The Oceanography and Ecology of the Ross Sea

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Abstract

The continental shelf of the Ross Sea exhibits substantial variations in physical forcing, ice cover, and biological processes on a variety of time and space scales. Its circulation is characterized by advective inputs from the east and exchanges with off-shelf regions via the troughs along the northern portions. Phytoplankton biomass is greater there than anywhere else in the Antarctic, although nitrate is rarely reduced to levels below 10 μmol L^{-1}. Overall growth is regulated by irradiance (via ice at the surface and by the depths of the mixed layers) and iron concentrations. Apex predators reach exceptional abundances, and the world's largest colonies of Adélie and emperor penguins are found there. Krill are represented by two species (*Euphausia superba* near the shelf break and *Euphausia crystallorophias* throughout the continental shelf region). Equally important and poorly known is the Antarctic silverfish (*Pleuragramma antarcticum*), which is also consumed by most upper-trophic-level predators. Future changes in the Ross Sea environment will have profound and unpredictable effects on the food web.

INTRODUCTION

Polar systems are being dramatically affected by a changing climate (Doney et al. 2012), but in other ways they are among the least impacted by human activity of all marine ecosystems (Halpern et al. 2008). The Ross Sea continental shelf (**Figure 1**) is an excellent example of this dichotomy: Its food web is largely pristine (industrial fishing has been limited and mostly impractical until recently owing to heavy ice conditions), but its chemistry is changing rapidly because of increasing carbon dioxide concentrations, decreased pH, and an aragonite saturation state approaching 1 (Orr et al. 2005, Matson et al. 2011). Sea-ice seasonality is also changing rapidly (Stammerjohn et al. 2008, 2012). As such, some aspects of this region's ecology and food web dynamics remain unperturbed, whereas others are rapidly responding to environmental changes (Smith et al. 2012). Both conditions make the Ross Sea continental shelf one of the Southern Ocean's most ideal "natural laboratories" to test hypotheses dealing with natural interactions and processes.

Climate change affects the Ross Sea shelf largely through the physical forcing of the environment. For example, ice concentrations in the Ross Sea sector—which lies between 130°W and 160°E and extends north to 50°S (Arrigo et al. 2008a), in contrast to the continental shelf alone—have been changing rapidly; unlike those in the West Antarctic Peninsula region, however, ice concentrations in the Ross Sea have been significantly increasing in extent (Comiso & Nishio 2008) and duration (Stammerjohn et al. 2012), and they are responsible for the modest net increase in Southern Ocean ice extent since 1979. Models of future atmospheric and ice conditions (e.g., Bracegirdle et al. 2008) suggest that this trend is transient and that in 50 years the Ross Sea will experience a substantial reduction in sea ice during austral summer driven by increased atmospheric temperatures and changes in winds. Hence, the changes being observed now (increased

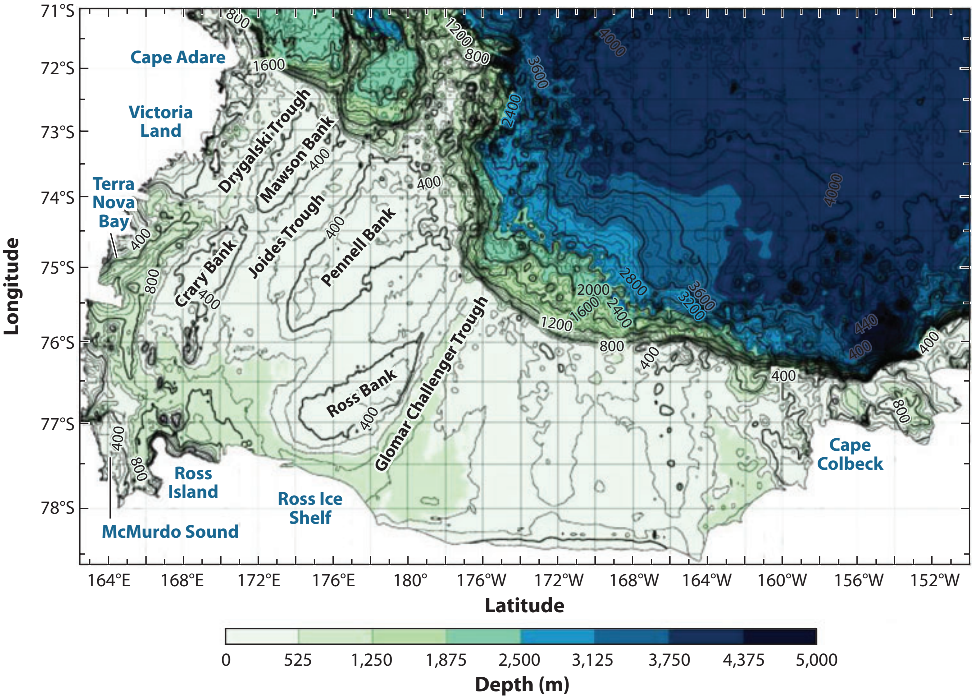

Figure 1

Bathymetric map of the Ross Sea. Based on the ETOPO1 bathymetry, with a contour interval of 100 m.

sea-ice cover in the entire Pacific sector, with substantial spatial variability on the continental shelf; Stammerjohn et al. 2008) may soon reverse. When that reversal occurs, some of the ecological and oceanographic changes that have been observed in the West Antarctic Peninsula (Montes-Hugo et al. 2009) may occur in the Ross Sea, albeit with substantial regional differences.

We review herein various aspects of Ross Sea oceanography and ecology, including the environmental settings, chemical oceanography, phytoplankton dynamics, and higher-trophic-level interactions. We particularly emphasize changes that we believe will occur in the near future, based on observed temporal trends both in the Ross Sea and elsewhere in the Southern Ocean as well as modeled impacts and predicted forcing. We also provide topics that deserve investigation to understand the Ross Sea's ecology, its linkages to other systems, and its role in global processes.

Katabatic winds: winds caused by higher-density air driven down a slope by gravity; in the Antarctic, they arise from cold, dense air masses created over elevated ice sheets by radiational cooling

Polynya: an area of reduced ice surrounded by higher concentrations of ice; they can arise either from melting or from wind-driven ice movements

Ice shelf: a thick, floating platform of glacial ice that has been driven by gravity over the ocean

THE PHYSICAL SETTING

Two important factors influence the climate and surface winds over the Ross Sea (Parish et al. 2006). First, the Ross Sea is one of the most active cyclogenetic regions in the world (Jones & Simmonds 1993, King & Turner 1997) and is thus often subject to strong storms. Second, the physiography of the region generates strong katabatic winds that flow from land over the ocean. The Transantarctic Mountains along the southern and western sides of the Ross Ice Shelf and the Victoria Land coast along with the elevated East Antarctic Ice Sheet immediately inland (Parish et al. 2006) are generation sites of katabatic winds that flow down glaciers and can extend over the coastal ocean, leading to areas of reduced ice concentration even in winter.

One example of this phenomenon is the Terra Nova Bay polynya (Bromwich & Kurtz 1984). Over the Ross Ice Shelf, which covers the southern half of the Ross Sea, extensive cold-air drainage (katabatic winds) occurs from the Siple Coast region in the east as well as from glacial valleys of the Transantarctic Mountains (Parish et al. 2006). The katabatic flow loses its forcing once it reaches the ice shelf, but a barrier wind along the mountains is created that leads to a persistent northward airflow along the western and central sections of the Ross Ice Shelf. This flow, which continues northward over the Ross Sea, is known as the Ross Ice Shelf air stream (Parish et al. 2006, Seefeldt & Cassano 2012). It results in areas of reduced ice concentration throughout the winter along the Ross Ice Shelf as ice is driven northward to create the Ross Sea polynya. This process continues through November, and as the solar heat input increases, open waters expand northward (**Figure 2**). This open water frequently extends off the shelf during austral summer and often (but not always) becomes contiguous with the open Pacific Ocean. Sea ice covers the Ross Sea quickly in early March and continues to thicken and expand throughout winter. Brine is rejected during ice formation, which subsequently sinks and helps to form High Salinity Shelf Water. Sea ice in the Ross Sea is generally annual, with some multiyear ice along the coast of Victoria Land and in the eastern slope region.

Inputs onto the shelf are dominated by flows from the southern limb of the Ross Gyre of saline and warm (>1°C) Circumpolar Deep Water (CDW) drawn from the Antarctic Circumpolar Current (Orsi & Whitworth 2005, Orsi & Wiederwohl 2009). On-shelf transport of CDW is critical to the heat and salt budgets, regional sea-ice cycle, and basal melt rate of the Ross Ice Shelf, as it is the oceanic source of heat (Smith et al. 2012). Different mechanisms (flow inertia around curved bathymetry, onshore advecting eddies in troughs, and atmospherically forced exchange) have been proposed for the on-shelf CDW transport (Klinck & Dinniman 2010), but the exact cause remains uncertain. Unlike in the southeast Pacific, where the southern boundary of the eastward Antarctic Circumpolar Current flows along the shelf break, the major dynamical obstacles to rising waters are the abrupt poleward diving of isopycnals found over the upper continental slope (Ainley & Jacobs 1981) and the westward-flowing slope current near the shelf break that carries

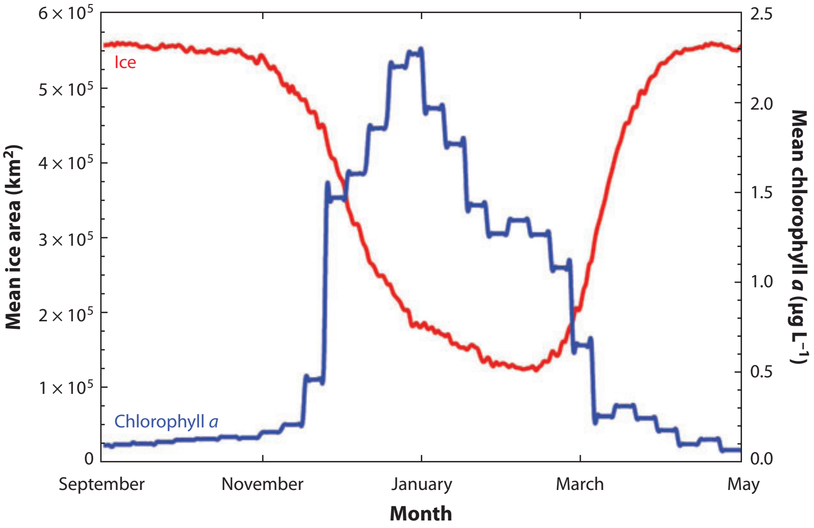

Figure 2

Temporal progression of ice area and chlorophyll *a* concentrations on the Ross Sea continental shelf. Sea-ice area is derived from special sensor microwave/imager (SSM/I) data from 1997 to 2012; chlorophyll *a* is estimated from Sea-Viewing Wide Field-of-View Sensor (SeaWiFS)–Moderate Resolution Imaging Spectroradiometer (MODIS)/Aqua data from the same period. Chlorophyll *a* concentrations at each time point have a different number of values used to estimate concentrations because they are dependent on cloud-free images.

a layer of cold and fresh Antarctic Surface Water (Whitworth et al. 1998). The Antarctic Surface Water enters the eastern Ross Sea near Cape Colbeck as a narrow coastal current that advects continental meltwater derived from upstream (Jacobs et al. 1985). Atmospheric cooling sustains sea-ice formation during winter, especially in the wind-driven polynyas, where ice is made continually because the relatively warm ocean waters are never insulated from the atmosphere by sea-ice cover. Ice formation increases sea-surface salinity and produces dense shelf water that fills most of the shelf's troughs, including under the floating Ross Ice Shelf. The mixture of meltwater from the base of the Ross Ice Shelf with shelf water emerges as less saline Ice Shelf Water, identified by temperatures below the surface freezing point (<-2.0°C), facilitated by the pressure-reduced freezing point of seawater, and indicating contact with the base of the ice shelf at depth. The shelf water flows northward along the western flank of the troughs, and when it reaches the shelf break sills, it increases the tilt of the isopycnals and facilitates inflow of modified CDW (MCDW; >0.5°C) at the base of the Antarctic Slope Front (Ainley & Jacobs 1981).

Because of the low stratification over the continental shelf, the circulation on much of the shelf is strongly forced by the bathymetry owing to potential vorticity constraints (Dinniman et al. 2003). Poleward extensions of MCDW are apparent over the western side of the many banks (Orsi & Wiederwohl 2009, Kohut et al. 2013) that are oriented southwestward–northeastward (**Figure 1**). The most conspicuous and persistent of these inflows appear as a subsurface "warm" core (>-1.5°C) (Jacobs & Giulivi 1998). Across the western shelf, MCDW inflows mix with surface waters. Enhanced mixing of shelf waters with MCDW at the Antarctic Slope Front, possibly driven by the strong tides along the continental slope (Whitworth & Orsi 2006, Padman et al. 2009), produces a variety of dense waters that ventilate adjacent ocean basins. In the Ross Sea, the export of cold Antarctic Bottom Water (<-1°C) is restricted to the regions off the Drygalski, Joides, and Glomar Challenger Troughs (Gordon et al. 2004). The less dense waters (<0.5°C) descend to mid-depths along much of the slope front and freshen the CDW layer of the Ross Gyre. Approximately 30% of the combined input of shelf water and Antarctic Surface Water to the Antarctic Bottom Water and CDW layers is attributable to Ross Sea production (Orsi et al. 2002).

ELEMENTAL CYCLES

Waters of the Ross Sea continental shelf are highly productive, sustaining an annual primary production of approximately 83.4 Tg C y^{-1}, equivalent to a mean shelf-wide productivity of 0.82 g C m^{-2} d^{-1} over a growing season of four months (Arrigo et al. 2008a). This production rate is as great as any in the entire Southern Ocean and is particularly noteworthy given the size of the Ross Sea continental shelf. Despite high rates of primary production, macronutrients (nitrate, phosphate, and silicate) are rarely depleted from surface waters during the growing season and on average are well above levels considered to saturate nutrient uptake (**Figure 3**). However, isolated locations do experience the complete removal of nitrate (Smith & Nelson 1985). The general lack of nutrient depletion is likely caused by two factors: iron availability and the low temperature-limited growth rates (along with a short growing season imposed by ice). Conversely, locations that exhibit more extreme macronutrient removal must have both adequate iron supplies and optimal irradiance conditions.

Low dissolved iron concentrations limit phytoplankton growth and biomass over much of the deep regions of the Southern Ocean (Boyd 2002). Although there are a number of potential sources of iron to surface waters of the Ross Sea, including atmospheric seafloor sediments, sea ice and glacial ice, MCDW intrusions, and mineral aerosols (Sedwick & DiTullio 1997) (**Figure 4**), there is evidence that iron availability can limit phytoplankton growth in the Ross Sea during parts of the growing season (Sedwick et al. 2000, Coale et al. 2005). Recent observations suggest that substantially reduced iron concentrations develop during spring, implying that continued growth and biomass accumulation during the summer months require inputs of "new" iron to surface waters during summer (Peloquin & Smith 2007, Sedwick et al. 2011). Given the spatial scale of the summer growth, the source of such inputs remains unclear, because atmospheric inputs (dust) are thought to be restricted to the few ice-free land areas (such as the Dry Valleys along the southern coast of Victoria Land). Little is known about the regeneration rates of iron in the surface waters of Antarctica, although irradiance has been suggested to be important in the photochemical alteration of iron bioavailability (Tagliabue & Arrigo 2005).

Primary production in waters overlying the exposed Ross Sea shelf appears to be characterized by relatively high export efficiencies, perhaps facilitated by the formation of organic aggregates (Asper & Smith 1999). The estimated f-ratios are approximately 50% (Asper & Smith 1999, Cochlan et al. 2002). This, along with the importance of the Ross Sea as an area of deep-water formation, suggests that the Ross Sea plays a significant role in the Southern Ocean carbon cycle as a major regional anthropogenic CO_2 sink (Arrigo et al. 2008b). The Ross Sea also constitutes a significant regional sink for silicic acid as a result of the preferential sedimentation of diatom-derived opal relative to organic carbon (Nelson et al. 1996), which leads to the formation of substantial diatomaceous deposits, suggesting that the Ross Sea plays a role in the global silica budget as well (DeMaster 2002).

THE ROSS SEA FOOD WEB: PLANKTON

Phytoplankton assemblages in the Ross Sea have been studied intensively for decades. In general, phytoplankton biomass and composition are coupled to ice distributions, the variations in mixed-layer depth, and irradiance availability. Smith & Gordon (1997) found that biomass is

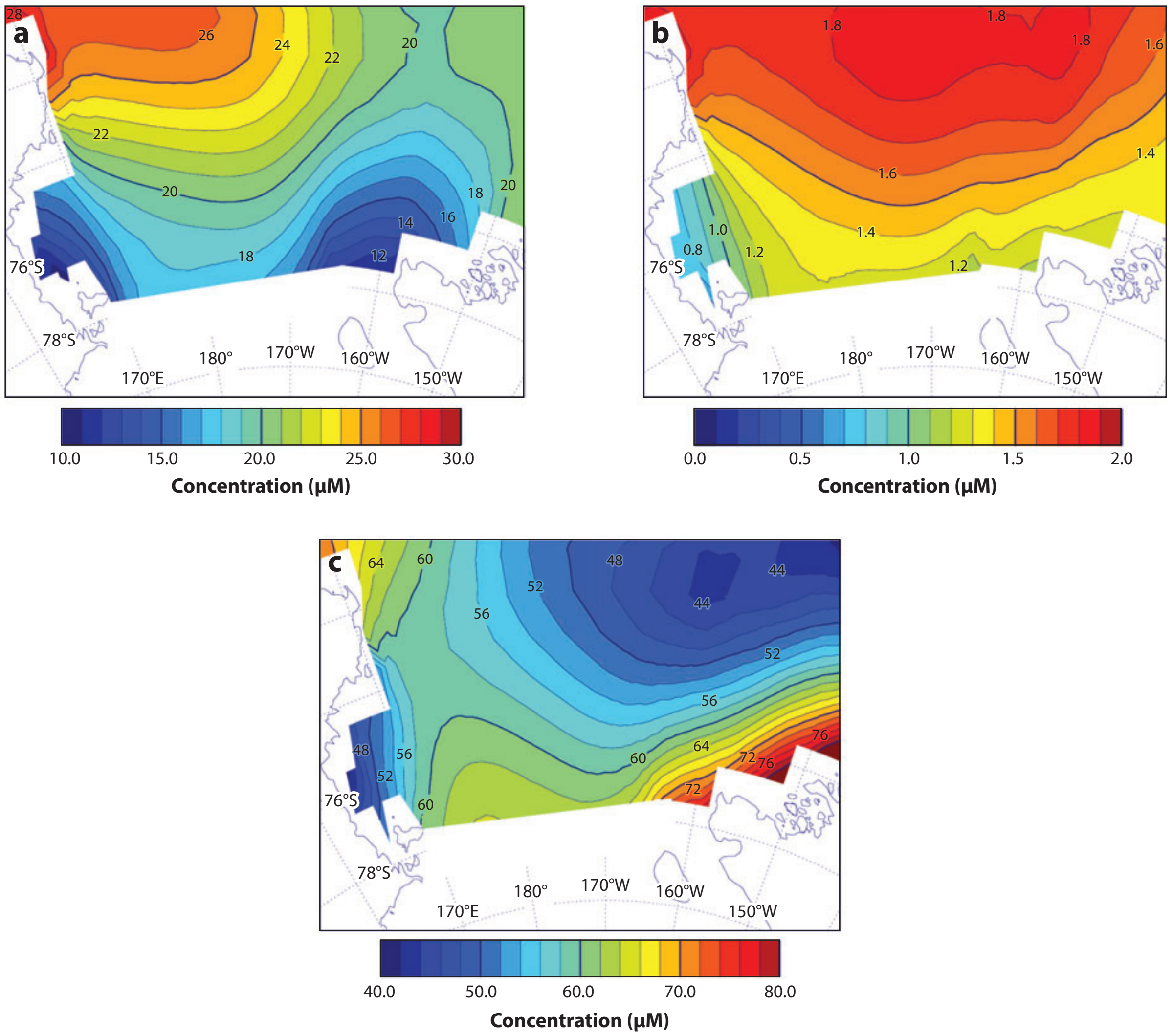

Figure 3

Spatial distribution of average January concentrations (10 m) of (*a*) nitrate, (*b*) phosphate, and (*c*) silicic acid on the Ross Sea continental shelf. Data taken from Garcia et al. (2010).

elevated by mid-November and that growth is proceeding rapidly by that time. This indicated that growth is initiated in late October, which was later confirmed by direct observations (Smith et al. 2000). Although satellite observations of ocean color during this period are often obscured by clouds (Arrigo & McClain 1994), those data also confirm that chlorophyll begins to increase in November (Arrigo & van Dijken 2004), when mixed layers in the Ross Sea shoal to depths that provide sufficient irradiance for growth. High, albeit light-limited, growth rates in spring in conjunction with low losses due to grazing and sinking are responsible for the large accumulation of biomass that is regularly observed in the southern shelf in late December. El-Sayed et al. (1983) described large accumulations of the haptophyte *Phaeocystis* near the Ross Ice Shelf, and Smith & Nelson (1985) reported massive accumulations (the largest accumulations of biogenic

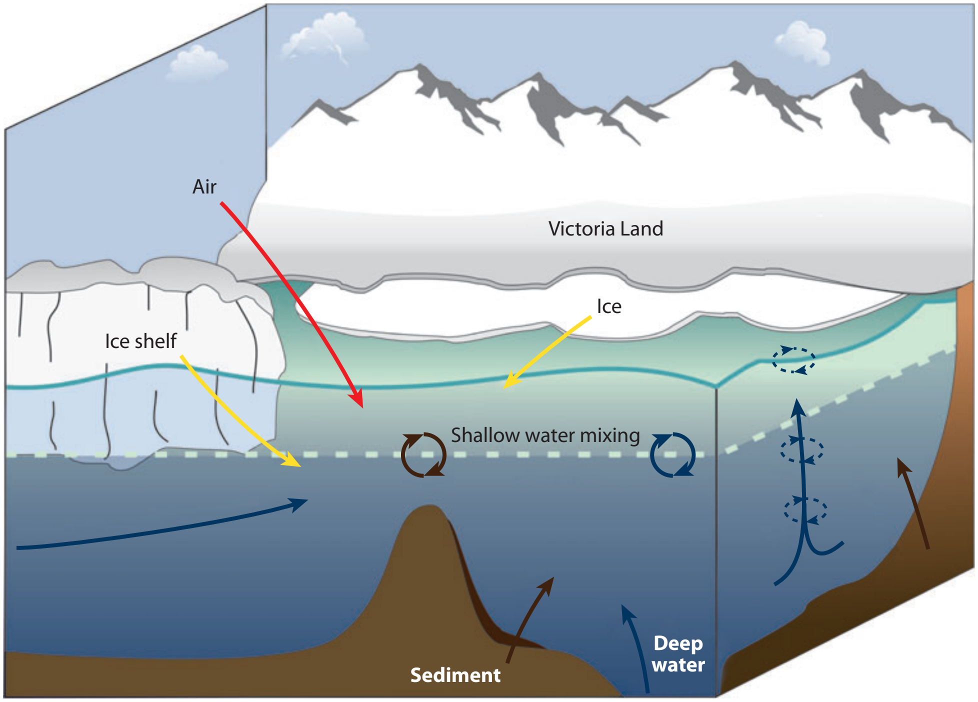

Figure 4

Schematic of the potential sources of iron to the Ross Sea. These include oceanic sources (*dark blue arrows*) (inputs in the modified Circumpolar Deep Water, inputs from under the ice shelf in the Ice Shelf Water, and vertical inputs via surface mixing and mesoscale eddies), sedimentary sources (*brown arrows*) (including any inputs that occur via resuspension of sediments and vertical mixing in shallow bank regions), atmospheric sources (*red arrows*) (from the Dry Valleys and Mount Erebus), and ice sources (*yellow arrows*) (via ice melt during spring and summer and from glacial sources). Inputs from hydrothermal vents are possible but have not been detected in the Ross Sea.

silica ever observed) of a diatom bloom off the coast of Victoria Land, both of which emphasize the variability in space as well as time.

The temporal dynamics of phytoplankton assemblages in the Ross Sea have been well documented in the past two decades. Spring biomass is generally dominated by *Phaeocystis antarctica* (Smith & Gordon 1997, Arrigo et al. 1999); its dominance is explained by its ability to photosynthesize under the reduced spring irradiances (Kropuenske et al. 2009) (**Figure 5**). Surface mixed layers in spring (November–mid-December) are approximately 50 m deep, whereas those in summer are often less than 10 m (Smith & Asper 2001). Chlorophyll concentrations in *P. antarctica* blooms can exceed 15 μg L^{-1}. These generally decrease rapidly to low levels over a two-week period, possibly as a result of aggregate formation and rapid sinking of intact colonies when growth becomes limited by iron availability (DiTullio et al. 2000, Smith et al. 2011b). The life cycle of *Phaeocystis* involves both solitary and colonial stages, including seasonal changes in the relative numbers of each (Mathot et al. 2000). The two forms are ecologically separate, with solitary forms being ingested by heterotrophic microplankton (Dennett et al. 2001, Smith et al. 2003) and colonies sinking and being remineralized at depth. After the seasonal decline of *P. antarctica*, phytoplankton assemblages are dominated by diverse populations of diatoms, which tend to dominate assemblages in austral summer in the shallower mixed layers and are often

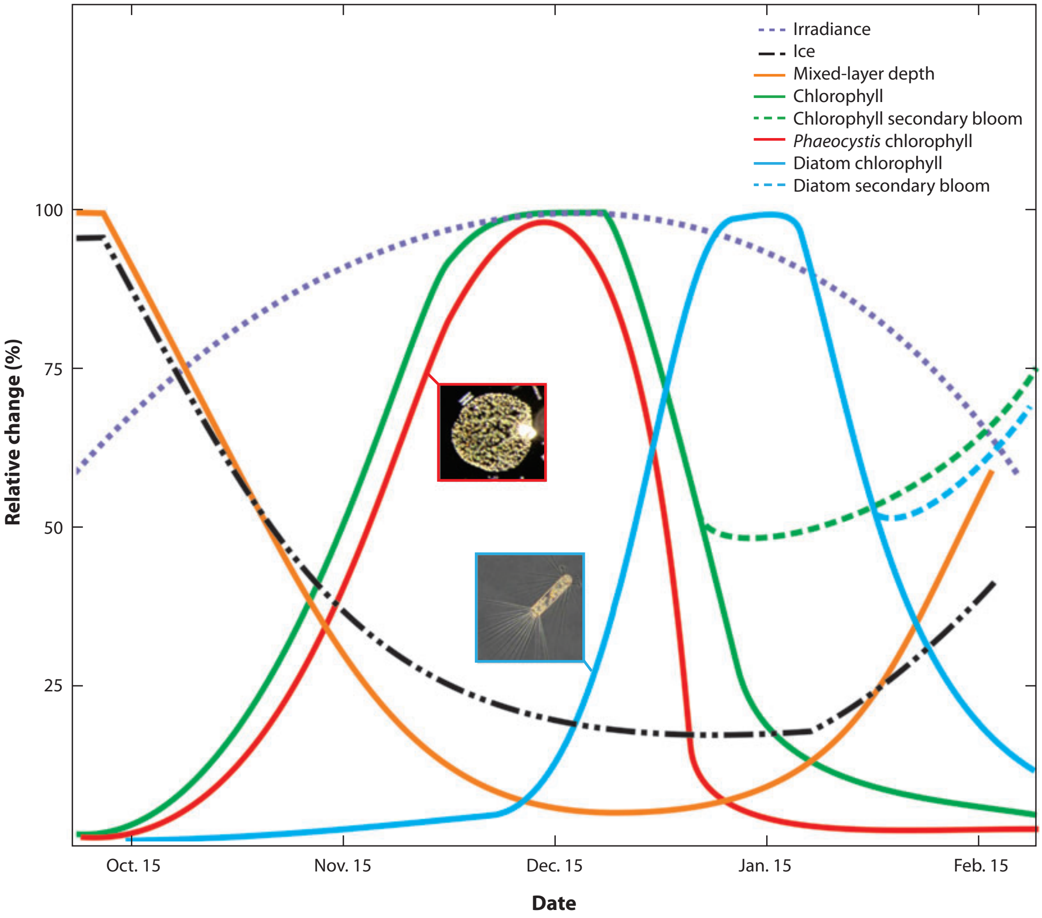

Figure 5

Conceptual representation of the temporal progression of several environmental variables and phytoplankton composition in the southern Ross Sea. Irradiance is maximal on December 21. Ice concentrations begin to decrease rapidly in November and reach their minimum in February, whereas the depths of the surface mixed layers begin to decrease in October and reach a minimum in January. Chlorophyll concentrations increase rapidly in November, become maximal in December, and then decrease even more rapidly in early January; alternatively, in January and February these concentrations can increase following the initial decrease. Spring increases in chlorophyll are due to the growth and accumulation of *Phaeocystis antarctica*, whereas summer increases are largely the result of the growth and accumulation of diatoms. A secondary diatom bloom can also occur in summer.

associated with sea- and glacial-ice melt (**Figure 5**). Other groups (dinoflagellates, cryptomonads, and silicoflagellates) occur in spatially restricted locations (Arrigo et al. 1999). Although this overall pattern is relatively predictable, significant interannual variations exist in the contributions of the various functional groups to total biomass (Smith et al. 2011b).

This regular seasonal sequence imposes constraints on biogeochemical cycling because the two dominant functional groups have markedly different elemental ratios and roles in food webs. *P. antarctica* has a C:N:P ratio of approximately 139:19:1, whereas diatoms have a ratio of 76:12:1 (Arrigo et al. 2000), thus potentially impacting deep-water concentrations of nutrients and sediments. Additionally, colonial *P. antarctica* is thought to be largely ungrazed by most mesozooplankton (Tagliabue & Arrigo 2003; but see Haberman et al. 2003), although pteropods may

Functional groups: conceptual groupings of species that have an ecological function in common (in terms of either the food web or biogeochemical cycles); examples include diatoms and coccolithophorids

Table 1 Estimates of net community production based on observed nutrient deficits (modeled after Smith et al. 2011b)

Time period	Annual production (g C m^{-2})	Annual production (g C m^{-2} d^{-1})
Nitrogen		
2001–2002	61.7	0.64
2003–2004	252	2.60
2004–2005	72.4	0.80
2005–2006 (n = 12)	89.8	0.98
2005–2006 (n = 58)	74.0	0.89
2010	58.8	0.71
Silicon		
2001–2002	35.0 (43.3%)	0.36
2003–2004	105 (58.5%)	1.08
2004–2005	27.9 (61.4%)	0.31
2005–2006 (n = 12)	11.5 (87.2%)	0.13
2005–2006 (n = 58)	27.9 (39.2%)	0.54
2010	14.0 (61.2%)	0.27

For silicon, numbers in parentheses are the percentage of production attributable to nondiatomaceous forms (largely *Phaeocystis antarctica*).

consume both solitary cells and colonies (Elliott et al. 2009). In contrast, diatoms are considered to be grazed at significant rates by zooplankton such as copepods and krill and can be incorporated into rapidly sinking fecal pellets, thereby minimizing remineralization in the water column and favoring their export to the benthos.

Phytoplankton growth, particularly diatom growth, has been experimentally shown to be iron limited in summer under conditions of high irradiance (Sedwick & DiTullio 1997, Sedwick et al. 2000). Through a variety of techniques, absolute growth rates have been found to range from 0 to 0.87 d^{-1} (Smith et al. 1999, 2000), rates that are similar to the temperature-limited rates predicted by Eppley (1972). Given the predictability of the seasonal assemblage pattern, the low dissolved iron concentrations in surface waters during much of the growing season (Sedwick et al. 2011), and the small differences in taxon-specific iron requirements (Garcia et al. 2009), seasonal changes in the assemblages may involve interactions between irradiance and iron (Boyd 2002). Peloquin & Smith (2007) observed diatomaceous blooms that occurred after the decline of *P. antarctica*, indicating additions of iron to the euphotic zone, although the mechanism by which this may occur remains unknown. Estimates of the contribution of diatoms to annual productivity in waters of the southern Ross Sea range from 38% to 61% (**Table 1**).

After the discovery of the ozone hole over Antarctica, concerns were expressed about the impact of increased UV radiation on phytoplankton productivity. However, owing to the rapid movement of the ozone hole over large spatial regions, the timing of the ozone hole (austral spring), and the depths of the mixed layers during that period, it was concluded that substantial decrease in productivity did not result from increased UV radiation fluxes (e.g., Lubin et al. 2004). Accurate assessments remain difficult to obtain, given the poor understanding of rates of vertical mixing and phytoplankton recovery to photochemical damage (Neale et al. 2012) as well as the lack of adequate methodological procedures to assess the damage.

Ozone hole: a springtime reduction in the amount of ozone in the stratosphere caused by the chemical reaction between ozone and chlorofluorohydrocarbons released by humans

In situ and satellite-based bio-optical estimates of primary productivity demonstrate the extreme productivity of the Ross Sea. The latter approach has the advantage of increased resolution in time and space, and is the most accurate means of assessing the shelf-wide productivity. Arrigo et al. (2008a) estimated that the mean net primary productivity for the entire Ross Sea sector of the Southern Ocean is 68.9 g C m^{-2} y^{-1} (189 mg C m^{-2} d^{-1}), which represents one-third of the total Southern Ocean annual production. Annual net primary production on the Ross Sea continental shelf (the site of the highest productivity in the Antarctic; Smith & Comiso 2008) is considerably higher, averaging 179 g C m^{-2} y^{-1}, and also shows the most interannual variability. Such high productivity and export efficiency (Sweeney et al. 2000) give rise to large air–sea gradients in $p\mathrm{CO}_2$, with seawater CO_2 levels often dropping below 200 μatm in summer. Radioisotope incorporation estimates indicate that carbon uptake can be as large as any measured in Antarctic waters (Wilson et al. 1986). Estimates of production derived from nutrient deficits support the large productivity of the southern Ross Sea (**Table 1**). Recent simulations indicate that waters of the Ross Sea continental shelf are responsible on average for more than 25% of the estimated total CO_2 uptake of the entire Southern Ocean (Arrigo et al. 2008b).

Biological fractionation of carbon isotopes has been used in the Ross Sea to discriminate between the productivity contributions of various functional groups. $\delta^{13}\mathrm{C}_{\mathrm{org}}$ values of particulate matter in the Ross Sea typically range from −20‰ to −35‰ (Villinski et al. 2000). Particulate organic carbon in ice can be enriched further and have $\delta^{13}\mathrm{C}_{\mathrm{org}}$ values of −15‰ (Arrigo et al. 2003). The two dominant functional groups, diatoms and *P. antarctica*, also have markedly different $\delta^{13}\mathrm{C}_{\mathrm{org}}$ values, with diatoms being more enriched with $^{13}\mathrm{C}$. When grown under reduced $p\mathrm{CO}_2$ conditions, however, all phytoplankton experience isotopic enrichment, and the magnitude of the discrimination is greatest at reduced $p\mathrm{CO}_2$ levels. Long (2010) found that diatoms are significantly enriched with $^{13}\mathrm{C}$ relative to *P. antarctica* (by approximately 6‰) and concluded that both environmental and taxonomic effects generate the observed Ross Sea $\delta^{13}\mathrm{C}_{\mathrm{org}}$.

Annual production is influenced by variations in large-scale climate variations (Lovenduski & Gruber 2005), particularly the Southern Annular Mode (SAM). This mode of climate variability is characterized by oscillations in the north–south gradient in atmospheric pressure that controls the strength of the westerly winds. During the positive phase of the SAM, the north–south pressure difference increases and westerly winds intensify, increasing the rate of Ekman divergence at the ocean surface and stimulating upwelling along the Antarctic Divergence. More important, the SAM was able to explain >64% of the interannual variance in chlorophyll *a* concentrations on the Ross Sea continental shelf, with the positive phase of the SAM being associated with increased phytoplankton biomass (Arrigo et al. 2008a). Westerly winds may continue to increase in coming decades (Le Quéré et al. 2007). Depending on the extent to which the sea-ice season increases (Stammerjohn et al. 2012), phytoplankton biomass on the Ross Sea shelf could also increase.

Bacteria (that is, heterotrophic prokaryotes) reach exceptionally high biomass levels in the Ross Sea—comparable to those found in productive waters of the North Atlantic, despite the near-freezing temperatures (Ducklow 1999). Abundances increase by more than an order of magnitude during the growing season. However, bacteria are a tiny fraction of total biomass relative to phytoplankton (approximately 2%) (Ducklow 1999). Bacterial biomass is loosely coupled to phytoplankton, with the peak in bacterial abundance coming approximately one month after the spring autotroph maximum, and bacterial production appears to be limited by labile dissolved organic carbon inputs (Ducklow 1999).

Micro- and mesozooplankton in the Ross Sea have received relatively little attention. Caron et al. (2000) conducted dilution experiments to assess microzooplankton grazing, but owing to the presence of colonial *P. antarctica*, most of these experiments (83%) failed to demonstrate significant ingestion rates. The biomass of microzooplankton has been quantified (Dennett et al. 2001), but the impact of this group on biogeochemical cycling remains poorly constrained. Investigations of mesozooplankton abundance and feeding are similarly limited. Deibel & Daly (2007) concluded that the overall biomass of mesozooplankton in the Ross Sea, despite the high regional primary production, is approximately 15% that of the Scotia Sea. *Calanoides acutus*, *Metridia gerlachei*, and *Euchaeta antarctica* are the dominant copepods (Hopkins 1987). Tagliabue & Arrigo (2003) suggested that zooplankton biomass is anomalously low as a result of the decoupling of grazers and phytoplankton growth, but this hypothesis has not been empirically tested. Sediment traps have collected substantial numbers of mesozooplankton fecal pellets, which at times constitute 100% of the flux (Dunbar et al. 1998, Smith et al. 2011b). This indicates that mesozooplankton ingestion of phytoplankton in the surface waters can at times be substantial. Ainley et al. (2006) have proposed that the low mesozooplankton abundance, particularly of euphausiids, is the result of a trophic cascade driven by the high abundance of mesopredators and apex predators, many of which feed heavily on krill and/or on small silverfish (*Pleuragramma antarcticum*) that in turn feed principally on krill, leading to reduced grazing. Antarctic krill (*Euphausia superba*) are largely absent from the inner continental shelf but occur along the shelf break; conversely, crystal krill (*Euphausia crystallorophias*) occur throughout the inner shelf region (Sala et al. 2002). Ingestion rates of krill, copepods, pteropods, and other zooplankton have yet to be studied in the Ross Sea.

THE ROSS SEA FOOD WEB: THE BENTHOS AND HIGHER TROPHIC LEVELS

The Ross Sea benthos is among the most diverse in the Southern Ocean (Clarke & Johnston 2003). The reasons for this richness likely stem from the diversity of habitats as determined by depth and currents (Barry et al. 2003). In addition, the northwest corner of the shelf, unlike other Antarctic shelves, was ice free during past glaciations (summarized in Ainley et al. 2010b). Barry et al. (2003) suggested that, other than depth, the most important factor controlling benthic diversity is the near-bottom current flow, which regulates the food supply. Bottom depths also vary substantially in the Ross Sea owing to the presence of troughs and banks, and the shallower areas are often devoid of soft sediments, which in turn restrict the types of fauna present. Conversely, the troughs are sites of active sediment biodeposition and are covered with organic-rich muds and diatomaceous oozes (Barry et al. 2003). In general, the amount of fine-grained sediment increases with depth, as does the organic matter concentration (Smith et al. 2007). Antarctic benthic communities, including those of the Ross Sea, are considered to be among the most ecologically stable in the world, characterized by a marked resistance to change in composition and high levels of biomass and endemism (Clarke & Johnston 2003). Many species show a circumpolar distribution, are eurybathic, and have slow growth rates coupled with an extraordinary longevity (Smith et al. 2007).

Notothenioids (a perch-like group) dominate the Ross Sea fish fauna, with the remainder being mostly liparids (snailfishes) and zoarcids; macrourids (eelpouts) occur in deeper waters of the slope (Eastman 2005, Ainley & Pauly 2013). Several species are endemic to the Ross Sea (Ainley et al. 2010b). Most Ross Sea fish are benthic, epibenthic, or cryopelagic (within the sea-ice brash), with the exception of two very important species, both notothenioids: Antarctic toothfish (*Dissostichus mawsoni*; ~2 m long, >100 kg as adults) and Antarctic silverfish. These two species inhabit the midlevel and surface waters as adults, employing fat and reduced skeletal elements to achieve buoyancy; young toothfish (<120 cm) are benthic. Silverfish are a major prey of almost every upper-trophic-level predator over the shelf, including toothfish, which in turn are fed upon by Weddell seals and killer whales (La Mesa & Eastman 2011). Silverfish may be the most important consumer of crystal krill.

The upper-trophic-level mesopredators in the Ross Sea are extraordinarily abundant, and include toothfish, Adélie and emperor penguins (*Pygoscelis adeliae* and *Aptenodytes forsteri*, respectively), seals, and cetaceans (Ballard et al. 2012). As an example of abundance, Adélie and emperor penguins in the Ross Sea represent 38% and 25% of their respective global populations, and Antarctic petrels (*Thalassoica antarctica*) in the Ross Sea represent 40% of theirs; seal and cetacean abundance is noteworthy as well (Ballard et al. 2012). The high diversity and abundance are maintained by a mosaic of habitats, defined vertically by depth of foraging and horizontally by sea-ice affinity and seasonal faunal movements (Ballard et al. 2012). The distribution of penguin colonies is well known (**Figure 6**). Squid, fish, emperor penguins, and Weddell (*Leptonychotes weddellii*) and crabeater (*Lobodon carcinophagus*) seals remain in the Ross Sea throughout the year; the other predators are present only from October to March. During spring and summer, Weddell seals and the two penguin species remain close to the coast for breeding, but the remaining species use various parts of the continental shelf, with habitats defined largely by sea ice.

FUTURE CHANGES IN THE ROSS SEA

Ice distributions in the Ross Sea are currently increasing by 5% per decade and more than balance the decreases observed in the Amundsen-Bellingshausen sector (Comiso et al. 2011, Stammerjohn et al. 2012). The ice-free period in the Ross Sea polynya has also decreased significantly, by more than two months (Stammerjohn et al. 2012), suggesting that the mean continental shelf productivity has also decreased substantially since 1980. Sizable interannual variability in production and export has been observed (Arrigo et al. 2003; Arrigo & van Dijken 2004; Smith et al. 2006, 2011a,b), and although annual production is clearly a function of ice, production at smaller spatial scales is also influenced by iron availability and vertical stratification (e.g., Long et al. 2011). All of these variables—ice distribution, iron concentrations, and vertical stratification—will change in the coming century, but the extent and direction of change are difficult to predict.

The westerly winds that encircle Antarctica have already been observed to be intensifying and moving southward (Marshall 2003), and the cold winds flowing northward over the Ross Sea have increased (Turner et al. 2009). At least for the next few decades, this is projected to lead to continued increases in sea-ice extent and ice season in the Ross Sea (Stammerjohn et al. 2012). However, air temperatures over the Ross Sea are predicted to increase substantially in the next century (by approximately 3°C by 2100; Bracegirdle & Stephenson 2012), leading to decreases in the local sea-ice extent and ice season. In addition, substantial freshening of the waters in several locations around the Ross Sea will likely continue (Jacobs et al. 2002, Jacobs & Giulivi 2010) as a result of advection of reduced-salinity waters from the Amundsen Sea, which itself is generated by increased basal ice shelf melting there. However, these changes also have interactive effects that are difficult to predict. For example, reduced salinity might enhance stratification, but increased winds and decreased ice cover may serve to decrease that stratification (similar to the Antarctic Peninsula region; Montes-Hugo et al. 2009).

Such changes would have substantial biological and ecological impacts. Primary production would increase substantially, given the overall control on annual timescales by ice. Phytoplankton composition would also change markedly, with the contribution of *P. antarctica* to total assemblage biomass decreasing and that of diatoms increasing. As diatoms are considered to be primary food sources for zooplankton such as copepods and crystal krill, their biomass may increase as well. Owing to their life history limitations and requirement for larval development at great depth, Antarctic krill would be unable to invade much of the continental shelf (Hofmann & Lascara 2000). Antarctic silverfish may increase in importance within the food web, as they spawn in winter in association with ice, forage as larvae and juveniles on copepods, and forage as adults on crystal krill. Higher-trophic-level predators (e.g., Adélie penguins, emperor penguins, and baleen

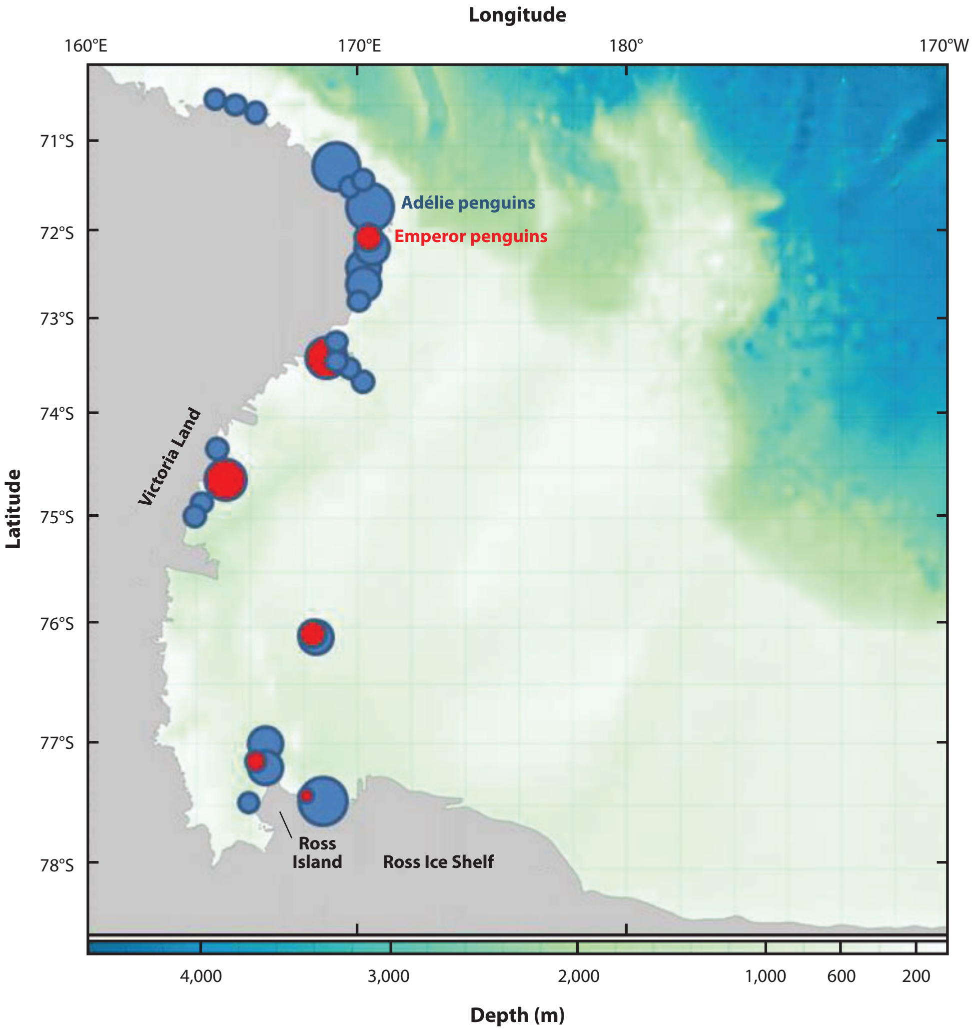

Figure 6

Distribution of Adélie and emperor penguins in the Ross Sea (modeled after Ainley et al. 2010c). An additional Emperor penguin colony is at Cape Colbeck (154°W; not shown). The sizes of the circles indicate the relative abundance of penguins. The assemblage of apex predators is sustained largely by foraging on three species: silverfish, crystal krill, and Antarctic krill (Pinkerton et al. 2010). There appears to be extreme competition for prey (e.g., Ainley et al. 2006), although it is decreased by vertical and spatial segregation during foraging. The apex predator is the ecotype-B orca (*Orca orcinus*), which feeds largely on seals and possibly emperor penguins. Slightly below orcas in the trophic pyramid are leopard seals (*Hydrurga leptonyx*), which are significant predators on seals and penguins. The ecotype-C killer whale (Ross Sea killer whale, likely a distinct species) and the Weddell seal are important predators of toothfish (Ainley & Siniff 2009).

whales) should respond positively to the increased availability of fish and krill. Regardless of the food web alterations, changes in the primary physical control—the distribution of ice—will bring about severe ecological disruptions.

The upper trophic levels have undergone noticeable changes over the past several decades. The number of Adélie penguins in the Ross Sea increased during the early 1970s in response to the reductions in stocks of Antarctic minke whales (*Balaenoptera bonaerensis*), a trophic competitor. They then decreased slightly as the whale population recovered, and later began to slowly increase again (Ainley et al. 2005, 2010a). Owing to increasing winds and the more persistent presence of coastal open water in contrast to the trends over the greater continental shelf, the reduced ice areas along the coast have increased in duration in nonsummer months (figure 3*b* in Parkinson 2002), leading to increased ice production (Comiso et al. 2011), enhanced penguin foraging efficiency, and increased breeding success and abundance (Ainley et al. 2010a). During the past decade, penguin colonies of the southern Ross Sea have begun to increase rapidly (LaRue et al. 2013), most likely as a result of increased silverfish availability (Ainley & Pauly 2013).

SUMMARY POINTS

1. The Ross Sea is largely unimpacted by direct human effects such as fishing but is being modified by changes in atmospheric composition (stratospheric ozone and greenhouse gases), which lead to changes in winds and altered temperatures. Such changes will continue in the coming decades, leading to profound ecological changes.
2. Ice concentrations have increased rapidly in the Ross Sea sector and are responsible for the net increase in ice concentrations found over the entire Southern Ocean. These increases have resulted in a greatly reduced open-ice season (by two months) in the Ross Sea polynya.
3. The circulation of the Ross Sea is well known and controlled largely by bathymetry. Important features such as dense water formation are forced by the large range in the seasonal heat budget. Significant freshening of waters is occurring, possibly through the advection of low-salinity water from the east.
4. The Ross Sea primary productivity is as great as any in the Antarctic, making it an important regional carbon sink. The primary control on annual cycles is irradiance, and in the summer the productivity is influenced by iron inputs and availability. Phytoplankton assemblages are dominated by the seasonal progression from *Phaeocystis antarctica* to diatoms, which structures the food web and trophic dynamics.
5. Large abundances of apex predators occur in the Ross Sea; conversely, zooplankton biomass appears to be lower than that of other regions in the Antarctic. The sizes of colonies of selected species are extraordinary and are the largest of any in the world.
6. The benthic assemblages are diverse and stable, and exhibit characteristics found throughout the Antarctic (e.g., large size, long life spans, and low growth rates) as well as a relatively high degree of endemism. Benthic biomass is largely controlled by food availability.
7. Future changes in the Ross Sea will be driven by global increases in atmospheric temperatures (projected to rise by approximately 3°C over the Ross Sea by 2100), as well as the behavior of the ozone hole. The resulting changes in air temperatures, winds, freshwater inputs, and amounts of offshore heat inputs will likely reduce summer ice cover substantially. Such changes will result in altered phytoplankton composition and production, changed krill availability, and modified apex predator abundance and reproductive success.

FUTURE ISSUES

1. The Ross Sea has been changing as fast as any region on Earth during the past four decades and will continue to do so in the coming century (albeit in a different direction). What will the ecosystem impacts be of the predicted changes in ice cover and atmospheric temperatures? Will the "natural" trophic structure and interactions be substantially modified?
2. Will the increased CO_2 concentrations and decreased pH of seawater impact all levels of the food web and benthos? Will the region remain a significant regional carbon sink?
3. To what extent will industrial fishing alter the food web of the entire region? How will those changes compare in magnitude with those of climate change?
4. How will the changes in physical forcing alter the formation of deep water and Ice Shelf Water in the coming century?
5. What will the full impacts of the recovery of the Antarctic ozone concentrations be on the oceanography and ecology of the Ross Sea continental shelf?

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Errata

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