West Antarctic Peninsula: An Ice-Dependent Coastal Marine Ecosystem in Transition

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Wilhelmina Bay near Nansen Island (62°18'0"S, 59°3'0"W), a popular cruise destination on the western Antarctic Peninsula. *Photo by Natasja van Gestel, Texas Tech University*

ABSTRACT. The extent, duration, and seasonality of sea ice and glacial discharge strongly influence Antarctic marine ecosystems. Most organisms' life cycles in this region are attuned to ice seasonality. The annual retreat and melting of sea ice in the austral spring stratifies the upper ocean, triggering large phytoplankton blooms. The magnitude of the blooms is proportional to the winter extent of ice cover, which can act as a barrier to wind mixing. Antarctic krill, one of the most abundant metazoan populations on Earth, consume phytoplankton blooms dominated by large diatoms. Krill, in turn, support a large biomass of predators, including penguins, seals, and whales. Human activity has altered even these remote ecosystems. The western Antarctic Peninsula region has warmed by 7°C over the past 50 years, and sea ice duration has declined by almost 100 days since 1978, causing a decrease in phytoplankton productivity in the northern peninsula region. Besides climate change, Antarctic marine systems have been greatly altered by harvesting of the great whales and now krill. It is unclear to what extent the ecosystems we observe today differ from the pristine state.

INTRODUCTION

The marine ecosystem of the western Antarctic Peninsula (WAP) extends 1,300 km from Alexander Island and the southern Bellingshausen Sea (70°S) to the northern tip of the peninsula and King George Island (62°S) at the southern end of Drake Passage (Figure 1). The Weddell Sea to the east and the Amundsen Sea to the west both include more southerly (higher latitude) embayments and are characterized by more extensive and persistent sea ice. The WAP region is distinctive among Antarctic regions, with its north-south geography and direct exposure to the prevailing westerly atmospheric and oceanic circulation. It is also distinct in its response to climate change, with strong sea ice decreases and rapid winter warming observed over the last three to five decades. The WAP system includes the immediate coastal region (0–300 m deep), the continental shelf region (300–1,000 m deep), and the continental slope region (> 1,000 m deep and about 200 km from the coast). The latter region is adjacent to where the Antarctic Circumpolar Current (ACC) flows.

In common with the Arctic, but distinct from other coastal ecosystems, the variations in sea ice distribution and the freshwater inputs from melting sea ice and glacial ice are the dominant influences on ecological and biogeochemical processes in Antarctic coastal systems. As in other coastal systems, geomorphology and bathymetry play critical roles in structuring the WAP ecosystem (Schofield et al., 2013, in this issue, address some aspects of this). In common with most of the world's coastal regions, the WAP system is profoundly affected by anthropogenic influences, including climate change, pollution, past exploitation of upper trophic level species such as whales and seals, and current exploitation of fish and krill stocks.

There is a rich history of oceanographic research in the region, starting with the Discovery Investigations of 1924–1951 (Hardy, 1967). With a strong focus on *Euphausia superba*, the Antarctic krill, these studies formed the foundation of all subsequent research in the region and, indeed, throughout the
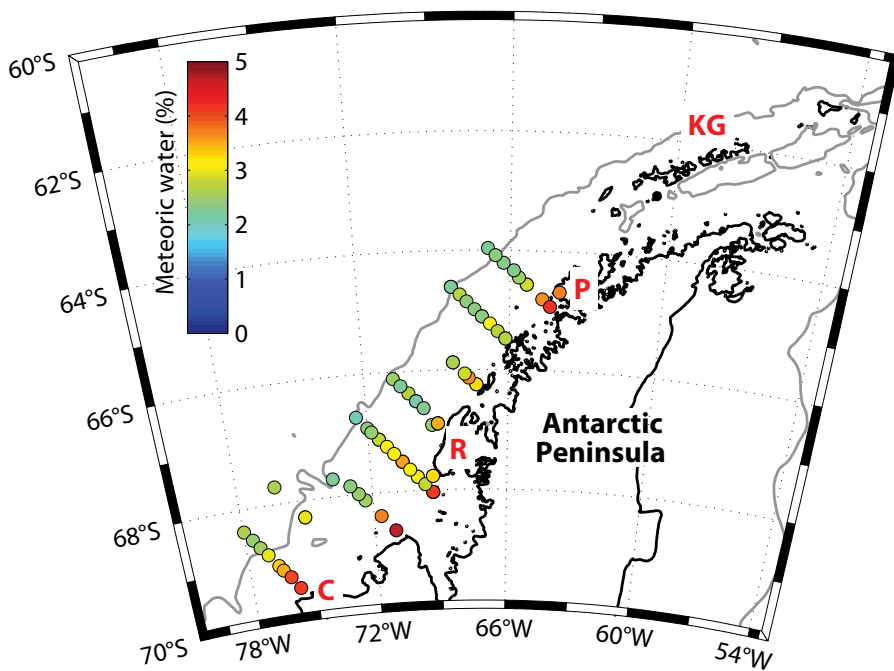
Figure 1. Map of study region along the western Antarctic Peninsula. The small dots are regular hydrographic stations, colored to indicate the percent meteoric water (predominantly glacial melt) in the water column in January 2011 (Meredith et al., 2013). Red letters show locations of Palmer (P) and Rothera (R) stations. KG = King George Island. C = Charcot Island. Hydrographic lines (colored dots) are 100 km apart (north to south) and 20 km apart (cross shelf). The continental shelf break is to the left.

Southern Ocean. More recently, interdisciplinary programs such as Research on Antarctic Coastal Ecosystem Rates (RACER; Huntley et al., 1991), FRUELA (a carbon flux study in the Antarctic Peninsula area; Anadón and Estrada, 2002), and SO GLOBEC (Southern Ocean Global Ocean Ecosystems Dynamics; Hofmann et al., 2004) have made fundamental contributions to our understanding of the region.

Palmer Long Term Ecological Research (PAL) began in 1990 (Ducklow et al., 2007; Steinberg et al., 2012) by recording semiweekly observations of nearshore processes at Palmer Station (64.8°S, 64.1°W) between October and April, and by conducting a regional-scale cruise in January (Figure 1) each austral summer. PAL was built on intensive studies of Adélie penguin demography and

feeding ecology carried out since the mid-1970s (Fraser and Trivelpiece, 1996) and on related oceanographic research (Ross et al., 1996). Operating since 1997, the Rothera Time Series (RaTS; Clarke et al., 2008) is a UK contribution to long-term research in the WAP region. The British Antarctic Survey (BAS) conducts this study year-round in the nearshore ocean environment close to Adelaide Island, at approximately 67°S (Figure 1), allowing an unprecedented range of physical, biogeochemical, and biological variables to be measured continuously throughout the seasons. In this paper, we describe the physical setting, ocean environment, and ecological structure and dynamics of the WAP coastal region based on research by PAL (Ducklow et al., 2012) and the BAS (Meredith et al., 2004; Clarke et al., 2007).

OCEANOGRAPHY AND CLIMATE

The WAP's coastal region (Martinson et al., 2008) is punctuated by islands, promontories, and small peninsulas, and includes a complex network of straits, bays, and passages between the islands and the continental mainland (Figure 1). A complex coastal circulation is associated with the irregular coastline and nearshore bathymetry, and it includes the recently described Antarctic Peninsula Coastal Current, which appears to be driven by winds and glacial meltwater inputs in the austral summer (Moffat et al., 2008). The coastal circulation may serve to retain or transport plankton within the coastal region, but the spatial and temporal distributions of these effects are not well established. Along the peninsula, the seafloor deepens abruptly to 200–300 m or deeper within a few kilometers of shore. It is bisected by the landward ends of several glacial-erosion submarine troughs and canyons that exceed 750 m in depth and extend across the continental shelf (Anderson, 1999). These features facilitate the upwelling of warm, nutrient-rich Upper Circumpolar Deep Water (UCDW) that may support enhanced, predictable food supplies for foraging penguins (Fraser and Trivelpiece, 1996; Schofield et al., 2013, in this issue).

The changing regional climate is discussed in detail elsewhere (Turner et al., 2009), but it should be noted here that the WAP exhibits among the most rapid rates of regional warming anywhere, especially in winter (+7°C since 1950, or five times the global annual mean). The average annual winter (JJA) and summer (DJF) air temperatures are –1.5, –4.9, and +1.4 °C, respectively, for the period

1989–2009 (http://oceaninformatics. ucsd.edu/datazoo/data/pallter/datasets). The ocean in the region is also warming greatly, with a rise in surface ocean temperature in excess of 1°C measured during the second half of the twentieth century (Meredith and King, 2005). Part of this upper-ocean warming is thought to be of atmospheric origin, with the transfer of heat facilitated by greater amounts of ice-free waters from spring to autumn. The deeper ocean has warmed tremendously as well (Martinson et al., 2008). A strong source of the heat input to the WAP region is the inflow of warm, mid-depth UCDW from the ACC, where warmer intrusions along the glacially scoured canyons impinge on the inner shelf regions (Martinson, 2012; Martinson and McKee, 2012). The warming from above and below has resulted in the rapid retreat of the majority of glaciers along the peninsula (Cook et al., 2005), with significant consequences for the coastal ecosystem.

FRESHWATER INPUTS FROM SEA ICE AND GLACIERS

The duration, extent, and seasonality of sea ice are the principal physical determinants of variability in ecosystem dynamics in coastal Antarctic marine ecosystems. Indeed, sea ice in the WAP region is highly variable year to year and is changing rapidly (Figure 2). The recent warming and increase in regional winds have resulted in significant shortening of the winter ice season (or, conversely, lengthening of the summer ice-free season). In the Palmer Station region in the north (Figure 2a), the ice season duration has become, on average, about 92 days shorter over 1979/80 to 2012/13 (± 41 days; or –2.7 ± 1.2 days/year,

p = 0.02). These seasonal sea ice changes are largely wind driven (Holland and Kwok, 2012; Maksym et al., 2012). Strong northerly winds drive the ice edge southward, delaying ice edge advance in autumn and accelerating its retreat in spring, often synoptically with each passing storm (Stammerjohn et al., 2003; Massom et al., 2008). Increased solar ocean warming in summer (due to earlier and longer ice-free conditions) is also contributing to the sea ice changes, acting as a positive feedback to enhance and sustain the rate of warming and sea ice retreat (Meredith and King, 2005; Stammerjohn et al., 2011). The WAP and southern Bellingshausen Sea show the largest and fastest Antarctic sea ice decreases, on a par with the largest regional decreases in Arctic sea ice (Stammerjohn et al., 2012).

The north-south oriented WAP presents a strong latitudinal climate gradient both in temperature and sea ice, characterized by a shorter ice season and more maritime conditions in the north (e.g., in the Palmer Station vicinity) and a longer ice season and more continental conditions in the south (e.g., in the Rothera Base vicinity). The region-wide decreases in sea ice are therefore manifested differently north to south (Figure 2). In the north, the sea ice season barely exists anymore (e.g., the 2006–2012 declining sea ice cover near Palmer Station shown in Figure 3a). In fact, there are indications that in recent times, relatively little sea ice grows in situ in the Palmer Station vicinity (compared to earlier years in the 1979-to-present satellite record; Stammerjohn et al., 2008a,b). The ice cover there is largely ephemeral, blowing in and out of the area with each passing weather system. Meanwhile, in the south, where there was once perennial ice cover, the summer season is now increasingly ice-free.

Embedded within these north-south seasonal sea ice changes are near-coastal changes as well. In autumn, the

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most notable feature is a tendency for open water to persist until early winter (June–July) in an elongated polynya-like feature extending from the northern tip of the peninsula to just south of Palmer Station (Turner et al., 2012). This feature, associated with ocean-warmed air temperatures, likely impacts species that require sea ice during this time of year (see below). In spring, with more frequent wind-driven sea ice retreats, sea ice is advected southward and piles up along the coast. This causes sea ice retreat to be early over the continental shelf but late along the coast (Massom et al., 2006; Smith et al., 2008), and this affects the timing and location of phytoplankton blooms in spring and the redistribution of freshwater.

A consequence of the rapidly retreating sea ice and the shortening sea ice season in the WAP region is the greater exposure of the ocean to the atmosphere and, consequently, greater mixing of the upper ocean due to both mechanical (wind-driven) processes and buoyancy-driven mechanisms. This greater vertical mixing spreads the glacial melt received by the nearshore ocean over progressively deeper layers, and, hence, it reduces surface concentrations. This has potentially significant consequences, especially for the availability of micronutrients supplied by glacial melt, which may be decreasing in the euphotic zone despite the possible increase in their overall supply due to accelerating deglaciation.

The spatial distribution of freshwater inputs from meteoric sources (Figure 1) allows the nearshore RaTS data, south of the PAL area, to be contextualized over the scale of the WAP shelf (Meredith et al., 2013). At the RaTS site itself, calculations based on the stable isotopes of oxygen in seawater ($\delta^{18}O$) indicate that meteoric water (predominantly in the form of glacial melt) dominates the oceanic freshwater budget, with values of up to 6% of the overall mass of the water (Meredith et al., 2013). By comparison, sea ice melt contributes much less (maximum around 2%). On the broader scale, particularly strong inputs of glacial melt are seen at specific coastal locations along the WAP, most notably close to Anvers Island (near Palmer Station), Adelaide Island (close to Rothera), Alexander Island, and Charcot Island (Figure 1). These locations correspond
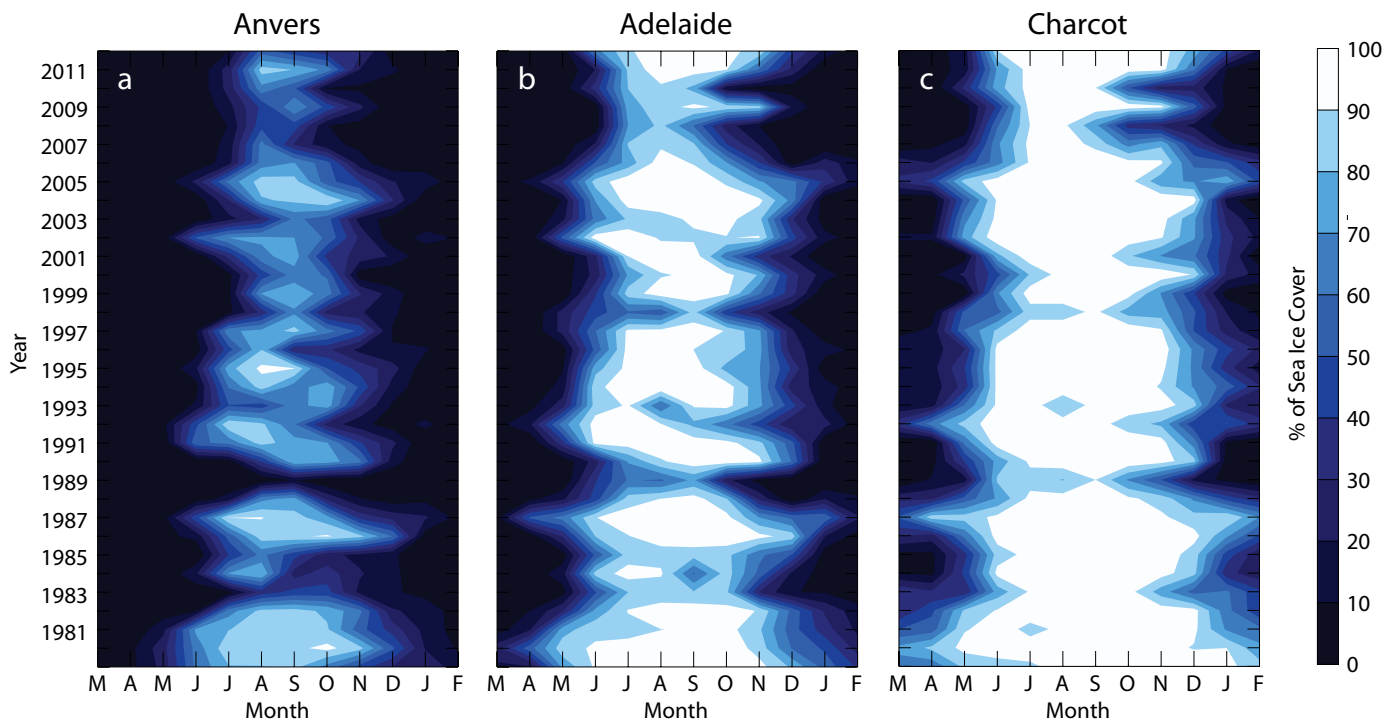
Figure 2. Changes in the ice season annual duration at three north-to-south sites (Anvers-Palmer, Adelaide-Rothera, and Charcot Island) along the western Antarctic Peninsula (Figure 1). The ice season has become shorter over the period from 1979 to 2012 (bottom to top), with trends toward a later autumn sea ice advance (left) and earlier spring sea ice retreat (right). Sea ice cover is derived from Scanning Multichannel Microwave Radiometer–Special Sensor Microwave/Imager (SMMR-SSM/I) data, as described in Stammerjohn et al. (2008a).

to regions of strong precipitation over the adjacent catchment areas on the peninsula, with strong consequent glacial discharge to the ocean. The exception is Charcot Island where the high freshwater concentration is presumed to be due to the southward nearshore circulation along the WAP, and possibly the recent collapse of the Wilkins Ice Shelf.

MIXED LAYER DEPTH, STRATIFICATION, AND PHYTOPLANKTON BLOOMS

Antarctic coastal regions experience intense phytoplankton blooms triggered by sea ice retreat. At the RaTS site at Rothera Base just inside the Antarctic Circle (67.5°S), phytoplankton experience about three weeks of complete darkness each year. In contrast, there is sunlight throughout the year at Palmer Station (64.8°S), but it is much reduced during winter (large incidence angle and short day length). From May through August (austral fall/winter), primary production rates at Palmer are near the limits of detection by the ^{14}C method, and chemolithotrophic organisms dominate the microbial assemblage (Grzymski et al., 2012). At Rothera Base, phytoplankton growth begins to exceed loss rates from respiration, grazing, and viral lysis soon after the winter minimum in solar irradiance (Venables et al., 2013), resulting in the large blooms that follow the ice retreat (Figure 3; see also Clarke et al., 2008), with peak chlorophyll *a* (Chl-*a*) typically occurring between November and February.

Freshwater inputs from melting sea ice in the coastal zone combine with glacial runoff to generate a strong cross-shelf gradient in summertime mixed layer depth (MLD; Figure 4a).

MLD clearly differentiates the shelf and coastal regions into two regimes: a narrow (40 km) coastal zone with summer MLD of approximately 5–10 m and a mid-shelf/slope region with MLD of 25–50 m or greater. Across the WAP, the mixed layer is deeper in winter than summer due to wind mixing and buoyancy loss (cooling and brine rejection from sea ice production in winter). Moreover, changes in winter MLD can affect vertical stratification in summer. For example, changes in sea ice during the preceding winter strongly influence interannual variability in summertime vertical stratification at the RaTS site in the south (Venables et al., 2013). This effect is produced by the greater exposure of the ocean to the atmosphere during winters with reduced sea ice coverage due primarily to wind-driven advection. The reduced sea ice coverage enables greater wind-induced mixing of surface waters and also increased buoyancy loss due to prolonged ice production. Combined, these effects produce
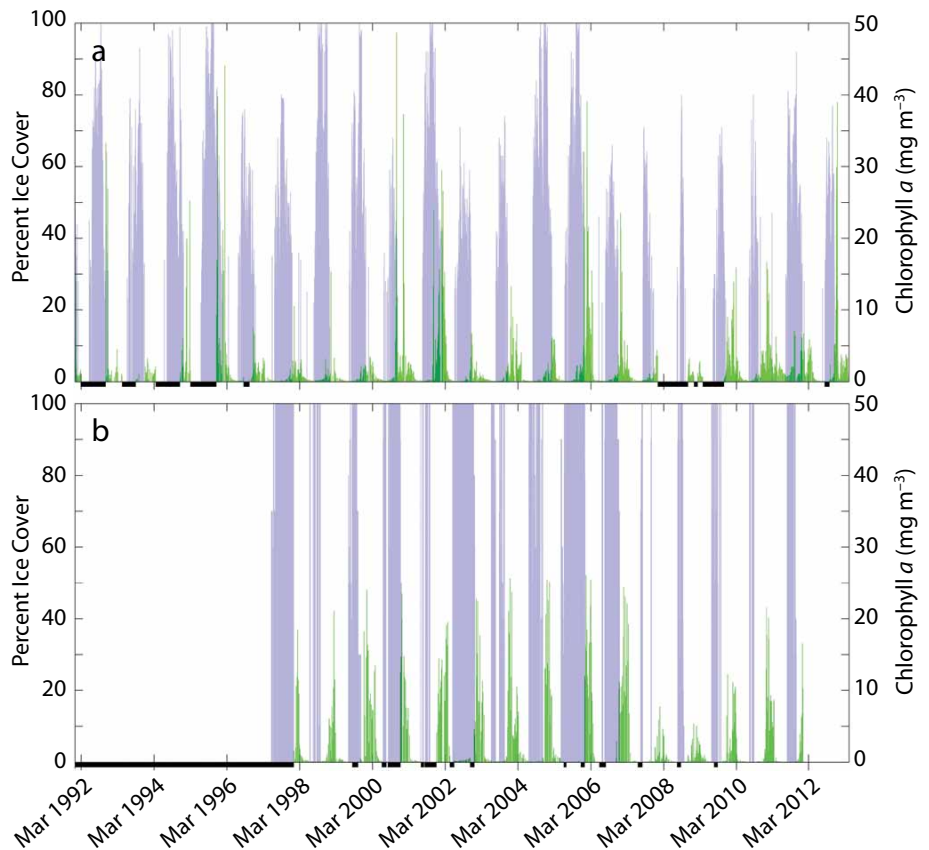

Figure 3. Time series of surface chlorophyll (upper 15 m, green) and sea ice cover (violet) at Palmer (a) and Rothera Stations (b). Sea ice cover is based on SMMR-SSM/I imagery at Palmer (see Figure 2) and local observations of fast ice concentration at Rothera. The darker green indicates chlorophyll under sea ice. Black bars indicate chlorophyll sampling gaps > 21 d. Sampling at Palmer was weekly after 1996 when ice and wind conditions permitted, with a gap for 2008–2009. Sampling at Rothera is weekly throughout the record, when ice and wind conditions permit. Note that ice cover at Rothera still reaches 100% in most years, at least briefly. In the Palmer Station region, the ice cover is almost always < 70%.

anomalously deep winter mixed layers during years with light ice cover. Year-round sampling showed that winter MLD exceeded 100 m in light ice years (Venables et al., 2013). In contrast, the winter MLD was just 25–50 m in years with heavier, longer-lasting sea ice cover. The mean summer stratification was about twice as great following high ice winters as following low ice winters. The differences in stratification, and resulting vertical mixing and light avail-ability, have clear implications for phyto-plankton growth (see graph of ice and Chl-*a* in Figure 3b).

There is a clear first-order relationship between shallow MLD and summertime primary production (Figure 4a,c). In low ice years, MLD at RaTS shoals at an approximately constant rate, from 100 m in early September to ~ 10 m by mid-December, whereas in high ice years, the winter MLD is already fairly

shallow (25–50 m). Although bloom initiation was the same in the high and low ice regimes, the bloom magnitude was greater in high ice years under the more stratified conditions and greater integrated mixed layer light availability. In the northern part of the WAP over the past three decades, primary production has declined as sea ice cover has dimin-ished and wind mixing has increased (Montes-Hugo et al., 2009). These changes at the base of the food web are beginning to reverberate through the entire coastal ecosystem as sea ice and winds continue to change.

Among the coastal systems in the Long Term Ecological Research (LTER) network (Table 1), there is a clear dis-tinction between the productivity of pelagic systems dominated by phyto-plankton and systems with macrophyte producers. The annual net primary production in the Palmer region is

about the same as near Bermuda in the oligotrophic subtropical open sea, and it is dwarfed by the marsh and seagrass systems of the eastern and western US coasts. Even so, primary production along the WAP and in other coastal regions of Antarctica is greater than in the open Southern Ocean because ice-edge phytoplankton blooms focus most of the annual primary production in a brief growing season, providing ample phytoplankton stocks for krill and other macrozooplankton herbivores (Ross et al., 2008).

SECONDARY PRODUCTION AND TOP PREDATORS

Traditionally, Antarctic marine ecosys-tems are believed to be dominated by the Antarctic krill *Euphausia superba* and its predators (Murphy et al., 2013). *E. superba* is a shrimplike crusta-cean zooplankter about 2–5 cm long (Figure 5). Antarctic krill form a critical link between diatom primary producers and the large stocks of marine mam-mals and seabirds, including the Adélie penguins that are the iconic species of Antarctic ecosystems. Distribution of krill around the continent is extremely variable and patchy, with large swarms reported to contain more than 100 indi-viduals per m^3 (Tarling et al., 2009). Krill stocks average about 200–6,000 mgC m^{-2} in areas of low to high krill concentra-tions, respectively (Pakhomov et al., 2002). Along the peninsula, *E. superba* stocks average 10–250 individuals per 1,000 m^3 (Ross et al., 2008), or ~ 85–2,125 mgC m^{-2}. Antarctic krill are usually thought to be a shelf-slope species found over the continental shelf and in the open sea, rather than in the immediate coastal zone (Atkinson et al.,
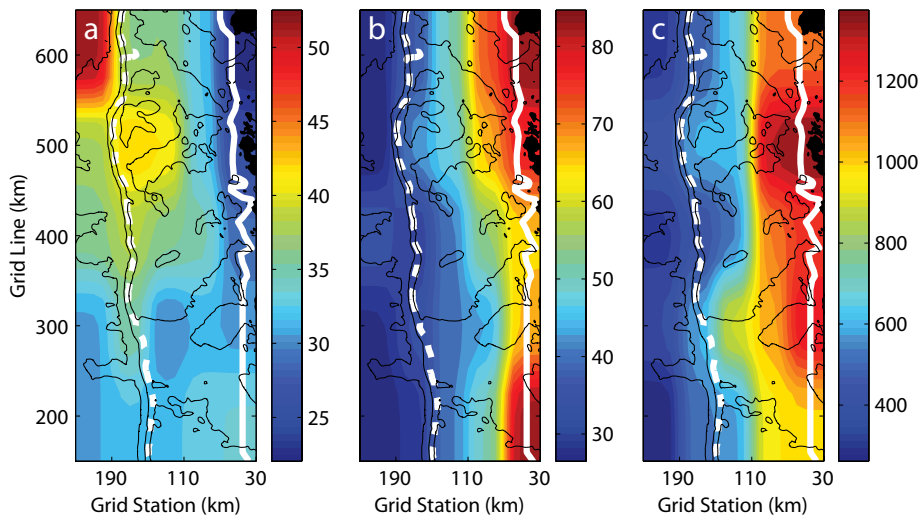

Figure 4. (a) Mixed layer depth (decibars; Martinson et al., 2008), (b) water column chlorophyll (mg m^{-2}), and (c) primary production rate (mgC m^{-2} d^{-1}) in the region between Anvers Island in the north and Marguerite Bay in the south. These plots are averaged for cruises undertaken from 1993 to 2012. The immediate coastal region in the south part of the study area (including the Rothera Time Series [RaTS] site at Rothera Base) is not contoured because Marguerite Bay extends more than 100 km farther to the east and is not surveyed regularly. The dashed and solid white lines denote the continental shelf break at > 1,000 m, and coastal zone < 300 m.

Table 1. Annual net primary production rates in selected coastal Long Term Ecological Research and oceanic sites.

Site	Primary Producer(s)	Rate (gC m⁻² yr⁻¹)	References
Palmer, Antarctica (PAL)	Phytoplankton (coastal 1993–2012)	180	Vernet et al. (2008)
	Macroalga *Himantothallus grandifolius*	16–56	Wiencke and Amsler (2012)
California Current Ecosystem (CCE)	Phytoplankton (coastal, upwelling, 1984–2013)	390	R. Goericke*
Bermuda Atlantic Time Series (BATS)	Phytoplankton (open sea)	157	Lomas et al. (2013)
Florida Coastal Everglades (FCE)	Seagrasses, macroalgae, periphyton, mangroves	853–1,166	Herbert and Fourqurean (2009); L. Collado-Vides, V.H. Rivera, J. Fourqurean*; Castañeda-Moya et al. (in press)
Georgia Coastal Ecosystems (GCE)	Marsh grasses (aboveground)	675	Pennings et al. (2012)
	Phytoplankton	280	Pennings et al. (2012)
Plum Island Ecosystems, MA (PIE)	Marsh grass (aboveground)	350	A. Giblin, J. Morris*
Santa Barbara Coastal, CA (SBC)	Kelp forest	1,200	Reed et al. (2008); Harrer et al. (in press)
Virginia Coast Reserve (VCR)	Seagrasses and marsh grass (aboveground)	300–450	Kirwan et al. (2012); K. McGlathery*

* personal communications, 2013

Figure 5. Some exemplary large organisms of the western Antarctic Peninsula (WAP). (a) The overstory brown macroalga *Cystosphaera jacquinotii*, which can co-dominate with other large brown algae in benthic communities along the WAP. The spherical structures are gas-filled floats that allow the alga to rise two or more meters off the bottom. The oblong structures are reproductive elements. *Photo by C.D. Amsler*. (b) Adult Antarctic krill *Euphausia superba*. The green color is from phytoplankton in the gut. *Photo by A. McDonnell*. (c) Adult Adélie penguin *Pygoscelis adeliae* and a two week-old chick at Torgersen Island, one kilometer from Palmer Station. *Photo by W. Fraser*

2008). The cold, fresh coastal zone is the preferred habitat of the crystal or ice krill *Euphausia crystallorophias*. More than 50 crystal krill individuals per 1,000 m^3 have been documented in the WAP study region (Ross et al., 2008).

These general patterns appear to be changing. Antarctic krill are locally abundant on the inner shelf near Palmer Station (> 100 individuals per 1,000 m^3; Ross et al., 2008), where they are the principal prey of the Adélie penguin *Pygoscelis adeliae*. The Adélie penguins that breed and forage in the Anvers Island area (near Palmer Station) have been studied intensively since 1975 (Fraser and Trivelpiece, 1996; Fraser and Hofmann, 2003). Cohorts of Antarctic krill year classes can be followed through four- to five-year cycles in Adélie penguin diet samples (Fraser and Hoffman, 2003). Significant krill recruitment events occurred in 1991–1992, 1995–1997, and 2000–2003, 2006–2007, and 2010–2011 (Figure 6; data derived after Fraser and Hoffman, 2003). Krill recruitment success is related to heavy winter sea ice (Fraser and Hoffman, 2003), and declining sea ice extent and duration in the Palmer Station region

may be contributing to the decline of the krill (Atkinson et al., 2004), as well as the Adélie population, as discussed further below.

Krill also support a large population of crabeater seals (*Lobodon carcinophagus*) and an increasing number of fur seals (*Arctocephalus gazella*, see below) throughout the region (Costa and Crocker, 1996; Chapman et al., 2004; Siniff et al., 2008). In addition to crabeaters, baleen whales (humpback, *Megaptera novaeangliae,* and minke, *Balaenoptera bonaernsis*) pursue krill into coastal fjords in the fall and winter. This large coastal assemblage of krill grazers is preyed on by leopard seals (*Hydrurga leptonyx*) and killer whales (*Orcinus orca*), and together all these species of ice-loving and ice-tolerant mammals and birds constitute one of the largest communities of warm-blooded top predators on the planet (Steinberg et al., 2012).

The classical explanation for the large stocks of "charismatic megafauna" in Antarctic coastal regions is that the food web is short and efficient, dominated by large-celled diatoms and Antarctic krill, the main prey of all the large predators (Knox, 2006). However, Antarctic

seas also harbor active microbial food webs (Hewes et al., 1990), initiated by increasing stocks of smaller-celled phytoplankton such as cryptophytes that are too small to be ingested by krill (Moline et al., 2004; Montes-Hugo et al., 2009; Huang et al., 2012). These small primary producers now account for 20–90% of the primary production in the Palmer region (recent work of author Sailley and colleagues) and are grazed by microzooplankton (Lori Garzio, Virginia Institute of Marine Science, and colleagues, *pers. comm.*, 2013). In turn, microzooplankton may constitute a large part of the krill diet. The extra trophic level between primary producers and krill causes a reduction in trophic efficiency. Even so, the measured primary production and krill stock in the region is sufficient to support present-day seal population levels and historical stocks of penguins 10 times larger than current levels (recent work of author Sailley and colleagues).

BENTHIC COMMUNITIES

Hard-substrate communities are widespread along the WAP benthos, particularly in the northern half of the region. Large perennial brown macroalgae dominate in shallow waters to depths of 40 m or greater, with biomass commonly in the range of 5–10 wet kg m^{-2} and coverage of the bottom commonly ranging above 80% (Wiencke and Amsler, 2012). *Desmarestia anceps* and *D. menziesii* usually dominate in shallower waters, with *Himantothallus grandifolius* dominating deeper, although other large brown algae such as *Cystosphaera jacquinotii* (Figure 5a) can co-dominate with *D. anceps* or *H. grandifolius* (Wiencke and Amsler, 2012). Estimates of primary productivity are available only for
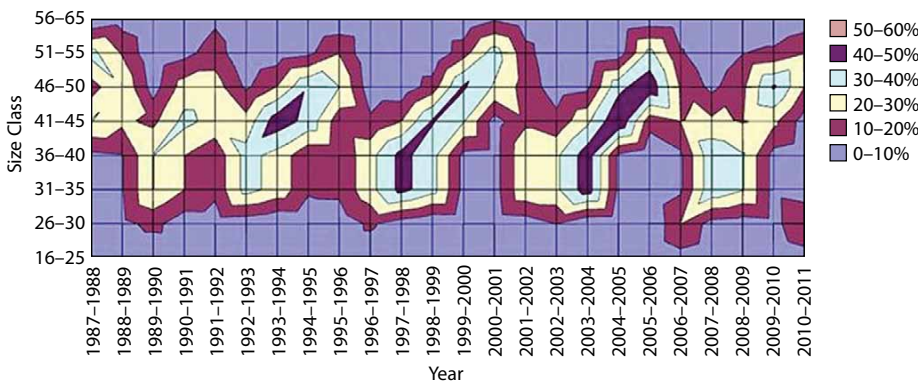

Figure 6. Size-frequency occurrence of Antarctic krill *Euphausia superba* in diet samples from nesting and actively foraging Adélie penguins at Palmer Station, 1987–2011. The diet composition data were obtained as described in Fraser and Hoffman (2003).

H. grandifolius and are in the range of 16–56 gC m^{-2} yr^{-1} (Wiencke and Amsler, 2012). Red macroalgae dominate the understory in these communities, but they are not as important in terms of cover or biomass but are very important in terms of species richness.

The macroalgal-dominated communities support rich assemblages of invertebrates, particularly amphipods (Huang et al., 2007), although gastropods and echinoderms are also abundant (White et al., 2012). Amphipod densities in *D. menziesii* and *D. anceps* canopies have been estimated at over 300,000 and 30,000 individuals m^{-2} of the benthos, respectively (Amsler et al., 2008). All of the dominant brown and most of the abundant red macroalgae are chemically defended from being consumed by amphipods and other grazers. As macroalgae in the northern and central WAP lose their dominance with increasing depths, rich communities of sessile invertebrates replace them. Sponges are usually the most important members of these communities. However, tunicates, bryozoans, and soft corals are also numerically important and any of these can co-dominate at specific locations.

WAP ECOSYSTEM RESPONSE TO ANTHROPOGENIC FORCING

The WAP region is warming faster than almost all other areas on the planet, and the extent, duration, and seasonality of sea ice cover are also rapidly changing. The extent to which these changes are anthropogenic in nature (as opposed to being part of natural variation of the climate system) is an ongoing subject of research. It has been hypothesized that the greater influx of warmer UCDW from the ACC is

the consequence of strengthening and southward-shifting winds over the Southern Ocean, often quantified by the movement of the Southern Annular Mode (SAM) to a more positive state. These atmospheric changes could induce stronger upwelling (Waugh et al., 2013) and onshelf flow at the WAP shelf break and, hence, permit greater quantities of warmer water to intrude along the canyons toward the coast. The SAM is also strongly implicated in the direct atmospherically forced changes impacting the WAP, along with the El Niño-Southern Oscillation phenomenon via teleconnections with the tropical Pacific. Movement of the SAM to a more positive state is well described (Marshall et al., 2004; Thompson et al., 2011), and it is increasingly seen that the depletion of stratospheric ozone is a key factor in this forcing, along with contributions from greenhouse gas emissions (Lee and Feldstein, 2013). However, these anthropogenic forcings will have natural variability superimposed, and not all aspects

of the WAP warming can currently be explained in terms of anthropogenic effects and changes in atmospheric circulation. Further research is needed; nonetheless, significant human impacts on the WAP climate are strongly implied.

Most native species in the region, from diatoms to whales, are ice-obligate, with successful completion of their life cycles requiring sea ice cover and a particular phenology of sea ice advance and retreat (Ducklow et al., 2012). Since at least the 1970s, rapid warming, sea ice loss, and, possibly, other related climate changes (Fraser et al., 2013, in this issue) have resulted in an 80% decline in the Adélie penguin population in the Palmer region (Figure 7). Concurrently, Gentoo penguins, a sub-Antarctic, non-ice-requiring species, are immigrating and successfully establishing breeding populations in the region. Gentoos now make up over half the total penguin breeding community. The conspicuous changes in penguins were just the first changes to be noted in the WAP (Ainley, 2002).
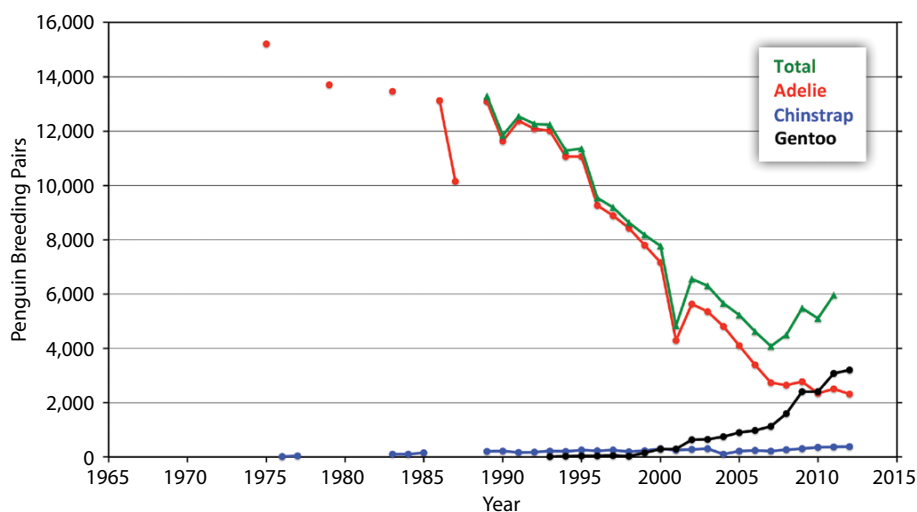

Figure 7. Population census data for Adélie, Chinstrap, and Gentoo penguins in the Palmer Station region, 1975–2012. After declining since the late 1970s, the total penguin population (breeding pairs) in the region has been increasing since 2008 due to the rapid growth and immigration of Gentoos in the region. Over half the penguins in the region now are Gentoos.

Changes in krill stocks, phytoplankton composition, and other ecosystem properties have now also been documented. A synthesis of these observations suggests possible future changes in ecosystem structure from dominance by krill toward a food web with more microbial herbivores and bacteria (recent work of author Sailley and colleagues).

Macroalgal assemblages in the southern WAP have much lower biomass and diversity than those described above for the northern WAP, and these southern WAP communities appear to be typical of those at similar latitudes around the continent (Wiencke and Amsler, 2012). The change occurs somewhere between 64°S and 67°S, unfortunately by far the least-studied area of the WAP in terms of benthic community structure. Moe and DeLaca (1976) hypothesized that the decrease is due to decreased annual irradiance because of increased sea ice cover. It seems likely that richer macroalgal-dominated communities typical of the northern WAP are expanding to the south as annual sea ice declines, but without either historical or current information on the nearshore benthic communities of this region, this hypothesis cannot be tested.

The striking decline of the Adélie penguins has made the WAP emblematic of polar climate change, but it would be a mistake to attribute the many ecological changes manifesting in the region as simple reflections of climate warming and sea ice loss alone. Although circumpolar ocean and atmospheric circulation partially isolate the continent of Antarctica from the rest of the global climate system, they do not form an impermeable barrier. Persistent organic pollutants (POPs), including DDT, DDE, PCBs, and more exotic compounds, "leapfrog" to both polar regions via successive cycles of volatilization, atmospheric transport, deposition, and revolatilization before condensing in cold, high-latitude areas (Dickhut et al., 2005). Ironically, net transport of volatile POPs from warmer to colder areas results in greater concentrations remote from source regions in the temperate zones and tropics. As an extreme example of this pattern, the glacier behind Palmer Station is a current source of DDT to the local food web, despite a worldwide ban on DDT production (Geisz et al., 2008). Once immobilized in polar regions, POPs enter and concentrate in phytoplankton and krill (Chiuchiolo et al., 2004) and in penguins, giant petrels, and skuas (Geisz, 2010). The consequences of POPs in Antarctic marine food chains are unknown. The body burdens are sublethal, but may influence responses to other stressors, including warmer temperatures, acidification, and altered ice and breeding phenologies.

Climate change and transequatorial pollutant transport notwithstanding, the most profound effects on the WAP system are likely the result of human predation. Whaling, sealing, and, later, harvesting of fish and krill have removed top and intermediate predators from the WAP system, an example of "fishing down the food web" (Pauly et al., 1998; Ainley and Pauly, 2013). The human exploitation of Antarctica began following the discovery of fur seal colonies in the South Shetland and South Orkney Islands in 1819–1820, resulting in extirpation of the population by 1904. Soon thereafter, whaling began in earnest, and few baleen whales were left for the taking by the 1920s (Ainley and Pauly, 2013). As articulated in the "Krill Surplus Hypothesis" (Laws, 1985), the near extirpation of the great whales from most Southern Hemisphere waters by the mid-twentieth century probably decreased predation pressure on Antarctic krill, leaving more food available for penguins and crabeater seals and leading to population increases in those species. But, this effect is complicated by several factors, including the recovery of baleen whales and fur seals following the (incomplete) moratorium on whaling in most sectors of Antarctica by the

> ## LIKE OTHER COASTAL REGIONS AROUND THE WORLD, THE [WESTERN ANTARCTIC PENINSULA] ECOSYSTEM IS EXHIBITING COMPLEX AND INCREASINGLY RAPID CHANGES DUE TO THE COMBINED EFFECTS OF CLIMATE CHANGE (PARTIALLY ANTHROPOGENIC), FISHERIES OVERHARVESTING, AND POLLUTION.

International Whaling Commission in 1982. Adding further to the puzzle, Adélies began to decline (not increase) in the late 1970s, even before the whale recovery began to take off, implicating climate change as an additional factor in Antarctic population dynamics (Fraser et al., 1992). This controversy rages on. Trivelpiece et al. (2011) note concurrent declines in ice-obligate Adélies and ice-avoiding Chinstrap penguins, and argue against a direct effect of sea ice decline and in favor of variations in krill availability (perhaps caused by ice decline) as the major controlling factor on penguin populations. In this issue, Fraser et al. (2013) indicate that the exposure of penguin colonies to prevailing winds and snow accumulation on north- vs. south-facing slopes has caused differential colony extinction rates in the Palmer region. Climate change, top-down effects resulting from fisheries harvests, and the entry of pollutants into the region all combine to drive changes in the Antarctic marine ecosystem. These changes are currently most prevalent on the WAP, but may threaten the rest of the Antarctic coastline in the future (Turner et al., 2009).

SUMMARY

Sea ice melting and glacier runoff strongly influence the coastal zone of the western Antarctic Peninsula, leading to very shallow mixed layers and locally high primary production. These conditions support sufficient krill stocks to feed both currently low and historically large populations of penguins and other predators. Primary production is low in comparison to most other coastal sites dominated by macrophytes, but similar to pelagic production in temperate

and subtropical sites. Like other coastal regions around the world, the WAP ecosystem is exhibiting complex and increasingly rapid changes due to the combined effects of climate change (partially anthropogenic), fisheries over-harvesting, and pollution. The Antarctic coastal system, once dominated by large organisms at all trophic levels, appears to be transitioning toward a microbe-dominated system. A paradox of the Southern Ocean is that it is simultaneously one of the most comprehensively protected of global marine systems, owing to the Antarctic Treaty, and one of the most impacted, as a consequence of rapid climate change, human exploitation, and the novel poleward transport of anthropogenic compounds.

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