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THE ROSS SEA IN A SEA OF CHANGE

BY WALKER O. SMITH JR., PETER N. SEDWICK, KEVIN R. ARRIGO,
DAVID G. AINLEY, AND ALEJANDRO H. ORSI

ABSTRACT. The Ross Sea, the most productive region in the Antarctic, reaches farther south than any body of water in the world. While its food web is relatively intact, its oceanography, biogeochemistry, and sea ice coverage have been changing dramatically, and likely will continue to do so in the future. Sea ice cover and persistence have been increasing, in contrast to the Amundsen-Bellinghshausen sector, which has resulted in reduced open water duration for its biota. Models predict that as the ozone hole recovers, ice cover will begin to diminish. Currents on the continental shelf will likely change in the coming century, with a projected intensification of flow leading to altered deep ocean ventilation. Such changes in ice and circulation will lead to altered plankton distributions and composition, but it is difficult at present to predict the nature of these changes. Iron and irradiance play central roles in regulating phytoplankton production in the Ross Sea, but the impacts of oceanographic changes on the biogeochemistry of iron are unclear. Unlike other Southern Ocean regions, where continental shelves are very narrow and Antarctic krill dominates the herbivorous fauna, the broad shelf of the Ross Sea is dominated by crystal krill and silverfish, which are the major prey items for higher trophic levels. At present, the Ross Sea is considered to be one of the most species-rich areas of the Southern Ocean and a biodiversity “hotspot” due to its heterogeneous habitats. Despite being among the best-studied regions in the entire Southern Ocean, accurate predictions of the impacts of climate change on the oceanography and ecology of the Ross Sea remain fraught with uncertainty.

INTRODUCTION

The Ross Sea, a large Antarctic embayment south of New Zealand, is an unusual region lying within the larger domain that is the Southern Ocean. It lies to the north of Earth's largest ice shelf, the Ross Ice Shelf (RIS), which covers an area of 520,000 km², with an average thickness of 370 m. The outer portion of the ice shelf floats on seawater that is modified during its transit beneath the shelf, and that mixes and exchanges with waters to the north over the continental shelf. The continental shelf north of the RIS covers an area of 466,000 km², with an average depth of ~ 530 m, and the shelf break occurs at ~ 700 m depth (Figure 1). However, of importance to the biota, small portions of the Ross Sea are shallower than 200 m (see Box 1). Numerous troughs running roughly in a north-south direction, carved by ice streams during past glacial periods, traverse the shelf. These troughs, and the intervening banks, influence regional circulation, sedimentation, and biogeochemical and biological processes. Unlike other Antarctic continental shelves, the northwest portion of the Ross Sea shelf was not glaciated during the previous glacial maxima, which is an important characteristic with regard to the composition of regional biota.

Following James Clark Ross's discovery of his namesake sea in 1841, extensive collections of its benthic biota were obtained by subsequent British "heroic" expeditions; indeed, the Ross Sea is the type locality for more than 400 marine species. Modern scientific investigations of the Ross Sea were initiated during the 1957 International Geophysical Year, and were continued through the 1980s by repeated cruises undertaken

by the US Navy and Coast Guard. Upon launch of the Research Vessel Icebreaker *Nathaniel B. Palmer* in 1992, scientific investigations in the Ross Sea greatly expanded in frequency, duration, and diversity. As a result, today the Ross Sea is one of the most intensively studied regions in the Southern Ocean, with investigations of geology, sedimentology, glaciology, oceanography, and marine biology of a number of trophic levels. The Ross Sea is also considered to be the least human impacted continental shelf on Earth, at least in terms of its biota (Halpern et al., 2008), displaying pristine ecological characteristics that are no longer observed in other shelf environments. In addition to direct observations, substantial advances in our understanding of the Ross Sea have been gained from satellite observations and deployments of in situ instrumentation.

Studies of the Ross Sea have greatly benefited from the presence of McMurdo Station, located adjacent to McMurdo

Sound on Ross Island. This station is the focus of much regional research and is the staging location for the supply of other bases and camps on the continent, including the South Pole. As such, supply vessels must reach McMurdo Station every summer, which has facilitated the entrance of research vessels into the area. Facilities at the station also support ocean-going research programs, as well as ocean research activities that make use of holes drilled in seasonal and semipermanent fast ice adjacent to the station, where water depths immediately offshore exceed 400 m. Additional research activities are being conducted from the Italian research base Mario Zucchelli, located in Terra Nova Bay 280 km to the north, and at Scott Base, operated by New Zealand.

In this article, we review the essential features of Ross Sea oceanography, including circulation and water mass characteristics, biogeochemical cycling, phytoplankton dynamics, and the

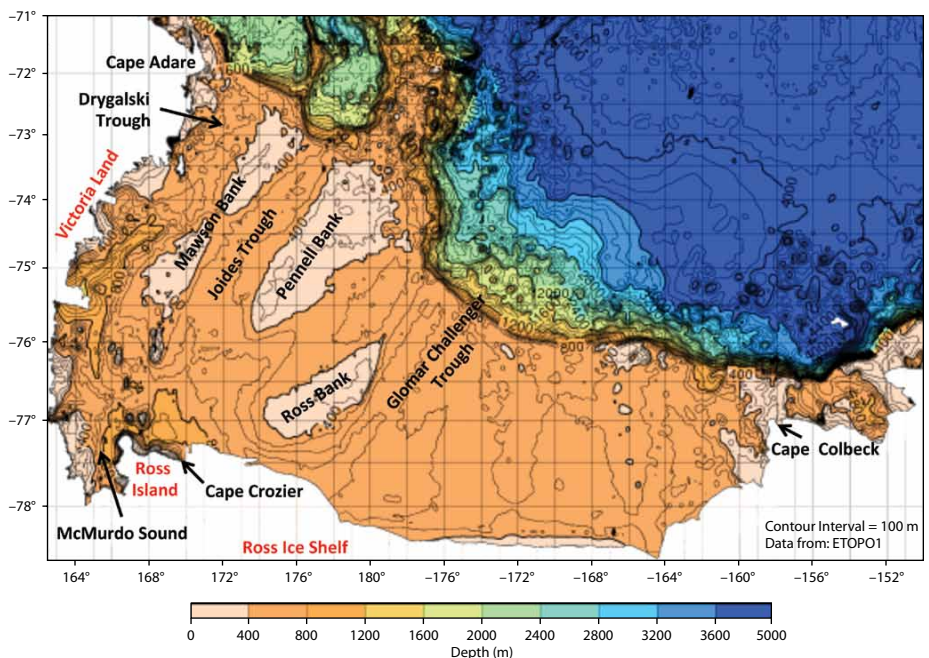


Figure 1. Map of Ross Sea bathymetry.

BOX 1 | ROSS SEA CONTINENTAL SHELF FEATURES

Summary of features of the Ross Sea continental shelf based on the bathymetry used in Orsi and Wiederwohl (2009), where the Ross Sea continental shelf is defined by the 700 m isobath leading to the continental slope and north of the Ross Ice shelf.

Area: $46.61 \times 10^4 \text{ km}^2$ (constituting 18% of the entire shelf region around Antarctica)

Volume: $24.75 \times 10^4 \text{ km}^3$

Areas (percentages) of Ross Sea continental shelf with water depths less than:

600 m	$31.23 \times 10^4 \text{ km}^2$	67.0%
500 m	$17.08 \times 10^4 \text{ km}^2$	36.6%
400 m	$1.82 \times 10^4 \text{ km}^2$	3.90%
300 m	$1.11 \times 10^4 \text{ km}^2$	2.37%
200 m	$0.56 \times 10^4 \text{ km}^2$	1.20%

ecology of higher trophic levels. We also discuss evidence of contemporary environmental change in the Ross Sea and predict that future changes are likely to be substantial within this century.

PHYSICAL OCEANOGRAPHY

Ice concentrations in the Ross Sea decrease rapidly in austral spring (Figure 2). Small areas of reduced ice concentrations are located throughout the winter near the Ross Ice Shelf, when ice is driven northward by strong winds off the ice shelf. This process continues through November, and as the solar heat input increases, open waters expand northward. Generally, this open water extends completely off the shelf during summer, and the open water region is contiguous with the open Pacific. Sea ice covers the Ross Sea quickly in March, and continues to thicken and form throughout winter.

The stratification of the Ross Gyre, a large cyclonic gyre to the north of the Ross Sea, is dominated by a $\sim 2,500 \text{ m}$ mid-depth layer of relatively saline and warm ($> 2^\circ\text{C}$) Circumpolar Deep Water

drawn from the bypassing Antarctic Circumpolar Current farther to the east (Figure 3; Orsi and Whitworth, 2005). Thereafter, the Antarctic Circumpolar Current hugs the continental slope of the Amundsen-Bellingshausen Seas (Orsi et al., 1995), allowing the uninterrupted surge of Circumpolar Deep Water ($> 1^\circ\text{C}$) over the bottom layer of the shelf (Jacobs et al., 1996). That is not the case over the $\sim 466,000 \text{ km}^2$ of Ross Sea shelf, where only thin layers of upwelled deep water are observed at intermediate depths (Orsi and Wiederwohl, 2009). However, on-shelf transport of Circumpolar Deep Water is critical to the heat and salt budgets, regional sea ice cycle, and primary productivity of the Ross Sea, as it is the oceanic source of heat and nutrients (Smith et al., 2007).

Unlike in the Southeast Pacific, the major dynamical obstacle to rising waters is the abrupt poleward-diving of isopycnals found over the Ross Sea upper continental slope (Ainley and Jacobs, 1981), and the westward sweep near the shelf break of the Slope Current that carries a thick layer of cold and fresh Antarctic Surface Water (Whitworth et al., 1998).

Antarctic Surface Water enters the Ross Sea around Cape Colbeck as part of a narrow coastal flow that, in addition to importing sea ice and icebergs, also incorporates continental meltwater derived from sea ice-air interactions farther upstream (Jacobs et al., 1985). This strong boundary current continues westward along the RIS, bringing low-salinity surface waters to an area that in winter develops the giant ($25,000 \text{ km}^2$) Ross Sea Polynya, the most active ($390 \text{ km}^3 \text{ yr}^{-1}$) “sea ice factory” around Antarctica. The much smaller ($\sim 3,000 \text{ km}^2$) Terra Nova Bay Polynya off Victoria Land generates considerably less ice ($59.2 \text{ km}^3 \text{ yr}^{-1}$; Martin et al., 2007). Atmospheric cooling sustains sea ice formation, increasing sea surface salinity and producing the dense Shelf Water that fills most of the continental shelf bottom layer, including under the RIS. The product of topographically controlled circulation and progressive basal melting emerges to the north at a few locations and at mid-depths, as less-saline Ice Shelf Water with a depressed ($< -2^\circ\text{C}$) freezing point. Mostly produced within the Ross Sea

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Polynya, the Shelf Water volume and salinity decrease seaward and to the east. Its circulation involves northward flow against the western flank of troughs, and, upon reaching the seaward sills, Shelf Water increases the background tilt of isopycnals, thus facilitating inflow of Modified Circumpolar Deep Water ($> 0.5^{\circ}\text{C}$) available at the base of the Slope Front (Ainley and Jacobs, 1981).

Poleward extensions of Modified Circumpolar Deep Water are apparent along and over the western side of banks (Orsi and Wiederwohl, 2009). After gradual attenuation and thinning along a ~ 300 km transit toward the RIS, the most conspicuous and persistent of these inflows appears to enter the sub-ice cavity near 173°W as a subsurface “warm” ($> -1.5^{\circ}\text{C}$) core (Jacobs and Giulivi, 1998). Across the wider western shelf, shallower Modified Circumpolar Deep Water inflows mix further with surface waters, bringing the nutrients that support observed high levels of primary productivity (Smith et al., 2007). Enhanced mixing of carbon-rich continental waters with Modified Circumpolar Deep Water at the Slope Front produces a variety of dense waters that, upon sinking down the continental slope, effectively ventilate adjacent ocean basins. In the Ross Sea, the export of cold Antarctic Bottom Water types ($< -1^{\circ}\text{C}$) is restricted to the slope regions off Drygalski, Joides, and Glomar Challenger Troughs, and supplies the abyssal layer offshore (Orsi et al., 1999; Gordon et al., 2004). The lighter mixtures ($< 0.5^{\circ}\text{C}$) only descend to mid-depths along much of the Slope Front, and freshen the voluminous Circumpolar Deep Water layer of the Ross Gyre. About 30% of the combined input of Shelf Water and Antarctic Surface Water to the Antarctic Bottom

Water and Circumpolar Deep Water layers is attributable to Ross Sea exports (Orsi et al., 2002).

BIOGEOCHEMICAL CYCLES

Waters over the Ross Sea continental shelf are among the most productive in the Southern Ocean, sustaining annual primary production of $\text{ca. } 23.4 \pm 9.98 \text{ Tg C yr}^{-1}$ (Arrigo et al., 2008a). Despite high rates of primary

production, macronutrients (nitrate, phosphate, and silicate) are rarely depleted from surface waters during the growing season; thus, the region may be described as a “high nutrient, high chlorophyll” regime (Smith and Gordon, 1997; Arrigo et al., 2008a). Moreover, primary production in the southern Ross Sea appears to be characterized by relatively high export efficiencies, perhaps facilitated by the formation of organic

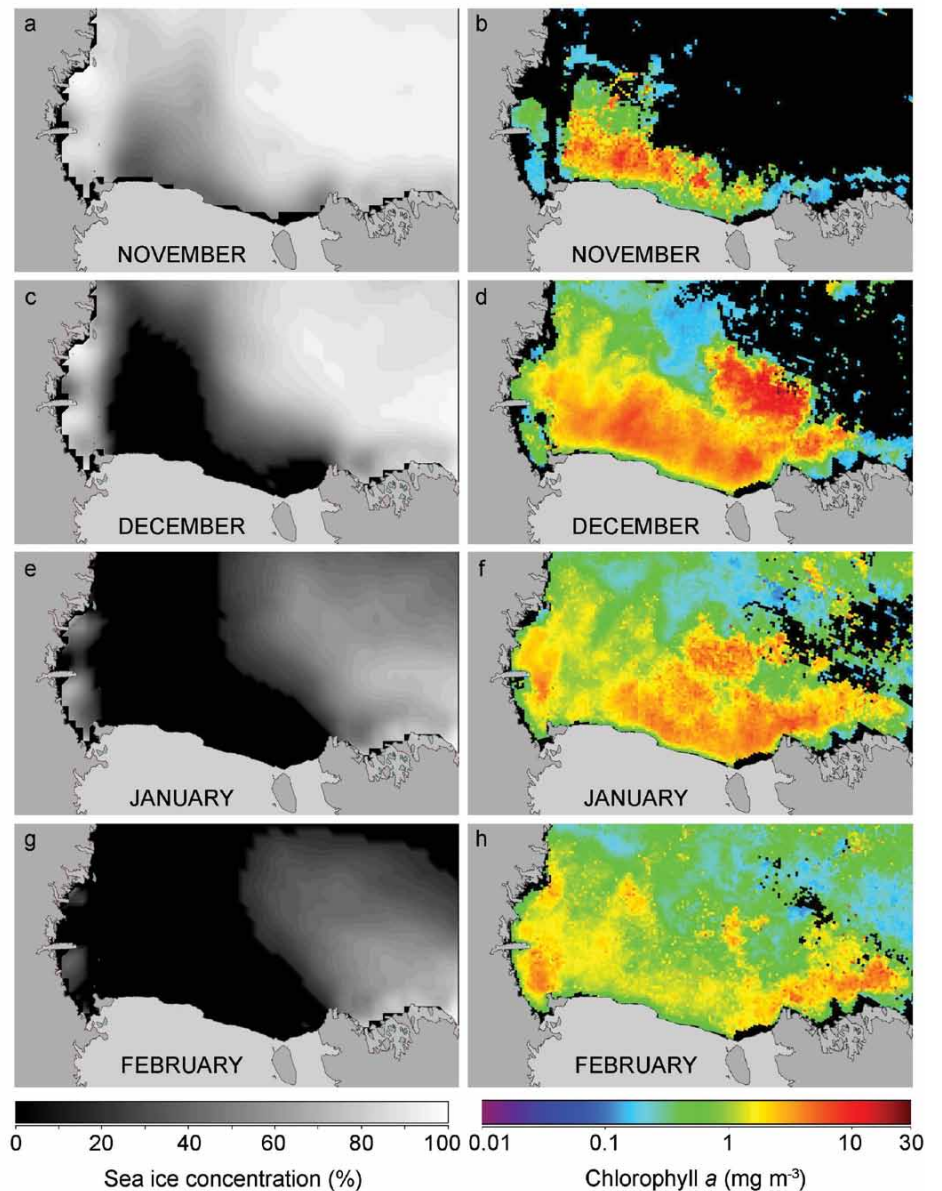


Figure 2. Mean ice concentrations in the Ross Sea during November, December, January, and February (a,c,e,g) and composite chlorophyll *a* concentrations during the same months (b,d,f,h), using data from both from the SeaWiFS and MODIS satellites during 1997–2011. Black represents ice or cloud cover.

aggregates (Asper and Smith, 2003), with estimated f -ratios of around 50% (Asper and Smith, 1999). (The f -ratio is the ratio of nitrate-based production to total production.) These high export efficiencies, and the importance of the Ross Sea as an area of deepwater formation (see earlier Physical Oceanography section), suggest that the Ross Sea plays a significant role in the Southern Ocean carbon cycle, specifically by serving as a major regional oceanic CO₂ sink (Arrigo et al., 2008b).

The high rates of primary and export

production in the Ross Sea also assign the region an important role in the regional cycling of other bioelements. Phytoplankton composition has been shown to affect the relative concentrations of dissolved inorganic carbon, nitrogen, and phosphorus in surface waters (Arrigo et al., 1999; Sweeney et al., 2000). In turn, these factors influence the carbon and nutrient characteristics of the shelf waters that contribute to oceanic deep waters (Orsi and Weiderwohl, 2009), and, ultimately, to

the air-sea exchange of CO₂. The Ross Sea also constitutes a significant regional sink for silicic acid as a result of the preferential burial of diatom-derived opal, relative to organic carbon, in sediments that accumulate on the inner shelf (Nelson et al., 1996). Finally, the Ross Sea continental shelf is thought to be a major source of the climatically active compound dimethylsulfide to the atmosphere (DiTullio and Smith, 1995). This organic sulfur compound is known to be produced by the haptophyte *Phaeocystis antarctica*, which is a major phytoplankton species in the Ross Sea (see next section on Plankton Dynamics).

There is an important critical nexus in the cycling of each of these bioelements in the Ross Sea with the supply and cycling of the essential micronutrient iron. It is now generally accepted that low dissolved iron concentrations limit phytoplankton growth rates and biomass over much of the Southern Ocean (Boyd, 2002), particularly in the remote surface waters of the Antarctic Circumpolar Current, which exhibit chronic iron deficiency (Figure 4). Although there are a number of potential sources of iron to surface waters of the Ross Sea, including seafloor sediments, sea ice and glacial ice, Modified Circumpolar Deep Water intrusions, and mineral aerosols (Sedwick and DiTullio, 1997), there is ample evidence that availability of iron limits primary production in the Ross Sea during the growing season. Indeed, one of the first examples of “iron limitation” of phytoplankton growth in the Southern Ocean was provided by shipboard experiments in the Ross Sea (Martin et al., 1990). Results of further field and modeling studies indicated that the Ross Sea is a seasonally iron-limited ecosystem, whereby a “winter reserve”

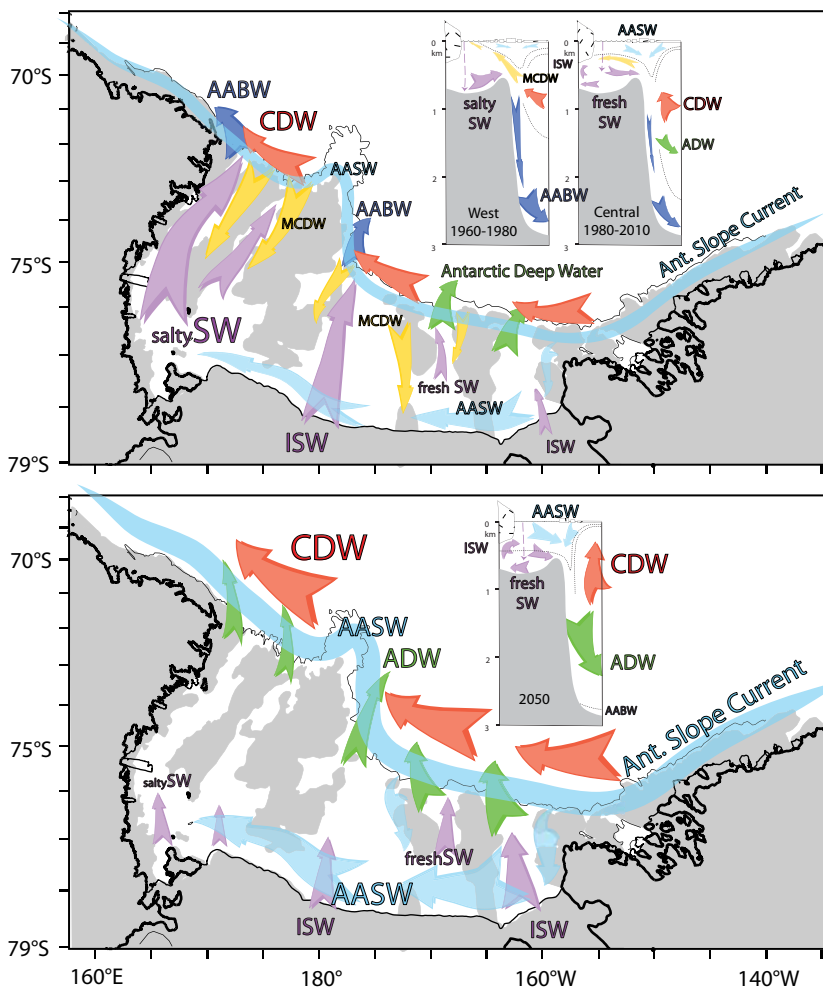


Figure 3. Potential changes in Ross Sea circulation and stratification. The upper panel illustrates the conditions observed during the past 50 years; the lower panel shows potential intensification of flow and air-sea-ice interactions leading to an alternative mode of deep ocean ventilation during the next century. Arrow width indicates the relative strength of each flow, and color represents individual water masses. Antarctic Surface Water (AASW): light blue. Shelf Water (SW): purple. Modified Circumpolar Deep Water (MCDW): orange. Circumpolar Deep Water (CDW): red. New Antarctic Deep Water: green. New Antarctic Bottom Water: dark blue.

of dissolved iron is depleted from surface waters during the growing season (Sedwick et al., 2000; Coale et al., 2003). However, more recent observations suggest that iron limitation can develop rapidly during the late spring, implying that continued growth and biomass accumulation during the summer months requires inputs of “new” iron to surface waters during summer (Peloquin and Smith, 2007; Sedwick et al., 2011).

PLANKTON DYNAMICS

Studies of phytoplankton in the Ross Sea have been as intensive as anywhere in the Southern Ocean. Smith and Gordon (1997) found Ross Sea biomass to be elevated by mid-November, and growth was proceeding rapidly by that time; they extrapolated back in time to suggest that growth was 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, those data also confirm that chlorophyll begins to increase in November (Arrigo and van Dijken,

2004), when mixed layers in the Ross Sea shoal to depths that provide sufficient irradiance for growth. This pattern is striking, as few other Southern Ocean regions, even those some 1,600 km north of the Ross Sea, bloom so early in the austral growing season. High, early season growth rates, coupled with low rates of grazing and sinking losses, are responsible for the large accumulation of biomass that is repeatedly observed in the Ross Sea in late December.

The temporal dynamics of phytoplankton assemblages in the Ross Sea are well known. The dominance of *Phaeocystis antarctica* (Smith and Gordon, 1997; Arrigo et al., 1999) in the spring biomass is generally explained by its ability to photosynthesize under the reduced irradiances found in spring (Smith et al., 2007). Surface mixed layers in spring are ~ 50 m, while those in summer can be less than 10 m. Chlorophyll concentrations in *P. antarctica* blooms can exceed $15 \mu\text{g L}^{-1}$, but generally rapidly decrease 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 (Smith et al., 2011b). The life cycle of *Phaeocystis* involves both solitary and colonial stages, and seasonal changes in the relative numbers of each have been observed (Smith et al., 2007). After the 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 associated with sea- and glacial-ice melt, and with other groups (dinoflagellates, cryptomonads, silicoflagellates) appearing in isolated locations (Arrigo et al., 1999). While this pattern is relatively predictable, significant interannual variations in the contribution to total biomass have been noted (Smith et al., 2006, 2011a).

This regular seasonal succession 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 ratios of 76:12:1 (Arrigo et al., 2000).

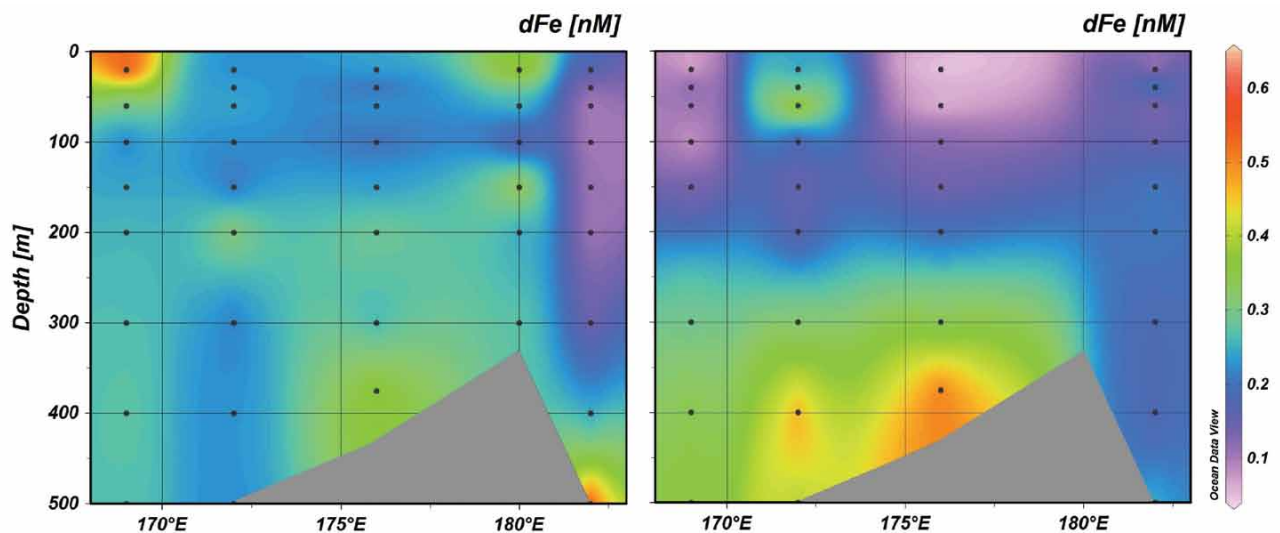


Figure 4. Interpolated zonal sections of dissolved iron (dFe) concentration in the Ross Sea Polynya along $76^{\circ}30'S$ in spring (October to November 1996, left panel) and summer (January to February 1997, right panel), showing the seasonal drawdown of dissolved iron in the upper water column. The shallow area is Ross Bank. Data are replotted from Coale et al. (2005).

Furthermore, these ratios are retained in material that sinks to depth, thus potentially impacting deepwater concentrations of nutrients and sediments (Dunbar et al., 2003). Additionally, *P. antarctica* is thought to be largely ungrazed by most mesozooplankton (Tagliabue and Arrigo, 2003), although pteropods may consume both solitary cells and colonies (Elliott et al., 2009). In contrast, diatoms are generally considered to be grazed at significant rates by zooplankton and incorporated into rapidly sinking fecal pellets, hence minimizing remineralization in the water column and favoring their export to the benthos.

Phytoplankton growth, particularly that of diatoms, has been experimentally shown to be iron limited in summer under conditions of high irradiance (Sedwick and DiTullio, 1997; Sedwick et al., 2000). Given the predictability of the seasonal assemblage pattern, as well as the low dissolved iron concentrations in surface waters during much of the growing season (Sedwick et al., 2011), and the likely small differences in taxon-specific iron requirements (Garcia et al., 2009), it appears that seasonal changes in the assemblages may involve interactions between irradiance and iron (Boyd, 2002). Peloquin and Smith (2007) also noted the occurrence of substantial diatomaceous blooms after the decline of *P. antarctica*, which implies additions of iron to the euphotic zone, although the mechanism for increasing iron remains unknown. Macronutrients (N, P, Si) rarely drop to limiting levels; indeed, seasonal nitrate removal is generally 15 μM , or about half of the winter concentrations.

Estimates of primary productivity have been based on both in situ measurements and satellite-based bio-optical

models. The latter have the advantage of increased temporal and spatial resolution, and are likely the most accurate means of assessing shelf-wide productivity. Arrigo et al. (2008a) estimate that the mean net primary productivity for the entire Ross Sea sector of the Southern Ocean is 69 $\text{g C m}^{-2} \text{ yr}^{-1}$, which is less than field-based extrapolations and earlier remote-sensing estimates but accurately reflects substantial variations in both space and time over this large oceanic region. Annual net primary production on the Ross Sea continental shelf is considerably higher, averaging 179 $\text{g C m}^{-2} \text{ yr}^{-1}$. Such high productivity and export efficiency gives rise to large air-sea gradients in $p\text{CO}_2$, with seawater CO_2 levels often dropping below 200 μatm in summer. Recent model simulations suggest that the Ross Sea continental shelf is responsible on average for more than 25% of the estimated total CO_2 uptake of the entire Southern Ocean (Arrigo et al., 2008b).

Annual net primary production in the Southern Ocean is influenced by large-scale climate variations (Lovenduski and 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 SAM phase, 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. SAM's impact is particularly strong in the Ross Sea, where it can explain 73% of the variance in sea surface temperatures, with cooler waters being associated with positive SAM phases (Arrigo et al., 2008a). More

important, SAM explains > 64% of the interannual variance in chlorophyll *a* concentrations on the Ross Sea continental shelf, with the positive phase of SAM associated with increased phytoplankton biomass (Arrigo et al., 2008a). Westerly winds are projected to increase in coming decades (le Quéré et al., 2007), suggesting that phytoplankton biomass on the Ross Sea shelf could increase in the future, albeit constrained ultimately by iron availability.

Finally, micro- and mesozooplankton in the Ross Sea have received relatively little attention compared to the temporal and spatial scales of phytoplankton studies in the region. Caron et al. (2000) conducted dilution experiments to assess microzooplankton grazing, but most (83%) failed to demonstrate significant ingestion rates. Microzooplankton biomass has been quantified (Dennett et al., 2001), but microzooplankton grazing's impact on biogeochemical cycling remains unclear. Investigations of mesozooplankton abundance and feeding are similarly limited to defined regions. Deibel and Daly (2007) concluded that overall biomass of mesozooplankton in the Ross Sea, despite high regional primary production, was ~ 15% that of the Scotia Sea. Tagliabue and Arrigo (2003) suggested that Ross Sea zooplankton were 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 comprise 100% of the flux (Smith et al., 2011b), suggesting that mesozooplankton ingestion in the surface waters can at times be substantial. Ainley et al. (2006) proposed that the low mesozooplankton abundance was the result of a trophic

cascade centered around the unusually high abundance of meso- and apex predators, many of which feed heavily on krill or on small fish that feed principally on krill. The resulting paucity of krill leads to reduced grazing on diatoms. Antarctic krill (*Euphausia superba*) are largely absent from the inner continental shelf, but occur in the outer portions of troughs and near the shelf break; conversely, the reciprocal pattern is seen in crystal krill (*E. crystallorophias*), which occur throughout the inner shelf region (Sala et al., 2002).

HIGHER TROPHIC LEVELS AND ECOLOGY

The Ross Sea benthic biota is considered to be one of the most species-rich in the Southern Ocean and a biodiversity “hotspot” (Clarke and Johnston, 2003). Of the few thousand species known from the Antarctic, more than 400 were first described from the Ross Sea, 40 of which are endemic, including mainly fish and invertebrates (Ainley et al., 2010a). The reasons for this richness likely stem from the diversity of habitats as defined 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. On the basis of bottom samples, Bullivant (1967) divided the fauna broadly into five communities. The most distinctive of them was the Pennell Bank assemblage and the assemblages around Ross Island; the most widespread were those of the deep shelf (over the deeper parts of the banks) and those in the muds of the troughs. Barry et al. (2003) suggest that the most important factor, other than depth, controlling benthic diversity is the near-bottom current flow, which regulates the food supply.

The fish fauna of the Ross Sea is composed of 95 species from 16 families and is dominated by notothenioids (a perch-like group; 64% of species), with the remainder being mostly liparids (snailfishes) and zoarcids (eelpouts; Eastman, 2005). 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*) and Antarctic silverfish (*Pleuragramma antarcticum*). These two species, despite their lack of swim bladders, inhabit the mid- to surface waters as adults; young toothfish (< 100 cm) are benthic. The extremely large toothfish (~2 m, > 100 kg as adults) have been called the “sharks of the Antarctic,” owing to their large size and voracious piscine diet, and the very abundant silverfish are known as “the herring of the Antarctic,” owing to their abundance and loose schooling behavior. Silverfish are a major prey of almost every upper trophic level predator over the shelf, including toothfish. Weddell seals and Ross Sea orcas feed upon the toothfish.

The upper trophic level predators in the Ross Sea are abundant and diverse, composed of 16 major species, including one fish (toothfish), Adélie and emperor penguins (*Pygoscelis adeliae*, *Aptenodytes forsteri*), seals, and cetaceans (Ballard et al., 2011). High proportions of world populations for several of these species reside in the Ross Sea (Table 1). The high diversity and abundance is maintained by a mosaic of habitats, defined vertically by depth of foraging and horizontally by sea ice affinity and seasonal movements, as well as a temporal component (Ballard et al., 2011). Thus, the distribution of apex predators, such as penguins, is both spatially and temporally

nonuniform (Figure 5). The squid, fish, emperor penguins, and Weddell (*Leptonychotes weddellii*) and crabeater (*Lobodon carcinophagus*) seals presumably remain in the Ross Sea year-round; the remainder are present only during October to March. During spring/summer, Weddell seals and the two penguin species remain close to the coast for breeding, and the squid is found along the slope; the remaining species use various parts of the continental shelf with habitats largely defined by sea ice, the marginal ice zone, polynyas, and other restricted environments.

This assemblage of apex and meso-predators is largely sustained by foraging on three species: silverfish and crystal krill over the shelf, and Antarctic krill over the slope (Ballard et al., 2011). Hence, close coupling is observed at this level of the food web. The vertical and spatial dimensions of foraging lessen the extreme competition for prey. The apex predator in the system 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 can be eaten by killer whales, but are significant predators on seals and penguins.

THE FUTURE

Evidence of significant annual, interannual, and decadal variability in Ross Sea water properties and sea ice characteristics emphasizes the region’s sensitivity to changing oceanographic and atmospheric forcing. During the winter of 2002, the Ross Sea shelf was anomalously covered with sea ice due to the presence of a grounded, massive iceberg; development of the Ross Sea Polynya was much suppressed (Martin et al., 2007); and the

following summer showed a record maximum of perennial ice cover (Comiso et al., 2011). Extensive hydrography collected that summer, while the massive tabular iceberg C-19 was still grounded, showed the rapid propagation of a high-salinity anomaly from Shelf Water in the Drygalski Trough to Antarctic Bottom Water off Cape Adare (Gordon et al., 2004). However, a longer record (1995–2006) revealed that the 2003 anomaly was a transient feature within a broader change occurring in the opposite direction: the salinity of both Shelf Water and Ice Shelf Water has declined by ~ 0.06 per decade (Budillon et al.,

2011). Indeed, 50 years (1958–2008) of summer measurements in the Ross Sea reveal widespread freshening (Jacobs and Giulivi, 1998, 2010). The salinity of the southwestern shelf has decreased by 0.03 per decade, a slower pace than either of its parent water masses, the Antarctic Surface Water in front of the RIS (0.08 per decade) and the Modified Circumpolar Deep Water at the RIS (0.04 per decade), but faster than its derivative, Antarctic Bottom Water off Cape Adare (0.008 per decade). Indeed, the Ross Sea sector dictates the trends of Antarctic ice cover growth and sea surface temperature cooling, with a 5%

per decade increase during 1978–2008 (Comiso, 2010).

Intensified southerly winds over the RIS, in response to stratospheric ozone-related amplification, and the migration of the Amundsen Low in the Southwest Pacific (Turner et al., 2009), affect sea ice production in the Ross Sea. When that center of cyclonic ice motion is displaced eastward (as in 2000, 2001, 2005), the northward export is stronger, wider, and perpendicular to the RIS, whereas it is narrow when the center is displaced either westward or northward (1995, 2006) and the inflow from the Amundsen-Bellingshausen Seas is

Table 1. Summary of the population sizes of upper trophic level predators in the Ross Sea, Antarctica, in the waters overlying the continental shelf and slope. Percentages reflect the portion of the world or Southern Ocean (by sector) population that occurs within the Ross Sea; sources of population estimates from Ballard et al. (2011).

Species	Number Individuals	Proportion of World Population (%)
Colossal squid <i>Mesonychoteuthis hamiltoni</i>	?	?
Antarctic toothfish <i>Dissostichus mawsoni</i>	?	?
Sperm whale <i>Physeter macrocephalus</i>	Few, extirpated	?
Arnoux's beaked whale <i>Berardius anuxii</i>	150?	?
Blue whale <i>Balaenoptera musculus</i>	~ 30?	?
Antarctic Minke Whale <i>Balaenoptera bonaerensis</i>	21,000	6 %
Ecotype C Killer Whale <i>Orcinus orca</i>	3,350	~ 50 %?
Ecotype A/B Killer Whale <i>Orcinus orca</i>	70	?
Weddell Seal <i>Leptonychotes weddellii</i>	30,000–50,000	50–72% Pacific sector
Crabeater Seal <i>Lobodon carcinophagus</i>	204,000	17% Pacific sector
Leopard Seal <i>Hydrurga leptonyx</i>	8,000	12% Pacific sector
Elephant seal <i>Mirounga leonina</i>	~ 100?	< 1%
Ross seal <i>Ommatophoca rossii</i>	~ 500?	?
Adélie Penguin <i>Pygoscelis adeliae</i>	3,000,000	38%
Emperor Penguin <i>Aptenodytes forsteri</i>	200,000	26%
Antarctic Petrel <i>Thalassoica antarctica</i>	5,000,000	30%
Snow Petrel <i>Pagodroma nivea</i>	1,000,000	?
South Polar Skua <i>Stercorarius maccormicki</i>	19,000?	Most in Pacific sector

stronger. There, the response is compounded with the heat anomaly from enhanced upwelling during positive SAM (Hall and Visbeck, 2002), as indicated by the observed increase of glacial and sea ice melt in that sector (Jacobs et al., 2011). From an ice-drift budget for the Ross Sea shelf during 1992–2008 and thin-ice production calculations, Comiso et al. (2011) estimated the trend of increase in sea ice produced within the Ross Sea Polynya at $2 \times 10^5 \text{ km}^3$ per winter, with tripled production ($6 \times 10^5 \text{ km}^3$ per winter) in 2008. This positive trend ruled out the Ross Sea Polynya as a potential source for the observed freshwater anomaly in the Ross Sea; instead, the estimated rate of salt content increase in Shelf Water is 0.023 per decade.

Explaining the half-century freshening in the Ross Sea requires knowledge of all oceanic heat and freshwater contributions. Antarctic Surface Water input along the slope and coastal currents with increasing amounts of meltwater

and precipitation, either exported in the Amundsen Sea or gained during transit, are likely the largest contributors. Enhanced freshwater input from local sources cannot be ruled out, but neither can a decreased Circumpolar Deep Water input reported by Jacobs and Giulivi (2010). Compared to the late 1970s, in 2007 a smaller, less-saline, colder (by $\sim 0.5^\circ\text{C}$), less-dense, and deeper ($\sim 100 \text{ m}$) “warm” core was found near the RIS. Between 1964 and 2004, an equal density loss was seen at both sides of the ASF: in the Circumpolar Deep Water primarily by warming ($\sim 0.5^\circ\text{C}$) and freshening (~ 0.05), and in Modified Circumpolar Deep Water by freshening (~ 0.17) and cooling ($\sim 1^\circ\text{C}$). Reduction of mixing rates at the Slope Front might be inferred from the thickening ($\sim 200 \text{ m}$) of Antarctic Surface Water with salinity decreasing at the same rate as near the RIS. In the past 50 years, Shelf Water freshening has been correlated to increasingly positive annual

SAM values, and this will likely continue to modify deep ocean ventilation until the ozone hole completely disappears (Jacobs and Giulivi, 2010).

Given the projected changes in both atmospheric and oceanic temperatures, it is expected that changes in the sea ice of the Southern Ocean eventually will parallel those observed in the Arctic, with reduced sea ice concentrations over broad scales, especially as stratospheric ozone concentrations recover (Thompson and Solomon, 2002). Recently, there has been a slight increase in sea ice extent over the entire Southern Ocean, a trend driven by increases in the Ross Sea sector that are greater than the losses in the Southwest Atlantic (Comiso, 2010). These patterns are projected to continue for the next few decades (Ainley et al., 2010b). However, as global temperatures continue to rise, ice concentrations in the Ross Sea will eventually start to decline. Presently observed changes have exhibited substantial

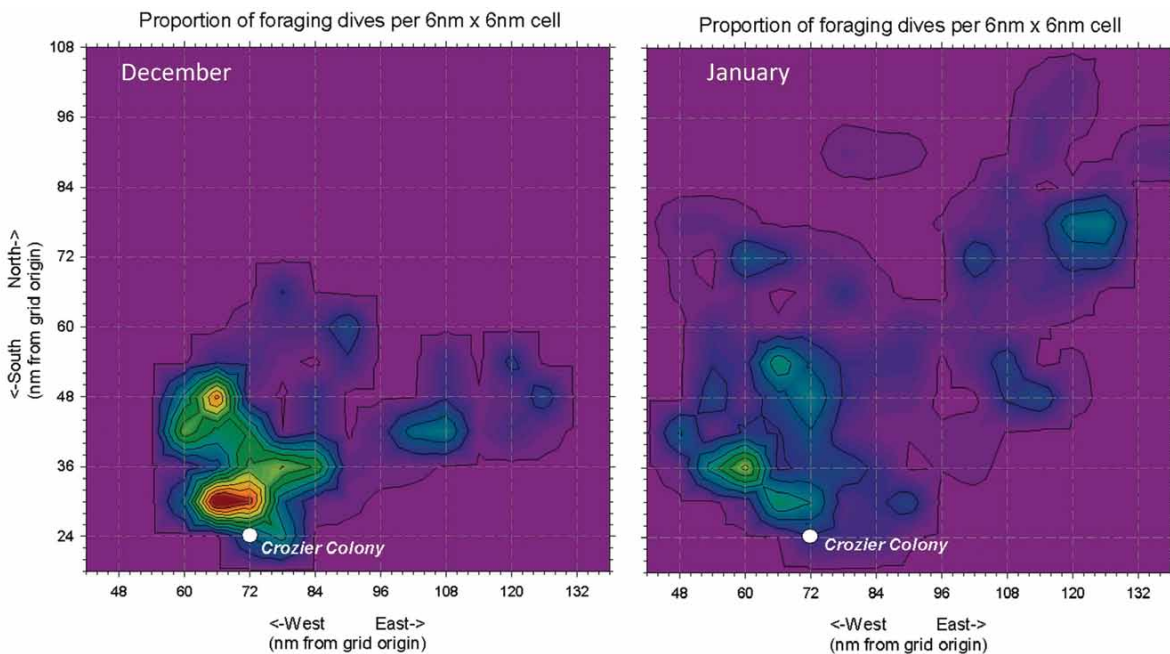


Figure 5. Geographic distribution of the percentage of foraging dives of Adélie penguins near the Cape Crozier rookery on Ross Island during December 2009 (left panel) and January 2010 (right panel), illustrating their nonrandom foraging behavior.

variations in space (Parkinson, 2002; Stammerjohn et al., 2008), with much uncertainty about how long these spatial variations will remain. While sea ice dynamics are a primary physical feature controlling phytoplankton productivity in the Ross Sea via irradiance, climate-altered air-sea interactions are difficult to predict. That is, should stratification induced by melting ice be weakened, mixed-layer depths might increase from wind events and result in a scenario similar to that observed in the West Antarctic Peninsula (Montes-Hugo et al., 2008), where reduced sea ice cover is correlated with increased mixed layer depths, increased cloudiness, decreased primary production, and reduced average size of phytoplankton. If a similar situation were to develop in the Ross Sea, *P. antarctica* might become more dominant, and diatoms might be less frequently encountered, although iron supply, which is likely related to sea ice extent, may also mediate that transition.

Another potential impact of climate change is through large-scale physical forcing. Winds over the Antarctic Circumpolar Current have increased and shifted poleward over the past several decades (Russell et al., 2006), leading to concerns that the sink for atmospheric CO₂ in the Southern Ocean is weakening (le Quéré et al., 2007). Models suggest that, at least in the West Antarctic Peninsula region, intrusions of Circumpolar Deep Water will increase with increased Antarctic Circumpolar Current speeds (Dinniman et al., in press). A similar exercise for the Ross Sea region suggests that the effect might be the same, with increased westerly winds driving more vigorous circulation of the Ross Gyre (Jacobs et al., 2002), which in turn increases Circumpolar Deep Water

intrusions onto the Ross continental shelf. Given that such intrusions are associated with increased phytoplankton biomass and productivity (although the exact mechanism is poorly known), such changes in large-scale atmospheric forcing might serve to increase primary productivity in the Ross Sea.

Changes may also be expected among the various biotic assemblages and biogeochemical cycles in the Ross Sea that are linked to phytoplankton production and composition. For example, altered phytoplankton assemblages may alter zooplankton ingestion and growth, which may impact the entire food web (Smith et al., 2007). Changes in surface-layer biomass and species composition may also modify the rate of export of organic matter (both in quantity and composition) to depth, and this might alter the benthic-pelagic coupling and the role of the Ross Sea as a regional CO₂ sink. Hence, understanding the changes in phytoplankton dynamics induced by climate change is critical to understanding certain food web and biogeochemical alterations in the Ross Sea. On the other hand, the biomass of zooplankton grazers is not directly linked to productivity; that is, it is lower than expected, and it appears to be strongly affected by top-down predation exerted by upper trophic levels (Ainley et al., 2006). Therefore, the upper parts of the Ross Sea food web potentially may be insulated from future changes in primary production.

Another major uncertainty concerns the processes that supply biologically available iron to surface waters of the Ross Sea and their responses to future climate-driven changes in this region. Critical unknowns include the quantitative importance of deep and nearshore waters, as well as the biological

availability of the particulate iron pool. The anticipated warming and freshening of surface waters (Jacobs et al., 2002; Jacobs, 2006), and eventual reductions in sea ice extent and convective mixing, might be expected to decrease the supply of iron to surface waters during the growing season, although these impacts might be tempered by increased inputs of iron-rich glacial and sea ice meltwater. Clearly, a rigorous assessment of the impacts of climate change on the distribution and biological sufficiency of iron in Antarctic waters must await major efforts to further the role of iron in this region.

The upper trophic levels have seen noticeable climate-related change over the past several decades. Adélie penguins in the Ross Sea, where 38% of the world population is located (Table 1), increased during the early 1970s in response to the industrial depletion of Antarctic minke whales (*Balaenoptera bonaerensis*), a trophic competitor, a trend that ceased when the whale population recovered (Ainley et al., 2007). These penguins began increasing again, coincident with a change in the composition of benthic invertebrate communities and a shift of the SAM to a persistently positive phase in the late 1970s and early 1980s (Ainley et al., 2010b). The SAM shift, along with a dramatic increase in the Antarctic ozone hole, led to a stronger polar vortex and increasing winds in the Southern Ocean (Thompson and Solomon, 2002). As a result, coastal polynyas became larger and more prevalent in the Ross Sea (Parkinson, 2002), which is favorable to penguin foraging efficiency and leads to increasing populations (Ainley et al., 2010b). Changes in the nearshore benthic communities were related to a lessening in the formation of anchor ice (Dayton, 1989). At a smaller temporal


scale, a number of Ross Sea vertebrate species (e.g., penguins and seals) have shown correlations of life history parameters with the El Niño-Southern Oscillation cycle (Testa et al. 1991; Wilson et al., 2001; Barber-Meyer et al., 2008; Rotella et al., 2012), although the linkages, possibly related to sea ice variability, remain obscure.

On the other hand, industrial fishing was initiated in the Ross Sea in 1996, the target being the long-lived Antarctic toothfish. At least at the periphery of this species' Ross Sea range, the abundance and size of fish have noticeably decreased (Ainley et al., in press). Similarly, the prevalence of toothfish-eating killer whales has decreased in the southern Ross Sea (Ainley et al., 2009), and the populations of competing Adélie penguins, which also prey on silverfish, has increased once more (recent work of author Ainley). Therefore, the relatively "slow" pace of climate-related change in the Ross Sea has potentially been exacerbated and enhanced by much faster, direct alteration of the food web by biotic extraction. The fate of upper trophic levels may be determined, in part, by the success of attempts to declare the entire Ross Sea a marine reserve (Ballard et al., 2011).

At the same time, the increasing winds led to expansion of the large-scale sea ice field in the Ross Sea sector (Stammerjohn et al., 2008). Modeling indicates that these changes resisted the general warming of the Southern Ocean (Jacobs, 2006) and will continue for the next few decades (Ainley et al., 2010b). One factor facilitating the expanding ice in the Ross Sea sector is increased Ekman transport of ice northward resulting from increased westerly winds over the Antarctic Circumpolar Current.

However, as ocean warming continues, sea ice will eventually begin to retreat in the Ross Sea sector (Turner et al., 2009). Identifying, quantifying, and modeling the key mechanisms directing the flow of waters at the edge of Antarctic continental and ice shelves, as well as the most relevant sea-ice-air interactions in the Ross Sea, are major current challenges, and improvements in our understanding of these processes are necessary if we are to better understand the Southern Ocean response to ongoing climate perturbations.

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