

# Trophic interactions within the Ross Sea continental shelf ecosystem

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The continental shelf of the Ross Sea is one of the Antarctic's most intensively studied regions. We review the available data on the region's physical characteristics (currents and ice concentrations) and their spatial variations, as well as components of the neritic food web, including lower and middle levels (phytoplankton, zooplankton, krill, fishes), the upper trophic levels (seals, penguins, pelagic birds, whales) and benthic fauna. A hypothetical food web is presented. Biotic interactions, such as the role of *Euphausia crystallorophias* and *Pleuragramma antarcticum* as grazers of lower levels and food for higher trophic levels, are suggested as being critical. The neritic food web contrasts dramatically with others in the Antarctic that appear to be structured around the keystone species *Euphausia superba*. Similarly, we suggest that benthic–pelagic coupling is stronger in the Ross Sea than in most other Antarctic regions. We also highlight many of the unknowns within the food web, and discuss the impacts of a changing Ross Sea habitat on the ecosystem.

**Keywords:** Ross Sea; neritic food web; bio–physical coupling; ecosystem function; ecosystem structure; pelagic–benthic coupling

## 1. INTRODUCTION

The Ross Sea continental shelf is a unique region of the Antarctic, both with regard to its physics and its ecology. Its broad shelf (the most extensive in the Antarctic), extreme seasonality (the region being in complete darkness during winter), numerous significant polynyas, extensive ice shelf (the largest in the Antarctic, covering half of the continental shelf), and substantial vertical and horizontal exchanges provide a dynamic environment for the biota. The food web appears to be substantially different from most other areas of the Southern Ocean, which are mostly pelagic overlying a deep benthos. In addition, the climate of the Ross Sea is changing, albeit not necessarily in the same manner as that of areas like the west Antarctic Peninsula (WAP), where temperatures have increased more rapidly than anywhere else on Earth in the past 50 years (Smith *et al.* 1999). Satellite data suggest that ice extent is *increasing* in the Ross Sea region by more than 5% per decade (in comparison, the reduction in the WAP is approximately 7% per decade; Kwok & Comiso 2002), as is the length of the ice season (Parkinson 2002). However, polynyas are increasing in extent as well (Parkinson 2002). For most of the biota, the impacts of these changes are poorly known, but should the trend continue, significantly altered biological dynamics can be expected.

## 2. THE PHYSICAL SETTING

The physical characteristics of the Ross Sea emphasize its unique nature (table 1). It is the largest continental shelf region in the Antarctic, but owing to the isostatic response of the continent to the mass of the ice cap, it remains relatively deep (mean depth is approx. 500 m). The shelf break occurs at approximately 800 m, with the slope reaching 3000 m. The currents on the Ross Sea continental shelf are characterized by a gyre-like circulation (figure 1). This circulation also extends under the ice shelf, although the details of the under-shelf circulation are poorly known. The water that exits is substantially cooled and modified, with potential temperatures less than  $-2^{\circ}\text{C}$  (the extreme temperature is possible due to the reduction in the freezing point with increased pressure). Most currents are coherent throughout the entire water column, and substantial seasonal variability in current velocities occurs (Dinniman *et al.* 2003). The deep canyons at the shelf break affect the deep circulation and facilitate intrusions of modified circumpolar deep water (MCDW) onto the shelf.

Much of the Ross Sea's physical oceanography is dominated by the presence of a large area of reduced pack ice cover surrounded by denser ice concentrations, the Ross Sea polynya. In winter, the polynya is formed by strong katabatic winds from the south that advect ice to the north. In turn, cold air temperatures drive significant ice formation, and the resultant fresh water removal creates cold, salty and therefore dense water that sinks, driving convective overturn. Aperiodic intrusions of MCDW also provide heat that increases ice ablation at the surface. Few oceanographic studies

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Table 1. The physical features and characteristics of the Ross Sea continental shelf.

variable	magnitude
area	187 000 km <sup>2</sup>
water depth	mean approximately 600 m (maximum at 1200 m, but with extensive banks (<200 m); shelf break at 800 m)
air temperatures	range from -60 to 10.1°C
water temperature	range from -1.86 to 3.2°C
salinity	range from 34.0 to 34.92 psu
circulation	controlled by bathymetry winds, and coriolis force, that generates the Ross Sea gyre; includes flow under the ice shelf; exchanges with slope via canyons
sediments	shallow areas often ice scoured with many boulders; troughs dominated by diatomaceous ooze with significant organic content
pack ice concentrations	range seasonally and interannually from ice free (except for isolated embayments) to 100% ice cover
polynyas	four described, the largest is the most extensive in the Antarctic
glacial inputs	owing to low temperatures, little run-off; much in the way of subsurface melt and icebergs generated from Ross Ice shelf and coastal glaciers
irradiance	photoperiod from 0 to 24 h; maximum irradiance in summer approximately 60 mol photons m <sup>-2</sup> d <sup>-1</sup>
nutrients	[NO <sub>3</sub> ] ranges from 15 to 30 μM; [Si(OH) <sub>4</sub> ] from 20 to 85 μM; [Fe] from 0.05 to 2 nM

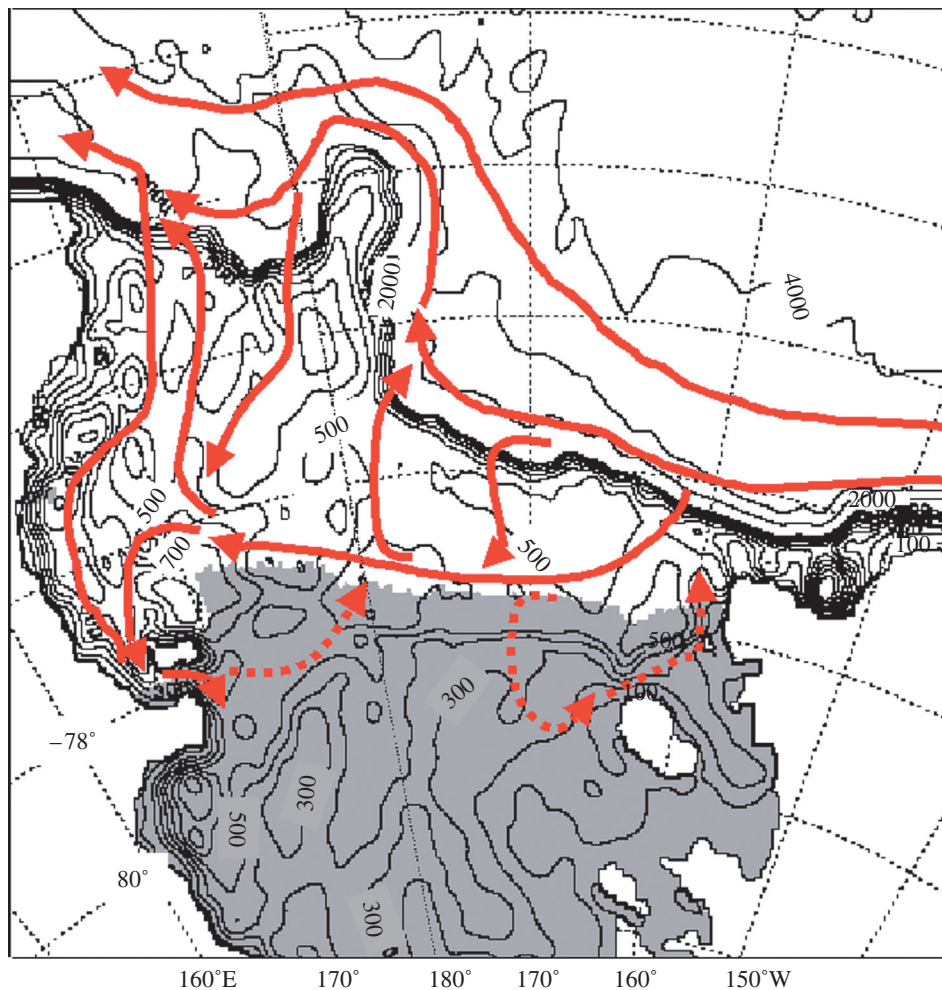


Figure 1. The general circulation of waters on the Ross Sea continental shelf. Shaded area is the location of the Ross Ice Shelf; depth contours in metres; dashed lines under the ice shelf represent currents derived from modelling but few direct observations. After Locarnini (1994), Jacobs & Giulivi (1998) and Dinniman *et al.* (2003).

have been conducted during winter in the Ross Sea, but early spring measurements near the ice shelf have observed a homogeneous mixed layer throughout the entire water column, suggesting that at some locations shelf waters are mixed to the bottom during winter.

Smaller polynyas also occur along the coast of Victoria Land, with notable examples being the Terra

Nova Bay Pennell Bank and the Ross Passage polynyas (Jacobs & Comiso 1989). The seasonal pattern of ice cover is well known from satellite imagery (figure 2; Jacobs & Comiso 1989; Jacobs & Giulivi 1998; Zwally *et al.* 2002). The Ross Sea polynya begins to expand rapidly in November as the heat budget becomes positive, facilitating melting and the cessation of ice

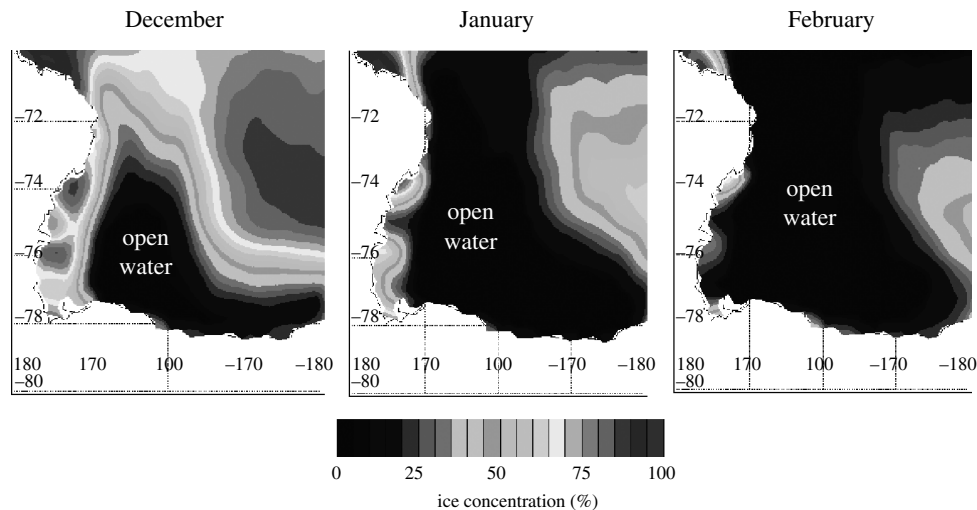


Figure 2. The seasonal progression of ice cover in the Ross Sea. Data provided by the National Snow and Ice Center, Boulder, CO, USA.

formation. The polynya extends to the northwest and east, and by mid-January much of the continental shelf is free of ice. Large variations among years occur, and these may result from large-scale processes controlling air pressure and storms (Jacobs & Comiso 1989; Ainley *et al.* 2005). An additional component is the presence of large icebergs that become grounded and restrict the advection of pack ice off the shelf (Arrigo *et al.* 2002). While icebergs of this size are relatively rare in the experience of humans, they have occurred regularly during the Holocene as the Ross Ice Shelf retreated; their occurrence can result in pack ice concentrations that are far greater than normally observed, and thus can have significant impacts on the food web. Pack ice begins to form in late February and March, and the continental shelf region quickly becomes ice covered with new pack ice by mid-March.

Exchanges with the continental slope and open ocean readily occur. Along the shelf break, upwelling of MCDW leads to the occurrence of a shelf break front (Ainley & Jacobs 1981; Jacobs & Comiso 1989). It has also been found that the Ross Sea is an important site of deep-water formation in association with formation of the Ross Sea polynya; that is, extremely cold, dense waters are formed, cascade off the shelf and expand throughout the southern Pacific sector. The magnitude of this water mass generation remains uncertain, but Locarnini (1994) suggested that the Ross Sea is responsible for nearly one-third of all deep water formed in the Southern Ocean. More recent estimates suggest that the region is responsible for 20% of the Antarctic deep water formed (Orsi *et al.* 1999). Ice (and hence fresh water) is advected off the shelf by winds, and deep-water intrusions onto the shelf also occur channelled by the several deep N–S troughs (Jacobs *et al.* 2002). These intrusions may be biologically important as sources of iron that fuel surface phytoplankton blooms (M. R. Hiscock *et al.* 1996–1997, unpublished work), and can be detected by the temperature and salinity characteristics of these waters, which are significantly different from the water masses on the shelf (figure 3; Jacobs *et al.* 2002). Unfortunately, we do not have a good understanding of the frequency or strength of these incursions.

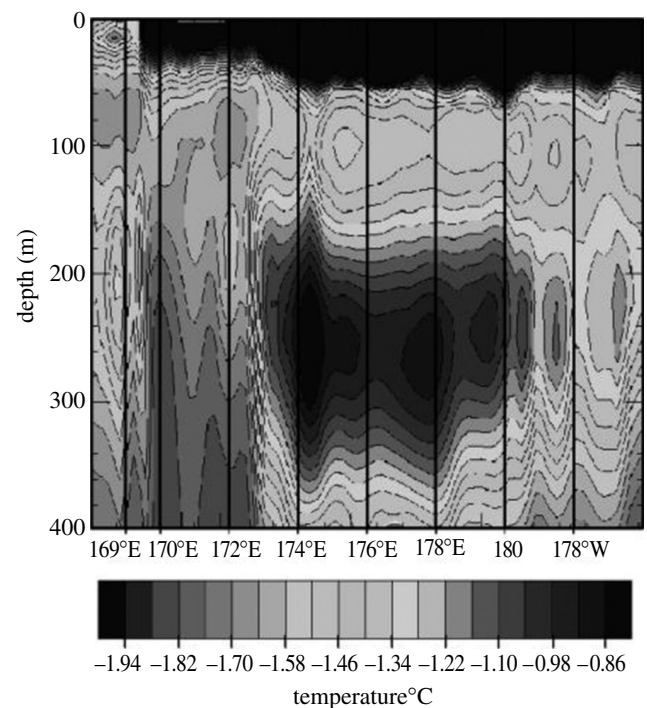


Figure 3. Temperature (°C) of the water in the southern Ross Sea (M. R. Hiscock *et al.* 1996–1997, unpublished work). Waters with a maximum subsurface temperature have their origin from the Antarctic Circumpolar Current and represent a significant cross-shelf flux of water, as well as a micronutrient input to the shelf.

### 3. THE BIOLOGICAL SETTING

The Ross Sea has a diverse biota in both the neritic and the benthic realms, and includes a substantial contribution to the overall diversity from both the ice and the shallow water littoral. Much is known of each of the trophic levels, but despite the long history of study (dating from the explorations of James Clark Ross in the mid-1800s), a great deal remains poorly known, and many biological interactions remain incompletely characterized.

#### (a) Lower trophic levels

The functional groups (groups of species that have a similar, unifying characteristic and ecological role) of

Table 2. Functional groups and the 'critical' species within each group in the Ross Sea.

functional group	critical species
<i>phytoplankton</i>	
diatoms	<i>Corethron coriophyllum</i> , <i>Pseudonitzschia</i> spp., <i>Fragilariopsis</i> spp., <i>Rhizosolenia</i> spp., <i>Thalassiosira</i> spp.
haptophytes	<i>Phaeocystis antarctica</i>
dinoflagellates	—
cryptophytes	—
<i>heterotrophic microplankton</i>	
dinoflagellates	—
choanoflagellates	—
<i>heterotrophic mesozooplankton</i>	
pteropods	<i>Limacina helicina</i>
copepods	<i>Calanoides acutus</i> , <i>Metridia gerlachei</i> , <i>Euchaeta antarctica</i>
euphausiids	<i>Euphausia crystallorophias</i> , <i>Euphausia superba</i> (near the shelfbreak)
<i>nekton</i>	
small fishes	<i>Pleuragramma antarcticum</i> , <i>Trematomus bernacchii</i> , <i>Pagothenia borchgrevinki</i> , myctophids (near the shelfbreak)
large fishes	<i>Dissostichus mawsoni</i>
<i>marine mammals and birds</i>	
seals	<i>Lobodon carcinophagus</i> , <i>Leptonychotes weddelli</i> , <i>Hydrurga leptonyx</i>
penguins	<i>Pygoscelis adeliae</i> , <i>Aptenodytes forsteri</i>
petrels	<i>Pagodroma nivea</i> , <i>Thalassoica antarctica</i>
whales	<i>Orcinus orca</i> , <i>Balaenoptera bonaerensis</i> , <i>Berardius amouxi</i>
<i>benthic fauna/flora</i>	
shallow, hard substratum: macroalgae, sponges, soft corals, amphipods, gastropods, bryozoans, echinoids, asteroids	<i>Himantothallus</i> , <i>Desmarestia</i> , <i>Phyllophora</i> , <i>Homaxinella balfourensis</i> , <i>Alcyonium</i> , <i>Paramoera walkeri</i> , Sertellidae, <i>Sterechinus neumayeri</i> , <i>Odontaster validus</i>
deeper (greater than 100 m), hard substratum: sponges, corals, polychaetes, barnacles, bryozoans	<i>Cinachyra</i> , <i>Errina</i> , <i>Bathylasma corolliforme</i> , <i>Serpula narconensis</i> , Microporellidae, Cabereidae, Tubuliporidae
soft substratum: bivalves, gastropods, polychaetes, echinoids, asteroids, ophiuroids echinoids, corals	<i>Laternula elliptica</i> , <i>Adamussium colbecki</i> , <i>Yoldia eightsi</i> , Syllidae, <i>Ctenocidaris</i> , <i>Acodontaster</i> , <i>Ophionotus</i> , <i>Ophiosparte</i> , <i>Ophiurolepis</i> , <i>Astrotoma</i>

the lower trophic levels, particularly phytoplankton, are well known. Functional groups include the diatoms, haptophytes, dinoflagellates and cryptophytes (table 2), but perhaps just as importantly, several functional groups commonly found in other oceans, such as coccolithophorids, cyanobacteria, chlorophytes and prochlorophytes, are nearly completely absent in the Ross Sea. Therefore, while the dated notion of a simplified, linear food chain supported by diatoms does not exist *sensu stricto*, some of the smaller components of the microbial food web are indeed absent; hence, the mean size of the 'average' primary producer is substantially larger than that of tropical and subtropical regions. The larger size potentially increases the net transfer to the higher trophic levels (e.g. Ryther 1969), but the type of phytoplankton also influences trophic transfer in the region.

Diatoms are common in waters overlying the Ross Sea continental shelf, and can be the dominant members of the phytoplankton. Pennate species (e.g. *Fragilariopsis* spp., *Pseudonitzschia* spp.) form large blooms, particularly near ice edges during summer (Smith & Nelson 1985; Fonda Umani *et al.* 2002; Garrison *et al.* 2003), and contribute substantially to vertical flux of biogenic material either directly or after incorporation into faecal pellets (Smith & Dunbar 1998; Accornero & Gowing 2003). Centric diatoms (e.g. *Corethron coriophyllum*, *Rhizosolenia* spp., *Thalassiosira*

spp.) are ubiquitous components as well. Autotrophic dinoflagellates are more poorly described, but have been detected in significant numbers in spring (Mathot *et al.* 2000). Cryptophytes can occur in large, isolated blooms (Arrigo *et al.* 1999) and seem to require the establishment of strong stratification via glacial run-off.

The haptophytes are another important functional group, dominated in the Ross Sea by *Phaeocystis antarctica*. *Phaeocystis* is known to be critical with regard to biogeochemistry, climate feedbacks and food webs, but its food-web connections in the Ross Sea remain elusive. It produces large amounts of dimethylsulphide (DMS, a volatile organic that is transported great distances and can influence cloud formation; Andreae 1990), has greatly different ratios of particulate C : N : P relative to diatoms (Arrigo *et al.* 1999; Sweeney *et al.* 2000), is largely ungrazed (Smith & Asper 2001), and can export significant quantities of organic matter to depth via aggregate formation (Smith & Dunbar 1998; DiTullio *et al.* 2000), although the majority of the biogenic material is remineralized within the water column (Smith & Asper 2000; Asper & Smith 2003). DMS derivatives, found in ice cores, have also become important proxies for pre-historical trends in ocean productivity (Curran *et al.* 2003). The general seasonal pattern of *P. antarctica* abundance appears to be rapid growth in spring, reaching a maximum in mid-to late December, and a rapid demise in January

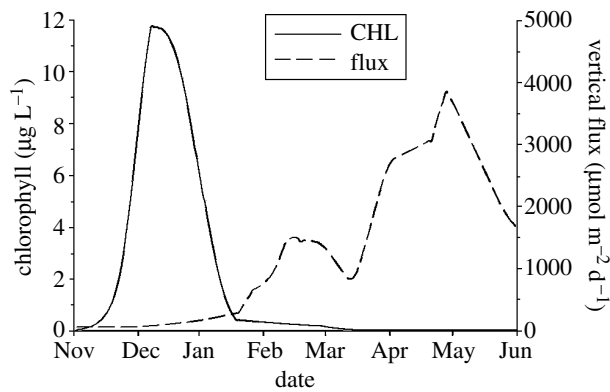


Figure 4. Temporal pattern of *Phaeocystis antarctica* abundance (as chlorophyll; CHL) and the vertical flux of particulate organic carbon to depth in the southern Ross Sea. *P. antarctica* biomass based on Tremblay & Smith (2007); flux data from Collier *et al.* (2000).

(figure 4). Its growth in late December is probably limited by *in situ* iron concentrations, as *P. antarctica* (as well as co-occurring diatoms) appears to become iron limited during summer (Olson *et al.* 2000). Furthermore, the iron requirements of *P. antarctica* are greater than those of diatoms (Coale *et al.* 2003), and coupled with its apparent ability to grow well at low irradiances (Moisan & Mitchell 1999) and relatively low grazing pressures provided by its life cycle (formation of large colonies that cannot be effectively grazed by small herbivores), may allow it to bloom early in the season.

Owing in part to the large amount of sea ice present, cryophilic algae in the Ross Sea are an important source of organic matter for the food web; the dynamics of this flora are better known in the Ross Sea than anywhere else in the Southern Ocean (Arrigo 2003). Ice algal biomass can be very large (up to three orders of magnitude greater than that of the underlying water; e.g. Sullivan *et al.* 1993), and on an annual, integrated basis ice algae contribute approximately 20% of the local production. The temporal dynamics of ice algae are quite different compared to those of phytoplankton, with the seasonal increase occurring prior to that of phytoplankton and the release into the water column (and subsequent flux and/or remineralization) occurring prior to the planktonic export (Arrigo *et al.* 1998*a,b*). It has been repeatedly suggested that ice algae 'seed' the water column upon ice melt (e.g. Smith & Nelson 1985), but little direct evidence exists concerning the physiological and ecological capabilities of ice algae once they are released into the water column. Similarly, the grazer crystal krill (also known as ice krill; *Euphausia crystallographias*) is considered to be an obligate ice form, but although it is considered to be the single most important grazer of neritic diatoms (Pakhomov & Perissinotto 1997), nearly nothing is known about its quantitative relationship with ice algae (see below). Despite the presumed importance of ice biota, little is known concerning the linkages between ice algae, the water column and the localized food web, and without that understanding a clear, quantitative understanding of food web transfers within the food web will remain elusive.

Bacterial biomass is low in spring, but both biomass and activity increase with the seasonal phytoplankton

bloom (Ducklow *et al.* 2000). Microbes both in the water column and the sea ice are involved (e.g. Lizotte 2003; Garrison *et al.* 2006). However, biomass does not increase to the same degree as phytoplankton, suggesting that the initial biomass and activity is limited by carbon and energy sources, whereas later in the season losses due to bacterivory become important (Caron *et al.* 2000). This is consistent with the two-order-of-magnitude increase in microzooplankton biomass (Dennett *et al.* 2001), with the microzooplankton probably using bacteria as a major food source, given the paucity of smaller phytoplankton (with the exception of solitary *P. antarctica*). Bacterial cells are also larger than those from warmer waters, with average cell lengths being approximately 1 µm (Ducklow *et al.* 2000).

Although the bacterial production and the microbial food web dependent on this production are unimportant in surface waters (relative to the amount of carbon processed via the autotrophic system; Ducklow 1999), various microzooplankton are present and active. Heterotrophic dinoflagellates are seasonally important consumers of autotrophic carbon, as are nanoplanktonic choanoflagellates (Dennett *et al.* 2001). The mean annual particulate carbon contribution of heterotrophic microplankton is not grossly different from that of other oceans, but the seasonal variations are extreme. Caron *et al.* (2000) found that microzooplankton grazing rates (as determined by dilution experiments) are extremely low, and most do not have significant rates of grazing. Smith *et al.* (2003) suggested that this results from colonial *P. antarctica* escaping grazing through their increased size, with small solitary *P. antarctica* cells being ingested.

Unlike the pelagic and slope waters of the Southern Ocean, where Antarctic krill (*Euphausia superba*) has been intensively investigated (Siegel 2005; Nicol 2006), surprisingly little is known about mesozooplankton (greater than 200 µm) in the Ross Sea and their role in food-web dynamics and biogeochemical cycles. Hopkins (1987) analysed the diet of the zooplankton, euphausiids and small fishes in McMurdo Sound, and found that the copepods *Calanoides acutus*, *Metridia gerlachei* and *Euchaeta antarctica* were important. The same species were found to be important in Terra Nova Bay and the northern shelf region as well (Carli *et al.* 1999; Zunini Sertorio *et al.* 1999). Crystal krill are presumed to be an important link between the ice and the water column, owing to their prominence in the diets of species in upper trophic levels, but there have been only a few efforts to quantify their biomass, distribution and rates of grazing in the Ross Sea (e.g. Azzali & Kalinowski 2000). Sala *et al.* (2002) found that *E. crystallographias* dominated on the continental shelf south of 74° S, but that *E. superba* was dominant near the shelf break. Azzali & Kalinowski (2000) did net tows and acoustic surveys for krill in the Ross Sea sector, and found large variations in space and time for both species. Hopkins (1987) found that the late summer biomass of crystal krill was only 10% that of total zooplankton in McMurdo Sound, and was approximately equal to that of small fishes. However, the grazing on crystal

krill is intense, leading to their presumed seasonal depletion by predators (e.g. adélie penguins *Pygoscelis adeliae*, Antarctic silverfish *Pleuragramma antarcticum* and minke whales *Balaenoptera bonaerensis*; Ainley *et al.* 2004, 2006), who then switch their diet to small fishes during early summer (Ainley *et al.* 2003a, 2006). Otherwise, crystal krill are long-lived, living to at least 5 years in age, and their turnover can be quite slow. Given their importance to neritic food webs, new ideas and data on their biomass, vertical and horizontal distribution, and life-history patterns are required, particularly in regard to their response to seasonal and interannual variation in sea-ice extent, polynya extent and timing, and predation.

An unusual feature of the Ross Sea is the relatively significant temporal uncoupling between surface production and the vertical flux of organic matter (figure 4). In many areas of the ocean and Antarctic, the export of organic matter to depth (in this case 500 m) is tightly coupled, as passive sinking of phytoplankton and phytodetritus is relatively rapid (of the order of  $10 \text{ m d}^{-1}$ ), and so sinking of particles can deliver particulate organic carbon (POC) to 500 m of the order of days to a few weeks (Lohrenz *et al.* 1992; Fischer *et al.* 1988; Smith & Dunbar 1998; Smith *et al.* in press). In the Ross Sea, the maximum in phytoplankton biomass and flux are, however, separated by some 4.5 months (figure 4). The production peak is due to the seasonal bloom of *P. antarctica*, whereas the flux maximum is much broader, occurs in May (winter), and is mediated by the pteropod *Limacina helicina* (Collier *et al.* 2000). Given that the yearly production is approximately  $100 \text{ g C m}^{-2}$ , and the January–June flux is approximately  $3.5 \text{ g C m}^{-2}$ , this suggests that the Ross Sea is neither highly retentive nor characterized by high rates of export relative to production (Grebmeier & Barry 2007), but the timing of flux is unusual and may influence benthic growth and survival.

### (b) Fishes

The fish fauna of the Ross Sea is overwhelmingly dominated by a single family, the notothenioids, and La Mesa *et al.* (2004) characterized this dominance as being ‘unparalleled in the fish fauna of any other marine ecosystem’. In the deeper portions of the Southern Ocean, including the Ross Sea continental slope, families such as Myctophidae and Liparidae contribute much more to the fish fauna (Eastman 1993). Most notothenioids as adults are benthic fishes having no swim bladders, but with reduced skeletal mineralization and concentrated lipid deposits they also have radiated to occupy mid-waters, especially for feeding (Eastman 1993). In the Ross Sea, notothenioids comprise 77% of all species and 91% of the biomass (Eastman & Hubold 1999). In addition to their overwhelming taxonomic dominance, notothenioids are extremely important within the food web of the Ross Sea, a pattern divergent from the Antarctic krill-dominated remainder of the Southern Ocean. As with other trophic groups, the fish fauna is also noteworthy for forms that are absent: there are no fast moving, piscine top predators such as sharks and tunas, but this is true for the entire Southern Ocean.

One species that occupies a critical role in the food web is the Antarctic silverfish *P. antarcticum*, which occurs high in the water column as 1- and 2-year olds, but otherwise descends to epibenthic depths later in life; as subadults, it comprises more than 90% of the biomass of mid-water fish (DeWitt 1970). It feeds largely on zooplankton, but is opportunistic and will ingest other forms, including its own larvae, mysids, amphipods and pteropods. It, in turn, is fed upon by flighted birds (South polar skuas *Stercorarius maccormicki*, snow petrels *Pelagodroma nivea* and Antarctic petrels *Thalassoica antarctica*), adélie and emperor (*Aptenodytes forsteri*) penguins, Weddell seals (*Leptonychotes weddellii*), Antarctic toothfish (*Dissostichus mawsoni*) and other fishes, minke (*B. bonaerensis*) and killer whales (*Orcinus orca*). In times and locations where crystal krill are absent, or at greatly reduced biomass, *P. antarcticum* may dominate energy transfer within the water column.

Another notothenioid that is commonly found in the Ross Sea is *D. mawsoni*, or Antarctic toothfish. It is epibenthic, although under fast ice it occurs in mid-depths (Fuiman *et al.* 2002), and as with other notothenioids, neutral buoyancy is achieved by both lipid inclusion and reduced skeletal calcification (Eastman 1993). This species is the largest fish in Antarctic waters (mean length and mass for 29 specimens in McMurdo Sound is 163 cm and 60 kg, respectively, and 70 kg specimens have been reported; Eastman 1993), and has recently become the target of a long-line fishery in the Ross Sea, especially along the continental slope (Horn 2002; Phillips *et al.* 2004). Given that toothfish grow and recruit slowly (approx.  $2 \text{ cm}$  and  $0.9 \text{ kg yr}^{-1}$ ; Eastman 1993), the fishery could quickly impact the biomass and distribution of the group and potentially disrupt the entire food web (in the sense of Jackson *et al.* 2001; Pauly & Maclean 2003; Pauly *et al.* 2005). The toothfish may be the ecological counterpart of sharks in warmer ecosystems; Eastman (1993) characterized toothfish as the most voracious piscine predator in the Southern Ocean. In the shallower portions of the Ross Sea, toothfish feed primarily not only on *P. antarcticum*, but also on cephalopods and mysids; 10% of its body mass is derived from body lipids. It, in turn, is a major food item for Weddell seals and killer whales (‘type C’; a form of orca which preys solely on fishes; Pitman & Ensor 2003); indeed, its vertical and horizontal distribution in McMurdo Sound may be strongly regulated by the deep-diving behaviour and foraging by seals and killer whales (e.g. Testa *et al.* 1985).

The cryopelagic notothenioid *Pagothenia borchgrevinki* is also common in the Ross Sea. Their diet is quite diverse, feeding on pteropods, copepods, amphipods, and occasionally larval *P. antarcticum* (La Mesa *et al.* 2004). They live in the upper 6 m of the water column, often on the underside of sea ice, and enter the ice as a refuge against predation (similar to the behaviour of krill; Brierly *et al.* 2002). They have substantial concentrations of blood antifreezes, which facilitate its cryopelagic lifestyle. Emperor penguins, skuas and Weddell seals are their main predators.

**(c) Upper trophic levels**

Unlike the remainder of the world ocean, the top-trophic levels of the Ross Sea remain intact, at least for the present, although the impacts of whaling in waters adjacent to the Ross Sea may have had an important impact (Ainley *et al.* 2006). A great deal is known about the numbers, distribution, diet and seasonal natural history patterns of the top predators: cetaceans, seals and birds, and increasing information is being garnered on toothfish (see above). Satellite imagery of chlorophyll (CHL) and the abundance of other top-trophic predators imply that the Ross Sea is one of the most productive stretches of ocean south of the polar front (Arrigo *et al.* 1998b). Owing to the paucity of information on prey distribution (i.e. of crystal krill and silverfish), virtually nothing is known on how variations in prey variability might affect annual or decadal variation in reproductive success or, ultimately, population size of these top predators. On the other hand, growing evidence indicates that feeding by the top predators during summer can affect the availability of their fish and krill prey, at least in the hundreds of square kilometers of ocean that border on concentrations of breeding animals (Testa *et al.* 1985; Ainley *et al.* 2004, 2006).

Cetacean, pinniped and avian biomass over the shelf is approximately 0.182, 0.068 and 0.070 g m<sup>-2</sup>, which are levels comparable to the richest top-trophic marine communities elsewhere (Ainley 1985). The members of these communities are pagophilic in their distributions, being associated with sea ice or its proximity (Ainley *et al.* 2003b). Except along the shelf break where blue (*Balaenoptera musculus*) and other large baleen whales once frequented, overfishing, sealing or whaling is not currently affecting ecosystem processes over the shelf, nor has widespread pollution been an issue as has occurred elsewhere. In the Ross Sea's coastal waters, the minke whale population was greatly impacted by whaling (standing stocks reduced by 40%; Branch & Butterworth 2001) that occurred throughout the Southern Ocean from 1960 to 1980, but has since recovered (Branch & Butterworth 2001), perhaps as a result of a reserve population that was protected in the pack ice where whaling ships did not venture. Currently, the cetacean population over the shelf is composed entirely of minke whales (about 14 000), killer whales (about 7500) and far fewer but unknown numbers of Arnoux's beaked whales (*Berardius arnouxii*; Ainley 1985; Ponganis & Kooyman 1995; Branch & Butterworth 2001). These whales, like most of the birds (see below), are probably absent from the shelf during winter, owing to darkness and the extensive sea ice present (Van Dam & Kooyman 2004).

Avian populations also have high standing stocks, but are species poor. Approximately 38 and 26% of the world population of adélie and emperor penguins reside during summer in the Ross Sea, or about 4 million penguins including breeding and non-breeding portions of populations (as extrapolated from Woehler 1993). An additional 6 million petrels, principally Antarctic and snow petrels, occur over the shelf and especially over waters at the shelf break front (Ainley *et al.* 1984; Ainley 1985).

Finally, the pinniped assemblage is composed of five species, dominated by the crabeater seal (*Lobodon carcinophagus*; about 200 000 individuals), but also includes the Weddell seal (about 32 000–50 000), leopard seal (*Hydrurga leptonyx*; 8000), Ross seal (*Omatophoca rossi*; 5000) and elephant seal (*Mirounga leonina*; less than 100; Stirling 1969; Ainley 1985). Except for the elephant seal, these species breed and probably occur in the Ross Sea region, if not the Ross Sea itself, continuously throughout the year. The Weddell seal occurs in areas of fast ice, such as McMurdo Sound, which supports the highest concentrations of this species in the world. The remaining seals are denizens of the pack ice, especially along the shelf break and the ice margins of the Ross Sea polynya (Ainley 1985; Ainley *et al.* 2003b).

All of these top predators prey principally on two organisms in waters over the shelf: the Antarctic silverfish and crystal krill (Eastman 1985, 1993; Ichii & Kato 1991; Ichii *et al.* 1998; Cherel & Kooyman 1998; Ainley *et al.* 2003b). The killer whale (type C; Pitman & Ensor 2003) and the Weddell seal also feed heavily on the toothfish (Calhaem & Christoffel 1969; Testa *et al.* 1985; Pitman & Ensor 2003; Kim *et al.* 2004). Near the shelf break, Antarctic krill (*E. superba*) and myctophid fish replace crystal krill in the diets of top predators (e.g. Ainley *et al.* 1984; Ichii *et al.* 1998). The squid, *Pyschroteuthis glacialis*, can also be important to predators near the shelf break (Ainley *et al.* 1984).

The Ross Sea polynya is practically devoid of top-trophic predators during spring, and these organisms are found later in the season in the diatom-dominated food webs characteristic of the marginal ice zone that rings the polynya (Ainley *et al.* 1984; Karnovsky *et al.* 2007). This pattern may be related to the grazing efficiency of zooplankton in regions with varying concentrations of diatoms and *P. antarctica*, which is purported to be largely ungrazed by mesozooplankton.

**(d) Benthos**

Antarctic benthic communities are considered to be among the most ecologically stable in the world, characterized by a marked resistance to change in composition and high levels of biomass (Brey & Clarke 1993, but see Dayton 1989), biodiversity and endemism (Brey *et al.* 1994; Arntz *et al.* 1997; Clarke & Johnston 2003). Many species show an essentially circumpolar distribution (Hedgpeth 1971; Richardson & Hedgpeth 1977; White 1984; Knox 1994), are eurybathic (Brey *et al.* 1996), and often have an extraordinary longevity (Dayton 1990; Arntz *et al.* 1994). Any explanation of the structure and distribution of benthic communities in the Ross Sea must include the differences in the environments (sea-ice cover, iceberg scouring and bottom geomorphology) occurring among sites, and the changes in the trophic dynamics and larval supply, which in turn are linked to local hydrodynamic features and primary production.

Barry *et al.* (2003) investigated the links between climate variability and the cascade of ecosystem processes related to the benthos in the Ross Sea. Owing to the large gradients and abrupt changes in environmental variables (annual radiation, ice concentrations and impacts, trophic inputs and hydrological

features) along the latitudinal gradient from Cape Adare (62° S) to McMurdo Sound (78° S), these variations might be expected to generate differences in the benthos (Berkman *et al.* 2005; Howard-Williams *et al.* 2006). Terra Nova Bay appears to be particularly rich, suggesting that community distribution is not always linearly related to latitudinal gradients. Whether this diversity and richness is due to sampling artefacts (the Italian research station is located there; hence sampling is more frequent and on smaller spatial scales) or true environmental richness (large productivity, diversity of bottom types, etc.) is uncertain. Variations in climatic, geographical and hydrological forcing represent barriers that result in anomalies in community and population distributions. Along the coast of Victoria Land, Terra Nova Bay, its polynya and the Drygalski glacier represent significant physical discontinuities that affect diversity, community structure and population genetics.

#### (e) Controls of benthic distribution

On the continental shelf, the role of ice disturbance (e.g. ice-cover persistence, anchor ice and ice scouring) is dominant, facilitating the occurrence of communities dominated by relatively opportunistic species (Gutt *et al.* 1996; Gutt 2001). Grounded icebergs not only affect the benthic communities, but also modify the regional hydrodynamic regimes, with significant attendant changes in primary production (Arrigo *et al.* 2002). In contrast, undisturbed benthic communities show a high level of stability, and contain a variety of large and potentially long-lived species controlled by food availability. Only below 500 m does the downward flux of organic material seem to regulate faunal distribution.

The role of pelagic organic matter in structuring Antarctic benthic communities, with inputs linked to local hydrology, is evident in McMurdo Sound, where there is an order of magnitude difference in benthic densities and organic input between the eastern and the western sides (Dayton & Oliver 1977; Barry 1988). The seasonal changes in quality and quantity of suspended organic matter and differences in particle flux (several orders of magnitude greater than in the offshore pelagic system) can be affected by terrestrial inputs, katabatic winds, resuspension and coastal morphology (Bathmann *et al.* 1991; Fabiano *et al.* 1997; Povero *et al.* 2001). Barry *et al.* (2003) found suspension feeders to be more abundant in shallow waters, while detritus feeders increased with depth.

A significant role has been assigned to 'latitudinal' variables (like the time and extent of ice cover or the lighted season) that could determine the community emergence, the movement of deep-living species towards the surface and a general faunal impoverishment towards the south (Berkman *et al.* 2004). The macroalgal distribution seems to corroborate this hypothesis. More information on the spatial and temporal distributions of benthic organisms is required to understand the high degree of spatial heterogeneity, the patchiness of the various assemblages and the variables that determine community composition.

#### (f) Hard-bottom benthic assemblage distribution and zonation

The hard-bottom habitat represents only a small fraction of the total Ross Sea benthos. It is largely present along the shore and usually covered by fast ice, but can occur in offshore reefs and seamounts where the bottom currents are intense and sediments are scoured and redeposited. The upper littoral fringe is generally azoic due to the severe physical conditions, but during the summer ephemeral assemblages, characterized by cyanobacteria and pennate diatoms, develop inside small pools, mainly fed by fusion waters from the land. The tidal zone (1.5–2 m wide) hosts a biological film composed of diatoms and cyanobacteria (Gambi & Mazzella 1992), which may reach high biomass (up to 900 mg CHL-*a* m<sup>-2</sup>; Dayton *et al.* 1986). In the most sheltered areas where the abrasive action of ice can be avoided, the green macroalgae *Prasiola crista* and *Urospora penicilliformis* are present (Cormaci *et al.* 1992a,b, 1996). Within this community, the grazing amphipod *Paramoera walkeri* reaches high densities (up to 6000 m<sup>-2</sup>; Gambi *et al.* 1994). Below the littoral zone, algal communities thrive (Zaneveld 1966, 1968), well structured in belts and quite homogeneous on a large spatial scale. Large brown algae (*Himantothallus grandifolius*, *Desmarestia menziesii* and *Desmarestia anceps*), rhodophytes (*Iridaea cordata* and *Phyllophora antarctica*) and encrusting algae, as well as diverse fauna of herbivores and their predators, characterize these belts. Particularly, rich populations of syllid polychaetes, tanaids and gastropods live associated with *Phyllophora* (Cattaneo-Vietti *et al.* 2000b).

The algal communities along Victoria Land differ significantly in their latitudinal distribution and composition. For example, *Himantothallus* and *Desmarestia* are absent south of Cape Hallett, and *Phyllophora* is found in shallower waters towards the south. In McMurdo Sound, the abundance of macroalgae is reduced, and their bathymetric range is narrower than elsewhere. An apparent north–south phytogeographical gradient, with algal belts decreasing in importance to the south, is probably due to decreased irradiance (total annual photon fluxes, as well as the number of days of 24 h photoperiods) and the longer persistence of the pack ice (which scours the seabed and reduces total irradiance by up to two orders of magnitude). The carnivorous sea star *Odontaster validus* and omnivorous sea urchin *Sterechinus neumayeri* are frequently observed, varying considerably in population densities from site to site.

In McMurdo Sound, from 20 to 25 m, anchor ice is an important disturbance, affecting up to 70% of the sea floor (Dayton *et al.* 1969, 1970; Battershill 1989; Dayton 1989), while similar disturbances are nearly absent from Terra Nova Bay. Thus, the shallow water benthos in the two areas can be significantly different. Fast growing sessile species, like the bush sponge *Homaxinella balfourensis* (extremely common at McMurdo), the soft coral *Alcyonium antarctica*, and hydroids (more common at Cape Hallett), are frequently observed, suggesting a role for ice scouring by small icebergs. In deeper waters (approx. 80 m), frondose algae are absent at Terra



Nova Bay, and the calcareous coralline alga *Clathromorphum*, on which sea-urchins feed, dominates; at McMurdo, the latter alga is replaced by *Phymatolithon* at a depth of approximately 60 m (Miller & Pearse 1991). From 70 to approximately 130 m, the benthos is dominated by diversified filter-feeding assemblages, dominated by sponges (which can attain high biomass; over 2–3 kg m<sup>-2</sup> wet weight), gorgonaceans and holothuroids.

The three-dimensional sponge–anthozoan assemblage (Bullivant 1967) is among the most complex communities present in the Ross Sea, and its complexity is comparable with temperate or even tropical communities. It has been described from McMurdo Sound (Dayton *et al.* 1974) and Terra Nova Bay (Cattaneo-Vietti *et al.* 1996, 2000c), with high diversity and biomass, as well as high rates of predation, competition and symbiosis (e.g. the intriguing diatom–sponge relationships; Bavestrello *et al.* 2000; Cerrano *et al.* 2000, 2004a,b). Structural differences arise mainly from the different role played by huge volcano sponges, the hexactinellids *Rossella racovitzae*, *Rossella nuda* and *Scolymastia joubinii*.

Below 120–130 m, hard-bottom outcrops become rare and is mainly colonized by the polychaete *Serpula narconensis* (Schiaparelli *et al.* 2000) and bryozoans, which become dominant in still deeper waters (200–350 m), forming dense mats near Cape Hallett. Elsewhere, the hard substratum is available only on seamounts, ridges or along the shelf break where the bottom currents are intense and sediments are scoured and redeposited. Some conspicuous sessile species, like the orange stylasterine coral (*Errina* sp.) and the Antarctic acorn barnacle (*Bathylasma corolliforme*), cover exposed rock surfaces. The stylasterine corals seem to be more common in the northern reaches of the Ross Sea (e.g. Pennell Bank, Cape Hallett, Cape Adare).

#### (g) Soft bottom benthic assemblage distribution and zonation

In the Ross Sea, soft sediments are relatively coarse, characterized by gravel or muddy sand through 400–500 m. In shallow waters (20–70 m), dense populations of benthic diatoms (up to 30–200 mg m<sup>-2</sup> CHL-*a*) favour surface deposit feeders such as crystal krill and infauna (characterized by the large bivalve *Laternula elliptica* (10–20 m<sup>-2</sup>) and the smaller *Limopsis* sp.). In some areas of Terra Nova Bay and McMurdo Sound, the bivalve *Adamussium colbecki* covers nearly 100% of the seabed, reaching 100–120 g m<sup>-2</sup> DW (soft tissues) and 60–80 m<sup>-2</sup> (Stockton 1984; Berkman 1990; Cerrano *et al.* 2001; Chiantore *et al.* 2000, 2001, 2002, 2003; Heilmayer *et al.* 2003). This bivalve processes approximately 14% of the total carbon flux and produces biodeposits that support active microbial production (Albertelli *et al.* 1998; Chiantore *et al.* 1998). The distribution of this species, which is generally considered to be circumantarctic, is not homogeneous along Victoria Land, becoming rarer at northern sites (Capes Hallett and Adare). Moreover, Terra Nova Bay and McMurdo Sound populations may be genetically distinct, as the dispersal capacity of larvae could be restricted to the pack ice where food and shelter are available (M. Guidetti *et al.* 2001, unpublished work).

In shallow waters, predators such as gastropods and the nemertean worms are locally abundant, while the echinoid *S. neumayeri* and the starfish *O. validus* remain abundant at all depths on both hard and soft substrata (Chiantore *et al.* 2002). As with sea urchins, differences were observed between the McMurdo and Terra Nova Bay populations, with specimens of the latter being more abundant but smaller than those from McMurdo Sound. Among echinoids, the pencil urchins (*Ctenocidaris* sp.), a euribathic group, seem to show a discontinuous distribution as well, being common in McMurdo Sound, absent in Terra Nova Bay, and occurring in northern sites.

The amount of fine-grained sediment increases with depth, as does the organic matter concentration. In these environments, the bivalve *Yoldia eightsi* reaches high densities (70–80 m<sup>-2</sup> at Terra Nova Bay); numerous species of ophiuroids and spatangoids are also found. Generally, the fine-grained sediments below 120 m is populated by tube building polychaetes (Gambi & Bussotti 1999; Gambi *et al.* 2000) and small bivalves (Cattaneo-Vietti *et al.* 2000c). Large deposits of siliceous sponge spicules can be found free in the sediments or densely packed in spicule mats greater than 1 m in thickness (Barthel 1992; Cattaneo-Vietti *et al.* 2000a). Within these mats, lives a rich and specialized community, dominated by the burrowing bivalve *Limatula hodgsoni*, many crustaceans and polychaetes. These spicules can represent more than 50% of the total dry weight of the sediment and can reach densities of 500 000 spicules g<sup>-1</sup>. These mats confirm the locally important role of sponges, which along with diatoms determine the texture and silica content of the sediments.

At the shallow depths of banks, iceberg-scouring effects are important. These perturbations occur continuously in front of Capes Hallett and Adare, where the continuous passage of tabular icebergs creates large troughs and pits, as well as berms of displaced sediment that may reach 8 m in height. Near Cape Hallett, the percentage of bottom area disturbed is approximately 30% (Berkman *et al.* 2005). The result is a mosaic of patches characterized by a temporal succession of ephemeral, fast growing, opportunistic species (Dayton *et al.* 1969; Dayton 1989, 1990; Lenihan & Oliver 1995). Only among the vagile fauna is the scouring activity less intense than expected: the iceberg movement probably causes a pressure wave in the sediments that triggers an escape response in the epifauna. Near Capes Hallett and Adare (from 150 and 250 m), the benthic communities are characterized by dense populations of ascidians, which are less common in the south where the iceberg impacts are less intense. These ascidian-dominated communities, with associated bivalves and ophiuroids, could be considered as intermediate successional stages following an iceberg disturbance.

From 450 to 500 m, bryozoan mats generally dominate in soft bottom substrata, forming the deep shelf mixed assemblage described by Bullivant (1967), but locally other taxa dominate, such as ophiuroids or *Cephalodiscus* spp. (Hemicordata), which maintain high densities near Coulman Island (Schiaparelli *et al.* 2004). Upon an increase in the mud fraction, the community becomes dominated by polychaetes and

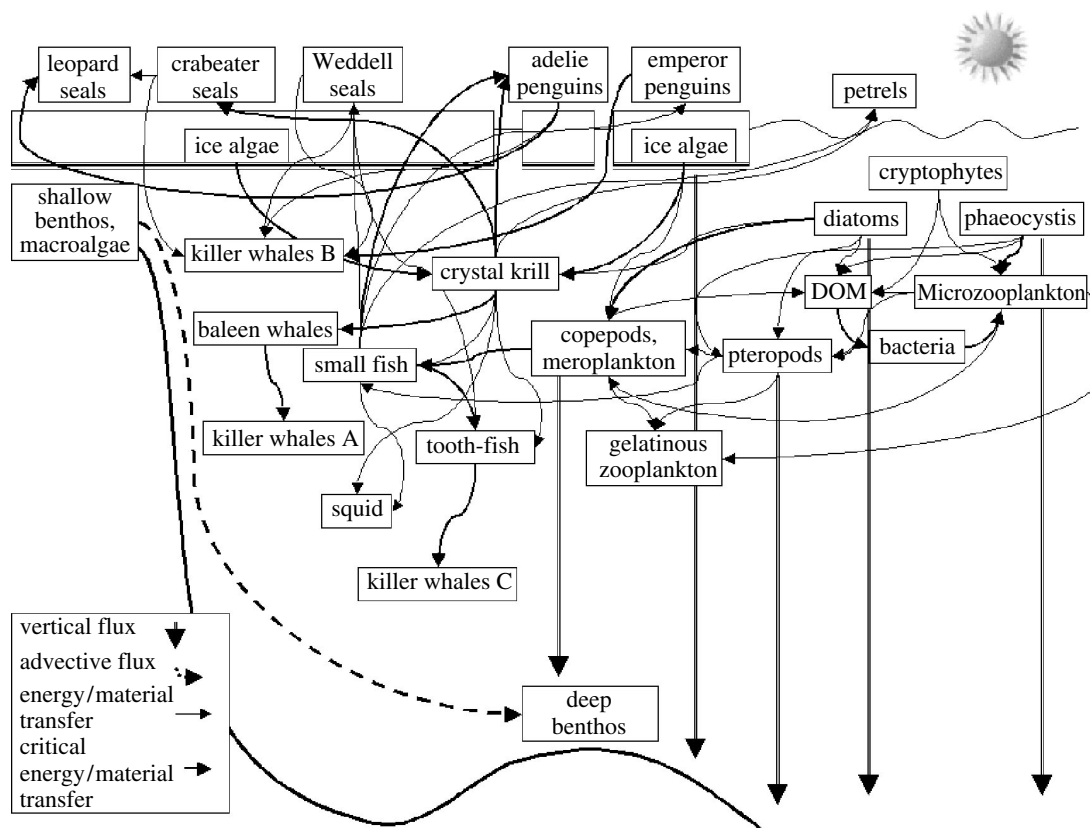


Figure 5. Schematic of a generalized Ross Sea continental shelf food web. DOM, dissolved organic matter.

ophiuroids (deep shelf mud-bottom assemblage) and is more unstructured, with a strong reduction in faunal density and biomass.

### 3. FOOD WEB AND BIOTIC INTERACTIONS

The food-web interactions within the Ross Sea are largely based on studies of diets of organisms (e.g. Ainley *et al.* 1984; Hopkins 1987), as well as distributions of prey and predators, but because the food web has a limited number of functional groups, a realistic food web of the Ross Sea can be deduced (figure 5). One obvious conclusion to be drawn from this depiction is that both crystal krill and silverfish are extremely important species in the food web over the shelf. What cannot be easily depicted are the temporal variations that are superimposed on these biotic interactions. Clearly, the strong seasonality in occurrence, abundance, distribution and activity of the various food-web components greatly influences energy transfer and stability; however, the time-scales of interactions are poorly described. Obviously, phytoplankton respond rapidly on daily, monthly and seasonal scales (largely as a function of irradiance), but it is unclear how quickly long-lived organisms such as crystal krill, toothfish, silverfish, the benthic fauna and top predators respond to these variations in production. These responses will in large part determine the ecosystem response to perturbations at the smaller scale, but without an understanding of the time-scales involved it will be difficult to predict the system responses to anthropogenically forced changes.

In general, the mid-water food web has a reduced number of species and groups (relative to non-polar regions), and the fauna are largely opportunistic

feeders. Owing to the depth, the benthos is relatively isolated from the surface waters (except in terms of coupling of food supply) and as far as we know does not exert a major, structuring role on the mid-water component. Further information on the vertical/seasonal movements of fishes and crystal krill could modify this conception. On the other hand, in shallow areas, detritus originating from concentrations of birds and mammals (e.g. carcasses, food remains), as well as that from sea ice, can be important to the benthic community. In this regard, the Weddell seal could be a critical species in coastal areas, preying intensively on toothfish (which in turn prey on smaller fish species), reducing their standing stocks to near zero where seal concentrations are high (Testa *et al.* 1985), and providing concentrated amounts of detrital material to the benthos. Food-web connections are strongly structured by ice dynamics, which further impose a marked seasonal influence on biotic interactions.

Smetacek & Nicol (2005) suggest that benthic–pelagic coupling in Antarctic waters is unimportant. While such generalizations may be true for regions removed from the continental shelf (depths greater than 1000 m) and driven by the exponential reduction in organic matter input to depth, it certainly is not true for the Ross Sea continental shelf. Indeed, coupling between the surface layer and benthos is quite strong (i.e. the flux of organic matter in the surface layer to the sediments and the relative amount of remineralization within the water column of that organic material), as it is in other polar systems of similar depth (Grebmeier & Barry 2007; C. R. Smith *et al.* 2006). This is also reflected in the relatively low importance of the microbial food web within the Ross Sea water column.

C. R. Smith *et al.* (2006) suggest, based on the lack of seasonal variability of labile organic matter in the sediments in the Antarctic Peninsula region, that variations in organic matter flux to the benthos from above are buffered by the pool of available organic matter in the sediments, and that even large annual variations in flux may not induce similar variations in benthic growth and biomass. Therefore, organisms in the soft benthos may be uncoupled from surface processes, but the importance of the flux of biogenic matter from the surface (and the percentage that enters the benthos) remains quite high.

Currents in the Ross Sea can often be quite energetic (greater than  $12 \text{ cm s}^{-1}$ , with tidal currents exceeding even these velocities; Dinniman *et al.* 2003), and often generate significant nepheloid layers in the bottom 50 m of the water column. Such resuspension of phytodetritus (of presumably high energetic value) would routinely provide suspension feeders enhanced concentrations of food, and also potentially transport organic matter vertically over relatively large distances (e.g. from the polynya to areas under ice where production is reduced). Such redistribution is known from the distribution of biogenic matter in sediments (Dunbar *et al.* 1989) and may be important in regulating the distribution and growth of suspension feeders in the Ross Sea.

#### 4. CONCLUSIONS

##### (a) *Uniqueness of the Ross Sea*

The Ross Sea continental shelf represents one extreme within a continuum of biomass, processes and temporal patterns found in the Antarctic. It is a wide continental shelf (widest in the Antarctic) and is the most spatially extensive, productive region in the Southern Ocean. Its phytoplankton blooms are predictable, and the observed spatial segregation of functional groups is temporally consistent (albeit with interannual variations; W. O. Smith *et al.* 2006). Top- and middle-trophic levels have not been substantially impacted by human activity, as is the case elsewhere on the globe including the remainder of the Southern Ocean (Jackson *et al.* 2001; Pauly *et al.* 2003), and there is no widespread pollution or overfishing. Unique attributes include the extreme importance of bivalves in coupling water column productivity to the seafloor, processing as much as 14% of the total carbon flux (Albertelli *et al.* 1998; Chiantore *et al.* 1998), a rate now unknown in other portions of the ocean (the entire Chesapeake Bay was once filtered over the course of a few days by oysters, but due to disease and overfishing, the oysters have nearly disappeared and the Bay is now flushed physically; Pauly & Maclean 2003), and the apparent depletion of prey in the foraging areas of dense concentrations of top predators (Ainley *et al.* 2004, 2006), a pattern not well documented elsewhere.

The apparent dependence of the upper portions of the food web on crystal krill and silverfish, two species whose ecology and dynamics are poorly known, is also unusual in the Antarctic. While copepods can be present and dominate grazing on phytoplankton in numerous areas of the Antarctic (Ashjian *et al.* 2004), the upper trophic levels in many regions of the

Southern Ocean (the so-called 'Antarctic Marine Ecosystem'; Beddington & May 1982; Bengtson & Laws 1985) are apparently structured only around the Antarctic krill, *E. superba*, which is present in the Ross Sea only near the shelf break. Differences between the two euphausiids are known (Knox 1994), but how these differences lead to differences in food-web structure is unclear. Similarly, many of the benthic communities (e.g. the sponge communities) are quite unusual and have not been observed elsewhere. Therefore, many of the aspects of the food web are unique to the Ross Sea, making it an excellent location to study the ecology and the biotic interactions of cold waters, as of yet free of direct anthropogenic impacts. Perhaps biochemical assessment of the various trophic levels (isotopes and fatty acids) will allow the quantitative relationships within the food web to be clarified.

##### (b) *Critical research needs*

The Ross Sea is changing, and a more complete understanding of the system's entire food web is needed in order to predict the ecological impacts of such change (and other changes) in the future. Some aspects of the food web are relatively well known (e.g. primary productivity, distributions, sea-ice microbial communities, and diet and numbers of some top-trophic predators, and the structure of benthic communities), but at each trophic level, there are substantial gaps in our understanding, for example follows:

- What controls the distribution and abundance of *P. antarctica*?
- How productive is *E. crystalloporphias*, and what is its distribution in space and time, especially during periods when ice covers the Ross Sea?
- What are the quantitative linkages with the ice biota and the water column?
- What is the impact of large, mobile animals such as whales on the entire food web?
- How does the benthos respond to short- and long-term changes in the physical and the biological forcing of the water column?

These and other questions are essential in order to address and make informed predictions about the response of the entire ecosystem to future changes.

We also do not have a clear understanding of the responses of various trophic groups to perturbations, or the time-scales of response. Recently, the Ross Sea has experienced massive iceberg calvings and groundings, which altered circulation and productivity; however, we do not know if these changes quantitatively impacted all trophic levels, or to what extent. As some of these icebergs have lasted a number of years, it would be surprising if there were no ecological effects of these disturbances, yet we know little of their impacts on long-lived organisms. We do know they have changed the genetic structure of penguin populations (Shepherd *et al.* 2005). Time-series data from a single location (or multiple sites) are needed to assess the long-term (decadal) responses of all trophic groups (and the interactions among groups) to change.

**(c) The Ross Sea and factors affecting change**

Stemming from interest in the behaviour and fate of the West Antarctic Ice Sheet, the Holocene and older climate and history of the Ross Sea embayment and the Ross Ice Shelf have been intensively studied (e.g. Stuiver *et al.* 1981; Berkman *et al.* 1998; Ingólfsson *et al.* 1998). In recent years, the climate of the region has been consistent with predictions of global climate models: a cooling of East Antarctica and a warming of West Antarctica (e.g. Kwok & Comiso 2002). Despite slightly warmer winter temperatures measured at Ross Island (Ainley *et al.* 2005), the Ross Sea ice extent has been increasing and the sea-ice season has been growing longer, in contrast to much of the ocean off West Antarctica (Parkinson 2002; Zwally *et al.* 2002). This may be related to increased wind strengths and variations in the Antarctic Oscillation (or Southern Annular Mode; Hall & Visbeck 2002). Further evidence for this is growth in the size of the Ross Sea polynya (Parkinson 2002).

Significant oceanographic changes in some water mass properties in the Ross Sea have also been observed. Jacobs *et al.* (2002) found a significant freshening of deeper water (the changes were up to 0.1 psu), consistent with increased basal melting of the West Antarctic Ice Shelves (which has recently been shown to be much greater than thought; Velicogna & Wahr 2006). Such changes could alter density-driven circulation, vertical mixing and biogeochemical processes on the shelf, but such alterations have as yet not been documented.

The effects of changing climate on most elements of the biota have not been directly studied. The responses of penguin populations to the changes in sea-ice extent and polynya size (which are climate related) have been recently assessed (Wilson *et al.* 2001; Ainley *et al.* 2005). During a period of low wind speeds and cold temperatures in the 1950s to early 1970s, sea-ice concentrations were enhanced, and adélie penguin populations were reduced. In the mid-1970s, coincident with a switch in the state of the Antarctic Oscillation leading to warmer winter temperatures and stronger winds, the ice became more divergent and penguin populations began to grow; growth levelled off in the late 1980s, as the Antarctic Oscillation again shifted and winds subsided. Coincident with the mid-1970s shifts, the benthic biota of McMurdo Sound also changed noticeably relative to the prevalence of anchor ice (less ice after mid-1970s; Dayton 1989), and Weddell seal populations may also have been affected by a decrease in ice thickness (Ainley *et al.* 2005).

Perhaps, no less important than climate change, the Ross Sea ecosystem has recently become the site of increased commercial fishing and whaling efforts (Horn 2002), coincident with the reduction of various stocks in the remainder of the Southern Ocean (Pauly *et al.* 2003). Therefore, climate-driven changes and those driven by human commerce may be occurring simultaneously, and an understanding of the importance of each to the structuring of the Ross Sea food web is essential to predict the complex reactions to such disturbances. Owing to the effects of large-scale fishing and whaling in the Southern Ocean, we do not know

what the structure and function of Antarctic ecosystems were prior to the top predator removal. While the Southern Ocean is often considered pristine (e.g. Smetacek & Nicol 2005), the large ecological changes that were induced by the removal of fishes and whales severely altered trophic linkages, and today the Ross Sea is where these linkages are closer to the 'natural' state than anywhere else in the Antarctic.

All ecosystems respond to change, and while the resilience of many systems to change is well known and quantified, this is not the case for the Ross Sea (or polar ecosystems in general). The responses of polar biota tend to be slower than those in more temperate regimes, and so the rates of ecosystem response may not be well coupled to the rates of environmental change, especially if forced by anthropogenic changes from outside the system. Understanding the nature of the ecological changes that will occur in the Ross Sea in future years will be a major challenge for both oceanographers and polar ecologists.

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