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TWO DECADES OF PELAGIC ECOLOGY OF THE WESTERN ANTARCTIC PENINSULA

BY DEBORAH K. STEINBERG, DOUGLAS G. MARTINSON, AND DANIEL P. COSTA



Photo credit: D. Steinberg

ABSTRACT. Significant strides in our understanding of the marine pelagic ecosystem of the Western Antarctic Peninsula (WAP) region have been made over the past two decades, resulting from research conducted aboard ARSV *Laurence M. Gould* and RVIB *Nathaniel B. Palmer*. These advances range from an understanding of the physical forcing on biology, to food web ecology (from microbes to top predators), to biogeochemical cycling, often in the larger context of rapid climate warming in the region. The proximity of the WAP to the Antarctic Circumpolar Current and WAP continental shelf bathymetry affects the hydrography and helps structure the biological community. Seasonal, spatial, and interannual variability at all levels of the food web, as well as the mechanisms supporting their production, are now more clearly understood. New tools and technologies employed in the region were critical for making this research possible. As a result, our knowledge of the WAP pelagic ecosystem during a time of rapid climate change has vastly improved.

INTRODUCTION

The marine pelagic ecosystem of the Western Antarctic Peninsula (WAP) region is one of the most seasonally productive on our planet, supporting extensive summer phytoplankton blooms and large stocks of Antarctic krill, seabirds, and marine mammals. The WAP comprises a diverse pelagic habitat, ranging from shallow coastal, to continental shelf, to deep continental slope subregions (Figure 1). The shelf is cut by deep channels and troughs that affect the hydrography and, in turn, help structure the region's biological community. As in other Antarctic coastal marine ecosystems, the production and life cycles of organisms here are intimately tied to the annual cycle and interannual variations in sea ice cover. The WAP differs from the rest of the Antarctic Continent, however, in that it is experiencing the most rapid warming of any marine ecosystem on Earth, with a 3°C increase in annual mean air temperature and a 6°C rise in mean winter temperature over the last six decades (Vaughan et al., 2003). The productive food web, unique geographical setting, and interactions between climate warming and the marine ecosystem

make the WAP a fascinating region in which to focus pelagic research.

This paper presents a brief overview of what we have learned over the past two decades from studies of the pelagic ecology of the WAP conducted on ARSV *Laurence M. Gould* and RVIB *Nathaniel B. Palmer*. This research ranges from large, interdisciplinary, multiyear, multi-investigator programs to smaller efforts focused on the role of a single species or process. The larger multidisciplinary programs began with the process-level program Research on Antarctic Ecological Rates (RACER; Huntley et al., 1991) with most cruises on R/V *Polar Duke*. They include the ongoing Palmer Long Term Ecological Research (PAL-LTER) project to investigate the role of climate change in structuring the pelagic ecosystem and its effects on WAP biogeochemical cycling (Ducklow et al., 2012a). Another large effort is the recently completed US Southern Ocean Global Ocean Ecosystems Dynamics (SO GLOBEC) program (Hofmann et al., 2011) with a primary goal to understand the physical and biological factors that contribute to overwintering success of

Antarctic krill, focusing on both krill and higher predators. The FOOD for Benthos on the ANtarctic Continental Shelf (FOODBANCS) program investigated connections between ecological processes in the water column and the benthos ("benthopelagic coupling") (Smith and DeMaster, 2008). Finally, a broad range of other studies covered the ecology, physiology, population dynamics, or behavior of important taxa. In this paper, we first set the stage with the WAP's physical environment, introducing the importance of physical forcing on biology, and then move through the food web from microbes to top predators, highlighting connections and effects on biogeochemical cycling.

PHYSICAL SETTING

As the eastern rim of the Bellingshausen Sea, the WAP marine environment is dominated by rugged coastal geography and the close proximity of the Antarctic Circumpolar Current (ACC) (Figure 1). The glacially sculpted coastline along the peninsula is highly convoluted, cut with numerous islands, deeps, bays, fjords, submarine canyons, and a series of embayments often interconnected by deep channels (Anderson, 2002). Its broad continental shelf averages ~ 430 m in depth (the "nominal depth") and

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roughly 300 km in width. The domain is naturally divided into three subregions—continental slope, shelf, and coastal regions—consistent with the bathymetry, ocean dynamics, water mass, and biological distributions (Martinson et al., 2008; Figure 1).

The ACC delivers Upper Circumpolar Deep Water (UCDW), the primary source of nutrients and heat to the WAP continental shelf region. The southernmost position of the ACC meets the continental slope once it passes the Ross Gyre and stays there throughout the entire Southeast Pacific region along the continental rim of the Amundsen-Bellinghousen Seas, riding up to the shelf-slope break along the peninsula (Figure 1). This location makes UCDW directly available to the WAP continental shelf. In this important respect,

the West Antarctic continental shelf is unique in Antarctica for this extended proximity of the ACC and delivery of warm UCDW. Klinck et al. (2004) show that at the intersection of the Marguerite Trough (Figure 1, center of yellow rectangle) and the shelf break, the oncoming ACC is driven into the northern wall of the trough, generating a pressure head that drives UCDW up the trough and transports it across the shelf (but below the shelf's nominal depth; Martinson and McKee, 2012). UCDW is mixed into shelf waters above the nominal shelf depth (above the Marguerite Trough conduit) via eddies shed at the continental shelf break (Moffat et al., 2009; Martinson and McKee, 2012). Circulation in the WAP is characterized by a large meandering cyclonic (clockwise) flow that sometimes breaks into

northern and southern cyclones with a small anticyclone separating them midway up the peninsula (Hofmann et al., 1996; Martinson et al., 2008).

Climate change is directly affecting the WAP marine system. Its most notable impact is on sea ice, whose temporal and spatial distribution plays a major role in upper ocean stratification and in the production, distribution, and life cycles of WAP species at all trophic levels (described below). Specifically, in the WAP and Bellingshausen Sea region, sea ice advances two months later and retreats more than one month earlier than elsewhere in the Antarctic, resulting in a greater than three month shorter ice season. In an area extending from the southern Bellingshausen Sea to the eastern Amundsen Sea, along and just offshore of the continental shelf break, the

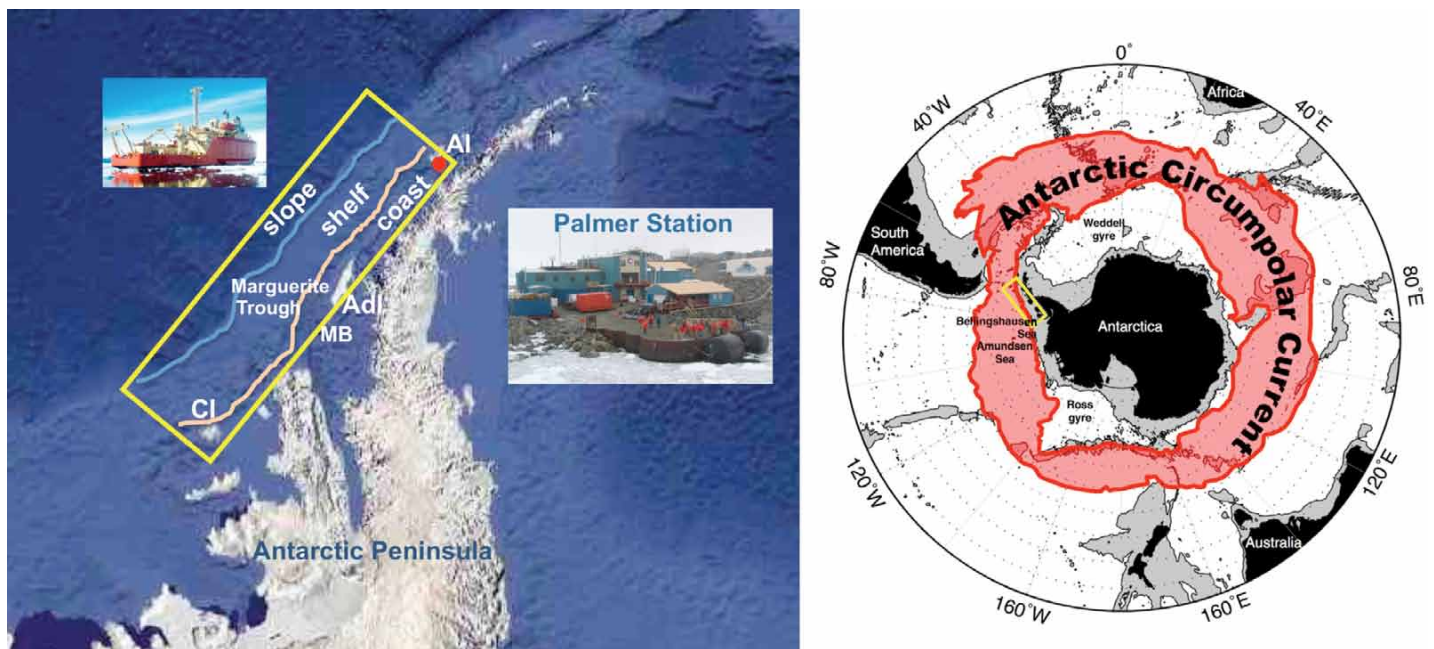


Figure 1. Western Antarctic Peninsula (WAP) and proximity to the Antarctic Circumpolar Current (ACC). (left panel) Map shows the sampling region of the Palmer Long Term Ecological Research (PAL-LTER) project (yellow rectangle) and encompasses the Southern Ocean Global Ocean Ecosystems Dynamics sampling region (approximately in the middle of the PAL-LTER sampling region, encompassing Marguerite Bay (MB)). The orange line separates the coastal from the shelf region, and the blue line separates shelf from deeper (> 750 m) slope waters. The red dot locates Palmer Station (right inset) on Anvers Island (AI); Adelaide Island (AdI) and Charcot Island (CI) are also indicated. ARSV *Laurence M. Gould* is shown in the left insert. (right panel) Location of the ACC (in red) in relation to the WAP (yellow rectangle). The ACC flows clockwise around Antarctica; west of the Antarctic Peninsula, its southern extent consistently hugs the shelf-slope break and supplies warm, nutrient-laden Upper Circumpolar Deep Water to shelf waters. Location of ACC adapted from Orsi et al., (1995); Martinson and McKee (2012)

seasonal sea ice season from 1979–2006 shortened by 83 days (updated from Stammerjohn et al., 2008a), and nearly all of the perennial (permanent) ice in this area has been lost (Stammerjohn et al., 2008b). Repeated sampling in the WAP by the *Gould* since its launch in 1997 has helped to document the dramatic warming of UCDW (Martinson et al., 2008). The UCDW is the major source of heat responsible for melting the bottom of the ice streams draining the West Antarctic Ice Sheet as they enter the Amundsen Sea Embayment, and is the likely source of heat dominating winter atmospheric warming in the WAP.

PRIMARY PRODUCTION AND MICROBIAL ECOLOGY

Investigations of WAP primary production commenced soon after the *Palmer* was commissioned and entered Antarctic service in 1992. One of the last RACER cruises, an early LTER cruise, and others used the *Palmer* from 1992 onward, supplementing earlier work aboard the *Polar Duke*. The major product of this pioneering research was to establish an understanding of the seasonal variability and mean levels of primary production, and to suggest the mechanisms supporting this production. In particular, local-to regional-scale diatom blooms over the shelf were found associated with intrusions of warm, nutrient-rich UCDW onto the shelf (Prézelin et al., 2000).

Investigations of the effects of ultraviolet (UV) radiation on phytoplankton growth and photosynthesis have been an important strand in phytoplankton research along the peninsula. This is another area with a rich “prehistory” of research preceding *Gould*- and *Palmer*-based cruises. Later, Neale and colleagues (Fritz et al., 2008) established

that Antarctic coastal phytoplankton assemblages are somewhat less sensitive to UV radiation and repair UV-induced damage to their photosynthetic systems more rapidly than their open ocean counterparts.

The major contributions to new understanding of phytoplankton ecology along the peninsula have come from the 15 annual LTER cruises conducted aboard the *Gould* since 1998 (Ducklow et al., 2012a). In synthesizing this research, Vernet et al. (2008) demonstrated that summertime primary productivity (PP) within the LTER study region exhibited strong interannual and regional variability related to the timing of sea ice retreat (see Maksym et al., 2012, in this issue). Spatial variability was characterized by enhanced PP rates in the inshore, coastal, and southern (e.g., Marguerite Bay, see Figure 1) regions and declining PP extending across the shelf into open ocean waters. Mixed-layer depth was the major proximal factor controlling PP rates, and both high PP and shallow mixed layers were associated with late sea ice retreat. More recent (2008–2011) and geographically extensive (south to Charcot Island; Figure 1) observations are consistent with these conclusions. The main conclusion from this research is that, to a first order, PP along the peninsula is light limited and that upper water column stability is conferred by melting sea ice (and glacier runoff; Dierssen et al., 2002). Vernet et al. (2008) did not detect a long-term trend (1995–2006) in PP rates. Although macronutrient concentrations generally remain above nonlimiting concentrations, the role of iron limitation remains an open question in WAP shelf waters.

The strong relationship between PP and sea ice, coupled with the sharp

decline in the duration of sea ice cover since 1978 (Stammerjohn et al., 2008b) suggest PP rates could be declining as well. Extracting a temporal trend required the greater temporal and spatial resolution of remotely sensed ocean color observations. Analyzing coastal zone color scanner (CZCS) and Sea-viewing Wide Field-of-view Sensor (SeaWiFS) imagery obtained over a nearly 30-year period (1978–1986 and 1998–2006) backed up by in situ observations from the *Gould*, the *Palmer*, and other vessels, Montes-Hugo et al. (2009) showed that surface chlorophyll *a* concentrations had declined over the WAP by 12%, with large decreases in the north and increases in the south, both associated with decreasing sea ice cover. The differential changes in chlorophyll (which explain about 60% of PP variability) in response to sea ice decline indicate the complexity of the sea ice-phytoplankton system. Decreasing PP in the north was associated with deeper mixed layers and increasing light limitation as a result of declining stability from reduced sea ice melting. In the south, areas previously covered by sea ice year-round are becoming open in summer as sea ice melt migrates southward, exposing new areas to sunlight. Here again, light appears to be the principal driver of PP variability.

Heterotrophic bacterioplankton decompose organic matter synthesized by primary producers and recycle nutrients. The foundation for bacterioplankton research along the peninsula comes from the RACER project and early LTER research (Karl et al., 1996). Coastal Antarctic waters present a challenging environment for bacteria, alternating between an extended period of darkness and extremely limited supplies of organic matter in winter, and

organic-matter-replete conditions during phytoplankton blooms in summer. Indeed, the abundance of *Bacteria* exceeds 1×10^9 cells per liter in summer, about as high as in rich temperate seas, but is an order of magnitude less abundant in winter and in deep water (Church et al., 2003). In contrast, *Archaea* were more abundant in winter and in deeper waters. These observations (some of the first in winter) were enabled by *Palmer's* ability to penetrate the sea ice covering the WAP shelf in winter.

The main factors governing variations in rates of bacterial secondary production (BP) are not well known, but 10 years of observations from the LTER cruises (2003–2012; Ducklow et al., 2012b) demonstrate close coupling between PP and BP over regional and interannual scales

(Figure 2). Chlorophyll is the best predictor of BP variability, indicating that local accumulation of organic matter is the principal source of sustenance for bacteria, at least in summer.

The role of temperature in regulating bacterial activity is a classic problem in microbial ecology. The governing paradigm is that temperature interacts with organic matter availability, and that low temperature (i.e., near the annual minimum) inhibits bacterial activity when organic matter is low (Pomeroy and Deibel, 1986). However, recent observations along the WAP showed no universal relationship between BP and temperature.

Historically, Antarctic marine ecosystems were believed to be simple, linear food chains where primary production

by diatoms was conveyed via krill to large consumers such as penguins, seals, and whales. We now know these systems harbor more complicated food webs made up of a microbial assemblage that includes microzooplankton (zooplankton $< 200 \mu\text{m}$, the majority of which are protozoa). There is a diverse assemblage of microzooplankton in the WAP that can ingest a major fraction of the daily primary and bacterial production, more so than can the macrozooplankton described below, at least in summer (Lori Price, Virginia Institute of Marine Science, *pers. comm.*, July 2012).

ZOOPLANKTON

The central role that the Antarctic krill, *Euphausia superba* (Figure 3), plays in the WAP's food web has been recognized for more than a century, so it is not surprising that the zooplankton community has remained a focus of research here. Most Antarctic top predators, including penguins, seals, and baleen whales depend upon krill for food, while krill themselves are major grazers of phytoplankton and through their metabolism recycle nutrients and export organic matter to depth. The last two decades of zooplankton studies in the WAP carried out on the *Gould* and the *Palmer* have revolved around a number of themes that include the importance of sea ice to krill and effects of climate change on zooplankton community structure, the importance and role of taxonomic groups other than krill, and how hydrography and water circulation affect zooplankton (physical-biological coupling).

Studies in the WAP indicate a relationship between seasonal and interannual ice dynamics and recruitment and abundance of krill, as well as abundance of other species. The algal community

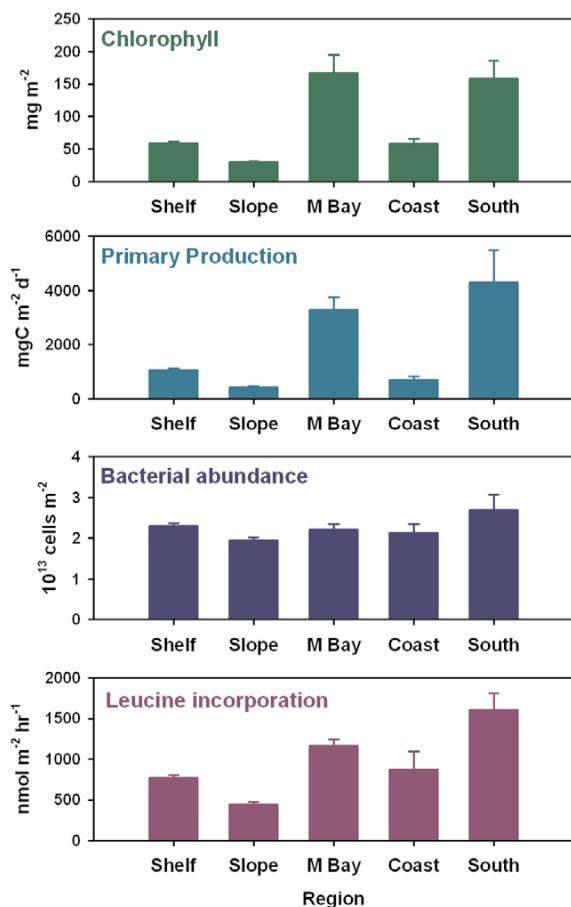


Figure 2. Long-term (2003–2011) regional averages for chlorophyll and bacterial stocks and rates of primary and bacterial production (all collected at 0–50 m) along the western Antarctic Peninsula. Shelf, oceanic (slope), and coastal stations are defined by bathymetry. See Figure 1 for location of Marguerite Bay (M Bay); south stations are located south of Marguerite Bay.

associated with sea ice provides food for developing larval krill when water column food resources are scarce, and thus years, or regions, with extensive winter sea ice should favor winter-over survival of larvae and subsequent recruitment to the juvenile stage. Decadal-scale climate fluctuations such as the El Niño-Southern Oscillation that affect sea ice dynamics have been linked to variability in krill reproductive and recruitment success (Quetin et al., 2003; Loeb et al., 2009). Larval krill adaptations, such as feeding on nonphytoplankton prey, delayed development, or shrinking in size, lend flexibility to their behavior, enabling them to survive the winter (Daly et al., 2004; Ross et al., 2004). Controls on distribution and abundance of other species have also been linked to seasonal sea ice dynamics. For example, Ross et al. (2008) demonstrate a negative correlation between salp (gelatinous, pelagic tunicate) abundance and both the timing of sea ice advance and duration of ice cover. Long-term climate warming

trends have also led to important changes in the WAP zooplankton community, such as an increase in the range and frequency of salp occurrence (Ross et al., 2008) and a decrease in krill in the northern WAP (recent work of author Steinberg and colleagues). These changes in the WAP are analogous to those over a larger region in the Southwest Atlantic sector of the Southern Ocean, where salps are increasing and krill are declining (Atkinson et al., 2004) coincident with the sea ice decline.

Partly as result of a changing zooplankton community, the importance of other dominant taxonomic groups besides krill in the WAP, such as copepods, salps, and pteropods (pelagic snails) are increasingly recognized (Figure 3). Based on 12 years of data from the PAL-LTER project, Ross et al. (2008) show patterns in the summer climatology of three krill species, salps (*Salpa thompsoni*), and pteropods (*Limacina helicina*) that are distinct and correlate with sea ice and with

cross-shelf gradients with high abundance either inshore (krill) or offshore at the outer shelf break (salps). In fall and winter, copepods usually dominated both abundance and biomass of zooplankton on or near the continental shelf in Marguerite Bay (Ashjian et al., 2004). Regional differences or temporal changes in zooplankton community structure in turn affect food web dynamics and biogeochemical cycling. In summer, grazing by salps, which have high ingestion rates, resulted in a distinct shift in the relative importance of the major macrozooplankton grazers from krill and pteropods near the coast and over the shelf to salps offshore at the shelf break; there was also a shift in highest grazing impact from krill and pteropods in the south to salps in the northern WAP (Bernard et al., 2012; Figure 4). This community shift also significantly increased overall macrozooplankton community grazing impact. Focused studies on salps indicate *Salpa thompsoni* produce fecal pellets that sink on average 700 m per day,



Figure 3. Zooplankton and fish of the western Antarctic Peninsula. Clockwise, starting from far left (with photo credits): Deploying a zooplankton net aboard ARSV Laurence M. Gould (D. Steinberg); Antarctic krill, *Euphausia superba* (D. Steinberg); pteropod, *Limacina helicina* (J. Cope); copepod, *Calanus propinquus* (M. Gleiber); Silverfish, *Pleuragramma antarcticum* (D. Steinberg). Center: chain of salps, *Salpa thompsoni* (L. Madin).

and defecation rates of salps can exceed that of krill (Phillips et al., 2009). Thus, changes in community structure from krill to salps could affect particle export in the WAP (Gleiber et al., in press).

Physical processes play a major role in structuring the WAP zooplankton community. WAP circulation acts both as a means of transport (the WAP is considered to be a source of krill for regions to the north and east) and as a retention mechanism (gyres in regions such as Marguerite Bay could retain krill locally) (Hofmann et al., 1996; Ashjian et al., 2004). While recent studies did not find a large population of krill overwintering on the shelf in Marguerite Bay (Ashjian et al., 2004), there was evidence of higher krill biomass in regions of weaker currents, suggesting avoidance of advection away from the area (Lawson et al., 2008). The sources of Antarctic krill recruitment into the WAP appear to be a mix of both local, with spawning and larval development in deep troughs or canyons, and advective, from offshore spawning habitats to onshore. These two sources are evidenced from net collections and acoustics (Wiebe et al., 2011) as well as genetic variation in WAP krill populations (Batta-Lona et al., 2011). In addition, genetic continuity among marine

benthic invertebrates living on the WAP and on South America continental shelves is maintained via transport of their pelagic larvae across the Drake Passage and polar front to the WAP (Scheltema et al., 2010).

FISHES

Pelagic fishes are an important component of the Antarctic food web as consumers of zooplankton (especially krill) and as prey for many top predators. Pelagic fish populations at the shelf break in most coastal regions of the Antarctic exhibit a distinct separation between off-shelf, mesopelagic, oceanic fauna and on-shelf, neritic fauna. This separation is not seen in the WAP, where UCDW forms a warmer layer in the mesopelagic over the shelf, and oceanic species mix with endemic neritic species (Donnelly and Torres, 2008; Cullins et al., 2011). The degree to which oceanic or neritic species dominate the WAP assemblage is dependent upon the subsurface temperature and salinity maxima, with colder, less-saline waters favoring neritic fauna (Donnelly and Torres, 2008). The dominant neritic fishes are the notothenioids, particularly *Pleuragramma antarcticum*, the Antarctic Silverfish (Figure 3), and they are able to survive in cold shelf

waters because of biological antifreezes in their blood (Cullins et al., 2011; and see Detrich et al., 2012, in this issue). Dominating the oceanic assemblage are mesopelagic myctophids—particularly *Electrona antarcticum*, paraplepidids, and bathylagids (Donnelly and Torres, 2008; Cullins et al., 2011), which lack antifreeze glycoproteins in their blood (Cullins et al., 2011) and thus can only occur on the WAP shelf where there is input of UCDW.

TOP PREDATORS

The large and persistent biomass of krill and other mid-trophic-level species in this region of the Southern Ocean sustains a large biomass of warm-blooded top predators, possibly the most important community of warm-blooded top predators in the world in terms of energy flux. A distinct advantage of working in the WAP is the ability to coordinate ship-based studies with demographic measurements on breeding colonies. As many of these colonies have long-term data sets, population trends can be correlated with dynamic oceanographic processes. Such information is essential for disentangling the role of climate change from food web interactions that have resulted from the

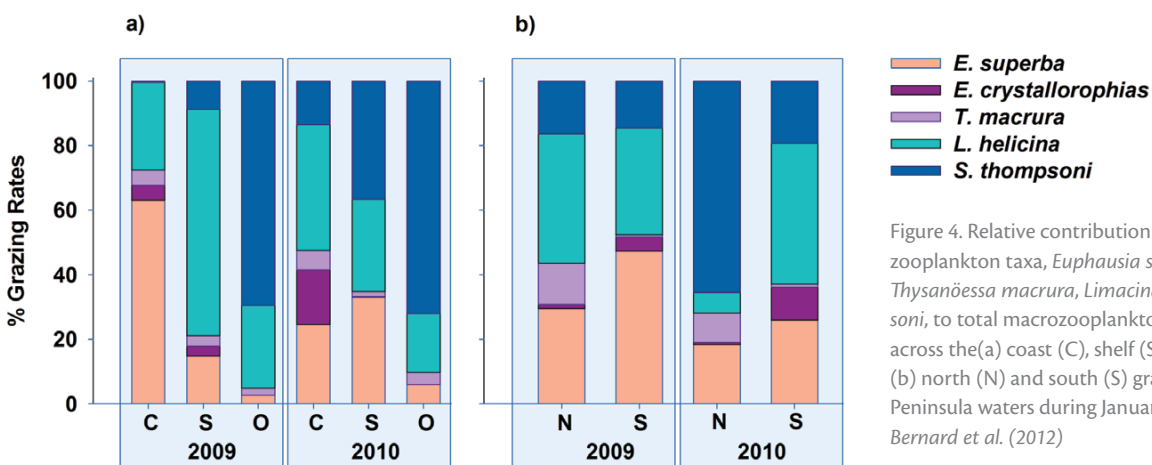


Figure 4. Relative contribution of the dominant macrozooplankton taxa, *Euphausia superba*, *E. crystallophias*, *Thysanöessa macrura*, *Limacina helicina*, and *Salpa thompsoni*, to total macrozooplankton community grazing rates across the (a) coast (C), shelf (S), and offshore (O) and the (b) north (N) and south (S) gradients of western Antarctic Peninsula waters during January 2009 and 2010. From Bernard et al. (2012)

human exploitation of top predators (Ainley et al., 2010; Trivelpiece et al., 2011, Ducklow et al., 2012a). This region has already witnessed the loss of the only Emperor Penguin colony in the WAP along with a reduction in all penguin species. This overall reduction in numbers has been accompanied by the replacement of Adélie penguins by Chinstrap and Gentoo penguins in the northern and mid-peninsula region; Adélie penguins rely on the winter sea ice while the latter species prefer open water (Ducklow et al., 2012a).

The WAP has been an area of intense research where new tools and technologies (electronic tracking, acoustic receivers, gliders, and stable isotopes) have been integrated with traditional approaches (*Palmer-* and *Gould-*based surveys, diet analysis, colony-based demographics) to significantly increase our understanding of the ecology, behavior, and physiology of top predators (Costa et al., 2010; Kahl et al., 2010). Surveys from studies conducted aboard the *Gould* and the *Palmer* revealed the presence of crabeater seals (*Lobodon carcinophagus*), leopard seals (*Hydrurga leptonyx*), Weddell seals (*Leptonychotes weddellii*), southern elephant seals (*Mirounga leonina*), and Antarctic fur seals (*Arctocephalus gazella*); however, only crabeater seals were present in large numbers (Chapman et al., 2004). The most commonly sighted cetaceans are humpback (*Megaptera novaeangliae*) and minke whales (*Balaenoptera bonaerensis*). These whales are most often sighted in the austral fall and winter along the continental shelf in coastal habitats, particularly fjords, where complex bathymetry and the presence of Circumpolar Deep Water concentrate their prey. Foraging habits of Adélie penguins and crabeater

seals are constrained by their need to periodically haul out on ice or land, whereas humpback and minke whales are more closely associated with proximity to their prey (Friedlaender et al., 2011). Visual whale surveys, coupled with penguin stomach content analysis and net tows to sample the prey field, indicate that humpback whales prefer larger, older krill and are more abundant in areas where penguins have the greatest foraging success (i.e., have full stomachs; Friedlaender et al., 2008). Humpback and minke whales appear to segregate their foraging activities by depth, as minke whale sightings were associated with deeper krill aggregations (Friedlaender et al., 2009).

Fronts are known to aggregate prey,

and seabirds were most frequently congregated during the winter near the ice edge, the Antarctic Polar Front, and the Shelf Break Front (Chapman et al., 2004). During summer, when both penguins and flying seabirds are constrained by their need to return to their breeding colonies, they were most associated with the Shelf Break Front and the southern boundary of the ACC (Ribic et al., 2011). During winter, a region of particularly high abundance of top predators, a biological “hotspot,” was identified within Marguerite Bay (Friedlaender et al., 2011; Figure 5). Marguerite Bay has a persistent polynya and a deep trough that facilitates the intrusion of UCDW onto the shelf and into the bay (Dinniman et al., 2011). Although forage

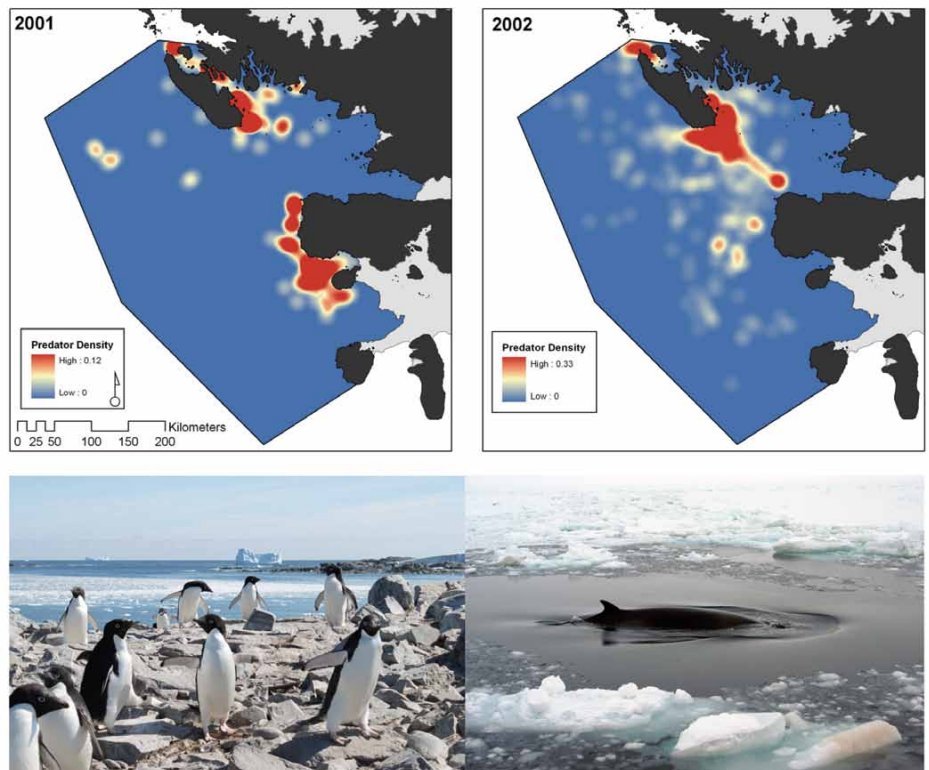


Figure 5. (top) Occurrence patterns of Adélie penguins, crabeater seals, and humpback and minke whales in the Marguerite Bay region, a “biological hot spot” during 2001 and 2002. Distributions of penguins and seals were derived from satellite tracking data, while visual surveys were used for the whales (from Friedlaender et al., 2011). (bottom left) Adélie penguin colony on Avian Island. D. Steinberg (bottom right) Minke whale surfacing near Palmer Station. D. Costa

success during the winter is unclear for most species, the mass and fat content of crabeater seals increased over the fall and winter, indicating successful foraging during the period of greatest winter darkness and highest ice cover (McDonald et al., 2008). A surprise finding based on stable isotope signatures from whiskers and scat analysis was that in addition to their primary prey, Antarctic krill, crabeater seals also consume fish (Hückstädt et al., 2012).

The movement patterns and foraging behavior of a variety of birds and mammals have been examined using satellite

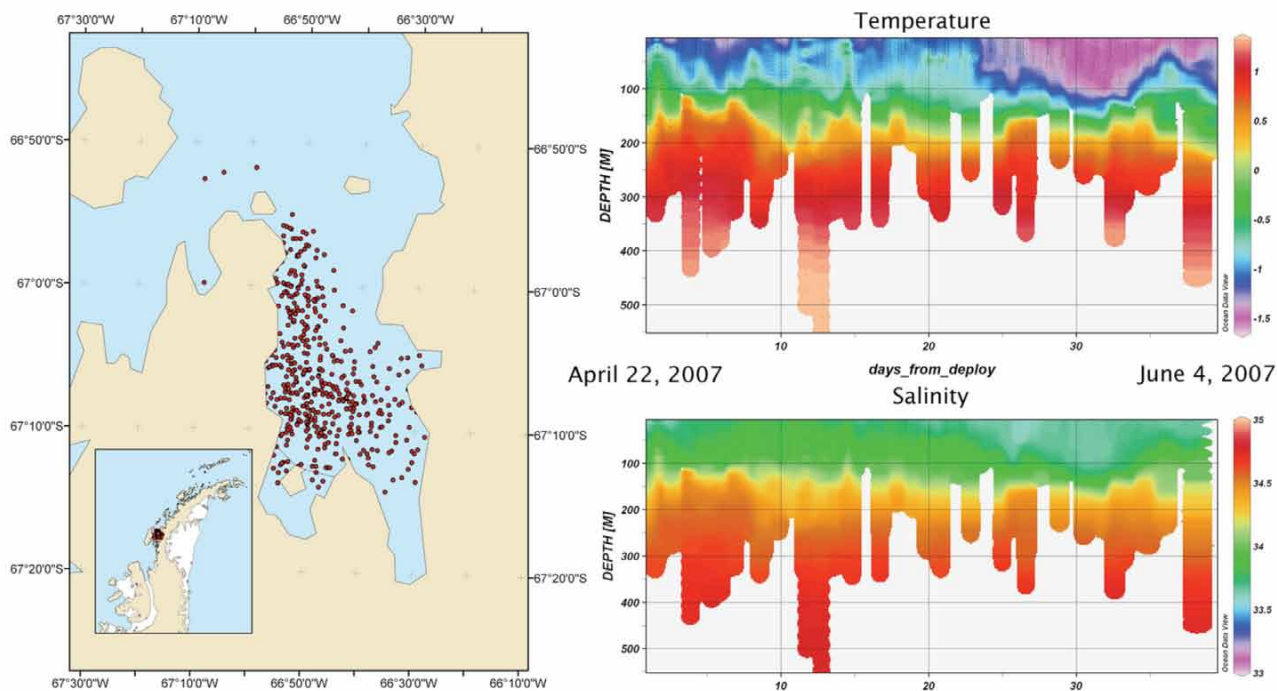
telemetry. Adélie penguins forage in shallow (< 200 m) waters near land and in the mixed layer (200–500 m) near the edges of deep troughs that cut across the continental shelf, even in winter (Erdmann et al., 2011). In the WAP, Weddell seals appear to be sedentary, remaining in the fjords, whereas crabeater seals move extensively along the continental shelf (as much as 664 km to northeast, 1,147 km to southwest), staying deep within the pack ice throughout the winter and closer to shore in regions where the change in bathymetry was greatest (Burns et al., 2004). Elephant seals moved along the

outer margins of the continental shelf and considerable distances offshore into pelagic waters (Costa et al., 2010). One elephant seal foraged 5,400 km to the west, well into the Amundsen and Bellingshausen Seas. These species partition their habitat by foraging depth and duration, with the longest and deepest dives by elephant seals.

Recently deployed conductivity-temperature-depth (CTD) tags on seals can collect salinity and temperature data along with animal behavior data. These tags reveal that elephant seals prefer UCDW, while crabeater seals prefer a



Figure 6. (top) A Weddell seal carrying a Sea Mammal Research Unit CTD (conductivity-temperature-depth) tag. *Photo courtesy of D. Costa.* (bottom left) Location of Weddell seal when CTDs were taken in the Lallemand Fjord, WAP. The small inset at lower left shows the location of the Lallemand Fjord just to the east of the northern tip of Adelaide Island. (bottom right) Smoothed temperature and temperature sections obtained from a single Weddell seal from April 22 to June 4, 2007. *Figure from Costa et al. (2010)*



lower range of temperature and salinity typically found on the inner shelf (Costa et al., 2010). The CTD-tagged seals have also provided oceanographic data in regions rarely visited by ships and can operate throughout the Antarctic winter (Figure 6; Costa et al., 2008, 2010). Oceanographic data collected by elephant seals provided insight into the unexpected breakup of the Wilkins Ice Shelf in 2008. Two sets of data were collected; the first relied on observations that elephant seals were diving deeper than the known bathymetry. These observations led to a refined bathymetry for this region, which uncovered a series of deep troughs that extend from the outer to the inner continental shelf near the Wilkins Ice Shelf (Padman et al., 2010). The second data set, temperature records recorded from the seals' tags, confirmed the flow of UCDW underneath the Wilkins Ice Shelf, which added heat and thus contributed to the breakup of the ice shelf (Padman et al., 2012). Other new technologies include the use of fixed, bottom-mounted moorings (Acoustic Recording Packages) and deployment of sonobuoys from the ships to record the calls of a variety of whale and seal species. These documented the year-round presence of blue whales (*Balaenoptera musculus*) and the seasonal presence of calling fin whales (*B. physalus*). Call frequency of both species was lower in areas of heavy ice cover (Širović and Hildebrand, 2011).

FLUX AND BENTHO-PELAGIC COUPLING

Particle flux in the WAP (as determined by a long-term, time-series sediment trap at 170 m over the shelf) exhibits extreme seasonal and interannual variability, with peak flux in summer following


the annual sea ice retreat and phytoplankton bloom (Ducklow et al., 2008). Zooplankton fecal pellets, mostly from krill, dominate particulate organic carbon (POC) flux over the WAP continental shelf; thus, climate-induced changes in plankton community structure could alter POC export (Gleiber et al., in press), as noted above. The connection between water column POC flux and benthic processes was explored in the FOODBANCS program (Smith and DeMaster, 2008). Interestingly, the seasonal response of the WAP-shelf benthic ecosystem is mild compared to the extreme seasonal variability in POC flux. Labile organic carbon from these seasonal flux pulses accumulates in the WAP sediments, resulting in a “food bank” that sustains benthic detritivores through the winter, with processes such as benthic feeding and sediment-community oxygen consumption relatively uninterrupted (Smith and DeMaster, 2008).

CONCLUSION

Clearly, the era of research supported by the *Palmer* and the *Gould* has resulted in significant increases in our understanding of the WAP pelagic ecosystem. Prior to this era, we had some understanding of the hydrography, the major “players” in the WAP food web and their life histories, and enough of a foundation to begin to answer: What drives production and distribution of WAP organisms over time and space? The effects of climate warming on the WAP region were just beginning to be recognized, but the effects, if any, on most organisms was unknown. The major contributions of the *Palmer* and the *Gould* era have been to make important connections between hydrography and biology, to enhance understanding of how community

structure can affect biogeochemical cycling, and to show the unprecedented effects of climate warming on ecosystem structure. The interdisciplinary, cooperative nature of many of the major programs supported by these ships was key to our success, as it will be in the future.

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