3.78	3.40	57.69	-	-	-
Dissostichus mawsoni	0.04	0.10	11.54	-	-	-
Aethotaxis mitopteryx	0.07	0.31	15.38	-	-	-
Channichthyidae						
Chionodraco hamatus	0.79	3.11	76.92	0.09	0.32	30
Chionodraco myersi	12.42	31.40	84.62	0.03	0.28	10
Chionobathyscus dewitti	0.03	0.12	7.69	-	-	-
Cryodraco antarcticum	1.77	5.28	92.31	-	-	-
Dacodraco hunteri	0.69	0.76	26.92	0.10	0.14	30
Neopagetopsis ionah	0.03	0.35	15.38	0.01	0.01	10
Pagetopsis maculatus	0.29	0.22	61.54	-	-	-
Pagetopsis macropterus	0.17	0.22	30.77	-	-	-
Chaenodraco wilsoni	1.15	1.42	65.38	-	-	-

Artedidraconidae						
Artedidraco loennbergi	0.65	0.05	57.69	-	-	-
Artedidraco orianae	0.75	0.24	61.54	-	-	-
Artedidraco shackletoni	0.25	0.06	46.15	-	-	-
Artedidraco skottsbergi	0.70	0.05	50.00	-	-	-
Dolloidraco longedorsalis	3.68	0.55	61.54	-	-	-
Pogonophryne barsukovi	0.10	0.14	23.08	-	-	-
P. lanceobarbata	0.12	0.05	19.23	-	-	-
P. macropogon	0.02	0.03	11.54	-	-	-
P. mormorata	0.31	0.15	53.85	-	-	-
P. permittini	0.06	0.05	11.54	-	-	-
P. phyllopogon	0.05	0.02	15.38	-	-	-
P. scotti	0.16	0.35	30.77	-	-	-
Histiodraco velifer	0.20	0.22	34.62	-	-	-
Bathydraconidae						
Gerlachea australis	0.94	0.45	46.15	-	-	-
Gymnodraco acuticeps	0.18	0.54	53.85	0.04	0.03	20
Akarotaxis nudiceps	0.02	<0.01	19.23	-	-	-
Bathydraco macrolepis	0.01	<0.01	3.85	-	-	-
Bathydraco marri	0.08	0.02	11.54	-	-	-
Cygnodraco mawsoni	0.37	0.86	50.00	-	-	-
Prionodraco evansii	1.93	0.14	42.31	-	-	-
Racovitzia glacialis	0.43	0.34	46.15	-	-	-
Non-Nothotheioidei:						
Zoarcidae						
Lycodichtys antarcticus	0.06	0.01	15.38	-	-	-
Ophthalmolycus amberensis	0.01	0.01	3.85	-	-	-
Zoarcidae sp.	0.06	0.02	15.38	-	-	-
Macrouridae						
Macrourus whitsoni	0.02	0.17	7.69	-	-	-
Myctophidae						
Gymnoscopelus sp.	0.04	0.11	3.85	-	-	-
Myctophidae sp.	-	-	-	0.03	0.01	10
Liparidae						
Careproctus sp.	0.01	<0.01	3.85	-	-	-
Paraliparis antarcticus	0.11	0.08	7.69	-	-	-
Paraliparis sp.	0.04	<0.01	7.69	-	-	-

Liparidae sp.	0.13	0.04	23.08	-	-	-
Anotopteridae						
Anotopterus pharao	-	-	-	0.11	3.93	30
Rajiidae						
Bathyraja maccaini	0.11	1.87	34.62	**-**	**-**	**-**
Bathyraja sp.	0.03	0.12	11.54	**-**	**-**	**-**
Species No.	**49** (42)			**9** (7)		
Species Richness	**6.326** (5.406)			**1.471** (1.103)		
Diversity	**2.037** (2.015)			**0.0378** (0.0268)		
Evenness	**0.5235** (0.5391)			**0.0172** (0.0138)		