TROPHIC DYNAMICS OF ANTARCTIC SHELF ECOSYSTEMS – FOOD WEBS AND ENERGY FLOW BUDGETS

UTE JACOB

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TROPHIC DYNAMICS OF ANTARCTIC SHELF ECOSYSTEMS –

FOOD WEBS AND ENERGY FLOW BUDGETS

TROPHISCHE DYNAMIK VON ÖKOSYSTEMEN DES ANTARKTISCHEN SCHELFS – NAHRUNGSNETZE UND ENERGIEFLUSS-BILANZEN

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In Memory of my grandfather Heinrich Kleine & Buddy
-much missed

"Precious and fragile things need special handling"
(Precious, M.L. Gore)

SUMMARY

Predicting impacts of environmental change on organisms and on the communities they belong to are of considerable concern to current ecological studies. The Southern Ocean is a useful model system for examining the responses of species and systems to environmental change, because as well as presenting a continuum of ecological complexity, the geographical location and isolation makes monitoring environmental change straightforward.

This thesis is an attempt to achieve deeper insights into the functioning of polar communities and ecosystems by analyzing trophic dynamics and energy flow patterns primarily in the high-Antarctic Weddell Sea. In order to achieve this goal, a number of approaches targeting different system aspects as well as system levels had to be developed: (i) Stable isotope signatures and diet information were combined to determine trophic position of and trophic interactions between organisms. (ii) A new multidimensional approach was developed to measure and to compare species trophic niche position and width. (iii) Food web descriptors were estimated to allow comparisons between different communities. (iv) A Mass balanced flow model was used to assess importance of trophic linkages and compartments.

The high trophic complexity of the food web of the Weddell Sea observed, results from the high trophic generality of most of the populations as well as their ability for vertical niche expansion. The numerous closely connected species with their trophic flexibility affect overall system properties such as stability and resilience.

It remains to be seen if the “loose” connectivity observed in the Weddell Sea food web leads towards stability, but it is likely that there are different ways of being robust related to different types of perturbations. “Change” is not limited to just the number of species in a community, but might include an alteration to such properties as precipitation, nutrient cycling and temperature, all of which are correlated with productivity.

The food web of the high-Antarctic Weddell Sea may be able to cope better, at least to a certain extent, with slowly changing environmental conditions than with dramatic short-term disturbances.

ZUSAMMENFASSUNG

Ein besseres Verständnis der Funktionsweise mariner Ökoysteme ist eine wichtige Voraussetzung für Prognosen zu Auswirkungen globaler Erwärmung auf Organismen und Systeme. Die außerordentliche Beständigkeit der ökologischen Zusammenhänge, sowie die geographische Lage und Isolation machen den südlichen Ozean zu einem der wertvollsten Modellsysteme, um die Auswirkungen von Klimaveränderungen auf einzelne Arten, aber auch das Zusammenwirken verschiedener Arten, zu untersuchen.

Ziel dieser Arbeit ist, durch die Analyse von Nahrungsnetzen des hochantarktischen Weddellmeeres und ihrer trophischen Dynamik genauere Kenntnis über die Funktion polarer Lebensgemeinschaften und Ökosysteme zu erlangen.

Um dieses Ziel zu erreichen, habe ich verschiedene Ansätze verwendet und entwickelt, die auf unterschiedliche Eigenschaften beziehungsweise auf die verschiedene Organisationsebenen des Ökosystems gerichtet sind: (i) Stabile Isotopensignaturen und Nahrungsanalysen wurden kombiniert verwendet, um die trophische Stellung von einzelnen Arten sowie die trophische Struktur des Gesamtsystems zu entschlüsseln (ii) Ein neuer multidimensionaler Ansatz wurde von mir entwickelt, um die Stellung und Weite der trophischen Nische verschiedener Arten miteinander zu vergleichen (iii) Ich habe Charakteristika von Nahrungsnetzen ermittelt und konnte so Unterschiede zwischen Antarktischen und borealen Systemen aufzeigen (iv) Mit Hilfe eines Gleichgewichtsmodells konnten die Energieflüsse im System quantifizierbar und vergleichbar gemacht werden, um so die Bedeutung der verschiedenen Arten für das System evaluieren zu können.

Die komplexe Struktur des Nahrungsnetzes im Weddellmeer ist auf das flexible Nahrungsspektrum der meisten Populationen zurückzuführen, genauso wie auf ihre Fähigkeit, die trophische Nische vertikal zu erweitern. Die zahlreichen eng vernetzten, hochflexiblen Arten, beeinflussen die Stabilität und Resilienz des Gesamtsystems.

Noch nicht ganz geklärt ist, ob die „lockere“ Verknüpfung, des Nahrungsnetzes des Weddellmeeres zu einer höheren Systemstabilität führt. Sehr wahrscheinlich gibt es jedoch eine Reihe von Systemeigenschaften, die auf wiederum verschiedene Arten von Veränderungen unterschiedlich reagieren. Veränderungen sind nicht nur auf die Anzahl der Arten beschränkt, sondern können auch Veränderungen von Eigenschaften

wie Niederschlag, Nährstoffkreisläufe und Temperatur beinhalten, die alle mit der Produktivität des Systems korreliert sind.

Meine Untersuchungen zeigen, dass das Nahrungsnetz des hochantarktischen Weddellmeeres belastbarer gegenüber Veränderungen ist als vermutet und bis zu einem bestimmten Grad auf langsame Veränderungen der Umwelt reagieren kann, während plötzlich abrupte Veränderungen irreversible Folgen für die Funktionsweise des Systems haben können.

“Never eat more than you can lift at once”

Miss Piggy

1 PREFACE

Ecosystem-level studies that consider trophic relationships are typically based upon system-specific knowledge of feeding relationships (Martinez 1991). Such feeding relationships combined to whole system food webs are useful tools for merging ecological subdisciplines as well as linking species to ecosystems. This stems from the fact that “who eats whom” appears to be the most central organizing concept in ecology (Martinez 1991; de Ruiter et al. 2005). Food web characterization is therefore required as an initial step in understanding an ecosystem (Link 2002). A major challenge of food web ecology is to improve our ability to quantify trophic interactions at the desired organizational scales, whether that will be individual consumers, populations, or entire food webs. The information needed is almost universally derived from analysis of consumer gut contents and provides fundamental information for bioenergetic models (Kitchell et al. 1977). Gut content analysis reveals the diet of a consumer at a particular place and time, and is often used to infer population level feeding. However, this approach can be limited in its capacity for reconstructing energy flow for entire food webs, as the amount of dietary data required for such studies can be prohibitive (Vander Zanden & Rassmussen 2002; Pinnegar et al. 2004). Diet analysis is also limited in its ability to capture trophic variability at finer scales of trophic organization, such as intra-population or individual-level diet specialization.

A number of inferential techniques have the potential to provide information on trophic relationships at a variety of organizational scales. These approaches include the use of fatty acid biomarkers (Grahl-Nielsen & Mjaavatten 1991; Nyssen et al. 2005) and stable isotope tracers (Minagawa & Wada 1984; Peterson & Fry 1987; Post 2002). The use of stable isotopes has emerged as a particularly powerful tool in food web studies, and is currently being used to address a variety of questions concerning trophic interactions that are of relevance to ecosystem management (Vander Zanden & Rassmussen 2002). The isotope approach can contribute to elucidating food web processes at two different scales that are particularly difficult to study using traditional techniques: that of whole food webs such as the mean number of trophic transfers between the bottom and the top species, the stratigraphy of a food web (in the sense of Cohen & Luczak 1992), i.e. the proportion of species at each level above the basal species) or, if some of the basal species have isotopic signatures that are different enough, the existence of separate or confluent pathways of matter transfer (Ponsard & Arditi 2001) as well as trophic variability occurring at the intra-population level (Vander Zanden & Rassmussen 2002).

To assess the relative importance of trophic linkages quantitative food web models and flow network analyses have been used (Baird & Ulanowicz 1989; Baird et al. 1991; Monaco & Ulanowicz 1997, Baird et al. 1998; Christian & Luzkovich 1999; Baird et al. 2004). Mass balance models such as ECOPATH WITH ECOSIM (Walters et al. 2000) analyse the amount of energy or matter flow along trophic links. They allow in-depth analysis of ecosystem structure and dynamics as well as the evaluation of effects of potential changes in environmental conditions.

One key aspect of food web theory is the question of how food webs can be described in a way that allows feasible comparisons between different communities, and at the same time serves to uncover general patterns inherent to all of them (Cohen et al. 1993). In this thesis we link food web theory to common patterns in energy flow and species characteristics, through investigating patterns in the trophic interactions of species. Combining food web theory with stable isotope signatures and balanced energy flow analyses (Raffaelli & Hall 1996; Ulanowicz 1996) provides a powerful set of tools which allow to demonstrate how in Antarctic marine food webs, with many closely connected species, community organisation and species trophic characteristics affect overall system properties.

2 OVERVIEW

2.1 The Structure of Antarctic Ecosystems and Trophic Interactions

Ecology is predominantly a science of interactions. A main purpose of ecological research is to understand ecological processes and the resultant patterns of distribution, abundance, diversity and interactions (McIntosh 1985; Underwood et al. 2000). Certain aspects of the ecology of Antarctic organisms have been reviewed regularly during the past (Hedgpeth 1971; Dell 1972; Clarke 1983; White 1984; Dayton 1990; Arntz et al. 1994; Clarke 1996; Arntz et al. 1997; Gray 2001), but with respect to the whole system even where to begin from is a difficult issue; we do not even know how many species are out there (Gutt et al. 2001; Clarke & Johnston 2003), let alone how they interact with each other and with the environment (Christianou 2003).

The marine Antarctic is characterized by low but relatively constant water temperatures, seasonal or permanent ice cover as well as seasonally variable food input from the water column (Hempel 1985; Clarke et al. 1988; Fahrbach et al. 1992; Arntz et al. 1994; Johannessen et al. 1996). The relatively low metabolism and productivity of Antarctic organisms as well as the longevity of most of them (Brey & Clarke 1993; Arntz et al. 1994; Brey et al. 1995, Chapelle & Peck 1995; Ahn & Sim 1998; Bluhm et al. 1998) appears to be mainly governed by food supply and temperature. Despite low individual productivity, Antarctic shelf benthos is characterized with intermediate to high diversity, comparatively high values of biomass and a patchy distribution of organisms (Dell 1972; White 1984; Highsmith & Coyle 1990; Grebmeier 1993; Piepenburg & Schmidt 1996; Arntz et al. 1997; Brey & Gerdes 1997; Gutt & Starmans 1998; Gerdes et al. 2005 PUBLICATION VII).

The marine Antarctic is composed of an interconnected system of functionally distinct hydrographic and biogeochemical subdivisions (Treguer & Jacques 1992) and includes open-ocean, frontal regions, shelf-slope waters, sea ice and marginal ice zones (e.g. Smith et al. 1995). Hureau (1994) proposed three main ecological zones within the Southern Ocean from South to the North, (i) the HIGH ANTARCTIC ZONE; (ii) the SEASONAL PACK ICE ZONE and (iii) the ICE FREE ZONE (FIG.1).

The HIGH ANTARCTIC ZONE is the region adjacent to the continent, which is covered by permanent ice most of the year. This zone covers all the coasts of the Antarctic continent, most of the continental shelf as well as Peter I. and Balleny Islands.

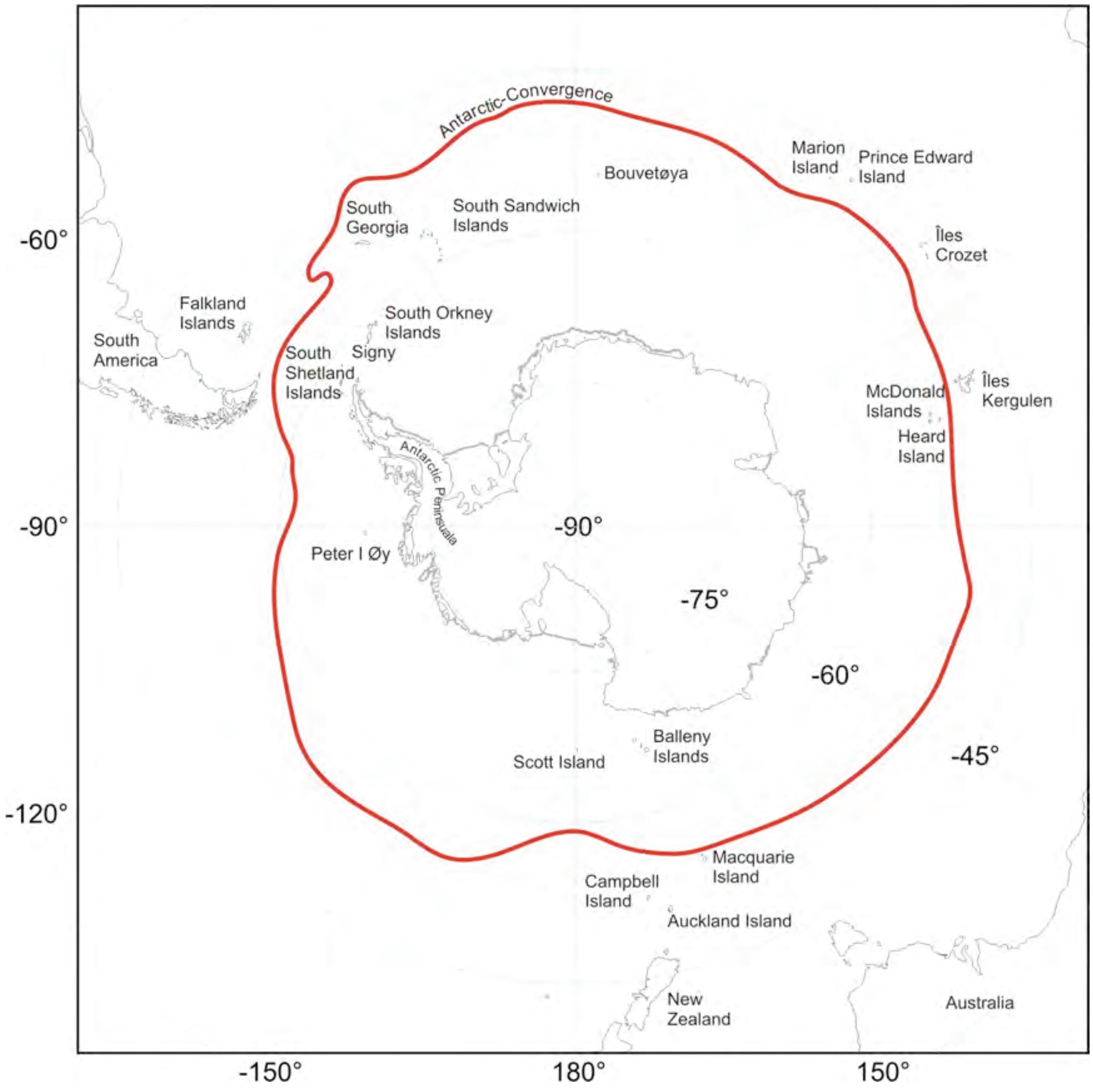

Figure 1: The Antarctic continent and adjacent areas in the Southern Ocean (modified from Bonner & Walton 1985)

It is characterized by the presence of the euphausiid *Euphausia crystallorophias*, demersal fishes of the genus Trematomus and few other pelagic nototheniids, e.g. *Pleuragramma antarcticum* (Hureau 1994). The rich epibenthic communities in the Weddell Sea and in the Ross Sea are known as “multi-storied” assemblages (Bullivant 1967; Andriashev 1968; Gutt 1991b; Gutt & Ekau 1996). Sponges are dominant members of many Antarctic benthic communities (Beliaev & Ushakov 1957; Koltun 1970; Dayton et al. 1970; Voss 1988; Barthel et al. 1990; Barthel 1995; Gatti 2002). They serve as (i) habitat for numerous other benthic organisms (Dearborn 1977; Gutt 1988; Wägele 1988; Barthel et al. 1991; Kunzmann 1992); as (ii) prey for many benthic invertebrates and vertebrates (McClintock 1994; Dahm 1997; Jacob et al.

2003 PUBLICATION IX) and (iii) the persistent skeletons of dead hexactinellids form major parts of the common Antarctic spicule mats. Thereby they modify substrate conditions for other benthic fauna (Barthel 1992; Barthel & Gutt 1992; Barthel 1995).

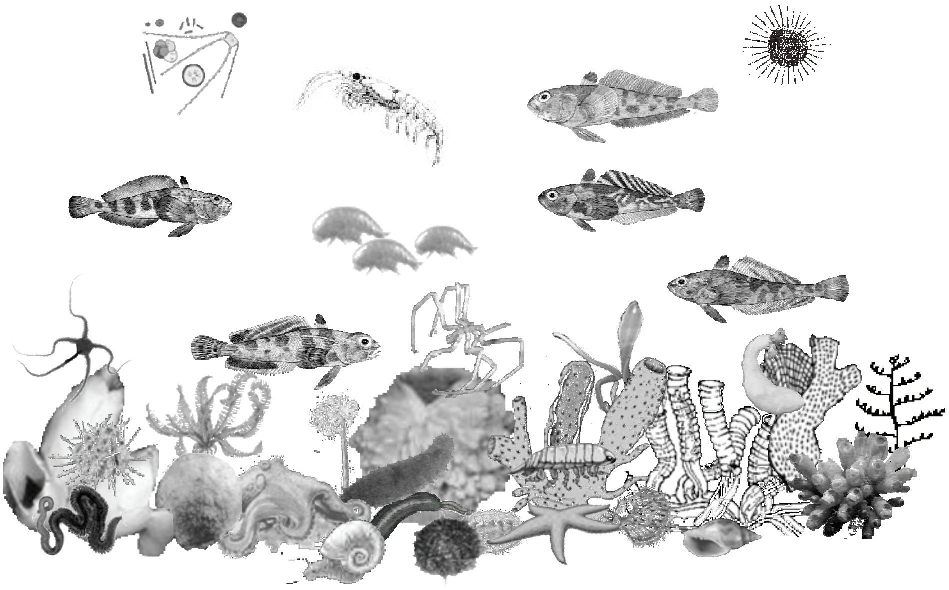

Figure 2: Simplified illustration of an eastern Weddell Sea shelf "multi-storied" community

The SEASONAL PACK ICE ZONE is limited to the north by the northern winter limit of the pack ice and to the south by the northern summer limit of the pack ice, as observed by satellites (Zwally et al. 1983). The South Orkney Islands, the South Sandwich Islands, the South Shetland Islands and the northern tip of the Antarctic Peninsula belong to the SEASONAL PACK ICE ZONE (Hureau 1994).

It is the most productive ecological zone of the Southern Ocean with highest concentrations of the Antarctic krill *Euphausia superba* (Marr 1962) and numerous myctophid fish species (Hureau 1994). Due to increasing commercial interest in krill, this area has received special attention during the past decade and to date, 89% of the global harvest of Antarctic krill has been taken from this area (Hewitt & Linen Low 2000). Along the coastal zones of the SEASONAL PACK ICE ZONE sea-ice impact appears to be less severe compared to the HIGH ANTARCTIC ZONE, although there is an intense impact of wave action and wind speed (Barnes 2005). In shallow water the seasonal growth of macroalgae is an important food source for benthic predators (Amsler et al. 1995; Jazdzewski et al. 2001). Consumption of some macroalgae by various fish and invertebrates (Iken et al. 1997; Iken 1999; Iken et al. 1999) and the assimilation of benthic macroalgal carbon through detrial food webs (Dayton 1990) link the high productivity of the shallow benthos with the pelagic food web (Dunton 2001; Corbisier et al. 2004). Measurements of $\delta^{13}C$, $\delta^{15}N$ and C/N for a variety of Antarctic Peninsula fauna and flora support the role of benthic brown algae to resident organisms and determine food web relationships among this diverse littoral fauna (Dunton 2001; Corbisier et al. 2004). Ophiuroids, mainly *Ophionotus victoriae*, characterize the benthic communities (Piepenburg et al. 2002; Manjon-Cabeza & Ramos 2003), as well as polychaetes, bivalves and crustaceans (Jazdzewski et al. 1986; Piepenburg et al. 2002).

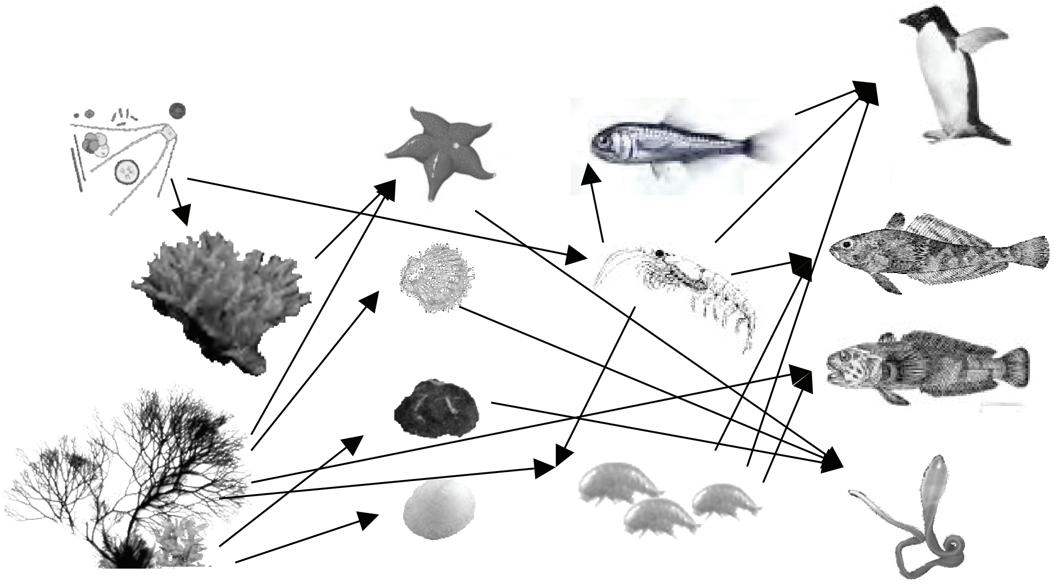

Figure 3: Simplified important pathways of the food web within the Seasonal Pack Ice Zone

The ICE FREE ZONE extends between the Subtropical Front to the North and the northern winter limit of pack ice to the South. Following this, the Ice Free Zone includes the following islands from West to East: South Georgia, Bouvet Island, Marion Island, the Prince Edward Islands, Crozet Island, Kerguelen Island, Heard and Macquarie Islands which constitute the Kerguelen Province. The Magellanic area and the Falkland Islands constitute a Patagonian Province (Hureau 1994). This region supports large populations of seabirds, cephalopods (Collins et al. 2004) and marine mammals, as well as commercial fisheries for toothfish *Dissostichus eleginoides* and icefish *Champsocephalus gunnari*. The trophic interactions and food web structure in the upper trophic levels of Antarctic pelagic waters appear to be a function of the vertical distribution of phytoplankton and their grazers, as well as of the mobility of the apex predators (Ainley et al. 1991). Top predators abundant in the ICE FREE ZONE are the Antarctic fur seal *Arctocephalus gazella*, the minke whale *Balaenoptera acutorostrata* (Brown & Lockyer 1984; de la Mare 1997; Tynan 1998; Reid et al. 2000) and numerous seabirds such as king penguin (*Aptenodytes patagonicus*), chinstrap penguin (*Pygoscelis antarctica*), Kerguelen petrel (*Pterodroma brevirostris*), blue petrel (*Halobaena caerulea*) and cape petrel (*Daption capense*), Antarctic prion (*Pachyptila desolata*), and southern giant fulmar (*Macronectes giganteus*) (Ainley et al. 1991; Ainley et al. 1992). The pelagic system is inhabited by meso- and bathypelagic fish species, whereas the coastal fish fauna is dominated by species like *Electrona antarctica*, *Patagonotothen guntheri, Notothenia rossii, Gobionotothen gibberifrons, Dissostichus eleginoides, Chaenocephalus aceratus* and the mackerel ice fish *Champsocephalus gunnari*. The simplified food web of Hopkins et al. (1993) illustrates the principal routes for energy to the top predators and highlights the importance of the intermediate trophic levels, krill as well as fish and squids, to energy flow through the pelagic system (Fig. 4).

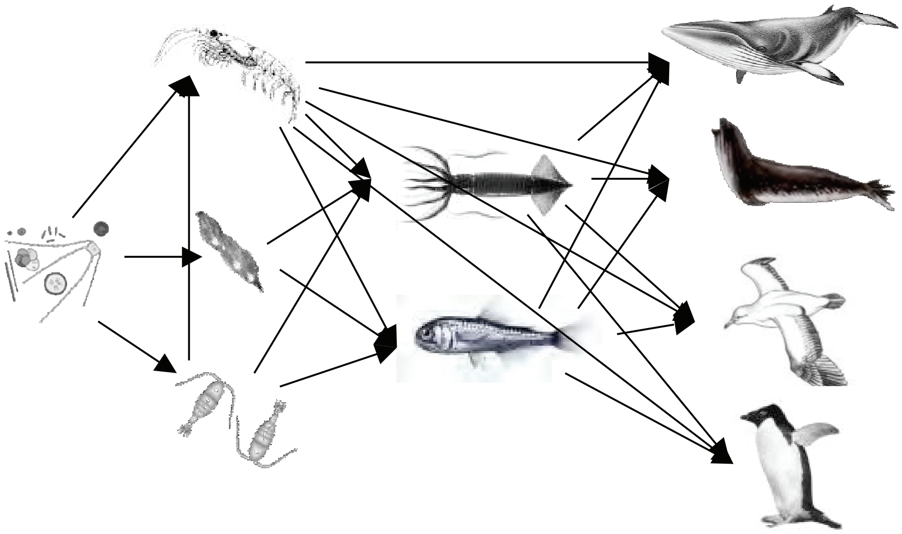

Figure 4: Major pathways from phytoplankton to apex predators in a simplified mid-water food web of the ICE FREE ZONE (modified after Hopkins et al. 1993)

There are at least three reasons for the observed high zooplankton concentrations, especially at South Georgia (Murphy et al. 1998; Boyd 2002; Murphy et al. 2004) and around the islands situated in the ICE FREE ZONE. Firstly, zooplankton is advected into the region by the Antarctic Circumpolar Current (ACC) from the northern part of the Antarctic Peninsula, an area of known high krill production (Hofman et al. 1998). Secondly, mixing of coastal and high Antarctic water masses, plus local nutrient enrichment of the waters by island run-off leads to locally high primary production relative to the surrounding ocean, which may support larger zooplankton populations (Øresland & Ward 1993; Atkinson 1996; Atkinson & Snyder 1997; Atkinson et al. 1999; Atkinson et al. 2001). Thirdly, local mixing between shelf and oceanic waters reduces the export of zooplankton out of the system (Boyd 2003). The data of Hopkins et al. (1993) indicate that most of the biomass and energy flow at intermediate and higher trophic levels in the ICE FREE ZONE can be accounted for by less than 20 species and these key species are predominant throughout the West Wind Drift south of the Polar Front (Hopkins et al. 1993).

Owing to its geographical isolation, Antarctica represents a pristine environment and has been identified as an important case study for the conservation of intact ecosystems (Chown & Gaston 2002). Antarctic marine ecosystems may be viewed as complex systems, which exhibit some degree of self-organization (Kay 1991; Schneider & Kay 1994; Bellamy & Lowes 1999; Boyd & Murray 2001). The annual advance and retreat of sea ice is a major physical determinant of spatial and temporal changes in the structure and function of the system (Andriashev 1968; Smith et al. 1995). The seasonal timing of such ecologically important events affects life histories of species at every trophic level (Smith et al. 1995). However, present knowledge of the functioning of polar benthic communities and ecosystems, in particular their trophic linkages and energy flow patterns is still fragmentary (e.g. Bluhm 2001), therefore the food web structure or even a balanced trophic model of such a system is a challenging task.

2.2 Food Web Ecology

The key role of trophic interactions and biomass fluxes in ecosystem functioning explains the continuous interest in topological community descriptions among ecologists. Food web studies were pioneered by Cohen (1978), Pimm (1982), Sugihara et al. (1989) and Cohen et al. (1990) and aimed at describing trophic links among species (Baird & Ulanowicz 1989; Warren 1989; Hall & Raffaelli 1991; Martinez 1991; Havens 1992; Polis 1991; Goldwasser & Roughgarden 1993). Comprehension of food web structure and of ecosystem functioning is necessary for a more efficient approach to resource management and endangered species conservation (Crowder et al. 1996; Loreau et al. 2001; Thebault & Loreau 2003). To figure out the complexity associated with highly diverse natural communities is by lumping taxonomically or functionally similar species, particular on their feeding relationships, into one of various trophic groupings (Chase & Leibold 2003).

Trophic Compartments and Trophic Links

It has long been noted that distribution, abundance and behaviour of organisms is influenced by interactions with other species (MacArthur 1955; de Ruiter et al. 2005). Species are linked with each other in webs of interactions, and consumption/predation is the key interaction within ecosystems (e.g. Martinez 1991; Sih et al. 1998; Christianou 2003). Progress in food-web research has been hampered in particular by a failure to standardize both the level of taxonomic resolution (Martinez 1991; Martinez 1992; Closs & Lake 1993; Hall & Raffaelli 1993) and the effort put into characterizing the compartments of the food web and detecting links between them (Cohen et al. 1993; Hall & Raffaelli 1993; Polis 1994; Jaarsma et al. 1998). To figure out the complexity associated with highly diverse natural communities is by lumping taxonomically or functionally similar species, particular on their feeding relationships, into one of various trophic groupings (Chase & Leibold 2003). These categories include (i) FUNCTIONAL GROUPS, where within trophic levels compartments perform in similar ways (e.g. benthic herbivores); (ii) GUILDS, a concept similar to functional groups but often also associated with taxonomic grouping (scavenging amphipods) and (iii) TROPHOSPECIES, a group of compartments that have identical linkage patterns within a food web (Yodzis 1988; Martinez 1991). We structure our system along taxonomic lines, i.e. one species = trophic compartment. Species, cluster and trophic species specify different aggregation levels of the more general term, species.

Most links in real food webs remain concealed in food web models. Cohen and Newman (1988) estimated that model webs that contain > 30 compartments typically include only about 20% of the links that are actually present (Pinnegar et al. 2004). “Does this lack of detailed knowledge really matter?” May (1988) suggested that “the way a food web model is constructed may tell us more about the psychology of the scientist involved than about real world ecology” (see Pinnegar et al. 2004). It might be true that model construction tends to reflect the specialism of the researcher constructing them, or the commercial interest of the society as a whole (e.g. emphasis given to commercially important species, like the Antarctic toothfish, *Dissostichus mawsoni* or charismatic species like whales, for example the Antarctic minke whales

Balaenoptera acutorostrata. Additionally, there is a tendency to over-aggregate organisms at the base of the food web (Hall & Rafaelli 1993), such as primary producers, bacteria, protozoans and nematodes, which are partly poorly characterised, but themselves highly interacting systems (Warren 1989; Walker 1985; Hall & Raffaelli 1991). Direct or indirect effects of one compartment on another depend on the nature of these interactions, which are neither unidirectional nor necessarily of equal effect in both directions. ”Basal” compartments are defined as non-predatory compartments usually they are autotrophic. ”Top” compartments are not preyed upon by other compartments. “Intermediate” compartments consume at least one other compartment and are consumed by at least one other compartment in the web. An “isolated” compartment is a compartment that has no other compartment reported as predators or prey (Briand & Cohen 1984). “Omnivores” feed on more than one trophic level (Pimm & Lawton 1978).

Irrespective of the number of links, the type of links (herbivorous, carnivorous, detritivorous and omnivorous) as well as the topology of the entire web can be expected to influence the system’s response to perturbations (Christianou 2003). Therefore one outstanding question will remain: “How does one provide advice or predictions, given that an infinite number model configurations are possible, and no one model can ever achieve perfection?” (Costanza & Sklar 1985; Pinnegar et al. 2004).

Trophic Position and Trophic Level

The trophic position of a trophic compartment is the exact position within a food web as defined by all links to or from this compartment. Research on trophic levels focuses on (i) patterns common to all ecological systems (Elton 1927; Lindeman 1942; Lawton 1978; Pimm & Lawton 1978; Pimm et al. 1991; Yodzis 1989; Martinez & Lawton 1995); (ii) patterns that distinguish types of systems (Hairston 1960; Briand & Cohen 1987; Moore et al. 1989; Polis & Strong 1996); and (iii) patterns that distinguish an organism’s role within ecological systems (Power 1990; Cabana & Rasmussen 1994; Brett & Goldman 1997; Pace et al. 1999; Schmitz et al. 2000; Williams & Martinez 2004).

Measuring trophic level is central to this wide range of ecological research and food web theory plays a prominent role in this measurement on a species-by-species level and whole system basis (Levine 1980; Adams et al. 1983; Williams & Martinez 2000;

Williams & Martinez 2004). Conventional diet analysis does not always help since species and individuals in the size spectrum (i) switch diet frequently, (ii) digest prey at different rates, and (iii) contain unidentifiable gut contents (Polunin & Pinnegar 2002). Diet analysis is labor intensive when applied to a whole system range of taxa and size classes and, moreover, estimates of trophic level are required for prey items, too. An appealing alternative to diet analysis is nitrogen stable isotope analysis ($\delta^{15}N$, Post 2002; Jacob et al. 2005 PUBLICATION I; Jacob et al. 2005 PUBLICATION II; Jacob et al. 2005 PUBLICATION IV). This provides estimates of trophic level, because in the tissue of consumers $\delta^{15}N$ is typically enriched (on average by 3.4 ‰) relative to their prey (Post 2002). Thus $\delta^{15}N$ reflects the trophic composition of assimilated diet over time (Post 2002b).

Food Web Descriptors

The construction of a food web comprises mapping of the interrelationships between the trophic compartments of an ecological community (DeAngelis 1992; de Ruiter et al. 2005). Common patterns within and between food webs can only be perceived with tools that allow to compare web structure across different systems, i.e. universal food web descriptors. The search for and interpretation of general patterns based on such descriptors has a long tradition in ecology (e.g. Gallopin 1972, Cohen 1978, Pimm 1982, Briand & Cohen 1984, Briand & Cohen 1987, Paine 1988, Lawton 1989) As food webs are complex objects, many summarizing system descriptors (indices) have been proposed to allow for ecologically meaningful comparisons between different webs (Fig.5; e.g. Cohen 1977; Cohen 1989; Pimm 1982; Briand & Cohen 1984; Lawton 1989; Sugihara et al. 1989; Pimm et al. 1991; Havens 1992; Jonsson et al. 2005). A food web is a structure of cross-linked food chains. Conventional descriptors of food webs are based on the number of trophic compartments (TC) in a food web and the number of links L between them (Hall & Raffaelli 1993).

A food chain is an ordered sequence of at least two species and run from a basal element to each top predator. Food chain length is the number of links within this particular path (Pimm 1982; Cohen et al. 1986; Hall & Raffaelli 1993). Linkage density (L/S) is the number of links per TC, connectance (C), the proportion of realised links within a web, is calculated as $2 \times L/(S^2\text{-}S)$ (Hall & Raffaelli 1993; Warren 1994), linkage complexity is calculated by $S \times C$ (Briand 1985). Trophic vulnerability (V) and trophic generality (G) of a TC are the number of predators and the number of prey items, respectively (Schoener 1989).

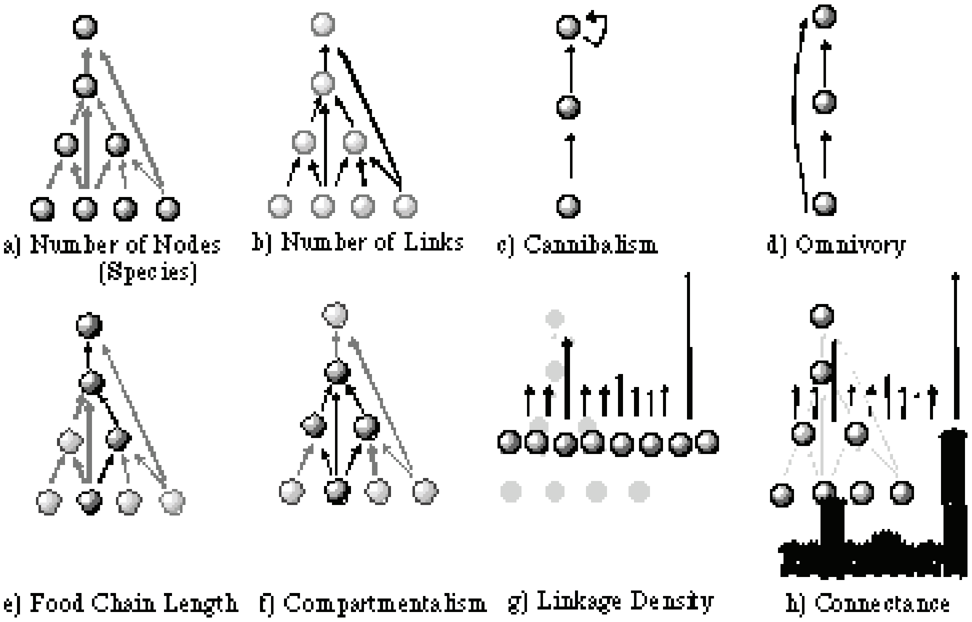

Figure 5: Food Web Descriptors useful for comparisons between different webs

Some of these descriptors are known to be very sensitive to model aggregation and the rate of identified links in a food web (Goldwasser & Roughgarden 1997; Bersier et al. 1999; Martinez et al. 1999; Link 2002a; Cattin-Blandenier 2004).

2.3 Body Size and Food Web Patterns

Size-based analyses of open marine food webs, where body size rather than taxonomic identity is the principal descriptor of an organism, provide alternative insights into food web structure and function that complement and extend those from taxon-based analyses (Jennings 2005). Predators are usually between one and three orders of magnitude larger than their prey (Jonsson et al. 2005; Cohen et al. 2003; Woodward & Hildrew 2002), and although there are some notable exceptions (e.g. host-parasite and some host-parasitoid systems, pack hunters and baleen whales) this general biological phenomenon illustrates the links between the trophic structure of whole communities and body size (Brown et al. 2004). The description of links between body size and trophic structure is hampered, however, by the unreliability or unsuitability of methods used to estimate trophic level (Jennings 2005). Across the whole food web, trophic level and body size are positively related (Fry & Quinones

1994; Jennings et al. 2002). Albeit species with a similar maximum body size can evolve to feed at different trophic levels, there are less small species feeding at high trophic levels than at low trophic levels (Jennings 2005). The overall trophic continuum across body-size classes shows that fixed (integer) trophic levels do not appropriately describe the structure of aquatic food webs (France et al. 1998). Accordingly, Jennings (2005) treats the parameter “trophic level” as a continuous measure. If the potential diet of a given predator is defined as a subset of the next largest predator’s diet, then a nested hierarchy of dietary niches will result, as it is widely observed in nature (e.g. Woodward & Hildrew 2002, Cushing et al. 2003). Hierarchical ordering of feeding niches is a central component of the recent niche models that have successfully reproduced many of the topological patterns seen in real food webs, including the prevalence of generalism and omnivory, from a relatively simple set of rules (e.g. Warren 1996, Williams & Martinez 2000, Cattin et al. 2004). If community niche space can be collapsed into a single axis, as suggested by these models, and if that axis is body size, then characterizing the size distributions within a food web will capture much of the biologically meaningful variation in a relatively straightforward manner (Woodward et al. 2005).

Regarding marine Antarctic Shelf Systems, the potential weakness with size-based analyses is that the proposed positive relationship between body size and trophic level is poorly developed here. In Antarctic Shelf Systems (i) the very large animals typically feed on very small prey (whales → myctophid fish → krill → phytoplankton, Jennings 2005; Jacob et al. 2005 PUBLICATION V), (ii) scavenging species, small in size, (e.g. amphipods, nemertines and gastropods) feed up and down the food chain irrespective of their size (Nyssen et al. 2003; Nyssen et al. 2005; Brose et al. 2005 PUBLICATION III; Jacob et al. 2005 PUBLICATION V), and (iii) large benthic and pelagic suspension & filter feeders, feed on very small suspended particulate organic matter (Orejas et al. 2003; Brose et al. 2005 PUBLICATION III; Jacob et al. 2005 PUBLICATION V).

2.4 Energy Flow and Mass Balance

One ecological approach towards community dynamics is the exchange of energy and matter between trophic compartments which constitute smaller and more manageable subsets of the whole system (Vandermeer 1969; Gilpin et al. 1986; Billick & Case

1994) Studies of energy budget and mass balance provide a quantitative answer to ecosystem level questions about rate and control of flux and cycling (Likens 1992)."ECOPATH WITH ECOSIM" (EwE) has emerged as one of the most popular approaches to ecosystem flow modelling, and one of the few (Fath and Patten 1999) that can address large-scale ecosystem issues. ECOPATH is based on a static flow model (Polovina 1984; Christensen & Pauly 1992) and uses mass balance principles to estimate flows (Polovina 1984; Christensen & Pauly 1992; Bundy et al. 2000). This software allows in-depth analysis of ecosystem structure and dynamics as well as the evaluation of potential changes in environmental conditions. The mass balanced ecosystem model analyses the flow of energy or matter along the trophic links. In the mass-balance master formulation, the size of inputs and initial stocks determine the overall constraint on the range of model behaviour. The inputs required to construct an ECOPATH network include biomass and production, diet composition, annual catch, ecotrophic efficiency, primary production, detritus biomass and food consumption per unit biomass (Pauly et al. 1993).

The master equation for each functional group (*i*) is:

$$B_{(i)}(P/B)_i EE_{(i)} - \sum_{\text{predators j}} B_{(j)}(Q/B)_j DC_{(j,i)} - EX_{(i)} = 0 \tag{1}$$

where $B_{(i)}$ is the total biomass for compartment *i*, $(P/B)_i$ is the production/ biomass ratio, $(Q/B)_j$ the consumption/ biomass ratio and $DC_{(i,j)}$ the fraction of compartment *i* in the average diet of consumer *j* (Christensen & Walters 2004). $EE_{(i)}$ is the ecotrophic efficiency, $P_{(i)}$ the total production rate, $Q_{(j)}$ the total consumption rate for consumer *j*, $EX_{(i)}$ the total export of compartment *i* out of the ecosystem. This system of linear equations can be solved, using standard matrix algebra, and provided that $DC_{(i,j)}$ and $EX_{(i)}$ are known or specified, entry is optional for any one of the other four main parameters ($B_{(i)}$, $(P/B)_i$, $(Q/B)_j$, $EE_{(i)}$) (Christensen & Walters 2004, Pinnegar et al. 2004).

The main limitation of ECOPATH models is subsequently their main assumption, that the ecosystem network is adequately represented by a set of simultaneous linear equations that is solved for a steady state at the compartment and system level, therefore a mass balanced model is a static description of the system. Thus multiple ECOPATH networks must be constructed and compared to investigate different management scenarios. However, static ECOPATH networks serve as a good starting point for building dynamic simulation models (Christensen & Pauly 1993). ECOSIM, a primarily biomass-based model, allows simulation of system dynamics, mainly under different regimes of exploitation starting from a static ECOPATH network. A specific goal of ECOSIM models is to simulate how a change in one or more compartments might affect the ecosystem over time (Trites et al. 1999).

Mass balance represents one way to integrate diverse information that is significant for management decisions pertaining to disturbance of ecosystems, for example, inputs of pollutants, climate change and exploitation. Mass balanced networks can be compared over different spatial and temporal scales. Comparisons of different network configurations are made by comparing goal functions, these include quantitative trophic structure, cycling index, number and quantitative importance of simple cycles, simple and cyclic path lengths and Ulanowicz' ascendancy, which measures the average mutual information in a system and is scaled by throughput (Christensen and Pauly 1992). The difference between total system capacity and ascendancy is a measure of system overhead. Overhead sets the limit on how much the ascendancy can increase and is a reflection of the system's strength in reserve from which it can draw to meet unexpected perturbations (Ulanowicz 1986; Ulanowicz & Puccia 1990; Ulanowicz & Kay 1991; Christensen & Pauly 1992).

Schalk et al. (1993) and Jarre-Teichmann et al. (1997) combined available data from the eastern Weddell Sea (Voß 1988; Priddle et al. 1992; Arntz et al. 1997; Brey & Gerdes 1997) to construct a conceptual model of the biomasses at and energy flows through the various trophic levels and compartments in the Weddell Sea ecosystem.

2.5 Stability Properties and Response to Ecosystem Disturbance

Understanding the structure and dynamics of ecological networks is critical for understanding the persistence and stability of ecosystems (Dunne et al. 2005). Food webs have played a major role in exploring the relationship between complexity and stability in natural communities (MacArthur 1955; Elton 1958, Gardner & Ashby 1970; May 1972; May 1973; Pimm 1984). Habitat fragmentation, degradation, and loss pose the most significant threats to the structure and persistence of populations and communities (Wilcox & Murphy 1985; Saunders et al. 1991; Debinski & Holt 2000; Fahrig 2003). Stability of ecosystems has received much attention in the literature (MacArthur 1955; Paine 1969; Paine 1992; Brose et al. 2003; Dambacher et al. 2003). Investigating the effect of biodiversity on the stability of ecological communities is complicated by the numerous ways in which models of community interactions can be formulated. Assuming the ecosystem was at an equilibrium state, does an ecosystems return to its original state or does it shift to a new state after a perturbation? Resilience is a measure of ecosystem stability which determines how rapidly an ecosystem returns to its original state after a perturbation (Neubert & Caswell 1997). This has led to differences in conclusions and interpretations of how the number of species in a community affects its stability (Ives & Hughes 2002). May's work inspired researchers to examine real world data (Pimm 1980) and one of the most important observations to emerge from all this activity was the "hyperbolic connectance law". This "law" states that there is a " hyperbolic" relationship between the number of species in a community and the proportion of possible links that are realised. Whether higher connectance does indeed coincide with decrease in overall stability (Haydon 1994, de Ruiter et al. 1995), or whether weak links aid or inhibit system stability (McCann et al. 1998, Neutel et al. 2002) remains to be seen (Pinnegar et al. 2004).

Trophic structure and strength of trophic linkages within the functional groups determine the communities' response to and ability to recover from perturbations (Christianou 2003). A shift in synchronicity between trophic levels, caused if compartments respond differently to perturbations (Stenseth & Mysterud 2002) in has been reported for terrestrial ecosystems. Records on studies for trophic decoupling (mismatch in food supply) in marine ecosystems are rare (Cushing 1975; Winder & Schindler 2004). However, trophic decoupling will have critical consequences in Antarctic marine systems, especially if keystone compartments (functional groups or species) are affected.

2.6 Thesis Outline

This thesis focuses on the trophic dynamics of Antarctic shelf ecosystems. Assuming that the emergent behaviour of an ecosystem is, at least partly, dependent on the properties and behaviour of the entities it is composed of (Christianou 2003), we looked into different entities of the ecosystem structure. My thesis consists of six core publications. For validation of trophic interactions we used a standardized method of determining stable isotope signatures (Jacob et al. 2005 PUBLICATION I) to determine the trophic position of Antarctic invertebrates and vertebrates (Jacob et al. 2005 PUBLICATION II; MINTENBECK et al. 2005 PUBLICATION VIII). We link food web theory (Brose et al. 2005 PUBLICATION III; Jacob et al. 2005 PUBLICATION V) to common patterns in energy flow (Jacob et al. 2005 PUBLICATION VI) and species characteristics, through investigating patterns in the trophic interactions of species (Brose et al. 2005 PUBLICATION III, Jacob et al. 2005 PUBLICATION IV). Feeding links for the food web models were obtained by synthesizing available information on 488 Antarctic invertebrates and vertebrates (see Appendix); distributions; diets; trophic links & levels and other parameters extracted from more than 500 publications that I standardized and made available for a large-scale database (Brose et al. 2005 PUBLICATION III).

Finally, I discuss whether the combination of food web theory with stable isotope signatures (Post 2002a) and balanced energy flow analyses (Raffaelli & Hall 1996; Ulanowicz 1996) provides a feasible set of tools which enables us to demonstrate how in Antarctic marine food webs, with many closely connected species, community organisation and species trophic characteristics affect overall system properties.

3 PUBLICATIONS

Below, the publications that constitute this thesis are listed and my share thereof is explained.

The core publications of the thesis:

PUBLICATION I.

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

The initial idea originates from myself and the third author. I developed the conceptual approach. Practical work was performed by myself and the second author. I wrote the manuscript together with the third author.

PUBLICATION II.

Jacob, U., Brey, T., Fetzer, I., Kaehler, S., Mintenbeck, K., Dunton, K., Struck, U., Beyer, K., Pakhomov, E.A., Arntz, W.E., (2005) Towards the Trophic Structure of the Bouvet Island Marine Ecosystem, *Polar Biology* (in press)

Sampling and laboratory work was conducted by myself, the fourth, the seventh, and the eighth author. I wrote the initial draft manuscript and all further versions, which resulted from discussion with the second author and later with all co-authors.

PUBLICATION III.

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., Francois Edwards, F., Harper-Smith, S., **Jacob, U**., Knapp, R.A., Mark E. Ledger, M.E., Memmott, J., Mintenbeck, K., Pinnegar, J.K., B.C. Rall, B.C., Rayner, T., Ruess, L., Ulrich, W., Warren, P., Williams, R.J., Woodward, G., Yodzis, P., Martinez, N.D., (2005) Body sizes of consumers and their resources. *Ecology* 86: 2545

The first author developed the conceptual frame, outline and design of the large scala database. He wrote the manuscript and it was discussed and improved by all the co-authors. I contributed feeding links for the food web model of the eastern Weddell Sea shelf which were obtained by synthesizing available information on Antarctic invertebrates and vertebrates; distributions; diets; body sizes; and other parameters extracted from more than 500 publications that I standardized and compiled for this database.

PUBLICATION IV.

Jacob, U., Brose, U., Mintenbeck, K., Morissette, L., Brey, T. (2005) A three-dimensional approach to consumer trophic niche width based on prey size, prey trophic position and prey mobility. (Manuscript)

I developed the idea for the use of trophic standard parameters to determine trophic niche width within a multidimensional space. The data analysis procedure was developed in close cooperation with the second and the fifth author. The manuscript was discussed and improved by all the co-authors.

PUBLICATION V.

Jacob, U., Brose, U., Rall, B.C., Brey, T., (2005) Food Web Complexity: What can we learn from an Antarctic marine system? (Manuscript Draft)

I conducted the data collection feasible for food web analysis. The data analysis procedure was developed in close cooperation with the second and the fourth author. I wrote the initial draft manuscript and all further versions, which resulted from discussion with all co-authors.

PUBLICATION VI.

Jacob, U., Morissette, L., Mintenbeck, K., Gutt, J., Gerdes, D., Arntz, W.E., Brey, T., (2005) A trophic flow model of the high Antarctic Weddell Sea shelf. (Manuscript Draft)

Data collection was performed by the seventh author and myself. The data analysis procedure was developed in close cooperation with the second and the seventh author. I wrote the initial draft manuscript and all further versions, which resulted from discussion with all co-authors.

Further publications related to my thesis:

PUBLICATION VII.

Brose, U., Jonsson, T., Berlow, E.L., 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., Cushing, L., Edwards, F., Harper-Smith, S., **Jacob, U**., Knapp, R.A., Ledger, M.E., Memmott, J., Mintenbeck, K., Pinnegar, J.K., Rayner, T., Ruess, L., Ulrich, W., Warren, P., Williams, R.J., Woodward, G., Martinez, N.D., (2005) Consumer resource boody size relationships. *Ecology* (submitted)

PUBLICATION VIII.

Gerdes, D., Brey, T., Mühlenhart-Siegel, U., **Jacob, U.**, (2005) Large scale patterns in Antarctic biomass and production (Manuscript)

PUBLICATION IX.

Mintenbeck, K., **Jacob, U.,** Brey, T., Knust, R., Arntz, W.E., (2005) Depth–dependent variability in $\delta^{15}N$ of marine POM consumers: the role of particle dynamics and organism trophic guild. *Marine Ecology Progress Series* (submitted)

PUBLICATION X.

Brodte, E., Graeve, M., **Jacob, U**., Knust, R., Pörtner, H.O., (2005) Adaptation to temperature or metabolism? - Lipid classes and fatty acid compositions of polar and temperate eelpouts (Manuscript)

PUBLICATION XI.

Heilmayer, O., Honnen, C., **Jacob, U**., Chiantore, C., Cattaneo-Vietti, R., Brey, T. (2005), Temperature effects on summer growth rates in the Antarctic scallop, *Adamussium colbecki*, *Polar Biology* 28: 523-527

PUBLICATION XII.

Jacob U., Terpstra S., Brey T., (2002), The role of depth and feeding in regular sea urchins niche separation – an example from the high Antarctic Weddell Sea. *Polar Biology* 26: 99-104

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

STABLE ISOTOPE FOOD WEB STUDIES- A CASE FOR STANDARDIZED SAMPLE TREATMENT

Ute Jacob, Katja Mintenbeck, Thomas Brey, Rainer Knust, Kerstin Beyer

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NOTE

Stable isotope food web studies: a case for standardized sample treatment

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ABSTRACT: Enrichment of the stable isotopes ^{13}C and ^{15}N across trophic levels is a commonly used tool in studies on organic matter flow and food webs. However, there is still no accepted standard for pre-analysis sample preparation. Thus, potential methodological bias in single studies may hamper comparability and scalability of data from different sources. Sample $CaCO_3$ content introduces a positive bias in $\delta^{13}C$ measurements and a negative bias in $\delta^{15}N$ measurements. The acidification of samples to remove inorganic carbonate significantly reduces both $\delta^{13}C$ and $\delta^{15}N$. As a standard procedure we recommend (1) acidifying samples with as little hydrochloric acid (HCl) as possible using the drop-by-drop technique, and (2) restraining from rinsing after HCl application.

KEY WORDS: Isotope signatures · Carbonates · Sample acidification

INTRODUCTION

Metabolic processing of ingested organic matter causes isotopic fractionation of ^{13}C:^{12}C and ^{15}N:^{14}N stable isotope pairs. Therefore, the stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ are proxies of the trophic distance of an organism from the origin of the corresponding food chain. Although the underlying physiological, biochemical and biophysical processes are not yet fully understood (Ponsard & Averbuch 1999), enrichment of the stable isotopes ^{13}C and ^{15}N across trophic levels is a commonly used tool in studies on organic matter flow and food webs in aquatic and terrestrial ecosystems. On average, $\delta^{13}C$ and $\delta^{15}N$ increase by 0.5 to 1 and 2.8 to 3.4‰, respectively, from one trophic level to the next (e.g. Minagawa & Wada 1984, Peterson & Fry 1987, Michener & Schell 1994). Early trophic stable isotope studies relied on $\delta^{13}C$ only (Fry 1984, Fry & Sherr 1984). The finding that $\delta^{13}C$ correlates with tissue fat content, whereas $\delta^{15}N$ does not, led to the parallel application of both isotope ratios in more recent studies (e.g. Fry 1988, Rau et al. 1991, 1992). Although the magnitude of variation in $\delta^{13}C$ fractionation is the major source of error in quantitative stable isotope models (Vander Zanden & Rasmussen 2001), $\delta^{13}C$ is still used as it serves as a valuable carbon source tracer (e.g. Lesage et al. 2001). The major methodological question regarding the simultaneous measurement of $\delta^{13}C$ and $\delta^{15}N$ is whether the removal of inorganic carbonate ($CaCO_3$, for instance in red algae, cnidarians, bryozoans, mollusks, echinoderms) from the sample will bias tissue stable isotope ratios (Fry 1988, Cloern et al. 2002). Carbon incorporated in tissue and in carbonate are of different origin and hence differ in $\delta^{13}C$; therefore, carbonate must be removed by acidification prior to mass spectrometry (Fry 1988, Rau et al. 1991, Cloern et al. 2002). It remains unclear, however, whether tissue isotopic ratios are affected by acidification or not; there is contradictory evidence regarding $\delta^{15}N$, whereas no significant impact on $\delta^{13}C$ has been reported (Bunn et al. 1995, Bosley & Wainright 1999, Pinnegar & Polunin 1999). Our study, based on 193 samples from 29 species (11 major taxa), analyzes (1) how sample $CaCO_3$ content affects stable isotope ratios, and (2) whether $\delta^{13}C$ and $\delta^{15}N$ are affected by sample acidification.

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MATERIALS AND METHODS

A total of 92 invertebrate samples (18 species among crustaceans, bryozoans, brachiopods, cephalopods, sponges, cnidarians, echiurids, polychetes, pantopods and echinoderms) and 101 fish samples (11 species) were collected for stable isotope analysis from fauna sampled along the Scotia Arc and the Antarctic Peninsula. Small organisms were analyzed whole, whereas in macro- and megafaunal specimens only body wall pieces or muscle tissue samples were used. All samples were kept frozen at –30°C until further analysis. Samples were lyophilisated for 24 h in a Finn-Aqua Lyovac GT2E and then ground to a fine powder. Each sample was split in half: one part was acidified to remove $CaCO_3$ in accordance with Fry (1988) and Cloern et al. (2002) by adding 1 mol l^{-1} hydrochloric acid (HCl) drop-by-drop until no more CO_2 was released, re-dried at 60°C without rinsing to minimize loss of DOM (dissolved organic matter) and ground again; the other half did not receive any further treatment. Stable isotope analysis was conducted with an isotope-ratio mass spectrometer (Thermo/Finnigan Delta plus, GeoBioCenter). Experimental precision (based on standard deviation of replicates of a peptone standard) was ≤0.15‰ for carbon and nitrogen.

A paired Student's *t*-test was used to evaluate whether stable isotope ratios differed between 'crude' and acidified samples. Sample $CaCO_3$ content had not been determined; hence, we used a $CaCO_3$ proxy to analyze the effect of $CaCO_3$ on stable isotope ratios:

$$\text{carbonate proxy} = \frac{[\text{C:N}]_{\text{crude}}}{[\text{C:N}]_{\text{acid}}} - 1 \qquad (1)$$

where $[\text{C:N}]_{\text{crude}}$ is the C:N ratio of a non-acidified sample and $[\text{C:N}]_{\text{acid}}$ is the C:N ratio of an acidified sample. This proxy should be linearly related to sample $CaCO_3$ content, provided that tissue C:N is independent of sample $CaCO_3$.

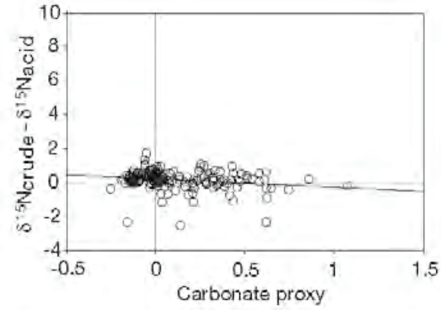

Fig. 1. Effect of sample $CaCO_3$ content on the difference in $\delta^{15}N$ between acidified and non-acidified samples. Sample $CaCO_3$ is approximated by the carbonate proxy $[\text{C:N}]_{\text{crude}}/[\text{C:N}]_{\text{acid}}$. Significant linear relation: $y = 0.248 - 0.486 \times x$, $r^2 = 0.047$, $p = 0.0033$, $N = 193$

RESULTS AND DISCUSSION

Surprisingly, a number of samples showed negative carbonate proxy values (Figs. 1 & 2). Analysis of presumably $CaCO_3$ free samples (fish and polychaete tissue) showed that, on average, acidification decreased tissue N content ($N_{acid} = -0.15N_{crude}$) proportionally more than tissue C content ($C_{acid} = -0.11C_{crude}$), thus causing higher C/N ratios in acidified samples. There is no need to correct the carbonate proxy value for this effect, as we assume it to be independent of sample $CaCO_3$ content.

$\delta^{15}N_{crude} - \delta^{15}N_{acid}$ was negatively related to sample $CaCO_3$ content (linear regression: df = 192, p = 0.0033, Fig. 1), whereas tissue $\delta^{13}C_{crude} - \delta^{13}C_{acid}$ was positively related to sample $CaCO_3$ content (linear regression: df = 192, $p < 0.0001$, Fig. 2). In samples containing no $CaCO_3$ (defined by carbonate proxy ≤ 0.03), acid treatment showed a significant negative effect on both $\delta^{15}N$ (paired *t*-test: mean difference = 0.320‰, SE = 0.037, df = 115, p = 0.0001) and $\delta^{13}C$ (paired *t*-test: mean difference = 0.117‰, SE = 0.044, df = 115, p = 0.0081).

The ongoing discussion of whether samples should be treated with HCl, how this treatment should be carried out, and what effect the treatment may have on isotope ratios as well as the contradictory findings (Bunn et al. 1995, Bosley & Wainright 1999, Pinnegar & Polunin 1999, McCutchan et al. 2003) shows that there is an urgent need for sample treatment standardization.

Regarding $\delta^{13}C$, our results indicate the expected positive relation between the acidification effect on $\delta^{13}C$ and sample $CaCO_3$ content (Fig. 2). The bias caused by $CaCO_3$ was in the range of the distance between subsequent trophic levels (0.5 to 1.0‰) at carbonate proxy values as low as 0.08 (Fig. 2). Regarding $\delta^{15}N$, this is the first study that demonstrates a significant negative, albeit weak, effect of sample $CaCO_3$ on tissue $\delta^{15}N$ (Fig. 1), the mechanism of which, however, remains unclear.

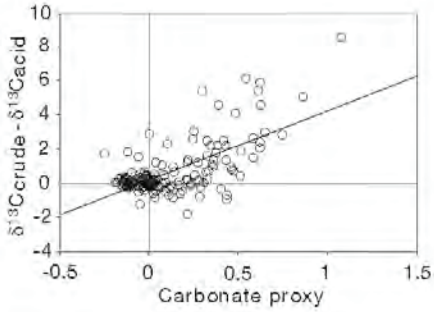

Fig. 2. Effect of sample $CaCO_3$ content on the difference in $\delta^{13}C$ between acidified and non-acidified samples. Sample $CaCO_3$ is approximated by the carbonate proxy $[\text{C:N}]_{\text{crude}}/[\text{C:N}]_{\text{acid}}$. Significant linear relation: $y = 0.181 + 4.08 \times x$, $r^2 = 0.449$, $p = 0.0001$, $N = 193$

The analysis of samples containing no $CaCO_3$ showed that acidification caused a significant (average = 0.117‰) decrease in $\delta^{13}C$. This deviation is (1) about 16% of the average shift of 0.5 to 1‰ from one trophic level to the next, (2) within the $\delta^{13}C$ variability observed in one trophic compartment (e.g. Rau et al. 1991, Vander Zanden & Rasmussen 2001, Cloern et al. 2002), and (3) in the range of measurement precision (≤0.15‰). $\delta^{15}N$ was also negatively affected (average = 0.320‰), but to a much lesser extent regarding the average shift of 2.8 to 3.4‰ from one trophic level to the next as well as $\delta^{15}N$ variability within one trophic compartment (e.g. Adams & Sterner 2000, Dunton 2001, Iken et al. 2001, Nyssen et al. 2002). The shift was, however, distinctly above measurement precision (≤0.15‰). Our findings support Bosley & Wainright's (1999) view that the way and extent to which $\delta^{15}N$ is affected by acidification depends on the methods applied, mainly on the rinsing of the acidified sample with distilled water. Our drop-by-drop acidification technique without subsequent rinsing appeared to produce, on average, little bias in $\delta^{15}N$ and low inter-sample variability in bias (Figs. 1 & 2). The 3 outliers in Fig. 1 were most likely to be caused by mistakes during sample processing.

CONCLUSION

Tissue samples must be acidified in order to make stable isotope data comparable across taxa with varying $CaCO_3$ content. Data from non-acidified but carbonate-free samples can be made comparable to data from acidified samples by the corresponding correction factors for $\delta^{13}C$ (–0.117‰) and $\delta^{15}N$ (–0.320‰). It remains to be seen, however, whether the factors found here are also valid for non-Antarctic ecosystems.

For future food web studies using $\delta^{13}C$ and $\delta^{15}N$ simultaneously, we recommend the following procedure to standardize sample treatment: (1) Acidify samples prior to stable isotope analysis by careful application of as little HCl as possible. Apply 1 mol l^{-1} HCl drop-by-drop until no further CO_2 development is visible.

(2) Dry acidified samples directly, do not rinse with water after acidification.

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TOWARDS THE TROPHIC STRUCTURE OF THE BOUVET ISLAND MARINE ECOSYSTEM

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Towards the trophic structure of the Bouvet Island marine ecosystem

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Abstract Although Bouvet Island is of considerable importance for Southern Ocean species conservation, information on the marine community species inventory and trophic functioning is scarce. Our combined study of stable isotopes and feeding relationships shows that (1) the marine system conforms to the trophic pattern described for other Antarctic systems within the Antarctic circumpolar current (ACC); (2) both the benthic and the pelagic subsystem are almost exclusively linked via suspended particulate organic matter (SPOM); and (3) there is no evidence of a subsystem driven by macroalgae. Bouvet Island can therefore be characterized as a benthic "oasis" within a self-sustaining open ocean pelagic system.

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Introduction

Bouvet Island (Bouvetøya, 54°72′60S, 3°24′E) is located just south of the Antarctic Polar Front (APF) and within the Antarctic circumpolar current (ACC, Fig. 1, Foldvik et al. 1981; Perissinotto et al. 1992). Owing to its geographical isolation (i.e. 2,590 km downstream of the South Sandwich Islands, 2,570 km upstream of the Prince Edward Islands and 1,600 km north of Queen Maud Land, Antarctica) the island represents a pristine environment and has been identified as an important case study for the conservation of intact ecosystems (Chown and Gaston 2002). Nevertheless, marked climate change and subsequent invasion of hitherto alien species have already affected other remote systems of the Southern Ocean (e.g. South Georgia; Bergstrom and Chown 1999; Chown and Gaston 2002; Gaston et al. 2003; Frenot et al. 2005) and may thus endanger the ecology of Bouvet Island, too. Unfortunately, to date, next to nothing is known about the Bouvet Island marine community species inventory and the trophic functioning of the system. From existing oceanographic, biogeographic and ecological data we can infer that (1) the pelagic compartment of the Bouvet ecosystem is part of the Antarctic surface water ecosystem (ASW; Perissinotto et al. 1992), i.e. we expect ASW species inventory and trophic structure; (2) the Bouvet inventory of top predatory birds and mammals, albeit enormous in numbers and biomass (Cooper et al. 1984; Croxall 1984; Haftorn 1986; Isaksen et al. 2000; Kirkman et al. 2001; Keith et al. 2002) resembles that of other Sub-Antarctic islands such as the Prince Edward Islands (Perissinotto et al. 1990; Perissinotto and McQuaid 1992; Pakhomov and Froneman 1999); and (3) the benthic compartment of the Bouvet ecosystem should be structured accordingly, with a typical macroalgal depth zonation and a fauna characteristic for systems shaped by strong currents, though species composition may differ from comparable sites such as the South Sandwich Islands (LAMPOS; Jacob et al.

2003; Arntz and Brey 2003) or the Prince Edwards Islands (Kaehler et al. 2000).

Here we present the first attempt towards a better understanding of the Bouvet Island food web based on stable isotope signatures of nitrogen and carbon and information on the diet of the most significant species.

Material and methods

Sampling of marine flora and fauna was conducted near Bouvet Island during RV "Polarstern" cruise ANT XXI/2 in 2003/2004 (Fig. 1, Arntz and Brey 2005). Four Agassiz trawl samples (mouth opening 3 m×1 m, 10 mm×10 mm cod end mesh size, 20 min trawl time) were taken between 100 and 550 m water depth. Abundant taxa were identified to species level whenever possible, and sampled for stable isotope analysis. Small organisms were sampled whole, whereas pieces of body wall or muscle tissue were sampled from macro and megafaunal specimens. A total of four macroalgal samples (Rhodophyta spp.), 96 invertebrate samples of benthic and hyperbenthic invertebrates referring to 15 different taxa (among them decapods, amphipods, bryozoans, crinoids, holothurians, nemerteans, cnidarians, polychaetes, pycnogonids and asteroids) and ten samples of the nototheniod fish *Lepidonotothen larseni* were collected (Table 1). All samples were kept frozen at −30°C until further analysis.

Stable isotope signatures

δ^{13}C and δ^{15}N signatures serve as proxies of the trophic distance of an organism from the primary food source of the corresponding food chain. δ^{13}C signatures are commonly used as valuable carbon source tracers (e.g. Lesage et al. 2001), whereas δ^{15}N values are a useful tool for detecting the trophic position and therefore the trophic hierarchy of the system. Samples were lyophilisated for 24 h in a Finn-Aqua Lyovac GT2E and then ground to a fine powder. Each sample was acidified to remove $CaCO_3$ in accordance with Fry (1988), Cloern et al. (2002) and Jacob et al. (2005) by adding 1 mol l^{-1} hydrochloric acid (HCl) drop-by-drop until CO_2 release stopped, re-dried at 60°C without rinsing to minimize loss of dissolved organic matter and ground again. Stable isotope analysis and concentration measurements of nitrogen and carbon were performed simultaneously with a THERMO/Finnigan MAT Delta plus isotope ratio mass spectrometer, coupled to a THERMO NA 2500 elemental analyzer via a THERMO/Finnigan Conflo II- interface. Stable isotope ratios are given in the conventional delta notation (δ^{13}C; δ^{15}N) relative to atmospheric nitrogen (Mariotti et al. 1984) and PDB (PeeDee Belemnite standard). Standard deviation for repeated measurements of lab standard material (peptone) proved to be better than 0.15‰ for nitrogen and carbon. Standard deviations of concentration measurements of replicates of our lab standard are $<3\%$ of the concentration analyzed.

In order to fill gaps in invertebrate and macroalgae species coverage, we added some stable isotope data referring to other sub-Antarctic localities, i.e. Prince Edward Island (Kaehler et al. 2000, 2005) and Anvers Island (Dunton 2001) (Fig. 1). Isotope signatures of Antarctic seabirds, mammals and particulate organic matter (POM) were taken from Rau et al. (1991, 1992), E.A. Pakhomov (unpublished data) and K. Mintenbeck (unpublished data). Data for the pelagic predatory squid *Kondakovia longimana* were taken from Wada et al. (1987).

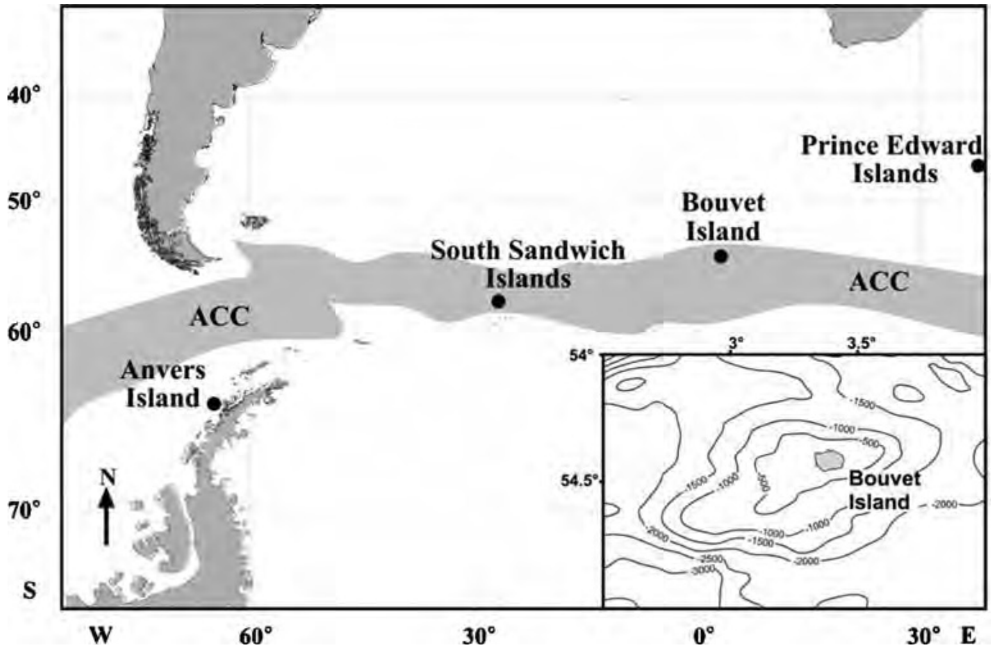


Fig. 1 Map showing Anvers Island, South Sandwich Islands, Bouvet Island and the Prince Edward Islands. *Grey band* indicates region of the Antarctic circumpolar current (ACC)

Table 1 Summary of taxa sampled, isotope signatures and the source of the data used to compile the trophic structure of the marine ecosystem of Bouvet Island

Taxa	Species	δ^{15}N range (‰)	δ^{13}C range (‰)	Reference
"POM"		−2.83 to 4.40	−30.23 to −21.17	Rau et al. (1991)
"POM"		0.92	−28.83	E.A. Pakhomov (unpublished data)
"POM"		2.10	−30.79	E.A. Pakhomov (unpublished data)
Phytodetritus		3.44	−19.15	Kaehler et al. (2000)
Chlorophyceae		5.86	−11.46	Dunton (2001)
Phaeophyceae		0.57 to 13.79	−35.31 to −13.22	Dunton (2001)
Rhodophyceae		1.02 to 9.36	−35.21 to −17.64	Dunton (2001)
Porifera		1.24 to 2.77	−22.06 to −21.79	Kaehler et al. (2000)
Hydroidea		2.55	−22.34	Kaehler et al. (2000)
Gorgonaria	*Primnoisis* sp.	4.60 to 7.77	−24.80 to −19.70	This study
Pennatularia		8.16	−25.71	This study
Nemertini	*Parborlasia corrugatus*	8.62 to 11.99	−26.96 to −23.19	This study
Bivalvia		3.81	−19.29 to −16.27	Kaehler et al. (2000)
Gastropoda		6.53	−26.54 to −12.79	This study
Cephalopoda		8.37	−19.12	Kaehler et al. (2000)
Squid	*Kondakovia longimana*		−25.37	Wada et al. (1987)
Polychaeta	*Polynoidae*	4.14 to 12.42	−25.10 to −17.43	This study
	Harmothoe spinosa	9.70	−23.33	This study
	Laetmonice producta	7.34 to 8.11	−25.30 to −23.46	This study
Copepoda		−1.59 to −1.06	−27.00 to −24.87	Kaehler et al. (2000)
Amphipoda		0.69 to 9.53	−25.03 to −18.06	This study
Isopoda		0.95 to 6.73	−25.89 to −15.32	Kaehler et al. (2000)
Decapoda		5.16 to 7.38	−24.18 to −17.01	This study
Chaetognatha		3.03	−23.39	Kaehler et al. (2000)
Pantopoda		6.20 to 10.55	−26.03 to −24.55	This study
Bryozoa		5.01 to 6.34	−24.73 to −24.63	This study
	Austroflustra spp.	5.38 to 5.95	−26.34 to −25.91	This study
Brachiopoda		3.81	−18.41	Kaehler et al. (2000)
Ophiuroidea	*Ophiurolepis* spp.	6.30 to 8.22	−18.87 to −16.37	Kaehler et al. (2000)
Asteroidea		6.07 to 10.70	−21.99 to −15.52	This study
	Porania antarctica glabra	10.23 to 11.39	−21.85 to −15.86	This study
Crinoidea	*Promachocrinus kerguelensis*	5.96 to 6.70	−21.45 to −19.10	This study
	Anthometra adriani	7.59 to 8.12	−21.12 to −12.40	This study
Holothuroid ea		5.70 to 7.39	−26.88 to −18.86	This study
	Echinopsolus acanthocola	6.10	−27.62	This study
	Bathyplotes bongraini	7.38	−23.25	This study
	Psolus antarcticus	4.93 to 9.22	−24.47 to −17.01	This study
	Taeniogyrus contortus	4.82 to 6.54	−27.29 to −24.33	This study
Ascidiacea		4.79 to 8.50	−26.00 to −24.37	This study
Pisces	*Lepidonotothen larseni*	8.00 to 9.93	−26.19 to −21.03	This study
Aves	*Pygoscelis adeliae*	5.34 to 12.39	−26.84 to −22.78	Dunton (2001)
	P. antarctica	6.91	−27.04	Dunton (2001)
	Daption capense	5.61 to 7.37	−28.45 to −26.14	Rau et al. (1992)
	Fulmares glacialoides	5.41 to 7.70	−28.71 to −25.97	Rau et al. (1992)
	Macronectes giganteus	8.71	−24.38	Mintenbeck (unpublished data)
	Pagodroma nivea	5.99 to 8.70	−28.48 to −25.95	Rau et al. (1992)
	Thalassoica antarctica	4.99 to 6.31	−29.07 to −27.08	Rau et al. (1992)
Mammalia	*Arctocephalus gazella*	7.13 to 8.75	−25.65 to −24.47	This study

Feeding relationships

Information on feeding links between species occurring in the Bouvet Island ecosystem was collected by a thorough literature search. Following the approach of Martinez (1991), a directional feeding link was assigned to any pair of species A and B whenever an investigator reports or assumes that A consumes B. Suspended particulate organic matter (SPOM) is considered as a non-predatory taxon as it includes significant resources (dead organic matter, nano- and micro-plankton) for many benthic invertebrates and is therefore itself a highly interacting system (Warren 1989; Walker 1985; Hall and Raffaelli 1991).

Results

Judging from the trawl sample debris, the seafloor around Bouvet Island was covered by coarse sands, stones and gravel (see also Arntz and Thatje 2005). Accordingly, the benthic system was dominated by typical hard bottom life forms. Crinoids (e.g. *Anthometra adriani*), holothurians (e.g. *Taeniogyrus contortus*) and asteroids (e.g. *Porania antarctica glabra*) were dominant in the Agassiz trawl samples. Red macroalgae and hydroids were also common, as well as bryozoans (mainly *Austroflustra* spp.) and some large sponges and gorgonians (mainly *Primnoisis* sp.). Other dominant

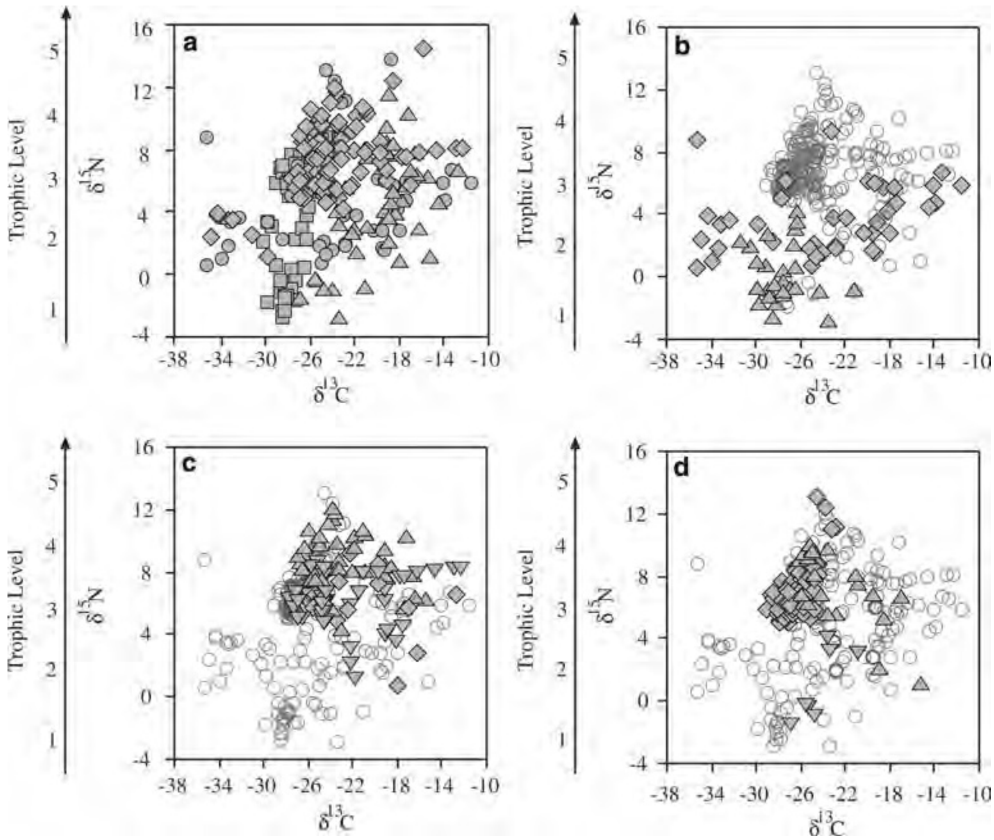


Fig. 2 $\delta^{15}N$ and $\delta^{13}C$ signatures of the marine flora and fauna of Bouvet Island. Signatures for missing compartments (e.g. zooplankton, and land-based predators) are added from other localities as described in the text, **a** (*filled circle*) Anvers Island, (*filled diamond*) Bouvet Island, (*filled triangle*) Prince Edward Islands, (*filled square*) Weddell Sea **b** (*filled diamond*) benthic primary producers, (*filled triangle*) pelagic primary producers; **c** (*filled triangle*) benthic predators, (*inverted triangle*) benthic suspension feeders, (*filled diamond*) benthic deposit feeders; **d** (*filled diamond*) land-based (*filled triangle*) predators, pelagic predators, (*inverted triangle*) zooplankton; (*open circle*) all signatures used in the study (Table 1)

elements were serpulid polychaetes, small amphipods (Caprellidae and Lyssianassidae), small pycnogonids and the nototheniid fish species *L. larseni* and *L. kempi*. Typical infaunal or epifaunal deposit feeders like echinoids, sipunculids and echiurids were absent (Arntz and Thatje 2005).

Stable isotope signatures

Among the food sources of the marine ecosystem of Bouvet Island, POM signatures ranged from −28.83 to −30.79 in $\delta^{13}C$ and from −0.92 to 2.10 for $\delta^{15}N$ (E.A. Pakhomov, unpublished data). Isotopic composition of macroalgae ranged from −11.5 to less than −35‰ in $\delta^{13}C$ and from 0.6 to 9.4‰ in $\delta^{15}N$ (Fig. 2b; Table 1).

With regard to $\delta^{15}N$ of the fauna, copepods had the lowest values. $\delta^{15}N$ values ranged between −1.06 and −1.59, $\delta^{13}C$ values between −24.87 and −27.0 (Table 1). The Adelie penguin (*Pygoscelis adeliae*) and benthic predators like the nemerteans had the highest values (Table 1).

Feeding relationships

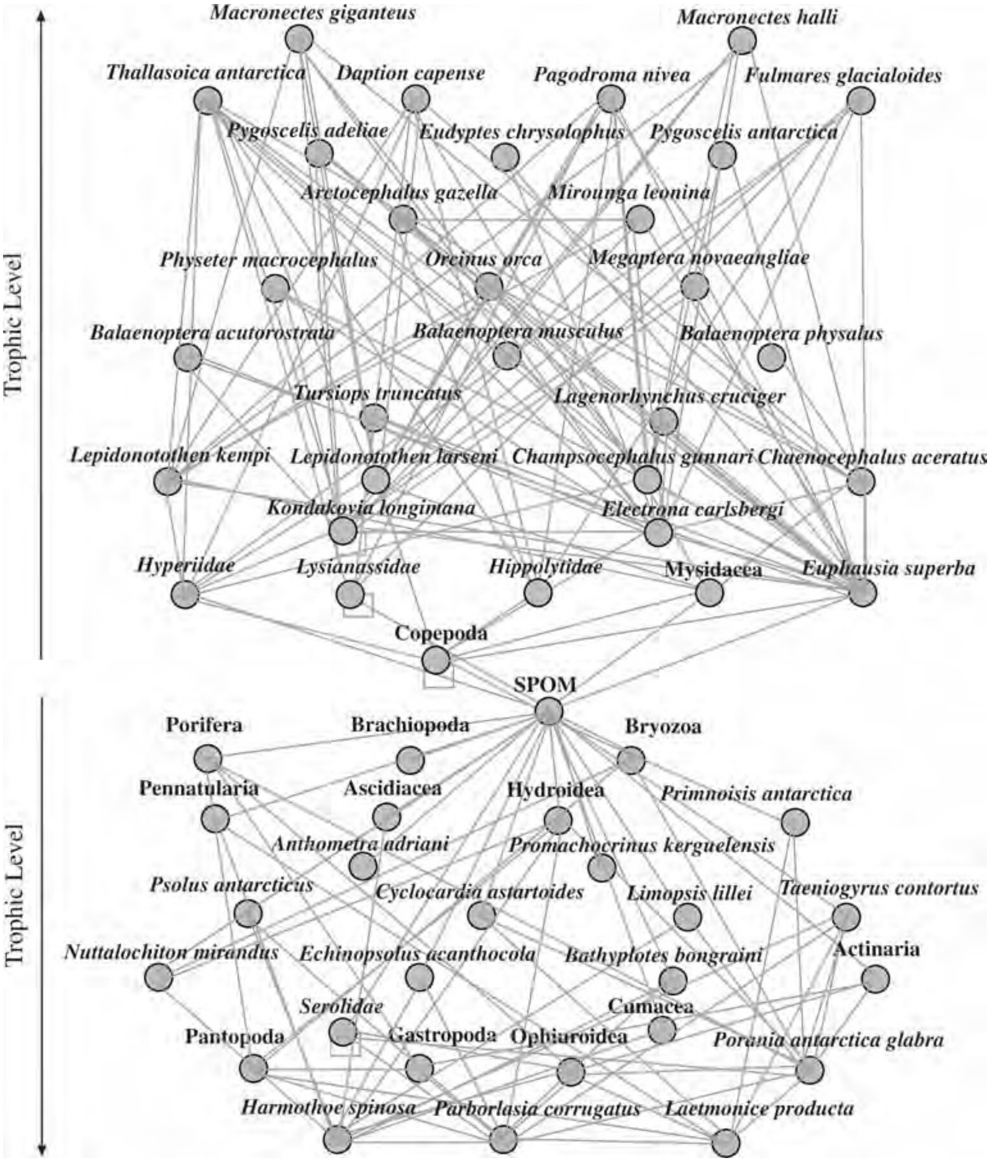
Two hundred and eighty-two feeding links connecting 58 different taxa were inferred from the literature. The preliminary food web shown in Fig. 3 indicates a distinct separation between (1) a bentho-demersal compartment highly entangled within itself and coupled to the SPOM box and (2) a pelagic compartment, coupled to the SPOM box and zooplankton.

Discussion

Scattered and missing data are one of the primary concerns when analyzing structural properties such as food webs of remote and poorly investigated systems (Connor and Simberloff 1978; Gaston 1996). On the other hand, stable isotope signatures are vulnerable to misinterpretation owing to their relative ease of use and assumed simplicity in interpretation (Gannes et al 1997; Schmidt et al. 2003). In order to compensate for these shortcomings we (1) combined information on general trophic hierarchy (stable isotope signatures $\delta^{13}C$ and $\delta^{15}N$) with information on trophic links (diet composition) as recommended by Vander Zanden et al. (2000) and (2) added data from other, ecologically comparable Sub-Antarctic locations.

Regarding the pelagic community as well as long ranging top predators (seabirds, mammals, pelagic cephalopods), there is no evidence that trophic position derived from stable isotope signatures or feeding relations differ distinctly between sites within the ACC (Fig. 1), as is to be expected in a uniform circum-Antarctic ACC pelagic system (Rau et al. 1991, 1992). This may be different in carbon isotope signatures of benthic macroalgae (Fischer and Wiencke 1992), which may be

Fig. 3 Conceptual model of the SPOM driven part of the Bouvet Island food web (macroalgae and grazers are not shown) based on all information available from Bouvet Island and comparable sites within the ACC. The SPOM box includes all living nano- and micro-plankton as well as dead organic matter. *Arrows* leading back to the group/species itself represent cannibalism



affected by local conditions such as light regime. Nevertheless, there is some evidence that such site-specific differences are smaller than the general differences between microalgae and macroalgae (Kaehler et al. 2000, 2005). With respect to substrate and hydrographic regime, the shallow water benthic environment (above 100 m) is likely to be quite similar around Bouvet Island, Anvers Island, South Sandwich Islands or the Prince Edward Islands (see e.g. Perissinotto et al. 1992). Therefore, we expect similar communities, mainly composed of macroalgae and their grazers (see e.g. Dunton 2001; Iken et al. 1997; Kaehler et al. 2000; Corbisier et al. 2004), and a suspension feeder-predator assemblage as encountered below 100 m. We know neither the extent nor the exact taxonomic composition of this macroalgae—grazer subsystem at Bouvet Island, albeit there is some anecdotal evidence of its existence: rocky surfaces in the swell zone appeared to be colonized by algae, and algal debris appeared to be present on some pebble beaches, as indicated by visual inspection from ship and helicopter.

Owing to the structural similarity of the system to other Sub-Antarctic and Antarctic open ocean systems (e.g. Hopkins 1993) and the conservative feeding behaviour of species, we assume the proposed food web to be representative for Bouvet Island. Given that both the isotope data and the feeding link data cover the major trophic groups from the pelagic and the benthic compartment, we are confident that our first attempt at the trophic structure of Bouvet Island is founded on a sound base.

Primary food sources

Unlike the shelf ice limited high Antarctic seas, which rely on pelagic primary production and ice algae production (Rau et al. 1991, 1992), many near shore Sub-

Antarctic ecosystems are heavily subsidized by carbon from benthic primary producers, i.e. microalgae and particularly macroalgae (Attwood et al. 1991; Fischer and Wiencke 1992; Dunton 2001; Kaehler et al. 2005).

Shallow-water primary producers are consumed by a variety of species covering a wide trophic range from exclusive herbivores, e.g. the gastropod *Laevilittorina antarctica*, to high level omnivores such as the fish species *Notothenia coriiceps/neglecta* (Barrera-Oro and Casaux 1990; Iken et al. 1997; Kaehler et al. 2000, 2005; Dunton 2001).

None of these known macroalgal consumers were found in our samples, indicating that they are restricted to the depth zone of macroalgal presence. Compared to SPOM as well as to potential consumer species, macroalgal isotopic signatures are particularly high in δ^{15}N (0.6–9.4‰) and stretch across an extremely wide range in δ^{13}C (< -35 to -11.5, Fig. 2b). Hence stable isotopes can provide no evidence that macroalgal matter enters the deeper part of the benthic food web analysed here in significant proportions, either directly or via the SPOM pool. However, it remains to be seen whether future sampling will indicate a relative importance of macroalgae or an absence of macroalgal consumers at Bouvet, if macroalgae are scarce. We do not have enough information on macroalgal abundance and distribution to exclude the possibility that some of the primary producers might be important, even though this seems unlikely at present.

Degradation and assimilation of macroalgal matter through detrital food webs is a common feature in many nearshore systems of temperate (Adin and Riera 2003) as well as Antarctic regions (Dunton and Schell 1987; Iken et al. 1997; Corbisier et al. 2004; Kaehler et al. 2005). Precondition for this pathway, however, are comparatively calm hydrographic conditions, which allow sedimentation of SPOM, formation of soft bottoms and development of the corresponding deposit feeding community. Such conditions exist in well-protected bays and coves such as Admiralty Bay and Potter Cove at King George Island or Palmer Station Bay at Anvers Island (Iken et al. 1997; Dunton 2001; Corbisier 2004), but not at Bouvet Island (e.g. average current speed > 30 cm/s, Hofmann 1985) and similarly exposed shores. Here, macroalgal production that is not consumed directly by herbivores is likely to be exported eastwards to the open ocean by the ACC. Therefore we assume pelagic primary production to be the principal food source of the Bouvet marine ecosystem. The ACC is a highly productive frontal area by itself, but Perissinotto et al. (1992) showed that over the Bouvet Island shelf plankton standing stock and production are even higher, most likely owing to the island mass effect which causes local upwelling (IME, Doty and Oguri 1956; Heywood et al. 1990).

Trophic structure

When macroalgae and grazers are excluded and all living nano- and micro-plankton as well as dead organic matter are summarized into one SPOM box, then this SPOM fuelled marine food web is clearly separated in a pelagic and a benthic part (Fig. 3). The benthic system is dominated by (1) a variety of suspension feeders which are all linked directly to SPOM and (2) mobile benthic predators. Competition between many suspension-feeding taxa may be reduced significantly by consumption of different size fractions and/or types of SPOM (Orejas et al. 2001). Among the predators, nemerteans, asteroids and polychaetes are quite flexible in their alimentation, as indicated by their wide range in stable isotope signatures (Fig. 2c) as well as by the many documented feeding links. This has also been observed on the eastern Weddell Sea shelf where most of the structuring compartments were regarded as omnivores (Jarre-Teichmann et al. 1997). Apparently, there exist only a few direct links between pelagic animals and benthic predators. Our data include the ophiuroid *Ophiurolepis* spp. (feeding on euphausiids, Dahm 1996). Other Antarctic benthic predators of pelagic animals not found here but known to be present in the ACC region are for example the hydrozoan *Tubularia ralphii* (copepods, Orejas et al. 2001) and the anthozoan *Anthomastus bathyproctus* (salps, Orejas et al. 2001).

The alimentation of the pelagic top predators (pelagic fish, squid, whales and land-based predators) appears to be much less variable than the one of the benthic predators. Pelagic predator isotope variability is lower (Fig. 2d) with diets consisting mainly of krill, hyperiid amphipods, mysids and decapods (Fig. 3; Dewitt et al. 1990; Mc Kenna 1991; Bushula et al. 2005).

Conclusions

At present, our Bouvet trophic model shows some obvious gaps, mainly with respect to the macroalgae-grazer complex as well as regarding the role of demersal fish species, which were absent in our samples but apparently play an important role in Antarctic shelf areas (Barrera-Oro and Casaux 1990; Gröhsler 1994; Brenner et al. 2001; Mintenbeck 2001).

Nevertheless, a rather clear picture emerges that shows Bouvet Island as a benthic "oasis" within a self-sustaining open ocean pelagic system. Except for the hitherto unknown macroalgae-grazer complex, the whole benthic food web is coupled directly to SPOM, and the detritus food web, which is typical for most benthic systems (Jarre-Teichmann et al. 1997), is missing completely.

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PUBLICATION III

BODY SIZES OF CONSUMERS AND THEIR RESOURCES

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BODY SIZES OF CONSUMERS AND THEIR RESOURCES

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Abstract. Trophic information—who eats whom—and species' body sizes are two of the most basic descriptions necessary to understand community structure as well as ecological and evolutionary dynamics. Consumer–resource body size ratios between predators and their prey, and parasitoids and their hosts, have recently gained increasing attention due to their important implications for species' interaction strengths and dynamical population stability. This data set documents body sizes of consumers and their resources. We gathered body size data for the food webs of Skipwith Pond, a parasitoid community of grass-feeding chalcid wasps in British grasslands; the pelagic community of the Benguela system, a source web based on broom in the United Kingdom; Broadstone Stream, UK; the Grand Cariçaie marsh at Lake Neuchâtel, Switzerland; Tuesday Lake, USA; alpine lakes in the Sierra Nevada of California; Mill Stream, UK; and the eastern Weddell Sea Shelf, Antarctica. Further consumer–resource body size data are included for planktonic predators, predatory nematodes, parasitoids, marine fish predators, freshwater invertebrates, Australian terrestrial consumers, and aphid parasitoids. Containing 16 807 records, this is the largest data set ever compiled for body sizes of consumers and their resources. In addition to body sizes, the data set includes information on consumer and resource taxonomy, the geographic location of the study, the habitat studied, the type of the feeding interaction (e.g., predacious, parasitic) and the metabolic categories of the species (e.g., invertebrate, ectotherm vertebrate). The present data set was gathered with the intent to stimulate research on effects of consumer–resource body size patterns on food-web structure, interaction-strength distributions, population dynamics, and community stability. The use of a common data set may facilitate cross-study comparisons and understanding of the relationships between different scientific approaches and models.

Key words: allometry; body length; body mass; body size ratio; food webs; parasitoid–host; predation; predator–prey.

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PUBLICATION IV

A THREE-DIMENSIONAL APPROACH TO CONSUMER TROPHIC NICHE WIDTH BASED ON PREY SIZE, PREY TROPHIC POSITION AND PREY MOBILITY

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MANUSCRIPT

A three-dimensional approach to consumer trophic niche width based on prey size, prey trophic position and prey mobility

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Abstract

The trophic niche is defined by just that subset of boundary conditions which refers to the species' diet. Trophic niche and trophic niche width are conceptually robust but difficult to quantify ecological parameters. We present 3-dimensional measure of trophic niche width, which is based on prey size, prey trophic position, and prey mobility. The suitability of this proxy is exemplified with the high Antarctic Weddell Sea ecosystem, where high trophic generality and vertical niche expansion in many species appears to be responsible for the observed overall high trophic complexity.

Introduction

The ecological niche of a species is defined as the n-dimensional hypervolume bounded by sets of conditions that are compatible with its persistence and success (Hutchinson 1957, Pilou 1972). The trophic niche is defined by just that subset of boundary conditions which refers to the species' diet. Although conceptually robust, it has proven difficult to find practical measures of trophic niche and trophic niche width that are simple to obtain, yet provide an adequate descriptor of the ecological position of the population examined (Ebenman and Nilsson 1982; Bolnick et al. 2002; Bearhop et al. 2004; Matthews and Mazumder 2004).

Initiated by Roughgarden (1972; 1974) numerous studies used continuous parameter such as food item diversity (Bolnick et al. 2003); item size range (Bolnick et al. 2003); item partitioning (Barnes and De Grave 2000) or consumer foraging behavior (Ebenman and Nilsson 1982) to determine a population's trophic niche width. Bearhop et al. (2004) proposed the variance in consumer stable isotope ratio as an easy to apply and robust measure of population trophic niche width. The shortcomings and potential pitfalls of this particular approach are discussed below. Many authors suggested that consistent niche width measures should be composed from multiple variables (Genner et al. 1999; Bolnick et al. 2002; Svanbäck and Persson 2004; Matthews and Mazumder 2004).

Here we introduce a 3-dimensional measure of trophic niche width, which is based on prey size, prey trophic position, and prey mobility, and demonstrate its suitability for comparisons of trophic niche width between populations of dominantly omnivorous consumer species of the high Antarctic Weddell Sea shelf.

Material & Methods

Trophic niche width dimensions and parameters

Our measure of trophic niche width combines the three dimensions (i) prey size, (ii) prey trophic position and (iii) prey mobility.

Prey size (P1) and prey trophic position (P2) reflect the consumer's handling capacity for resource species of different body sizes and trophic levels, respectively (Cohen & Newman 1985; Woodward & Hildrew 2002, Cohen 1978; Warren 1996; Williams and Martinez 2000). Prey trophic position indicates the significance of a consumer with respect to the vertical extension of the food web, i.e. the number of trophic levels. The more levels are accessed by a single consumer, the more trophic flexibility is obtained by this consumer, and the higher is its potential impact on the food web structure. Prey mobility (P3) is a qualitative measure of the consumer's capability of handling prey of different agility.

Body size determinations are standardized by the following procedure: average body length is converted into body mass M by

$$M \text{ (g wet mass)} = \pi/6 * \text{size}^3 \text{ (cm)}$$

following Cohen et al. (1993) and Brose et al. (2005). In order to obtain an even distribution within the interval [0, 1], a sigmoid transfer function is applied to the ln (M) data

$$x = (1 + e^{-\ln (M)*\text{Gain}})^{-1}$$

where the optimum value of "Gain" is found by iterative minimisation of variance among frequencies classes of the distribution.

Trophic position is determined by stable nitrogen isotope signatures ($\delta^{15}N$), as the stable isotope pair ^{15}N:^{14}N serves as a proxy of the trophic distance of a consumer from the origin of the corresponding food chain (Post 2002, Matthews & Mazumder 2004).

To achieve an even distribution of data within the interval [0, 1], stable isotope values are first normalized and subsequently converted by a sigmoid transfer function

$$y = (1 + e^{-\delta 15N *\text{Gain}})^{-1}$$

Mobility is categorized according to a 4-level scale: $z = 0$ for sessile or passively floating species, $z = 0.25$ for crawlers, $z = 0,5$ for facultative swimmers, and $z = 1.0$ for obligate swimmers.

Trophic Niche Position

The position of a consumer's trophic niche in the 3-dimensional space circumscribed by prey size x, prey trophic position y and prey mobility z is defined by the coodinates referring to then mean values of x,y, and z across all prey items.

Trophic Niche Width

We combine the ranges of the three parameters prey size x, prey trophic position y and prey mobility z into the composite index of population trophic niche width TNW3.

This index is defined by the maximum Euclidean distance (ED) between all prey items of a consumer. For two prey items (*P;Q*) in a three dimensional space *ED* is computed by:

$$\mathrm{ED}_{P,Q} = \sqrt{(p_x - q_x)^2 + (p_y - q_y)^2 + (p_z - q_z)^2} \quad (1)$$

where *x* is the prey size, *y* is prey trophic position and *z* prey mobility.

Real world example data

Suitability of our trophic niche width approach is tested with a food web data set from the high Antarctic Weddell Sea shelf ecosystem (Arntz & Brey 2001, Brose et al. 2005, Jacob et al. (unpublished)). 489 species, most of which are benthic invertebrates and fish species, where treated as consumer populations. Diet composition of each species was inferred from field observations, stomach content-, stable isotope- and predation analyses. 16200 feeding links have been documented. Average body size of resource species populations was taken from published accounts (Brose et al. 2005). Trophic position of resource species populations was determined by stable nitrogen isotope ratios (Rau et al. 1991, 1992, Jacob et al., unpublished data).

Results

Trophic niche width dimensions and parameters

The average resource body size ranged from 0.00021 to 856.61 cm across all prey populations of the Weddell Sea shelf ecosystem. Prey trophic position varied distinctly between prey species, $\delta^{15}N$ isotopic signatures of the resource populations ranged from –0.23 ‰ for diatoms like *Thalassiosira antarctica* to 14.78 ‰ for the asteroid *Cycethra verrucosa mawsoni*. If we assume a trophic enrichment of 3.4 ‰ per trophic level (Cabana & Rasmussen 1994; Post 2002), the resource populations cover about 4.4 trophic levels.

All mobility levels are well presented; sessile or floating items like porifera, bryozoans, detritus and diatoms, crawlers like asteroids, echinoids and holothurians, facultative swimmers like some amphipods, crinoids and octopods, and obligate swimmers like copepods, euphausiids, squid and fish.

The combination of the three parameters clearly distinguishes groups of consumer populations that share a high amount of similar prey items (Fig.1).

The composite index TNW3 ranges from 0.0000047 in heterotrophic dinoflagellates to 1.37 in the omnivorous ophiuroid *Ophiosparte gigas*. Trophic niche width appears to be independent of size and of trophic position (Fig.2b, c, d). It is, however, closely coupled to generality, i.e. definition (Fig. 2a).

The distribution of niche width values reflects that the marine Antarctic contains both, populations with large and with small trophic niches (Fig. 3).

Discussion

It appears intuitively obvious that trophic position and trophic niche width of a species/population is not a one-dimensional measure but is constrained by the species' capacity regarding numerous different ecological dimensions (Hutchinson 1957, Ebenman & Nilsson 1982, Chase & Leibold 2003, Bolnick et al. 2003; Matthews & Mazumder 2004). To identify and measure the full set of parameters that define trophic niche width (e.g. nutritional quality of prey species; prey preference) is most likely beyond the capacity of any scientific endeavour. Therefore we look for a subset of parameters, which provides a sufficient and reliable estimate of trophic niche width, but yet can be obtained with justifiable effort even in an open marine system.

We assume that the measure of trophic niche width introduced here can serve this purpose, as its parameters prey size, prey trophic position, and prey mobility (i) refer to distinctly different as well as trophically significant ecological properties and (ii) represent a reasonable trade off between information obtained and measurement effort.

The measure of the prey size reflects the resource size range a consumer can handle. Usually ratios of consumer body size to resource body size are computed in order to make comparisons across a large size range reasonable (Cohen et al. 1993, Memmott et al. 2000, Brose et al. 2005). Such ratios were found to be correlated to interaction strength patterns in real ecosystems, which in turn determine food web stability (Emmerson & Raffaelli 2004). The most accurate way of determining body size would be to measure the actual size of all items consumed for each consumer individual and each resource species. This is not manageable in a system with more than a very few species. In order to allow rapid determination of body size by a standardized procedure we chose a simplified approach, obviously at the expense of accuracy. Firstly, we take average body size of resource species populations from published accounts (Brose et al. 2005). The latter does not necessarily resemble average size of consumed items of this resource, e.g., the consumer may be restricted to a certain part of the whole size range. Secondly, we derivate body mass from body length, which is much easier and faster to determine, by a standard formula that assumes a spherical body shape (Cohen et al. 1993). This indirect estimate introduces a body shape related bias. The body size concept becomes problematic, too, when dealing with detritus, which may consist of unconsolidated mixed matter to a large extent.

There are two options for the determination of the trophic position of a resource species, (i) food web models based on stomach content analysis and (ii) stable isotope ratios, which lead to almost identical results (Kline & Pauly 1998, Williams & Martinez 2004, Pauly & Watson 2005). Regarding trophic relationships, $\delta^{15}N$ signatures proved to be more reliable than $\delta^{13}C$ (e.g. Fry 1988, Rau et al. 1991, 1992), as the magnitude of variation in $\delta^{13}C$ fractionation is the major source of error in quantitative stable isotope models (Vander Zanden & Rasmussen 2001) due to correlation with tissue fat content and a small trophic step-size. It appears obvious that a consumer gains the more trophic flexibility and impact on food web structure the more trophic levels it can access. Hence omnivory appears to be a significant indicator of trophic niche width. Williams & Martinez (2004) measured omnivory by the standard deviation of the trophic levels of the consumed resource items, i.e. their measure is weighted by diet composition. Our index of trophic prey position, in contrast, is a straightforward measure of maximum trophic range.

The measure of the prey mobility reflects the consumer's capability of handling prey of different agility. All qualitative levels of mobility are well-presented, sessile or floating items, crawlers, facultative swimmers and obligate swimmers. Although categories chosen, might appear extremely simplified they reflect the generalist behaviour of most consumer populations. They are able to capture prey species along the mobility dimension, irrespective of their own mobility. For example, the anemone *Isotealia antarctica* (mobility:) is able to devour the medusa *Periphylla periphylla*. Mobile prey species such as large medusae or fish, which get close enough to the bottom in shallow-water are likely to be captured by the anemone's tentacles.

Shortcuts to measure trophic niche width via the variability of $\delta^{15}N$ in the consumer population as proposed by Bearhop et al. (2004), appear to be questionable. Consider a consumer population with feed on a wide trophic range from primary producers to carnivores. If each consumer individual has exactly the same diet composition, than each individual will have the same $\delta^{15}N$ and variability between individuals will be zero. Furthermore, the stable isotope approach is hindered by the absence of a testable model for trophic step enrichment (Ponsard & Averbuch 1999; Adams & Sterner 2000), the magnitude of the $\delta^{15}N$ variation is sensitive to the feeding rate, excretion rate, the degree of isotopic discrimination during food absorption (Ponsard & Averbuch 1999; Vanderklift & Ponsard 2003; Olive et al. 2003), the type of tissue used (Schmidt et al. 2004) and sample treatment (Jacob et al. 2005). Therefore, stable isotope analysis appears at its most powerful when combined with conventional approaches (Vander Zanden et al. 2000; Post 2003; Matthews & Mazumder 2004, Bearhop et al. 2004).

To define a population's trophic niche width, we established a proxy based on prey size, prey trophic position, and prey mobility the range of prey sizes. To relay on any of these axes alone, would lead to biased information, (i) isotope signatures can be biased by analytical assumptions, (ii) diet compositions are confounded by variation in assimilation efficiencies among diet items (Williams & Martinez 2004) or taxonomic resolution, and (iii) body size ratios are affected by resolution (Brose et al. 2005). But the combination of these three dimensions leads to a reliable estimate of a population's niche width as separation in a multidimensional niche space allows coexistence as high overlap along one niche dimension typically is accompanied by separation on another dimension (MacArthur & Pianka 1966; MacArthur & Levins 1967; Krebs et al. 1974; Kie & Bowyer 1999; Stewart et al. 2003).

In order to make comparisons among and in-between food webs a standardized approach to methodology, taxonomic resolution and effort is needed (Thompson & Townsend 2000). We used the population level to provide a sufficient and reliable estimate of trophic niche width, because it can be obtained with justifiable effort even in large open systems. We are aware that individual specialization can comprise a major part of the population's niche width, as it facilitates frequency dependent interactions that can affect the population's stability, the amount of intra-specific competition, fitness-function shapes, and the populations' capacity to diversify and to specialize rapidly (Bolnick et al. 2003). To apply our niche width approach to individual variation, the influence of ecological sex dimorphisms (Shine 1991), ontogenetic diet changes (Post 2003), and resource polymorphisms (Skulason &

Smith 1995) on the individual's trophic niche have to be considered (Bolnick et al. 2003) and respective dimensions have to be added.

In our example system of the Antarctic Weddell Sea, the composite index of population trophic niche width TNW3 ranges from 0.0000047 in heterotrophic dinoflagellates to 1.37 in the omnivorous ophiuroid *Ophiosparte gigas*. TNW3 tends to be highest in benthic predators and scavengers and shows no obvious correlations to consumer size, trophic level or mobility (Fig. 2). This reflects common trophic traits within the marine Antarctic marine (i) scavenging species, small in size, (e.g. amphipods, nemertines and gastropods) feed up and down the food chain irrespective of their size, (ii) large benthic suspension feeders feed on very small suspended particulate organic matter, phytoplankton or phytodetritus (Orejas et al. 2003; Brose et al. 2005), and (iii) the very largest animals like seals and whales feed on very small prey down the food chain. The pattern observed reflects that the high trophic complexity of the Weddell Sea shelf ecosystem results from the high trophic generality of most of the populations as well as their ability for vertical niche expansion

Conclusions

Our study indicates that the three parameters prey size, prey trophic position and prey mobility may be sufficient to construct a meaningful index of trophic niche width.

It remains to be seen whether this approach is feasible for all types of ecosystems, and whether it can be used to address further questions regarding (i) species distribution along environmental gradients, (ii) similarity of coexisting species, (iii) the role of species in community succession and assembly, and (iv) patterns of biodiversity.

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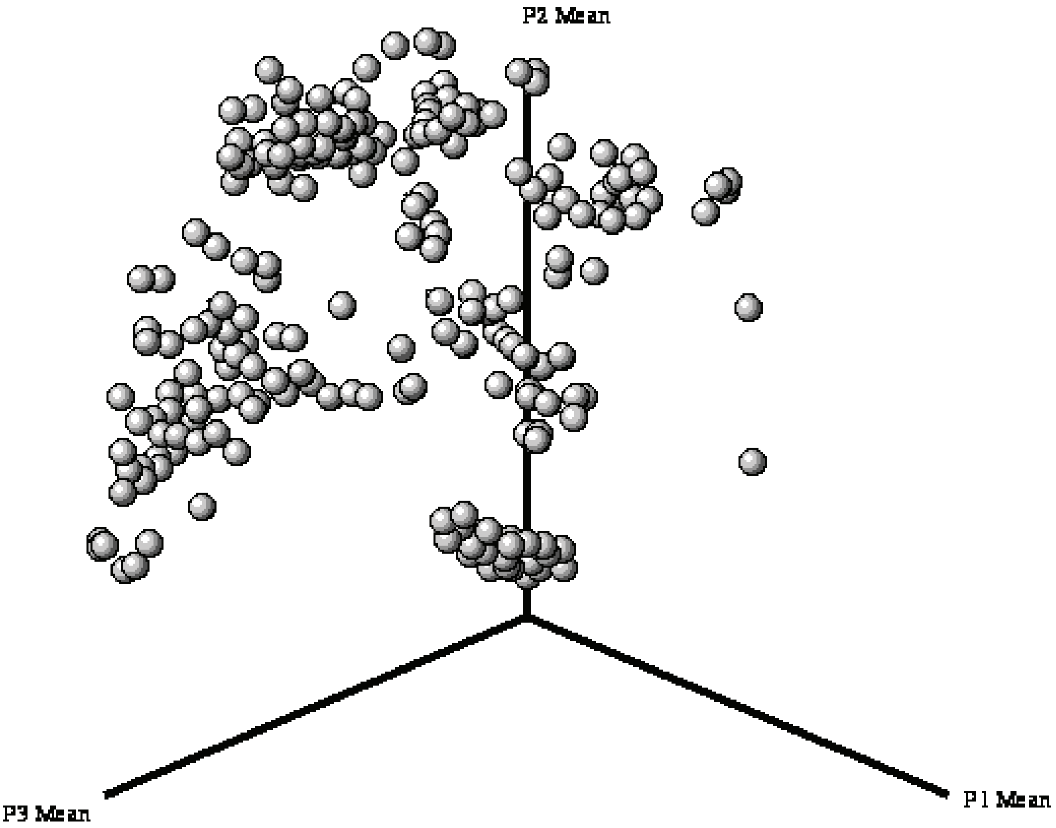

Figure 1: Mean trophic niche width of the consumer populations along the three dimensions (P1 prey size; P2 prey trophic position; P3 prey mobility)

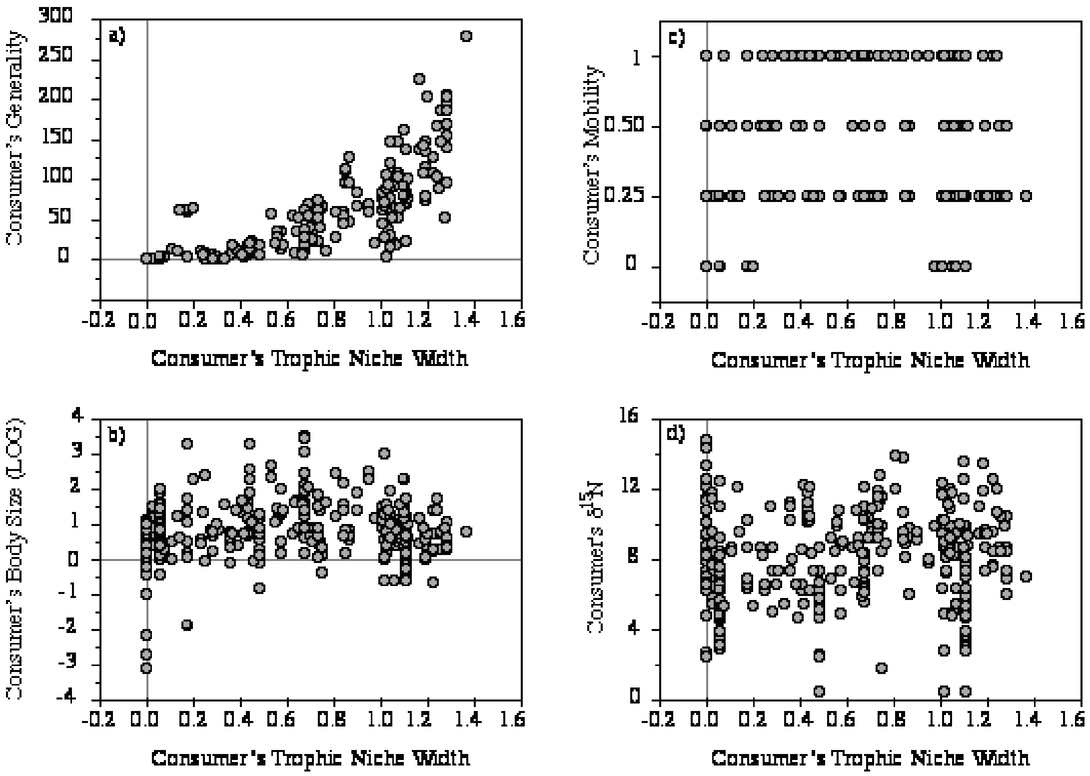

Figure 2: Mean trophic niche width of the consumer populations in relation to consumer properties (a) generality; b) body size; c) mobility; d) trophic poition)

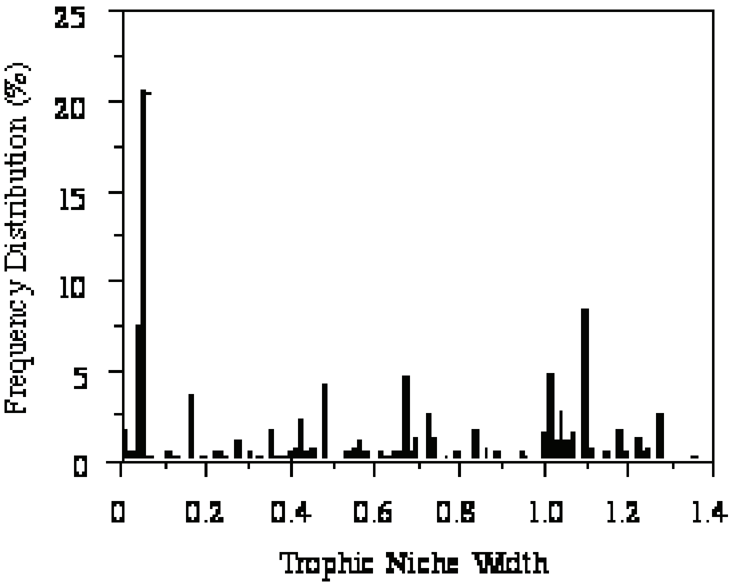

Figure 3: Distribution of population niche width values of the high Antarctic Weddell Sea

PUBLICATION V

FOOD WEB COMPLEXITY:
WHAT CAN WE LEARN FROM AN ANTARCTIC MARINE SYSTEM?

Ute Jacob, Ulrich Brose, Björn C. Rall, Thomas Brey

MANUSCRIPT

Food Web Complexity:

What can we learn from an Antarctic Marine System?

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Abstract

Assessing the trophic structure of food webs and the functional role of the entities it is composed of is essential for the evaluation of direct or indirect impacts of environmental change on marine communities. The Southern Ocean food web has often been described as simple in comparison with other marine systems, partly due to the numerical importance of Antarctic krill and the proposed major path of energy transfer leading from primary producers to krill and to krill consumers. The use of topological food web descriptors demonstrates the high complexity of high-Antarctic Weddell Sea food web.

Introduction

Ecosystem-level studies that consider trophic relationships are typically posited upon system-specific knowledge of feeding relationships (Martinez 1991). Such feeding relationships combined to whole system food webs are useful tools for merging ecological subdisciplines as well as linking species to ecosystems. As food webs are complex objects, many summarizing system descriptors have been proposed to enable ecologically meaningful comparisons between different webs (e.g. Cohen 1977; Cohen 1989; Pimm 1982; Briand & Cohen 1984; Lawton 1989; Sugihara et al. 1989; Pimm et al. 1991; Havens 1992; Jonsson et al. 2005). It seems to be likely that marine ecosystems differ inherently from terrestrial or freshwater counterparts due to (i) their openness, (ii) the orders of magnitude in size across the species, and (iii) their unique relationship between the number of species and connectivity (Steele 1985; Cohen 1994; Link 2002; Link et al. 2005).

The Southern Ocean ecosystem exhibits a number of unique features, e.g. a ±25 million years long history of biogeographic isolation (Clarke 1985; Hempel 1985; Clarke et al. 2005; Barnes 2005; Thatje et al. 2005), and, in form of the annual formation and retreat of sea ice, the geographically most extensive seasonal oscillation pattern of the world. Consequently, there are a number of quite obvious unique ecological features such as a high degree of endemism (Arntz et al. 1994; Arntz et al. 1997) or the occupation of the “pelagic swarm fish niche” by euphausiid crustaceans (Ichii 1990; Bergstrom et al. 1990; Daly & Macaulay 1991; Sprong & Schalk 1992; Ritz 1994; Verity & Smetacek 1996; Ritz 2002).

Pioneering trophic studies of the Southern Ocean ecosystem focused on a seemingly simple pelagic food chain consisting of about three trophic levels (primary production - krill - krill predators, Tranter 1982), whereas little attention was paid to the “microbial loop” or to organisms below the size of large diatoms and to the benthic food web (Knox 1970; Clarke 1985). The Antarctic continental Sea shelf exhibits a complex three-dimensional community with large biomass, intermediate to high diversity, and patchy distribution of organisms (Dayton 1990; Arntz et al. 1994; Gutt & Starmans 1998, Teixidó et al. 2002, Gerdes et al. 2003). In large areas the benthic fauna is dominated by epibenthic suspension feeders, which can cover the sediment completely (Dayton et al. 1974; Voss 1988; Teixidó et al. 2002).

It is well known that the "trophic" approach towards ecosystem can be limited in its capacity for reconstructing feeding relationships for entire food webs, as the amount of dietary data required for such studies can be prohibitive, as it increases exponentially with system complexity (Vander Zanden & Rassmussen 2002; Pinnegar et al. 2004). Our example ecosystem, the high-Antarctic eastern Weddell Sea shelf and slope region, is known to be rich in species (Gutt et al. 2001; Clarke & Johnston 2003) and trophically complex and highly interconnected (Jacob et al. 2005), i.e. we are still far from knowing the entire food web. Nevertheless, we attempt to apply food web theory tools to the limited information available in order to evaluate whether we can achieve meaningful insights and, if so, how compares this high-Antarctic system to terrestric and aquatic ecosystems analyzed in a similar way.

Material & Methods

Food Web Properties

Information on species inventory of the eastern Weddell Sea and on feeding links between these species was collected by a thorough literature search. Data from more than 500 publications were standardized and compiled for a large-scale database (Brose et al. 2005a). Following the approach of Martinez (1991), a directional feeding link was assigned to any pair of species A and B whenever an investigator reports or assumes that A consumes B. Species were not divided further into functional different trophic species such as larvae, juveniles, adults, but treated as "adults".

Top species have prey but no predators while basal species have predators but no prey, whereas intermediate species have both prey and predators (Briand & Cohen 1984). The sum of top and intermediate species divided by the sum of intermediate and basal species is the predator-to-prey ratio. As food webs are complex objects, many summarizing system descriptors have been proposed to allow comparisons between different webs (e.g. Cohen 1977; Cohen 1989; Pimm 1982; Briand & Cohen 1984; Lawton 1989; Sugihara et al. 1989; Pimm et al. 1991; Havens 1992; Jonsson et al. 2005). Basic metrics calculated for the unlumped food web are the number of species S and the number of links L between them (Hall & Raffaelli 1993)

Summary ecosystem descriptors are Linkage Density DL, i.e. the number of links per species

$DL = L/S$;

Connectance C, i.e. the proportion of realised links within a web (Hall & Raffaelli 1993; Warren 1994)

$C = 2 \times L/(S^2-S)$;

Linkage Complexity CL; i.e. explanation (Briand 1985)

$CL = S \times C$;

and Predator/Prey ratio PP, i.e. explanation (Cohen 1977)

PP = .

Species Trophic Vulnerability V and species Trophic Generality G, i.e. the number of predators and the number of prey items of one species (Schoener 1989), are the basis of the ecosystem descriptors Mean Trophic Vulnerability V_M and Mean Trophic Generality G_M

$V_M = V/S$ and $G_M = G/S$

Results

Based on the data base and the definitions and procedures described above we obtained an unlumped food web consisting of 491 species, most of which are benthic invertebrates and fish species. Particulate organic matter (POM), sediment (SED) and phytodetritus (DET) are considered as non-predatory species as they serve as important resources for most benthic invertebrates and are themselves highly interacting systems (Warren 1989, Walker 1985, Hall & Raffaelli 1991).

In some species the very poor taxonomic resolution of prey items would have biased estimates. Here we used information about these species' size, behaviour, and stable isotope signatures (Brose et al. 2005a; Jacob et al. 2005; Jacob et al., unpublished data) to deduce their feeding habits and the corresponding most likely feeding links.

In total, 16200 feeding links were identified between the 491 species. Linkage density DL amounts to 33.20, Connectance C to 0.135, and Linkage Complexity CL to 33.19. Mean Trophic Vulnerability V_M was 32.46, whereas Trophic Vulnerability V ranged from 0 in 32 top species to 96 in the copepod *Calanus propinquus* there are, however, 225 links to phytodetritus. Mean Trophic Generality G_M was 33.35 whereas Trophic

Generality G ranged from 0 for basal species to 278 for the omnivorous ophiuroid *Ophiosparte gigas* (Tab.1).

Discussion

Despite of being far from complete, our Weddell Sea data set differs from other well-known food webs in general in three of its properties: (i) there are a lot more feeding links detected; (ii) the value of mean linkage density is higher than usually reported; and (iii) phytodetritus is one of the most important resources. The value for the mean number of interactions per species confirms that this is a highly connected food web, although estimated values for connectance are not out of the range of reported values for other food webs (Tab.1) as one could have expected. The whole concept of connectance is based on identifiable discrete food items, i.e. single-celled or multi-celled individuals. This approach becomes problematic when dealing with detritus as a food source, counted as one link but consisting of unconsolidated mixed matter to a large extent. With respect to the number of links from phytodetritus to its consumers, we followed a conservative approach here as we introduced a single virtual "phytodetritus species". As there are 59 phytoplankton species in our system, one could argue that there exist 59 feeding links from phytoplankton to each consumer of phytodetritus. This would change all parameters significantly and make the Weddell Sea system even more unique in terms of connectivity and complexity.

Given that our data do not cover the size range and trophic levels across the life history of these consumers, it is feasible that including egg, larval and juvenile interactions would increase the linkage density and connectance even more.

Common features of the Weddell Sea system are the differences in foraging behaviour and the extreme high degree of omnivory of marine consumers explain the high linkage density observed. Most fish species and invertebrates are opportunistic generalists with a high trophic generality (Dahm 1996; Brenner et al. 2002; Mintenbeck 2001; Jacob et al. 2003; Jacob et al. 2005a+b) they are quite flexible in their alimentation, as indicated by the high number of documented feeding links.

"If food webs have a structure, then so what? Why is network anatomy so important to characterize?" Strogatz asks. "Because structure always affects function," he answers (Pimm 1982; Strogatz 2001; Pimm 2002). Connectance, linkage density, etc., these are all indicators for how communities change and respond to perturbations

(Christianou 2003; Pimm 2002; Dunne et al. 2005). Only a few marine systems have been analyzed according to food web theory so far (Link 2002), and food web descriptors estimated stand apart from those of their terrestrial and freshwater counterparts (Tab.1, Link 2002; Link et al. 2005). Therefore, to gain deeper insights in the structure of the complex marine system of the Weddell Sea body size analyses may be useful to assess community and ecosystem level responses to environmental change (Laymann et al. 2005; Brose et al. 2005b) as ratios of consumer and resource body sizes were found to be correlated to interaction strength patterns in real ecosystems which in turn determine food web stability (Emmerson & Raffaelli 2004; Brose et al. 2005b).

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Table 1: Food web characteristics of 17 different webs including the eastern Weddell Sea shelf

Food Web	Number of Species S	Top Species	Intermediate Species	Basal Species	Number of Links L	Linkage Density L/S	Connectance C $2 \times L/(S^2\text{-}S)$	Predator/Prey ratio	Reference
Benguela system	29	0	27	2	203	7.00	0.241	0.93	Yodzis 1998
Caribbean reef	50	0	47	3	556	11.12	0.222	0.94	Opitz 1996
Northeastern US Shelf	79	3	74	2	1403	17.76	0.225	1.01	Link 2002
Scotch Broom	85	50	34	1	223	2.63	0.031	2.40	Memmott et al. 2000
Canton Creek	102	26	22	54	697	6.83	0.067	0.63	Townsend et al. 1998
Chesapeake Bay	31	10	16	5	68	2.19	0.071	1.24	Baird & Ulanowicz 1989
Coachella Valley	29	0	26	3	262	9.03	0.312	0.90	Polis 1991
El Verde	155	20	107	28	1509	9.74	0.063	0.94	Waide & Reagan 1996
UK grassland	61	19	34	8	97	1.59	0.026	1.26	Dawah et al. 1995
Little Rock Lake	92	1	79	12	997	10.84	0.118	0.88	Martinez 1991
Skipwith Pond	25	1	23	1	197	7.88	0.312	1.00	Warren 1989
St. Marks Eastuary	48	9	33	6	221	4.60	0.096	1.08	Christian & Luczkovich 1999
St. Martin	42	7	29	6	205	4.88	0.116	1.03	Goldwasser & Roughgarden 1993
Stony Stream	109	19	29	61	829	7.61	0.070	0.53	Townsend et al. 1998
Ythan Estuary 1991	83	31	47	5	395	4.76	0.057	1.50	Hall & Raffaelli 1991
Ythan Estuary 1996	124	49	70	5	579	4.67	0.038	1.59	Huxham et al. 1996
Weddell Sea Shelf	491	32	394	62	16200	33.20	0.135	0.93	This study

PUBLICATION VI

ENERGY FLOW OF AN HIGH ANTARCTIC ECOSYSTEM – THE WEDDELL SEA SHELF

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MANUSCRIPT DRAFT

Energy Flow of a high Antarctic Ecosystem – The Weddell Sea Shelf

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Abstract

Mass balanced ecosystem models analyse the flow of energy along trophic links. They allow in depth analysis of ecosystem trophic structure as well as the evaluation of effects of potential changes in environmental conditions. Here we present a mass-balanced trophic model of the eastern Weddell Sea shelf using the ECOPATH software.

Introduction

Constructing mathematical models to simulate the behavior of ecosystems is the focus of much research in biological sciences today. A comprehensive understanding of the structure, function, and regulation of major ecosystems is necessary to face the world's ever-growing environmental problems (Mann 1988; Pahl-Wostl 1993; Gaedke 1995). Models facilitate prediction of ecosystem behaviour over time as a function of specified human impact, such as fishing, or changes in the environment (pollution, climate changes etc.). Demand for accurate predictions encourages biologists to quantify and compact the complex interactions of organisms in an ecosystem into predictive computer models to guide ecological management and analysis of choices and tradeoffs.

There has been considerable interest in ecosystem approaches to natural resource management, and this has been particularly in the marine environment (e.g. Link 2002a, Christensen et al. 1996, Pinnegar et al. 2004, Link 2005). However, there remains little consensus concerning the conceptual and analytical tools that should be used to study ecosystems (Walters et al. 1997). “Ecopath with Ecosim” (EwE) has emerged as one of the most popular approaches, and one of the few (Fath and Patten 1999) that can address large-scale ecosystem issues. Keeping in mind its limitations (Christensen and Walters 2004, Plaganyi and Butterworth 2004) this software has been used for policy exploration and scenario modelling (Pitcher and Cochrane 2002). Several comprehensive studies on the trophic interactions between marine organisms have been conducted using EwE (Polovina 1984; Opitz 1993; Morissette 2001), but studies on Antarctic communities are scarce (Jarre-Teichmann et al. 1997; Bredesen 2003). The goal of this study is to combine knowledge on feeding relationships, the trophic hierarchy and biomass flow of the community of the high Antarctic Weddell Sea to identify important trophic flows and groups.

Material & Methods

Basic Modelling

Originally proposed by Polovina (1984), Ecopath is a program for balancing steady state food web models. In the mass-balance master formulation, the size of inputs and trophic compartments determine the overall constraint on the range of model behaviour. The inputs required to construct an ECOPATH network include biomass and production, diet composition, annual catch, ecotrophic efficiency, primary production, detritus biomass and food consumption per unit biomass (Pauly et al. 1993).

The master equation for each functional group (*i*) is:

$$B_{(i)}(P/B)_i EE_{(i)} - \sum_{\text{predators j}} B_{(j)}(Q/B)_j DC_{(j,i)} - EX_{(i)} = 0 \tag{1}$$

where $B_{(i)}$ is the total biomass for compartment *i*, $(P/B)_i$ is the production/ biomass ratio, $(Q/B)_j$ the consumption/ biomass ratio and $DC_{(i,j)}$ the fraction of compartment *i* in the average diet of consumer *j* (Christensen & Walters 2004). $EE_{(i)}$ is the ecotrophic efficiency, $P_{(i)}$ the total production rate, $Q_{(j)}$ the total consumption rate for consumer *j*, $EX_{(i)}$ the total export of compartment *i* out of the ecosystem. This system of linear equations can be solved, using standard matrix algebra, and provided that $DC_{(i,j)}$ and $EX_{(i)}$ are known or specified, entry is optional for any one of the other four main parameters ($B_{(i)}$, $(P/B)_I$, $(Q/B)_j$, $EE_{(i)}$) (Christensen & Walters 2004, Pinnegar et al. 2004).

Input Data & Model Structure

To date the largest Ecopath food web thought to have been published is that of Mackinson et al. (2001); with 59 trophic groups; East Florida Shelf, whereas the smallest consisted of only 7 trophic groups, Moreau et al. 1993; Lake Tanganyika, Burundi, (see Pinnegar 2004). In this study we use 52 trophic compartments to describe the trophic structure of the estern Weddell Sea shelf. We defined the compartments based on information of taxonomic criteria, trophic role, size and diet information (Appendix A), data were pedigreed according to quality of data. We thus defined one detrial compartment, and the following 51 living groups: seabirds (3 groups); marine mammals (9 groups); demersal fish (5 groups); pelagic fish (2 groups); cephalopoda (3 groups); benthic predators and scavengers (11 groups); benthis suspension feeders (8 groups); benthic deposit feeders (5 groups); pelagic crustaceans (2 groups); zooplankton (2 groups) and primary producer (2 groups) (Tab.1).

Results & Disscussion

Balancing the Model

The model of the eastern Weddell Sea shelf could not be balanced with the initial estimates. Balancing an Ecopath model relies on an iterative process involving manual implementations that need to be rigorously conducted. Each step of this process must be based on ecological hypotheses that are realistic. For this reason, the balancing process can be viewed as a fertile explanatory phase where ecological hypotheses are formulated in the confrontation of local knowledge and model constraints (Bozec et al. 2004; Kavanagh et al. 2004). The degree of energy balance of each functional group is usually determined in ECOPATH by examining the ecotrophic efficiency (EE). A value of EE less than 1 for a group indicates that, the group is not consumed in noticeable amounts by any other group, a value near or equal 1 indicates that the group is heavily preyed upon. For most groups the ecotrophic efficiency should be close to one.

To balance the model we used automatic mass balancing. The diet matrix has low confidence compared to other parameters. After diet, the biomass values are the next lee well known quantities. Therefore the automated mass balance routine is designed to adjust at least input values of diet and biomass (Kavanagh 2002; Kavanagh et al. 2004). Automatic mass balance leads to new input values (Tab.2), mainly in order to meet the requierements of the benthic omnivores and scavengers. Biomass of porifera, as one of the most common prey items, was estimated two times higher than found in the box cores, in contrast biomass of most of the benthic predators was adjusted one to two times lower than estimated.

The major flows in the ecosystem are illustrated in Fig. 1. The components of the system are arranged on the vertical axis according to their trophic level. In Ecopath, a routine allow to analyze the whole ecosystem by aggregating trophic groups into discrete trophic levels, based on an approach described by Ulanowicz (1995). First, fractional trophic levels are assigned all trophic groups modeled in the system. Primary producers and detritus are given a trophic level of one, and for each of the 49 consumers the mean weighted trophic level is then calculated as one plus the sum of the trophic levels of its prey multiplied by the prey's proportion in the diet. (Christensen 1995). The benthic compartments are placed between trophic level 2.0 for benthic supension and deposit feeders, excluding anthozoans and hydrozoans, which are partly preying on zooplankton (Orejas et al. 2001) and 3.6 for benthic cephalopods, such as *Pareledone charcoti*. Top predators like whales, seals, and fish occupy distinctly higher trophic levels, placed between level 3.2 for small pelagic fish and myctophids up to level 4.7 for killer and sperm whales.

Mixed Trophic Impacts

The mixed trophic impacts between the 52 trophic compartments in the model were computed following Ulanowicz & Puccia (1990) (Fig.2). The concept of mixed trophic impacts assesses the direct and indirect impact a change of biomass of a given compartment on the biomass of another compartment (Ulanowicz & Puccia 1990; Jarre-Teichmann et al. 1997). An increase in nanophytoplankton and microphytoplankton positively impacts all pelagic consumers such as mesozooplankton, and krill but also suspension feeding invertebrates. Overall there appear to be a highly interacting benthic system as well as a highly interacting pelagic system. The benthic system is dominated by suspension feeders, which are all linked directly to the primary producers and the detritus box and by mobile benthic predators. Among the predators, nemerteans, asteroids and polychaetes are quite flexible in their alimentation, as indicated by their wide range of trophic impacts on a variety of prey items (Fig.2). Therefore most of the structuring compartments can be regarded as omnivores (Jarre-Teichmann et al. 1997). Although only a few, there exist some direct links between pelagic animals and benthic predators. Our data include the ophiuroid *Ophiurolepis spp*. (feeding on euphausiids, Dahm 1996), the hydrozoan *Tubularia ralphii* (copepods, Orejas et al. 2001) and the anthozoan *Anthomastus bathyproctus* (salps, Orejas et al. 2001).

The pelagic system includes fish, squid, whales, seals penguins and seabirds. There the impacting compartments are the squid and fish species as well as the top predators, the killer whale and the leopard seal.

The present study of the eastern Weddell Sea shelf benefited from a large amount of data on its biological communities. The model provided valuable insights on the trophic structure and allowed to state some hypotheses for the main structuring compartments of the Weddel Sea web. The main limitation of the model is the probable the unequally resolution of data. For some compartments there are only guesstimates regarding their trophic role within the community. Research trawls hardly ever catch squid. We have no effective means of sampling their abundance or of assessing their ecology but beeing aware that they are important pelagic consumers with high trophic impacts on the pelaggic community.

The proximate role played by seals and whales is obvious: they are predators and consumers of fish and invertebrates. Less intuitive is their ultimate role (dynamic and structural) within the ecosystem. The limited information available suggests that some perform a dynamic role by transferring nutrients and energy, or by regulating the abundance of other species.

Food web linkages ultimately determine the fate and flux on every population in an ecosystem. Although there are be numerous interactions, few are of the magnitude to drive whole-system dynamics. Therefore we need to broaden our understanding and better our resolution of this complex web on every scale.

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Table 1: Input parameters for the mass balanced model of the eastern Weddell Sea shelf

	Code	Trophic Compartment	Biomass (g C m^2)	Production/ Biomass	Consumption/ Biomass	Production/ Consuption
	1	Nanophytoplankton	0.031	224.000	-	-
	2	Microphytoplankton	0.335	224.000	-	-
	3	Mesozooplankton	1.340	7.000	4.500	-
	4	Gelatineous zooplankton	0.170	50.000	250.000	-
	5	Krill	0.480	2.000	8.250	-
	6	Mysidacea	0.017	0.750	-	0.207
	7	Porifera	45.300	0.007	0.007	-
	8	Bryozoa	0.536	0.216	-	0.301
	9	Brachiopoda	0.017	0.288	-	0.023
	10	Sessile Polychaetes	0.004	0.259	-	0.512
	11	Bivalvia	0.494	0.385	-	0.209
	12	Holothuria (SF)	0.538	0.443	-	0.150
	13	Crinoida	0.167	0.478	1.000	-
	14	Anthozoa & Hydrozoa	0.368	0.221	-	0.301
	15	Cumacea & Tanaidacea	0.066	0.687	-	0.207
	16	Decapoda	0.044	0.587	-	0.276
	17	Octopoda	0.275	2.000	-	0.194
	18	Amphipoda	0.344	0.918	-	0.207
	19	Isopoda	0.187	0.801	-	0.207
	20	Pantopoda	0.025	0.986	-	0.362
	21	Nemertini	0.328	0.376	-	0.266
	22	Polynoid Polychaetes	7.361	0.539	-	0.603
	23	Gastropoda	0.091	0.489	-	0.369
	24	Ophiuroidea	1.429	0.783	-	0.226
	25	Ascidians	1.431	0.114	-	0.230
	26	Asteroidea	1.750	0.331	-	0.295
	27	Echinoida & Cidaroida	0.324	0.521	-	0.064
	28	Polyplacophora	0.009	0.439	-	0.194
	29	Holothuroida (DF)	0.538	0.443	-	0.150
	30	Irregularia	0.009	0.200	-	0.064
	31	Sipuncula & Echiurida	0.203	0.242	-	0.150
	32	Scaphopoda	0.009	0.479	-	0.150
	33	Small Squid	0.109	2.500	12.000	-
	34	Large Squid	0.064	3.000	15.000	-
	35	Small demersal fish	0.410	0.800	4.243	-
	36	Large demersal fish	0.293	0.550	3.274	-
	37	Small pelagic fish	0.135	0.250	4.802	-
	38	myctophids	1.596	0.950	7.406	-
	39	toothfish	0.023	0.265	1.600	-
	40	Rock cod	0.065	0.305	2.286	-
	41	Icefish	0.007	0.570	2.912	-
	42	Crabeater Seal	0.064	0.110	5.798	-
	43	Ross Seal	0.001	0.220	11.382	-
	44	Weddell Seal	0.002	0.220	11.382	-
	45	Leopard Seal	0.005	0.150	5.343	-
	46	Small cetaceans	0.00001	0.049	7.200	-
	47	Minke Whales	0.001	0.095	4.800	-
	48	Baleen Whales	0.00001	0.065	4.800	-
	49	Sperm Whales	0.00006	0.065	4.200	-
	50	Killer Whales	0.00004	0.060	4.800	-
	51	Seabirds	0.00001	0.140	65.624	-
	52	Empeor penguin	0.0026	0.240	64.236	-
	53	Penguins	0.0001	0.221	62.027	-

Table 3 Summary statistics for the balanced model of the eastern Weddell Sea shelf in comparison to the Weddell Sea shelf model in 1997 (Jarre-Teichmann et al. 1997)

Statistic	Model 2005 value (g C m^2)	Model 1997 value (g C m^2)
Sum of all consumption	67.1	121.8
Sum of all exports	42.9	5.8
Sum of all respiratory flows	34.14	69.4
Sum of all flows to detritus	51.5	63.5
Total system throughput	204.1	260.5

Appendix

Source for the Original Input Parameters for the preliminary model version

1. **Nanophytoplankton**: biomass (Jarre-Teichmann et al. 1997, Brey unpublished data), production (Jarre-Teichmann et al. 1997, Brey unpublished data)
2. **Microphytoplankton**: biomass (Jarre-Teichmann et al. 1997, Brey unpublished data), production (Jarre-Teichmann et al. 1997, Brey unpublished data)
3. **Mesozooplankton**: biomass (Voronina et al. 1980, Voronina 1998, Fisher et al. 2004), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
4. **Gelatinous zooplankton**: biomass (Pages et al. 1996, Pages 1997, Brey unpublished data), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
5. **Krill**: biomass (Siegel 1986), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
6. **Mysidacea**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
7. **Porifera**: biomass (Gatti 2002, Gerdes et al. 2005), production (Gatti 2002), consumption (Gatti 2002), diet (Brose et al. 2005)
8. **Bryozoa**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
9. **Brachiopoda** biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
10. **Sessile Polychaetes**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
11. **Bivalvia**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
12. **Holothuria (SF)**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
13. **Crinoida**; biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
14. **Anthozoa & Hydrozoa**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
15. **Cumacea &Tanaidacea**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
16. **Decapoda**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
17. **Benthic cephalopods**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
18. **Amphipoda**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
19. **Isopoda**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
20. **Pycnogonida**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)

21. **Nemertini**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
22. **Polychaeta**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
23. **Gastropoda**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
24. **Ophiuroidea**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
25. **Ascidians**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
26. **Asteroida**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
27. **Echinoids & Cidaroids**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
28. **Polyplacophora**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
29. **Holothuria (DF)**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
30. **Irregular sea-urchins**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
31. **Sipuncula & Echiurida**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
32. **Scaphopoda**: biomass (Gerdes et al. 2005), production (Brey unpublished data), consumption (Brey unpublished data), diet (Brose et al. 2005)
33. **Large Squids**: biomass (Clarke 1985, Rodhouse 1997), production (Pauly & Christensen 1996), consumption (Pauly & Christensen 1996), diet (Kear 1992, Kock 1987, Laws 1985, Nemoto et al. 1988, Nemoto et al. 1985, Nicol & Endo 1997, Rodhouse & White 1995, Rodhouse et al. 1992)
34. **Small Squids**: biomass (Clarke 1985, Rodhouse 1997), production (Pauly & Christensen 1996), consumption (Pauly & Christensen 1996), diet (Kear 1992, Kock 1987, Laws 1985, Nemoto et al. 1988, Nemoto et al. 1985, Nicol & Endo 1997, Rodhouse & White 1995, Rodhouse et al. 1992)
35. **Small demersal fish**: biomass (CCAMLER 1994, Kock 1992), production (Daniels 1983, Kock 1992, Radtke et al. 1989, Shlibanov 1990), consumption (Kock 1981, Kock 1992, Shust & Pinskaya 1978), diet (Burchett et al. 1983, Casaux 1998, Everson 1981, McKenna Jr. 1991, Reid & Arnould 1996, Richardson 1975, Targett 1981, Vachi & la Mesa 1995, Mintenbeck 2001, Bredesen 2004)
36. **Large demersal fish**: biomass (CCAMLER 1994, Kock 1992), production (Barrera Oro & Tomo 1988, Csirke 1987, Kock 1992), consumption (Barrera-Oro & Tomo 1988, Kock 1992), diet (Burchett et al. 1983, Croxall et al. 1988, Croxall et al. 1985, Everson 1981, Everson 1984, Fischer & Hureau 1985, Kock 1981, Kock 1987, Kock & Jones 2002, Reid et al. 1996, Target 1981, Mintenbeck 2001, Bredesen 2004)
37. **Small pelagic fish**: biomass (Kock 1992, Torres et al. 1984), production (Kunzmann 1986), consumption (Kock 1992, Kunzmann 1986), diet (Gon & Heemstra 1990, Hubold & Hagen 1997, Wohrmann et al. 1997)
38. **Myctophid fish**: biomass (Lubivoma et al. 1983, Phleger et al. 1997; Sabourenkov 1991), production (Linkowski 1987), consumption (Hulley 1990), diet (Greely et al. 1999, Hoddell 1996, Hopkins 1985, Hopkins et al. 1993, Hopkins & Torres 1989, Kock 1987, Lancraft et al. 1991, Nishikawa & Tsuda 2001, Phleger et al. 1997, Piatkowski et al. 1994, Rowedder 1979, Bredesen 2004)
39. **Toothfish**: *Dissostichus mawsoni*: biomass (Reid & Nevitt 1998), production (Kock et al. 1985), consumption (Kock 1992), diet (de la Rosa et al. 1997, Duhamel 1981, Fischer & Hureau 1985, Gonzales & Rodhouse 1998, Kock 1987, McKenna Jr. 1991, Tarverdiyeva 1972)
40. **Antarctic rockcod**: e.g. *Notothenia marmorata*: biomass (Barrera-Oro et al. 2000, Burchett & Ricketts 1984, Jones et al. 2000, Kock 1992), production (Tankevich 1990), consumption (Freytag 1980), diet (Burchett 1983, Hurau 1970, Kock 1992, Linkowski et al. 1983, McKenna Jr. 1991, Tarverdiyeva 1972)

41. **Icefish**: *Champsocephalus gunnari*: biomass (CCAMLER 1994, Kock 1992, Jones et al. 2000, Kock 2005), production (Kock 1992), consumption (Kock 1981, Kock 2005), diet (Agnew et al. 1998, Kock & Everson 1997, McKenna Jr. 1991, Kock 2005)
42. **Crabeater seals**: body mass (Trite & Pauly 1998), population size (Erickson & Hanson 1990), production (Croxall 1987), consumption (Innes et al. 1987, Trites et al. 1999), diet (Bengtson & Laws 1985, Croxall et al. 1985, Lowry et al. 1988, Oritzland 1977, Pauly et al. 1998, Siniff & Stone 1985, Stone & Meier 1981, Walker et al. 1998, Bredesen 2004)
43. **Ross seals**: body mass (Trites & Pauly 1998), population size (Siniff & Stone 1985), production (Croxall 1987), consumption (innes et al. 1987, Trites et al. 1999, Bredesen 2004), diet (Bengtson & Laws 1985, Croxall et al. 1985, Harwood & Croxall 1988, Ortizland 1977, Plötz et al. 1991, Pauly et al. 1998, Plötz et al. 2001)
44. **Weddell seals**: body mass (Trites & Pauly 1998), population size (Siniff & Stone 1985), production (Croxall 1987), consumption (innes et al. 1987, Trites et al. 1999, Bredesen 2004), diet (Bengtson & Laws 1985, Croxall et al. 1985, Harwood & Croxall 1988, Ortizland 1977, Plötz et al. 1991, Pauly et al. 1998, Plötz et al. 2001)
45. **Leopard seals**: body mass (Trites & Pauly 1998), population size (Siniff & Stone 1985), production (Croxall 1987), consumption (Innes et al. 1987, Trites et al. 1999), diet (Bonner 1982, Croxall et al. 985, Lowry et al. 1988, Walker et al. 1998)
46. **Small cetaceans**: (including the dolphins *Lagenorhynchus cruciger* and *Tursiops truncates*) body mass (Trites & Pauly 1998), population size (Brown & Lockyer 1984, International Whaling Commission 1995, Kasamatsu & Joyce 1995; Leatherwood et al. 1988, Tamura & Ohsumi 2001, Branch & Butterworth 2001a), production (Evans & Stirling 2001), consumption (Kasamatsu & Joyce 1995, Sergant 1969), diet (Goodall & Galeazzi 1985; Pauly et al. 1998)
47. **Minke whales**: body mass (Trites & Pauly 1998), population size (International Whaling Commission 2003, Branch & Butterworth 2001b), production (Evans & Stirling 2001), consumption (Laws 1977; Lockyer 1981; Ohsumi 1979), diet (Ichii & Kato 1991, Kawamura 1994, Pauly et al. 1998)
48. **Baleen whales**: (including blue whales, fin whales, humpack whales, sei whales and southern right whales), body mass (Trites & Pauly 1998), population size (Chapman 1988, Branch & Butterworth 2001a), production (Evans & Stirling 2001, Bredesen 2004), consumption (Laws 1977, Lockyer 1981), diet (Mackintosh 1972; Nemoto 1959, Pauly et al. 1998, Tamura & Ohsumi 2000)
49. **Sperm whales**: body mass (Trites & Pauly 1998), population size (Branch & Butterworth 2001a, Whitehead 2002), production (Evans & Stirling 2001, Bredesen 2004), consumption (Laws 1977, Lockyer 1981); diet (Knox 1994, Nemoto et al. 1988, Pauly et al. 1998; Brose et al. 2005)
50. **Killer whales**: body mass (Trites & Pauly 1998), population size (International Whaling Commission 1995; Branch & Butterworth 2001a), production (Evans & Stirling 2001), consumption (Laws 1977, Lockyer 1981); diet (Goodall & Galeazzi 1985, Pauly et al. 1998, Kasamatsu et al. 2000, Bredesen 2004, Brose et al. 2005)
51. **Seabirds**: body mass (Croxall 1984), population size (van Franeker 1992, van Franeker et al. 1997), production (Croxall 1984, Knox 1994, Bredesen 2004), diet (Ainley et al. 1992, Hopkins et al. 1993, Favero et al. 1997)
52. **Empeor penguin**: body mass (Williams 1995), population size (Croxall et al. 1984, Prince & Croxall 1996), production (Croxall & Prince 1983), consumption (Croxall et al. 1985), diet (Croxall 1984, Croxall 1985, Croxall & Davis 1999)

4 SYNTHESIS

The susceptibility of the large marine Antarctic ecosystem to change makes it an ideal case to study the effect of environmental change on the systems' trophic structure and dynamics (Ciannelli et al. 2005; Smetacek & Nicol 2005). But knowledge of the functioning of Antarctic communities and ecosystems, in particular on their trophic connections and energy flow patterns is still fragmentary (e.g. Bluhm 2001).

"Who eats whom" appears to be the most central organizing concept in ecology (Martinez 1991; de Ruiter et al. 2005) and therefore food web characterization is required as an initial step in understanding an ecosystem (Link 2002). Marine ecosystems, however, appear to differ inherently from terrestrial or freshwater counterparts due to (i) their openness, (ii) the orders of magnitude in size across the species, and (iii) their unique relationship between the number of species and connectivity (Steele 1985; Cohen 1994; Link 2002; Link et al. 2005; Jacob et al. 2005 PUBLICATION V).

But if so, "does food-web theory work for marine ecosystems?" (Link 2002; Link et al. 2005). Only a few marine systems have been analyzed according to food web theory so far (Link 2002), most of them were coastal, enclosed or embayed (Arreguin-Sanchez et al. 1993; Gomes 1993; Mendoza 1993), and food web descriptors estimated stand apart from those of their terrestrial and freshwater counterparts (Link 2002; Link et al. 2005; Jacob et al. 2005 PUBLICATION V). Thus, the jury is still out on this question.

4.1 What is the origin of such complex community patterns?

To grasp the complexity associated with highly diverse natural communities the concept of functional diversity, which is defined as "those components of biodiversity that influence how an ecosystem operates or functions" (Tilman 2001) is used. This concept predicts that increased functional diversity will facilitate ecosystem functioning due to greater resource use complementarity (Hooper 1998; Tilman 2001; Petchey 2003) among species in a community (Trenbath 1974; Harper 1977; Tilman et al. 1997; Loreau 1998).

The discussion of whether biodiversity determines ecosystem functioning (Schulze & Mooney 1993) has lead to numerous experimental studies (Tilman 1999; Kinzig et al.

2001; Loreau et al. 2001; Loreau et al. 2002; Petchey et al. 2004). Recent attention has turned to the characterization of functionally significant components of biodiversity (Díaz & Cabido 2001; Hooper et al. 2002; Petchey et al. 2004). The concept of functional diversity is closely related to niche theory, where separation in a multidimensional niche space allows coexistence as high overlap along one niche dimension typically is accompanied by separation on another dimension (MacArthur & Pianka 1966; MacArthur & Levins 1967; Krebs et al. 1974; Kie & Bowyer 1999; Stewart et al. 2003; Jacob et al. 2005 PUBLICATION IV).

In PUBLICATION IV we have illustrated how the niche concept can be used to define a species' trophic requirements. It might be used to address further questions including (i) species distribution along environmental gradients, (ii) similarity of coexisting species, (iii) the role of species in community succession and assembly, and (iv) patterns of biodiversity.

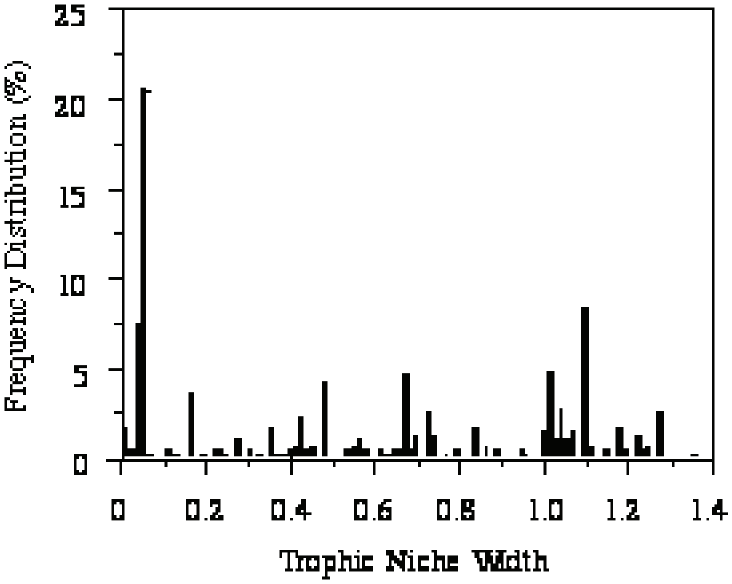

Figure 4.6 Frequency distribution of trophic niche width values of the eastern Weddell Sea shelf community (Jacob et al. 2005 PUBLICATION IV)

The composite index of population trophic niche width in the Weddell Sea system ranges from 0.0000047 in heterotrophic dinoflagellates to 1.37 in the omnivorous ophiuroid *Ophiosparte gigas*. The distribution of niche width values reflects that the marine Antarctic contains both, populations with large and with small trophic niches (Fig. 4.6).

➔ The high trophic complexity of the Weddell Sea shelf ecosystem results from the high trophic generality of most of the populations as well as their ability for vertical niche expansion.

4.2 How stable is the marine Antarctic system and what governs its ability to respond to environmental change?

In 1955 MacArthur proposed the DIVERSITY-STABILITY HYPOTHESIS. This thesis predicts that ecological communities increase in energetic efficiency (productivity) and in the ability to recover from disturbance with an increase in the number of species in the system (McArthur 1955). Sugihara (1982) and Christianou (2003) point in a similar direction when they state that the stability of an ecological community is determined by given trophic characteristics of the entities it is composed of and of the network of interactions linking these entities together.

Early food web studies and models indicate that omnivory destabilizes ecological communities (Pimm 1982; Pimm et al. 1993), whereas more recent conceptual syntheses suggest that omnivory is a stabilizing factor (Fagan 1997, Neutel et al. 2001, Williams & Martinez 2004). It appears obvious, however, that a consumer gains the more trophic flexibility and impact on food web structure the more trophic levels it can access (Jacob et al. 2005 PUBLICATION IV).

Given the high dietary overlap and generalist feeding nature of most of the species of the Weddell Sea shelf, plus the well documented capacity of diet switching of many species in this system (e.g. Dahm 1997; Brenner et al. 2002; Jacob et al. 2003), it appears that there are few trophic links of outstanding exclusivity and strength. One exception is the krill species *Euphausia superba* that is the common and often the dominant food source of many pelagic predators.

➔ It remains to be seen if "loose" connectivity as observed in the Weddell Sea food web leads towards stability, but it is likely that there are different ways of being robust related to different types of perturbations (Melian & Bascompte 2002; Christianou 2003). Antarctic food webs may be able to cope better, at least to a certain extent, with slowly changing environmental conditions than with dramatic short term disturbances such as volcano eruptions (e.g. Deception Island, Gallardo 1975) or loss of large shelf ice sheets (e.g. Larsen B, Domack et al. 2005).

4.3 How will the extinction of a threatened species or the addition of an invasive species influence Antarctic marine ecosystems?

During the last decades, there has been increasing recognition that external forcing – either anthropogenic (Parsons 1996; Jackson et al. 2001; Verity et al. 2002) or environmental (McGowan et al. 1998; Stenseth et al. 2002; Chavez et al. 2003) can profoundly impact entire communities, causing a rearrangement of their internal structure (Pauly et al. 1998; Anderson & Piatt 1999; Steele & Schuhmacher 2000) and a deviation from their original succession (Odum 1985; Schindler 1985; Winder & Schindler 2004). Growing concern about how species loss or species gain will affect ecosystems has stimulated numerous studies (Ehrlich & Ehrlich 1988; Naeem et al. 1994; Sala et al. 2000; Chapin et al. 2000; Terborgh et al. 2001).

Species Loss

Most recent studies on species loss assumed that species go extinct randomly, but species often go extinct in order of their sensitivity to a stress that intensifies through time, such as a gradual change in salinity or temperature (Ives & Cardinale 2004). So far there is little evidence of temperature change in Antarctic waters, but models predict average global sea temperatures to rise by around 2°C by 2100 (Peck 2005). Such rise would take many Antarctic marine species beyond their survival limits (Mark 2004; Peck 2005). Accordingly, changes of only a few degrees can have significant impacts on predator-prey relationships, too, e.g. shifts in interaction strength or trophic decoupling, with profound ecological consequences (Aronson & Blake 2001).

Investigations on temperature tolerance in Antarctic fish species (Mark et al. 2002; Pörtner et al. 2004; Mark et al. 2004a; Mark et al. 2004b) indicates that most species are quite stenothermal, but at least some could keep pace with slow and moderate warming of Antarctic waters, especially deep water species like the eelpout *Pachycara brachycephalum* (Wells et al. 1990; Di Prisco 2000; Mark 2004).

The sensitivity of an individual species to environmental change depends not only on the direct impact of change on that particular species, but also on indirect effects caused by changes in abundances of other species. Moreover, as species go extinct, links within the food web are severed, changing the pathways through which indirect effects operate (Ives & Cardinale 2004).

Consequences of species loss depend on the extent of compensation created by food-web interactions. Compensation is defined here as the increase of abundance in some species when their competitors and/or predators decrease due to environmental stress. Compensation makes communities as a whole more resistant to stress because it allows to rebalance the flow network by re-adjusting species densities. However, if extinction progresses, the potential for compensation and thus resistance capacity will decrease. Changes in the food web structure caused by successive extinctions make it extremely difficult to predict which species will show compensation. This unpredictability argues for "whole-ecosystem" approaches to biodiversity conservation, as seemingly insignificant species may become important after other species go extinct (Ives & Cardinale 2004).

One specific example of species loss from the Antarctic is the loss of the great whales. ECOPATH models had been constructed to address questions concerning ecosystem interactions and the role of large whales (Bredesen 2003; Trites et al. 2004). One model represented the 1900s (i.e., after the extensive hunting of pinnipeds had ceased, but before whaling began), and was used to explore the effects of removing whales from the ecosystem. The second model, corresponding to the 1990s (i.e., present day) was used to address the recovery of whale populations. Biomass during the 1990s was dominated by krill and other zooplankton, while whales, seals and birds contributed relatively little to overall biomass of the ecosystem (Bredesen 2003; Trites et al. 2004). The simulated whaling resulted in an increase of *Notothenia rossii*, *Dissostichus eleginoides* and *Champsocephalus gunnari*. Biomass of Antarctic fur seals did not increase, in contrast to the observed trend of Antarctic fur seal populations over the last century (Payne 1977; Boveng et al. 1998). Removing 10% of the baleen whale biomass each year reduced the biomass of the whale population to about 5% of its original size in about 50 years. Cessation of whaling after 50 years resulted in whale biomass recovering to only about 10% of its original biomass at the end of 100 years of simulation (Bredesen 2003; Trites et al. 2004).

Both models suggest that removal of large whales had little measurable effect on lower trophic levels or on the dynamics of other species in the system. The populations of large whales, however, once reduced to low numbers, take a long and maybe indefinite time to recover (Bredesen 2003; Trites et al. 2004).

Despite these model findings, empirical evidence indicates that the removal of so many large predators has affected the interactions at virtually all trophic levels (Laws 1962; Bengston & Laws 1985; Croxall 1992; Kock & Shimadzu 1994; Woodward et al. 2005). Higher resolution models may be able to reproduce these patterns, too.

➔ Loss of large bodied consumers, like whales, leads to a permanent shift of equilibrium trophic structure.

Species Gain

Invasive species are considered to be a leading threat to biodiversity worldwide (Coblentz 1990; Soulé 1990; Wilcove & Bean 1994; Vander Zanden et al. 2004a). Their impact on native species, communities, and ecosystems has been widely recognized for decades (Elton 1958; Lodge 1993a; Lodge 1993b; Simberloff 1996; Sakai et al. 2001). Typical consequences of species invasions are (i) no observable impacts on native species, (ii) alteration of the pattern of species interactions in the rest of the community (Schaffer 1981; Leibold & Wilbur 1992; Lawler & Morin 1993; Wotton 1994; McCann et al. 1998; McCann 2000), (iii) extinction of native species, and (iv) alteration of ecosystem processes (Spencer et al. 1991; Lodge 1993a; Vitousek et al. 1996; Strayer et al. 1999; Vander Zanden et al. 2004a; Gurevitch & Padilla 2004). Marked climate change and subsequent invasion of hitherto alien species have already affected terrestrial systems of the Southern Ocean (e.g. Marion Island: the house mice, Smith & Steenkamp 1990; South Georgia: the carabid *Trechisibus antarcticus*, Bergstrom and Chown 1999, Chown and Gaston 2002, Gaston et al. 2003; Frenot et al. 2005) and invasion of alien species may thus endanger the ecology of marine Antarctic ecosystem, too.

To characterize vulnerable communities, Vander Zanden et al. (2004a) presented a conceptual framework for modelling invader occurrence and impact. The species invasion process is composed of three steps or filters (Fig. 4.2). The corresponding modelling approach of Vander Zanden et al. (2004b) is based on the understanding of among-system variability, food web interactions between the invader and the target ecosystem, and the development of quantitative models to classify communities according to both invader occurrence and impact. The first filter identifies which communities are accessible to invading species, the second filter identifies which communities are capable of supporting invading species and the third filter identifies which communities would be adversely impacted if invasive species were able to establish (Vander Zanden et al. 2004a+b)).

Actually the return of large decapod crabs is discussed as one of the most likely and maybe already ongoing invasions of the Antarctic system (Feldmann & Tshudy 1989; Clarke et al. 2005; Thatje et al. 2005). They are excluded from Antarctica due to the low temperatures prevailing there since about 35 million years, but warming of Antarctic waters might allow the return of "bone crushers" such as lithodid crabs (Fig. 4.2).

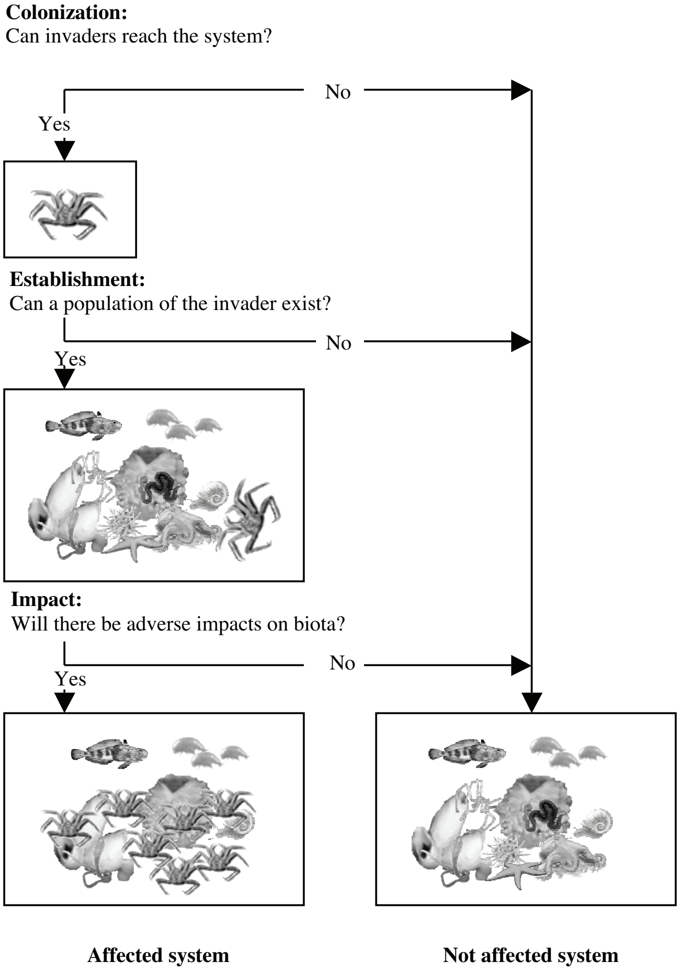

Figure 4.2: Modelling approach for predicting invader occurrences and impacts in Antarctic communities (modified from Vander Zanden et al. 2004a)

➔ Whether and how species gain will impact Antarctic communities remains to be seen. Deeper insights in food web interactions between the invader and the target system are required.

4.4 Future Perspectives

Antarctic ecosystems, with their low level of direct human impact, have been identified as an important case study for the conservation of intact ecosystems (Chown and Gaston 2002). The Southern Ocean shows signs of warming (Gille 2002) and climatic anomalies are known to affect the physical and biological environment at regional scales (Fraser & Hoffman 2003; Smith et al. 2003; Trathan & Murphy 2003; Forcada et al. 2005). Although the linkages between global climate perturbation and community responses are only just being explored (e.g. Fraser & Hoffmann 2003; Trathan et al. 2005; Dunne et al. 2005), environmental change potentially starts to affect Antarctic krill, *Euphausia superba*, and it's consumers, including numerous species of seabirds and marine mammals (Boyd & Murray 2001; Reid & Croxall 2001; Forcada et al. 2005).

In general, organisms have three mechanisms for coping with change: they can (i) use physiological flexibility, (ii) evolve new adaptations, and (iii) migrate to better sites (Peck 2005). The combination of restricted physiological capacities (e.g. stenothermy), long generation times and restricted available dispersal ranges results in slow rates of adaptation that make most Antarctic species the least capable of responding appropriately to environmental change (Peck 2005).

Perturbations are not random in their negative and positive impacts on species' interactions. Emerging evidence shows that species partly are declining as a result of environmental changes ("losers" Fig. 4.3) and are being replaced by a smaller number of expanding species ("winners" Fig. 4.4) that thrive in perturbed environments (McKinney & Lockwood 1999).

Figure 4.3: On the losing side, large Antarctic whales, near extinction after whaling activity (Bredesen 2003; Trites et al. 2004) (© Photographs: A. Rose)

According to the Redundancy Hypothesis (Ehrlich & Ehrlich 1981; Walker 1992) species may be functionally expendable (Johnson et al. 1996). The suggestion is that, in some communities, some species are "redundant"; they could be lost without much effect on the structure and functioning of the whole community (Gitay et al. 1996). This would suggest that, "most species are superfluous, more like passengers than rivets, and only a few key ones are pilots needed to keep the plane flying" (Walker 1992).

Even if losing species do not become completely extinct, they will probably be reduced to small trophic compartments and become insignificant compared to the driving forces of the trophic structure of the given system (McKinney & Lockwood 1999).

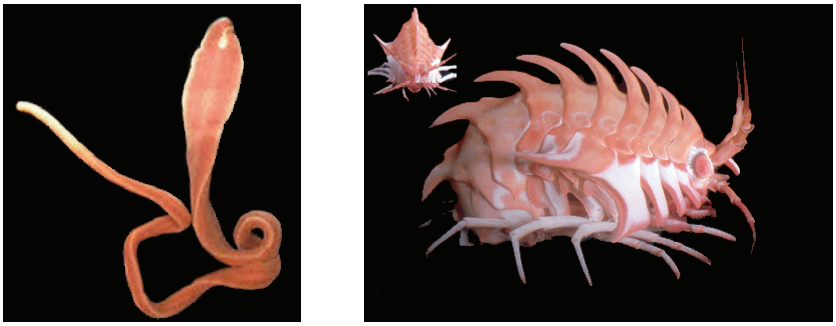

Figure 4.4: On the winning side, benthic voracious and highly flexible scavengers like the nemertean *Parborlasia corrugatus* or benthic epimerid amphipods (© Photographs: M. Rauschert)

An understanding of the dynamic relations between species is an indispensable step towards the comprehension of change in Antarctic food web structure due to ecosystem disturbance. Future research should be focused on:

➔ Networks incorporating both qualitative and quantitative information; they will provide more insight into the relationship between connectivity distribution, connectivity correlation and their importance to ecosystem response to perturbation.

➔ The relationship between distribution, biomass and trophic function for Antarctic species, as species loss and species gain do influence ecosystem function. We already know that removing key species such as ecosystem "engineers" or certain top predators may have dramatic effects.

➔ The relationship among body size and trophic position in complex food webs. Jonsson & Ebenman (1998) show that for simple food chains, resilience decreases if the ratio between predator and prey interaction strength decreases with increasing trophic position. Documenting the distribution of interaction strengths for all links within complex Antarctic marine food webs is probably not achievable. If more tractable metrics could be used as surrogate-correlates of interaction strength, then we would be able to evaluate the effects on the stability and ecosystem functioning of systems following environmental change and subsequently species loss and species gain (McCann 2000; Loreau et al. 2001; Emmerson & Raffaelli 2004).

The fundamental uncertainty about the sustainability of ecological systems following human impacts argues for the preservation of as many species as possible (Bolger 2001) because "costs of being wrong when pursuing the optimist's policies are far greater and less reversible than the costs of being wrong when pursuing the sceptic's policies" (Davies et al. 1994; Costanza et al. 2000). Although the requisite decision criteria remain to be fully developed, the ability to predict "the climate if not the weather" is a promising intersection between food web theory and resource management (Link et al. 2005). Translating food web descriptors and network metrics into management decision criteria remains a key area of research (Link 2005; Link et al. 2005).

5 ACKNOWLEDGEMENTS

$$\int c(i)\, e^{n} C_{\in} = f(u^{n})^{*}$$

The whole always exceeds the sum of the parts, this thesis is a plot that has thicken with each layer of colour that every person has added - Thank you to everyone involved!

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“ A quirky story of the eccentric thoughts of some truly mad individuals…![*1]

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*Devine, B., Cohen, J.E., (1992) Absolute Zero Gravity. Simon & Schuster, New York

[*1] Praise for „Reflections of a Summer Sea“, by Trevor Norton, „Choice of the Month“, The Bookseller

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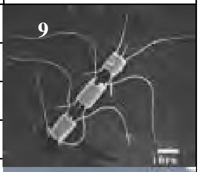
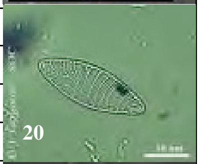
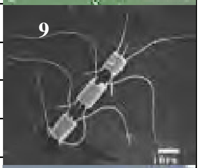
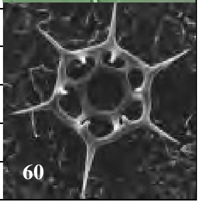
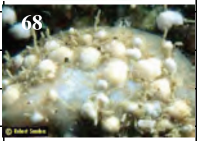
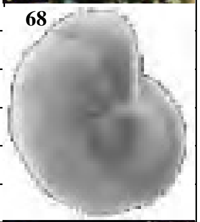
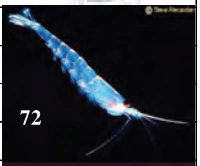
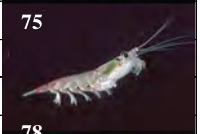
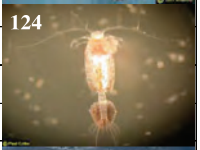
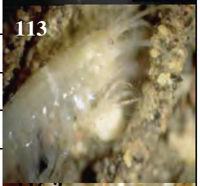
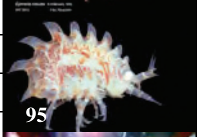
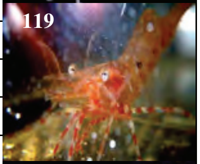
7 APPENDIX

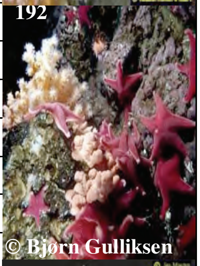
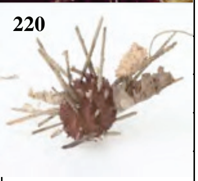
Table 1: List of Species used for food web analysis. Identification of different feeding types was obtained via an extensive literature research and own measurements. Species' trophic position was inferred from stable isotope analysis following Cabana & Rasmussen (1994).

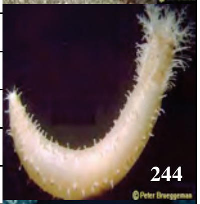
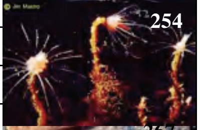
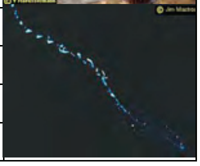
Trophic Position	Code	Taxonomy	Common Name	Illustration
-0.23	1	*Actinocyclus actinochilus*	Diatom	
-0.23	2	*Actinocyclus spiritus*	Diatom	
-0.23	3	*Adenocystis utricularis*	Diatom	
-0.23	4	*Azpeitia tabularis*	Diatom	
-0.23	5	*Banquisia belgicae*	Diatom	
-0.23	6	*Chaetoceros bulbosum*	Diatom	
-0.23	7	*Chaetoceros concavicornis*	Diatom	
-0.23	8	*Chaetoceros criophilum*	Diatom	
-0.23	9	*Chaetoceros dichaeta*	Diatom	
-0.23	10	*Chaetoceros flexuosum*	Diatom	
-0.23	11	*Chaetoceros neglectum*	Diatom	
-0.23	12	*Chaetoceros pelagicus*	Diatom	
-0.23	13	*Chaetoceros socialis*	Diatom	
-0.23	14	*Corethron cryophilum*	Diatom	
-0.23	15	*Coscinodiscus oculoides*	Diatom	
-0.23	16	*Cylindrotheca closterium*	Diatom	
-0.23	17	*Eucampica antarctica*	Diatom	
-0.23	18	*Fragilariopsis curta*	Diatom	
-0.23	19	*Fragilariopsis cylindrus*	Diatom	
-0.23	20	*Fragilariopsis kerguelensis*	Diatom	
-0.23	21	*Fragilariopsis linearis*	Diatom	
-0.23	22	*Fragilariopsis nana*	Diatom	
-0.23	23	*Fragilariopsis obliquecostata*	Diatom	
-0.23	24	*Fragilariopsis pseudonana*	Diatom	
-0.23	25	*Fragilariopsis rhombica*	Diatom	
-0.23	26	*Fragilariopsis ritscheri*	Diatom	
-0.23	27	*Fragilariopsis separanda*	Diatom	
-0.23	28	*Fragilariopsis sublinearis*	Diatom	
-0.23	29	*Fragilariopsis vanheurckii*	Diatom	
-0.23	30	*Manguinea fusiformis*	Diatom	
-0.23	31	*Manguinea rigida*	Diatom	
-0.23	32	*Navicula glaciei*	Diatom	
-0.23	33	*Navicula schefterae*	Diatom	
-0.23	34	*Nitzschia kerguelensis*	Diatom	
-0.23	35	*Nitzschia lecointei*	Diatom	
-0.23	36	*Nitzschia neglecta*	Diatom	
-0.23	37	*Odontella weissflogii*	Diatom	

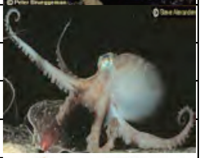
Trophic Position	Code	Taxonomy	Common Name	Illustration
-0.23	38	*Porosira glacialis*	Diatom	 63
-0.23	39	*Porosira pseudodenticulata*	Diatom	
-0.23	40	*Proboscia alata*	Diatom	 68
-0.23	41	*Proboscia inermis*	Diatom	
-0.23	42	*Proboscia truncata*	Diatom	
-0.23	43	*Pseudonitzschia heimii*	Diatom	
-0.23	44	*Pseudonitzschia liniola*	Diatom	 68
-0.23	45	*Pseudonitzschia prolongatoides*	Diatom	
-0.23	46	*Pseudonitzschia subcurvata*	Diatom	
-0.23	47	*Rhizosolenia antennata*	Diatom	
-0.23	48	*Stellarima microtrias*	Diatom	
-0.23	49	*Thalassiosira antarctica*	Diatom	
-0.23	50	*Thalassiosira australis*	Diatom	 72
-0.23	51	*Thalassiosira frenguelliopsis*	Diatom	
-0.23	52	*Thalassiosira gracilis*	Diatom	
-0.23	53	*Thalassiosira gracilis expecta*	Diatom	
-0.23	54	*Thalassiosira gravida*	Diatom	 75
-0.23	55	*Thalassiosira lentiginosa*	Diatom	
-0.23	56	*Thalassiosira ritscheri*	Diatom	
-0.23	57	*Thalassiosira trifulta*	Diatom	 78
-0.23	58	*Thalassiosira tumida*	Diatom	
-0.23	59	*Trichotoxon reinboldii*	Diatom	
2.72	60	*Dictyocha speculum*	Silicioflagellate	
2.72	61	*Phaeocystis antarctica*	Cilliate ????	 81
2.72	62	*Silicioflagellates*	Silicioflagellate	
2.72	63	*Bodo saltans*	Choanoflagellate	
2.72	64	*Amphidinium hadai*	Dinoflagellate	
2.72	65	*Gyrodinium lachryma*	Dinoflagellate	 86
2.72	66	*Parvicorbucula socialis*	Cilliate	
	67	*Cassidulinoides parkerianus*	Foraminifera	
	68	*Cibicides refulgens*	Foraminifera	
	69	*Globocassidulina crassa*	Foraminifera	 124
	70	*Lenticulina antarctica*	Foraminifera	
	71	*Neogloboquadrina pachyderma*	Foraminifera	
2.78	72	*Euphausia crystallorophias*	Euphausiacea	
3.29	73	*Euphausia frigida*	Euphausiacea	 109
5.42	74	*Thysanoessa macrura*	Euphausiacea	
3.50	75	*Euphausia superba*	Euphausiacea	
6.36	76	*Ampelisca richardsoni*	Amphipoda	
9.65	77	*Abyssorchomene rossi*	Amphipoda	 108
9.50	78	*Abyssorchomene plebs*	Amphipoda	
8.65	79	*Abyssorchomene nodimanus*	Amphipoda	
8.65	80	*Eusirus antarcticus*	Amphipoda	 96
9.09	81	*Eusirus perdentatus*	Amphipoda	
8.65	82	*Alexandrella mixta*	Amphipoda	
9.23	83	*Tryphosella murrayi*	Amphipoda	

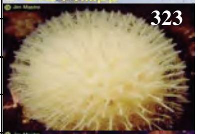
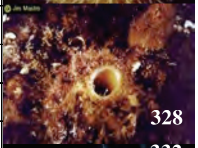
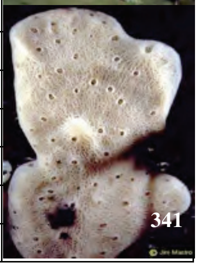
Trophic Position	Code	Taxonomy	Common Name	Illustration
10.50	84	*Waldeckia obesa*	Amphipoda	
12.10	85	*Parschisturella ceruviata*	Amphipoda	
8.65	86	*Paramoera walkeri*	Amphipoda	
8.65	87	*Epimeriella walkeri*	Amphipoda	
5.58	88	*Cyllopus lucasi*	Amphipoda	
4.63	89	*Hyperiella dilatata*	Amphipoda	
0.44	90	*Vibilia antarctica*	Amphipoda	
0.44	91	*Vibilia stebbingi*	Amphipoda	
4.63	92	*Hyperia macrocephala*	Amphipoda	
8.10	93	*Epimeria similis*	Amphipoda	
8.65	94	*Epimeria robusta*	Amphipoda	
8.65	95	*Epimeria macrodonta*	Amphipoda	
8.65	96	*Epimeria rubrieques*	Amphipoda	
7.90	97	*Epimeria georgiana*	Amphipoda	
8.65	98	*Melphidippa antarctica*	Amphipoda	
8.65	99	*Oediceroides emarginatus*	Amphipoda	
8.65	100	*Oediceroides calmani*	Amphipoda	
8.65	101	*Maxilliphimedia longipes*	Amphipoda	
8.65	102	*Gnathiphimedia mandibularis*	Amphipoda	
10.60	103	*Echiniphimedia hodgsoni*	Amphipoda	
11.30	104	*Iphimediella cyclogena*	Amphipoda	
8.50	105	*Paraceradocus gibber*	Amphipoda	
8.65	106	*Liljeborgia georgiana*	Amphipoda	
8.65	107	*Momoculodes scabriculosus*	Amphipoda	
8.65	108	*Uristes gigas*	Amphipoda	
8.50	109	*Eurythenes gryllus*	Amphipoda	
8.65	110	*Bathypanoploea schellenbergi*	Amphipoda	
9.30	111	*Pseudorchomene coatsi*	Amphipoda	
8.65	112	*Heterophoxus videns*	Amphipoda	
8.65	113	*Haplocheira plumosa*	Amphipoda	
8.65	114	*Oradarea edentata*	Amphipoda	
4.90	115	*Djerboa furcipes*	Amphipoda	
8.65	116	*Rhachotropis antarctica*	Amphipoda	
4.88	117	*Themisto gaudichaudii*	Amphipoda	
6.18	118	*Primno macropa*	Amphipoda	
8.09	119	*Notocrangon antarcticus*	Decapoda	
7.03	120	*Chorismus antarcticus*	Decapoda	
7.82	121	*Nematocarcinus lanceopes*	Decapoda	
3.03	122	*Rhincalanus gigas*	Copepoda	
3.71	123	*Calanus propinquus*	Copepoda	
3.85	124	*Calanoides acutus*	Copepoda	
2.78	125	*Metridia gerlachei*	Copepoda	
7.00	126	*Euchaeta antarctica*	Copepoda	
5.69	127	*Eucopia australis*	Mysidacea	
5.84	128	*Euchaetomera antarcticus*	Mysidacea	
6.36	129	*Antarctomysis maxima*	Mysidacea	

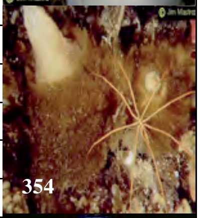
Trophic Position	Code	Taxonomy	Common Name	Illustration
10.26	130	*Ceratoserolis meridionalis*	Isopoda	
8.64	131	*Frontoserolis bouveri*	Isopoda	
11.50	132	*Natatolana obtusata*	Isopoda	
11.28	133	*Natatolana oculata*	Isopoda	
6.56	134	*Natatolana meridionalis*	Isopoda	
7.28	135	*Munna globicauda*	Isopoda	
11.80	136	*Serolis bouveri*	Isopoda	
7.25	137	*Serolis polita*	Isopoda	
8.64	138	*Gnathia calva*	Isopoda	
8.23	139	*Glyptonotus antarcticus*	Isopoda	
8.64	140	*Austrosignum grande*	Isopoda	
10.73	141	*Aega antarctica*	Isopoda	
8.64	142	*Arcturidae*	Isopoda	
5.04	143	*Conchoecia hettacra*	Ostracoda	
4.90	144	*Alacia hettacra*	Ostracoda	
4.90	145	*Alacia belgicae*	Ostracoda	
4.90	146	*Metaconchoecia isocheira*	Ostracoda	
4.90	147	*Boroecia antipoda*	Ostracoda	
4.76	148	*Conchoecia antipoda*	Ostracoda	
	149	*Nototanais antarcticus*	Tanaidacea	
	150	*Peraeospinosus pushkini*	Tanaidacea	
	151	*Nototanais dimorphus*	Tanaidacea	
6.83	152	*Eudorella splendida*	Cumacea	
6.83	153	*Vaunthompsonia indermis*	Cumacea	
6.83	154	*Camylaspis maculata*	Cumacea	
6.83	155	*Diastylis mawsoni*	Cumacea	
6.83	156	*Ekleptostylis debroyeri*	Cumacea	
7.71	157	*Pentanymphon antarcticum*	Pantopoda	
7.53	158	*Ammothea carolinensis*	Pantopoda	
9.60	159	*Colossendeis scotti*	Pantopoda	
8.50	160	*Nymphon gracillimum*	Pantopoda	
1.80	161	*Pelegobia longicirrata*	Polychaeta	
8.49	162	*Rhynchonereella bongraini*	Polychaeta	
9.89	163	*Laetmonice producta*	Polychaeta	
9.91	164	*Harmothoe spinosa*	Polychaeta	
9.46	165	*Harmothoe crosetensis*	Polychaeta	
9.46	166	*Harmothoe hartmanae*	Polychaeta	
8.70	167	*Polyeunoa laevis*	Polychaeta	 © Bjørn Gulliksen
9.60	168	*Barrukia cristata*	Polychaeta	
11.80	169	*Eulagisca gigantea*	Polychaeta	
10.50	170	*Eunoe spica*	Polychaeta	
8.49	171	*Eunoe hartmanae*	Polychaeta	
8.49	172	*Eunoe spica spicoides*	Polychaeta	
4.97	173	*Vanadis antarctica*	Polychaeta	
8.49	174	*Pista spinifera*	Polychaeta	
5.15	175	*Phyllocomus crocea*	Polychaeta	

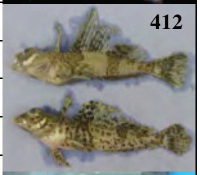
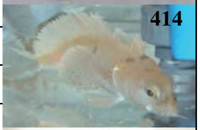
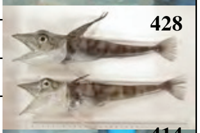
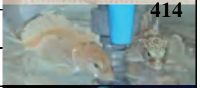
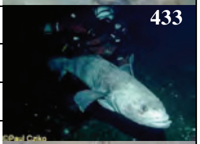
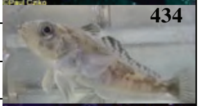
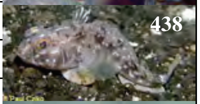
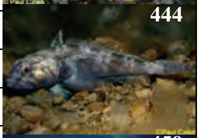
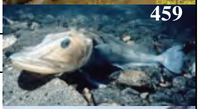
Trophic Position	Code	Taxonomy	Common Name	Illustration
7.23	176	*Terebella ehlersi*	Polychaeta	 188
8.49	177	*Eucranta mollis*	Polychaeta	
6.64	178	*Promachocrinus kerguelensis*	Crinoida	
7.11	179	*Anthometra adriani*	Crinoida	
11.01	180	*Acodontaster conspicuus*	Asteroida	
10.85	181	*Acodontaster capitatus*	Asteroida	
10.42	182	*Acodontaster hodgsoni*	Asteroida	 189
9.80	183	*Bathybiaster loripes*	Asteroida	
11.83	184	*Cuenotaster involutus*	Asteroida	
11.01	185	*Diplasterias brucei*	Asteroida	
8.75	186	*Luidiaster gerlachei*	Asteroida	
9.42	187	*Labidiaster annulatus*	Asteroida	
11.01	188	*Lophaster gaini*	Asteroida	
11.01	189	*Notasterias armata*	Asteroida	 192 © Bjørn Gulliksen
11.01	190	*Solaster dawsoni*	Asteroida	
11.01	191	*Odontaster meridionalis*	Asteroida	
11.01	192	*Odontaster validus*	Asteroida	
8.82	193	*Kampylaster incurvatus*	Asteroida	
14.78	194	*Cycethra verrucosa mawsoni*	Asteroida	
11.17	195	*Notasterias stolophora*	Asteroida	
14.37	196	*Notioceramus anomalus*	Asteroida	 203
10.08	197	*Perknaster sladeni*	Asteroida	
11.01	198	*Pteraster affinis aculeatus*	Asteroida	
13.33	199	*Perknaster densus*	Asteroida	
11.01	200	*Perknaster fuscus antarcticus*	Asteroida	
10.10	201	*Macroptychaster accrescens*	Asteroida	 204
10.86	202	*Lysasterias perrieri*	Asteroida	
9.86	203	*Psilaster charcoti*	Asteroida	
9.92	204	*Porania antarctica*	Asteroida	
11.59	205	*Porania antarctica glabra*	Asteroida	
7.32	206	*Ophioperla koehleri*	Ophiuroida	 213
6.00	207	*Ophionotus victoriae*	Ophiuroida	
9.40	208	*Ophioceres incipiens*	Ophiuroida	
6.90	209	*Ophiurolepis brevirima*	Ophiuroida	
7.32	210	*Ophiurolepis gelida*	Ophiuroida	
7.00	211	*Ophiosparte gigas*	Ophiuroida	 217
7.32	212	*Ophiacantha vivipara*	Ophiuroida	
7.32	213	*Ophiacantha antarctica*	Ophiuroida	
9.44	214	*Astrotoma agassizii*	Ophiuroida	
7.32	215	*Astrochlamys bruneus*	Ophiuroida	
7.32	216	*Gorgonocephalus chilensis*	Ophiuroida	
5.98	217	*Sterechinus neumayeri*	Echinoida	 220
8.90	218	*Sterechinus antarcticus*	Echinoida	
9.25	219	*Ctenocidaris gigantea*	Cidaroida	
9.58	220	*Ctenocidaris spinosa*	Cidaroida	
9.25	221	*Notocidaris mortenseni*	Cidaroida	

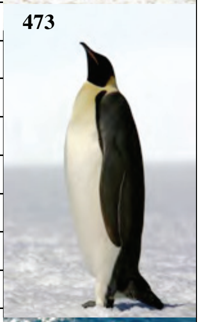
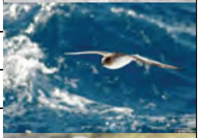
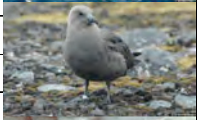
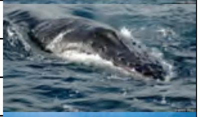
Trophic Position	Code	Taxonomy	Common Name	Illustration
9.60	222	*Abatus curvidens*	Irregularia	
7.83	223	*Abatus cavernosus*	Irregularia	
7.39	224	*Abatus nimrodi*	Irregularia	
7.39	225	*Abatus shackeltoni*	Irregularia	
9.25	226	*Austrocidaris canaliculata*	Cidaroida	
9.25	227	*Aporocidaris milleri*	Cidaroida	
9.25	228	*Ctenocidaris perrieri*	Cidaroida	
9.25	229	*Ctenocidaris geliberti*	Cidaroida	
7.69	230	*Mesothuria lactea*	Holothuria	
6.30	231	*Achlyonice violaecuspidata*	Holothuria	
6.44	232	*Bathyplotes gourdoni*	Holothuria	
8.44	233	*Bathyplotes bongraini*	Holothuria	
7.69	234	*Scotoplanes globosa*	Holothuria	
7.69	235	*Molpadia musculus*	Holothuria	
11.50	236	*Ypsilocucumis turricata*	Holothuria	
8.88	237	*Psolidium incertum*	Holothuria	
7.69	238	*Trachythyone parva*	Holothuria	
7.69	239	*Laetmogone wyvillethompsoni*	Holothuria	
7.69	240	*Pseudostichopus mollis*	Holothuria	
7.69	241	*Pseudostichopus villosus*	Holothuria	
7.69	242	*Elpidia glacialis*	Holothuria	
7.69	243	*Chiridota weddellensis*	Holothuria	
6.40	244	*Ekmocucumis steineni*	Holothuria	
7.69	245	*Ekmocucumis turqueti*	Holothuria	
7.69	246	*Abyssocucumis liouvillei*	Holothuria	
5.90	247	*Psolus dubiosus*	Holothuria	
6.97	248	*Psolus charcoti*	Holothuria	
6.33	249	*Psolus antarcticus*	Holothuria	
6.95	250	*Echinopsolus antarcticus*	Holothuria	
7.69	251	*Ekmocucumis grandis*	Holothuria	
5.47	252	*Taeniogyrus contortus*	Holothuria	
4.83	253	*Silicularia rosea*	Hydrozoa	
4.83	254	*Tubularia ralphii*	Hydrozoa	
4.83	255	*Oswaldella antarctica*	Hydrozoa	
4.83	256	*Monocaulus parvula*	Hydrozoa	
4.67	257	*Rhodalia miranda*	Siphonophora	
6.62	258	*Atolla wyvillei*	Siphonophora	
2.60	259	*Dimophyes arctica*	Siphonophora	
5.05	260	*Diphyes antarctica*	Siphonophora	
4.67	261	*Bargmannia sp*	Siphonophora	
6.20	262	*Solmundella bitentaculata*	Scyphozoa	
6.20	263	*Dipulmaris antarctica*	Scyphozoa	
6.20	264	*Desmonema glaciale*	Scyphozoa	
4.92	265	*Periphylla periphylla*	Scyphozoa	
9.88	266	*Urticinopsis antarctica*	Actinaria	
9.88	267	*Isotealia antarctica*	Actinaria	

Trophic Position	Code	Taxonomy	Common Name	Illustration
9.88	268	*Edwardsia meridionalis*	Actinaria	
9.88	269	*Isosicyonis alba*	Actinaria	
6.32	270	*Primnoisis antarctica*	Gorgonaria	
5.34	271	*Gersemia antarctica*	Gorgonaria	
5.34	272	*Clavularia frankliniana*	Gorgonaria	
6.24	273	*Primnoella spp*	Gorgonaria	
5.40	274	*Ainigmaptilon antarcticus*	Gorgonaria	
5.20	275	*Armadillogorgia cyathella*	Gorgonaria	
6.32	276	*Alcyonium antarcticum*	Alcyonaria	
6.32	277	*Anthomastus bathyproctus*	Alcyonaria	
8.78	278	*Nuttallochiton mirandus*	Polyplacophora	
8.49	279	*Callochiton gaussi*	Polyplacophora	
7.37	280	*Notaeolidia gigas*	Gastropoda	
12.10	281	*Austrodoris kerguelensis*	Gastropoda	
7.37	282	*Trophon longstaffi*	Gastropoda	
7.37	283	*Tritonia antarctica*	Gastropoda	
7.37	284	*Aegires albus*	Gastropoda	
10.80	285	*Bathydoris clavigera*	Gastropoda	
7.37	286	*Tritoniella belli*	Gastropoda	
11.89	287	*Harpovoluta charcoti*	Gastropoda	
7.37	288	*Puncturella conica*	Gastropoda	
10.24	289	*Neobuccinum eatoni*	Gastropoda	
7.70	290	*Marseniopsis mollis*	Gastropoda	
6.50	291	*Marseniopsis conica*	Gastropoda	
9.60	292	*Parmaphorella mawsoni*	Gastropoda	
7.37	293	*Amauropsis rossiana*	Gastropoda	
7.37	294	*Newnesia antarctica*	Gastropoda	
7.37	295	*Falsimargarita gemma*	Gastropoda	
7.37	296	*Marginella ealesa*	Gastropoda	
7.37	297	*Pontiothauma ergata*	Gastropoda	
7.37	298	*Probuccinum tenuistriatum*	Gastropoda	
6.18	299	*Nacella concinna*	Gastropoda	
2.48	300	*Clione limacina*	Pteropoda	
2.48	301	*Clione antarctica*	Pteropoda	
2.48	302	*Clio pyramidata*	Pteropoda	
2.48	303	*Limacina helicina antarctica*	Pteropoda	
9.30	304	*Pareledone charcoti*	Octopoda	
8.75	305	*Pareledone antarctica*	Octopoda	
6.55	306	*Psychroteuthis glacialis*	Squid	
6.55	307	*Morotheuthis ingens*	Squid	
6.55	308	*Alluroteuthis antarcticus*	Squid	
6.55	309	*Galitheuthis glacialis*	Squid	
6.90	310	*Kondakovia longimana*	Squid	
6.55	311	*Gonatus antarcticus*	Squid	
6.55	312	*Mesonychoteuthis hamiltoni*	Squid	
6.55	313	*Martialia hyadesi*	Squid	

Trophic Position	Code	Taxonomy	Common Name	Illustration
7.07	314	*Cyclocardia astartoides*	Bivalvia	
6.48	315	*Yolida eightsi*	Bivalvia	
5.65	316	*Laternula elliptica*	Bivalvia	
7.19	317	*Limopsis lillei*	Bivalvia	
8.26	318	*Limopsis marionensis*	Bivalvia	
5.28	319	*Lissarca notorcadensis*	Bivalvia	
2.88	320	*Propeleda longicaudata*	Bivalvia	
3.48	321	*Cadulus dalli antarcticus*	Scaphopoda	
7.22	322	*Dentalium majorinum*	Scaphopoda	
12.50	323	*Cinachyra antarctica*	Porifera	
9.20	324	*Cinachyra barbata*	Porifera	
6.29	325	*Bathydorus spinosus*	Porifera	
5.58	326	*Iophon radiatus*	Porifera	
11.00	327	*Kirkpatrickia variolosa*	Porifera	
4.53	328	*Rossella racovitzae*	Porifera	
3.90	329	*Stylocordyla borealis*	Porifera	
6.29	330	*Homaxinella balfourensis*	Porifera	
6.29	331	*Scolymastra joubini*	Porifera	
6.29	332	*Latrunculia apicalis*	Porifera	
6.29	333	*Latrunculia brevis*	Porifera	
6.29	334	*Tetilla leptoderma*	Porifera	
6.29	335	*Haliclona dancoi*	Porifera	
6.29	336	*Mycale acerata*	Porifera	
4.66	337	*Rossella antarctica*	Porifera	
5.71	338	*Rossella tarenja*	Porifera	
6.29	339	*Haliclona tenella*	Porifera	
6.29	340	*Clathria pauper*	Porifera	
6.29	341	*Calyx arcuarius*	Porifera	
6.29	342	*Isodyctia toxophila*	Porifera	
6.29	343	*Isodyctia cavicornuta*	Porifera	
6.29	344	*Isodyctia steifera*	Porifera	
6.29	345	*Axociella nidificata*	Porifera	
7.61	346	*Rossella nuda*	Porifera	
6.29	347	*Tenorium papillatum?*	Porifera	
6.29	348	*Tenorium semisuberites*	Porifera	
6.29	349	*Tedania oxeata*	Porifera	
6.29	350	*Tedania tantula*	Porifera	
6.29	351	*Tedania vanhoeffeni*	Porifera	
6.29	352	*Phorbas areolatus*	Porifera	
6.29	353	*Phorbas glaberrima*	Porifera	
6.29	354	*Polymastia invaginata*	Porifera	
6.29	355	*Polymastia isidis*	Porifera	
6.29	356	*Scolymastra joubini*	Porifera	
5.49	357	*Beroe cucumis*	Ctenophora	
5.49	358	*Lyrocteis flavopallidus*	Ctenophora	
5.49	359	*Callianira antarctica*	Ctenophora	

Trophic Position	Code	Taxonomy	Common Name	Illustration
12.55	360	*Baseodiscus antarcticus*	Nemertean	
11.40	361	*Lineus longifissus*	Nemertean	
8.63	362	*Parborlasia corrugatus*	Nemertean	
6.70	363	*Phascolion strombi*	Sipuncula	
7.05	364	*Golfingia nordenskjoeldi*	Sipuncula	
7.05	365	*Golfingia mawsoni*	Sipuncula	
7.05	366	*Golfingia ohlini*	Sipuncula	
7.05	367	*Golfingia anderssoni*	Sipuncula	
7.05	368	*Golfingia margaritacea*	Sipuncula	
8.18	369	*Alomasoma belyaevi*	Echiurida	
6.99	370	*Echiurus antarcticus*	Echiurida	
8.33	371	*Hamingia spp*	Echiurida	
8.20	372	*Maxmuelleria faex*	Echiurida	
4.76	373	*Alloeoflustra angusta*	Bryozoa	
4.80	374	*Camptoplites tricornis*	Bryozoa	
4.76	375	*Nematoflustra flagellata*	Bryozoa	
4.76	376	*Austroflustra vulgaris*	Bryozoa	
4.63	377	*Melicerita obliqua*	Bryozoa	
4.76	378	*Systenopora contracta*	Bryozoa	
3.13	379	*Flustra antarctica*	Bryozoa	
4.76	380	*Fasciculipora ramosa*	Bryozoa	
4.76	381	*Reteporella hippocrepis*	Bryozoa	
4.76	382	*Lageneschara lyrulata*	Bryozoa	
4.70	383	*Isoschizoporella tricuspis*	Bryozoa	
4.76	384	*Cabasea curvata ??*	Bryozoa	
4.76	385	*Chondriovovelum adeliensis ??*	Bryozoa	
4.76	386	*Bostrychopora dentata*	Bryozoa	
6.23	387	*Liothyrella uva*	Brachiopoda	
6.70	388	*Magellania joubini*	Brachiopoda	
6.70	389	*Magellania fragilis*	Brachiopoda	
6.70	390	*Crania lecointei*	Brachiopoda	
6.70	391	*Composothyris racovitzae ??*	Brachiopoda	
6.52	392	*Liothyrella uva antarctica*	Brachiopoda	
5.33	393	*Eukrohnia hamata*	Chaetognatha	
5.01	394	*Sagitta gazellae*	Chaetognatha	
5.16	395	*Sagitta marri*	Chaetognatha	
5.76	396	*Sagitta maxima*	Chaetognatha	
6.60	397	*Cephalodiscus spp*	Pterobranchia	
6.19	398	*Molgula pedunculata*	Ascidian	
6.19	399	*Ascidia challengeri*	Ascidian	
6.19	400	*Corella eumyota*	Ascidian	
6.19	401	*Aplidium vastum*	Ascidian	
6.19	402	*Synoicum adareanum*	Ascidian	
6.56	403	*Cnemidocarpa verrucosa*	Ascidian	
6.19	404	*Sycozoa sigillinoides*	Ascidian	
6.19	405	*Pyura bouvetensis*	Ascidian	

Trophic Position	Code	Taxonomy	Common Name	Illustration
6.19	406	*Pyura discoveryi*	Ascidian	
6.19	407	*Pyura setosa*	Ascidian	
6.19	408	*Pyura tunicata ??*	Ascidian	
0.42	409	*Salpa thompsoni*	Salpa	
0.42	410	*Salpa gerlachei*	Salpa	
0.42	411	*Ihlea racovitzai*	Salpa	
12.00	412	*Artedidraco orianae*	Pisces	
11.84	413	*Artedidraco loennbergi*	Pisces	
12.53	414	*Artedidraco shackeltoni*	Pisces	
13.50	415	*Dolloidraco longedorsalis*	Pisces	
11.83	416	*Pogonophryne marmorata*	Pisces	
11.63	417	*Pogonophryne phyllopogon*	Pisces	
13.61	418	*Pogonophryne permitini*	Pisces	
11.41	419	*Pogonophryne scotti*	Pisces	
13.61	420	*Pogonophryne barsukovi*	Pisces	
10.67	421	*Cygnodraco mawsoni*	Pisces	
9.58	422	*Gerlachea australis*	Pisces	
10.74	423	*Gymnodraco acuticeps*	Pisces	
9.84	424	*Prionodraco evansii*	Pisces	
10.08	425	*Racovitzia glacialis*	Pisces	
8.23	426	*Chaenodraco wilsoni*	Pisces	
11.74	427	*Chionodraco hamatus*	Pisces	
11.20	428	*Chionodraco myersi*	Pisces	
12.25	429	*Cryodraco antarcticus*	Pisces	
12.79	430	*Dacodraco hunteri*	Pisces	
10.11	431	*Pagetopsis maculatus*	Pisces	
12.30	432	*Aethotaxis mitopteryx*	Pisces	
9.07	433	*Dissostichus mawsoni*	Pisces	
9.43	434	*Trematomus eulepidotus*	Pisces	
9.03	435	*Trematomus lepidorhinus*	Pisces	
12.57	436	*Trematomus loennbergii*	Pisces	
8.17	437	*Trematomus nicolai*	Pisces	
10.69	438	*Trematomus pennellii*	Pisces	
10.85	439	*Trematomus scotti*	Pisces	
9.04	440	*Pleuragramma antarcticum*	Pisces	
11.98	441	*Notothenia marmorata*	Pisces	
11.98	442	*Notothenia coriiceps*	Pisces	
11.12	443	*Trematomus bernacchii*	Pisces	
9.08	444	*Trematomus hansoni*	Pisces	
11.60	445	*Macrourus holotrachis*	Pisces	
9.57	446	*Macrourus whitsoni*	Pisces	
8.46	447	*Electrona antarctica*	Pisces	
11.75	448	*Harpagifer antarcticus*	Pisces	
9.22	449	*Bathylagus antarcticus*	Pisces	
8.52	450	*Notolepis coatsi*	Pisces	
8.32	451	*Gymnoscopelus braueri*	Pisces	

Trophic Position	Code	Taxonomy	Common Name	Illustration
8.32	452	*Gymnoscopelus opisthopterus*	Pisces	
8.32	453	*Gymnoscopelus nicholsi*	Pisces	
8.05	454	*Protomyctophum bolini*	Pisces	
9.99	455	*Pagetopsis macropterus*	Pisces	
8.88	456	*Muraenolepis marmoratus*	Pisces	
10.04	457	*Muraenolepis microps*	Pisces	
13.83	458	*Pachycara brachycephalum*	Pisces	
8.11	459	*Champsocephalus gunnari*	Pisces	
6.71	460	*Fulmarus glacialoides*	Aves	
5.57	461	*Thalassoica antarctica*	Aves	
6.25	462	*Halobaena caerulea*	Aves	
6.47	463	*Daption capense*	Aves	
7.19	464	*Pagodroma nivea*	Aves	
7.84	465	*Pterodroma brevirostris*	Aves	
12.13	466	*Macronectes halli*	Aves	
12.13	467	*Macronectes giganteus*	Aves	
6.65	468	*Procellaria aequinoctialis*	Aves	
8.28	469	*Oceanites oceanicus*	Aves	
5.40	470	*Sterna vittata*	Aves	
5.85	471	*Sterna paradisaea*	Aves	
6.38	472	*Pachyptila desolata*	Aves	
10.28	473	*Aptenodytes forsteri*	Penguin	
8.54	474	*Pygoscelis adeliae*	Penguin	
6.08	475	*Lobodon carcinophagus*	Seal	
7.75	476	*Hydrurga leptonyx*	Seal	
8.01	477	*Arctocephalus gazella*	Seal	
6.91	478	*Mirounga leonina*	Seal	
9.26	479	*Ommatophoca rossii*	Seal	
13.92	480	*Leptonychotes weddelli*	Seal	
10.17	481	*Balaenoptera musculus*	Whale	
10.17	482	*Balaenoptera physalus*	Whale	
10.17	483	*Balaenoptera acutorostrata*	Whale	
10.17	484	*Physeter macrocephalus*	Whale	
10.17	485	*Megaptera novaeangliae*	Whale	
10.17	486	*Orcinus orca*	Whale	
10.50	487	*Lagenorhynchus cruciger*	Dolphin	
10.50	488	*Tursiops truncates*	Dolphin	

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