CHAPTER 7

THE ROSS SEA CONTINENTAL SHELF: REGIONAL BIOGEOCHEMICAL CYCLES, TROPHIC INTERACTIONS, AND POTENTIAL FUTURE CHANGES

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7.1 INTRODUCTION

The Ross Sea continental shelf, lying between Cape Adare, Victoria Land (71°17′ S, 170°14′ E) and Cape Colbeck, Marie Byrd Land (77°07S, 157°54W) and stretching from the continent north to the 800 m isobath (Figure 7.1), is a unique region of the Antarctic, both with regard to its physics and its ecology. It is now clear that the various regions among Antarctic continental shelf systems have unifying characteristics, but also marked regional differences (e.g., Arrigo & van Dijken, 2003). Among cold water continental shelves, the Ross Sea is the least impacted by anthropogenic factors of any on Earth (Halpern *et al.*, 2008). Its broad extent (the widest in the Antarctic, and covering ca. 433,000 km^2), extreme seasonality of its trophic linkages (its high-latitude Antarctic location induces complete darkness during winter), numerous polynyas (regions of open water surrounded by sea ice), a massive ice shelf – the Ross Ice Shelf (RIS, the largest in the world, covering nearly half of the continental shelf) and substantial vertical and horizontal exchanges, both with waters of the continental slope (between 800–3000 m) and with those under the RIS, provide a dynamic environment. It is because of these characteristics that the Ross Sea food web differs from those in many other areas of the Southern Ocean (Knox, 2006).

The climate of the Ross Sea is changing rapidly, as are other areas of the Antarctic, such as the west Antarctic Peninsula (WAP) region. However, the direction of environmental change in the Ross Sea is opposite that of the WAP. Satellite data suggest that sea ice coverage is *increasing* in the Ross Sea region by more than 5% per decade (in the WAP it has decreased by ca. 7% per decade; Comiso & Nishio, 2008), and the length of the ice-free season has significantly decreased by ca. 60 days since 1979 (Parkinson, 2002; Stammerjohn *et al.*, 2008). However, owing in part to increasing wind
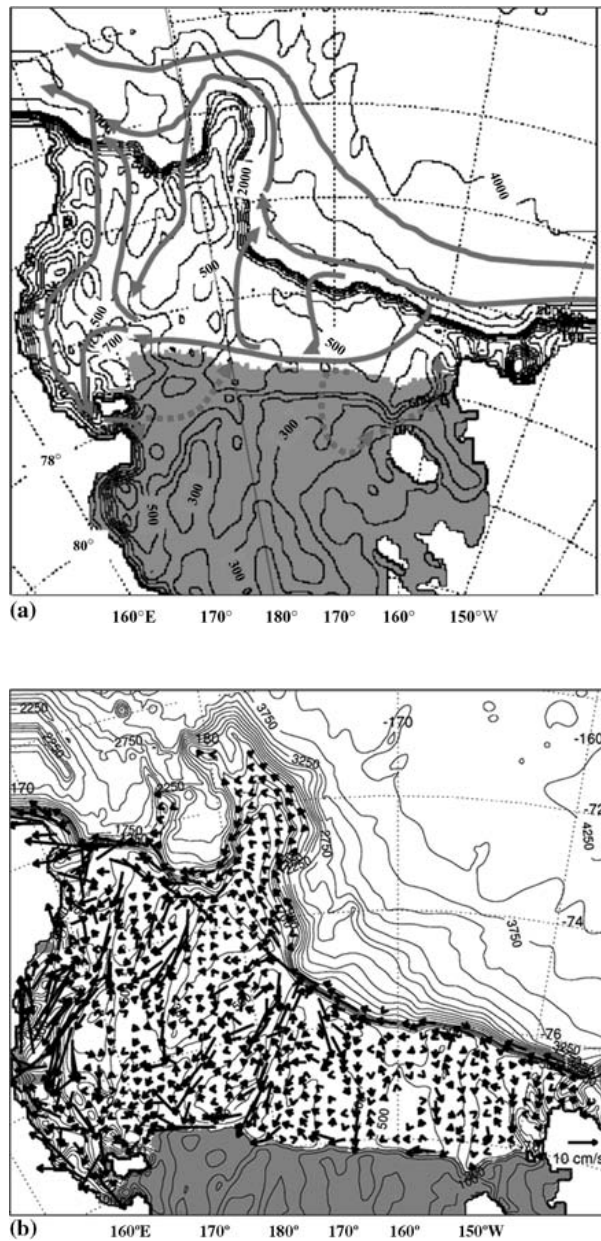
Figure 7.1 (a) General circulation of waters on the Ross Sea continental shelf (Smith *et al.*, 2007). Heavy dotted line is the dateline; shaded area is the location of the Ross Ice Shelf. Depth contours in meters. Dashed lines under the ice shelf represent currents derived from modeling but few direct observations. After Locarini (1994), Jacobs and Giulivi (1998), and Dinniman *et al.* (2003). (b) Mean velocity on the Ross Sea continental shelf as determined by a high-resolution coupled numerical model (Dinniman *et al.*, 2003, 2007). The vectors represent mean annual flow at 20 m; velocities below $1.0\,\mathrm{m\,s}^{-1}$ are not shown.

strength over the Southern Ocean (Russell *et al.*, 2006), certain Ross Sea polynyas are increasing in area (Parkinson, 2002). Therefore, at a smaller scale sea ice cover is decreasing in the west and increasing in the eastern portion of the Ross Sea continental shelf. For most of the biota other than penguins (which benefit from larger, more predictable polynyas), the impacts of these changes to date have not been detected (e.g., Ainley *et al.*, 2005, 2010a), but should the trend continue, significantly altered biological dynamics can be expected, especially for those species that require open water or sea ice cover at specific times in their life cycle.

7.2 PHYSICAL SETTING

The physical characteristics of the Ross Sea emphasize its unusual nature (Table 7.1). It is the largest continental shelf 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 ca. 600 m; Anderson, 1999). Although the shelf break occurs at $\sim$800 m, within the shelf there are banks with depths shallower than 250 m and troughs with depths > 1200 m. The character of the shelf sediments is highly variable and among the best known in the Southern Ocean, and a significant portion of the northwestern continental shelf, unlike the remainder of the continent's, remained unglaciated during past glacial maxima (Anderson, 1999).

The circulation of the Ross Sea Gyre, just north of the slope (see Jacobs *et al.*, 2002; Dinniman *et al.*, 2003, 2007) is clockwise, being driven by the westerly winds of the Antarctic Circumpolar Current and easterly winds at its southern edge (Figure 7.1a, b). A northward boundary current occurs along the western Ross Sea coast (Victoria Land), completing the circulation. Flow is vigorous along the shelf break (up to $0.25\,\mathrm{m\,s}^{-1}$). The circulation over the Ross Sea continental shelf consists of two clockwise rotating gyres (Figure 7.1a, b), which are synchronized with the clockwise circulation of the larger-scale Ross Sea Gyre (Jacobs *et al.*, 2002; Dinniman *et al.*, 2003, 2007). The continental shelf circulation extends under the RIS (e.g., Dinniman *et al.*, 2007; Figure 7.2), although the details of the under-shelf circulation have yet to be fully investigated. Most currents are coherent throughout the water column, and substantial seasonal variability in current velocities occurs (Dinniman *et al.*, 2003, 2007).

Table 7.1 The physical features and characteristics of the Ross Sea continental shelf

Variable	Magnitude
Area	433,000 km^2
Water depth	Mean ca. 600 m; shelf break at 800 m; but with extensive shallower banks ($<$ 200 m)
Air temperature	Ranges from -60 to $10.1\,°C$
Water temperature	Ranges from -1.86 to $3.2\,°C$
Salinity	Ranges from 34.0–34.92
Circulation	Controlled by bathymetry 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 oozes with significant organic content
Pack ice concentrations	Range seasonally and interannually from ice free (except for isolated embayments) to 100% ice cover
Glacial inputs	Owing to low temperatures, little runoff; much in the way of subsurface melt and icebergs generated from Ross Ice Shelf and coastal glaciers
Irradiance	Photoperiod from 0–24 h; Maximum irradiance in summer ca. 60 mol photons m^{-2} d^{-1}
Nutrients	[NO$_3$] ranges from 15–30 µM; [Si(OH)$_4$] from 20–85 µM; [Fe} from 0.05–2 nM

Few oceanographic studies have been conducted during winter in the Ross Sea, but early spring measurements near the RIS have observed a homogeneous mixed layer
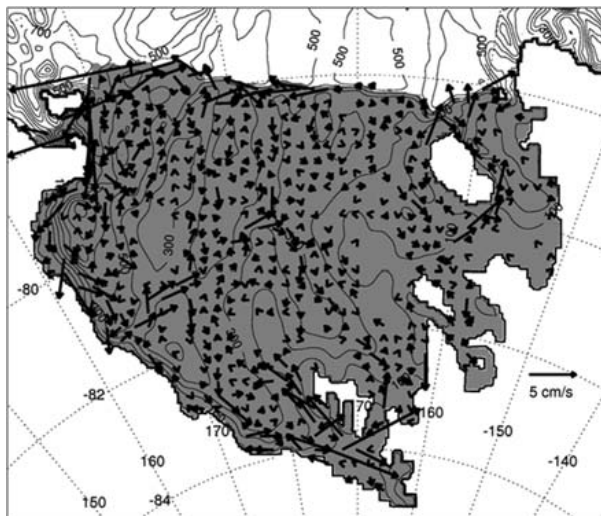

Figure 7.2 Circulation under the Ross Ice Shelf as determined by a high-resolution coupled numerical model originally described by Dinniman et al. (2003, 2007). The vectors represent mean annual flow at 20 m below the ice-water interface. Velocities below 0.25 m s^{-1} are not shown. Contour lines below ice shelf represent water column thickness.

throughout the entire water column (http://usjgofs. whoi.edu/jg/dir/jgofs/southern/), demonstrating that at some locations (such as near the ice shelf) waters are mixed to the bottom during winter.

Temperature and salinity distinguish a variety of water masses in the Ross Sea (Jacobs et al., 1970; Hofmann & Klinck, 1998). The historical hydrographic data for this area have been compiled into a climatology that has been used to revise and update the understanding of the water mass structure of the Ross Sea (Orsi & Wiederwohl, 2009). At the surface is Antarctic Surface Water (AASW), which in summer is warmed by solar radiation to $> -1.5\,°C$, with salinity around 34.0 (Orsi & Wiederwohl, 2009). The thermohaline characteristics of this water show considerable scatter that is produced by variable heating and sea ice melt. Below the AASW is a warm, oceanic water mass, Circumpolar Deep Water (CDW), which rises to about 500 m at the continental shelf break. This water originated in the North Atlantic as North Atlantic Deep Water, and as a consequence is low in oxygen, high in nutrients, and has retained its relatively high temperature (maximum of $1.5\,°C$ in the Ross Sea region Orsi & Wiederwohl, 2009). The CDW cools during its travel around the Ross Gyre and arrives at the shelf break with temperatures between 0 and $1\,°C$ (now called modified CDW or MCDW). This water can be detected by its temperature and salinity characteristics, which are

significantly different from the water masses on the shelf (Figure 7.3; Jacobs *et al.*, 2002; Orsi & Wieder-wohl, 2009); furthermore, its dissolved oxygen concentrations are lower relative to surrounding water masses. Along the shelf-break, especially in the western, steeper portion, upwelling of MCDW leads to the occurrence of a shelf-break front (Ainley & Jacobs, 1981).

The troughs (mean depth of ca. 800 m) that subdivide the Ross Sea continental shelf (typically formed by glacial action during glacial maxima) terminate at the shelf break, providing a north-south conduit for movement of this deep oceanic water onto the shelf (Jacobs *et al.*, 2002; Dinniman *et al.*, 2003). This water intrudes onto the continental shelf and floods the area between
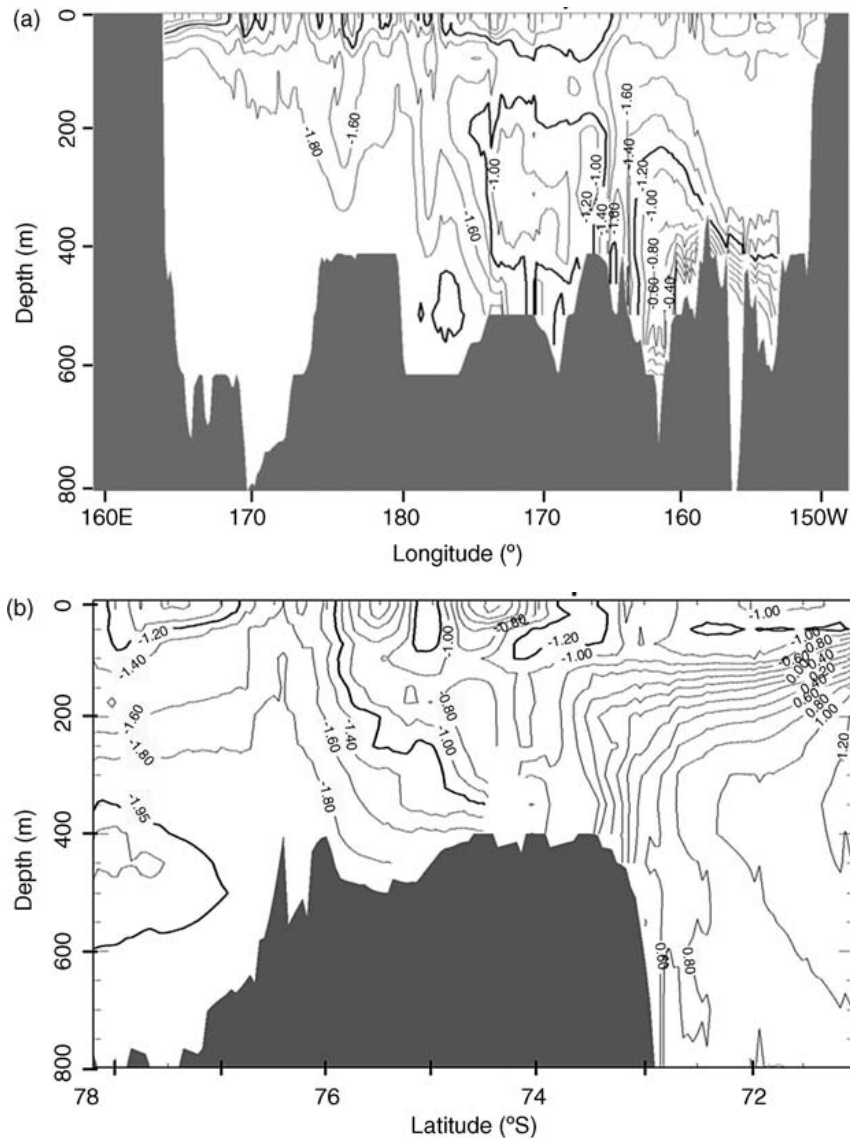

Figure 7.3 Temperature (°C) of the water in the southern Ross Sea: (a) east-west section at 76° 30′ S, and (b) north–south section along 180°. Data derived from a modified numerical model originally described by Dinniman *et al.* (2003, 2007). Waters with a subsurface temperature maximum originate from the ACC and represent a significant cross-shelf flux of water, as well as a potential micronutrient input to the shelf and to the surface.

200 m and the bottom, providing heat and nutrients. The warmer water provides a deep habitat for many organisms and the nutrients, when mixed to the surface, support high rates of primary production. The MCDW intrusions may be biologically important by stimulating phytoplankton blooms (Peloquin & Smith, 2007), but the exact mechanism remains uncertain. The intrusion process is episodic, but occurs throughout the year (Dinniman et al., 2003).

The warm MCDW flows under the RIS at specific locations (Figure 7.3), melting the glacial ice. The freshened melt-water is buoyant, and thus a vertical circulation is produced. The cold ($<-2.0\,°C$, the extreme low temperature made possible due by the decreased freezing point at increased pressures) and freshened (34.62) water produced is called Ice Shelf Water (ISW). This distinctive water exits from the western parts of the RIS, but due to its density remains at ca. 300 m. A shallow variety is also produced within 100 m of the surface, but is not detected far from the edge of the RIS. The densest water in the Ross Sea occurs mainly in the west, being composed of two slightly different forms. High Salinity Shelf Water (HSSW) is cold and salty ($<-1.9\,°C$, >34.6), having been produced by the extreme conditions in the coastal polynyas along the western side of the Ross Sea north of McMurdo Sound. Low Salinity Shelf Water (LSSW) is slightly less dense ($<-1.8\,°C$, 34.4–34.6), being produced in the central and eastern Ross Sea. Both of these water masses are generated in the winter during convective overturning due to strong surface cooling and brine rejection.

Antarctic Bottom Water (AABW) is formed in the Ross Sea by mixing of the cold, dense shelf water with MCDW (Whitworth et al., 1998). The western Ross Sea is one of three primary source regions in the Antarctic that contribute the bulk of AABW to the global deep ocean (see Muench et al., 2009 and references therein). The dense bottom water exits the Ross Sea in energetic, bottom-trapped flows that move down the continental slope with mean velocities of 0.4–0.6 m s^{-1} (Gordon et al., 2004, 2009), and occasional maximum observed velocities that approach 2 m s^{-1} (Visbeck & Thurnherr, 2009). Analyses of time series from a moored current meter array, high-resolution hydrographic profiles (Gordon et al., 2004, 2009; Whitworth & Orsi, 2006), and high-resolution microstructure profiles (Muench et al., 2009) from the AABW outflow region in the western Ross Sea, coupled with analyses of simulated circulation fields obtained for the Ross Sea from a three-dimensional primitive equation numerical model (Padman et al., 2009), show that mixing via tidal currents is a critical component of the dynamics of the dense shelf water outflows (Muench et al., 2009). The identification of the importance of tidal flows to the circulation of the Ross Sea and ultimately to the larger-scale global circulation has important implications for future field programmes and models that are developed to study the hydrographic structure and circulation of the Ross Sea. Explicit inclusion of the dynamics of the tides in the Ross Sea is required for an accurate representation of the overall circulation.

Glacial ice and sea ice have strong influences on the water properties of the Ross Sea continental shelf. The seasonal pattern of ice cover and polynya formation in the Ross Sea is well known from comparisons of sequential distributions of sea ice coverage derived from satellite observations (see Figure 7.4; Jacobs & Giulivi, 1998; Zwally et al., 2002; Smith & Comiso, 2008). Sea ice is a seasonal and transient feature and covers the Ross Sea in winter. All but the most eastern Ross Sea is free of sea ice by late summer (January and February), after which sea ice begins forming again.

Polynyas are essentially winter features; that is, they are generated and maintained in winter, but enlarge during spring and summer, when they have been described as being in a 'post-polynya' phase – with the surrounding sea ice having disappeared in at least one direction (Arrigo, 2007). The Ross Sea Polynya (RSP) is consistently detected throughout winter, although its size may be greatly restricted to a small region along the RIS. The RSP expands rapidly in November as the heat budget becomes positive, facilitating the cessation of ice formation and inducing melting. The post-polynya enlarges to the north and east, and by mid-January much of the continental shelf is free of sea ice. Large variations occur among years, and these may result from large-scale processes controlling air pressure and storms (Jacobs & Comiso, 1989; Ainley et al., 2005).

The RSP opens due to both warm water at depth (sensible heat) and strong northerly katabatic winds (latent heat export) off the RIS. Other coastal polynyas, such as the Terra Nova Bay (TNB) polynya, remain open during the winter due to offshore katabatic winds, allowing continual freezing of ocean water and export of sea ice that together result in significant salt fluxes. The combination of winter cooling and brine rejection creates some of the densest water in the ocean, making the western Ross Sea an important site for deep-water formation (Orsi & Wiederwohl, 2009).
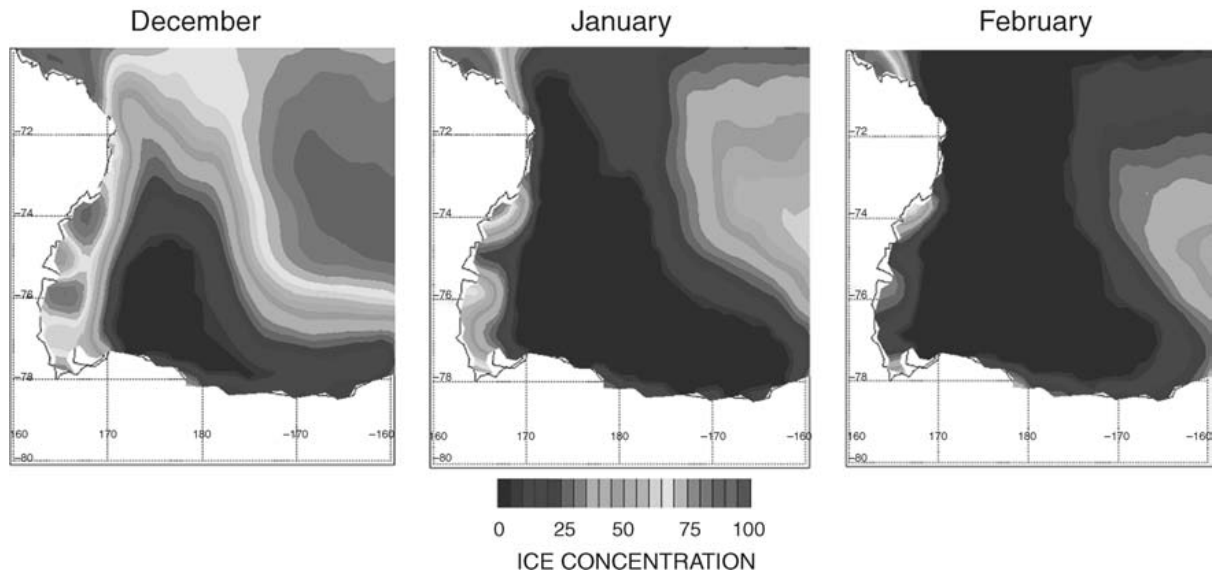
Figure 7.4 The seasonal progression of ice cover in the Ross Sea. Data provided by the National Snow and Ice Center, Boulder, CO, USA. (*See the colour version of this figure in Plate section.*)

As described above, the cold, dense water formed here cascades off the shelf and expands throughout the southern Pacific sector (Orsi *et al.*, 1999; Orsi *et al.*, 2002). The volume of the water generated has been estimated to be responsible for 20% (Orsi *et al.*, 1999) to 33% (Locarnini, 1994) of all deep water formed in the Southern Ocean. Smaller polynyas also occur along the coast of Victoria Land, with notable examples being the Ross Passage and Pennell Bank Polynyas (Jacobs & Comiso, 1989). These polynyas are affected by the upwelling of warm MCDW (Jacobs & Comiso, 1989).

An additional component of sea ice dynamics is the occasional presence of large ($\sim$5000 to 10,000 km^2) icebergs that become grounded and restrict the advection of pack ice off the shelf (Arrigo *et al.*, 2002). While icebergs of this size are (apparently) rare, they have occurred regularly during the Holocene as the RIS retreated; their occurrence results in pack ice concentrations that are far greater than normally observed, and thus can have significant impacts on the food web by decreasing primary productivity, altering migration patterns of megafauna, and disrupting trophic dynamics (Arrigo *et al.*, 2002; Ainley *et al.*, 2006).

Analyses of sea ice records derived from satellite passive microwave sensors, which began in 1978, have revealed variable trends in sea ice coverage (Stammerjohn & Smith, 1997; Liu *et al.*, 2004; Parkinson, 2004) and length of the sea ice season (Parkinson, 2002; Stammerjohn *et al.*, 2008) depending on scale in the Ross Sea sector. At the regional scale ice extent and the length of seasonal coverage is increasing, but at smaller scales some coastal polynyas are growing in spatial extent and duration of ice-free days. The underlying causes appear to be connected to large-scale global climate variability, as mediated through winds and the Southern Annular Mode (SAM). Parkinson (2004) provides a review of modelling and observational studies that address the response of Southern Ocean sea ice to large-scale climate forcing. Features of the global climate system such as the Antarctic Dipole (Yuan & Martinson, 2000, 2001), Southern Annular Mode (SAM: Hall & Visbeck, 2002; Simmonds & King, 2004) and El Niño-Southern Oscillation (Yuan & Martinson, 2000; Yuan, 2004) affect the Ross Sea, but interannual variability in sea ice coverage of this region makes identification of trends, linkages and attribution of cause difficult (Parkinson, 2004). Nevertheless, increasing large-scale winds are increasing ice extent and season and increasing the importance of polynyas (Russell *et al.*, 2006; Stammerjohn *et al.*, 2008; Ainley *et al.*, 2010c).

7.3 BIOLOGICAL SETTING

The Ross Sea has a diverse biota in both the neritic and benthic realms, and includes a substantial contribution from both the ice and shallow water littoral to the overall biodiversity. Indeed, its benthos has been described as a biodiversity hotspot (Clarke & Johnston, 2003), and its fish fauna is evolutionarily distinct (Eastman & Ainley, 2009). More than 40 vertebrate species are endemic to the Ross Sea, including >400 type specimens of birds, fish and invertebrates (Ainley *et al.*, 2010b). Individual components of trophic levels and interactions between trophic levels have been the focus of many national and international research programs in the Ross Sea (e.g., JGOFS: Smith *et al.*, 2000; Anderson & Smith, 2001). However, despite the long history of study (dating from the explorations of James Clark Ross in the mid-1800s) much remains to be learned, and many biological interactions remain incompletely characterized. While several long-term data sets exist, the lack of comprehensive data, while not unusual for marine systems, limits our ability to predict responses of the Ross Sea ecosystem to environmental and human perturbations, both of which are now having detectable effects (Dayton, 1989; Ainley *et al.*, 2005, 2010c). In the context of the global ocean, the Ross Sea food web is as yet relatively unexploited by humans or affected by other anthropogenic factors (Halpern *et al.*, 2008; Ainley, 2010), and therefore offers an opportunity to investigate largely unperturbed continental shelf food web processes.

7.3.1 Lower trophic levels

Primary production and biomass in the Ross Sea is substantial, accounting for as much as 28% of the annual production of the Southern Ocean ($4410\,\mathrm{Tg\,C\,yr}^{-1}$; derived from a model using chlorophyll concentrations; Arrigo *et al.*, 1998b). The mean biomass observed is as great as anywhere in the Southern Ocean (see Figure 7.5), with average annual chlorophyll concentrations of about $2\,\mu\mathrm{g\,L}^{-1}$, nearly an order of magnitude greater than in waters with depths greater than 1000 m. Such averages represent only those days with cloud- and ice-free locations, and do not include the vanishingly small values in winter. Other continental shelf regions have similar mean chlorophyll levels, but when productivity is modeled using short-term pigment concentrations, incident irradiance, euphotic zone
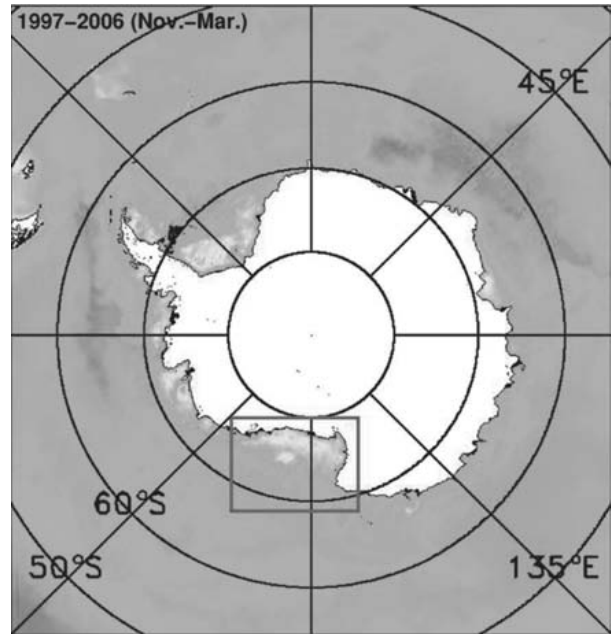

Figure 7.5 Annual climatology of the pigments in the Ross Sea region derived from SeaWiFS. Each pixel is the mean of all data available from November through March from 1997–2009. From Smith and Comiso (2008). (*See the colour version of this figure in Plate section.*)

depth and photosynthesis/irradiance responses, then the large primary production of the Ross Sea continental shelf becomes apparent (Arrigo *et al.*, 2008; Smith & Comiso, 2008). In addition, weekly maxima in productivity are substantially greater in the Ross Sea than in either the West Antarctic Peninsula or Weddell Sea (Smith & Comiso, 2008). A climatology based on discrete samples demonstrates the temporal trends in biomass usually observed: rapid increase in November upon ice removal, a unimodal maximum in late December, with a rapid decrease to low levels prior to the complete cover by ice in March (see Figure 7.6). A similar climatology derived from satellite pigment determinations shows a similar pattern, although specific regions show differences, likely due to biases introduced by differences in sampling (Figure 7.7). The production in the Ross Sea is supported by both water-column and sea-ice microbial processes.

The functional groups (species that have a similar, unifying characteristic and ecological role, Hood *et al.*, 2006) of the lower trophic levels, particularly phytoplankton, are well known. The important functional
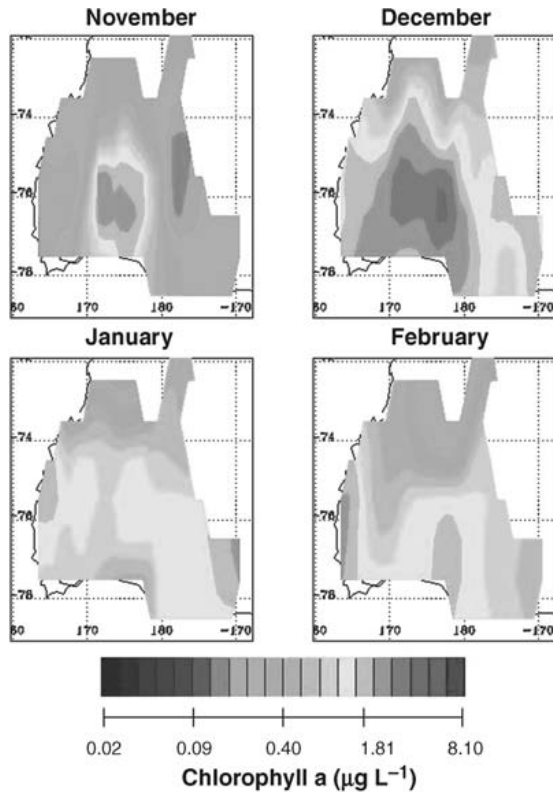
Figure 7.6 Monthly climatology based on a compendium of discrete measurements of chlorophyll a from 1983–2005 (from Smith et al., 2010). (*See the colour version of this figure in Plate section.*)

groups found in the Ross Sea include diatoms, haptophytes, dinoflagellates, silicoflagellates and cryptophytes (Table 7.2), but just as importantly, several functional groups commonly found in other oceans, such as coccolithophorids, cyanobacteria, chlorophytes, and prochlorophytes, are almost completely absent in the Ross Sea. Therefore, while the 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 that are of central importance in temperate and tropical settings (e.g., Li *et al.*, 1992) are indeed absent; hence, the mean size of the 'average' primary producer is substantially larger than that of nonpolar regions. The larger size potentially increases the net transfer efficiency to the higher trophic levels (e.g., Ryther, 1969), but the type of functional group also influences trophic transfer in the region.

Diatoms attain high biomass in waters overlying the Ross Sea continental shelf, and often are dominant members of the phytoplankton. Pennate species (e.g., *Fragilariopsis* spp., *Pseudonitzschia* spp.) form large blooms, particularly near the expanding ice edge 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 fecal pellets (Smith & Dunbar, 1998; Accornero & Gowing, 2003). Centric diatoms (e.g., *Corethron criophillum*, *Rhizosolenia* spp., *Thalassiosira* spp.) are ubiquitous components as well.
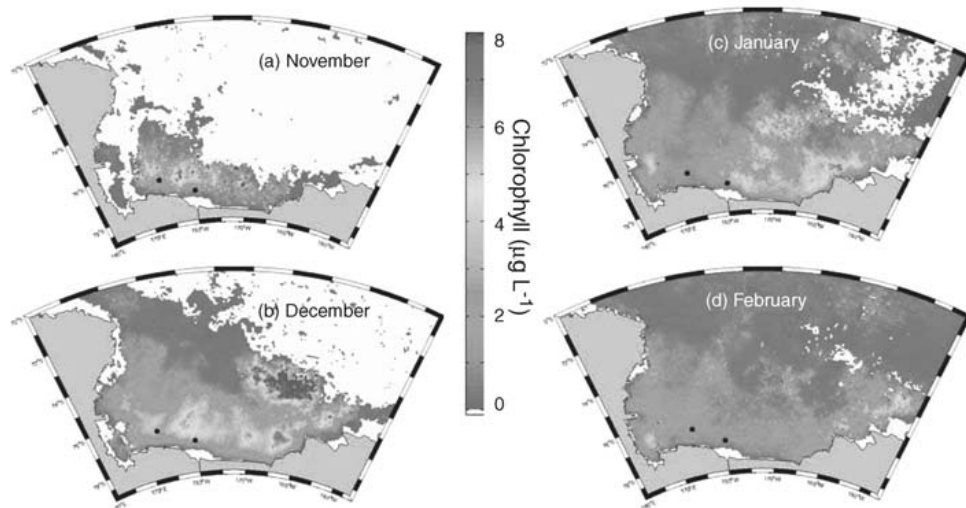

Figure 7.7 Mean monthly chlorophyll concentrations in the Ross Sea as derived from the SeaWiFS satellite estimates from 1997–2009. (a) November, (b) December, (c) January, and (d) February (from Smith et al., 2011a). (*See the colour version of this figure in Plate section.*)

Table 7.2 Functional groups and the 'critical' species within each group in the Ross Sea

Functional group	Critical species
Phytoplankton	
Diatoms	*Corethron coriophyllum, Pseudonitschia spp., Fragilariopsis spp., Rhizosolenia spp., Thalassiosira spp.*
Haptophytes	*Phaeocystis antarctica*
Dinoflagellates	
Cryptophytes	
Heterotrophic microplankton	
Dinoflagellates	
Choanoflagellates	
Heterotrophic mesozooplankton	
Pteropods	*Limacina helicina*
Copepods	*Calanoides acutus*, *Metridia gerlachei*, *Euchaeta antarctica*
Euphausiids	*Euphausia crystallorophias*
Nekton	
Small fishes	*Pleuragramma antarcticum, Trematomus bernacchii, Pagothenia borchgrevinki*
Large fishes	*Dissostichus mawsoni*
Marine mammals and birds	
Seals	*Lobodon carcinophagus, Leptonychotes weddelli, Hydrurga leptonyx*
Penguins	*Pygoscelis adeliae*, *Aptenodytes forsteri*
Petrels	*Pagodroma nivea*, *Thalassoica antarctica*
Whales	*Orcinus orca*, *Balaenoptera bonaerensis*
Benthic fauna/flora	
Shallow, hard substratum: macroalgae, sponges, soft corals, amphipods, gastropods, bryozoans, echinoids, asteroids	*Himantothallus, Desmarestia, Phyllophora, Homaxinella balfourensis, Alcyonium, Paramoera walkeri*, Sertellidae, *Sterechinus neumayeri, Odontaster validus*
Deep (>100 m), hard substratum: sponges, corals, polychaetes, barnacles, bryozoans	*Cinachyra, Errina, Bathylasma corolliforme, Serpula narconensis,* Microporellidae, Cabereidae, Tubuliporidae
Soft substratum: bivalves, gastropods, polychaetes, echinoids, asteroids, ophiuroids echinoids, corals	*Laternula elliptica, Adamussium colbecki, Yoldia eightsi,* Syllidae, *Ctenocidaris, Acodontaster, Ophionotus, Ophiosparte, Ophiurolepis, Astrotoma*

Autotrophic dinoflagellates are more poorly described, but have been observed in significant numbers (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. In portions of the Ross Sea, a significant proportion of diatoms remain ungrazed (Arrigo *et al.*, 2003).

Haptophytes are another important functional group, and in the Ross Sea one species, *Phaeocystis antarctica*, is dominant. *Phaeocystis* is known to be

critical to biogeochemical cycles, climate feedbacks, and food webs, but its specific trophic connections in the Ross Sea remain elusive. It produces large amounts of dimethylsulphide (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 apparently largely ungrazed (DiTullio & Smith, 1996; Caron *et al.*, 2000), and can export significant quantities of organic matter to depth
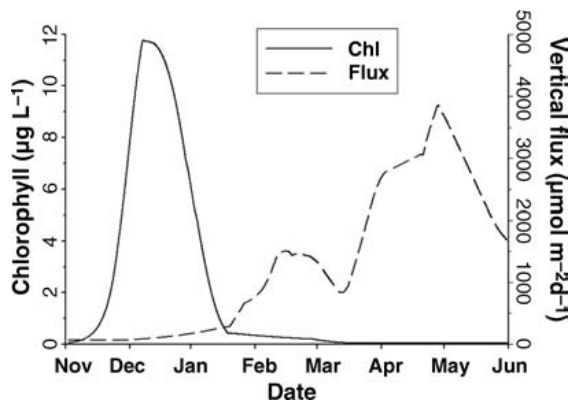
Figure 7.8 Temporal pattern of *Phaeocystis antarctica* abundance (as chlorophyll; CHL) and the vertical flux of particulate organic carbon to depth in the southern Ross Sea. *P. antarctica* biomass based on Tremblay and Smith (2007); flux data from Collier et al. (2000).

via aggregate formation (Smith & Dunbar, 1998; DiTullio *et al.*, 2000). The general, seasonal pattern of *P. antarctica* abundance is characterized by rapid growth in spring, being initiated in early November and reaching a maximum in mid- to late December, and a rapid demise in January (Figure 7.8). Its growth in late December is likely 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; Sedwick *et al.*, 2007) and, coupled with its ability to grow well at low irradiance (Moisan & Mitchell, 1999), relatively low grazing pressures provided by its life cycle (formation of large colonies that cannot be effectively grazed by small herbivores) and its ability to survive freezing in ice and long periods of darkness (Figure 7.9; Tang *et al.*, 2009) may allow it to bloom early in the season.

While the overall climatology of biomass and nutrient removal is established, substantial variations in space and time occur, especially among years. Using in situ fluorescence measurements, Smith *et al.* (2006, 2011a) demonstrated substantial differences in biomass through time at one location, as well as large differences among years (Figure 7.10a, b). In 2003–2004 the fluorescence at the two sites analyzed was similar to the climatological mean, in that biomass was high in late December, but declined rapidly thereafter. The unusual feature of this year was a large

summer increase (also noted in satellite images; Peloquin & Smith, 2007) that has been called a secondary bloom. The primary bloom consisted of *P. antarctica*, whereas the secondary bloom was driven by diatoms. At the eastern site (Figure 7.10b) the primary bloom was not recorded, likely because it had disappeared from the water column by the time of mooring deployment. In 2004–2005 a primary bloom was observed at both locations, but no secondary bloom. Furthermore, a large number of short-lived fluorescence excursions were noted at the eastern site that likely were related to both advective and mixing events (Smith *et al.*, 2011a). In 2005–2006, fluorescence at both sites was similar to the previous year initially, and also declined to low levels in January. However, marked diel fluctuations were noted; indeed, such diel patterns were seen in all years, but were a much greater percentage of the absolute fluorescence in 2005–2006 due to the low surface biomass. These results clearly demonstrate the magnitude of spatial and temporal variations on a variety of time scales, and suggest that such variations might have important food web and biogeochemical impacts.

Owing in part to the large amount of sea ice, cryophilic algae are an important source of organic matter for the Ross Sea 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 basis ice algae contribute from 4–20% of primary production (Arrigo *et al.*, 1998b; Pinkerton *et al.*, 2010). The temporal dynamics of ice algae are quite different compared to those of phytoplankton, with a seasonal increase occurring prior to that of phytoplankton, and the release into the water column (and subsequent flux and/or remineralization) occurring prior to substantial planktonic growth (Arrigo *et al.*, 1998a, b). It repeatedly has been suggested that ice algae 'seed' the water column upon ice melt (e.g., Smith & Nelson, 1985; Garrison *et al.*, 2003), but little direct evidence exists concerning the physiological and ecological capabilities of ice algae once they are released into the water column. Despite the presumed importance of ice biota, little is known specifically about the linkages between ice algae, the water column, and the food web and regional biogeochemistry; furthermore, virtually nothing is known concerning the ice communities in winter – the survival strategies, and physiological acclimations. Without that
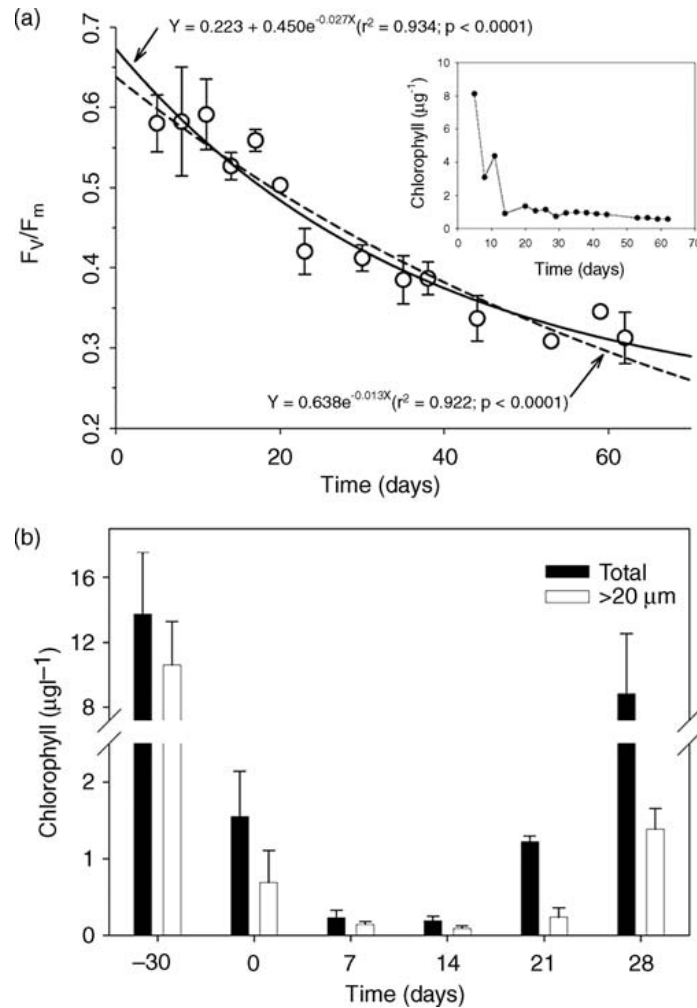
Figure 7.9 (a) Response of *Phaeocystis antarctica* photosynthetic capacity to prolonged darkness. Chlorophyll a concentrations are shown in the inset. The line represents an exponential decline with time, and the dashed line represents an exponential decline with a threshold. (b) Response of *P. antarctica* to 30 days of being frozen in ice. Solid bars represent both colonial and solitary cells; open bars represent colonies. From Tang *et al.* (2008).

understanding, a quantitative depiction of food web relationships and transfers will remain elusive.

Shallow, near-shore regions along the coast of Victoria Land can support substantial concentrations of macroalgae, periphyton, or microbenthic algae (Bunt, 1963). There appears to be marked gradient in macrophyte abundance, with large kelp communities occurring along the coast in the north (Cape Hallett), but largely disappearing in the south near Ross Island, likely due to physical/ice disruptions. While these forms can contribute to the food web and carbon inputs

locally, their contribution to the continental shelf is quite restricted.

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 in production and remineralization of organic matter (e.g., Lizotte, 2003, Garrison *et al.*, 2006). However, biomass does not increase to the same degree as phytoplankton, suggesting that the spring biomass and activity may be limited by carbon and energy sources, whereas later in the summer
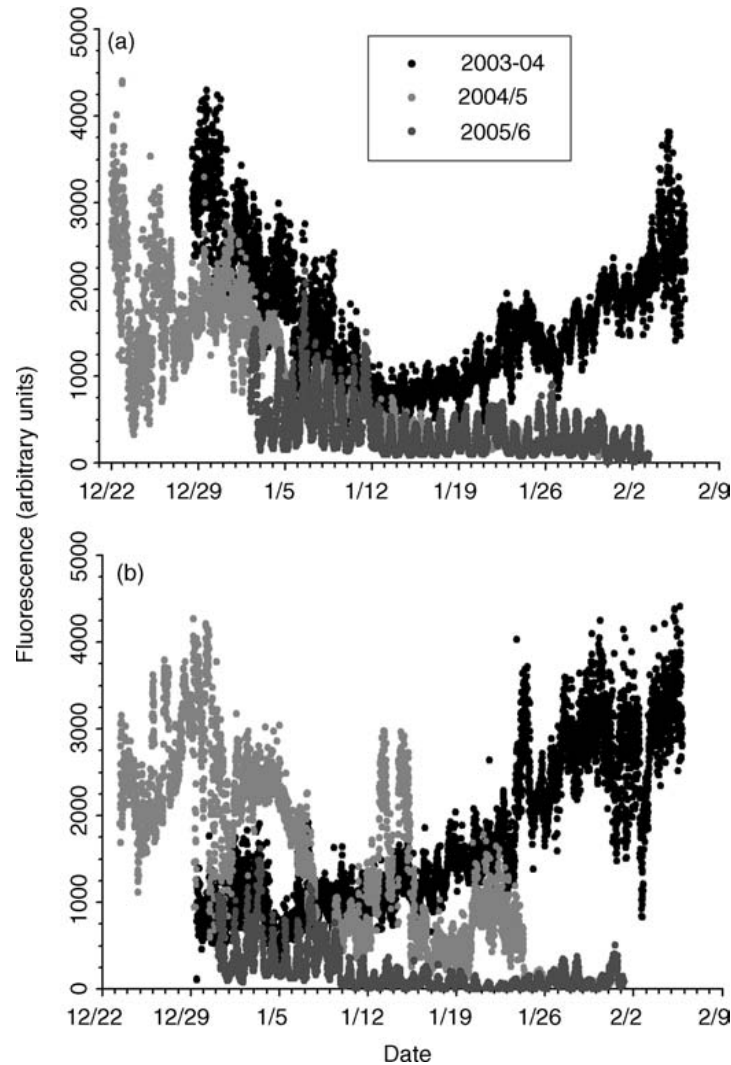
Figure 7.10 In situ fluorescence measurements collected from late December through early February in 2003–04, 2004–05, and 2005–06 at a) 77° S, 172.5° E and b) 77.8° S, 180°. Depths of the measurements were 19, 5 and 6 m at 77° S, 172.5° E and 19, 16 and 16 m at 77.8° S, 180°. Data were collected every 10 minutes, but only plotted every 3 hours. Adapted from Smith et al. (2011a).

losses due to bacterivory may balance growth and become quantitatively 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 likely using bacteria and small algae (such as solitary forms of *P. antarctica*) as a major food source. Bacterial cells are also larger than those from warmer waters, with average cell lengths being approximately 1 μm (Ducklow *et al.*, 2000).

Recently it was reported that prokaryotic assemblages (as detected by molecular analyses) exhibited a strong stratification within the water column, and reflected both the influence of light (autotrophic processes) and water mass formation (physical processes; Celussi *et al.*, 2009); however, a differentiation of major prokaryotic groups (e.g., Eubacteria, Archaea) was not provided.

Although bacterial production and the microbial food web is 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, 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 experiments did not show 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. Tang *et al.* (2008) found that a chemical signal also may reduce grazing on *P. antarctica*, but the ecological significance of this impact is uncertain.

7.3.2   Mid-trophic levels

Surprisingly little is known about Ross Sea mesozooplankton ($>200\,\mu$m) and their role in food web dynamics and biogeochemical cycles. Hopkins (1987) analyzed the diet of the zooplankton, euphausiids and small fish in McMurdo Sound, and found that the copepods *Calanoides acutus*, *Metridia gerlachei*, and *Euchaeta antarctica* were important prey items. The same species were found to be important for organisms in Terra Nova Bay and the northern shelf region as well (Carli *et al.*, 1999). Deibel and Daly (2007) note that the biomass of smaller zooplankton (copepods, etc.) is high, and that of krill is low (i.e., an order of magnitude lower than in the Scotia Sea). This contrasts with upper level predators, which are more abundant than most other Southern Ocean locations (Ainley *et al.*, 2010b).

The biology, physiology and ecology of Antarctic krill (*Euphausia superba*) has been intensively investigated throughout the Southern Ocean (Siegel, 2005; Nicol, 2006; Atkinson *et al.*, 2008), though less so in the pelagic and slope waters of the Ross Sea (Deibel & Daly, 2007). Antarctic krill predominates in waters overlying the slope and in the outer portions of troughs where CDW intrudes southward; over the inner shelf it is replaced by crystal krill *E. crystallorophias* (Ainley *et al.*, 2010b). Crystal krill *Euphausia crystallorophias* is an important link between the sea ice, the water column, and upper trophic levels, owing to its prominence in the diets of upper trophic level species (e.g., Ainley

et al., 1984, 2003a; Ichii *et al.*, 1998), but there have been only a few efforts to quantify its biomass, distribution and rates of grazing (e.g., Azzali & Kalinowski, 1999; Sala *et al.*, 2002; Taki *et al.*, 2008). This krill species, also known as ice krill, is an obligate ice form, and is considered to be the single most important grazer of neritic diatoms (Pakhomov & Perissinotto, 1997). Nearly nothing, however, is known about its quantitative relationship with ice algae. Sala *et al.* (2002), elaborated upon further by Taki *et al.* (2008) and supported by predator diets (e.g., Ainley *et al.*, 2010b), quantified the dominance of *E. crystallorophias* on the shelf south of 74° S, but that of *E. superba* along the shelf break. Net tows and acoustic surveys for krill in the Ross Sea sector (Azzali & Kalinowski, 1999; Sala *et al.*, 2002) found notable patchiness for both species, but in all these direct samplings the abundance of krill was surprisingly sparse. Hopkins (1987) found that the late summer biomass of crystal krill (a period when most ice algae had disappeared and grazing pressure by whales likely had increased dramatically) was only 10% that of total zooplankton in McMurdo Sound, and was approximately equal to that of small fishes. However, the foraging upon crystal krill is intense, leading to its presumed seasonal depletion by predators (e.g., Antarctic silverfish *Pleuragramma antarcticum,* Adélie penguins *Pygoscelis adeliae*, and Minke whales *Balaenoptera bonaerensis*; Ainley *et al.*, 2004, 2006), and resulting in increased predation pressure on alternative prey, such as small fish during early summer (Ainley *et al.*, 2003a, 2006). Indeed, in the late summer silverfish become cannibalistic, with larger individuals foraging on the larvae (Eastman, 1985).

Crystal krill can live about five years (Deibel & Daly, 2007) and as a result can impact the Ross Sea food web at multiple scales and trophic levels through their roles as prey items, predators and contributors to biogeochemical cycling. The importance of crystal krill to the food web remains to be assessed, and new ideas and data on their biomass, vertical and horizontal distribution, and life-history patterns, particularly with regard to their response to seasonal and interannual variation in sea ice extent, polynya extent and timing, and predation, are urgently needed. Other taxa (e.g., gelatinous forms such as ctenophores and cnidaria) are present, but little is known concerning their impacts on the food web of the Ross Sea.

An unusual feature of the Ross Sea is the relatively significant temporal uncoupling between surface production and the vertical flux of organic matter (Figure 7.8). In many areas of the ocean and Antarctic,

the export of organic matter to depth (in this case 200–1000 m) is tightly coupled to surface production, as passive sinking of phytoplankton and phytodetritus is relatively rapid (on the order of 10–100 m d^{-1}), and so sinking of particles can deliver POC to 600 m on the order of days to weeks (Asper *et al.*, 1992; Smith & Dunbar, 1998; DiTullio *et al.*, 2000; Smith *et al.*, 2011b). In the Ross Sea the maximum in phytoplankton biomass and flux can be, however, separated by some 4.5 months (Figure 7.8). The production peak is due to the seasonal bloom of *P. antarctica* and occurs in late December, whereas the flux maximum is much broader, occurs in May (winter), and in 1996–1997 was mediated by the pteropod *Limacina helicina* (Collier *et al.*, 2000). In other years, a marked maximum occurs in late February, and based on the elemental characteristics, is driven by phytodetritus (Dunbar *et al.*, 1998; Smith *et al.*, 2011b). The contribution of diatoms and *P. antarctica* to the phytodetrital flux is a function of the surface distributions of the two functional groups (Smith & Dunbar, 1998). The yearly production is ca. 100 g C m^{-2} (Smith & Gordon, 1997; Tremblay & Smith, 2007; Arrigo *et al.*, 2008), and the January–June flux is ca. 3.5 g C m^{-2}, suggesting that the Ross Sea is neither highly retentive nor characterized by high rates of export relative to production (Grebmeier & Barry, 2007). However, the timing of flux is unusual and may influence benthic growth and survival. It should be noted, however, that biogeochemical budgets suggest that export from the surface layer is at least an order of magnitude greater than that determined by sediment traps (Sweeney *et al.*, 2000; Smith *et al.*, 2006), so that current understanding of benthic–pelagic coupling may be biased.

The Ross Sea, like the rest of the Southern Ocean, experiences numerous short-term storms (Smith *et al.*, 2011a). These storms are reduced in frequency and intensity during summer months, but still occur regularly. Such events may induce deeper mixing of surface layers, resulting in net movement of organic matter to depth at time scales associated with these high-frequency events (a few days; Smith *et al.*, 2011a). Such an increase in vertical flux has been modeled in other ocean areas (Waniek, 2003), but data that are adequate to allow similar studies for the Southern Ocean and Ross Sea are lacking. However, given the intensity of the storms that impact the Ross Sea, it is likely that they increase the rate and timing of flux to depth, and thus have the potential to impact water column biota.

7.3.3   Fishes and mobile predators

The Ross Sea fish fauna, like much of the Antarctic's continental shelves, 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 deeper portions of the Southern Ocean, including the Ross Sea continental slope, such families as Myctophidae, Liparidae, and Macrouridae occur (Eastman, 1993). Most notothenioids are benthic fishes having no swim bladders, reduced skeletal mineralization and concentrated lipid deposits; they have radiated, however, by modulating lipids in the tissues to occupy mid-waters, especially Antarctic silverfish, *Pleuragramma antarcticum,* and the top-predator, Antarctic toothfish *Dissostichus mawsoni* (Eastman, 1993). In the Ross Sea, in an impressive radiation of ecotypes, notothenioids comprise 77% of all species and 91% of biomass (Eastman & Hubold, 1999). In addition to their overwhelming dominance, notothenioids are equally important as crystal krill as prey for mesopredators within the Ross Sea food web, a pattern divergent from the Antarctic krill-dominated systems that occur throughout the rest 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, a condition that is true for the entire Southern Ocean, except at its northernmost periphery (i.e., around South Georgia and Kerguelen islands) where sharks occasionally are observed. The presence of the very large, slow-moving Antarctic toothfish as well as a low density of mid-water fishes as prey are likely responsible for the absence of sharks but not elasmobranches (rays, skates; Eastman, 1993; see below).

Antarctic silverfish, like crystal krill, occupy a central role in the Ross Sea food web. This species occurs near the surface as 1- and 2-year-olds, and 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 (crystal krill, copepods), but is opportunistic and will ingest other prey, including 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*), minke whales and ecotype-C

orcas (*Orcinus orca*; see Pitman & Ensor, 2003, for a description of ecotypes). During times and in locations where crystal krill are absent or at greatly reduced biomass, *P. antarcticum* may provide the dominant pathway for energy transfer to the upper trophic levels of the Ross Sea marine food web.

Another notothenioid of great ecological importance in the Ross Sea, at the least as a predator, is the Antarctic toothfish. Its egg, larvae and small juveniles are undescribed, but it is thought that they spawn infrequently during winter in the ice-covered waters near sea mounts to the north of the Ross Sea (Hanchet *et al.*, 2008). As subadults and adults, the species is epibenthic, although under fast ice it occurs in mid-depths almost to the surface (Fuiman *et al.*, 2002). As with other notothenioids, neutral buoyancy is achieved by both lipid inclusions (10% of its mass is derived from lipids) and reduced skeletal calcification (Eastman, 1993). This species is by far the largest fish in Antarctic waters (mean length and mass for 29 specimens in McMurdo sound were 163 cm and 60 kg, respectively; Eastman, 1993; Horn, 2002; Brooks & Ashford, 2008), and recently has become the target of a long-line fishery in the Ross Sea and waters to the north (Phillips *et al.*, 2004). Given that toothfish spawn irregularly and grow slowly (at least as subadults: ca. 2 cm and $0.9 \, \text{kg} \, \text{y}^{-1}$; Eastman, 1993), the fishery likely will quickly impact the biomass and distribution of the group, possibly disrupting the food web (in the sense of Jackson *et al.*, 2001; Pauly & Maclean, 2003; Pauly *et al.*, 2005; Baum & Worm, 2009). Indeed, adult toothfish no longer can be caught in McMurdo Sound (DeVries *et al.*, 2008), at the southern edge of the species' range, with potential effects on the abundance of fish-eating killer whales, for which large toothfish are an important dietary item (Ainley *et al.*, 2010a). Eastman (1993) characterized toothfish as the most voracious piscine predator in the Southern Ocean; hence, toothfish may be the ecological counterpart of sharks in warmer ecosystems. Over the Ross Sea shelf toothfish feed primarily on *Pleuragramma antarcticum*, but also on cephalopods and mysids; in slope waters it preys mainly on benthic elasmobranches and near-bottom macrourid fishes (Eastman, 1985; Fenaughty *et al.*, 2003). In turn, it is a major food item for Weddell seals and killer whales (Type C; Ainley & Siniff, 2009; Ainley *et al.*, 2010a); its vertical and horizontal distribution in McMurdo Sound may be strongly controlled by the foraging by seals and killer whales (e.g., Testa *et al.*, 1985).

The cryopelagic notothenioid *Pagothenia borchgrevinki* also is common in the Ross Sea. Its diet is diverse, feeding on pteropods, copepods, amphipods, and larval silverfish (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 platelet layer as a refuge against predation (similar to the behavior of krill; Brierley *et al.*, 2002). The species has substantial concentrations of blood antifreezes, which facilitate its cryopelagic life style. Emperor penguins and Weddell seals are its main predators.

Squid, especially *Psychroteuthis glacialis* and *Gonatus antarcticus*, are important prey of many upper trophic level predators in the Ross Sea (Ainley *et al.*, 1984; Fenaughty *et al.*, 2003; La Mesa *et al.*, 2004), but as elsewhere in the Southern Ocean, little is known of their biomass or natural history.

7.3.4 Upper trophic levels

Unlike the remainder of the world ocean, the top trophic levels of the Ross Sea have been relatively unexploited, and trophic linkages remain intact, at least for the present, although the impacts of whaling on the populations of the Ross Sea are poorly defined (Ainley, 2010). Although it is the least affected stretch of ocean on Earth (Halpern *et al.*, 2008), this is not to say that the Ross Sea is 'pristine' and unimpacted by human activity. This region is responding to the large-scale climate signals that are affecting the rest of the Antarctic and world oceans (Parkinson, 2004; Stammerjohn *et al.*, 2008), and the long-term effects of these influences on the Ross Sea food web are only beginning to become evident (Dayton, 1989; Ainley *et al.*, 2010c). However, much is known about the abundance, distribution, diet and natural history patterns of the top predators: cetaceans, seals and birds, and increasing information is being garnered on toothfish, which can be combined with modeling studies to develop response scenarios.

Satellite-derived chlorophyll distributions and the abundance of other top-trophic predators imply that the Ross Sea is one of the most productive regions of ocean south of the Polar Front (see above). Due to the paucity of surveys of prey abundance (i.e., crystal krill, Antarctic krill, cephalopods, and Antarctic silverfish), virtually nothing is known on how variations in prey variability might affect long-term variations in reproductive success or population size of top predators. Conversely, growing evidence indicates that feeding by

the top predators during summer affects the availability of their fish and krill prey, at least in the 100s km^2 of ocean that border on large concentrations of breeding animals (Testa *et al.*, 1985; Ainley *et al.*, 2004, 2006). This indicates a delicate balance in this system. Moreover, the high primary productivity and substantial densities of top predators, but the low abundance of grazers, suggest a possible system-wide trophic cascade, i.e., 'reciprocal predator–prey effects that alter the abundance, biomass, or productivity of a population, community, or trophic level [down through] more than one link in a food web' (Pace *et al.*1999; Baum & Worm, 2009).

Cetacean, pinniped and avian biomass over the shelf during the early 1980s were determined to be approximately 0.182, 0.068, 0.070 g wet weight m^{-2}, which are levels comparable to the richest top-trophic marine communities elsewhere (Ainley, 1985). Since then, the populations of both penguins and minke whales have increased significantly owing to climate and ecological interactions (Ainley *et al.*, 2005, 2007; Ainley, 2010) and toothfish have decreased (see above). The members of these communities are pagophilic in their distributions, being associated with sea ice or its boundaries (Ainley *et al.*, 2003b). Except along the continental slope where blue (*Balaenoptera musculus*) and, to a lesser degree, fin (*B. physalus*) whales once frequented, over-fishing, sealing or whaling have not affected ecosystem processes over the shelf (Ainley, 2010), nor has widespread pollution been an issue as elsewhere (Halpern *et al.*, 2008). In the Ross Sea's coastal waters the minke whale population, which likely expanded into the habitat vacated by the great whales (Ainley, 2010), was reduced by whaling (standing stocks reduced by 40%; Branch & Butterworth, 2001) that occurred during the 1970s and early 1980s. It has since recovered (Branch & Butterworth, 2001), perhaps as a result of a reserve population that was protected in the pack ice where whaling ships could not work. Currently, the cetacean population over the shelf is composed entirely of Antarctic minke whales (about 21,000, or 6% of the world population), killer whales (about 3000; mostly type-Cs), and far fewer but unknown numbers of Arnoux's beaked whales (*Berardius arnouxii*; Ainley, 1985; Branch & Butterworth, 2001; Brownell & Ainley, 2009). These whales, like most of the birds (see below), are likely absent from the shelf during winter, owing to darkness and the extensive sea ice present (Van Dam & Kooyman, 2004). Sperm whales, *Physeter macrocephalus*, are beginning to return to waters of the Ross Sea

continental slope, perhaps numbering into the hundreds (Myashita *et al.*, 1995), although they were greatly reduced in the 20th century as a result of range contraction, as the Pacific stock was heavily exploited in the warmer part of its range during the 18th and 19th centuries (Ainley, 2010). They are known to feed on toothfish and squid, including the colossal squid *Mesonychoteuthis hamiltoni*, which potentially are an important over the continental slope.

Avian populations also have high standing stocks, but are species poor. Approximately 38% and 26% of all Adélie and Emperor penguins reside during summer in the Ross Sea, or about 4 million penguins, including breeding and non-breeding individuals (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); the numbers of Antarctic petrels are in the range of 30% or more of the world population. As noted above, Adélie penguin populations increased as minke whales were removed from slope and more northern waters during the 1970–1980s (where the penguins winter), at the same time that increasing winds were enhancing penguins' access to prey by making polynyas more predictable (Ainley *et al.*, 2005, 2007).

Finally, the pinniped assemblage is composed of five species, dominated by the crabeater seal (*Lobodon carcinophagus*; about 200,000 individuals), but also including Weddell seals (about 20,000–32,000), leopard seals (*Hydrurga leptonyx*, 8000), Ross seals (*Omatophoca rossi*; 5000) and a few elephant seals (*Mirounga leonina*; Ainley, 1985). Except for the elephant seal, these species likely breed in the Ross Sea region 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. If the total Antarctic population of Weddell seals as determined by genetic methods is correct (Curtis *et al.*, 2009), then the Ross Sea may possess about half of the world population of this species. The remaining seals are denizens of the pack ice, especially along the shelf-break and the ice margins of the RSP; Ross seals do not occur in the open waters over the shelf (Ainley *et al.*, 2003b).

All of these top predators prey principally on two organisms in waters over the shelf: Antarctic silverfish and crystal krill (Eastman, 1985, 1993; Ichii and Kato, 1991; Ichii *et al.*, 1998; Cherel & Kooyman, 1998, Ainley *et al.*, 2003b). Toothfish are also an important prey to Type-C orcas and Weddell seals (Testa

et al., 1985; Pitman & Ensor, 2003; Ainley & Siniff, 2009, Ainley *et al.*, 2010a). Near the shelf-break Antarctic krill and myctophids replace crystal krill in the top predators' diets (Ainley *et al.*, 1984; Ichii *et al.*, 1998). *Pyschroteuthis glacialis* (squid) can also be important in diets near the shelf break (Ainley *et al.*, 1984). The central portion of the RSP is nearly devoid of top predators during spring, but these organisms are found later in the season in the diatom-dominated food webs characteristic of the marginal ice zone around 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 *Phaeocystis antarctica*.

7.3.5 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 by high biomass levels (Brey & Clarke, 1993), biodiversity, and endemism (Brey *et al.*, 1994; Arntz *et al.*, 1997; Clarke & Johnston, 2003, Thrush *et al.*, 2006). Many species show a circumpolar distribution (Hedgpeth, 1971; Richardson & Hedgpeth, 1977; Knox, 2006), are eurybathic (Brey *et al.*, 1996), and often have an extraordinary longevity (Dayton, 1990; Arntz *et al.*, 1994). The structure and distribution of benthic communities in the Ross Sea is largely a function of the environmental differences (sea ice cover, iceberg scouring, bottom geomorphology, current velocities) among sites, as well as 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. Because of the large gradients and abrupt changes in environmental variables (radiation, ice concentrations, and hydrological features) 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; Thrush *et al.*, 2006). Barry *et al.* (2003) described five main species assemblages distributed over the shelf, as a function of slope and current velocity, which affected food availability. Terra Nova Bay and eastern McMurdo Sound appear to be particularly rich areas, suggesting that community distribution is not always linearly related to latitudinal gradients. Variations in climatic, geographic and hydrological forcing represent barriers that result in anomalies in community and population distributions (Barry *et al.*, 2003).

Controls of benthic distribution

On the continental shelf the role of ice disturbance (e.g., ice cover persistence, anchor ice, ice scouring) is dominant, facilitating communities dominated by opportunistic species (Gutt *et al.*, 1996; Gutt, 2001). Grounded icebergs along the coast and in the shallowest portions of the shelf not only affect the benthos, but also modify the regional oceanography, with significant attendant changes in production and trophic interactions (Arrigo *et al.*, 2002). In contrast, undisturbed benthic communities show a high degree of stability, and contain a variety of large and long-lived species controlled by food availability. Below 500 m the flux of the organic material seems to regulate faunal distribution. The role of organic matter in structuring Antarctic benthic communities 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). Barry *et al.* (2003) found suspension feeders more abundant in shallow waters, while detritus feeders increased with depth.

Hard bottom benthic assemblage distribution and zonation

The hard bottom littoral habitat represents only a small component of the Ross Sea benthos. It is usually covered by fast-ice, but can occur in offshore reefs and seamounts where the bottom currents are intense and sediments are scoured. The tidal zone (1.5–2 m range) develops a biological film composed of diatoms and cyanobacteria (Gambi & Mazzella, 1992), which may reach high biomass (up to 900 mg Chl a m^{-2}; Dayton *et al.*, 1986). Below the littoral zone algal communities thrive (Zaneveld, 1968). Phaeophytes (*Himantothallus grandifolius*, *Desmarestia menziesii* and *D. anceps*), rhodophytes (*Iridaea cordata* and *Phyllophora antarctica*), and encrusting algae, as well as a diverse fauna of herbivores and their predators, characterize these belts.

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 macroalgal abundance is reduced, and their bathymetric range is narrower. An apparent north–south gradient, with algal belts decreasing in importance to the south, is probably due to decreased irradiance (total annual photon fluxes) and the persistence of the pack ice (which can scour the seabed and reduces total irradiance by two orders of magnitude).

The carnivorous sea star *Odontaster validus* and omnivorous sea urchin *Sterechinus neumayeri* are frequent fauna components. In shallow areas of McMurdo Sound, anchor ice is an important disturbance, affecting up to 70% of the sea floor (Dayton *et al.*, 1969, 1970; Battershill, 1989; Dayton, 1989). Fast growing sessile species, like the bush sponge *Homaxinella balfourensis*, the soft coral *Alcyonium antarctica*, and hydroids occur, suggesting a role for ice scouring by small icebergs. In deeper waters (ca. 80 m), frondose algae are absent at TNB, and the calcareous coralline alga *Clathromorphum*, on which sea-urchins feed, dominates; at McMurdo the latter alga is replaced by *Phymatolithon* at 60 m (Miller & Pearse, 1991). Through 130 m the benthos is dominated by diversified filter-feeding assemblages, such as sponges (which can attain high biomass), gorgonaceans and holothuroids. The sponge-anthozoan assemblage (Bullivant, 1967) is among the most complex communities in the Ross Sea. It has been described from McMurdo Sound (Dayton *et al.*, 1974) and Terra Nova Bay (Cattaneo-Vietti *et al.*, 1996, 2000), with high diversity, biomass, and rates of predation, competition and symbiosis (e.g., diatom-sponge relationships; Bavestrello *et al.*, 2000; Cerrano *et al.*, 2000, 2004a, b). Structural differences arise mainly from the different role played by volcano sponges and the hexactinellids *Rossella racovitzae*, *R. nuda* and *Scolymastia joubinii*. Below 130 m the polychaete *Serpula narconensis* (Schiaparelli *et al.*, 2000) and bryozoans are common. Some sessile species, like the orange stylasterine coral (*Errina* sp.) and the Antarctic acorn barnacle (*Bathylasma corolliforme*), cover exposed rock surfaces.

Soft bottom benthic assemblage distribution and zonation

In the Ross Sea soft sediments are relatively coarse, characterized by gravel or muddy sand through 500 m. In shallow (< 70 m) waters dense populations of benthic diatoms favour surface deposit feeders, such as crystal krill, and infauna (e.g., the bivalves *Laternula elliptica* and *Limopsis* sp.). In TNB and McMurdo Sound, the bivalve *Adamussium colbecki* can cover nearly 100%

of the seabed (Stockton, 1984; Cerrano *et al.*, 2001; Chiantore *et al.*, 2001, 2002, 2003). This bivalve processes ca. 14% of the total organic flux and produces biodeposits that support active microbial production (Albertelli *et al.*, 1998). In shallow waters predators such as gastropods and the nemertean worms can be abundant, while the echinoid *Sterechinus neumayeri* and the starfish *Odontaster validus* remain abundant at all depths on both hard and soft substrata (Chiantore *et al.*, 2002).

The amount of fine-grained sediments and organic matter increases with depth. In these environments the bivalve *Yoldia eightsi* reaches high densities; numerous species of ophiuroids and spatangoids also occur. Generally, the fine-grained sediments below 120 m are characterized by tube-building polychaetes (Gambi & Bussotti, 1999; Gambi *et al.*, 2000) and small bivalves (Cattaneo-Vietti *et al.*, 2000). Large deposits of sponge spicules can be found in the sediments or in spicule mats >1 m in thickness (Barthel, 1992). Within these mats live a specialized community, dominated by the burrowing bivalve *Limatula hodgsoni*. These mats confirm the locally important role of sponges, which with diatoms determine the texture and silica content of the sediments.

Iceberg scouring is important on the shallow banks. Near Cape Hallett the bottom area disturbed covers ca. 30% (Berkman *et al.*, 2005), resulting in a mosaic of patches characterized by a temporal succession of opportunistic species (Dayton *et al.*, 1969; Dayton, 1989; Lenihan & Oliver, 1995). 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 450–500 m bryozoan mats dominate in soft bottom areas, forming the deep shelf mixed assemblage described by Bullivant (1967), but locally other taxa occur, such as ophiuroids or *Cephalodiscus* spp. (Hemicordata). Upon an increase in mud, the community becomes dominated by polychaetes and ophiuroids and is less structured, with a strong reduction in faunal density and biomass.

7.4 FOOD WEB AND BIOTIC INTERACTIONS

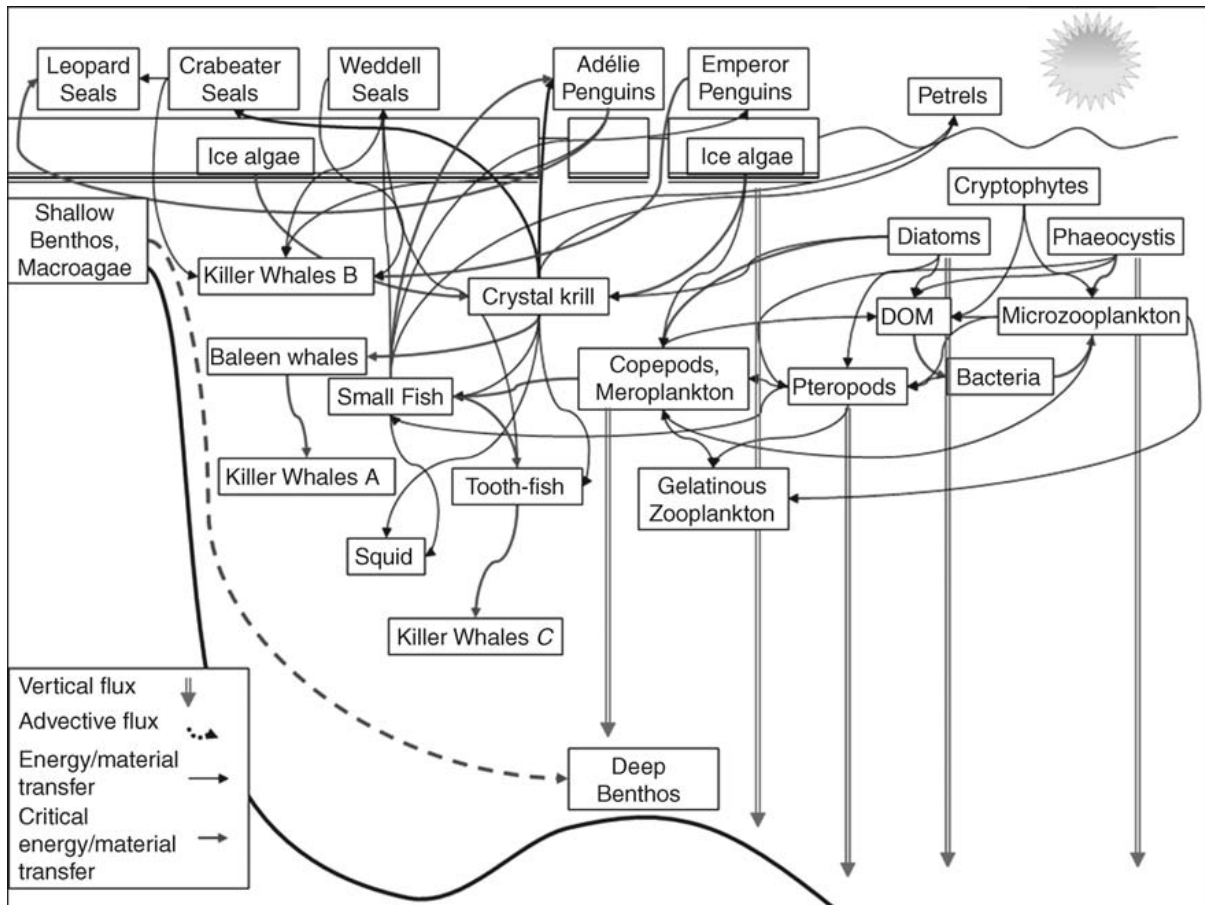The food web interactions within the Ross Sea are largely based on studies of diets of organisms (e.g., Ainley

Figure 7.11 Schematic of a generalized Ross Sea continental shelf food web. Not all taxonomic groups are included, particularly if their quantitatively impacts have yet to be established (e.g., sperm whales). The Ross Sea continental shelf is also spatially variable, and this schematic is largely based on southern Ross Sea data and observations. Variations in time on a variety of time scales also occur but are not pictured. (*See the colour version of this figure in Plate section.*)

et al., 1984; Hopkins, 1987; Barry *et al.*, 2003; La Mesa *et al.*, 2004), as well as distributions of prey and predators, but because the food web has a limited number of functional groups, a potential food web of the Ross Sea can be approximated (Figure 7.11). One conclusion from these linkages is that both crystal krill and Antarctic silverfish are extremely important species in the middle-trophic levels of the water-column food web, and that the rain of biotic particles from the surface layer is tremendously important to the benthos. What cannot be as easily depicted are the temporal variations that are superimposed on these biotic interactions, especially in view of the lack of winter data and biological strategies used to survive the winter, aproductive period. The

strong seasonality in occurrence, abundance, distribution and activity of the various food web components greatly influences energy transfer, resilience and stability of the ecosystem; 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 primary production. These responses will in large part determine the ecosystem response to perturbations at the smaller scale, and without an understanding of the time scales involved, it will be difficult to predict the system responses to

anthropogenically forced changes. While Pinkerton *et al.* (2010) have initiated a modeling exercise to describe the food web, their results so far mainly point out the gaps in knowledge, which are greatest for the benthos and middle-trophic levels.

In general, the mid-water food web has a reduced number of species and groups (relative to nonpolar regions), and the fauna are largely opportunistic feeders. Because of the depth, the benthos is relatively isolated from the surface waters (except in terms of coupling of food supply and iceberg disturbance; Barry *et al.*, 2003; Grebmeier and Barry, 2007), and may not exert a major, structuring role on the mid-water component. Further information on the vertical/seasonal movements of fish and crystal krill, which for instance recently has been seen feeding on detritus in McMurdo Sound (Deibel & Daly, 2007), could modify that conception. The Weddell seal could be a critical species in coastal areas, preying intensively on toothfish (which in turn prey on smaller fish species), and reducing their standing stocks to near zero where seal concentrations are high (Testa *et al.*, 1985). Food web connections are strongly structured by ice dynamics, which further impose a marked seasonal influence on biotic interactions.

Smetacek and Nicol (2005) suggested that benthic–pelagic coupling in Antarctic waters is unimportant. While such generalizations may be true for regions removed from the continental shelf (depths > 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 (that is, 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 (Grebmeier & Barry, 2007; Mincks *et al.*, 2005). This is also reflected in the relatively minor importance of the microbial food web within the Ross Sea water column. Mincks *et al.* (2005), based on the lack of seasonal variability of labile organic matter in the sediments, suggested 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 short-term surface production, but the importance of biogenic matter flux (and the percentage that enters the benthos) remains high.

Currents in the Ross Sea can be energetic, especially in the outer portion ($> 0.12\,\mathrm{m\,s^{-1}}$, with tidal currents exceeding even these velocities; Dinniman *et al.*, 2003, 2007; Gordon *et al.*, 2009; Whitworth & Orsi, 2006; Muench *et al.*, 2009), and often generate significant nepheloid layers 50 m from the bottom. 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 large distances (e.g., from the polynya to areas under ice where production is reduced). Indeed, trophic communities are richest and of greatest biomass in areas of stronger currents (Barry *et al.*, 2003). 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. Similarly, the outflow of water with low particulate organic concentrations from under the Ross Ice Shelf might be expected to reduce the biomass and diversity of the benthic fauna in specific areas.

7.5 CONCLUSIONS

7.5.1 Uniqueness of the Ross Sea

The Ross Sea continental shelf represents one extreme within a continuum of oceanographic conditions, 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; Smith *et al.*, 2006). Top- and middle-trophic levels have not yet been substantially, negatively 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; Ballance *et al.*, 2006; Blight & Ainley, 2008), and presently there is no widespread pollution or over-fishing (Halpern *et al.*, 2008). 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), a rate documented from other portions of the ocean (estimates suggest that eastern oysters (*Crassostrea virginica*) once filtered the volume of Chesapeake

Bay in about one month; Newell, 1988), 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 in marine systems (see Baum & Worm, 2009).

The apparent dependence of the upper portions of the food web on both krill and fish, involving species whose ecology and dynamics are poorly known (silverfish, crystal krill), is also unusual in the Antarctic, or at least little studied in other high-latitude shelf areas. While copepods can dominate grazing on phytoplankton in numerous areas of the Antarctic (Atkinson *et al.*, 1996; 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 primarily around the Antarctic krill, *E. superba*, which is present in the Ross Sea only near the shelf break. Copepods are important in the diets of smaller fish over the Ross Sea shelf (La Mesa *et al.*, 2004), as are crystal krill. Differences between the two euphausiids (Antarctic and crystal krill) are known (Knox, 2006), but how these differences lead to differences in food web structure is unclear. Thus many aspects of the food web are unique to the Ross Sea, and along with its relatively unimpacted ecology by human impacts, which makes it an excellent location to study the ecology and biotic interactions of cold waters. Perhaps biochemical assessment of the various trophic levels (isotopes, fatty acids) will allow the quantitative relationships within the food web to be clarified.

7.5.2 Potential impacts of climate change

'Climate' change, or large-scale physical changes induced by human activity, has had substantial impacts on the Southern Ocean and Ross Sea in a number of ways. First, the Antarctic Ozone Hole (AOH) has increased fluxes of high-energy UV radiation (Thompson & Solomon, 2002). Models have suggested that this atmospheric perturbation will decrease with time, since the reaction gases have a finite residence time; however, the same models appear to have underestimated the residence times, and the AOH is not recovering as fast as predicted (Russell *et al.*, 2006). Thus far, increased UV may have decreased larval survival of some species, altered phytoplankton composition and productivity, and contributed to physiological impairments, but

quantitfying ecosystem impacts have remained elusive (Karentz, 1994). It is likely that acclimation to changed conditions and the dynamics of the AOH itself have served to minimize system-wide impacts (Neale *et al.*, 2009).

Second, increases in atmospheric CO_2 have resulted in global temperature changes, which in turn have resulted in increases in temperatures in the ocean. Indeed, CDW, moving southward (and sinking) from mid-latitudes where it is at the surface, has been found to have warmed when sampled near the Antarctic continental margin (Jacobs, 2006). This heat input in turn has contributed to the collapse of several Antarctic ice shelves (Velicagna & Wahr, 2006), as well as subsurface melting of the seaward end of the Pine Island Glacier in Ellsworth Land, upstream from the Ross Sea. The addition of the melt-water has decreased the shelf water and surface salinity within the Ross Gyre (Jacobs *et al.*, 2002). Ecosystem effects of this change in ocean climate, if any, are not known.

The AOH and mid-latitude air warming has led to an acceleration of winds overlying the Antarctic Circumpolar Current (Thompson & Solomon, 2002; Russell *et al.*, 2006). This, in turn, has affected the pressure systems involved in the SAM (i.e., the Antarctic 'dipole' involving opposing pressure centres over the Ross Sea and Antarctic Peninsula), which has led to accelerated and warming northerly winds in the Southwest Atlantic and the opposite in the Ross Sea sector (Vaughan *et al.*, 2004; Stammerjohn *et al.*, 2008). The ultimate result is decreasing extent and persistence of sea ice off the SW Atlantic sector, and, again, the opposite in the Ross Sea sector. All models predict that atmospheric temperatures will continue to increase (e.g., Sarmiento *et al.*, 1998), and there is no reason to expect that the waters of the ACC will not warm as well.

Third, the biological response (increased productivity due to increased stratification) largely should balance the effects of gas exchange, and the Southern Ocean as a whole will remain close to its present state as a small sink of CO_2 (Sarmiento & le Quéré, 1996; Takahashi *et al.*, 2009). Of note, Arrigo *et al.* (2009) estimated that the Ross Sea continental shelf, by virtue of its large annual production, is responsible for up to 28% of the total air–sea exchange of CO_2 of the entire Southern Ocean. Hence, understanding the impacts of temperature changes (and the related ice concentration and vertical mixed layer changes) is of overriding

importance to the genesis of a predictive understanding of the Ross Sea ecosystem.

The current atmospheric CO_2 concentrations will ensure continued increases in ocean surface water concentrations. In recent years it has been shown that elevated CO_2 levels can have a direct impact on phytoplankton productivity and assemblage composition through the physiological limitations of carbon uptake. That is, some species have the ability to convert bicarbonate (the prevalent form of inorganic carbon at pH values near 8.0) using the enzyme carbonic anhydrase, which gives them a distinct advantage over forms that do not. In manipulations using natural assemblages and altered CO_2 concentrations, Tortell et al. (2002) found that under elevated CO_2 levels phytoplankton assemblages changed in composition, but not biomass. In similar experiments in the Ross Sea, phytoplankton showed a much more modest effect (Tortell et al., 2008), although an effect was still discernable using present techniques. Feng et al. (2010) found that other elements (such as iron) had a much greater effect than CO_2. Although such direct effects in the Ross Sea are apparently small, full system impacts of elevated carbon dioxide levels have yet to be assessed.

Fourth, increased CO_2 concentrations can result in ocean acidification (Doney et al., 2009) by shifting the carbonate equilibrium and decreasing the pH of seawater. This effect is most critical in areas where aragonite and carbonate dissolution equilibria are close to conditions of undersaturation. Orr et al. (2005) modeled the global impacts of ocean acidification and concluded that the Southern Ocean, and specifically those regions farthest south like the Ross Sea, would be the first among all regions in the world oceans to be negatively impacted. Such effects are most critical for calcareous organisms. The Ross Sea has a large number of benthic organisms that use aragonite in their shells and body parts, and by shifting the dissolution dynamics, it is expected that larval survival, growth, and reproductive success will be decreased. Pteropods are another important calcareous component of the food web, serving as important grazers of phytoplankton, food for various mid-level trophic groups, and as agents facilitating vertical export of organic matter. This group is exceedingly difficult to investigate experimentally, but it is reasonable to expect that their abundance and activity might decrease under decreased pH values that can reasonably be expected with further ocean acidification.

Finally, the increased winds that have resulted from mid-latitude warming and the AOH (Russell et al., 2006), have caused the Ross Sea's latent heat polynyas to become larger and more persistent (Parkinson, 2002). Through the 1990s this likely contributed to increases in the populations of Adélie penguins in the Ross Sea, owing to enhanced access to the ocean, the Ross Sea otherwise having been choked with sea ice for much longer seasonally a few decades ago (Ainley et al., 2005). Although winds are predicted to increase further and possibly influence polynya persistence as well, it appears that benefits to the penguin populations have already reached an asymptote (Ainley et al., 2010c). The increased winds have also caused a thinning of sea ice, in part contributing to the polynya response, which could well have negative impacts on emperor penguins, which depend on long-lasting fast ice on which to breed (Ainley et al., in press).

7.5.3 Conservation and the role of commercial fishing activity in the Ross Sea

As important as climate change, the Ross Sea has recently become the site of increased commercial fishing and whaling (Stevenson et al., 2008), 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. Because the effects of large-scale whaling in the Southern Ocean date to an era that precedes modern ecology, we can only guess about the structure and function of Antarctic ecosystems prior to whale removal (Ballance et al., 2006); however, the removal of demersal fish from the SW Atlantic and Indian Ocean sectors appears to have had profound effects on their predators (Ainley & Blight, 2008). While the Southern Ocean is often categorized as 'pristine' (e.g., Smetacek & Nicol, 2005), the large ecological changes that were induced by the removal of fish 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 (and the entire ocean). We could learn a great deal about how Antarctic food webs once were structured by increasing attention to the Ross Sea before it suffers the same fate as more accessible waters.

7.5.4 Research needs and future directions

The Ross Sea is changing, and projections of the impacts of this change (and other changes) require a more complete understanding of the entire food web and trophic interactions in this system. 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,

• What controls the distribution, morphotype and abundance of *Phaeocystis antarctica*, and to what extent is it used within the food web?

• What are the biological strategies used by all trophic levels to survive the extreme winter environment of the Ross Sea?

• How productive is *E. crystallorophias*, and what is its distribution in space and time, especially during periods when ice covers the Ross Sea?

• What is the impact of large, mobile animals such as whales, penguins and toothfish on the entire food web, and particularly on the abundance and distribution of prey species such as crystal krill and silverfish?

• How does the benthos respond to short- and long-term changes in the physical and biological forcing of the water column?

• How does the entire Ross Sea ecosystem respond to severe reduction of the most important piscine predator owing to increased fishing pressure? To changes in large-scale physical forcing?

• What alterations will continued climate change impart on the Ross Sea ecosystem?

The answers to these and other questions are essential in order to make informed projections and evaluations of the response of the ecosystem to predicted future changes (see Ainley *et al.*, 2010c). Sustained long-term oceanographic and biological monitoring programs are urgently needed to better understand the long-term (decadal, centennial) responses and the interactions among all trophic groups to environmental change, as well as the trophic coupling at smaller space and time scales. These measurement systems, combined with coupled environmental-ecosystem-socioeconomic modelling structures, will allow better understanding of the consequences and long-term (decadal, centennial) responses, the interactions among all trophic groups to environmental change, and guidance as to manage-ment and policy approaches needed for mitigating the effects of these changes.

REFERENCES

Accornero, A. & Gowing, M.M., 2003 Annual sedimentation pattern of zooplankton fecal pellets in the Southern Ross Sea: what food webs and processes does the record imply? In: *Biogeochemistry of the Ross Sea* (eds. G.R. DiTullio & R.B. Dunbar). American Geophysical Union, Washington, DC, 261–278.

Ainley, D.G. 1985 The biomass of birds and mammals in the Ross Sea, Antarctica. In: *Antarctic Nutrient Cycles and Food Webs* (eds. W.R. Siegfried, P.R. Condy & R.M. Laws). Springer Verlag, Berlin, 498–515.

Ainley, D.G. 2010 A history of the exploitation of the Ross Sea, Antarctica. *Polar Record.*, **46** (238): 233–243.

Ainley, D.G. & Blight, L.K. 2008 Ecological repercussions of historical fish extraction from the southern ocean. *Fish and Fisheries* **10**, 13–38.

Ainley, D.G. & Jacobs, S.S. 1981 Seabird affinities for ocean and ice boundaries in the Antarctic. *Deep-Sea Research* **28**, 1173–1185.

Ainley, D.G. & Siniff, D.B. 2009 The importance of Antarctic toothfish as prey of Weddell Seals in the Ross Sea: a review. *Antarctic Science* **21**, 317–327.

Ainley, D.G., Ballard, G., Ackley, S.T., Blight, L.K., Eastman, J.T., Emslie, S.D. Lescroël, A., Olmastroni, S., Townsend, S.E., Tynan, C.T., Wilson, P. & Woehler, E., 2007 Paradigm Lost, or, is top-down forcing no longer significant in the Antarctic marine ecosystem? *Antarctic Science* **19**, 283–290.

Ainley, D.G., Ballard, G., Barton, K.J., Karl, B.J., Rau, G.H., Ribic, C.A., Wilson, P.R. 2003a Spatial and temporal variation of diet within a presumed metapopulation of Adélie Penguins. *Condor* **105**, 95–106.

Ainley, D.G., Ballard, G., Dugger, K.M. 2006 Competition among penguins and cetaceans reveals trophic cascades in the Ross Sea, Antarctica. *Ecology* **87**, 2080–2093.

Ainley, D.G., Ballard, G., Olmastroni, S. 2010a An apparent decrease in the prevalence of 'Ross Sea killer whales'

in the southern Ross Sea. *Aquatic Mammals* **35**, 335–347.

Ainley, D.G., Ballard, G. & Weller, J. 2010b Ross Sea bioregionalization, Part I: Validation of the 2007 CCAMLR Bioregionalization Workshop Results towards including the Ross Sea in a representative network of marine protected areas in the Southern Ocean. CCAMLR Document WG-EMM-10/11, Hobart.

Ainley, D.G., Clarke, E.D., Arrigo, K., Fraser, W.R., Kato A., Barton, K.J. & Wilson, P.R. 2005 Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. *Antarctic Science* **17**, 171–182.

Ainley, D.G., O'Connor, E.F. & Boekelheide, R.J. 1984 The marine ecology of birds in the Ross Sea, Antarctica. *Ornithological Monographs* **32**, 1–97.

Ainley. D.G., Ribic, C.A., Ballard, G., Heath, S., Gaffney, I., Karl, B.J., Barton, K.R., Wilson, P.R. & Webb, S. 2004 Geographic structure of Adélie Penguin populations: size, overlap and use of adjacent colony-specific foraging areas. *Ecological Monographs* **74**, 159–178.

Ainley, D.G., Russell, J., Jenouvrier, S., Woehler, E., Lyver, P.O., Fraser, W.R. & Kooyman, G.L. 2010c Antarctic penguin response to habitat change as earth's troposphere reaches 2°C above pre-industrial levels. *Ecological Monographs* **80**: 49–66.

Ainley, D.G., Tynan, C.T. & Stirling, I. 2003b Sea ice: a critical habitat for polar marine mammals and birds. In: *Sea ice: an introduction to its physics, biology, chemistry and geology* (Eds. D.N. Thomas & G.S. Dieckmann). Blackwell Science, London, 240–266.

Albertelli, G., Cattaneo-Vietti, R., Chiantore, M., Pusceddu, A. & Fabiano, M. 1998 Food availability to an *Adamussium* bed during the austral summer 1993/94 (Terra Nova Bay, Ross Sea). *Journal of Marine Systems* **17**, 425–434.

Anderson, J.B. 1999 *Antarctic marine geology*. Cambridge, UK: Cambridge University Press.

Anderson, R.F. & Smith, W.O. Jr., 2001 The US Southern Ocean Joint Global Ocean Flux Study: volume two. *Deep-Sea Research II* **48**, 3883–3891.

Andreae, M.O. 1990 Ocean-atmosphere interactions in the global biogeochemical sulfur cycle. *Marine Chemistry* **30**, 1–29.

Arntz, W., Brey, T. & Gallardo, V.A. 1994 Antarctic zoobenthos. *Oceanography and Marine Biology* **32**, 241–304.

Arntz, W., Gutt, J. & Klages, M. 1997 Antarctic marine biodiversity: an overview: In: *Antarctic communities: species, structure and survival* (eds. B. Battaglia, J. Valencia & D.W.H. Walton). Cambridge University Press, London, 3–14.

Arrigo, K.R. 2003 Primary production in sea ice. In: *Sea ice: an introduction to its physics, chemistry, biology and geology* (eds. D.N. Thomas & G.S. Dieckmann). Blackwell Science Ltd, Oxford, 143–183.

Arrigo, K.R. 2007 Physical control of primary productivity in Arctic and Antarctic polynyas. In: *Polynyas: windows to the world's oceans* (eds. W.O. Smith, Jr. & D.G. Barber). Elsevier, Amsterdam, 223–238.

Arrigo, K.R. & van Dijken, G.L. 2003 Phytoplankton dynamics within 37 Antarctic coastal polynya systems. *Journal of Geophysical Research* **108** 3231, doi: 10.1029/2001JC000856.

Arrigo, K.R., van Dijken, G.L., Ainley, D.G., Fahnestock, M.A. & Markus, T. 2002 The impact of the B-15 iceberg on productivity and penguin breeding success in the Ross Sea, Antarctica. *Geophysical Research Letters* **29**, doi: 10.1029/2001glo14160.

Arrigo, K.R., van Dijken, G.L. & Bushinsky, S., 2008 Primary production in the Southern Ocean, 1997–2006. *Journal of Geophysical Research* **113**, C08004, doi: 10.1029/2007JC004551.

Arrigo, K.R., van Dijken, G.L. & Long, M. 2009 Coastal Southern Ocean: a strong anthropogenic CO_2 sink. *Geophyiscal Research Letters* **35**, doi: 10.1029/2008GL035624.

Arrigo, K.R., Robinson, D.H., Worthen, D.L., Dunbar, R.B., DiTullio, G.R., Van Woert, M. & Lizotte, M.P. 1999 Phytoplankton community structure and the drawdown of nutrients and CO_2 in the Southern Ocean. *Science* **283**, 365–367.

Arrigo, K.R., Worthen, D.L., Dixon, P. & Lizotte, M.P. 1998a Primary productivity of near surface communities within Antarctic pack ice. In: *Antarctic sea ice: biological processes, interactions, and variability* (eds. M.P. Lizotte & K.R. Arrigo). American Geophysical Union, Washington, D.C., 23–43.

Arrigo, K. R, Worthen, D.L. & Robinson, D.H. 2003 A coupled ocean-ecosystem model of the Ross Sea: 2. Iron regulation of phytoplankton taxonomic variability and primary production. *Journal of Geophysical Research* **108**, 3231, doi: 10.1029/2001JC000856.

Arrigo, K.R., Worthen, D.L., Schnell, A. & Lizotte, M.P. 1998b Primary production in Southern Ocean waters. *Journal of Geophysical Research* **103**, 15,587–15,600.

Ashjian, C.J., Rosenwalks, G.A., Wiebe, P.H., Davis, C.S., Gallager, S.M., Copley, N.J., Lawson, G.L. & Alatalo, P. 2004 Distribution of zooplankton on the continental shelf off Maguerite Bay, Antarctic Peninsula, during austral fall and winter, 2001. *Deep Sea Research II* **51**, 2073–2092.

Asper, V.A., Deuser, W.G., Knauer, G.A. & Lohrenz, S.E. 1992 Rapid coupling of sinking particle fluxes between surface and deep ocean waters. *Nature* **357**, 670–672.

Atkinson, A., Shreeve, R.S., Pakhamov, E.A., Priddle, J., Blight, S.P. & Ward, P. 1996 Zooplankton response to a phytoplankton bloom near South Georgia, Antarctica. *Marine Ecology Progress Series* **144**, 195–210.

Atkinson, A., Siegel, V., Pakhomov, E.A., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt, K., Fretwell, P., Murphy, E.J., Tarling, G.A. & Fleming, A.H. 2008 Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology Progress Series* **362**, 1–23.

Azzali, M. & Kalinowski, J. 1999 Spatial and temporal distribution of krill (*Euphausia superba*) biomass in the Ross Sea

(1989–1990 and 1994). In: *Ross Sea ecology* (eds. F.M. Faranda, L. Guglielmo & A. Ianora). Springer-Verlag, Berlin, 433–456.

Ballance, L., Pitman, R.L., Hewitt, R.P., Siniff, D.B., Trivelpiece, W. Z., Clapham, P. J. & Brownell, R. L., Jr., 2006 The removal of large whales from the Southern Ocean: evidence for long-term ecosystem effects? In: *Whales, whaling and ocean ecosystems* (eds. J.A. Estes, D.P. Demaster, D.F. Doak, T.E. Williams & R.L. Brownell, Jr). University of California Press, Berkeley, CA, 215–230.

Barry, J.P. 1988 Hydrographic patterns in McMurdo Sound, Antarctica, and their relationship to local benthic communities. *Polar Biology* **8**, 377–391.

Barry, J.P., Grebmeier, J.M., Smith, J. & Dunbar, R.B. 2003 Bathymetric versus oceanographic control of benthic megafaunal patterns in the Ross Sea, Antarctica. *Antarctic Research Series* **78**, 327–354.

Barthel, D. 1992 Do hexactinellids structure Antarctic sponge associations? *Ophelia* **36**, 111–118.

Battershill, C.N. 1989 Distribution an abundance of benthic marine species at Cape Armitage, Ross Island, Antarctica. Initial results. *New Zealand Antarctic Records* **9**, 35–52.

Baum, J.K. & Worm, B. 2009 Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology* doi: 10.1111/j.1365-2656.2009.01531.x.

Bavestrello, G., Arillo, A., Calcinai, B., Cattaneo-Vietti, R., Cerrano, C., Gaino, E., Penna, A. & Sarà, M. 2000 Parasitic diatoms inside Antarctic sponges. *Biological Bulletin* **198**, 29–33.

Beddington, J.R. & May, R.M. 1982 The harvesting of interacting species in a natural ecosystem. *Scientific American* **247**, 62–69.

Bengtson, J.L. & Laws, P.M., 1985 Trends in crabeater seal age at maturity: an insight into Antarctic marine interactions. In: *Antarctic nutrient cycles and food webs* (eds. W.R. Siegfried, P.R. Condy & R.M. Laws). Springer-Verlag, Berlin Heidelberg, 669–675.

Berkman, P.A., Cattaneo-Vietti, R., Chiantore, M., Howard-Williams, C., Cummings, V., Kvitek, R. 2005 Marine research in the Latitudinal Gradient Project along Victoria Land, Antarctica. *Scientia Marina* **69** (suppl), 57–63.

Blight, L.K. & Ainley, D.G. 2008. Southern Ocean not so pristine. *Science* **321**, 1443.

Branch, T.A. & Butterworth, D.S. 2001 Southern hemisphere Minke Whales: standardized abundance estimates from the 1978/79 to 1997/98 IDCR-SOWER surveys. *Journal of Cetacean Research and Management* **3**, 143–174.

Brey, T. & Clarke, A. 1993 Population dynamics of marine benthic invertebrates in Antarctic and sub-Antarctic environments: are there unique adaptations? *Antarctic Science* **5**, 253–266.

Brey, T., Klages, M., Dahm, C., Gorny, M., Gutt, J., Hain, S., Stiller, M., Arntz, W.E., Wägele, J-W. & Zimmermann, A. 1994 Antarctic benthic diversity. *Science* **368**, 297.

Brey, T., Dahm, C., Gorny, M., Klages, M., Stiller, M. & Arntz, W. E. 1996 Do Antarctic benthic invertebrates show an extended level of eurybathy? *Antarctic Science* **8**, 3–6.

Brierley, A.S., Fernandes, P.G., Brandon, M.A., Armstrong, F., Millard, N.W., McPhail, S.D., Stevenson, P., Pebody, M., Perrett, J., Squires, M., Bone, D.G. & Friffins, G. 2002 Antarctic krill under sea ice: elevated abundance just south of the ice edge. *Science* **295**, 1890–1892.

Brooks, C.M. & Ashford, J.R. 2008 Spatial distribution and age structure of the Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica. CCAMLR WG-FSA-08-18. Hobart.

Brownell, R.L., Jr. & Ainley, D.G. 2009 Antarctic toothfish and macrourids are likely important prey of Arnoux's beaked whales in the Ross Sea region. *CCAMLR paper EMM 09-02*, Hobart, Australia.

Bullivant, J.S. 1967 Ecology of the Ross Sea benthos. *New Zealand Oceanographic Institute Memoirs* **32**, 49–75.

Bunt, J.S. 1963 Diatoms of Antarctic sea ice as agents of primary production. *Nature* **199**, 1254–1257.

Carli, A., Pane, L. & Stocchino, C. 1999 Planktonic copepods in Terra Nova Bay (Ross Sea): distribution and relationship with environmental factors. In: *Ross Sea ecology* (eds. F.M. Faranda, L. Guglielmo & A. Ianora), Springer, Berlin, 309–322.

Caron, D.A., Dennett, M.R., Lonsdale, D.J., Moran, D.M. & Shalapyonok, L. 2000 Micro-zooplankton herbivory in the Ross Sea, Antarctica. *Deep-Sea Research II* **47**, 3249–3272.

Cattaneo-Vietti, R., Bavestrello, G., Cerrano, C., Sara', M., Benatti, U., Giovine, M. & Gaino, E. 1996 Optical fibres in an Antarctic sponge. *Nature* **383**, 397–398.

Cattaneo-Vietti, R., Chiantore, M., Schiaparelli, S. & Albertelli, G. 2000 Shallow and deep-water mollusc distribution at Terra Nova Bay (Ross Sea, Antarctica). *Polar Biology* **23**, 173–182.

Celussi, M., Paolia, A., Crevatin, E., Bergamasco, A., Margiotta, F., Saggiomo, V., Fonda Umani, S. & Del Negro, P. 2009 Short-term under-ice variability of prokaryotic plankton communities in coastal Antarctic waters (Cape Hallett, Ross Sea). *Estuarine, Coastal and Shelf Science* **81**, 491–500.

Cerrano, C., Arillo, A., Bavestrello, G., Calcinai, B., Cattaneo-Vietti, R., Penna, A., Sarà, M. & Totti, C., 2000. Diatom invasion in the Antarctic hexactinellid sponge *Scolymastra joubini*. *Polar Biology* **23**, 441–444.

Cerrano, C., Calcinai, B., Cucchiari, E., Di Camillo, C., Nigro, M., Regoli, F., Sara', A., Schiaparelli, S., Totti, C. & Bavestrello, G., 2004b Are diatoms a food source for Antarctic sponges? *Chemistry and Ecology* **20**, 57–64.

Cerrano, C., Calcinai, B., Cucchiari, E., Di Camillo, C., Totti, C. & Bavestrello, G. 2004a The diversity of relationships between Antarctic sponges and diatoms: the case of *Mycale acerata* (Porifera, Demospongiae). *Polar Biology* **27**, 231–237.

Cerrano, C., Puce S., Chiantore, M., Bavestrello, G. & Cattaneo-Vietti, R. 2001 The influence of the epizooic hydroid

Hydractinia angusta on the recruitment of the Antarctic scallop *Adamussium colbecki*. *Polar Biology* **24**, 577–581.

Cherel, Y. & Kooyman, G.L. 1998 Food of Emperor Penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctica. *Marine Biology* **130**, 335–344.

Chiantore, M., Cattaneo-Vietti, R., Berkman, P.A., Nigro, M., Vacchi, M., Schiaparelli, S. & Albertelli, G. 2001 Antarctic scallop (*Adamussium colbecki*) spatial population variability along the Victoria Land coast, Antarctica. *Polar Biology* **24**: 139–143.

Chiantore, M., Cattaneo-Vietti, R., Elia, L., Guidetti, M. & Antonini, M. 2002 Reproduction and condition of the scallop *Adamussium colbecki* (Smith, 1902), the sea-urchin *Sterechinus neumayeri* (Meissner, 1900) and the sea-star *Odontaster validus* Koehler, 1911 at Terra Nova Bay (Ross Sea): different strategies related to inter-annual variations in food availability. *Polar Biology* **22**, 251–255.

Chiantore M., Cattaneo-Vietti, R. & Heilmayer, O. 2003 Antarctic scallop (*Adamussium colbecki*) annual growth rate at Terra Nova Bay. *Polar Biology* **26**, 416–419.

Clarke, A. & Johnston, N.M. 2003 Antarctic marine benthic diversity. *Oceanography and Marine Biology* **41**, 47–114.

Coale, K.H., Wang, X., Tanner, S.J. & Johnson, K.S. 2003 Phytoplankton growth and biological response to iron and zinc addition in the Ross Sea and Antarctic Circumpolar Current along 170°W. *Deep-Sea Research II* **50**, 635–653.

Collier, R., Dymond, J., Honjo, S., Manganini, S., Francois, R. & Dunbar, R. 2000 The vertical flux of biogenic and lithogenic material in the Ross Sea: moored sediment trap observations 1996–1998. *Deep-Sea Research II* **47**, 3491–3520.

Comiso, J.C. & Nishio, F. 2008 Trends in the sea ice cover using enhanced and compatible AMSR-E, SSM/I and SSMR data. *Journal of Geophysical Research* **113**, doi:10.1029/2007JC004257.

Curtis, C., Stewart, B.S.,& Karl, S.A. 2009 Pleistocene population expansion of Antarctic seals. *Molecular Ecology* **18**, 2112–2121.

Dayton, P.K. 1989 Interdecadal variation in an Antarctic sponge and its predators from oceanographic climate shifts. *Science* **245**, 1484–1496.

Dayton, P.K. 1990 Polar benthos. In: *Polar Oceanography*, Part B, (ed. W.O. Smith, Jr.). Academic Press, San Diego, 631–685.

Dayton, P.K. & Oliver, J.S. 1977 Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science* **197**, 55–58.

Dayton, P.K., Robilliard, G.A. & DeVries, A.L. 1969 Anchor ice foundation in McMurdo Sound, Antarctica, and its biological effects. *Science* **163**, 273–274.

Dayton, P.K., Robilliard, G.A. & Paine, R.T. 1970 Benthic faunal zonation as a result of anchor ice at McMurdo Sound, Antarctica. In: *Antarctic ecology* (M. Holdgate). Academic Press, London, 244–257.

Dayton, P.K., Robilliard, G.A., Paine, R.T., & Dayton, L.B. 1974 Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecological Monographs* **44**, 105–128.

Dayton, P.K., Watson, D., Palmisano, A., Barry, J.P., Oliver, J.S. & Rivera, D. 1986 Distribution patterns of benthic microalgal standing stock at McMurdo Sound, Antarctica. *Polar Biology* **6**, 207–213.

Deibel, D. & Daly, K.L. 2007 Zooplankton processes in Arctic and Antarctic polynyas. In: *Polynyas: windows to the world* (eds. W.O. Smith, Jr., & D.G. Barber), Elsevier, San Diego, pp. 271–232.

Dennett, M.R., Mathot, S., Caron, D.A., Smith, W.O. Jr. & Lonsdale, D. 2001 Abundance and distribution of phototrophic and heterotrophic nano- and microplankton in the southern Ross Sea. *Deep-Sea Research II* **48**, 4019–4038.

DeVries, A.L., Ainley, D.G. & Ballard, G. 2008 Decline of the Antarctic toothfish and its predators in McMurdo Sound and the southern Ross Sea, and recommendations for restoration. *CCAMLR Paper* EMM 08/xx, Hobart, Tasmania.

DeWitt, H.H. 1970 The character of the midwater fish fauna of the Ross Sea, Antarctica. In: *Antarctic ecology*, Volume 1 (ed. M.W. Holdgate). Academic Press, London, 305–314.

Dinniman, M.S., Klinck, J.M. & Smith, W.O. Jr., 2003 Cross-shelf exchange in a model of Ross Sea circulation and biogeochemistry. *Deep-Sea Research II* **50**, 3103–3120.

Dinniman, M.S., Klinck, J.M., Smith, W.O. Jr., 2007 The influence of sea ice cover and icebergs on circulation and water mass formation in a numerical circulation model of the Ross Sea, Antarctica. *Journal of Geophysical Research* **112**, C11013, doi: 10.1029/2006JC004036.

DiTullio, G.R. & Smith, W.O. Jr., 1996 Spatial patterns in phytoplankton biomass and pigment distributions in the Ross Sea. *Journal of Geophysical Research* **101**, 18,467–18,478.

DiTullio, G.R. *et al.*, 2000 Rapid and early export of *Phaeocystis antarctica* blooms in the Ross Sea Antarctica. *Nature* **404**, 595–598.

Doney, S.C., Fabry, V.J., Feely, R.A. & Kleypas, J.A. 2009 Ocean acidification: the other CO$_2$ problem. *Annual Review of Marine Science* **1**, 169–192.

Ducklow, H.W. 1999 The bacterial content of the oceanic euphotic zone. *FEMS Microbiology-Ecology* **30**, 1–10.

Ducklow, H.W., Dickson, M.-L., Kirchman, D.L., Steward, G., Orchardo, J., Marra, J. & Azam, F. 2000 Constraining bacterial production, conversion efficiency and respiration in the Ross Sea, Antarctica, January-February, 1997. *Deep-Sea Research II* **47**, 3227–3248.

Dunbar, R.B., Leventer, A.R. & Mucciarone, D.A. 1998 Water column sediment fluxes in the Ross Sea, Antarctica: atmospheric and sea ice forcing. *Journal of Geophysical Research* **103**, 10741–10760.

Dunbar, R.B., Leventer, A.R. & Stockton, W.L. 1989 Biogenic sedimentation in McMurdo Sound, Antarctica. *Marine Geology* **85**, 155–179.

Eastman, J.T. 1985 *Pleuragramma antarcticum* (Pisces, Nototheniidae) as food for other fishes in McMurdo Sound, Antarctica. *Polar Biology* **4**, 155–160.

Eastman, J.T. 1993 *Antarctic fish biology: evolution in a unique environment.* Academic Press, London.

Eastman, J.T. & Ainley, D.G. 2009 The Ross Sea as a unique evolutionary site. CCAMLR Document WG-EMM-09/13, Hobart.

Eastman, J.T. & Hubold, G. 1999 The fish fauna of the Ross Sea, Antarctica. *Antarctic Science* **11**, 293–304.

Fenaughty, J.M., Stevens, D.W. & Hanchet, S.M. 2003 Diet of the Antarctic toothfish (*Dissostichus mawsoni*) from the Ross Sea, Antarctica (CCAMLR statistical subarea 88.1). *CCAMLR Science* **10**: 1–10l.

Feng, Y., Hare, C.E., Rose, J.M., Handy, S.M., DiTullio, G.R., Lee, P., Smith, W.O. Jr., Peloquin, J., Tozzi, S., Sun, J., Zhang, Y., Dunbar, R.B., Long, M.C., Sohst, B. & Hutchins D. 2010 Interactive effects of CO_2, irradiance and iron on Ross Sea phytoplankton. *Deep-Sea Research I* **57**: 587–595.

Fonda Umani, S., Accornero, A., Budillon, G., Capello, M., Tucci, S., Cabrini, M., del Negro, P., Monti, M. & de Vitto, C. 2002 Particulate matter and plankton dynamics in the Ross Sea Polynya of Terra Nova Bay during the austral summer 1997/98. *Journal of Marine Systems* **36**, 29–49.

Fuiman, L.A., Davis, R.W. & Williams, T.M. 2002 Behavior of midwater fishes under the Antarctic ice: observations by a predator. *Marine Biology* **140**: 815–822.

Gambi, M.C. & Bussotti, S. 1999 Composition, abundance and stratification of soft-bottom macrobenthos from selected areas of the Ross Sea shelf (Antarctica). *Polar Biology* **21**, 347–354.

Gambi, M.C., Buia, M.C., Mazzella, L., Lorenti, M. & Scipione, M.B. 2000 Spatio-temporal variability in the structure of benthic populations in a physically controlled system off Terra Nova Bay: the shallow hard bottoms. In: *Ross Sea ecology* (eds. F.M. Faranda, L. Guglielmo & A. Ianora). Springer, Berlin, 527–538.

Gambi, M.C. & Mazzella, L. 1992 Quantitative and functional studies on coastal benthic communities of Terra Nova Bay (Ross Sea, Antarctica): hard bottoms. In: *Symposium Oceanografia in Antartide* (eds. V.A. Gallardo, O. Ferretti & H.I. Moyano). Centro EULA, Universitad de Concepción, Chile. ENEA, 409–415.

Garrison, D.L., Gibson, A., Coale, S.L., Gowing, M.M., Okolodkov, Y.B., Fritsen, C.H. & Jeffries, M.O. 2006 Sea-ice microbial communities in the Ross Sea: autumn and summer biota. *Marine Ecology Progress Series* **300**, 39–52.

Garrison, D.L., Gibson, A., Kunze, H., Gowing, M.M., Vickers, C.L., Mathot, S. & Bayre, R.C. 2003 The Ross Sea Polynya Project: diatom- and *Phaeocystis*-dominated phytoplankton assemblages in the Ross Sea, Antarctica, 1994 and 1995. In: *Biogeochemistry of the Ross Sea* (eds. G.R. DiTullio & R.B. Dunbar), American Geophysical Union, Washington, DC, 53–76.

Gordon, A.L., Orsi, A.H., Muench, R.D., Huber, B.A., Zambianchi, E. & Visbeck, M. 2009 Western Ross Sea continental slope gravity currents. *Deep-Sea Research II* **55**, 796–817.

Gordon, A.L., Zambianchi, E., Orsi, A., Visbeck, M., Giulivi, C.F., Whitworth T. III & Spezie, G. 2004 Energetic plumes over the western Ross Sea continental slope. *Geophysical Research Letters* **31**, doi 10.1029/2004GL020785.

Grebmeier, J.M. & Barry, J.P. 2007 Benthic processes in polynyas. In: *Polynyas: windows to the world* (eds. W.O. Smith, Jr. & D.G. Barber), Elsevier, San Diego, 363–390.

Gutt, J. 2001 On the direct impact of ice on marine benthic communities, a review. *Polar Biology* **24**, 553–564.

Gutt, J., Starmans, A., Dieckmann, G., 1996. Impact of iceberg scouring on polar benthic habitats. *Marine Ecology Progress Series* **137**, 311–316.

Hall, A., Visbeck, M. 2002 Synchronous variability in the Southern Hemisphere atmosphere, sea ice, and ocean resulting from the annular mode. *Journal of Climate* **15**, 3043–3057.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.B., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. & Watson. R. 2008 A global map of human impact on marine ecosystems. *Science* **319**, 948–951.

Hanchet, S.M., Rickard, G.J., Fenaughty, J.M., Dunn, A. & Williams, M.J.H. 2008 A hypothetical life cycle for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region. *CCAMLR Science* **15**, 35–53.

Hedgpeth, J.W. 1971 Perspectives of benthic ecology in Antarctica. In: *Research in Antarctica* (ed. L.O. Quasim), American Association for the Advancement of Science, Washington, 93–136.

Hofmann, E.E. & Klinck, J.M. 1998 Thermohaline variability of the waters overlying the West Antarctic Peninsula continental shelf. In: *Ocean, ice and atmosphere: interactions at the continental margin* (eds. S. Jacobs & R. Weiss), Antarctic Research Series, American Geophysical Union, Washington, DC, **75**, 67–81.

Hood, R.R. *et al.*, 2006 Pelagic functional group modeling: progress, challenges and prospects. *Deep-Sea Research II* **53**, 459–512.

Hopkins, T.L. 1987 Midwater food web of McMurdo Sound, Ross Sea, Antarctica. *Marine Biology* **96**, 93–106.

Horn, P.L. 2002 Age and growth of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mawsoni*) in waters from the New Zealand subantarctic to the Ross Sea, Antarctica. *Fisheries Research* **56**, 275–287.

Ichii, T. & Kato, H.H. 1991 Food and daily food consumption of southern Minke Whales in the Antarctic. *Polar Biology* **11**, 479–487.

Ichii, T., Shinohara, N., Kujise, Y., Nishiwaki, S. & Matsuoka, K. 1998 Interannual changes in body fat condition index of Minke Whales in the Antarctic. *Marine Ecology Progress Series* **175**, 1–12.

Jackson, J.B.C. *et al.*, 2001 Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–638.

Jacobs, S.S. 2006 Observations of change in the Southern Ocean. *Philosophical Transactions of the Royal Society, London, series A* **364**, 1657–1681.

Jacobs, S.S. & Comiso, J.C. 1989 Sea ice and oceanic processes on the Ross Sea continental shelf. *Journal of Geophysical Research* **94**, 18195–18211.

Jacobs, S.S. & Giulivi, C.F. 1998 Interannual ocean and sea ice variability in the Ross Sea. *Antarctic Research Series* **75**, 135–150.

Jacobs, S.S., Amos, A.F. & Bruchausen, P.M. 1970 Ross Sea oceanography and bottom water formation. *Deep-Sea Research* **17**, 935–962.

Jacobs, S.S., Giulivi, C.F. & Mele, P.A. 2002 Freshening of the Ross Sea during the late 20th century. *Science* **297**, 386–389.

Karentz, D. 1994 Ultraviolet tolerance mechanisms in Antarctic marine organisms. *Antarctic Research Series* **62**, 93–110.

Karnovsky, N., Ainley, D.G. & Lee, P. 2007 The impact and importance of production in polynyas to top-trophic predators: two case histories. In: *Polynyas: windows to the world's oceans* (eds. W.O. Smith & D. Barber). Elsevier, San Diego, 391–410.

Knox, G.A. 2006 *Biology of Southern Ocean*. CRC Press, Boca Raton, FL.

La Mesa, M., Eastman, J.T. & Vacchi, M. 2004 The role of notothenoioid fish in the food web of the Ross Sea shelf waters: a review. *Polar Biology* **27**, 321–338.

Lenihan, H.S. & Oliver, J.S. 1995 Anthropogenic and natural disturbances to marine benthic communities in Antarctica. *Ecological Applications* **5**, 311–326.

Li, W.K.W., Dickie, P.W., Irwin, B.D. & Wood, A.M. 1992 Biomass of bacteria, cyanobacteria, prochlorophytes, and photosynthetic eucaryotes in the Sargasso Sea. *Deep-Sea Research* **39**, 501–519.

Liu, J., Curry, J.A. & Martinson, D.G. 2004 Interpretation of recent Antarctic sea ice variability. *Geophysical Research Letters* **31**, doi: 10.1029/2003GL018732.

Lizotte, M.P. 2003 The microbiology of sea ice. In: *Sea ice: an introduction to its physics, chemistry, biology and geology* (eds. D.N. Thomas & G.S. Diekmann), Blackwell Science Ltd, Oxford, 183–210.

Locarnini, R.A. 1994 Water masses and circulation in the Ross Gyre and environs. Ph.D. Dissertation, Texas A&M University, College Station, Texas, USA.

Mathot, S., Smith, W.O. Jr., Carlson, C.A. & Garrison, D.L. 2000 Estimate of *Phaeocystis* sp. carbon biomass: methodological problems related to the mucilaginous nature of the colonial matrix. *Journal of Phycology* **36**, 1049–1056.

Miller, K.A. & Pearse, J.S. 1991 Ecological studies of seaweeds in McMurdo Sound, Antarctica. *American Zoologist* **31**, 35–48.

Mincks, S.L., Smith, C.R. & DeMaster D.J. 2005 Persistence of labile organic mater and microbial biomass in Antarctic shelf sediments: evidence of a 'sediment food bank'. *Marine Ecology Progress Series* **300**, 3–19.

Moisan, T.A. & Mitchell, B.G. 1999. Photophysiological acclimation of *Phaeocystis antarctica* Karsten under light limitation. *Limnology and Oceanography* **44**, 247–258.

Muench, R., Padman, L., Gordon, A. & Orsi, A. 2009 A dense water outflow from the Ross Sea, Antarctica: mixing and the contribution of tides. *Journal of Marine Systems* **77**, 369–387.

Myashita, T., Kato, H. & Kasuya, T. 1995 World wide map of cetacean distribution based on Japanese sighting data. National Research Institute of Far Seas Fisheries, Shimizu, Japan.

Neale, P.J., Jeffrey, W.H., Sobrino, C., Pakulski, J.D., Phillips-Kress, J., Baldwin, A.J., Franklin, L.A. & Kim, H.-C. 2007 Inhibition of phytoplankton and bacterial productivity by solar radiation in the Ross Sea polynya. In: Smithsonian Institution Scholarly Press, Washington, D.C., pp. 299–308.

Newell, R.I.E. 1988 Ecological changes in the Chesapeake Bay: are they the result of overharvesting the American oyster, *Crassostera virginica*? In: *Understanding the estuary: advances in Chesapeake Bay research* (eds. M.P. Lynch & E.C. Krome), Chesapeake Bay Consortium Research Publication 129 (CBT/TRS 24/88), Gloucester Pt., VA, 536–546.

Nicol, S. 2006 Krill, currents, and sea ice: *Euphausia superba* and its changing environment. *BioScience* **56**, 111–119.

Olson, R.J., Sosik, H.M., Chekalyuk, A.M. & Shalapyonok, A. 2000 Effects of iron enrichment of phytoplankton in the Southern ocean during late summer: active fluorescence and flow cytometric analyses. *Deep-Sea Research II* **47**, 3179–3200.

Orr, J.C. et al. 2005 Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437**, 681–686.

Orsi, A.H. & Wiederwohl, C.L. 2009 A recount of Ross Sea waters. *Deep-Sea Research II* **56**, 778–795.

Orsi, A.H., Johnson, G.C. & Bullister, J.L. 1999 Circulation, mixing, and production of Antarctic bottom water. *Progress in Oceanography* **43**, 55–109.

Orsi, A.H., Smethie, W.M. & Bullister, J.L. 2002 On the total input of Antarctic waters to the deep ocean: a preliminary estimate from chlorofluorocarbon measurements. *Journal of Geophysical Research* **107**, 1–14.

Pace, M. L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F., 1999 Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* **14**, 483–488.

Padman, L., Howard, S.L., Orsi, A.H. & Muench, R.D. 2009 Tides of the Northwestern Ross Sea and their impact on dense outflows of Antarctic Bottom Water. *Deep-Sea Research II* **55**, doi: 10.1016/j.dsr2.2008.10.026.

Pakhomov, E.A. & Perissinotto, R. 1997 Spawning success and grazing impact of *Euphausia chrystallorophias* in the Antarctic shelf region. In: *Antarctic communities: species, structure and survival* (eds. B. Battaglia, J. Valencia &

D.W.H. Walton). Cambridge University Press, Cambridge, 187–192.

Parkinson, C.L. 2002 Trends in the length of the Southern Ocean sea-ice season. *Annals of Glaciology* **34**, 435–440.

Parkinson, C.L. 2004 Southern Ocean sea ice and its wider linkages: insights revealed from models and observations. *Antarctic Science* **16**, 387–400.

Pauly, D., Alder, J., Bennett, E., Christensen, V., Tyedmers, P. & Watson, R. 2003 The future for fisheries. *Science* **302**, 1359–1361.

Pauly, D. & Maclean, J. 2003 *In a perfect ocean: the state of fisheries and ecosystems in the North Atlantic Ocean.* Island Press, Washington, DC.

Pauly, D., Watson, R. & Alder, J. 2005 Global trends in world fisheries: impacts on marine ecosystems and food security. *Philosophical Transactions of the Royal Society B* **360**, 5–12.

Peloquin, J. & Smith, W.O. Jr., 2007 Phytoplankton blooms in the Ross Sea, Antarctica: interannual variability in magnitude, temporal patterns, and composition. *Journal of Geophysical Research* **112**, doi: 10.1029/2006JC003816.

Phillips, N.L., Blackwell, R.G. & Hanchett, S.M. 2004 Standardized CPUE analysis of the Antarctic toothfish fishery in CCAMLR subarea 88.1 from 1988/89 to 2003/04. *CCAMLR WS-FSA-04/25*, Hobart, Australia.

Pinkerton, M.H., Bradford-Grieve, J.M. & Hanchet, S.M. 2010 A balanced model of the food web of the Ross Sea. *CCAMLR Science* (in press).

Pitman, R.L. & Ensor, P. 2003 Three forms of killer whales in Antarctic waters. *Journal of Cetacean Research and Management* **5**, 1–9.

Richardson, M.D. & Hedgpeth, J.W. 1977 Antarctic soft-bottom macrobenthic community adaptation to a cold stable highly productive, glacially affect environment. In: *Adaptations within Antarctic ecosystems* (ed. G. Llano). Smithsonian Institution, Washington DC, 181–196.

Russell, J.L., Dixon, K.W., Gnanadesikan, A., Stouffer, R.J. & Toggweiler, J.R. 2006 The Southern Hemisphere westerlies in a warming world: propping open the door to the deep ocean. *Journal of Climate* **19**, 6382–6390.

Ryther, J.H. 1969 Photosynthesis and fish production in the sea. *Science* **166**, 72–76.

Sala, A., Azzali, M. & Russo, A. 2002 Krill of the Ross Sea: distribution, abundance and demography of *Euphausia superba* and *Euphausia crystallorphias* during the Italian Antarctic Expedition (January-February 2000). *Scientia Marina* **66**, 123–133.

Sarmiento, J.L. & le Quéré, C. 1996 Oceanic carbon dioxide uptake in a model of century-scale global warming, *Science*, **274**, 1346–1350.

Sarmiento, J.L., Hughes, T.M.C., Stouffer, R.J. & Manabe, S. 1998 Simulated response of the ocean carbon cycle to anthropogenic climate warming, *Nature*, **393**, 245–249.

Schiaparelli, S., Cattaneo-Vietti, R. & Chiantore, M. 2000 Adaptive morphology of *Capulus subcompressus* Pelseneer, 1903 (Gastropoda: Capulidae) from Terra Nova Bay, Ross Sea (Antarctica). *Polar Biology* **23**, 11–16.

Sedwick, P., Garcia, N.S., Risemen, S.F., Marsay, C.M. & DiTullio, G.R. 2007 Evidence for high iron requirements of colonial *Phaeocystis antarctica* at low irradiance. *Biogeochemistry* **83**, 83–97.

Siegel, V. 2005 Distribution and population dynamics of *Euphausia superba*: summary of recent findings. *Polar Biology* **29**, 1–22.

Simmonds, I. & King, J.C. 2004 Global and hemispheric climate variations affecting the Southern Ocean. *Antarctic Science* **16**, 401–413.

Smetacek, V. & Nicol, S. 2005 Polar ocean ecosystems in a changing world. *Nature* **437**, 362–368.

Smith, W.O. Jr. & Comiso, J.C. 2008 The influence of sea ice on primary production in the Southern Ocean: a satellite perspective. *Journal of Geophysical Research* **113**, doi: 10.1029/2007JC004251.

Smith, W.O. Jr. & Dunbar, R.B. 1998 The relationship between new production and vertical flux on the Ross Sea continental shelf. *Journal of Marine Systems* **17**, 445–457.

Smith, W.O. Jr. & Gordon. L.I. 1997 Hyperproductivity of the Ross Sea (Antarctica) polynya during austral spring. *Geophysical Research Letters* **24**, 233–236.

Smith, W.O. Jr. & Nelson, D.M. 1985. Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. *Science* **227**, 163–166.

Smith, W.O. Jr., Ainley, D.G. & Cattaneo-Vietti, R. 2007 Trophic interactions within the Ross Sea continental shelf ecosystem. *Philosophical Transactions of the Royal Society, London, series B* **362**, 95–111.

Smith, W.O. Jr., Anderson, R.F., Moore, J.K., Codispoti, L.A. & Morrison, J.M., 2000 The US Southern Ocean Joint Global Ocean Flux Study: an introduction to AESOPS. *Deep-Sea Research II* **47**, 3073–3094.

Smith, W.O. Jr., Asper, V., Tozzi, S., Liu, X. & Stammerjohn, S.E. 2011a Continuous fluorescence measurements in the Ross Sea, Antarctica: scales of variability. *Progress in Oceanography* **88**, 28–45.

Smith, W.O. Jr., Dennett, M.R., Mathot, S. & Caron, D.A. 2003 The temporal dynamics of the flagellated and colonial stages of *Phaeocystis antarctica* in the Ross Sea. *Deep-Sea Research II* **50**, 605–618.

Smith, W.O., Jr., Shields, A.R., Dreyer, J., Peloquin, J.A. & Asper, V. 2011b Interannual variability in vertical export in the Ross Sea: magnitude, composition, and environmental correlates. *Deep-Sea Research I* **58**: 147–159.

Smith, W.O., Jr., Shields, A.R., Peloquin, J.A., Catalano, G., Tozzi, S., Dinniman, M.S. & Asper, V.A. 2006 Interannual variations in nutrients, net community production, and

biogeochemical cycles in the Ross Sea. *Deep-Sea Research II* **53**: 815–833.

Stammerjohn, S.E. & Smith, R.E. 1997 Opposing Southern Ocean climate patterns as revealed by trends in regional sea ice coverage. *Climatic Change* **37**, 617–639.

Stammerjohn, S.E., Martinson, D.G., Smith, R.E., Yuan, X. & Rind, D. 2008 Trends in Antarctic seasonal sea ice retreat and advance and their and their relation to El Niño-Southern Oscillation and Southern Annular Mode variability. *Journal of Geophysical Research* **113**, doi: 10.1029/2007JC004269.

Stevenson, M.L., Hanchet, S.M. & Dunn, A. 2008 A characterisation of the toothfish fishery in subareas 88.1 and 88.2 from 1997–98 to 2007–08. CCAMLR Document WG-FSA-08/22.

Stockton, W.L. 1984 The biology and ecology of the epifaunal scallop *Adamussium colbecki* on the west side of McMurdo Sound, Antarctica. *Marine Biology* **78**, 171–178.

Sullivan, C.W., Arrigo, K.R., McClain, C.R., Comiso, J.C. & Firestone, J. 1993. Distributions of phytoplankton blooms in the Southern Ocean. *Science* **262**, 1832–1837.

Sweeney, C., Smith, W.O. Jr., Hales, B., Hansell, D.A., Carlson, C.A., Codispoti, L.A., Gordon, L.I., Millero, F.J. & Takahashi, T. 2000 Nutrient and TCO_2 uptake and export ratios in the Ross Sea. *Deep-Sea Research II* **47**, 3395–3422.

Takahashi, T. *et al.*, 2009 Climatological mean and decadal change in surface pCO_2, and net sea-air CO_2 flux over the global ocean. *Deep-Sea Research II* **56**, 554–577.

Taki, K., Yabuki, Y., Noiri, Y., Hayashi, T. & Naganobu, M. 2008 Horizontal and vertical distribution and demography of euphausiids in the Ross Sea and its adjacent waters in 2004/2005. *Polar Biology* **31**, 1343–1356.

Tang, K.W., Smith, W.O. Jr., Elliott, D.T. & Shields, A.R. 2008 Colony size of *Phaeocystis antarctica* (Prymnesiophyceae) as influenced by zooplankton grazers. *Journal of Phycology* **44**, 1372–1378.

Tang, K.W., Smith, W.O. Jr., Shields, A.R. & Elliott, D.T. 2009 Survival and recovery of *Phaeocystis antarctica* (Prymnesiophyceae) from prolonged darkness and freezing. *Philosophical Transactions of the Royal Society, Series B* **276**, 81–90.

Testa, J.W., Siniff, D.B., Ross, M.J. & Winter, J.D. 1985 Weddell Seal - Antarctic Cod interactions in McMurdo Sound, Antarctica. In: *Antarctic nutrient cycles and food webs* (eds. W.R. Siegfried, P.R. Condy & R.M. Laws). Springer Verlag, Berlin, 561–565.

Thompson, D.W.J. & Solomon, S. 2002. Interpretation of recent Southern Hemisphere climate change. *Science* **296**, 895–899.

Thrush, S., Dayton, P., Cattaneo-Vietti, R., Chiantore, M., Cummings, V., Andrew, N., Hawes, I., Kim, S., Kvitek, R. & Schwarz, A.M. 2006 Broad-scale factors influencing the biodiversity of coastal benthic communities of the Ross Sea. *Deep-Sea Research II* **53**, 959–971.

Tortell, P.D., DiTullio, G.R., Sigman, D. & Morel, F.M.M. 2002 CO_2 effects on taxonomic composition and nutrient utiliza-tion in an Equatorial Pacific phytoplankton assemblage. *Marine Ecology Progress Series* **236**, 37–43.

Tortell, P.D., Payne, C.D., Li, Y., Trimborne, S., Jost, B., Smith, W.O., Riesselmann, C., Dunbar, R.B., Sedwick, P. & DiTullio, G.R., 2008 CO_2 sensitivity of Southern Ocean phytoplankton. *Geophysical Research Letters* **35**, doi: 10.1029/2007GL032583.

Tremblay, J.-E. & Smith, W.O. Jr., 2007 Phytoplankton processes in polynyas. In: *Polynyas: windows to the world's oceans* (eds. W.O. Smith & D. Barber). Elsevier, Amsterdam, 239–270.

Vaughan, D.G., Marshall, G.J., Connolley, G.M., Parkinson, C., Mulvaney, R., Hodgson, D.A., King, J.C., Pudsey, C.J. & Turner, J. 2004 Recent rapid regional climate warming on the Antarctic Peninsula. *Climatic Change* **60**, 243–274.

Van Dam, R.P. & Kooyman, G.L. 2004 Latitudinal distribution of penguins, seals and whales observed during a late autumn transect through the Ross Sea. *Antarctic Science* **16**, 313–318.

Velicagna, I. & Wahr, J. 2006 Measurements of time-variable gravity show mass loss in Antarctica. *Science* **311**, 1754–1756.

Visbeck, M., Thurnherr, A. 2009 High-resolution velocity observations of the Drygalski Trough gravity plume. *Deep-Sea Research II* **55**, 835–842.

Waniek, J.J. 2003 The role of physical forcing in initiation of spring blooms in the northeast Atlantic. *Journal of Marine Systems* **39**, 57–82.

Whitworth, T. III & Orsi, A. 2006 Antarctic bottom eater production and export by tides in the Ross Sea. *Geophysical Research Letters* **33**, doi: 10.1029/2006GL026357.

Whitworth, T. III, Orsi, A.H., Kim, S.-J. & Nowlin, W.D. Jr., 1998 Water masses and mixing near the Antarctic Slope Front. *Antarctic Research Series* **75**, 1–27.

Woehler, E.J. 1993 *The distribution and abundance of Antarctic and subantarctic penguins*. Scientific Committee on Antarctic Research, Cambridge, UK.

Yuan, X. 2004 ENSO-related impacts on Antarctic sea ice: a synthesis of phenomenon and mechanisms. *Antarctic Science* **16**, 415–425.

Yuan, X. & Martinson, D.G. 2000 Antarctic sea ice extent variability and its global connectivity. *Journal of Climate* **3**, 1697–1717.

Yuan, X. & Martinson, D.G. 2001 The Antarctic dipole and its predictability. *Geophysical Research Letters* **28**, 3609–3612.

Zaneveld, J.S. 1968 Benthic marine algae, from Ross Island to Balleny Islands. In: *Primary productivity and benthic marine algae of the Antarctic and Subantarctic*. Antarctic Map Folio Series, Folio 10, American Geographic Society, New York, 10–12.

Zwally, H.J., Comiso, J.C., Parkinson, C.L., Cavalieri, D.J. & Gloersen, P. 2002 Variability of Antarctic sea ice 1979–1998. *Journal of Geophysical Research* **107**, doi: 10.1029/2000JC000733.