From: Ute Jacob, Aaron Thierry, Ulrich Brose, Wolf E. Arntz, Sofia Berg, Thomas Brey, Ingo Fetzer, Tomas Jonsson, Katja Mintenbeck, Christian Möllmann, Owen Petchey, Jens O. Riede and Jennifer A. Dunne, The Role of Body Size in Complex Food Webs: A Cold Case. In Andrea Belgrano and Julia Reiss, editors:
Advances in Ecological Research, Vol. 45,
Amsterdam, The Netherlands, 2011, pp. 181-223.
ISBN: 978-0-12-386475-8

Academic press.

The Role of Body Size in Complex Food Webs: A Cold Case

UTE JACOB,[1,*] AARON THIERRY,[2,3] ULRICH BROSE,[4]
WOLF E. ARNTZ,[5] SOFIA BERG,[6] THOMAS BREY,[5]
INGO FETZER,[7] TOMAS JONSSON,[6] KATJA MINTENBECK,[5]
CHRISTIAN MÖLLMANN,[1] OWEN L. PETCHEY,[8] JENS O. RIEDE[4]
AND JENNIFER A. DUNNE[9,10]

[1]*Institute for Hydrobiology and Fisheries Science, University of Hamburg, Grosse Elbstrasse 133, Hamburg, Germany*
[2]*Department of Animal and Plant Sciences, Alfred Denny Building, University of Sheffield, Western Bank, Sheffield, United Kingdom*
[3]*Microsoft Research, JJ Thompson Avenue, Cambridge, United Kingdom*
[4]*J.F. Blumenbach Institute of Zoology and Anthropology, Systemic Conservation Biology Group, Georg-August University Göttingen, Göttingen, Germany*
[5]*Alfred Wegener Institute for Polar and Marine Research, P.O. Box 120161, Bremerhaven, Germany*
[6]*Ecological Modelling Group, Systems Biology Research Centre, University of Skövde, Skövde, Sweden*
[7]*Department of Environmental Microbiology, Helmholtz Centre for Environmental Research—UFZ, Permoserstr. 15, Leipzig, Germany*
[8]*Institute of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, Zürich, Switzerland*
[9]*Santa Fe Institute, Santa Fe, New Mexico, USA*
[10]*Pacific Ecoinformatics and Computational Ecology Lab, Berkeley, California, USA*

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*Corresponding author. E-mail: ute.jacob@uni-hamburg.de

ADVANCES IN ECOLOGICAL RESEARCH VOL. 45 0065-2504/11 $35.00

DOI: 10.1016/B978-0-12-386475-8.00005-8

ABSTRACT

Human-induced habitat destruction, overexploitation, introduction of alien species and climate change are causing species to go extinct at unprecedented rates, from local to global scales. There are growing concerns that these kinds of disturbances alter important functions of ecosystems. Our current understanding is that key parameters of a community (e.g. its functional diversity, species composition, and presence/absence of vulnerable species) reflect an ecological network's ability to resist or rebound from change in response to pressures and disturbances, such as species loss. If the food web structure is relatively simple, we can analyse the roles of different species interactions in determining how environmental impacts translate into species loss. However, when ecosystems harbour species-rich communities, as is the case in most natural systems, then the complex network of ecological interactions makes it a far more challenging task to perceive how species' functional roles influence the consequences of species loss. One approach to deal with such complexity is to focus on the functional traits of species in order to identify their respective roles: for instance, large species seem to be more susceptible to extinction than smaller species. Here, we introduce and analyse the marine food web from the high Antarctic Weddell Sea Shelf to illustrate the role of species traits in relation to network robustness of this complex food web. Our approach was threefold: firstly, we applied a new classification system to all species, grouping them by traits other than body size; secondly, we tested the relationship between body size and food web parameters within and across these groups and finally, we calculated food web robustness. We addressed questions regarding (i) patterns of species functional/trophic roles, (ii) relationships between species functional roles and body size and (iii) the role of species body size in terms of network robustness. Our results show that when

analyzing relationships between trophic structure, body size and network structure, the diversity of predatory species types needs to be considered in future studies.

I. INTRODUCTION

Human activity is affecting ecosystems on a global scale to such an extent that few, if any, pristine ecosystems remain. This begs the question as to what characterises an undisturbed food web and how human induced disturbances such as habitat destruction, overexploitation, introduction of alien species and climate change might be expected to affect the structure and functioning of ecosystems (Dirozo and Raven, 2003). Indeed, there are growing concerns that disturbances on ecosystems, via changes in species richness, species composition and trophic structure will affect and seriously threaten important ecosystem functions (Thomas *et al*., 2004). In the light of these potential threats, a key question ecologists must now answer is how will such losses affect the diversity, structure and functioning of the world's ecosystems?

Attempting to answer this question has stimulated much of the interest in understanding the relationships between biodiversity and ecosystem functioning (Schulze and Mooney, 1993) and has led to numerous experimental studies over the past couple of decades (Balvanera *et al*., 2006; Cardinale *et al*., 2006; Loreau *et al*., 2001, 2002; Naeem *et al*., 1994; Petchey and Gaston, 2006; Petchey *et al*., 2004a; Tilman, 1991). These and other studies have shown that there is not necessarily a simple linear relationship between biodiversity and ecosystem function and have led to a more recent focus on functional diversity instead of species richness *per se* and on how to identify and characterise functionally significant components of biodiversity (Díaz and Cabido, 2001; Petchey *et al*., 2004b; Reiss *et al*., 2009).

Clearly, the effects of species loss ultimately have to be studied in natural systems to understand the full range of possible responses within the complex, multispecies networks of interacting taxa, such as described within the context of food web research (Reiss *et al*., 2009). Here, loss of a few species can potentially trigger a cascade of extinctions and other marked changes in food web structure (Bascompte *et al*., 2005; Borer *et al*., 2005).

There is increasing evidence that unexpected cascades of species extinctions and the pathways of restoration and recovery depend on the complex nature of species-rich communities (Bascompte and Stouffer, 2009; Dunne *et al*., 2004). From a conservation perspective, information on species functional roles is therefore desirable if we are to predict the likelihood of species extinctions and their potential effects on structure and function of the entire ecosystem (Memmott, 2009).

Dynamical and structural food web models, which describe the interactions between multiple species, have often focused on the relationship between complexity and stability in ecological communities, and this approach has a long history (e.g. MacArthur, 1955; May, 1972; McCann, 2000; McCann *et al.*, 1998, Tilman and Downing, 1994). They have the potential to increase our understanding of the effects of perturbations on the structure and functioning of ecosystems and can be used as predictive tools in ecosystem management, but only recently have such models ceased to be based on networks that are randomly ordered and parameterized (Brose *et al.*, 2008; Otto *et al.*, 2007). Traditionally, food webs are illustrated by a food web graph and described by various statistical food web metrics (such as average food chain length, number/fraction of basal, intermediate and top species, etc.). These are used to capture the trophic complexity of these webs and, as such, they are useful, but they also have limitations. First of all, these tools may capture important aspects of trophic structure but might reveal little about the functioning of the system. For example, how robust is the food web to disturbances and what is the contribution of individual species to community robustness? To address this issue, species characteristics that affect community-level properties need to be identified, and the distribution of these characteristics among the constituent species needs to be described and analyzed. This calls for augmenting traditional food web descriptions with additional information on species characteristics that affect community-level properties. There are now growing efforts to incorporate data on organismal traits into food web analyses. Recent approaches include the trivariate or so-called MN-web (a food web with data on body sizes, *M*, and abundance, *N*, of species; after Brown *et al.*, 2011; Cohen *et al.*, 2003; Jonsson *et al.*, 2005; Layer *et al.*, 2010, 2011; McLaughlin *et al.*, 2010; Mulder *et al.*, 2011; O'Gorman *et al.*, 2010), the trophochemical web (a food web with stoichiometric data on species, Sterner and Elser, 2002) and a growing awareness of the importance of body size for many species traits and, by extension, food web attributes (e.g. Brose *et al.*, 2006a,b; Riede *et al.*, 2011; Woodward *et al.*, 2005). Several size-based approaches to estimate trophic interaction strengths and to parameterize food web models have also recently been developed (e.g. Berg *et al.*, 2011; Brose *et al.*, 2008; O'Gorman and Emmerson, 2010; Otto *et al.*, 2007) as well as new techniques to analyse community viability (Ebenman and Jonsson, 2005) and the contribution of every species to community robustness (Berg *et al.*, 2011). Taken together, these new developments in food web ecology have the potential for yielding an improved understanding of controls on food web structure, as well as elucidating the ways in which perturbations may affect natural ecosystems (Woodward *et al.*, 2010a). Much of this work is still in its infancy, and the possible insights gained from these approaches have only started to be explored. We assume that the functional characteristics of the species that make up a food web (i.e. foraging behaviour and feeding strategy) will affect the properties of the entire community, and this should therefore enable us to develop a classification scheme for the functional roles of consumers.

Recent research has shown that species from higher trophic levels (Pauly *et al.*, 1998), large-bodied or slow-growing species, with late maturity tend to decline or go extinct more rapidly than those that are smaller (Cardillo, 2003; Layer *et al.*, 2011; McKinney, 1997). This suggests that some life-history traits like body size are linked to susceptibility to extinction and thus may be more likely to trigger secondary extinctions. Body size is a useful 'super-trait' for collapsing many functional attributes of a given species into a single, relatively easy to measure dimension. Along with temperature, it largely determines an individual's basal metabolic rate and its growth rate, which in turn are associated with natural mortality rates, longevity, age at maturity and reproductive output (Brose *et al.*, 2005a,b; Castle *et al.*, 2011; Ings *et al.*, 2009; Peters, 1983; Woodward *et al.*, 2010a; Yvon-Durocher *et al.*, 2011).

A recent study (Riede *et al.*, 2011) has shown that predator body mass increases with trophic level across a variety of predator types and across ecosystems (marine, stream, lake and terrestrial). These results supported theoretical predictions that predators are, on an average, larger then their prey and that they are, on average, more similar in size to their prey at higher trophic levels than at the base of the food web (Jonsson *et al.*, 2005; Layman *et al.*, 2005; Romanuk *et al.*, 2011). There are some apparent exceptions, including interactions between herbivore and plants, parasite–host relationships and benthic stream invertebrates as well as some marine benthic invertebrates, for which a different kind of size–structure seems to apply, that is, different feeding strategies enable most benthic invertebrates to feed on prey items larger then themselves (Riede *et al.*, 2011).

Most food web studies are from relatively species-poor networks (i.e. low species/node numbers), and thus fairly simply structured networks, such as Tuesday Lake (Cohen *et al.*, 2003; Jonsson *et al.*, 2005), and/or from communities that to some extent have been disturbed, such as the acidic Broadstone stream (Woodward *et al.*, 2005). Few studies are from species-rich, highly complex communities, and for this reason, our knowledge about what characterises such systems is poor. Further, for large, species-rich food webs, a food web graph and traditional food web statistics can do little more than conveying a fraction of the immense complexity of these entangled webs (e.g. Woodward *et al.*, 2008), and new complementary ways of describing food web structure that are linked to functional attributes are needed.

We aimed to address this gap in our current knowledge by characterising the species-rich and pristine Weddell Sea food web and developing a new classification scheme for the functional roles of consumers to describe and analyse the trophic complexity of this system. The Weddell Sea food web data represent a unique opportunity to analyse an exceptionally large and relatively undisturbed complex community from a large and globally important three-dimensional ecosystem within the marine Antarctic (Arntz *et al.*, 1994; 1997). In contrast to the previous pioneering trophic studies of the Weddell Sea ecosystem, which focused on a simple pelagic food chain (Tranter, 1982), the data set analyzed here reveals an extraordinarily complex food web that includes the benthos (see Brose *et al.*, 2006a,b; Jacob, 2005). This complexity reflects the high species numbers (Brey *et al.*, 1994; Gutt *et al.*, 2004), the great variety of foraging strategies (e.g. Brenner *et al.*, 2001; Dahm, 1996; Nyssen *et al.*, 2002), the enormous range in body mass of species and the large proportion of omnivorous species in the system (Jacob *et al.*, 2003; 2005).

Because of the highly resolved nature of the data, we were able to classify the key functional roles of many species. We did this by focussing on consumers in this food web and developing a new classification scheme (i.e. sorting consumers into 11 different categories) which takes different consumer traits into account and includes feeding strategy (predator, grazer, etc.), prey type (herbivore, etc.), motility and habitat. Based on the recent theoretical advances described above, we assume that these consumer characteristics and their body size will determine food web properties and that we can therefore analyse the contribution of different species categories to community robustness.

Food web robustness estimates the impact of species loss on one aspect of food web stability: that is, its potential to experience secondary extinctions based on its topology (*sensu* Dunne *et al.*, 2002). To investigate how robust the Weddell Sea food web is to the loss of species, we carried out a topological extinction analysis (Dunne *et al.*, 2002, 2004; Staniczenko *et al.*, 2010). In this approach, computer simulations are used to investigate how susceptible a food web is to sequential collapse as a result of secondary extinction cascades.

To summarize, we focus on what traits characterise the consumers in a large pristine food web and how the robustness of this food web depends on the sequence in which these species are assumed to go extinct. We aimed to explore (i) how body size is correlated with network structure (i.e. the trophic level of a species or its generality/vulnerability) over all species in the Weddell Sea and across a variety of consumer feeding types and (ii) the role of species characteristics such as body size regarding network robustness to provide first steps towards the understanding on how body size of a species constraints the likelihood of extinctions.

II. METHODS

A. The Weddell Sea Data Set

The Southern Ocean (Figure 1) ecosystem exhibits a number of unique features, including ~25 million years of bio-geographic isolation (Barnes, 2005; Clarke, 1985; Hempel, 1985) and, in the form of the annual formation

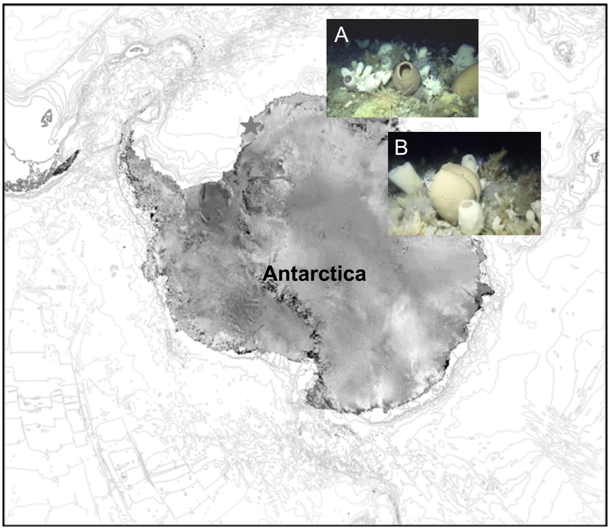

Figure 1 Map of Antarctica. Grey star indicates the study area. Photographs (©Julian Gutt, AWI) illustrate the three-dimensional structure of the benthic Weddell Sea community (A) and the habitat provisioning nature of most of the species (B).

and retreat of sea ice, the geographically most extensive seasonal environmental oscillation pattern in the world. Consequently, there are a number of unusual ecological features, such as a high degree of endemism (Arntz *et al.*, 1994, 1997) and the occupation of the 'pelagic swarm fish niche' by euphausiid crustaceans (Bergstrom and Chown, 1999; Ichii and Kato, 1991).

The high Antarctic Weddell Sea shelf (Figure 1) is situated between 74 and 78°S with a length of approximately 450 km. Water depth varies from 200 to 500 m. Shallower areas are covered by continental ice, which forms the coastline along the eastern and southern part of the Weddell Sea. Due to the weight of the continental ice, the shelf edge lies 500–600 m below sea level. The shelf area contains a complex three-dimensional habitat with large biomass, intermediate to high diversity in comparison to boreal benthic communities and a spatially patchy distribution of organisms (Arntz *et al.*, 1994; Dayton, 1990; Teixido *et al.*, 2002).

The early 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), with little attention being paid to organisms below the size of krill or to members of the benthic food web (Clarke, 1985). However, the rich epibenthic communities in the Weddell Sea (Arntz *et al.*, 1994) are dominated by large filter feeding sponges which serve as habitats and food sources for numerous other benthic invertebrates and vertebrates and which therefore support the high species richness observed (e.g. see photographs in Figure 1A and B). Most of the Weddell Sea food web consumers are benthic invertebrates and fish species, with four trophic entities (phytodetritus, sediment, bacteria and particulate organic matter (POM)), forming important basal resources (Hall and Raffaelli, 1991; Warren, 1989).

We compiled a species list that encompasses 489 consumer and resource species from the high Antarctic Weddell Sea (over 500 publications were analyzed and standardized: for a full description of the methods used and a full list of these publications see Jacob, 2005). This marine food web, which includes all the food web data available for the high Antarctic Weddell Sea collected since 1983, is one of the most highly resolved marine food webs documented to date, although it is a summary web that ignores seasonal changes. Diet composition of each species was observed from a combination of field observations and stomach content analyses performed between 2001 and 2004 (see Jacob, 2005). Expert ecologists specialized in different species assisted with identification and sample provision. A list of taxonomic keys used can be found in Jacob (2005). In some species, that is, benthic grazers and suspension feeders, poor taxonomic resolution of prey items would have biased estimates. Here, we used information obtained in the laboratory about these species' size, behaviour and stable isotope signatures (Brose *et al*., 2005a; Jacob *et al*., 2005) to deduce their feeding habits. Stable isotope analysis was performed for ~600 species and ~3100 individuals in total and included mainly sponges, fishes and benthic invertebrates. In brief, stable isotope (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 (Fry, 1988). δ^{13}C signatures are commonly used as carbon source tracers, whereas δ^{15}N values are a useful tool for detecting the trophic position and therefore the trophic hierarchy of the system (Post, 2002). 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) and Jacob *et al*. (2005). 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 NA2500 elemental analyzer via a THERMO/Finnigan Conflo II-interface. Stable isotope ratios are given in the conventional delta notation (d^{13}C; d^{15}N) relative to atmospheric nitrogen and PDB (PeeDee Belemnite standard).

For the food web construction, following the approach of Martinez (1991), a directional feeding link was assigned to any pair of species A and B whenever an investigator reports that A consumes B. Species were not divided further into larvae, juveniles or adults but treated as 'adults': consequently, with the data used here, we cannot address ontogenetic diet shifts.

The average body mass of the species populations was either directly measured (>90%) or in case of marine mammals and seabirds taken from published accounts (Brose *et al.*, 2005a).

B. Functional Consumer Classification of the Weddell Sea Food Web

Although characterising the relationship between ecosystem functioning and biodiversity is a challenging task, it is widely accepted that functional diversity of organisms sustains ecosystem functioning (e.g. Loreau *et al.*, 2001; Reiss *et al.*, 2009; Schulze and Mooney, 1993). This, however, raises the fundamental issue of how best to classify a functional species and how to assign functional traits. That is, what are the characteristics that determine the effect of a species on an ecosystem? Categorising different types of predation is one way to classify the extent to which species interact with each other. Instead of focusing on what they eat (which is covered by the traditional food web approach of who-eats-whom), we here classify consumers by feeding mode, and the general nature of the interaction (i.e. herbivorous, carnivorous or omnivorous) between predator and prey species. More specifically, we consider the feeding strategy, habitat, and mobility of the consumer and trophic type/position of the prey as important characteristics of consumer species. We suggest that these are useful additions to traditional descriptions of food web structure that will aid in linking food web structure to ecosystem functioning.

In this chapter, consumer species are grouped into 11 categories based on four suites of traits: feeding strategy, prey type, motility and habitat. Within each of these four groupings, four sub-groups were identified, outlined below.

The four main feeding strategies considered are:

(1) *Predator*: If the consumer feeds upon the prey species that it has directly killed, either via an active hunt for prey or via a sit-and-wait strategy for prey to approach within striking distance, it is considered a predator. Such a consumer need not consume the entirety of their prey to fall into this category but only parts of the prey. In contrast, parasites do not necessarily kill their hosts.

(2) *Scavenger*: If, in at least some of the feeding interactions that the consumer takes part, the prey species has already been killed by some previous event, then the consumer is considered a scavenger. As above, the entire prey item need not to be consumed entirely during the interaction.

(3) *Grazer*: A consumer species that feeds by grazing. In the process, they may either kill their prey species (like zooplankton species preying on

unicellular algae) or merely damage it (as in the case of herbivorous urchins only preying on a small part of benthic macroalgae).

(4) *Filtering*: A consumer that actively or passively filters their prey species out of the water column, that is, a suspension feeder.

A second set of traits that encompasses four main prey types, which are:

(1) *Herbivore*: A consumer that feeds on plant material only.
(2) *Carnivore*: A consumer that feeds on other animals only.
(3) *Omnivore*: A consumer that feeds on both animals and plants, as well as dead and alive material and therefore on more than one trophic level.
(4) *Detritivore*: A consumer that feeds on dead animals and plants and/or dissolved organic matter only.

The third trait set deals with mobility and habitat measures and distinguishes the various mechanisms for maintaining position and moving around in the marine environment. Each species was assigned to a mobility category according to whether it is (1) a 'sessile or passive floater', (2) a 'crawler', (3) a 'facultative swimmer', or (4) an 'obligate swimmer'.

The fourth and last trait set describes the physical position of a species within the environment. The species are described as (1) benthic, if the species lives on the seafloor; (2) pelagic, if the species lives close to the surface; (3) benthopelagic, if it moves between and links both environments; or (4) land-based, if the consumer is not aquatic but feeds predominantly in the marine realm.

Applying these classifications, we derived 11 groups, (bearing in mind that not all combinations are possible): carnivorous benthic predators (e.g. most fish species and nemertines), carnivorous benthic suspension feeders (e.g. the hydrozoan *Tubularia ralphii* or copepods, Orejas, 2001), carnivorous pelagic predators (e.g. squids and fishes), carnivorous land-based predators (e.g. the Leopard seal), detritivorous/herbivorous grazers (e.g. most sea urchins), herbivorous/detritivorous benthic suspension feeders (e.g. all Porifera), omnivorous benthic predators (e.g. amphipods), omnivorous benthic predator/scavengers (e.g. most seastars), omnivorous benthopelagic predators (e.g. fishes), omnivorous land-based predators/scavengers (e.g. seabirds) and omnivorous pelagic predators (e.g. omnivorous copepods).

C. Food Web Parameters

Many summarizing indices or food web metrics have been proposed previously to allow for comparisons between different food webs across ecosystems (e.g. Cohen *et al.*, 1993; Jonsson *et al.*, 2005; Pimm, 1982; Pimm *et al.*, 1991). Conventional descriptors of food webs are based on the number of nodes or species, S, in a food web and the number of links, L, between them (Hall and Raffaelli, 1993).

A food chain is an ordered sequence of at least two species that runs from a basal species (i.e. a primary producer or detritus) to a top predator. Food chain length is the number of links within this particular path (Hall and Raffaelli, 1993; Pimm, 1982).

Linkage density (L/S) is the number of links per species (S), connectance (C), the proportion of realised links within a web, is calculated as $2 \times L/(S^2 - S)$ (Hall and Raffaelli, 1993; Warren, 1989), linkage complexity is calculated by $S \times C$ (Briand, 1985). Trophic vulnerability (V) and trophic generality (G) of a species are the numbers of its predator and prey species, respectively (Schoener, 1989).

With respect to the number of links from detritus 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 between phytodetritus and any species that feeds upon it. This would change all parameters significantly and make the Weddell Sea system even more unique in terms of linkage density and generality.

There are various ways to calculate the trophic height of a species within a food web. The prey averaged trophic height is the TL calculation many prior studies have used, which is equal to 1 plus the mean trophic height of all the consumer's trophic resources (Williams and Martinez, 2004). Here, we use the short-weighted trophic height, where the prey averaged trophic height is weighted by the shortest chain within the network, as it is a better estimate of trophic height (Williams and Martinez, 2008).

D. Data Analysis: Statistics, Extinction Scenarios and Robustness of Weddell Sea Food Web

To explore whether species body mass was correlated with trophic level as well as whether a consumer's trophic generality and vulnerability (e.g. Memmott *et al.*, 2000) are related to the functional consumer classifications, we conducted simple pairwise correlations between body size and trophic level for all parameters for the entire set of species. We also conducted this analysis for all consumers combined (i.e. ignoring categories). The analysis was performed using R.

To investigate robustness of the Weddell Sea food web, we carried out computer simulations that quantified how susceptible the food web was to collapse as a result of secondary extinction cascades. The method employed is as follows: first, a species is removed from the network; following this, any non-basal species that loses all of its prey items, or cannibalistic species that loses all of its prey items except itself, are deemed to have gone secondarily extinct and are then removed from the web (Dunne *et al.*, 2002). The simulation next checks to see if any further extinctions occur as a consequence of the loss of those species which went secondarily extinct. Once the cascade ends, another species is selected for removal (using criteria described below) and the process repeats itself until the web is reduced to half its original species richness. Given this algorithm, basal species may experience primary removals but not secondary extinctions.

The propensity of the web to suffer secondary extinctions (its robustness) is then quantified as the fraction of species that had to be removed in order to result in a loss of at least 50% of the species (i.e. primary species removals plus secondary extinctions). A value of robustness for the web was calculated in the following way:

$$\text{Robustness} = \frac{N-1}{\frac{1}{2}S-1}$$

where N is the number of removals and S is the original species richness. The value of robustness can range from 0 where the web collapsed to half its original species richness following the first removal to 1 in the case where there are no secondary extinctions.

The sequential orders of the species removed (the primary extinctions) are based on specific species traits. In this study, we based the orders on three traits: a species' generality (the number of its prey species), vulnerability (the number of its predator species) and average body mass, removing species in both increasing and decreasing order of each trait. There was also a random order (1000 implementations of which were run), which served as a reference point. Consequently, in total, we had seven distinct extinction orders. Those orders based on a species' links updated the sequence following each round of extinction to take into account links lost in the previous round. If trait values were tied (e.g. if two species had the same number of prey), then the one to be removed was chosen at random. All computer simulations were carried out using R (Code: Thierry unpublished).

III. RESULTS

A. The Weddell Sea Food Web Data Set

The Weddell Sea food web dataset consisted of 488 species (out of which 420 species are consumers, see Appendix), and 16,200 feeding links were documented (Figure 2). This included all the food web data available for the high

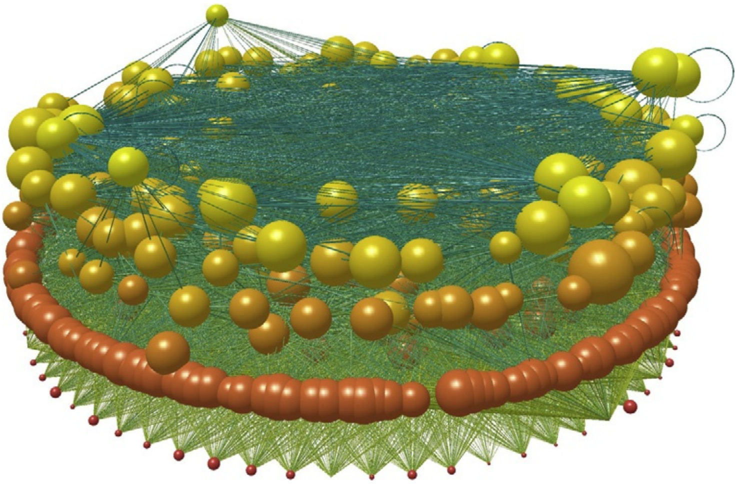

Figure 2 Food web of the high Antarctic Weddell Sea. The vertical axis displays the short-weighted trophic level (Williams and Martinez, 2008). Nodes are scaled relative to body size. Image created with FoodWeb3D (Williams, 2010; Yoon *et al*., 2004).

Antarctic Weddell Sea collected since the 1983. The web had a relatively low connectance of 0.067 in comparison with other marine webs (Table 1), where connectance varied between 0.22 for the Northeast US Shelf system (Dunne *et al*., 2004; Link, 2002) and 0.24 for the Benguela food web (Yodzis, 1998; food web analyzed in Dunne *et al*., 2004). Linkage density was the highest reported so far with 33.19, in comparison with 7.0 for the Benguela web and 17.8 for the Northeastern US Shelf. In the Weddell Sea food web, 6.7% of the Weddell Sea species were top predators, (species with no consumers), 79.7 % were intermediate species (with predators and prey) and 13.6% species were basal species (primary producers which are only prey). The percentages of intermediate and top species were well in the range with the Benguela and Northeastern US Shelf system, but in comparison, the higher percentage of basal species (13.6% vs. 3–7%) reflected the better resolution at the basal level (i.e. Dunne *et al*., 2004). The high degree of omnivory (67.8%) was comparable with omnivory values reported for other marine webs (Dunne *et al*., 2004).

These results reflected common features of the Weddell Sea system, differences in foraging behaviour and the extreme high degree of omnivory of marine consumers, and explained the high linkage density observed. Most fish and marine invertebrate species were opportunistic generalists with a high trophic generality (Brenner *et al*., 2001; Dahm, 1996; Jacob *et al*., 2003, 2005) as indicated by the high number of documented feeding links.

Table 1 Topological food web properties for four marine food webs (Taxa = number of taxa, C = connectance ($L/S2$), L/S = links per species, TL = mean trophic level, T = % top species, I = % intermediate species, B = % basal species, Omn = % omnivorous species)

	S	C	L/S	TL	T	I	B	Omn	Reference
Benguela	29	0.24	7.0	3.2	0	93	7	76	Yodzis (1998)
Caribbean Reef	50	0.22	11.1	2.9	0	94	6	86	Opitz (1996)
NE US Shelf	81	0.22	17.8	3.1	4	94	3	78	Link (2002)
Weddell Sea	492	0.07	33.19	2.5	6.7	79.7	13.6	67.27	Jacob (2005)

Data analyzed in Dunne *et al.* (2004).

B. Functional Consumer Classification of the Weddell Sea Food Web

Average body mass of Weddell Sea shelf species stretched across 22 orders of magnitude, from 1.53×10^{-14} g in small unicellular algae to 8.58×10^{8} g in baleen whales. The trophic level calculated via the diet matrix ranged from 1 in the primary producers up to 4.9 in a predatory scavenging seabird. Detritus and planktonic copepods had the highest vulnerability (220 predators for detritus and 146 for copepods) whereas the nemertean *Parborlasia corrugatus* had no reported predators at all due to its toxic skin (i.e. Jacob, 2005). The species with the highest generality was an omnivorous benthic ophiuroid with 246 prey items. Species with the lowest generality were either benthic grazers who only preyed on detritus, which was problematic, as detritus may consist of an unconsolidated mixture of dead material from many sources.

All mobility levels were represented; sessile or floating species, such as Porifera, bryozoans, detritus and diatoms; crawlers, such as asteroids, echinoids and holothurians; facultative swimmers, such as some amphipods, crinoids and octopods; and obligate swimmers such as copepods, euphausiids, squids, fishes and whales.

The assignment of predatory, feeding type and environmental classifications (i.e. our 11 groups) resulted in five major combined consumer categories and/or species trophic roles. The first group included carnivorous crawling and swimming benthic predators ($n = 34$), swimming carnivorous benthopelagic ($n = 19$), swimming pelagic predators ($n = 35$) and swimming land-based predators ($n = 17$): this group included all those species that only feed on alive prey of trophic heights higher than one.

The second group encompassed omnivorous crawling benthic predators ($n = 24$), swimming omnivorous benthopelagic ($n = 19$) and swimming pelagic predators ($n = 35$): this category included all those species that feed on alive prey of higher trophic levels but also at lower trophic levels (i.e. plants and detritus).

A third group was made up of herbivorous crawling benthic predators ($n=34$), swimming omnivorous benthopelagic ($n=1$) and swimming pelagic predators ($n=23$): this included all those species that feed on lower trophic levels (i.e. plants and detritus).

The fourth groups were omnivorous crawling benthic predators and scavengers ($n=75$), swimming benthopelagic ($n=40$), swimming pelagic ($n=22$) and swimming land-based ($n=4$) omnivorous benthic predators and scavengers, which included all those species that feed on alive prey but also recently killed prey items.

Finally, there was a fifth group that included herbivorous/detritivorous crawling benthic grazers ($n=39$), swimming herbivorous/detritivorous pelagic grazers ($n=12$) and sessile herbivorous/detritivorous benthic suspension feeders ($n=112$).

There was not a significant relationship between a species body mass and trophic level across all consumer species (Figure 3). However, if we separated the data using the feeding classifications listed above, it became clear that there were certain functional groups in which a relationship exists, and others where it was absent. The relationship between trophic level and body size was significant in all true carnivorous predator types (carnivorous pelagic predators r^2: 0.46, p: 0.0056; carnivorous benthic predators r^2: 0.49, p: 0.0527) and in all land-based predator types (carnivorous land-based predators r^2: 0.49, p: 0.0453) (Figure 4, Table 2). In all other trophic types, especially omnivorous predator/scavenger types as well as detritivorous

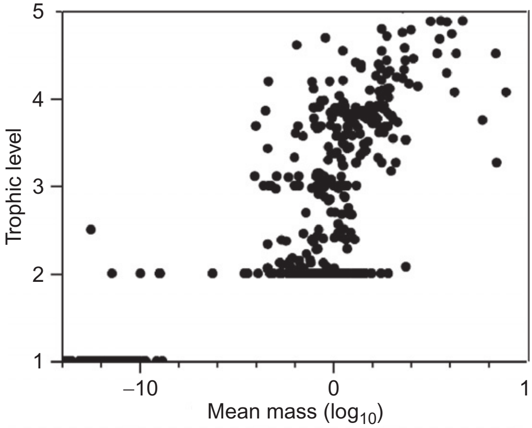

Figure 3 Pairwise relationships between body mass and trophic position across all species of the high Antarctic Weddell Sea.

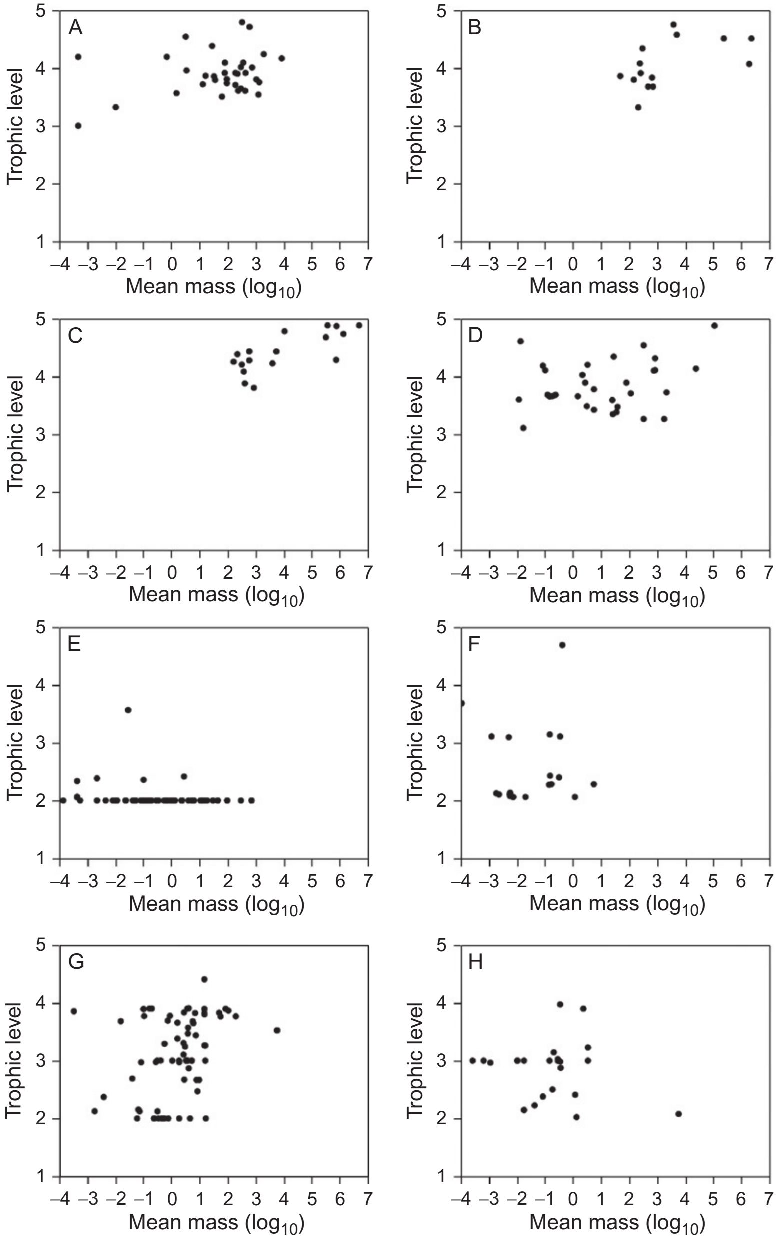

Figure 4 Pairwise relationships between species body size and trophic position separated according predatory types, (A–D) illustrating the albeit weak but significant relationships between trophic level and body mass (A: carnivorous benthic predators, B: carnivorous benthopelagic predators, C: carnivorous land-based and D: carnivorous pelagic predators), (E–H), illustrating the non-significant relationships for the E: suspension feeders, F: omnivorous pelagic predators, G: omnivorous predators and scavengers and H: omnivorous benthic predators.

Table 2 List of the results of the pairwise relationships between species body mass and trophic position across the different dominant consumer types

Predatory type	r^2	p-Value
Carnivorous benthic predator	0.4948	0.0527
Carnivorous benthic suspension feeder	–	–
Carnivorous pelagic predator	0.4587	0.0056
Carnivorous land-based predator	0.4912	0.0453
Detritivorous/herbivorous grazer	–	–
Herbivorous/detritivorous benthic suspension feeder	−0.0377	0.6933
Omnivorous benthic predator	−0.3142	-
Omnivorous benthic predator/scavenger	0.1226	0.2947
Omnivorous benthopelagic predator	–	–
Omnivorous land-based predator/scavenger	0.1542	0.8458
Omnivorous pelagic predator	−0.0664	0.7705

(Correlation coefficient: r^2; Significant probability: p). Values are displayed for predatory groups with numbers larger than 1.

grazers and benthic suspension feeders, the relationship was not significant (Figure 4, Table 2).

The correlations between body size, generality or vulnerability of the Weddell Sea species revealed that the medium-sized species had the highest numbers of predators and prey (Figure 5A and B). An exception here in terms of the vulnerability were the high values for phytodetritus, the various diatoms and POM, which are important basal food sources within the Weddell Sea food web.

C. Extinction Scenarios and Robustness of the Weddell Sea Food Web

When species were systematically removed from the food web in our simulations, potential secondary extinctions varied among the different types of removal sequences we applied (Figure 6). Several clear trends emerged: we found that, of the six trait-based sequences, removing species in order of decreasing vulnerability lead to the fastest collapse of the web (Figure 6). Removing species in order of decreasing generality or increasing mass also caused many secondary extinctions, with the order based on generality collapsing sooner: in both these cases, no secondary extinctions occurred until approximately 75 species were removed (Figure 6). The last three trait-based extinction orders all had a robustness of one and caused no cascades (Figure 6). Random removals normally resulted in high robustness and were

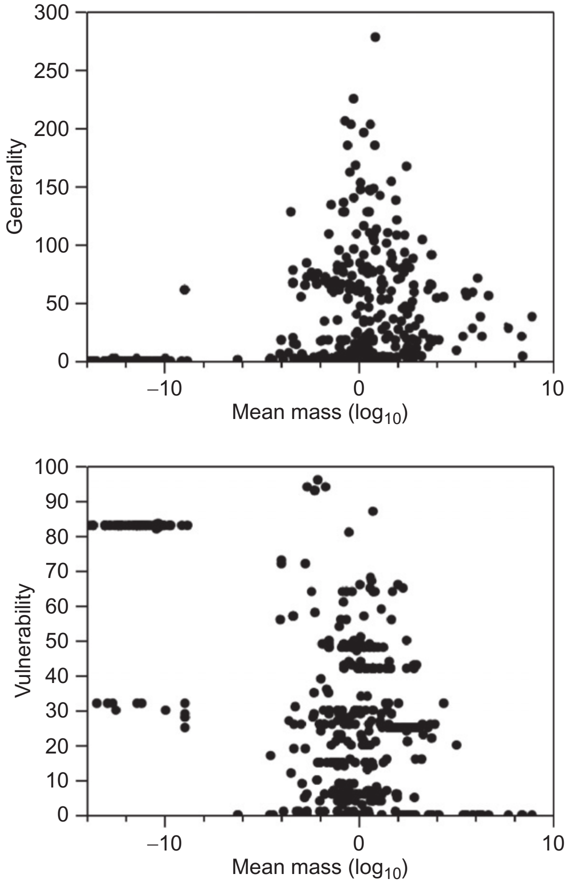

Figure 5 Pairwise relationships between species body mass and generality and body mass and vulnerability.

very rarely found to result in robustness as low as the trait-based orders, which caused collapse due to cascades (Figure 7).

IV. DISCUSSION

A. Implications of This Study

Here, we have demonstrated that grouping species by their traits (other than simply body size) is an ecological meaningful way to approach the complexity found in natural food webs. We have used a popular approach

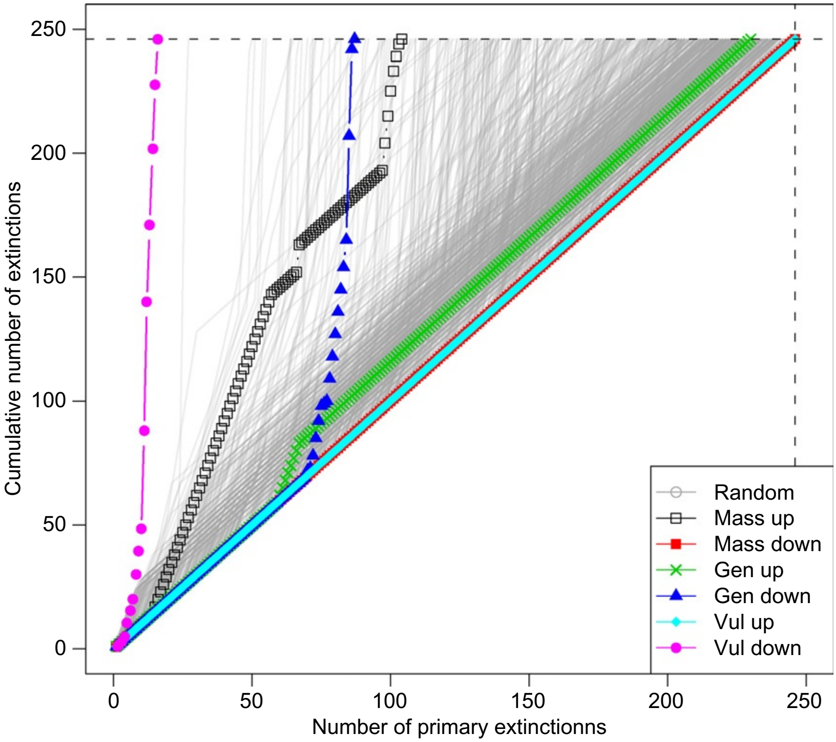

Figure 6 The relationship between the number of species removed and the cumulative number of extinctions (both removals and species which went secondary extinct). The dashed lines indicate the point at which half of the original species richness is reached. The different colours indicate the different extinction orders. Gen stands for generality and Vul for vulnerability. Up stands for removing the species with the lowest value of the trait to the highest. Down stands for removing the species with the highest value of the trait to the lowest.

to analyse this food web complexity by regressing body size of species against food web parameters (trophic height) and found that when we separated the data according to our classification system, that is, when we added additional traits to the information on body size, stronger food web patterns emerged.

Our extinction simulations have shown that it has been the removal of small to medium-sized, and not large, organisms that caused a cascade of secondary extinctions. It appears that larger-bodied species can be lost without causing a direct collapse of the network topology that will affect other species. This finding is surprising given that large species are assumed and have been proven to cause trophic cascades (Raffaelli, 2007).

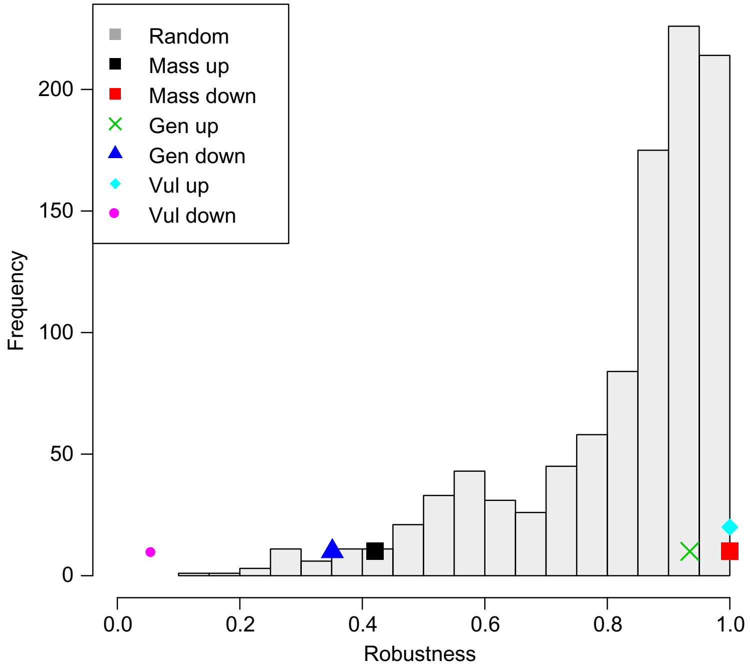

Figure 7 A histogram of the values of robustness for the 1000 random extinction orders. The coloured circles represent the three extinction orders, which resulted in secondary extinctions. The value of robustness was calculated by the method described in the text.

B. The Weddell Sea Food Web and Functional Consumer Classification

With the relatively low level of direct human impact, the Antarctic has been identified as an important case study for the conservation of intact ecosystems (Chown and Gaston, 2002). Certain aspects of the ecology of Antarctic organisms have been reviewed regularly during the past (Arntz *et al*., 1994; Clarke and Johnston, 2003; Dayton, 1990), but with respect to the whole system, deciding where to begin to characterise communities and ecosystems remains a challenging issue; we still do not know how many species are present, although incidence-based coverage estimators of species richness range between 11,000 and 17,000 species (Gutt *et al*., 2004; Clarke and Johnston, 2003). It is even more uncertain as to how these species all interact, so any attempts to characterise local food webs represent important advances in our understanding of Antarctic ecology.

Despite being far from complete (489 species vs. 17,000 potential species), the Weddell Sea food web dataset presented here differs from many other well-known food webs in general in three of its key properties: (i) there are many more feeding links detected than previously reported for marine food webs (e.g. Dunne *et al.*, 2004; Woodward *et al.*, 2010b); (ii) the basal species of the food web are (relatively) highly resolved and not lumped as phytoplankton or primary producers (but see Brown *et al.*, 2011; Layer *et al.*, 2010, 2011) and (iii) detritus is one of the most important food sources as reflected by its high trophic vulnerability (Jacob, 2005; see also Layer *et al.*, 2011, Mulder *et al.*, 2011).

The high number of feeding links can be explained by the generalist feeding nature of most of the species of the Weddell Sea shelf and their well-documented capacity of diet shifting in response to availability (e.g. Brenner *et al.*, 2001; Jacob *et al.*, 2003). This confirms early suggestions by Glasser (1983) that if resource abundances are highly variable and frequently tend to be scarce, as in the high Antarctic indicated by the pulsed phytoplankton bloom, consumers will be more likely be adapted to use many alternative resources, as reflected by the high trophic vulnerability of detritus which is also true for Broadstone Stream (Layer *et al.*, 2011) where all primary consumers depend on detritus as the most important food source.

Here, we use body size as a trait and a number of functional classifications of predatory types to understand the trophic role of the Weddell Sea consumer species. The 'trophic level' of a species is the vertical position within a food web, as defined by all links to or from this species (Gilljam *et al.*, 2011), and as such is typically described by a continuous, rather than an integer, scale. Research on trophic levels focuses on (i) patterns common to all ecological networks (Elton, 1927; Pimm *et al.*, 1991; Riede *et al.*, 2011; Yodzis, 1998); (ii) patterns that distinguish types of systems (Riede *et al.*, 2011) and (iii) patterns that distinguish an organism's role within ecological networks (Elton, 1927; Riede *et al.*, 2011; Williams and Martinez, 2004). Usually, predators are between one and three orders of magnitude larger than their prey (Cohen *et al.*, 2003; Jonsson *et al.*, 2005; Woodward and Hildrew, 2002), and the trophic level is positively correlated with body size, and although there are some notable exceptions (e.g. host–parasite and some host–parasitoid systems; see Henri and Van Veen, 2011, 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; Riede *et al.*, 2011). Across the whole food web, trophic level and body size are often positively related (Jennings *et al.*, 2002; Riede *et al.*, 2011). Although species with a similar maximum body size can evolve to feed at different trophic levels, there are fewer small species feeding at high trophic levels than at low trophic levels (Jennings *et al.*, 2002), and many of these 'unusual' patterns may be due to artefacts arising from the common practice of using species-averaged data (Gilljam *et al.*, 2011; Woodward *et al.*, 2010b).

In general, body size is positively correlated to trophic position and generality of consumers (Cohen *et al.*, 2003; Peters, 1983; Riede *et al.*, 2010, 2011). However, this relationship is poorly developed in the Weddell Sea system. Very large animals can feed on very small prey (whales → myctophid fish → krill → phytoplankton); small omnivorous species (e.g. amphipods, nemertines and gastropods) feed up and down the food chain, seemingly irrespective of their size (Nyssen *et al.*, 2002; Jacob, 2005), and large benthic and pelagic suspension and filter feeders feed on small POM. These findings support a recent study which showed that predators on intermediate trophic levels do not necessarily feed on smaller or prey similar in size but depending on their foraging strategy have a wider prey size range available (Riede *et al.*, 2011).

It needs to be borne in mind that size-based analyses based on species average body size can obscure the size–structure of ecological communities. Gilljam *et al.* (2011) found that prey mass as a function of predator mass was consistently underestimated when species mass averages were used instead of the individual size data. For the Weddell Sea data, ontogenetic stages would certainly shift some of the observed patterns in the sense that in true carnivores the relationship between trophic level and body mass would become even more apparent, whereas in benthic omnivorous predators and scavengers, the pattern observed should not change substantially as the prey size range available for a scavenger remains the same.

Species of intermediate size, such as the ophiuroid *Ophiosparte gigas,* have the highest generality, whereas the most important food source with the highest vulnerability was phytodetritus. There was no strong correlation of generality and body size, intermediate-sized based species have the highest generality whereas larger predators have more specialized diet. This reflects the high degree of complexity of the Weddell Sea shelf ecosystem, which results from the opportunistic feeding behaviour observed (Brenner *et al.*, 2001; Jacob *et al.*, 2003) and from different predatory types of most of the benthic invertebrate species.

When dealing with natural communities at large spatial scales, logistical constraints prevent measuring traits across all species in a perfectly consistent and comparable manner and, consequently, several important caveats concerning the reliability and interpretation of the resulting data come readily to mind. The usefulness of functional feeding categories has not been clearly demonstrated before in marine systems, although it is well established in freshwaters where it has been used for several decades in the context of trophic ecology (e.g. Cummins and Klug, 1979; Ledger *et al.*, 2011). Difficulties with the correct assignment to functional feeding groups have contributed to the inability to consider these metrics previously in marine studies. However, gaining the distribution of predatory types will be useful to understand how ratios of consumer and resource body sizes are correlated to network structure, interaction strength patterns and food web robustness, especially, with respect to predatory types (i.e. benthic predators/ scavengers) where the proposed positive relationship between body mass and trophic level does not hold true (Riede *et al*., 2011). Future research involving the relationships between functional traits and ecosystem functioning, in combination with size-based analyses (e.g. Gilljam *et al*., 2011; Woodward *et al*., 2010b), should aim to focus on the role of different predatory types, however simple the classification might seem, as this information appears to provide meaningful additional insights into network structure beyond those simply related to size *per se*.

Here, as in the vast majority of food web studies to date, we considered a summary food web (cf. webs listed in Ings *et al*., 2009), ignoring potential seasonal changes and differences among ontogenetic stages as well. It is clear that intraspecific variation related to ontogeny, body size (Cianciaruso *et al*., 2009) or diet breadth (Bolnick *et al*., 2003) could comprise a major part of a species trophic role (Gilljam *et al*., 2011; Melián *et al*., 2011; Woodward *et al*., 2010b). Further, because it can facilitate frequency-dependent interactions that can affect a population's stability, the amount of intraspecific competition, fitness-function shapes and the populations' capacity to diversify and to specialize rapidly may be key to understanding network structure and dynamics (Bolnick *et al*., 2003, Yvon-Durocher *et al*., 2011). Future research involving different ontogenetic stages, for example, larval and adult fish, as well as incorporating information on seasonal differences in food web structure and functioning, is clearly needed. Incorporating ontogenetic stages in the Weddell Sea data set would definitely add to the complexity observed, whereas taking into account, seasonal changes have a smaller impact on the overall structure, all herbivores depend on phytodetritus all year round, a slight change will include marine mammals and some seabirds which use the Weddell Sea only in summer as feeding grounds (Jarre-Teichmann *et al*., 1997) although the task is logistically challenging: the results of the current chapter nonetheless represent an important first step before we can move towards these more highly resolved approaches.

C. Extinction Scenarios the Robustness of the Weddell Sea Food Web

The influence of extinction risk on trophic vulnerability and species life histories are both complex and specific to the source of the threat (Purvis *et al*., 2000). Further, such relationships depend on the species sensitivity to a stress that intensifies through time, such as a gradual change in salinity or temperature (Ives and Cardinale, 2004). While the relationship between functional traits and the susceptibility of extinction risk is complex, recent research does suggest some clear and consistent patterns, namely, that smaller species are apparently less vulnerable to extinction than larger species (Cardillo, 2003; McKinney, 1997). In the light of this, it is perhaps heartening that in our topological simulations it was the sequences of deletions based on the removal of small, and not large, organisms that caused a cascade of secondary extinctions. It appears that within the Weddell Sea network, larger bodied species can be lost without causing a direct collapse of the network topology, which is the opposite case in other marine systems, where the loss of large apex predators has lead to multiple trophic cascades (i.e. Myers *et al.*, 2007; Raffaelli, 2007).

We should of course interpret these findings with a great deal of care. A major caveat, which needs to be borne in mind with such topological analysis, is that population dynamics are ignored and therefore no top-down extinctions, or other indirect effects, can occur (Montoya *et al.*, 2009). Further, the strength of the bottom-up extinctions will be reduced in the absence of population dynamics, as species need to lose all their prey items before going extinct and not just part of their diet, this need not be the case in real ecosystems (Ebenman and Jonsson, 2005). There are a range of studies showing the strong effect of top-down control (e.g. Berger *et al.*, 2001; Borrvall and Ebenman, 2006; Estes and Palmisano, 1974; Reisewitz *et al.*, 2006; Terborgh *et al.*, 2006) and the importance of considering interaction strength when analyzing the response of perturbations in ecological communities (e.g. McCann *et al.*, 1998; Montoya *et al.*, 2009; Novak *et al.*, 2011) and hence the analysis of topological robustness should be considered only as a best-case scenario.

Despite these considerations, there are several studies that have used mass-balanced models of population dynamics to examine the role of large whales and the consequences of their loss within the Antarctic food web. These studies indicate weak top-down control in these systems (Bredesen, 2003; Trites *et al.*, 2004) and suggest that the removal of large whales might have little measurable effect on lower trophic levels or on the population dynamics of other species in the food web. It is also worth noting that, in these models, once the populations of large whales were reduced to small numbers, they take a long time to recover (Bredesen, 2003; Trites *et al.*, 2004).

Secondary extinction cascades can occur from a body mass-based sequence of primary extinctions suggesting the importance of trophic size–structure for this system. It is also intriguing that this is despite the lack of any clear relationships between body mass and vulnerability, generality, or trophic level when examined across all species in the network. That is to say, the robustness analysis still makes clear the importance of the smaller species near the base of the food web that provide and channel energy for the many larger species of this system.

Our results also reinforce the findings of other studies regarding the importance of the highly connected species for robustness (Dunne *et al.*, 2002; Eklöf and Ebenman, 2006; Petchey *et al.*, 2008), with both in- and out-links being important. The suddenness of the collapse when removing the most vulnerable species (only approximately 25 primary removals within this sequence were required for the system to collapse to half of its size) reiterates the importance of detritus and planktonic copepods (the two most vulnerable species) for the Antarctic food web. It is also interesting that there is no positive relationship between generality and body mass, unlike as has often been observed in other systems (e.g. Woodward *et al.*, 2005). As has been found in some other studies (e.g. Digel *et al.*, 2011), the Weddell Sea web is perhaps rendered more susceptible to the loss of generalist predators, at least when undergoing a topological-based extinction simulation, and then would be expected in webs with a stronger generality allometry, where the loss of larger more specialized species causes more trophic cascades (Myers *et al.*, 2007).

V. CONCLUSION

Assuming that the emergent behaviour of an ecosystem is, at least partly, dependent on the properties and behaviour of the species it is composed of, we looked into different properties and how they are distributed within the overall ecosystem structure. We only focused on a small number of traits and simple predatory classifications and, although the total number of traits in marine consumers is potentially almost infinite, our data analyzed here and results clearly reflect the generalist trophic ecology of most species in the Weddell Sea.

An understanding of the relations between species functional roles and ecosystem structure is an indispensable step towards the comprehension of change in Antarctic or any other food web structure due to global change and subsequent biodiversity loss and gain (Woodward *et al.*, 2010a). This paves the road towards understanding the role of the functional and life-history traits of species, and the many services provided by ecosystems, the relationship between functional traits and to species taxonomy, ecological network structure, functioning and dynamics.

Our study clearly emphasizes that species body size and species classification in terms of trophic or functional roles are one key to understanding why certain species are abundant while others are rare, and how species functional roles may change in response to species loss.

ACKNOWLEDGEMENTS

This work was stimulated by fruitful discussions with members of the ESF Network SIZEMIC, especially with members of the three European Science Foundation funded SIZEMIC Working Groups led by O. P., U. T., Frank van Veen and Julia Reiss. Katja Mintenbeck is funded by the German Research Foundation (DFG, SSP 1158 Antarktisforschung, Project MI 1391/1).

APPENDIX

Table A1 Species list of the high Antarctic Weddell Sea Food Web

Species	Code	Environment
Actinocyclus actinochilus	1	Pelagic
Actinocyclus spiritus	2	Pelagic
Actinocyclus utricularis	3	Pelagic
Azpeitia tabularis	4	Pelagic
Banquisia belgicae	5	Pelagic
Chaetoceros bulbosum	6	Pelagic
Chaetoceros concavicornis	7	Pelagic
Chaetoceros criophilum	8	Pelagic
Chaetoceros dichaeta	9	Pelagic
Chaetoceros flexuosum	10	Pelagic
Chaetoceros neglectum	11	Pelagic
Chaetoceros pelagicus	12	Pelagic
Chaetoceros socialis	13	Pelagic
Corethron criophilum	14	Pelagic
Coscinodiscus oculoides	15	Pelagic
Cylindrotheca closterium	16	Pelagic
Eucampia antarctica	17	Pelagic
Fragilariopsis curta	18	Pelagic
Fragilariopsis cylindrus	19	Pelagic
Fragilariopsis kerguelensis	20	Pelagic
Fragilariopsis linearis	21	Pelagic
Fragilariopsis nana	22	Pelagic
Fragilariopsis obliquecostata	23	Pelagic
Fragilariopsis pseudonana	24	Pelagic
Fragilariopsis rhombica	25	Pelagic
Fragilariopsis ritscheri	26	Pelagic
Fragilariopsis separanda	27	Pelagic
Fragilariopsis sublinearis	28	Pelagic
Fragilariopsis vanheurckii	29	Pelagic
Manguinea fusiformis	30	Pelagic

Table A1 (*continued*)

Species	Code	Environment
Manguinea rigida	31	Pelagic
Navicula glaciei	32	Pelagic
Navicula schefterae	33	Pelagic
Nitzschia kerguelensis	34	Pelagic
Nitzschia lecointei	35	Pelagic
Nitzschia neglecta	36	Pelagic
Odontella weissflogii	37	Pelagic
Porosira glacialis	38	Pelagic
Porosira pseudodenticulata	39	Pelagic
Proboscia alata	40	Pelagic
Proboscia inermi	41	Pelagic
Proboscia truncata	42	Pelagic
Pseudo-Nitzschia heimii	43	Pelagic
Pseudo-Nitzschia liniola	44	Pelagic
Pseudo-Nitzschia prolongatoides	45	Pelagic
Pseudo-Nitzschia subcurvata	46	Pelagic
Rhizosolenia antennata	47	Pelagic
Stellarima microtrias	48	Pelagic
Thalassiosira antarctica	49	Pelagic
Thalassiosira australis	50	Pelagic
Thalassiosira frenguelliopsis	51	Pelagic
Thalassiosira gracilis	52	Pelagic
Thalassiosira gracilis expecta	53	Pelagic
Thalassiosira gravida	54	Pelagic
Thalassiosira lentiginosa	55	Pelagic
Thalassiosira ritscheri	56	Pelagic
Thalassiosira trifulta	57	Pelagic
Thalassiosira tumida	58	Pelagic
Trichotoxon reinboldii	59	Pelagic
Dictyocha speculum	60	Pelagic
Phaeocystis antarctica	61	Pelagic
Silicioflagellata	62	Pelagic
Bodo saltans	63	Pelagic
Amphidinium hadai	64	Pelagic
Gyrodinium lachryama	65	Pelagic
Parvicorbucula socialis	66	Pelagic
Cassidulinoides parkerianus	67	Benthic
Cibicides refulgens	68	Benthic
Globocassidulina crassa	69	Benthic
Lenticulina antarctica	70	Benthic
Neogloboquadriana pachyderma	71	Benthic
Euphausia crystallorophias	72	Pelagic
Euphausia frigida	73	Pelagic
Thysanoessa macrura	74	Pelagic
Euphausia superba	75	Pelagic

(*continued*)

Table A1 (*continued*)

Species	Code	Environment
Ampelisca richardsoni	76	Benthopelagic
Abyssorchomene rossi	77	Benthopelagic
Abyssorchomene plebs	78	Benthopelagic
Abyssorchomene nodimanus	79	Benthopelagic
Eusirus antarcticus	80	Benthopelagic
Eusirus perdentatus	81	Benthopelagic
Alexandrella mixta	82	Benthopelagic
Tryphosella murrayi	83	Benthopelagic
Waldeckia obesa	84	Benthopelagic
Parschisturella ceruviata	85	Benthopelagic
Paramoera walkeri	86	Benthopelagic
Epimeriella walkeri	87	Benthopelagic
Cyllopus lucasii	88	Pelagic
Hyperiella dilatata	89	Pelagic
Vibilia antarctica	90	Pelagic
Vibilia stebbingi	91	Pelagic
Hyperia macrocephala	92	Pelagic
Epimeria similis	93	Benthopelagic
Epimeria robusta	94	Benthopelagic
Epimeria macrodonta	95	Benthopelagic
Epimeria rubrieques	96	Benthopelagic
Epimeria georgiana	97	Benthopelagic
Melphidippa antarctica	98	Benthopelagic
Oediceroides emarginatus	99	Benthopelagic
Oediceroides calmani	100	Benthopelagic
Maxilliphimedia longipes	101	Benthopelagic
Gnathiphimedia mandibularis	102	Benthopelagic
Echiniphimedia hodgsoni	103	Benthopelagic
Iphimediella cyclogena	104	Benthopelagic
Paraceradocus gibber	105	Benthopelagic
Liljeborgia georgiana	106	Benthopelagic
Momoculodes scabriculosus	107	Benthopelagic
Uristes gigas	108	Benthopelagic
Eurythenes gryllus	109	Benthopelagic
Bathypanoploea schellenbergi	110	Benthopelagic
Pseudorchomene coatsi	111	Benthopelagic
Heterophoxus videns	112	Benthopelagic
Haplocheira plumosa	113	Benthopelagic
Oradarea edentata	114	Benthopelagic
Djerboa furcipes	115	Benthopelagic
Rhachotropis antarctica	116	Benthopelagic
Themisto gaudichaudii	117	Pelagic
Primno macropa	118	Pelagic
Notocrangon antarcticus	119	Benthic
Chorismus antarcticus	120	Benthic
Nematocarcinus lanceopes	121	Benthic
Rhincalanus gigas	122	Pelagic

Table A1 (*continued*)

Species	Code	Environment
Calanus propinquus	123	Pelagic
Calanoides acutus	124	Pelagic
Metridia gerlachei	125	Pelagic
Paraeuchaeta antarctica	126	Benthopelagic
Eucopia australis	127	Benthopelagic
Euchaetomera antarcticus	128	Benthopelagic
Antarctomysis maxima	129	Benthopelagic
Ceratoserolis meridionalis	130	Benthic
Frontoserolis bouvieri	131	Benthic
Natatolana obtusata	132	Benthic
Natatolana oculata	133	Benthic
Natatolana meridionalis	134	Benthic
Munna globicauda	135	Benthic
Serolella bouveri	136	Benthic
Serolis polita	137	Benthic
Gnathia calva	138	Benthic
Glyptonotus antarcticus	139	Benthic
Austrosignum grande	140	Benthic
Aega antarctica	141	Benthic
Arcturidae	142	Benthic
Conchoecia hettacra	143	Benthic
Alacia hettacra	144	Benthic
Alacia belgicae	145	Benthic
Metaconchoecia isocheira	146	Benthic
Boroecia antipoda	147	Benthic
Conchoecia antipoda	148	Benthic
Nototanais antarcticus	149	Benthic
Peraeospinosus pushkini	150	Benthic
Nototanais dimorphus	151	Benthic
Eudorella splendida	152	Benthic
Vaunthompsonia indermis	153	Benthic
Camylaspis maculata	154	Benthic
Diastylis mawsoni	155	Benthic
Ekleptostylis debroyeri	156	Benthic
Pentanymphon antarcticum	157	Benthic
Ammothea carolinensis	158	Benthic
Colossendeis scotti	159	Benthic
Nymphon gracillimum	160	Benthic
Pelagobia longicirrata	161	Pelagic
Rhynchonereella bongraini	162	Benthic
Laetmonice producta	163	Benthic
Harmothoe spinosa	164	Benthic
Harmothoe crosetensis	165	Benthic
Harmotoe hartmanae	166	Benthic
Polyeunoa laevis	167	Benthic
Barrukia cristata	168	Benthic
Eulagisca gigantea	169	Benthic

(*continued*)

Table A1 (*continued*)

Species	Code	Environment
Eunoe spica	170	Benthic
Eunoe hartmanae	171	Benthic
Eunoe spica spicoides	172	Benthic
Vanadis antarctica	173	Benthic
Pista spinifera	174	Benthic
Phyllocomus crocea	175	Benthic
Terebella ehlersi	176	Benthic
Eucranta mollis	177	Benthic
Promachocrinus kerguelensis	178	Benthic
Anthometra adriani	179	Benthic
Acodontaster conspicuus	180	Benthic
Acodontaster capitatus	181	Benthic
Acodontaster hodgsoni	182	Benthic
Bathybiaster loripes	183	Benthic
Cuenotaster involutus	184	Benthic
Diplasterias brucei	185	Benthic
Luidiaster gerlachei	186	Benthic
Labidiaster annulatus	187	Benthic
Lophaster gaini	188	Benthic
Notasterias armata	189	Benthic
Solaster dawsoni	190	Benthic
Odontaster meridionalis	191	Benthic
Odontaster validus	192	Benthic
Kampylaster incurvatus	193	Benthic
Cycethra verrucosa mawsoni	194	Benthic
Notasterias stylophora	195	Benthic
Notioceramus anomalus	196	Benthic
Perknaster sladeni	197	Benthic
Pteraster affinis aculeatus	198	Benthic
Perknaster densus	199	Benthic
Perknaster fuscus antarcticus	200	Benthic
Macroptychaster accrescens	201	Benthic
Lysasterias perrieri	202	Benthic
Psilaster charcoti	203	Benthic
Porania antarctica	204	Benthic
Porania antarctica glabra	205	Benthic
Ophioperla koehleri	206	Benthic
Ophionotus victoriae	207	Benthic
Ophioceres incipiens	208	Benthic
Ophiurolepis brevirima	209	Benthic
Ophiurolepis gelida	210	Benthic
Ophiosparte gigas	211	Benthic
Ophioperla ludwigi	212	Benthic
Ophiacantha antarctica	213	Benthic
Astrotoma agassizii	214	Benthic
Astrochlamys bruneus	215	Benthic
Gorgonocephalus chiliensis	216	Benthic

Table A1 (*continued*)

Species	Code	Environment
Sterechinus neumayeri	217	Benthic
Sterechinus antarcticus	218	Benthic
Ctenocidaris gigantea	219	Benthic
Ctenocidaris spinosa	220	Benthic
Notocidaris mortenseni	221	Benthic
Abatus curvidens	222	Benthic
Abatus cavernosus	223	Benthic
Abatus nimrodi	224	Benthic
Abatus shackeltoni	225	Benthic
Austrocidaris canaliculata	226	Benthic
Aporocidaris milleri	227	Benthic
Ctenocidaris perrieri	228	Benthic
Ctenocidaris gilberti	229	Benthic
Mesothuria lactea	230	Benthic
Achlyonice violaecuspidata	231	Benthic
Bathyplotes gourdoni	232	Benthic
Bathyplotes bongraini	233	Benthic
Scotoplanes globosa	234	Benthic
Molpadia musculus	235	Benthic
Ypsilocucumis turricata	236	Benthic
Psolidium incertum	237	Benthic
Trachythyone parva	238	Benthic
Laetmogone wyvillethompsoni	239	Benthic
Pseudostichopus mollis	240	Benthic
Pseudostichopus villosus	241	Benthic
Elpidia glacialis	242	Benthic
Chiridota weddellensis	243	Benthic
Ekmocucumis steineni	244	Benthic
Ekmocucumis turqueti	245	Benthic
Abyssocucumis liouvillei	246	Benthic
Psolus dubiosus	247	Benthic
Psolus charcoti	248	Benthic
Psolus antarcticus	249	Benthic
Echinopsolus acanthocola	250	Benthic
Ekmocucumis turqueti turqueti	251	Benthic
Taeniogyrus contortus	252	Benthic
Silicularia rosea	253	Benthic
Tubularia ralphii	254	Benthic
Oswaldella antarctica	255	Benthic
Monocaulus parvula	256	Benthic
Rhodalia miranda	257	Pelagic
Atolla wyvillei	258	Pelagic
Dimophyes arctica	259	Pelagic
Diphyes antarctica	260	Pelagic
Bargmannia	261	Pelagic
Solmundella bitentaculata	262	Pelagic
Dipulmaris antarctica	263	Pelagic

(*continued*)

Table A1 (*continued*)

Species	Code	Environment
Desmonema glaciale	264	Pelagic
Periphylla periphylla	265	Pelagic
Urticinopsis antarctica	266	Benthic
Isotealia antarctica	267	Benthic
Edwardsia meridionalis	268	Benthic
Isosicyonis alba	269	Benthic
Primnoisis antarctica	270	Benthic
Gersemia antarctica	271	Benthic
Clavularia frankiliana	272	Benthic
Primnoella	273	Benthic
Ainigmaptilon antarcticus	274	Benthic
Armadillogorgia cyathella	275	Benthic
Alcyonium antarcticum	276	Benthic
Anthomastus bathyproctus	277	Benthic
Nuttallochiton mirandus	278	Benthic
Callochiton gaussi	279	Benthic
Notaeolidia gigas	280	Benthic
Austrodoris kerguelenensis	281	Benthic
Trophon longstaffi	282	Benthic
Tritonia antarctica	283	Benthic
Aegires albus	284	Benthic
Bathydoris clavigera	285	Benthic
Tritoniella belli	286	Benthic
Harpovoluta charcoti	287	Benthic
Puncturella conica	288	Benthic
Neobuccinum eatoni	289	Benthic
Marseniopsis mollis	290	Benthic
Marseniopsis conica	291	Benthic
Parmaphorella mawsoni	292	Benthic
Amauropsis rossiana	293	Benthic
Newnesia antarctica	294	Benthic
Falsimargarita gemma	295	Benthic
Marginella ealesa	296	Benthic
Pontiothauma ergata	297	Benthic
Probuccinum tenuistriatum	298	Benthic
Nacella concinna	299	Benthic
Clione limacina	300	Pelagic
Clione antarctica	301	Pelagic
Clio pyramidata	302	Pelagic
Limacina helicina antarctica	303	Pelagic
Pareledone charcoti	304	Benthic
Pareledone antarctica	305	Benthic
Psychroteuthis glacialis	306	Pelagic
Moroteuthis ingens	307	Pelagic
Alluroteuthis antarcticus	308	Pelagic
Galiteuthis glacialis	309	Pelagic
Kondakovia longimana	310	Pelagic
Gonatus antarcticus	311	Pelagic

Table A1 (*continued*)

Species	Code	Environment
Mesonychoteuthis hamiltoni	312	Pelagic
Martialia hyadesi	313	Pelagic
Cyclocardia astartoides	314	Benthic
Yolida eightsi	315	Benthic
Laternula elliptica	316	Benthic
Limopsis lillei	317	Benthic
Limopsis marionensis	318	Benthic
Lissarca notorcadensis	319	Benthic
Propeleda longicaudata	320	Benthic
Cadulus dalli antarcticum	321	Benthic
Fissidentalium majorinum	322	Benthic
Cinachyra antarctica	323	Benthic
Cinachyra barbata	324	Benthic
Bathydorus spinosus	325	Benthic
Iophon radiatus	326	Benthic
Kirkpatrickia variolosa	327	Benthic
Rossella racovitzae	328	Benthic
Stylocordyla borealis	329	Benthic
Homaxinella balfourensis	330	Benthic
Scolymastra joubini	331	Benthic
Latrunculia apicalis	332	Benthic
Latrunculia brevis	333	Benthic
Tetilla leptoderma	334	Benthic
Haliclona dancoi	335	Benthic
Mycale acerata	336	Benthic
Rossella antarctica	337	Benthic
Rossella tarenja	338	Benthic
Haliclona tenella	339	Benthic
Clathria pauper	340	Benthic
Calyx arcuarius	341	Benthic
Isodyctia toxophila	342	Benthic
Isodyctia cavicornuta	343	Benthic
Isodyctia steifera	344	Benthic
Axociella nidificata	345	Benthic
Rossella nuda	346	Benthic
Tentorium papillatum	347	Benthic
Tentorium semisuberites	348	Benthic
Tedania oxeata	349	Benthic
Tedania tantulata	350	Benthic
Tedania vanhoeffeni	351	Benthic
Phorbas areolatus	352	Benthic
Phorbas glaberrima	353	Benthic
Polymastia invaginata	354	Benthic
Polymastia isidis	355	Benthic
Anoxycalyx joubini	356	Benthic
Beroe cucumis	357	Pelagic
Lyrocteis flavopallidus	358	Pelagic
Callianira antarctica	359	Pelagic

(*continued*)

Table A1 (*continued*)

Species	Code	Environment
Baseodiscus antarcticus	360	Benthic
Lineus longifissus	361	Benthic
Parborlasia corrugatus	362	Benthic
Phascolion strombi	363	Benthic
Golfingia nordenskojoeldi	364	Benthic
Golfingia mawsoni	365	Benthic
Golfingia ohlini	366	Benthic
Golfingia anderssoni	367	Benthic
Golfingia margaritacea margaritacea	368	Benthic
Alomasoma belyaevi	369	Benthic
Echiurus antarcticus	370	Benthic
Hamingia	371	Benthic
Maxmuelleria faex	372	Benthic
Flustra angusta	373	Benthic
Camptoplites tricornis	374	Benthic
Nematoflustra flagellata	375	Benthic
Austroflustra vulgaris	376	Benthic
Melicerita obliqua	377	Benthic
Systenopora contracta	378	Benthic
Flustra antarctica	379	Benthic
Fasciculiporoides ramosa	380	Benthic
Reteporella hippocrepis	381	Benthic
Lageneschara lyrulata	382	Benthic
Isoschizoporella tricuspis	383	Benthic
Caulastraea curvata	384	Benthic
Chondriovelum adeliense	385	Benthic
Bostrychopora dentata	386	Benthic
Liothyrella uva	387	Benthic
Magellania joubini	388	Benthic
Magellania fragilis	389	Benthic
Crania lecointei	390	Benthic
Compsothyris racovitzae	391	Benthic
Liothyrella uva antarctica	392	Benthic
Eukrohnia hamata	393	Pelagic
Pseudosagitta gazellae	394	Pelagic
Sagitta marri	395	Pelagic
Pseudosagitta maxima	396	Pelagic
Cephalodiscus	397	Benthic
Molgula pedunculata	398	Benthic
Ascidia challengeri	399	Benthic
Corella eumyota	400	Benthic
Aplidium vastum	401	Benthic
Synoicum adareanum	402	Benthic
Cnemidocarpa verrucosa	403	Benthic
Sycozoa sigillinoides	404	Benthic
Pyura bouvetensis	405	Benthic
Pyura discoveryi	406	Benthic
Pyura setosa	407	Benthic

Table A1 (*continued*)

Species	Code	Environment
Pyura tunicata	408	Benthic
Salpa thompsoni	409	Pelagic
Salpa gerlachei	410	Pelagic
Ihlea racovitzai	411	Pelagic
Artedidraco orianae	412	Demersal
Artedidraco loennbergi	413	Demersal
Artedidraco skottsbergi	414	Demersal
Dolloidraco longedorsalis	415	Demersal
Pogonophryne marmorata	416	Demersal
Pogonophryne phyllopogon	417	Demersal
Pogonophryne permitini	418	Demersal
Pogonophryne scotti	419	Demersal
Pogonophryne barsukovi	420	Demersal
Cygnodraco mawsoni	421	Demersal
Gerlachea australis	422	Benthopelagic
Gymnodraco acuticeps	423	Demersal
Prionodraco evansii	424	Demersal
Racovitzia glacialis	425	Bathydemersal
Chaenodraco wilsoni	426	Benthopelagic
Chionodraco hamatus	427	Demersal
Chionodraco myersi	428	Demersal
Cryodraco antarcticus	429	Demersal
Dacodraco hunteri	430	Demersal
Pagetopsis maculatus	431	Demersal
Aethotaxis mitopteryx	432	Benthopelagic
Dissostichus mawsoni	433	Pelagic
Trematomus eulepidotus	434	Benthopelagic
Trematomus lepidorhinus	435	Benthopelagic
Trematomus loennbergii	436	Benthopelagic
Trematomus nicolai	437	Benthopelagic
Trematomus pennellii	438	Demersal
Trematomus scotti	439	Demersal
Pleuragramma antarcticum	440	Demersal
Notothenia marmorata	441	Demersal
Notothenia coriiceps	442	Demersal
Trematomus bernacchii	443	Demersal
Trematomus hansoni	444	Benthopelagic
Macrourus holotrachys	445	Benthopelagic
Macrourus whitsoni	446	Benthopelagic
Electrona antarctica	447	Pelagic
Harpagifer antarcticus	448	Demersal
Bathylagus antarcticus	449	Pelagic
Notolepis coatsi	450	Pelagic
Gymnoscopelus braueri	451	Pelagic
Gymnoscopelus opisthopterus	452	Pelagic
Gymnoscopelus nicholsi	453	Pelagic
Protomyctophum bolini	454	Pelagic
Pagetopsis macropterus	455	Demersal

(*continued*)

Table A1 (*continued*)

Species	Code	Environment
Muraenolepis marmoratus	456	Benthopelagic
Muraenolepis microps	457	Benthopelagic
Pachycara brachycephalum	458	Demersal
Champsocephalus gunnari	459	Pelagic
Fulmarus glacialoides	460	Land-based
Thalassoica antarctica	461	Land-based
Halobaena caerulea	462	Land-based
Daption capense	463	Land-based
Pagodroma nivea	464	Land-based
Aphrodroma brevirostris	465	Land-based
Macronectes halli	466	Land-based
Macronectes giganteus	467	Land-based
Procellaria aequinoctialis	468	Land-based
Oceanites oceanicus	469	Land-based
Sterna vittata	470	Land-based
Sterna paradisaea	471	Land-based
Pachyptila desolata	472	Land-based
Aptenodytes forsteri	473	Land-based
Pygoscelis adeliae	474	Land-based
Lobodon carcinophaga	475	Land-based
Hydrurga leptonyx	476	Land-based
Arctocephalus gazella	477	Land-based
Mirounga leonina	478	Land-based
Ommatophoca rossii	479	Land-based
Leptonychotes weddelli	480	Land-based
Balaenoptera musculus	481	Benthopelagic
Balaenoptera physalus	482	Benthopelagic
Balaenoptera acutorostrata	483	Benthopelagic
Physeter macrocephalus	484	Benthopelagic
Megaptera novaeangliae	485	Benthopelagic
Orcinus orca	486	Benthopelagic
Lagenorhynchus cruciger	487	Benthopelagic
Tursiops truncatus	488	Benthopelagic

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