

CHAPTER 5

THE MARINE SYSTEM OF THE WESTERN ANTARCTIC PENINSULA

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5.1 INTRODUCTION

The marine ecosystem of the West Antarctic Peninsula (WAP) extends for ~1500 km from the Bellingshausen Sea near 75° S, 80° W to the northern tip of the peninsula near 63° S, 60° W, and from the mostly glaciated coast in the east across the continental shelf to the shelf break in the west. The shelf is about 200 km wide and averages 430 m in depth. The shelf break is defined by steep, rapidly deepening bathymetry between 750 and 3000 m (Figure 5.1). The glacially-sculpted coastline along the peninsula is highly convoluted, with numerous islands, deeps, bays, fjords, often

interconnected by channels, sometimes as deep as 900 m. The domain is divided into three sub-regions (continental slope, shelf and coastal regions of Figure 5.1B), defined by bathymetry, ocean dynamics, water mass and biological distributions.

This region at its widest extent includes three of the four circumpolar Antarctic marine ecosystem types or biomes defined by Treguer & Jacques (1992): the Permanently Open Ocean Zone (POOZ); Sea Ice Zone (SIZ), and bordering the continent, the Coastal and Continental Shelf Zone (CCSZ). The Polar Front Zone *per se* is not in our study region but the Southern Antarctic Circumpolar Current Front (SACCF) impinges on the

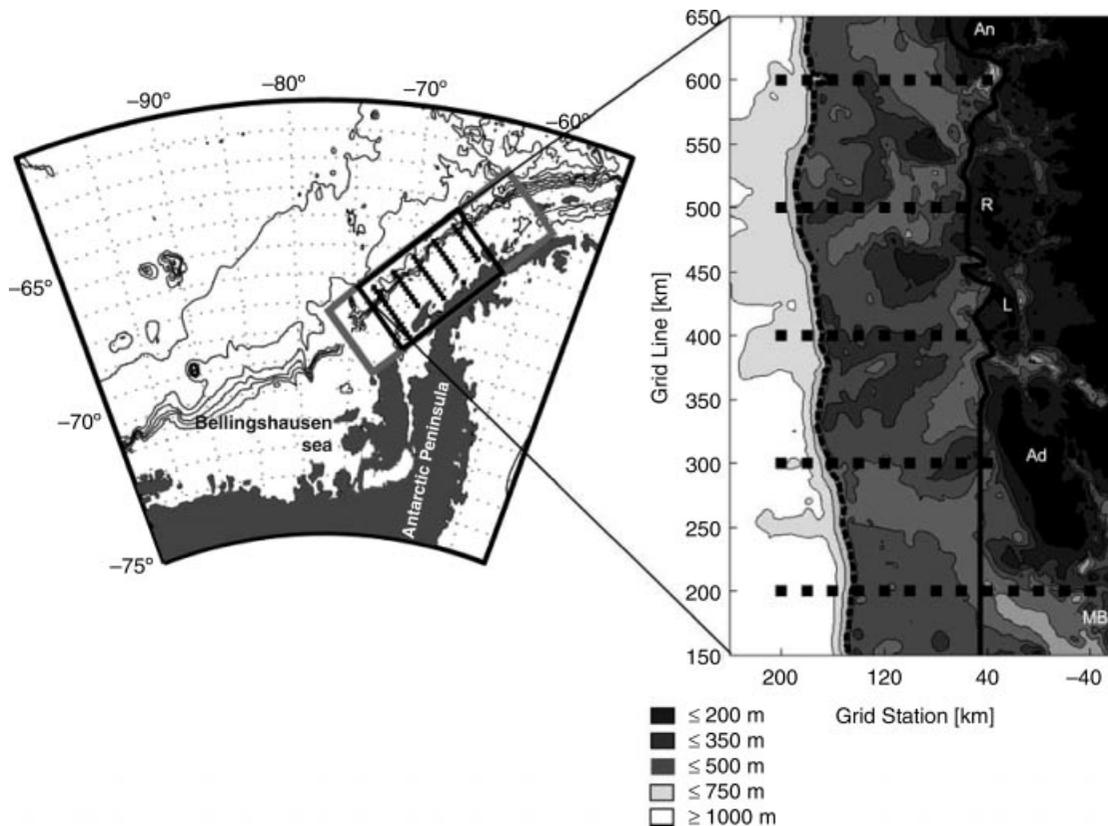


Figure 5.1 Left: Palmer Station Long Term Ecological Research (LTER) study region along the WAP showing sampling grid (bold black box) with labeled contoured bathymetry (750 m intervals). Right (inset): The main sampling grid occupied each January since 1993 consists of stations (small squares 10 km apart) arranged in 10 onshore to offshore lines spaced 100 km apart along the Peninsula (only lines 200–600 shown); stations proceed offshore from an arbitrary 0 line defining the peninsular coastline. An, R, Ad: Anvers, Renaud and Adelaide Islands; MB: Marguerite Bay. Continental shelf break indicated by dashed bold line (slope to left) and shelf-coastal sub-regions separated by solid bold line.

continental shelf (see below). Like other SI2, the WAP ecosystem is very productive, supporting large stocks of marine mammals and birds, as well as the Antarctic krill, *Euphausia superba* (Ross *et al.*, 1996b). The dynamics of the ecosystem are dominated by the seasonal growth, extent and retreat of sea ice and their interannual variations. The northern part of the Antarctic Peninsula is also among the most rapidly warming regions on Earth, having experienced a 2 °C increase in annual mean atmospheric temperature since 1950. The surface ocean west of the peninsula has also warmed significantly. Meredith and King (2005) demonstrate warming of over 1 °C since 1955–1964. In the past two decades, dramatic responses of the ecosystem

to the climate and ocean warming have been documented. In this chapter we synthesize studies of rapid climate change and ecosystem responses to it, proposing the WAP marine system as a premier example of the more generalized phenomenon experienced globally. Results from the Palmer Antarctic Long-Term Ecological Research project (PAL-LTER; Ross *et al.* 1996a; Smith *et al.*, 2003b), RACER (Huntley *et al.*, 1991), Southern Ocean GLOBEC (Hofmann *et al.*, 2004), Rothera Oceanographic and Biological Time Series (RaTS; Clarke *et al.*, 2008; www.antarctica.ac.uk/rats) and other studies are reviewed.

The life cycles of organisms in the Antarctic coastal marine ecosystem depend profoundly on the annual

cycle and interannual variations in sea ice cover (Ross *et al.*, 1996a; Smith *et al.*, 1998). We begin by discussing recent climate changes and their effects on the duration and extent of sea ice, then proceed to some of the principal components of the upper ocean pelagic ecosystem. This review does not cover marine mammals, fish or seabirds other than penguins in detail, and is limited to the pelagic system. Benthopelagic exchanges are lessened in importance because Antarctic continental shelves are > 300 m deep, well below the winter mixed layer. Benthic systems are reviewed by Clarke *et al.* (2007) and this volume and by Smith *et al.* (2006).

5.2 CLIMATE AND ICE

5.2.1 Surface air temperature

Significant changes have occurred over the last half century in the Antarctic Peninsula (AP) region, including the northwestern Weddell and southern Bellingshausen Seas, as revealed by instrument records, station observations, satellite data, and paleoenvironmental records (Domack *et al.*, 2003; Turner *et al.*, 2009a). Surface air temperature records in particular reveal a warming in winter (June–August) of 6.1°C over 1951–2008 (~1°C per decade), a warming rate that exceeds any other observed globally (Vaughan *et al.*, 2003). The paleo-records provide a longer-term history of change in the AP region and lend perspective for understanding the most recent (half century) warming trend, showing it to be unique within the last few millennia (Domack *et al.*, 2003; Smith *et al.*, 1999b; Vaughan *et al.*, 2003).

The British Antarctic Survey (BAS) meteorological observations (<http://www.antarctica.ac.uk/met/gjma/temps.html>) at Faraday/Vernadsky station (65°15' S, 64°16' W) have been especially useful given their length (over five decades), consistency, and quality control. Here we update and augment our earlier analyses of these data (Smith & Stammerjohn, 2001; Smith *et al.*, 1996) with the addition of data through 2008. Figure 5.2a shows the Faraday/Vernadsky annual average air temperatures from 1951 to 2008 (N = 58). The linear trend (solid line) determined by the least squares slope and its standard error are $0.054 \pm 0.015^\circ \text{C/year}$ ($N_{\text{eff}} = 26.7$, $p < 0.01$). Monthly and seasonal analyses show that the warming trend in Faraday/Vernadsky air temperatures is strongest during the mid-winter months and peaks in July at $0.124 \pm 0.044^\circ$

C/year ($N_{\text{eff}} = 33.8$, $p < 0.01$). This represents a 7.2°C increase in July temperatures over 1951 to 2008. Spring and summer trends are not as pronounced. The record from Rothera (further south on the WAP, 67°34' S, 68°08' W) shows strong temporal coherence to Faraday/Vernadsky (Figure 5.2), displaying similar trends, but with mean annual temperatures averaging a few degrees cooler (King, 1994; Smith *et al.*, 1996). Spatial coherence of surface air and sea surface temperature in the Antarctic Peninsula region is also displayed in infrared satellite observations (Comiso, 2000). Changes in the annual progression of temperature and the amount of variability associated with those temperatures suggests a climate shift along the WAP where continental influences from the south are giving way to increasing maritime influences from the north (R.C. Smith *et al.*, 1999).

5.2.2 Sea ice

Concurrently, various trends have been detected in Antarctic sea ice, showing that the magnitude and direction are strongly dependent on the region and time interval studied (Cavalieri *et al.*, 1997; Comiso & Nishio, 2008; Parkinson, 2004; Stammerjohn & Smith, 1997; Turner *et al.*, 2009b; Watkins & Simmonds, 2000; Zwally *et al.*, 2002). Here we analyze the trends over 1979–2007 (N = 29) using Version 2 of GSFC Bootstrap SMMR-SSM/I derived sea ice data (http://nsidc.org/data/docs/daac/nsidc0079_bootstrap_seaice.gd.html). In contrast to the Southern Ocean as a whole, but consistent with the observed AP warming, the annual mean sea ice extent has trended down in the WAP region. Figure 5.2b shows the mean annual sea ice extent for the Southern Ocean (inset) and the Palmer LTER region. The Southern Ocean trend is positive ($11786 \pm 4632 \text{ km}^2/\text{year}$, $N_{\text{eff}} = 26.0$, $p = 0.01$), representing a 2.8% increase relative to the mean ($1.2 \times 10^7 \text{ km}^2$) over 29 years. In contrast, the trend in the Palmer LTER region is strongly negative (-1312 ± 720 , $N_{\text{eff}} = 14.4$, km^2/year , $p = 0.05$), representing a 41% decrease relative to the mean (92052 km^2) over 29 years.

As shown by Smith and Stammerjohn (2001) winter sea ice duration is decreasing considerably faster than maximum winter sea ice extent in the Palmer LTER and greater western Antarctic Peninsula region (i.e., winter sea ice still roughly extends as far northward as before but does not remain there as long). To better assess

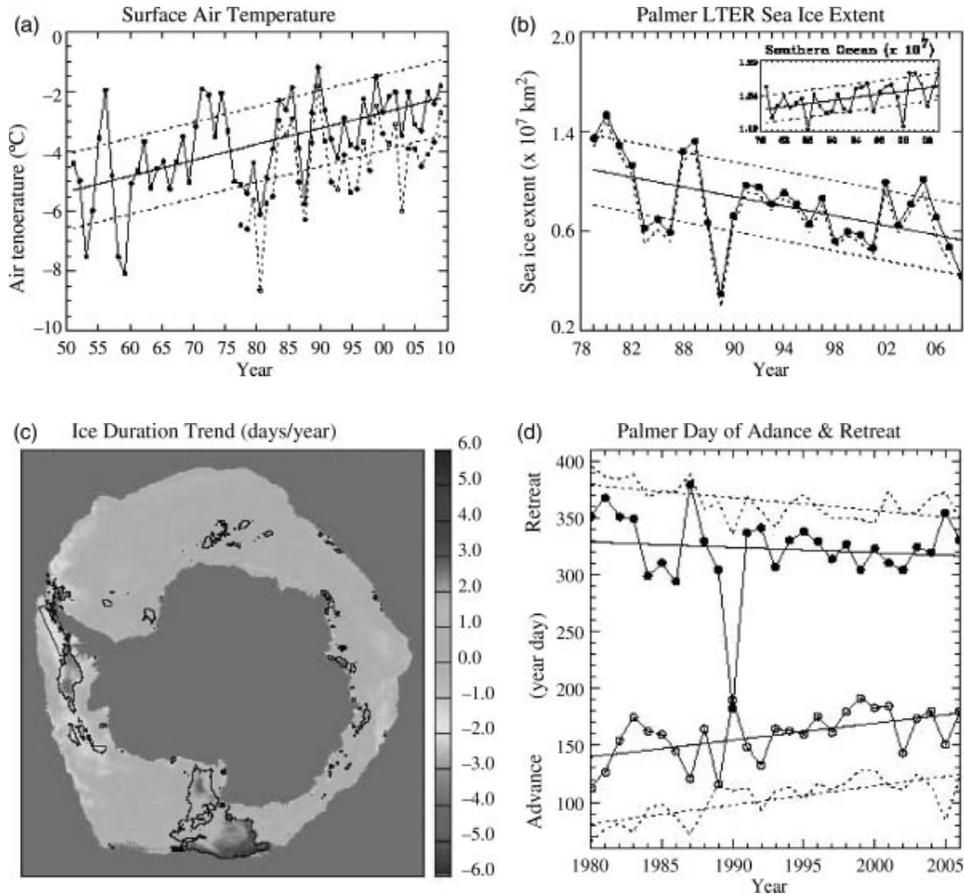


Figure 5.2 Annual average air temperature recorded at Faraday/Vernadsky Station ($65^{\circ}15'S$, $64^{\circ}16'W$) from 1951 to 2008, with linear regression fit (solid) and ± 1 standard deviation (dotted) about this fit. Annual average air temperature recorded at Rothera Station ($67^{\circ}34'S$, $68^{\circ}08'W$) from 1977–2008 is shown by the dotted curve. (b) Annual average sea ice extent for the Palmer LTER region and for the Southern Ocean (inset) from 1979 to 2008 with linear regression fit as in (a). Sea ice extent was derived from Version 1 (solid) and Version 2 (dotted) of the GSFC Bootstrap SMMR-SSM/I 1979–2007 ($N=29$) time series (see text). The 2008 data are preliminary estimates based on the Near Real Time Sea Ice data product (<http://nsidc.org/data/nsidc-0081.html>). (c) Spatial map of trend (days/year) in ice season duration over 1979/08 to 2006/07. The rectangular box west of the AP denotes the Palmer LTER large-scale grid, and the black contour signifies the area where the trend is significant at $p < 0.01$. (d) Time series (1979/80 to 2006/07) of day of advance (bottom solid with open circles, Palmer LTER; dotted, southern Bellingshausen Sea) and day of retreat (top solid with closed circles, Palmer LTER; dotted, southern Bellingshausen Sea), showing the linear regression fit. The time series are plotted such that e.g. year 1980 corresponds to the 1979–80 sea ice retreat and the subsequent 1980 sea ice advance. (Figure updated from Ducklow *et al.* 2007). (See the colour version of this figure in Plate section)

changing seasonality daily GSFC SMMR-SSM/I sea ice data are used to map for a given location when sea ice first arrives (day of advance) and last departs (day of retreat) during a sea ice year (mid-Feb of current year to mid-Feb of subsequent year), with the difference being ice season duration. Figure 5.2c shows the spatial

distribution of the trend in ice season duration over 1979–2007 for the Southern Ocean (similar to the 1979–2002 trend pattern in ‘ice season length’ reported by Parkinson (2004) and in sea ice concentration reported by Liu *et al.* (2004)). The rectangular box west of the AP denotes the Palmer LTER large-scale

grid, while the black contour indicates where the duration trend is significant at $p < 0.01$. The WAP region shows a decreasing trend in ice season duration, with a regional average decrease of 59 days in the Palmer LTER region over 1979–2007 (-2.11 days/year); further to the south (i.e., southern Bellingshausen Sea) ice duration decreased by 79 days (-2.82 days/year). Elsewhere in the Southern Ocean, ice season duration increased, particularly in the western Ross Sea, with a regional average increase of 59 days ($+2.11$ days/year).

As shown in Figure 5.2d, the decreasing trend in ice season duration in the WAP region is due to a strong trend towards a much later autumn sea ice advance (44 and 48 days over 1979–2007 for the Palmer LTER (solid) and southern Bellingshausen Sea (dotted) regions, respectively), and a somewhat earlier spring sea ice retreat (15 and 31 days, respectively). As expected, sea ice advance comes earlier (in the year) in the southern Bellingshausen Sea region than in the more northern Palmer LTER region, and vice versa for spring sea ice retreat. We also note that there is a stronger correlation between the advance and retreat time series when, as plotted in Figure 5.2d, spring sea ice retreat is correlated against the subsequent autumn advance ($R = -0.80$ for the southern Bellingshausen Sea region), than when the autumn advance is correlated against the subsequent spring retreat ($R = -0.44$). This is true for Arctic sea ice advance and retreat as well (Stammerjohn *et al.*, 2009). However, unlike the AP and southern Bellingshausen Sea region, trends in Arctic sea ice retreat are stronger than in sea ice advance (e.g., for the East Siberian–Chukchi–Beaufort Sea region, sea ice advance is ~ 26 days later and sea ice retreat ~ 35 days earlier over 1979–2006), but sea ice duration is decreasing faster by 29% in the AP and southern Bellingshausen Sea region than in the East Siberian–Chukchi–Beaufort Sea region (83 versus 59 day decrease over 1979–2006, respectively). Turner *et al.* (2009a) showed recently that the increasing sea ice in the Ross Sea is dependent on an intensification in the southerly winds in the sector, with ozone depletion being the most likely primary underlying cause.

5.2.3 Climate co-variability

Numerous studies have shown air temperature and sea ice in the AP region to be sensitive to variability in (1) the Southern Oscillation (Kwok & Comiso, 2002a;

Simmonds & Jacka, 1995; Smith *et al.*, 1996), (2) the El Niño Southern Oscillation (ENSO) (Harangozo, 2000; Marshall & King, 1998; Meredith *et al.*, 2004, 2008; Rind *et al.*, 2001; Yuan & Martinson, 2000), and (3) the Southern Annular Mode (SAM) (Hall & Visbeck, 2002; Lefebvre *et al.*, 2004; Marshall *et al.*, 2004; Simmonds, 2003; Thompson & Solomon, 2002; van den Broeke & Lipzig, 2003). Other studies offer general reviews of climate co-variability and the high latitude teleconnection in the Southern Ocean (Carleton, 2003; Parkinson, 2004; Simmonds & King, 2004; Turner, 2004; Yuan, 2004). Yuan (2004) provides a thorough conceptualization of the potential mechanistic linkages between polar and lower latitude ocean and atmospheric processes and shows that the Southeast Pacific undergoes the largest extra-tropical surface temperature response to ENSO on Earth. A few studies in particular have analyzed the high latitude response in the Southeast Pacific to the combined effect of ENSO and SAM variability (Fogt & Bromwich, 2006; Kwok & Comiso, 2002b; Liu *et al.*, 2004; Stammerjohn *et al.*, 2008b).

Figure 5.3 summarizes some of the highlights of climate co-variability in the Palmer LTER region: (a) Palmer LTER sea ice extent negatively co-varies with Faraday/Vernadsky air temperature (1979–2008 annual, $R = -0.93$, with highest monthly correlations in late spring/early winter, R (Jun) = -0.87); (b) 10-year running correlations show that since the 1990s correlations decreased, along with large multiyear swings in positive/negative sea ice anomalies; (c) Palmer LTER sea ice extent and the Southern Oscillation Index (SOI; the standardized sea-level pressure difference between Tahiti and Darwin, Australia) negatively co-vary (1979–2008 annual, $R = -0.52$, with highest monthly correlation in spring, R (Nov) = -0.61); and (d) 10-year running correlations show again decreased correlations since the 1990s (less so for smoothed time series, dotted lines), while the longer view provided by the Faraday/Vernadsky air temperature record shows that correlations with SOI were stronger in the 1960s to mid-1970s in addition to the 1980s. Similar results to (c) and (d) are obtained when an ENSO index (e.g., Niño3.4) is used. Additionally, though not shown, Palmer sea ice extent negatively co-varies with SAM variability (1979–2008 annual, $R = -0.41$, with highest monthly correlations in spring, R (Nov) = -0.53).

Concurrent with decreased climate co-variability with Palmer LTER sea ice extent in the 1990s is increased

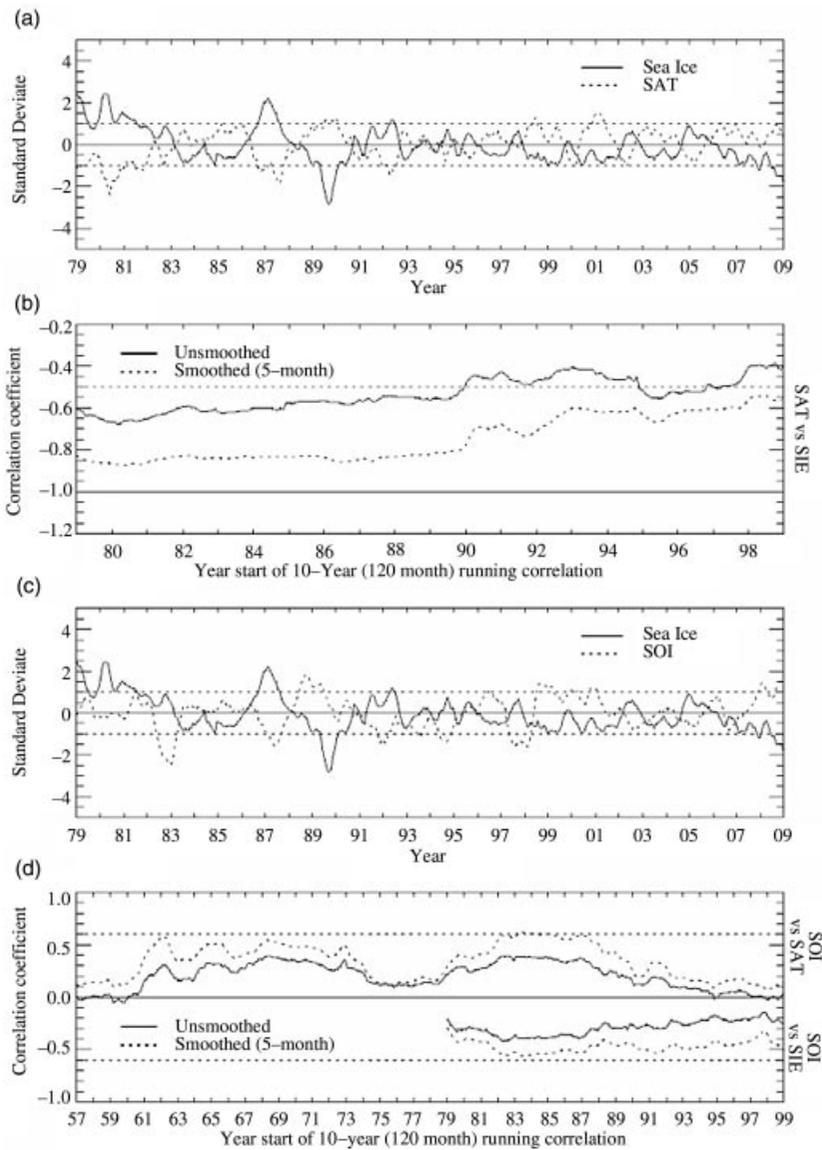


Figure 5.3 Monthly standard deviates (smoothed by 5-month running means) from January 1979 to December 2008. Monthly standard deviates were determined by dividing the anomaly (for the month and year in question) by the standard deviation of the anomaly (for the month in question). (a) Faraday/Vernadsky air temperature (dotted) and Palmer LTER sea ice extent (solid), (b) 10-year (120 month) running correlations between unsmoothed (solid) and smoothed (dotted) time-series of Faraday/Vernadsky air temperature and Palmer LTER sea ice extent; the smoothing was by 5-month running means, (c) Palmer LTER sea ice extent (solid) and Southern Oscillation Index (SOI) (dotted), and (d) 10-year (120 month) running correlations between unsmoothed (solid) and smoothed (dotted) time-series of Faraday/Vernadsky air temperature and SOI (positive correlations from 1957 to 1998), and between unsmoothed (solid) and smoothed (dotted) time-series of Palmer LTER sea ice extent and the SOI (negative correlations from 1979–1998).

seasonal variability (Smith *et al.*, 1998; Smith & Stammerjohn, 2001; Stammerjohn *et al.*, 2008a). Increased seasonal variability between the 1980s and 1990s is captured by the degree of persistence in monthly sea ice extent anomalies, which decreased from 12–13 months in the 1980s to two months in the 1990s (based on autocorrelation analysis). Increased seasonal variability is largely a result of increased variability in the timing of sea ice advance and retreat in the 1990s (Stammerjohn *et al.*, 2008a; 2008b), and this has direct implications for the marine ecosystem. The life histories of most polar marine species have evolved to be synchronized with the seasonality of sea ice (Ross *et al.*, 1996a; Smith *et al.*, 1995). Therefore, the marine ecosystem may be more sensitive to changes in the seasonal timing of sea ice advance and retreat than to overall changes in magnitude of winter sea ice extent (Smith *et al.*, 2003a, b), thus providing further impetus to understand the increased variability in sea ice advance and retreat.

As indicated by Figure 5.2, we have analyzed the variability and trends in the timing of sea ice advance and retreat. In contrast to results shown in Figure 5.3d, correlations between the timing of sea ice advance and retreat against ENSO and SAM variability are stronger (than for monthly sea ice extent) and markedly increase in the 1990s (Stammerjohn *et al.*, 2008a, b). Thus, given the increased seasonal variability of sea ice in the WAP region, monthly sea ice extent may not be the best variable for examining this relationship, as we seem to better capture sea ice sensitivity to ENSO and SAM variability by restricting our focus to the periods of sea ice advance and retreat.

This is not surprising given that the high latitude atmospheric response to ENSO intensified during austral spring–summer (Fogt & Bromwich, 2006) and SAM became more positive during summer–autumn (Marshall, 2003; Turner *et al.*, 2009b). The strengthening of the high latitude atmospheric circulation in the 1990s during large ENSO events appears to be related to stronger and more *sustained* periods of co-variability between ENSO and SAM during spring-to-autumn. Concurrently, the positive trend in SAM (Marshall, 2003; Thompson *et al.*, 2000) is implicated in asymmetrically strengthening the high latitude response to La Niña over El Niño events, thus helping to explain the overall negative sea ice response. Despite the strengthening of the high latitude atmospheric circulation in both spring and autumn, the sea ice response appears greater during the autumn sea ice advance than during the spring

retreat (Stammerjohn *et al.*, 2008b). This may be due in part to sea ice advance being more sensitive to climate variability than its retreat. The northward expansion of sea ice during advance is not physically constrained by a continental boundary, and can quickly occur (relative to the retreat) given the ability to rapidly vent ocean heat, especially during cold air outbursts. In contrast, sea ice retreat is constrained both physically (by the Antarctic continent, but also by increasing sea ice thickness, to the south) and thermally (weaker air-sea temperature contrasts driving weaker ice growth).

Within the context of the rapid warming of the AP region, we summarize our current findings as follows. The strongest trends in surface air temperature are during mid-winter months, peaking in July, with a 6.1°C increase since 1951. In contrast the strongest trends in sea ice are occurring during spring–summer when sea ice is retreating and during the subsequent autumn when sea ice is advancing. The trend towards a later advance and earlier retreat results in decreased winter sea ice duration. Concurrently, a decrease in sea ice concentration has also been observed for the greater WAP region (Vaughan *et al.*, 2003; Liu *et al.*, 2004). As suggested by others (Harangozo, 2006; Meredith & King, 2005; Vaughan *et al.*, 2003), decreased winter sea ice duration and concentration are changes that would conceivably increase winter ocean heat flux, both to the overlying atmosphere through leads and other openings, as well as to the underside of sea ice and marine glaciers (though attempts to quantify this show mixed results; see next section). Therefore, the rapid warming in winter in the AP region may largely be due to changes occurring in the atmospheric circulation during austral spring, summer and autumn that are negatively affecting the advance and retreat such that winter sea ice duration and concentration are decreasing, and ocean winter heat flux is increasing.

5.3 PHYSICAL OCEANOGRAPHY

The most voluminous source of ocean heat and nutrients in the Southern Ocean is Upper Circumpolar Deep Water (UCDW), transported by the Antarctic Circumpolar Current (ACC). The climatological southern edge or boundary of the ACC (SBACC, defined in Orsi *et al.* (1995) as the southern limit of Upper CDW characteristics) lies along the continental shelf break in the WAP region (Martinson *et al.*, 2008;

Orsi *et al.*, 1995). To the north is the southern ACC Front (SACCF, the southernmost current core of the ACC). The close proximity of the ACC to the broad continental shelves of the WAP (including the shelves of the Amundsen and Bellingshausen Seas at the base of the WAP to the southwest) makes this region oceanographically unique in the Antarctic.

Fundamental to the WAP is the relationship of shelf water masses to those of the ACC, in particular the UCDW. Martinson *et al.* (2008), wishing to relate shelf waters to those delivered to the region by the ACC, restrict the definition of UCDW to that as it occurs in the ACC immediately offshore of the WAP (hereafter referred to as “ACC-core UCDW”). When ACC-core UCDW is swept onto the shelf, mixing cools it to form modified UCDW (M-UCDW). Unmodified UCDW incursions occasionally survive short distances on the shelf (see Figure 5.4). Incursions most consistently move onto the shelf at the northern end of the large cross-shelf channel (Marguerite Trough) at the 300 cross-shelf line (Figure 5.1, Figure 5.4). Incursions of UCDW are consistent with the dynamic topography (circulation), indicating interactions of the ACC with shelf

bathymetry as the key physical mechanism driving the appearance of UCDW on the shelf.

Winter Water (WW) is prevalent throughout the Antarctic polar waters. This water is formed at or very near the freezing point – being the remnant winter mixed layer water – but here the summer values are well above freezing due to vertical mixing with the warmer waters above and below (Klinck, 1998; Martinson *et al.*, 2008; D.A. Smith *et al.*, 1999). The most conspicuously absent Antarctic water masses on the WAP shelf are the low- and high-salinity shelf waters (LSSW, HSSW) found at depth in numerous shelf locations around the continent. These waters, near the freezing point, with 34.6 salinity delimiting LSSW from HSSW, are notable for their role in deep and bottom water formation (Gill, 1973). This absence is consistent with the notion that bottom waters do not form in the WAP region today. LCDW is not commonly seen on the WAP shelf.

UCDW is quickly modified (cooled by mixing) as it moves across the shelf, cooling approximately linearly with distance from the slope (source) of the ACC-core UCDW. The significance of the cooling of this relatively warm water (3–4°C above the freezing point) on the

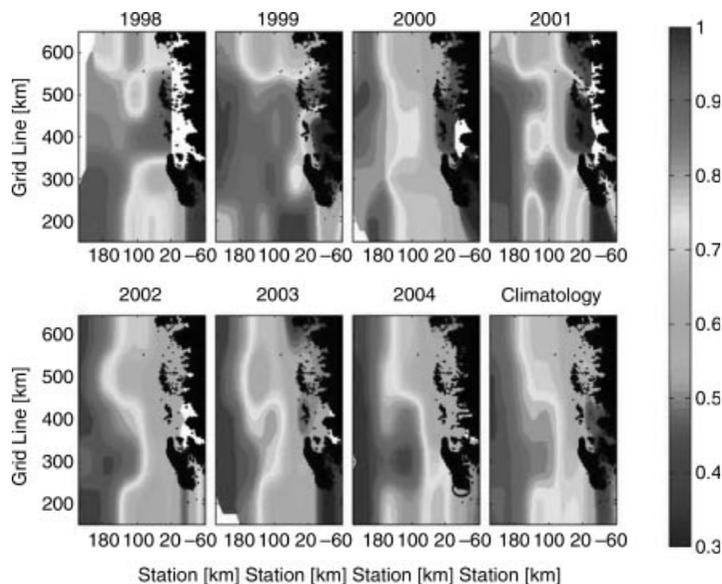


Figure 5.4 When Upper Circumpolar Deep Water (UCDW, see text) moves onto the continental shelf, it is quickly mixed to form cooler and fresher modified version of UCDW, making it difficult to track how that water from the ACC moves onto the shelf. In some locations the water makes short incursions onto the shelf with minimal modification allowing us to better track entry points and paths for moving onto the shelf. These annual maps show the location and extent of the short incursions of nearly unmodified UCDW for noted years. The actual colors correspond to the degree of UCDW modification (given as fraction of pure UCDW). (See the colour version of this figure in Plate section)

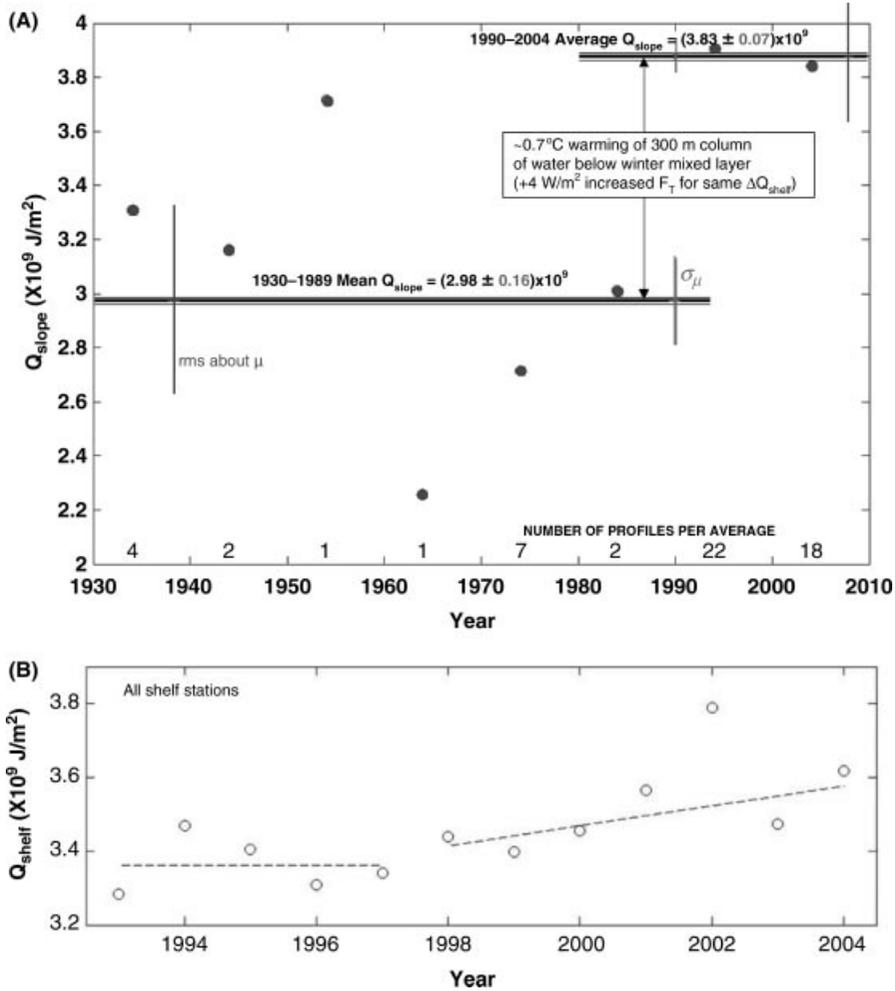


Figure 5.5 (A) Heat content (relative to freezing) of ACC slope water that has direct access to continental shelf, serving as source of ocean heat on the shelf. A considerable jump in this heat content occurs after the 1980s. Specifically, Q_{slope} averages $(2.98 \pm 0.16) \times 10^9 \text{ J/m}^2$ for the 17 stations pre-1990 vs $(3.83 \pm 0.07) \times 10^9 \text{ J/m}^2$ post-1990 stations (uncertainty in mean value shown about horizontal means as fine lines; scatter about means given by vertical bars). This is equivalent to a uniform warming of the $\sim 300 \text{ m}$ thick layer by 0.7°C . (B) More directly, heat content of this water on shelf, which is linearly related to the ocean heat flux, shows a jump in 1998, comparable to a 3 Wm^2 heat flux, followed by a linearly increasing trend of another 3 Wm^2 per year (excluding 2002 which is an unusually large outlier).

continental shelf is that the heat is passed from the water either to the atmosphere through leads and other openings or to the underside of ice (both sea ice and marine glaciers) thus melting it. This is important given the role of glacial ice melt to rising sea level, and the ocean heat is the only source of enough heat to melt this ice (the heat content of water is ~ 4700 times larger

than that of a comparable volume of air at the same temperature above freezing). The ocean heat content (Martinson *et al.*, 2008) has risen steadily along the WAP since 1998, with 84% of the increase due to increased upwelling, and 21% due to a light warming of the UCDW (Figure 5.5; the 1998 increase coincides with a regime shift observed in other variables across

the grid, including sea ice and other climate variables, Stammerjohn *et al.*, 2008b). Figure 5.5 shows that the increase in heat content is substantial relative to the average heat content in decades preceding 1990; enough of an increase sufficient to cause a 0.7°C warming of the upper 300 m of the water column below the winter mixed layer. This increase is a profound change in the physical environment and underlines the role of ocean circulation as the principal driver translating climate warming into ecosystem changes on the WAP shelf. The heat content is also a proxy for nutrient fluxes because UCDW is the primary imported source of these as well as heat; see below.

5.4 NUTRIENTS AND CARBON

5.4.1 Nutrients and UCDW intrusions

Surface macronutrient (nitrate, silicate and phosphate) concentrations generally persist at high levels in the Southern Ocean as a result of three factors: high concentrations in deep water, deep winter mixing that resupplies the surface layer following biological depletion, and micronutrient (iron) limitation. Nitrate and silicate concentrations below the main pycnocline average 33 and $95\ \mu\text{M}$, respectively, seaward of the shelf break in WAP region. Occasionally, in years with large phytoplankton blooms, or in areas of large phytoplankton accumulation, surface nitrate and phosphate may be nearly depleted. On average, surface nitrate and silicate are depleted from 30 to $< 15\ \mu\text{M}$ and from 80 to $60\ \mu\text{M}$, respectively between November and February at inshore stations near Palmer Station (Figure 5.6). Similar seasonal variations are observed in nearshore waters further south in northern Marguerite Bay (Clarke *et al.*, 2008). Seasonal nutrient depletions reflect diatom dominance (or lack thereof) in phytoplankton blooms (Figure 5.6 and see below). For example, the NO_3 and PO_4 are regularly depleted in Ryder Bay, but silicate is not, indicating bloom dominance by non-diatom phytoplankton (Clarke *et al.*, 2008).

UCDW intrusions (see above) have been implicated as sources of nutrients for phytoplankton over the shelf region (Prézélin *et al.*, 2000, 2004). From a comprehensive, multiseason, multiyear study of nutrients, hydrography and phytoplankton community composition throughout the WAP region including Marguerite Bay, Prézélin *et al.* (2004) concluded that shelf-break upwelling of episodic, nonseasonal UCDW intrusions

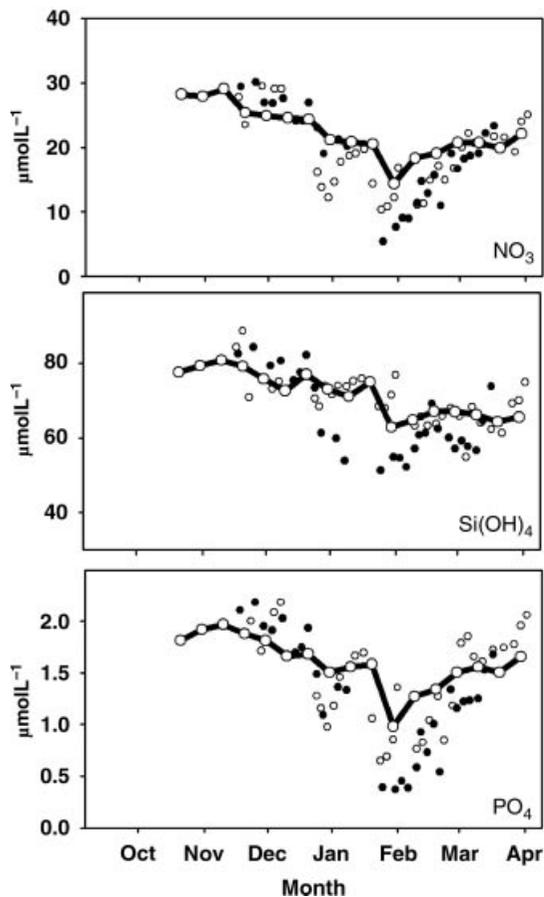


Figure 5.6 Surface layer nutrient utilization showing seasonal depletion at inshore time series station E near Palmer Station, 1994–2007. The solid lines show the mean (climatological) levels in 15-day intervals. The open circles (no line) are for 1995–1996, when phytoplankton were dominated by non-diatom species, as indicated by the lack of silica depletion relative to N and P. The solid circles are for 2001–2002, a year with a large diatom bloom (depletion of N, P and Si).

stimulated subsurface (i.e., below depths detected by remote sensing) diatom growth in the outer to midshelf region. In fact, upwelling is not necessary to bring nutrients onto the shelf: UCDW enters above the seafloor at the shelf break, flooding the water column to the base of the pycnocline. Following the entry onto the shelf, UCDW-associated nutrients can be mixed into the surface layer by several mechanisms including turbulent diffusive mixing, active erosion of the pycnocline by surface mixing, and elevation of the pycnocline

by upwelling. In addition, active erosion of the pycnocline in winter associated with brine rejection during sea ice growth may contribute additional upward nutrient transport. The latter two processes greatly dominate the vertical fluxes by a factor of 4 to 20. Nutrient concentrations track temperature in the UCDW, therefore it is likely that increased nutrient inputs have accompanied the increase in heat flux onto the shelf since 1990 (Figure 5.5). It is worth noting that bulk budgets for heat and salt at the WAP generally require levels of mixing that exceed those directly measured on research cruises, raising the question of where the major mixing events happen, and by which processes. Wallace *et al.* (2008) identified wind-driven coastal upwelling and internal tides as being potentially important mechanisms in this context, both of which occur near-shore and on time scales that would not be routinely sampled on cruises. Quantification of the mixing induced by these processes requires further work.

Serebrennikova and Fanning (2004) investigated nutrient variability in the Marguerite Bay (Figure 5.1) region during Southern Ocean-GLOBEC in 2001–2002. UCDW, supplied to the shelf by intrusions of the ACC, is characterized in this region by nitrate and silicate concentrations of 33–36 and 80–100 μM , respectively. They concluded from a detailed seasonal study of water mass properties, cross-shelf sections and a transect along the Marguerite Trough (Figure 5.1), that UCDW intrusions had essentially the same nutrient concentrations as water already over the shelf, and that UCDW was not a net source of higher nitrate or silicate concentrations, at least in this region. In contrast to the findings of Prézelin *et al.* (2004), they suggested that UCDW intrusions resulted in dilution, rather than enrichment, of high silicate concentrations already present over the shelf. They further suggested that the high (> 100 μM) concentration of silicate encountered in bottom water was caused by dissolution of opal in the bottom sediments. The results obtained by Serebrennikova and Fanning (2004) also contrast for example, with sections in the Ross Sea that show MCDW as a clear source of excess dissolved silica in summer (Gordon *et al.*, 2000).

5.4.2 Carbon cycle

Here we focus on the roles played by the WAP marginal ice zone and coastal region in atmosphere-ocean

CO_2 exchange and particle sedimentation. These processes are linked through the action of physical-chemical and biological processes driving the Solubility and Biological Carbon Pumps (Ducklow *et al.*, 2001b; Volk & Hoffert, 1985) that transport dissolved inorganic carbon (DIC or TCO_2) as well as dissolved organic carbon (DOC) against the vertical concentration gradient toward long-term storage in the deep ocean (Feely *et al.*, 2001). The Southern Ocean below 50° S, with 10% of the total ocean area, is responsible for $\sim 20\%$ of the global ocean CO_2 uptake (0.47 of 2.2 Pg C yr^{-1} ; Takahashi *et al.*, 2009) and about 10% of the anthropogenic CO_2 uptake (Sabine *et al.*, 2004). Arrigo *et al.* (2008) state that Antarctic continental shelves, currently not included in such estimates, act as powerful CO_2 sinks. Polar continental shelves covered by seasonal sea ice have been hypothesized to act as rectified (one-way) CO_2 pumps, due to the phasing of sea ice cover and biological activity. Sea surface temperature is more constant near Antarctica (relative to lower-latitude systems) and the CO_2 partial pressure ($p\text{CO}_2$) excursion in seawater governing air–sea CO_2 exchange is almost entirely due to biological drawdown and respiration (Takahashi *et al.*, 2009). In nearshore areas dilution of seawater with high DIC by glacial meltwater with negligible DIC is also important. Yager *et al.* (1995) found that the Northeast Water polynya on the Greenland Shelf was strongly undersaturated in the summer, ice-free season. They proposed the ‘seasonal rectification hypothesis’, stating that in marginal ice zones, the ice-free season coincides with the summer period of low $p\text{CO}_2$, when the regions act as atmospheric sinks. At other times of the year, when ocean $p\text{CO}_2$ could be well above saturation, the water is covered by sea ice and gas exchange is prevented. In spring, primary production may consume excess dissolved inorganic carbon even before the ice cover recedes. Yager *et al.* (1995) and Miller *et al.* (2002) used estimates of CO_2 exchange in the ice-free season as an *annual* average for air–sea gas exchange, leading to very areal high estimates of the air-to-sea flux. The Ross Sea polynya may function as such a sink for atmospheric CO_2 because it is strongly undersaturated in CO_2 in summer in response to *Phaeocystis* and diatom blooms (Takahashi *et al.*, 2002; Peloquin & Smith, 2007) and covered by ice during the rest of the year.

Whether the WAP shelves act as rectified or even unrectified net annual CO_2 sinks is not established. The area is characterized by large spatial and temporal

variability and by the co-occurrence of various biological (e.g., respiration and photosynthesis) and physical (e.g., heating, cooling, ice formation and ablation, melting, freshening and dilution) processes, all of which makes understanding and budgeting very challenging. Carrillo *et al.* (2004) studied these variations in detail using high spatial resolution underway mapping of surface $f\text{CO}_2$ and $f\text{O}_2$ (f = fugacity, similar to $p\text{CO}_2$) during cruises in January and July 1997. Different regions of the LTER grid showed different patterns of CO_2 and O_2 over- and undersaturation, resulting from spatial variation in dominance of physical or biological processes. Even in summer, dissolved CO_2 was near atmospheric equilibrium in some regions, particularly offshore and toward the north part of the grid. This pattern leads to some doubt regarding the universality of the rectified sink hypothesis. Within the last two decades, sea ice duration has declined by over 50 days (see above), with more of the change due to a later ice advance in the fall (see above). How declining sea ice will impact net annual CO_2 exchange is a rich area for new global change research.

Positive net community production (NCP) is the dominant biological process in the inshore areas and especially in Marguerite Bay, leading to strong drawdown of DIC and undersaturation of dissolved CO_2 ($p\text{CO}_2 < 200$ ppm). Serebrennikova and Fanning (2004) estimated NCP from total inorganic N and Si drawdown over the growing season. They found that NCP estimated from net N utilization was 3.8 ± 1.9 and $2.8 \pm 1.3 \text{ Mol C m}^{-2} \text{ y}^{-1}$ in Marguerite Bay (MB) in 2001 and 2002. NCP estimated from Si utilization was 1.1 and $0.9 \text{ mol C m}^{-2} \text{ y}^{-1}$ suggesting diatoms were responsible for about 30% of the annual NCP. The estimates for NCP in MB are comparable to estimates made in the hyperproductive Ross Sea by Sweeney *et al.* (2000a, b; 3.9 ± 0.9) but the range in MB was $0.6\text{--}9.6 \text{ mol C m}^{-2} \text{ y}^{-1}$. NCP for January 2008, calculated from biological O_2 supersaturation, constrained by measurements of $[\text{O}_2]/[\text{Ar}]$ ratios in the mixed layer (Emerson *et al.*, 1991; Hendricks *et al.*, 2004; Reuer *et al.*, 2007; Spitzer & Jenkins, 1989) is summarized in Figure 5.7. Carbon NCP is calculated from O_2 NCP/1.4, according to the stoichiometry given by Laws (1991). The measured NCP ranged from -2 to $52 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (-1.2 to $37 \text{ mmol C m}^{-2} \text{ day}^{-1}$), with an average of $13 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ($9.6 \text{ mmol C m}^{-2} \text{ day}^{-1}$). The highest NCP were found in the northern coastal area, with lower NCP in the south. NCP in the offshore area were very low.

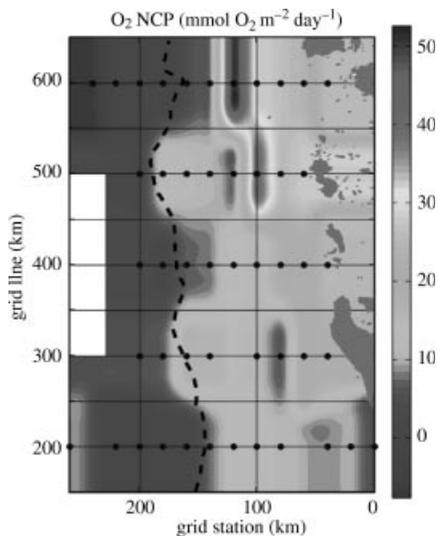


Figure 5.7 Integrated O_2 Net Community Production above the mixed layer depth in the Palmer LTER sampling region (as in Fig. 1) for Jan., 2008. Black dots are the stations where samples were collected. Dashed line indicates the continental shelf break. (See the colour version of this figure in Plate section)

5.4.3 Dissolved organic carbon

There have been few measurements of DOC in the WAP shelf region. DOC concentrations in January range $45\text{--}50 \mu\text{M}$, against a deepwater background concentration of $39 \mu\text{M}$ (Ducklow *et al.*, 2007). Carlson *et al.* (1998) showed that DOC accumulation was similarly low in the Ross Sea (cf. Bermuda summertime DOC of $60\text{--}70 \mu\text{M}$ and Hawaii, $>90 \mu\text{M}$) and suggested that Antarctic plankton systems funnel most of the seasonal NPP through the particulate, not dissolved, carbon pools. This may be true in the WAP as well. But Doval *et al.* (2002) reported DOC concentrations averaging about $75 \mu\text{M}$ at four stations in the Bransfield and Gerlache Straits near Palmer Station. DOC concentrations in Ryder Bay, Adelaide Island generally lie in the range $60\text{--}80 \mu\text{M}$, with some values exceeding $100 \mu\text{M}$ (Clarke *et al.*, 2008). Recently Manganelli *et al.* (2009) reported a few high DOC concentrations from a single cruise (summer 2004) in the Drake Passage north of the Peninsula ranging from $60\text{--}130 \mu\text{M}$. These values are in sharp contrast to most other observations in the region and need to be substantiated with additional data.

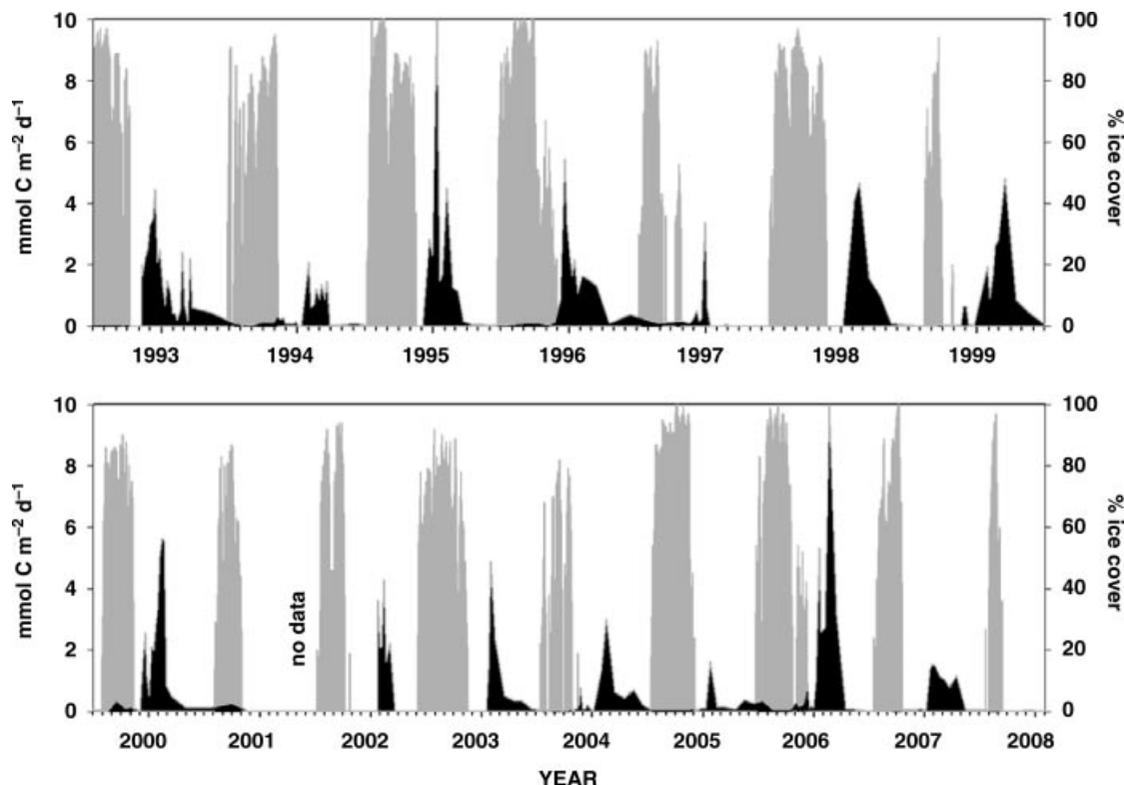


Figure 5.8 Particulate carbon sedimentation and sea ice cover in the midshelf region of the West Antarctic Peninsula, 64.5 South, 66 West. The time-series sediment trap is moored at 170 m in 350 m bottom depth. Sea ice cover is averaged over a circle with radius 25 km centered on the trap site, and determined from the GSFC Bootstrap SMMR-SSMI time series data provided by the US National Snow and Ice Data Center, Boulder, CO. There were no sedimentation data in Jan. 2001 to Jan 2002 due to trap failure. The other apparent blank segments in the time series are very low, nonzero fluxes (e.g., 1997–98). Trap data 1993–2002 courtesy D. Karl and C. Carrillo, Univ. of Hawaii. All data available at <http://oceaninformatics.ucsd.edu/datazoo/data/pallter/datasets>.

5.4.4 Sedimentation and export

The carbon budget in the WAP is strongly influenced by vertical sedimentation (Karl *et al.*, 1991b). Palmer LTER has maintained a sediment trap moored at 64.5° S, 66° W since 1993, about 100 km from Palmer Station in 350 m water depth (trap depth 170 m) and seaward of the Palmer Deep trough west of Anvers Island. As elsewhere in Antarctic marginal ice zones (Fischer *et al.*, 2002; Wefer *et al.*, 1988), particle flux in the WAP exhibits extreme seasonality (Figure 5.8), with a strong peak in the summer following the ice retreat and phytoplankton bloom (Ducklow *et al.*, 2008). The du-

ration, amplitude and annual total flux all exhibit significant interannual variability (Figures 5.8, 5.9). In particular, the annual sedimentation varied by nearly an order of magnitude over the 17-year observation period. Total annual flux is not related to local annual primary production. Other biological factors besides total primary production probably influence the patterns and magnitude of sedimentation. In addition, the area over which to average surface biological and sea ice properties depends on the size of the virtual collecting funnel of the overlying water column, and specifying this area depends on better resolution of the surface current velocity fields (Siegel & Deuser, 1997).

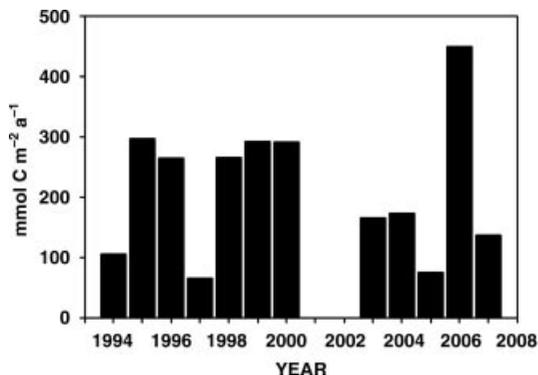


Figure 5.9 Annual sedimentation at 170 meters in the Palmer LTER Study area, 64.5° S, 66° W. The annual integrals are based on 21 individual samples collected over the course of each year, with an interval ranging from 7–30 days, depending on season and expected flux (data for 1993–2000 collected by D.M. Karl and C.J. Carrillo, Univ. Hawaii for PAL-LTER). The data were integrated from July to July and plotted at the intervening January for each year. The width of each bar spans the sampling year.

5.5 PHYTOPLANKTON DYNAMICS

5.5.1 Seasonal scale dynamics

The WAP is a highly productive marine ecosystem characterized by large phytoplankton blooms (Hart, 1942; Nelson & Smith, 1991; Prézelin *et al.*, 2000; Smith *et al.*, 2008). In coastal waters off Palmer Station, primary production averages 176 g C m⁻² over the growing season (range 47–351 g C m⁻² season⁻¹). This is about the same as the primary production measured by similar techniques (¹⁴C-incorporation) at subtropical sites like Bermuda and Hawaii, but is achieved in half the time. Similar seasonal production was observed in other ice edge areas of Antarctica, such as the Ross Sea (168 g C m⁻² season⁻¹; Smith Jr. *et al.*, 2000). Seasonally, phytoplankton growth is timed when solar illumination increases and sea ice melts, leaving open water from October through March/April (Moline & Prézelin, 1996; Smith *et al.*, 2001). Generally, mean productivity rates exhibit onshore to offshore gradients with high productivity rates (~1000 mg C m⁻² d⁻¹) found onshore compared to offshore waters (~100 mg C m⁻² d⁻¹; Vernet *et al.*, 2008). Phytoplankton blooms along the WAP are dominated by large (>20 microns) diatoms

(Hart, 1942; Holm-Hansen & Mitchell, 1991); however, over the last two decades there has been an increased recognition that nano- (<20 microns) and picoplankton (<2 microns) are also important to the WAP phytoplankton community (Buma *et al.*, 1991; Hewes *et al.*, 1990; Jacques & Panouse, 1991; Villafañe *et al.*, 1993) especially in the offshore waters (Vernet *et al.*, 2008). The dominant nano-flagellate taxa in the northern WAP are cryptomonads (Garibotti *et al.*, 2003a; Krebs, 1983; Whitaker, 1982), which have often been associated with low salinity water (Moline *et al.*, 2004). Further south, in Ryder Bay, Adelaide Island, phytoplankton biomass is dominated by large diatoms, although the prymnesiophyte *Phaeocystis antarctica* may be numerically most abundant (Annett *et al.*, 2010). The timing and magnitude of these blooms is largely a function of vertical mixing which determines the availability of light and nutrients.

5.5.2 Role of light

Light is a key factor regulating phytoplankton growth in the WAP. In the Southern Ocean, high wind speeds result in deep upper mixed layer depths (UML), which decrease the overall light available to phytoplankton (Mitchell *et al.*, 1991; Nelson & Smith, 1991; Sakshaug *et al.*, 1991). The importance of light in regulating phytoplankton growth is consistent with numerous observations. The first observation is that macronutrients are generally high throughout much of the WAP and do not appear to limit growth (Martin *et al.*, 1990a). Secondly, phytoplankton biomass accumulates when the upper mixed layer depth is shallow (Garibotti *et al.*, 2005; Mitchell & Holm-Hansen, 1991; Moline *et al.*, 1997; Vernet *et al.*, 2008) (see Figure 5.10A). Shallow mixed layers have been associated with low wind speeds over weekly time scales (Moline, 1998) and/or are associated with buoyant surface plumes due to sea ice and glacial melt (Dierssen *et al.*, 2002; Klinck, 1998; Smith Jr. & Nelson, 1985). This results in linear correlations between the average primary production and the timing of the sea ice retreat or summer mixed layer depth (Vernet *et al.*, 2008). Given this relationship, the concentration of chlorophyll a is often not correlated with nutrients but is inversely related to wind speed (Figure 5.11).

The importance of light to phytoplankton biology in WAP is reflected in cellular photosynthetic properties.

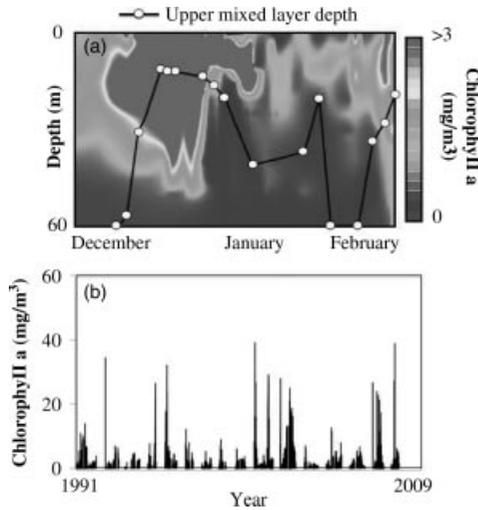


Figure 5.10 Dynamics of chlorophyll a at Palmer Station. A) phytoplankton bloom during the austral summer of 1991/1992. The bloom dynamics were described by Moline et al. (1998). The black line indicates the upper mixed layer depth. B) The inter-annual variability in surface chlorophyll since the LTER was initiated in 1992. (See the colour version of this figure in Plate section)

Photoacclimation in phytoplankton involves cells optimizing the absorption of incident light and/or maximizing the utilization of the absorbed light (often quantified as the maximum quantum yield of carbon fixation,

ϕ_{max}). These adjustments reflect time-dependent metabolic processes, therefore the acclimation state measured at any time integrates the recent light history of the cells. During periods of intense mixing, cells do not have adequate time to photoacclimate to a specific light condition and the photosynthetic properties adjust to the mean light level within the UML. Under these conditions photoacclimation parameters exhibit limited or no depth-dependency (Cullen & Lewis, 1988; Lewis et al., 1984). Conversely, during periods of water column stability, cells acclimate to incident light levels and photosynthetic parameters exhibit depth-dependent changes. Hence, as mixing decreases, the vertical water column variability in the photosynthetic parameters should increase.

Both the phytoplankton pigmentation and ϕ_{max} show signatures consistent with active photoacclimation emphasizing the importance of light to phytoplankton growth in the WAP. Phytoplankton absorption and cellular pigmentation are closely tied to recent light history. Chlorophylls and most carotenoids absorb light for photosynthesis, while some carotenoids function as photoprotective pigments (Bidigare et al., 1987; Demers et al., 1991). In diatoms, the carotenoids diadinoxanthin (DD) and diatoxanthin (DT) function as a photoprotective system, undergoing a light-regulated de-epoxidation and epoxidation reaction known as the xanthophyll cycle. These pigments dissipate excess energy by non-photochemical fluorescence quenching (Arsalane et al., 1994; Olaizola et al., 1994). In the WAP, when the UML shallows, there is a strong coherence of

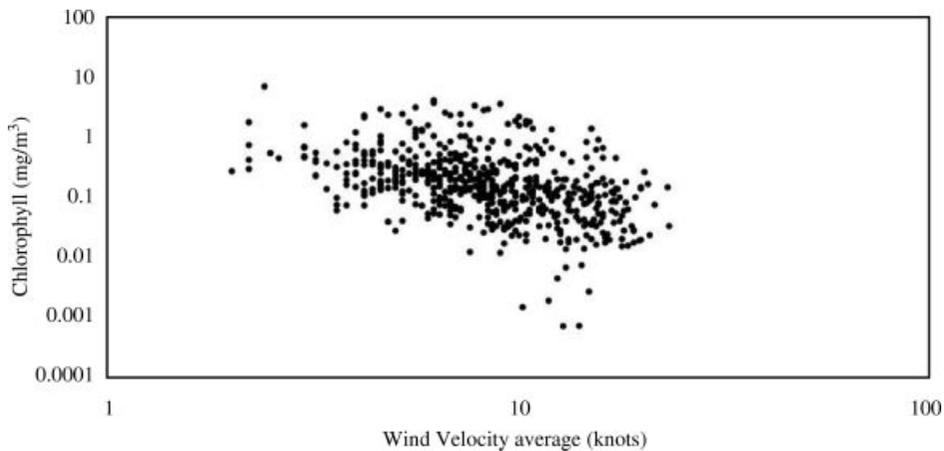


Figure 5.11 The relationship between wind and chlorophyll biomass.

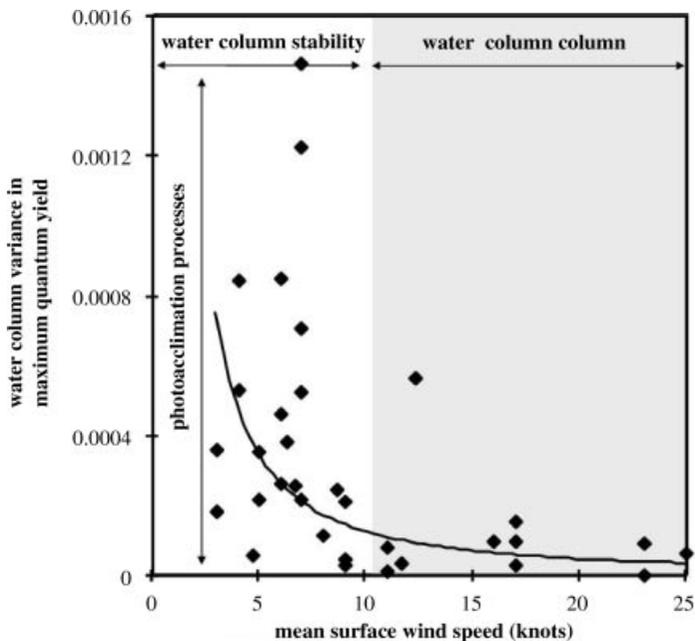


Figure 5.12 The relationship between water column variance in the maximum quantum yield for carbon fixation (Y-axis) and the 3-day average surface wind speed (X). Wind speeds less than 11 knots have been associated with stable water columns (Moline *et al.*, 1996).

the cells increasing photoprotective pigments when cells are confined to the upper water column (Moline, 1998). The kinetic response of the xanthophyll pool observed in WAP occurs on similar timescales as vertical mixing (Denman & Gargett, 1983). The co-occurrence is consistent with the interpretation that phytoplankton are adapted to dim light conditions when the UML is deep and cells adjust as they are confined near the surface when the UML shallows. Similarly ϕ_{\max} shows patterns consistent with photoacclimation being strongly tied to mixing. The mean water column variance in ϕ_{\max} , estimated from photosynthesis-irradiance parameters (Moline *et al.*, 1995) and cellular absorption estimated from pigment measurements (Bidigare *et al.*, 1989), is significantly higher during periods of low wind ($<20 \text{ km h}^{-1}$) compared to periods of high wind ($>20 \text{ km h}^{-1}$) (Figure 5.12, $p < 0.001$). Sustained wind speeds $>20 \text{ km h}^{-1}$ for several days appeared to be the threshold for water column destratification and mixing in this region (Moline & Prézelin, 1996). These patterns illustrate that phytoplankton are continually adjusting the physiology to optimize light utilization in this dimly lit oceanic environment.

5.5.3 Role of nutrients

While light history and mixing are central to regulating the productivity in these coastal waters, it has been suggested that nutrients play a major role in the offshore waters of the WAP. Most important has been the realization over the last few decades of the importance of micronutrients in regulating phytoplankton growth (Boyd *et al.*, 2000; Coale *et al.*, 2004; Martin *et al.*, 1990a). Shelf-wide surveys of the WAP during austral summer have found several regions of upwelling of subsurface intrusions of warm ($>1.5 \text{ C}$) Upper Circumpolar Deep Water (UCDW) that fuel high phytoplankton productivity rates by supplying macro- and micronutrients (Prézelin *et al.*, 2000). The importance of the micronutrients, especially iron, has been suggested as particularly critical (Boyd *et al.*, 2000; Coale *et al.*, 2004; Martin *et al.*, 1990a). The strongest evidence of micronutrient limitation to date in the WAP is found in offshore and slope areas where upwelled waters result in subsurface phytoplankton maxima (Garibotti *et al.*, 2003b; Prézelin *et al.*, 2000, 2004) in contrast to the surface blooms that dominate

the nearshore waters (Vernet *et al.*, 2008). The limited number of coastal measurements suggests ample iron concentrations (Martin *et al.*, 1990b). Micronutrients (iron) entrained from sediments might be significant in explaining local-scale variability in the productivity in specific regions of the WAP; however, it does not appear to be limiting the overall regional productivity (Sedwick *et al.*, 2007). More data are required to better quantify these nutrient-light interactions

5.5.4 Annual variability in phytoplankton

Phytoplankton biomass shows significant interannual variability. The 18-year time series of chlorophyll, collected at Palmer Station, shows the annual peak chlorophyll can vary by 5-fold year to year (see Figure 5.10B). Large productivity years appear to occur every 3–4 years (cf. Peloquin and Smith, 2007) and wind forcing remains the best environmental variable in predicting the magnitude of the phytoplankton blooms year to year. There is no discernable secular trend in the phytoplankton productivity in the local nearshore Palmer Station data set, in contrast to significant changes observed for the WAP as a whole. Both primary productivity and phytoplankton biomass appear to have decreased in the northern WAP. Recently, an analysis of the productivity measured with the Coastal Zone Color Scanner (CZCS, 1979–1986) and Sea-Viewing Wide Field-of-View Sensor (SeaWiFS, 1998–2006) (Montes-Hugo *et al.*, 2009) showed that chlorophyll concentrations have declined by a factor of over two in the northern regions of the WAP (north of 64° S). These declines have been associated with an increase, up to 60%, in surface winds combined with an increase in overcast skies (Montes-Hugo *et al.*, 2009). These factors increase light limitation in phytoplankton. Additionally, recent declines of chlorophyll over the northern WAP might also be partially related to a greater advection of relatively poor chlorophyll waters coming from the Weddell Sea into the Bellingshausen Sea through the Bransfield and Gerlache Straits (Barcena *et al.*, 2002). The declines observed in satellite observations have been confirmed by the ship-based radioisotope incubation results that have declined by >50% in the near-shore waters in the northern segments of the LTER grid (Vernet *et al.*, 2008).

While the northern WAP has experienced declines, the southern waters of the WAP (63.8 to 67.8° S,

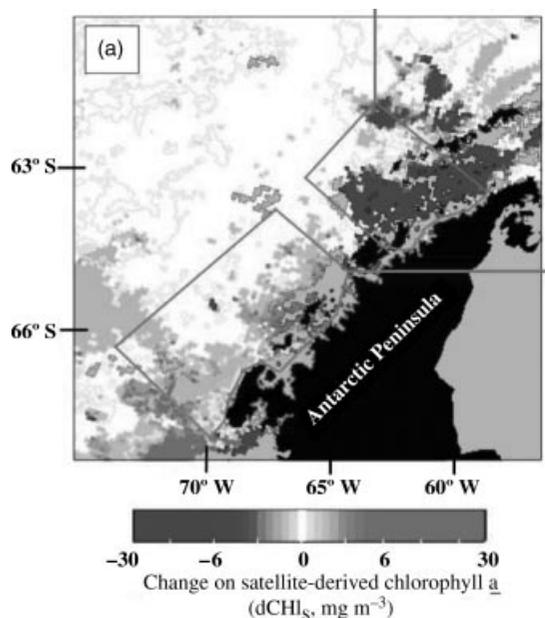


Figure 5.13 The variation of phytoplankton biomass over the WAP region. Average of pixel-by-pixel absolute difference in satellite-derived chlorophyll a concentration between the mean January observations for 1978 to 1986 and mean January observations for 1998 to 2006. Positive dChl_s corresponds to an increase of surface Chl with respect to the 1970s. (See the colour version of this figure in Plate section)

64.4° to 73.0° W) have seen a significant increase in phytoplankton biomass (66% on average; Montes-Hugo *et al.*, 2009) (see Figure 5.13). The increases were largely associated with two productive years (2005 and 2006), which were characterized by very low levels of sea ice, cloud cover, and wind. Unlike the northern WAP, the decrease in summer sea ice extent in the southern WAP has occurred in areas that were previously ice-covered most of the year. Therefore, the increase in ice-free summer days translates into more favourable conditions in the UML (e.g., increased light) for phytoplankton growth. Together, these environmental changes are expected to enhance photosynthesis and favour chlorophyll accumulation due to lower light limitation. These regional trends have likely contributed to the observed changes in the higher trophic levels such as regional declines in krill (Atkinson *et al.*, 2004) and Adélie penguins (see below).

5.6 MICROBIAL ECOLOGY

As in other marine systems (Ducklow, 1999), bacterioplankton in Antarctic waters directly utilize small molecular weight dissolved organic matter (DOM), derived ultimately from phytoplankton production. Bacteria complete the microbial loop by converting the DOM into biomass, then being consumed by protozoan and microzooplankton bacteriovores (Karl, 1993). In the WAP, heterotrophic prokaryote stocks contain a significant proportion of planktonic *Archaea* (Church *et al.*, 2003; Massana *et al.*, 1998; Murray *et al.*, 1998), but as yet these organisms remain uncultivated and we do not know their modes of nutrition, metabolic and trophic status or roles in the plankton system. Church *et al.* (2003) showed seasonal and depth-related variations in the relative and absolute abundances of *Archaea* vs. *Bacteria* along the WAP, with a greater proportion of the *Archaea* in deeper waters and during the winter. The *Archaea* increased in absolute abundance by about 40% from summer to winter in WAP surface waters, and also varied at depth, suggesting a dynamic and active population.

Total prokaryote (hereafter 'bacteria,' including varying proportions of *Archaea*, with unknown metabolic identities; and heterotrophic *Bacteria*) abundance is greater in the summer than winter, but does not vary as conspicuously as in the Ross Sea, where bacterioplankton undergo an annual bloom (Ducklow *et al.*, 2001a). Total abundance is generally $\sim 10^8$ cells L^{-1} in winter (July) and reaches to about 10^9 cells L^{-1} in January (Church *et al.*, 2003), that is, about the same range as in the temperate North Atlantic, but less than in the Ross Sea (Ducklow *et al.*, 2001a and see below).

Heterotrophic bacteria in Antarctic coastal waters must ultimately depend on phytoplankton production for organic matter (there are no terrestrial inputs of organic matter), so in some sense the two groups must be coupled by material flows in the plankton food web. In the RACER (Research on Coastal Antarctic Ecosystem Rates) Project, Karl and colleagues (Bird & Karl, 1991, 1999; Karl *et al.*, 1991a) carried out intensive seasonal (summer, December to March 1987; spring, November 1989) investigations of microbial processes in the northern Antarctic Peninsula and Drake Passage. They observed that bacteria were not correlated with chlorophyll during the spring phytoplankton bloom in the Gerlache Strait, with no bacterial response to increased Chl $> 2.5 \mu g L^{-1}$ (Bird & Karl, 1999). Bacterial biomass was $< 2\%$ of the total

plankton biomass and bacterial production (BP) was $\sim 3\%$ of the co-occurring primary production. They concluded that the bacterial response to the diatom bloom was suppressed by heterotrophic nanoplankton (HNAN) populations that consumed growing bacteria as the phytoplankton bloomed, and kept BP:PP low, i.e., the HNAN exerted top-down control. Bird and Karl concluded that, at least in their study area and during the spring bloom period, the microbial loop was uncoupled from primary producers, but they added that the uncoupling was not necessarily more widespread in space and time, and could be expressed more strongly in other seasons.

Bird and Karl (1999) diagnosed top-down control by computing the ratio of bacterial cells per individual HNAN in the standing stock of plankton samples taken at various times of the bloom cycle. Figure 5.14 reproduces the observations of Bird and Karl (1999) along with observations from the Ross Sea polynya. There were only about 100 bacteria per HNAN in the Gerlache Straits, and an order magnitude more in the Ross Sea over the full growth season. There were consistently fewer HNAN available to graze on bacterial cells in the Ross Sea than in the Gerlache Strait. The Bacteria: HNAN ratio approached 10,000 in some samples in the Ross Sea. The striking contrast in predator-prey ratios between the two regions suggests fundamental differences in food-web structure. For example, the notable release of bacteria from predation by HNAN in the Ross Sea suggests that the bacteriovores (HNAN) are more heavily preyed upon than in the WAP region. In general, there are fewer Antarctic krill in the central Ross Sea, an observation not consistent with the trophic cascade hypothesis. Salps or other mucus net feeders like pteropods could exert such top-down control on HNAN and initiate a trophic cascade favouring bacteria. The idea has not been tested.

Moran and colleagues studied phytoplankton-bacteria coupling in the Bransfield Strait (Moran & Estrada, 2002; Moran *et al.*, 2001). They provided a clear operational definition of phytoplankton-bacterial coupling by focusing specifically on the release of recently-synthesized DOC from active phytoplankton (14% of total particulate plus dissolved primary production). In a series of carefully-analyzed time course experiments, they showed that the released DOC met the metabolic requirement of bacteria in the same region studied in RACER and concluded that bacteria and phytoplankton were strongly coupled. They also concluded that BP was a very low fraction (mean $1.5 \pm 0.4\%$) of the total

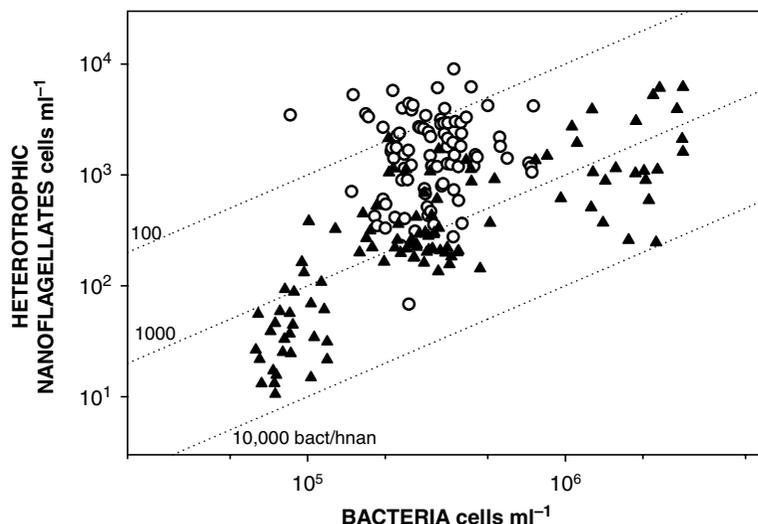


Figure 5.14 The ratio of bacterial to heterotrophic nanoflagellate (bacteriovore, HNAN) abundance in the Gerlache Strait, WAP (open circles) and the Ross Sea (closed triangles). The dotted lines indicate fixed ratios of 100, 1000 and 10,000 bacteria per HNAN. Gerlache data courtesy D. Bird, Université de Québec a Montréal.

particulate plus dissolved production but termed the coupling ‘strong’ nonetheless.

Seasonal sampling of primary and bacterial production rates over four growing seasons (November to

April) in the nearshore region at Palmer Station buttresses the observations of low bacterial production of previous investigators (Figure 5.15). Like other properties, there was substantial short-term and interannual

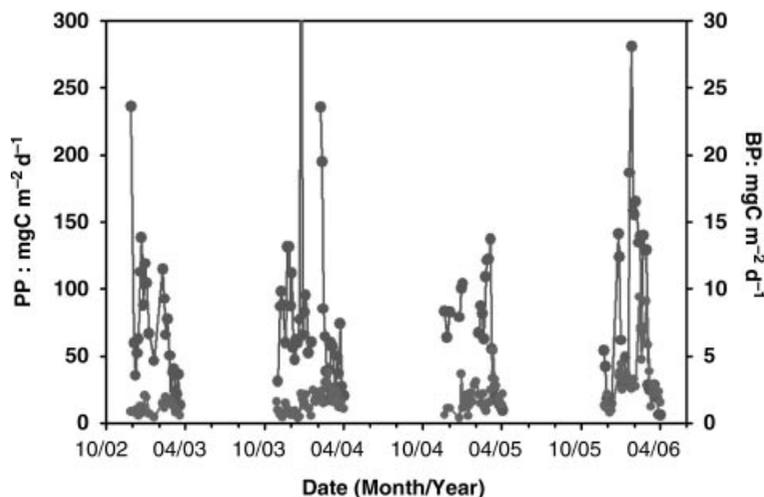


Figure 5.15 Primary (PP, green) and bacterial (BP, red) production rates at LTER Station E, 64.8 South, 64.0 West, ca 2 km from Palmer Station in 200 meters water depth. PP and BP are estimated approximately semiweekly between late October and late March each year from 4 to 6 discrete depth samples incubated with ^{14}C -bicarbonate and ^3H -leucine, respectively. The BP axis is scaled to be 10% of the PP axis so if a BP symbol is superimposed on a PP symbol for the same date, the BP:PP ratio is 0.1. Over the course of these four years individual daily BP:PP ratios ranged from 0.01 to 0.38, with a mean of 0.05 (N=113). (See the colour version of this figure in Plate section)

variability in the temporal patterns and of BP and PP. But in general BP was low, averaging less than $3 \text{ mmol C m}^{-2} \text{ d}^{-1}$, somewhat less than at Bermuda (Carlson *et al.*, 1996). However, PP is lower in Bermuda and so the BP:PP ratio is much lower at Palmer (1–4%), compared with 14% at Bermuda.

Why is BP:PP so low? Low temperature is an obvious candidate, and has been a subject of previous research (Pomeroy & Deibel, 1986). But temperature alone is not sufficient to explain low bacterial activity in cold waters (Kirchman *et al.*, 2009), and there are well-documented interactions between temperature and bacterial physiology in the utilization of dissolved organic compounds by bacteria (Pomeroy & Wiebe, 2001). It also appears that the supply of DOM from plankton sources is attenuated in some cold water food webs. As Moran and Estrada (2002) showed, the flux of recently-produced DOC to bacteria is just 14% of the total PP. If this supply is used at 15% efficiency (Carlson *et al.*, 1999), the resulting BP:PP would be $0.14 \times 0.15 = 2\%$, in the absence of uncoupled DOM sources like semilabile DOM or mesozooplankton excretion. This idea is explored further below.

5.7 ZOOPLANKTON

5.7.1 Community composition and distribution

Zooplankton community structure and distribution in the waters west of the Antarctic Peninsula (WAP) is broadly associated with latitudinal and cross-shelf zones delineated by seasonal variations in pack-ice cover, as well as by frontal regions of water masses such as the southern boundary of the Antarctic Circumpolar Current (Ross *et al.*, 2008; Ward *et al.*, 2004). The dominant zooplankton taxa in the WAP region include krill, copepods, salps (pelagic tunicates), and pteropods (pelagic snails) (Ashjian *et al.*, 2004; Loeb, 2007; Ross *et al.*, 2008). Krill are the best studied due to their central importance as prey for seabirds, seals and whales. A recent analysis of a 12-year (1993–2004) time-series in summer zooplankton abundance in the WAP (Ross *et al.*, 2008) updated through 2009 (Figure 5.16) indicates that the numerically dominant epipelagic meso- and macrozooplankton $\geq 2 \text{ mm}$ include three species of euphausiids (*Euphausia superba*, Antarctic krill, which compose $\sim 14\%$ of total abundance calculated over the whole grid for the time series;

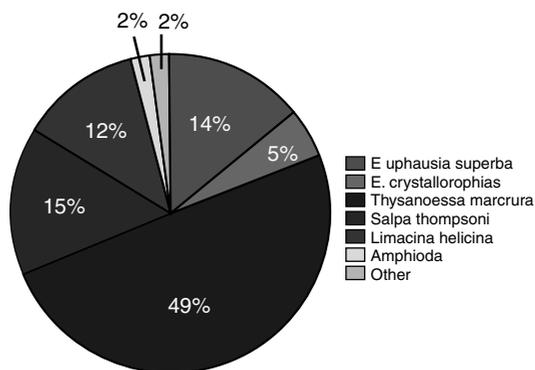


Figure 5.16 Mean summer (January) abundance of numerically dominant epipelagic meso- and macrozooplankton $\geq 2 \text{ mm}$ as a fraction of total abundance. Data are from 1993–2009 (with exclusion of 2008 – not yet analyzed). Other category includes chaetognaths, other pelagic gastropods, other crustacea (e.g., ostracods, copepods, mysids, other species of euphausiids), fish larvae, polychaetes, ctenophores, Hydrozoa, etc. Zooplankton were sampled with a $2 \text{ m} \times 2 \text{ m}$ frame, $700 \mu\text{m}$ mesh net towed obliquely 0–120 m. (Updated from Ross *et al.*, 2008.)

Thysanoessa macrura, $\sim 49\%$; *Euphausia crystallorophias*, ice krill, $\sim 5\%$), the shelled pteropod *Limacina helicina* ($\sim 12\%$), and the salp *Salpa thompsoni* ($\sim 15\%$). Patterns in the climatological distributions of these five species are distinct and correlate with sea ice parameters. Common features in summer include higher abundance in the north compared to the south, and cross-shelf gradients with highs in abundance either inshore (krill) or offshore at the outer slope (salps, Figure 5.17; Ross *et al.*, 2008). Salps appear to be increasing as more oceanic, lower phytoplankton conditions develop in the northern region. However, salps do also occur over the shelf in the north and a large salp bloom in 2009 occurred at a slope station (160) in the south resulting in ‘off the chart’ mean abundance for the time series (Figure 5.17). Using smaller mesh nets, Ashjian *et al.* (2004) found copepods (large and small) usually dominated both abundance and biomass of zooplankton on or near the continental shelf at Marguerite Bay in the fall and winter, with highest abundances offshore. The dominant larger copepod species in the WAP include calanoid copepods such as *Calanus acutus*, *C. propinquus*, *Gaedius* spp., *Metridia gerlachei*, *Rhincalanus gigas*, and *Paraeuchaeta* spp. (Ashjian *et al.*, 2004; Ross *et al.*, 1996b).

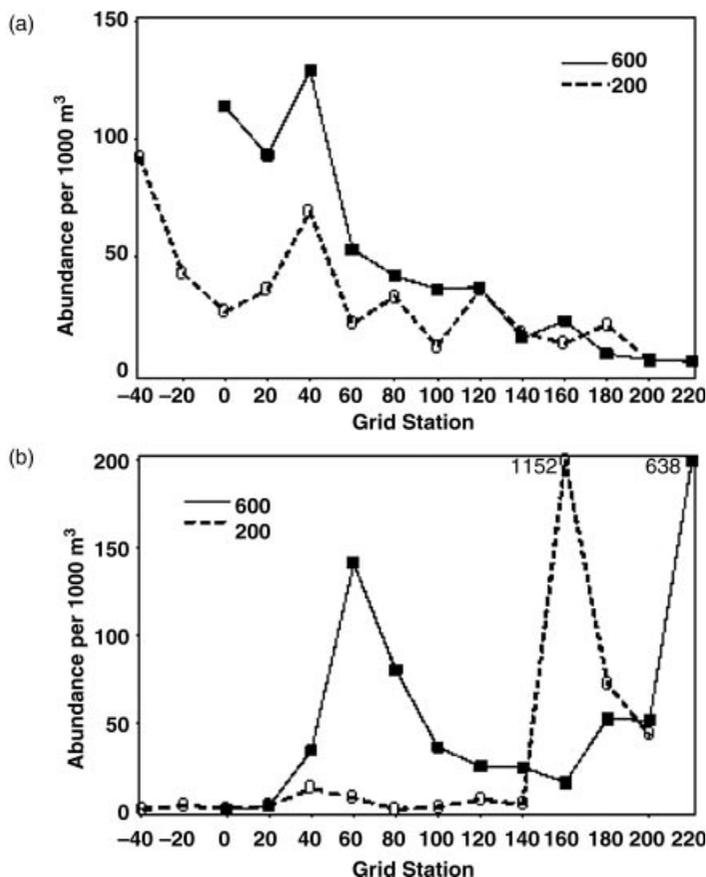


Figure 5.17 Comparison of mean abundance of (a) *Euphausia superba* and (b) *Salpa thompsoni* within the Palmer LTER region. Data are from 1993–2009 (with exclusion of 2008 – not yet analyzed). Abundance data shown for the northern 600 line (solid line), and more southern 200 line (dashed line), in the standard grid stations from nearshore (–40 line) to offshore (220 line). Abundance data were not estimated from Delta distribution as in Ross *et al.* (2008). Note off-chart values for salps in (b) for 160 and 220 lines. (*E. superba* figure updated from Ducklow *et al.*, 2007.)

Vertical distributions of zooplankton species along the WAP vary considerably with life history stage, season, time of day, and location. *E. superba* are thought to spawn in the late summer offshore along the peninsula shelf (Fach *et al.*, 2002; Hofmann *et al.*, 1998; Siegel, 2005) or possibly in deeper canyons on the continental shelf (Brinton, 1991). The embryos sink, hatch at depth, and larvae undergo development as they ascend. In addition to this ontogenetic migration, adult *E. superba* may undergo diel vertical migrations (DVM) (Cresswell *et al.*, 2009; Hernandez-Leon *et al.*, 2008; Tarling & Johnson, 2006), but this behaviour appears to be highly dependent upon location and season in the

WAP, and there is evidence from modeling and acoustics studies that DVM behaviour in krill is flexible depending upon food availability and predator concentrations (Cresswell *et al.*, 2009). A number of copepod species, such as *C. acutus*, *C. propinquus*, and *R. gigas*, ontogenetically migrate, occurring in upper waters in spring/summer and at depth in winter in the WAP (Ashjian *et al.*, 2008; Quetin *et al.*, 1996; Ross *et al.*, 1996b), as elsewhere in the Southern Ocean (Schnack-Schiel, 2001; Smith & Schnack-Schiel, 1990). Some copepod species such as *Metridia gerlachei* also undergo DVM (Hernandez-Leon *et al.*, 2008). *Salpa thompsoni* migrate vertically on the order of 500 m

day⁻¹ (Nishikawa & Tsuda, 2001), and also undergo an ontogenetic migration, whereby the asexual solitary stage overwinters deep and ascends to surface layers in spring/summer where they release chains of the sexual aggregate stage (Foxton, 1966; Lancraft *et al.*, 1991).

5.7.2 Long-term trends and climate connections

The role of decadal-scale climate fluctuations such as ENSO in shaping zooplankton community distribution and composition in the WAP and adjacent areas is increasingly recognized. Anomalies in climatological distribution and abundance of zooplankton in the WAP revealed episodic recruitment in Antarctic krill (Ross *et al.*, 2008). The episodic pattern in krill recruitment was two strong year classes in succession followed by three or four moderate or poor year classes. The mechanism underlying the strong link between the krill recruitment index and ENSO is most likely the effects of seasonal sea ice dynamics on both reproduction and winter-over survival of the resulting larvae (Quetin & Ross, 2003). Focused fall- and winter-time studies of krill larvae development (Frazer *et al.*, 2002; Quetin *et al.*, 2003) indicated highest growth rates in late winter, likely a combination of factors such as day length, water column and sea ice primary production, and food concentration. In the adjacent South Shetland–Elephant Island and Bransfield Strait area, krill reproductive and recruitment success and seasonal ice extent exhibited a three- to five-year periodicity and was also significantly correlated with ENSO variability (Loeb *et al.*, 2009). How these climate fluctuations affect krill life history and population distribution is of particular interest in the WAP where successful overwintering of high abundance shelf populations, particularly larval stages, is thought to replenish northern populations (Ashjian *et al.*, 2008).

The mechanisms driving variability in the temporal/spatial distribution of the shorter-lived, more oceanic species were less complex and more direct than those for the longer-lived euphausiids (Ross *et al.*, 2008). Salps have been more consistently present across the shelf post-1999 and the range of the pteropod *L. helicina* has been expanding. With shorter life spans, these two species can respond more quickly to the increasing heat content on the shelf in this region. There is a negative correlation between salps and ice advance and the

number of ice days, and a positive correlation between the presence of ice krill and the day of ice retreat. These results suggest that several environmental controls on distribution and abundance of these species were linked to seasonal sea ice dynamics (Ross *et al.*, 2008).

There are also effects of longer-term climate warming on zooplankton communities in the WAP, although effects on some taxa remain to be elucidated. The PAL record of zooplankton distributions over the 1993–2004 period suggests salps are increasing their range and frequency of occurrence in the northern region (Ross *et al.*, 2008), and a long-term increase in abundance of salps is also documented further north in the Elephant island region (Loeb, 2007). Larger-scale analysis of the southern ocean indicates salps have been expanding their range southward paralleling the loss of sea ice (Ashjian *et al.*, 2004; Pakhomov *et al.*, 2002). Any increase in salps in the PAL study region is likely a direct effect of the ice-free oceanic waters, which are increasingly flooding the shelf region, and the preference of salps for ice-free waters. While salps are increasing, krill appear to be declining over a larger region in the SW Atlantic sector (Atkinson *et al.*, 2004), including the Elephant Island region (Loeb, 2007; Siegel *et al.*, 1998), coincident with the sea ice decline. Krill abundance does not show a trend in the PAL region (Ross *et al.*, 2008).

5.7.3 Grazing and biogeochemical cycling

Zooplankton play a key role in food webs as grazers of primary production and in export of particulate organic carbon (POC) to depth via production of fecal pellets. The fraction of the NPP grazed by krill or salps in the WAP, estimated by grazing models incorporating experimental and theoretical estimates of ingestion, was on average 6% or less of the net primary production (NPP), but was quite variable with year and season, reaching as high as 76% for krill and 37% for salps (Ross *et al.*, 1998). In this study, higher grazing impact from krill occurred onshore and in the south, while salp grazing impact was higher offshore and in northern transects. Estimates of copepod grazing impact are also variable, presumably reflecting temporal and spatial changes in grazer abundance relative to primary production. For example, estimates of copepod removal of NPP near South Georgia was on average 36%, but ranged from 5–102% (Pakhomov *et al.*, 1997). The impact of pteropod feeding on removal of NPP in

the PAL area is unknown, but may be important as pteropods can account for a high percentage of the measured zooplankton community grazing in adjacent areas of the WAP and elsewhere in the southern ocean (Bernard & Froneman, 2009; Hunt *et al.*, 2008). While krill, salps, copepods, and pteropods are all potentially important meso- and macrograzers in the WAP, the role of microzooplankton (microflagellates, ciliates, heterotrophic dinoflagellates, and early life history stages of some crustacea) is little known. These major grazers of pico- and nanophytoplankton account for the majority of the loss of primary production in much of the world's ocean (Calbet & Landry, 2004). The one published study of microzooplankton grazing for the WAP shows that, while there was considerable variability in phytoplankton growth (0.02 to 1.16 day^{-1}), and grazing by microzooplankton (-0.04 to 0.69 day^{-1}), in six of their 12 experiments phytoplankton growth was balanced by microzooplankton grazing (Tsuda & Kawaguchi, 1997).

Zooplankton fecal pellets, mostly from krill, comprise the dominant fraction of the POC flux over the WAP continental shelf (Figure 5.18) (Wefer *et al.*, 1988). Changes in zooplankton community composition, biomass, and distribution in the WAP (as tied to climate change, sea ice dynamics, food availability and other factors) could thus effect biogeochemical cycling in the WAP. For example, a switch from a krill- to a salp-dominated ecosystem in the WAP could significantly alter carbon flux. Salps are non-selective filter feeders that efficiently re-package microplankton into large, rapidly sinking fecal pellets, greatly enhancing

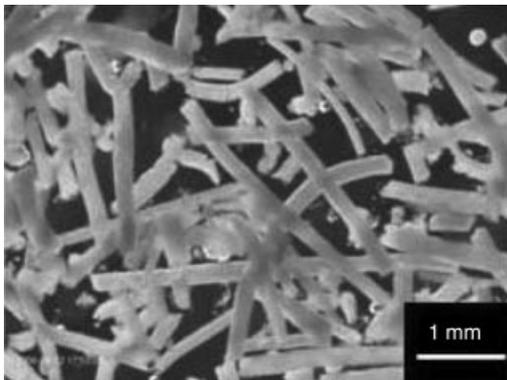


Figure 5.18 Sediment trap sample from Jan. 2006 comprised almost exclusively of krill fecal pellets. From PAL time-series trap located in northern shelf region deployed at 170 m. (See the colour version of this figure in Plate section)

the efficiency of C transport to depth (Michaels & Silver, 1988; Pakhomov *et al.*, 2006; Phillips *et al.*, 2009). *Salpa thompsoni* produce fecal pellets sinking on average 700 day^{-1} (Phillips *et al.*, 2009), and defecation rates of salps can exceed those of krill (Pakhomov, 2004; Pakhomov *et al.*, 2006; Phillips *et al.*, 2009). Thus significant vertical flux of particulate organic carbon and nitrogen due to range expansion and increases in abundance of salps could occur.

5.8 PENGUINS

The western Antarctic Peninsula region harbours breeding populations of five of the world's 17 recognized penguin species (Williams, 1995). Among these, Emperor (*Apdenodytes forsteri*) and Adélie (*Pygoscelis adeliae*) penguins are considered true Antarctic species, and exhibit life histories that are closely linked to the presence of sea ice (Ainley, 2002; Ainley *et al.*, 1992; Fraser *et al.*, 1992; Williams, 1995). The three remaining penguins, Gentoo (*P. papua*), Chinstrap (*P. antarctica*) and Macaroni (*Eudyptes chrysolophus*) are regarded as sub-Antarctic species, with life histories that are characterized by ice avoidance (Fraser *et al.* 1992; Williams 1995). Although the historical record indicates that Emperor and Macaroni penguins were never abundant in the WAP (less than a few hundred breeding pairs of each), the combined total population of the three other species numbers close to 1.5 million breeding pairs (Fraser & Trivelpiece, 1996; Woehler, 1993). These three penguin species comprise the dominant component of WAP regional avian biomass, an axiom that holds true even in winter due to their propensity to remain associated with their preferred polar or sub-polar habitats (Erdmann *et al.*, 2011; Fraser *et al.*, 1992; Polito & Trivelpiece, 2008; Trivelpiece *et al.*, 2007).

Penguins in the WAP are important consumers, a trophic position they also hold in virtually all sectors of Antarctica due to their relatively high abundance and dominance of local and regional avian biomass. However, in contrast to other regions of Antarctica, and particularly in the case of Adélie penguins, their diets in the WAP are almost exclusively represented by one prey species, *Euphausia superba*, the Antarctic krill (Ainley, 2002; Fraser & Hofmann, 2003; Volkman *et al.*, 1980). As mobile, long-lived, upper-trophic level predators, penguins and other seabirds integrate the effects of variability in the physical and biological environment over large spatial and temporal scales (Fraser &

Trivelpiece, 1996). As indicated previously, the marine environment of the WAP is experiencing some of the most rapid and significant warming on Earth, with the loss of sea ice possibly the most dramatic manifestation of change (Figure 5.2). Research on penguins whose life histories exhibit opposing affinities to sea ice not surprisingly provided some of the first evidence linking these changes in the physical environment to the biological responses of top predators (Fraser *et al.*, 1992). More importantly, this research established the importance of understanding the role of life history strategies within the context of the overall marine ecosystem response to climate variability. This focus is now a subject of interest spanning a suite of polar organisms (Forcada & Trathan, 2009; Moline *et al.*, 2008; Siniiff *et al.*, 2008).

One of the mechanisms by which climate warming induces change in ecosystem structure and function is by disrupting the evolved life history strategies of key component species (Rhodes & Odum, 1996). Certainly one of the most striking trends observed in the penguin population data is the change in community composition during the last three decades as ice-dependent Adélie penguins have decreased and ice-intolerant Chinstrap and Gentoo penguins have increased in the northern and mid-Peninsula region (Figure 5.19). The latter two species are the product of populations only recently established (1976 and 1994, respectively). This may be a unique event in the Palmer Station

area given paleoecological evidence indicating that these two sub-Antarctic species have not been present locally for at least the past 700 years (Emslie *et al.*, 1998). This implies that the environmental conditions promoting these population increases are unprecedented within the temporal limits of this record.

Although the precise causal mechanisms associated with these population trends remain equivocal (Forcada *et al.*, 2006; Fraser & Trivelpiece, 1996), analyses focused especially on the longer-term Adélie penguin data suggest that interactions between regional, and local-scale processes are involved, and both can be linked directly to the effects of rapid climate warming. There is wide concurrence that regional-scale trends are forced by a gradual decrease in the availability of winter sea ice (Fraser *et al.*, 1992). However, based on work at Palmer Station specifically, a more local source of population forcing has also been identified. This appears to be related to increasing snow precipitation in the WAP (Thompson *et al.*, 1994), which affects Adélie penguin colonies breeding where snow accumulations are enhanced by landscape aspect and prevailing winds during spring storms. These colonies have over the last 35 years decreased significantly faster than colonies where wind-scour abates snow accumulations (Fraser & Patterson, 1997; Patterson *et al.*, 2003), a pattern now observed in continental Antarctica as well (Bricher *et al.*, 2008). Interestingly, Palmer area populations of the ice-intolerant Chinstrap and Gentoo

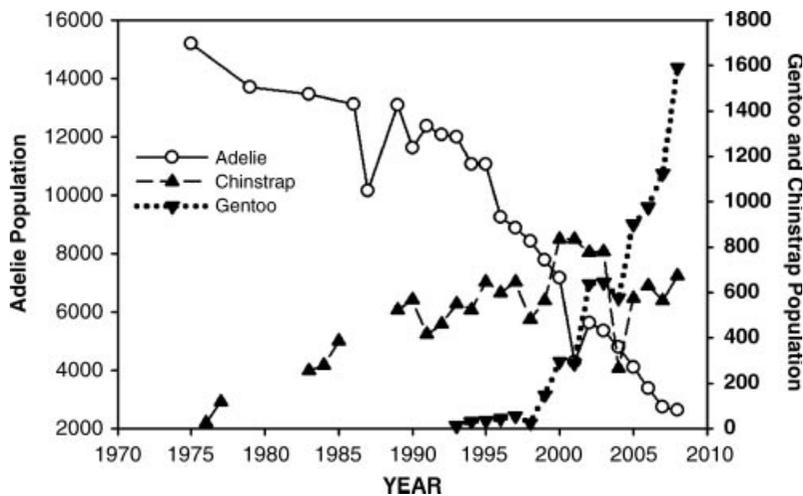


Figure 5.19 Population trends for three penguin species in the Anvers Island vicinity, 1975–2008. Data updated from Ducklow *et al.* (2007).

penguins have maintained their sub-Antarctic breeding chronologies (Williams, 1995), hence by breeding approximately three weeks later than Adélie penguins, Chinstrap and Gentoo penguins in effect permit spring melt to circumvent the negative effects of snow accumulation.

These two scales of processes operate by producing a spatial and/or temporal mismatch between needed resources and critical aspects of a species' life history, a long-established concept (cf. Cushing, 1969) that is now re-emerging as an important paradigm linking our understanding of marine and terrestrial ecosystem dynamics (Durant *et al.*, 2007; Edwards & Richardson, 2004; Fraser & Hofmann, 2003; Moline *et al.*, 2008). What remains a key challenge, however, is integrating a food-web perspective within the context of these dynamics. Changes in the abundance and availability of prey must surely have a role in altering the threshold states that lead to optimal habitat conditions for one species but suboptimal conditions for another (Fraser & Trivelpiece, 1996; Fraser *et al.*, 1992), yet integrating these factors into a model with sea ice as a key determinant of changes in predator populations has been problematic (Smith *et al.*, 1999b). Palmer Station Adélie penguin responses to changes in krill abundance are temporally coherent with those of other krill-dependent predators over spatial scales that include the northern WAP and much of the southwest Atlantic sector of the Southern Ocean (Clarke *et al.*, 2007; Fraser & Hofmann, 2003; Murphy *et al.*, 2007). The response variables are diverse, encompassing a range of factors from changes in foraging trip durations to population trajectories, and involve other predator groups besides penguins. The causal mechanisms that determine how the presence or absence of sea ice tips the balance in favour of one life history strategy over another may actually operate over much smaller scales than previously thought. These scales may encompass, for example, the factors that determine access to local breeding sites or traditional wintering areas (Erdman *et al.*, 2011; Fraser & Trivelpiece, 1996), and incorporate predator responses that result from species-specific competitive abilities for local prey resources (Lynnes *et al.*, 2002, 2004).

5.8.1 Contaminants in penguins

Persistent organic pollutants (POPs) reach polar regions by long-range atmospheric transport where snow, ice

and associated microbial communities serve as conduits for introducing them into the marine ecosystem (Chiuchiolo *et al.*, 2004; Risebrough *et al.*, 1976; Wania, 1997). Lipophilic POPs accumulate in fatty tissues and may biomagnify through the food web, thus accumulating in higher trophic level predators such as Adélie penguins. This species forages over relatively small distances close to breeding colonies in the summer and follows the sea ice edge in the winter (Volkman *et al.*, 1980, Fraser & Trivelpiece, 1996, Ainley, 2002, Fraser & Hofmann, 2003). Moreover, as a true Antarctic species, they are restricted to regions south of the Antarctic convergence, hence making excellent candidates for examining baseline pollution levels and long-term trends of contaminants in the Southern Ocean ecosystem (Sladen *et al.*, 1966; van den Brink *et al.*, 2009; van den Brink, 1997). Indeed, investigations of long-term trends of Σ DDT (p,p'-DDT + p,p'-DDE) in Adélie penguins has revealed an unexpected consequence of climate change along the WAP.

Global use and emission of DDT have declined by >90% and >80% since the late 1960s (Li & Macdonald, 2005). Building on data collected during and just following peak use of DDT (Risebrough *et al.*, 1976; Sladen *et al.*, 1966; Subramanian *et al.*, 1986), it is now evident that Σ DDT levels have not declined in the Palmer Archipelago population of Adélie penguins over more than 40 years (Geisz *et al.*, 2008). Adélie penguin eggs collected and analyzed from 2004–2006 revealed no significant change in contaminant concentration from those analyzed in the mid 1970s (Geisz *et al.*, 2008, Risebrough *et al.*, 1976). Similarly, Σ DDT in adult Adélie penguin subcutaneous fat, carrying 75–90% of the body burden (Subramanian *et al.*, 1986), follows model predictions for steady state showing an increase in Σ DDT concentrations during the 1960s and 70s, but no significant decline from peak detection (Geisz *et al.*, 2008). In contrast, Σ DDT decreased significantly from 1975 to 2003 in Arctic seabird eggs with half-lives of 9–20 years (Braune, 2007; Braune *et al.*, 2001). In the absence of current sources, Σ DDT in penguin eggs would likewise decline.

The continued steady state is not necessarily surprising given the uninterrupted use of DDT in the Southern Hemisphere, but air, snow, sea ice and water samples collected near the Antarctic Peninsula during 2002 indicate very little recent DDT deposition (Chiuchiolo *et al.*, 2004). Measurable levels of Σ DDT were found in glacier runoff and with recent melting rates for the Western Antarctic Ice Sheet indicate that 1–4 kg/y

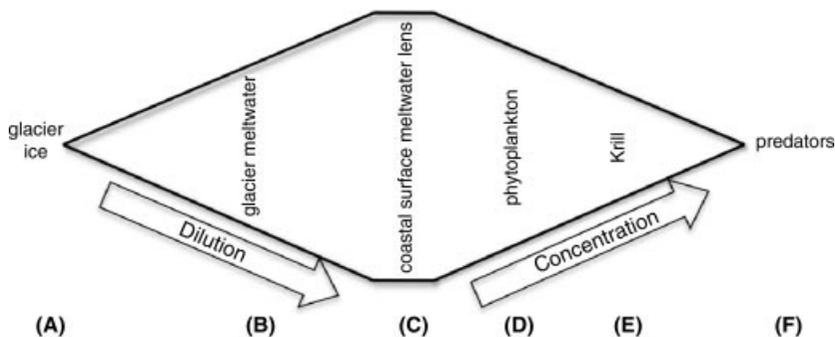


Figure 5.20 A conceptual model demonstrating the movement of relic POPs, deposited on glacier ice during peak use, into the Antarctic marine ecosystem. Contaminants are locked in layered glacier ice (A). Surface meltwater percolates through glacier ice and combines with basal meltwater to dilute contaminant concentrations (B). Glacial meltwater disperses contaminants into coastal seawater (C) where phytoplankton communities are stabilized in the freshwater lens (D). Lipophilic POPs are scavenged by algal bloom communities (D), biomagnified by krill consuming these phytoplankton (E), and further biomagnified and concentrated as they move up the food web to Adélie penguins (F).

Σ DDT are currently released into the Antarctic marine environment due to glacier ablation (Geisz *et al.*, 2008). Arctic and alpine lake systems likewise exhibit elevated contaminant levels where hydrology is heavily influenced by glacial runoff (Bizzotto *et al.*, 2009; Blais *et al.*, 2009; Bogdal *et al.*, 2009).

Existing data would indicate seasonal exposure to elevated concentrations of contaminants in glacier meltwater sufficiently maintains the body burdens of Σ DDT in Adélie penguins given that these predators are strongly coupled with their prey spatially and temporally over small scales (Fraser & Hofmann, 2003; Geisz *et al.*, 2008). A conceptual model (Figure 5.20) demonstrates how relic contaminants are likely transferred following seasonal glacier melt. A calculated ice column inventory for Σ DDT (Risebrough *et al.*, 1976) indicates that there is $>8 \mu\text{g}$ Σ DDT per m^2 of glacier ice on the Antarctic Peninsula (Geisz *et al.*, 2009). Though basal melt dominates glacier loss in the Antarctic, surface melt and meltwater percolation through glaciers (Figure 5.20A) are demonstrated as an important mechanism for total ice loss in the presence of atmospheric warming (Steig *et al.*, 2009; van den Brink *et al.*, 2009). The glacier meltwater lens extends at least 100 km offshore and stabilizes the surface layer permitting phytoplankton to remain in a favourable light environment (Figure 5.20B–D, Dierssen *et al.*, 2002). Diatom communities scavenge contaminants in this stable and expansive environment, which is illustrated by a near shore gradient of Σ DDT, primarily p,p'-DDT, in

phytoplankton (Chiuchiolo *et al.*, 2004). Seasonal diatom blooms are consumed by krill, the primary food source of Palmer area Adélie penguins (Figure 5.20D–F). During the breeding season (October–February), these penguins forage within the region affected by meltwater, consuming relic glacial Σ DDT that has biomagnified through the Antarctic marine food web. Though Σ DDT concentrations are below threshold levels for effects in these seabirds, the measurable contaminant, in combination with regional warming along the WAP, has provided a mechanism to trace ecosystem processes in the Antarctic marine food web.

5.9 MARINE MAMMALS

The marine mammals of the WAP include five pinniped species and, conservatively, at least nine species of cetaceans. Like the penguins, both the pinnipeds and cetaceans are composed of species whose life histories also exhibit varying affinities to sea ice. Thus, the pack ice seals, Crabeater (*Lobodon carcinophagus*), Weddell (*Leptonychotes weddellii*), Leopard (*Hydrurga leptonyx*) and Ross (*Ommatophoca rossii*), are ice-obligate species whose distribution, abundance, reproduction and foraging ecology are closely tied to the presence of sea ice, while Southern Elephant (*Mirounga leonina*) and Fur (*Arctocephalus gazella*) seals tend to winter and forage in open water and marginal ice zones, but reproduce on land (Burns *et al.*, 2004;

Costa & Crocker, 1996; Gales *et al.*, 2004). Among cetaceans, Minke (*Balaenoptera bonaerensis*) and Killer (*Orcinus orca*) whales exhibit life histories with affinities to sea ice while the other known species tend to be ice-avoiding, feeding in the WAP during the summer, but migrating north during austral winter to reproduce (Bonner, 1998; Pitman & Ensor, 2003; Sirovic *et al.*, 2004).

Although these megafauna are one of the most conspicuous features of the WAP marine ecosystem, they are also among the least well known, a characteristic that holds true for Antarctica and the Southern Ocean in general. Indeed, for cetaceans and the pack ice seals in particular, it is probably not possible at the moment to give even firm order-of-magnitude estimate of standing stocks along the WAP (Costa & Crocker, 1996), a region so under-sampled that surveys are still discovering both new species (Pitman & Ensor, 2003) and new populations of known species (Pitman & Ensor, 2003; Sirovic *et al.*, 2004). Nevertheless, what seems most clear about the role of the WAP in the ecology of these marine mammals is its significance as a feeding ground. Apart from the ice-dependent species that are tied to the region year round, the other species clearly migrate into the region for the sole purpose of feeding during austral summer (most of the whales; Freidlander *et al.*, 2008; 2009), or in autumn following reproduction in the sub-Antarctic (Fur and Southern Elephant seals; Bonner, 1998; Costa *et al.*, 2008; Siniff *et al.*, 2008). Although fish and squid are fed upon by all these species to varying degrees, Antarctic krill is by far the most important single component in the diets of these marine mammals. As a result, the distribution and abundance of krill (including marine physical and biological properties affecting these variables) strongly regulates where these mammals occur in space and time (Burns *et al.*, 2004; Chapman *et al.*, 2004; Freidlander *et al.*, 2006, 2008, 2009; Ribic *et al.*, 2008; Siniff *et al.*, 2008).

Given both this dependence on krill and life histories that exhibit different affinities to sea ice, it is conceivable that WAP marine mammal populations have exhibited trends not too dissimilar from those previously discussed for penguins (Figure 5.19). Atkinson *et al.* (2004), for example, have shown that declining sea ice is associated with a significant decrease in krill abundance in the WAP and Southwest Atlantic sector of the Southern Ocean. However, thus far only trends in some pinniped populations show convincingly that they may be responding to these perturbations. The

most conspicuous among these include dramatic increases in Fur and Southern Elephant seals, two ice-avoiding species, and decreases in Crabeater and Weddell seals, two ice-dependent species (Bonner, 1985; Erickson & Hanson, 1990; Laws, 1985). Although climate-induced population changes are suspected for marine mammals in other Antarctic sectors as well (e.g., Minke whales and Fur and Southern Elephant seals; Branch & Butterworth 2001; Hucke-Gaete *et al.*, 2004; McMahon *et al.*, 2005; Weimerskirch *et al.*, 2003) data interpretation is potentially confounded by many factors, including nonlinearities in observed trends (Forcada *et al.*, 2005), and in particular the fact that these species are recovering from massive population declines induced by human harvesting. Understanding these changes is complicated by massive human removal of whales and several fish stocks from Antarctic seas between 1950 and 1980 (Ainley and Blight, 2008). As indicated by Smetacek and Nicol (2005), disentangling the effects of human exploitation, climate change and changing modes of top-down control exerted by large predators is a major scientific and societal challenge facing Antarctic science.

5.10 SYNTHESIS: FOOD WEBS OF THE WAP

Inverse analysis techniques can be used to synthesize measurements such as those reviewed here into end-to-end food web models for the West Antarctic Peninsula. Adopted from the physical sciences by Vezina and Platt (1988), inverse analysis uses an input food-web compartment structure and a set of specified biological rules to solve for the multiple fluxes within a food web using limited data inputs. Using the inverse approach, Daniels *et al.* (2006) solved for an internally-consistent, mass-balanced food web (36 flows in total) for the Palmer Station region in January 1996.

In our updated analysis, we revise the Daniels *et al.* compartments and constraints to reflect the latest data and current understanding of the system. In particular, we assign consumption pathways to krill, salp, and microzooplankton compartments, and include *Pleuogramma* (Antarctic silverfish, which feed on krill and are in turn consumed by penguins) in our analysis. Updated literature values were also available to constrain krill production (Shreeve *et al.*, 2005), salp grazing (Perissinotto *et al.*, 1997) and egestion (Perissinotto *et al.* 1997; Phillips *et al.*, 2009), zooplankton respiration (Alcaraz

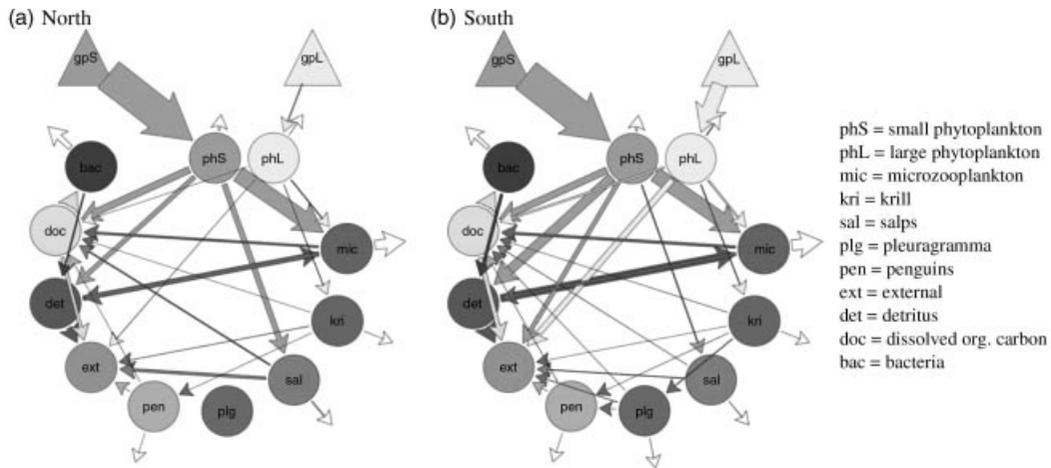


Figure 5.21 Inverse model reconstructions for foodwebs in the northern (Palmer Station) and southern (Avian Island) penguin foraging regions along the western Antarctic Peninsula. Note the greater relative abundance of large phytoplankton (phL) in the south, but overall dominance by smaller cells (phS) in both regions, leading to larger inputs of primary production into microzooplankton (mic) than krill (kri). Nonetheless the model satisfies metabolic needs for observed krill stocks in both regions. In these diagrams, some trophic exchanges (arrows) are permitted by the model but did not appear as nonzero flows in model solutions (e.g., detritus and microzooplankton consumption by krill and salps), further demonstrating that large phytoplankton production was sufficient to meet krill requirements. Note also greater flows through salps in the north, where greater sea ice declines may be stimulating salp blooms. (See the colour version of this figure in Plate section)

et al., 1998) and vertical export (Anadon *et al.*, 2002; Doval *et al.*, 2002; Ducklow *et al.*, 2008). Summertime measurements from Adélie penguin foraging regions near Palmer Station (north) and Adelaide Island (south) constrain the model. Flow through the food web is driven mainly by primary producer inputs and zooplankton biomass (Figure 5.21). The magnitude of fluxes and direction of flows are controlled by the size distribution of primary production because krill and salps are restricted to feeding within particular cell size classes. Despite four-fold variations in measured krill and salp biomass, most primary production is by small cells (Montes-Hugo *et al.*, 2008, 2009), suggesting a more prominent role for microzooplankton than previously estimated. Model results show that microzooplankton consumed 47% (South) to 60% (North) of primary production directly, and respired 25–30% of total primary production.

Adélie penguin populations are an order of magnitude larger in the South, driving a twenty fold variation in the fraction of primary production ultimately consumed by penguins (0.01% in the North on a krill diet and 0.2% in the South, where they feed on both krill and *Pleuragramma*). In addition, 35% (North) to

50% (South) of primary production is exported as detritus or DOC. By contrast, sediment trap measurements suggest exports of less than 5% of primary production, raising concerns about trap underestimation. These results therefore imply a smaller role for the ‘traditional’ Antarctic food chain linking diatoms, krill, and penguins, and greater significance for the microbial loop.

5.11 CONCLUSIONS

The marine pelagic ecosystem West Antarctic Peninsula, dominated by diatom primary producers, krill and a great variety of upper level vertebrate consumers, is similar in its structure and dynamics to other Antarctic shelf regions, with the exception of the Ross Sea system (Smith Jr. *et al.*, 2007). The Ross Sea is dominated by *Phaeocystis antarctica*, and has fewer krill than the WAP (Ducklow *et al.*, 2006). However, the WAP differs from all other Antarctic systems in one important respect: it is experiencing the most rapid warming of any marine ecosystem in the planet. Recently resolved changes in the regional climate and sea ice are now understood to

affect all levels of the food web, from top predators whose life histories exhibit different affinities to sea ice to fish, krill, phytoplankton and bacteria. Changes in these ecosystem components appear to be modulated by global teleconnections with ENSO and other modes of climate variability. Clarke *et al.* (2007) present a schematic view of a Southern Ocean food web in which primary production is channeled through krill, salps and other zooplankton toward three general fates: passage to higher predators, sinking to benthic food webs and transfer into the microbial food web. In the WAP, most production appears to move up through the food chain to the higher predators or into bacteria. Only a few per cent of the primary production sinks through the deep (300–700 m) water column to the benthos. Whether these modes of ecosystem function will change in importance with further warming (or indeed, if they have already changed) is unknown.

A major challenge for Antarctic scientists involves not only documenting ecosystem responses at all levels of biotic organization (genome to planetary), but also establishing a mechanistic understanding of the linkages between climate, sea ice, biogeochemical processes and lower to upper trophic levels. The WAP is fortuitously characterized by a relatively simplified marine ecosystem (though one still demonstrating complex dynamics and feedbacks), rapid climate warming and a well-populated scientific infrastructure. These factors present the international community of Antarctic scientists and policymakers with an unparalleled opportunity for observing and understanding the interactions between climate change and marine ecosystem response.

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