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# Multiscale control of bacterial production by phytoplankton dynamics and sea ice along the western Antarctic Peninsula: A regional and decadal investigation

Hugh W. Ducklow [a,*], Oscar Schofield [b], Maria Vernet [c], Sharon Stammerjohn [d], Matthew Erickson [a]

[a] The Ecosystems Center, Marine Biological Laboratory, 7 MBL St. Woods Hole, MA 02543, USA
[b] Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, NJ 08901-8525, USA
[c] Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, CA 92093-0210, USA
[d] Institute of Arctic and Alpine Research, University of Colorado, Campus Box 450, Boulder, CO 80309-0450, USA

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ABSTRACT

We present results on phytoplankton and bacterial production and related hydrographic properties collected on nine annual summer cruises along the western Antarctic Peninsula. This region is strongly influenced by interannual variations in the duration and extent of sea ice cover, necessitating a decade-scale study. Our study area transitions from a nearshore region influenced by summer runoff from glaciers to an offshore, slope region dominated by the Antarctic Circumpolar Current. The summer bacterial assemblage is the product of seasonal warming and freshening following spring sea ice retreat and the plankton succession occurring in that evolving water mass. Bacterial production rates averaged 20 mg C $m^{-2}$ $d^{-1}$ and were a low (5%) fraction of the primary production (PP). There was significant variation in BP between regions and years, reflecting the variability in sea ice, chlorophyll and PP. Leucine incorporation was significantly correlated ($r^2$ ranging 0.2–0.7, $p<0.001$) with both chlorophyll and PP across depths, regions and years indicating strong phytoplankton–bacteria coupling. Relationships with temperature were variable, including positive, negative and insignificant relationships ($r^2<0.2$ for regressions with $p<0.05$). Bacterial production is regulated indirectly by variations in sea ice cover within regions and over years, setting the levels of phytoplankton biomass accumulation and PP rates; these in turn fuel BP, to which PP is coupled via direct release from phytoplankton or other less direct pathways.



## 1. Introduction

Antarctic coastal and shelf waters exhibit high rates of primary productivity (Smith et al., 2000) that support large stocks of upper level consumers including seabirds, seals and whales (Smetacek and Nicol, 2005) and possibly constitute an important sink for atmospheric $CO_2$ (Arrigo et al., 2008). As in other marine ecosystems, net primary production (PP) flows both to a microbial foodweb and to higher trophic levels (Clarke et al., 2007). The relative allocation of organic matter flow between these two pathways is governed by phytoplankton cell size, dissolved organic matter (DOM) release and other variables (Legendre and Rassoulzadegan, 1996). The rich Antarctic production system might be expected to deliver large amounts of organic matter for bacterial utilization; yet paradoxically, bacterial production (BP) rates in the Ross Sea, Antarctica (Ducklow et al., 2001a) and in the Arctic Ocean (Kirchman et al., 2009a) are significantly lower on average, than in other, lower latitude ocean ecosystems. Moreover BP rates are low relative to the local PP, as well as in an absolute sense. That is, a smaller fraction of the PP is incorporated into bacterial biomass than in other, mostly better-studied ecosystems.

Two contrasting explanations for the low bacterial to primary production ratio (BP:PP) are: 1) the flux of labile organic matter to bacteria is low; or 2) low temperature inhibits bacterial activity. There is a long-standing debate about the role of low temperature as an explanation for low microbial rates in cold water (Pomeroy and Wiebe, 2001). Kirchman et al. (2009b) provided a critical review of the factors potentially influencing BP rates in polar seas. Their review found that the latest analyses do not indicate that cold temperatures *per se*, are the principal factor regulating bacterial growth. There are few direct measurements of the availability or flux of labile dissolved organic matter. There are some indications that top–down effects suppress bacterial stocks, and thus BP rates (Bird and Karl, 1999), but there is no *a priori* reason to suggest that bacterivory or viral lysis is more intense than in other systems.

Antarctic coastal and shelf waters remain sparsely sampled due to the remote location and difficulty of access even under ice-free conditions in summer. The western Antarctic Peninsula (WAP) region is experiencing rapid climate warming, resulting in a gradient of sea ice cover, ranging from a region of decreasing sea ice duration in the south to a now ice-free summer season in the north (Montes-Hugo et al., 2009; Stammerjohn et al., 2008a). The Palmer Antarctica Long Term Ecological

* Corresponding author. Tel.: +1 508 289 7193.
*E-mail addresses:* hducklow@mbl.edu (H.W. Ducklow), oscar@marine.rutgers.edu (O. Schofield), mvernet@ucsd.edu (M. Vernet), sharon.stammerjohn@colorado.edu (S. Stammerjohn).

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Research program initiated a new series of measurements of bacterial abundance and production rates in 2002–03 to investigate the biogeochemical importance of bacteria in the regional carbon cycle (Daniels et al., 2006; Ducklow et al., 2006b) and to test hypotheses about the regulation of bacterial processes in polar seas. Here we examine the resulting large, regional-scale, multiyear dataset of bacterial production measurements in relation to bacterial and phytoplankton stocks and primary production rates, with associated physical and sea ice properties collected each summer from 2003 to 2011.

The overall goal of this paper is to investigate the regional-scale distribution and interannual variability of BP in the west Antarctic Peninsula area in the context of local hydrography and coupling to PP by phytoplankton. We begin by describing the hydrography of the study area and placing our regional-scale, summertime observations in a seasonal context. Next we present vertical profiles of phytoplankton and bacterial properties in the different hydrographically-defined regions of the study area. Then we analyze the bacterial distributions at a range of spatial and temporal scales (local/annual to regional/decadal) primarily through regressions with phytoplankton (PP, Chl) properties. Finally we examine long-term (climatological) distributions and decadal records of phytoplankton and bacterial properties, and relate them to variations in sea ice and climate forcing. We conclude that accumulation of phytoplankton biomass regulates BP in the Antarctic Peninsula region. Phytoplankton biomass has increased in the south and decreased in the north in response to climate change and sea ice decline (Montes-Hugo et al., 2009); however as yet we are unable to say if these changes in the ecosystem have impacted other microbial processes. BP is greater in the south region, where phytoplankton biomass is also high, and where there is sea ice in summer. But, BP:PP is greater in the north region, indicating a complex and dynamic picture of bacteria-phytoplankton relationships.

## 2. Materials and methods

### 2.1. Study area and sampling

The PAL study region encompasses a roughly 200×700 km area along the western Antarctic Peninsula, extending from the coast in the east across the continental shelf to the offshore, continental slope region, and from Anvers Island in the north to Charcot Island in the south (Fig. 1). The study area is divided into coastal, shelf and offshore (slope) regions on the basis of bathymetry, hydrographic properties and ecology (Martinson et al., 2008). The mean depth of the shelf is 430 m. Annually-occupied hydrographic stations were spaced 20 km apart along cross-shelf lines 100 km apart (Waters and Smith, 1992). Marguerite Bay, immediately south and east of Adelaide Island, experiences the largest phytoplankton bloom in the region. Stations south of Marguerite Bay typically have sea ice cover in January, in contrast to the northern region. Thus, we differentiated Marguerite Bay and the southern part of the study area (lines 100, 000 and −100) from the northern stations on the 200–600 lines (Fig. 1). All stations on the 200 to 600 lines, including stations in Marguerite Bay were sampled in 2003–08 resulting in comprehensive sampling of the shelf region. Occasional stations were sampled in the coastal region (triangles in Fig. 1). Sampling on the Southern (−100, 000 and 100) lines started in 2009. Stations sampled after 2009 are given in Supplementary Table S1. The full study region is described in detail elsewhere (Ducklow, 2008; Ducklow et al., 2006a).

The regional-scale datasets reported here were obtained during annual summer cruises aboard ARSV Laurence M Gould in 2003–2011, occurring roughly between 01 January and 10 February each year (Table S1). At each station, sampling consisted of one or more hydrocasts with a Seabird CTD-rosette system and 24 Niskin-type 12-liter bottles fitted with Vicor™ silicone springs. In general, two bottles were closed at each of 12 depths, extending from the surface to the bottom, irrespective of bottom depth, and with sampling concentrated in the upper 50–100 m. Usually 4–6 samples were obtained in the upper 50 m. One of the two Niskin bottles at each depth was subsampled into 5% HCl-washed, deionized and seawater-rinsed polycarbonate bottles for bacterial and biogeochemical assays. The other bottle was dedicated to phytoplankton measurements.

Seasonal time-series sampling was performed at Station E, 5 km from Palmer Station (Fig. 1; 64.48° S, 66.04° W) approximately every 4 days between late October and late March in 2002–06 and 2008–11. Sampling and analyses were similar to the cruise-based sampling but using Zodiac boats as sampling platforms, and Go-Flo bottles hung individually at preselected depths on the hydrowire.

### 2.2. Analytical methods

Chlorophyll (Chl) and PP rates and corresponding bacterial abundance and BP rates were determined at every hydrostation. Water samples from this region include both bacterial and archaeal cells in varying proportions. Autofluorescent picoplankton are <1% of the total count. In the upper 100 m in summer, >80% of the total picoplankton count is bacterial (Church et al., 2003), and the counts are termed bacterial for simplicity. As with abundance, we term the leucine incorporation data (see below) as indicating heterotrophic bacterial production (BP) rates, recognizing that some small and variable fraction might be attributed to other, nonbacterial, organisms.

Chl and PP measurements were conducted on samples from the euphotic zone (0.1–1% of surface irradiance) as determined from PAR measurements made prior to each CTD cast, as described in Vernet et al. (2008). PP was measured by C14 bicarbonate incorporation in 24-hour deck incubations. Chl was assayed fluorometrically on acetone extracts. Bacterial abundance was determined at all depths sampled from surface to bottom. Samples for abundance determinations were preserved in 2% formaldehyde, kept frozen at −80 °C and returned to the home laboratory for flow cytometric analysis using SYBR-Green (Invitrogen, Carlsbad, CA). Sample analyses took place 3–6 months after each cruise. Flow cytometer samples from 2003 to 2007 were assayed on a Beckman–Coulter EPICS Altra at Virginia Institute of Marine Science. Samples for 2007–11 were assayed using a Becton–Dickinson FacsCalibur at the Marine Biological Laboratory in Woods Hole. Results for the two instruments were compared on the entire 2007 sample set and did not differ significantly. The analytical protocols of Gasol and del Giorgio (2000) were followed throughout.

BP rates were derived from rates of $^{3}$H-leucine incorporation measured on samples extending over the upper 50–100 m. The leucine assays followed a procedure modified from the protocol originally proposed by Smith and Azam (1992). Briefly, triplicate 1.5 ml samples were incubated in the dark for ~3 h with $^{3}$H-leucine (MP Biomedical, Santa Ana, CA; >100 Ci/mmol, 20–25 nM final concentration) in 2.0 ml microcentrifuge tubes (Axygen SCT-200, Union City, CA). Incubations were maintained within 0.5 °C of the *in situ* temperature in refrigerated circulator baths and terminated by the addition of 0.1 ml of 100% trichloroacetic acid (TCA). Samples were concentrated by centrifugation, rinsed with 5% TCA and 70% ethanol and air-dried overnight prior to radioassay by liquid scintillation counting in Ultima Gold cocktail (Perkin-Elmer, Waltham, MA). Blank values of TCA-killed samples were subtracted from the average of the triplicates for each discrete depth sample.

### 2.3. Data analysis

The coefficient of variation of triplicate flow cytometric counts was 5%. The coefficient of variation of triplicate leucine assays was 6%. The mean blank value was 90 dpm. These estimates include the analytical precision and sample pipetting and processing errors. The limit of detection for leucine incorporation rates (ten times the background for a 3 h incubation) is <1 pmol $l^{-1}$ $h^{-1}$ (~0.05 mg C $m^{-3}$ $d^{-1}$). Bacterial abundance was converted to carbon biomass using 10 fg C $cell^{-1}$

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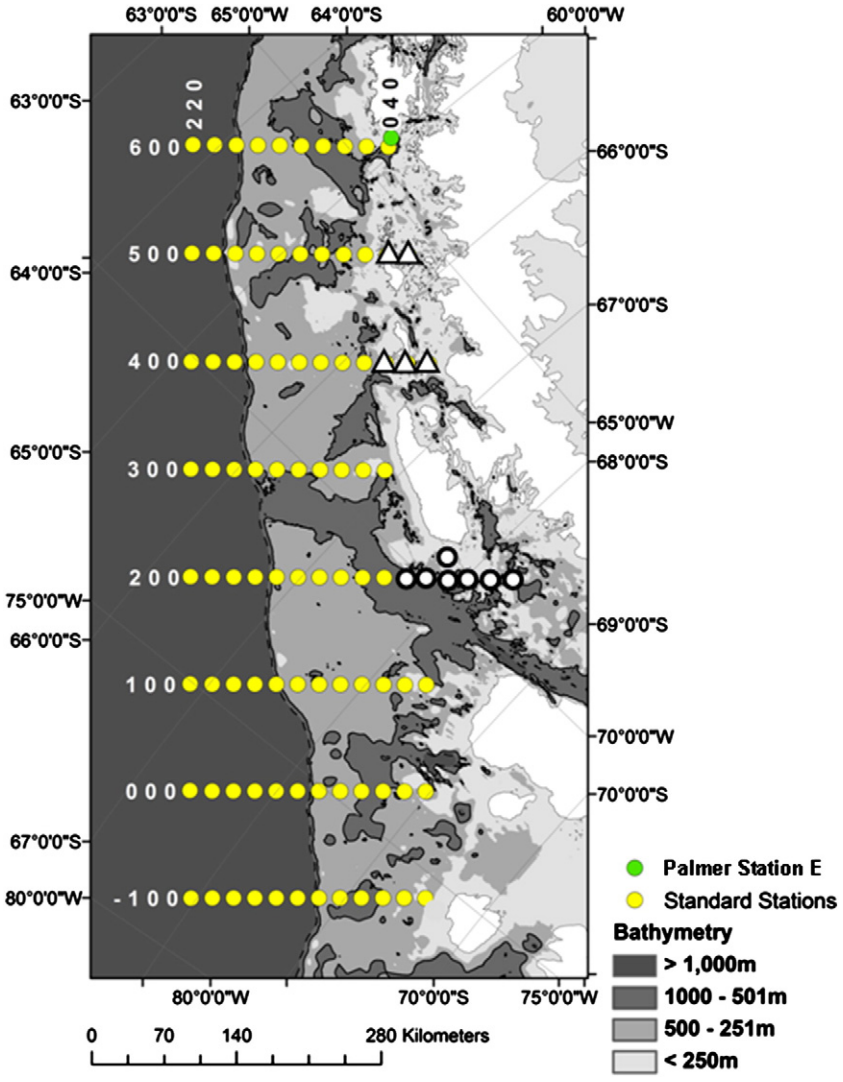


**Fig. 1.** Map of Palmer LTER study region along the Antarctic Peninsula (white). Palmer Station E is 5 km south of Anvers Island, (green dot). Hydrographic lines are 100 km apart, north to south. The standard on to offshore hydrographic stations (yellow dots) are 20 km apart. All stations >1000 m deep are Slope stations. Stations on the 200–600 lines<1000 m deep are termed Shelf stations. The triangles and white circles show Coastal and Marguerite Bay stations, respectively. Stations <1000 m deep south of the 200 line and Marguerite Bay are called South stations (the 100, 000 and −100 lines), and were not occupied prior to 2008. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Fukuda et al., 1998). Leucine incorporation rates were converted to bacterial carbon production using 1.5 kg C $mol^{-1}$ (Ducklow et al., 2000; Kirchman et al., 2009b). Chl, PP, bacterial abundance and leucine incorporation rate data exhibited relatively little variability below 50 m (see below). Bacterial properties were therefore integrated to 50 m to provide a consistent comparison across regions and years. This depth range encompassed the euphotic zone in all but a few cases. Integration depths were obtained by linear interpolation between sample depths if necessary. Statistical analyses were performed with Systat (ver. 13, Systat Inc. Chicago IL). Regression analyses of discrete depth values were confined to the upper 20 m (approximating the summer mixed layer) to remove the effect of depth-related variability.

All data considered in this paper are available at the Palmer LTER DataZoo: http://oceaninformatics.ucsd.edu/datazoo/data/pallter/datasets.

## 3. Results

### 3.1. Seasonality and hydrography

In this paper, we present observations obtained at the regional scale (Fig. 1) over nine years, 2003–11. Each year's cruise provides a snapshot of midsummer (January) conditions in the marginal sea ice zone to the west of the Antarctic Peninsula, (usually) following the annual sea ice retreat. These midsummer observations can be placed in the seasonal context by comparison with twice-weekly time series sampling undertaken at Palmer Station between October and March each field season. This comparison assumes that the seasonal cycle is similar in the nearshore and offshore regions. Water column (0–50 m) integrated leucine incorporation rates are low in the Austral spring (Fig. 2), around 200 nmol $m^{-2}$ $h^{-1}$, corresponding to a mean volumetric rate of ~5 pmol $l^{-1}$ $h^{-1}$, or a bacterial production rate of about 5–10 mg C $m^{-2}$ $d^{-1}$. Peak annual rates (~1000 nmol $m^{-2}$ $h^{-1}$) occur in mid-January to early February, coincident with the summer cruise period. There are few BP measurements from winter (i.e., April to September), when rates are typically <5 pmol $l^{-1}$ $h^{-1}$ (Ducklow, unpublished data).

We are principally concerned with the ecological and biogeochemical character of the upper 50 m of the water column in summer, the illuminated zone and season in which most biological activity occurs. In summer Antarctic Surface Water (AASW) is a freshened and warmed version of the sea ice-produced Winter Water (WW). It is freshened by spring sea ice melt and subsequently warmed by

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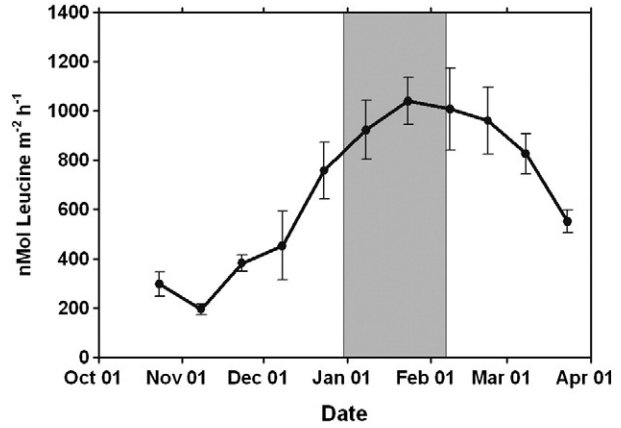


**Fig. 2.** Climatological (mean) seasonal cycle of the water column (0–50 m) $^{3}$H-leucine incorporation rate at nearshore Station E, Palmer Station, Antarctica. Observations from February 2003–March 2011 (excluding the 2006–07 and 2007–08 field seasons) were binned into 15-day intervals for this plot. The gray-shaded box indicates the period of the annual summer regional survey cruise (ca. Jan 01–Feb 06). Error bars are standard errors of the mean.

exposure to solar radiation (Fig. 3). The AASW typically overlies a remnant amount of the colder, saltier WW. In summer the water in the upper 50 m can be warmed and/or freshened considerably, depending on location and the time since sea ice retreat. Vertical profiles of temperature and salinity (Fig. 4) show that warming and freshening were on average restricted to the upper 50 m, with most change occurring in the upper 20 m encompassing the summer mixed layer. Different regions also exhibited varying characteristics: for example, in summer, waters in the Marguerite Bay and South regions were fresher and colder (<0 °C) due to more recent or ongoing ice melt (including sea ice, brash ice and glacier melt), whereas shelf and oceanic waters were typically warmer and saltier due to longer exposure to solar warming and relatively less *in situ* sea ice melt and/or longer exposure to wind mixing with the underlying saltier WW. This mosaic of characteristics reflects regional variations in the seasonal modification of the summer mixed layer with the underlying WW, setting the stage for plankton succession, including development of phytoplankton and bacterial properties following ice retreat and the spring phytoplankton bloom.

### 3.2. Phytoplankton stocks and production

We observed considerable interannual and regional variability in midsummer Chl and PP. For example, in 2009, an early ice retreat year, both rates and stocks were very low, with few discrete values even reaching the 2003–11 means (Fig. 5C,D). In years with later ice retreat (e.g., 2005, Fig. 5A,B), peak Chl and PP exceeded 10 mg m$^{-3}$ and 100 mg C m$^{-3}$ d$^{-1}$, respectively. Maximum Chl concentrations were nearly always in the surface mixed layer and declined with depth. Local hydrography showed variable relationships with Chl and PP (Supplemental Fig. S1), whereas regional differences were more distinct. For example, PP tended to be highest in Marguerite Bay, and lowest in the offshore slope region, irrespective of salinity or temperature. In the coastal region, PP was weakly but significantly ($p<0.001$) inversely related to both salinity and temperature, with the highest surface PP values occurring in cold, fresh nearshore waters (Supplementary Fig. S1 C,D; Supplementary Table S2).

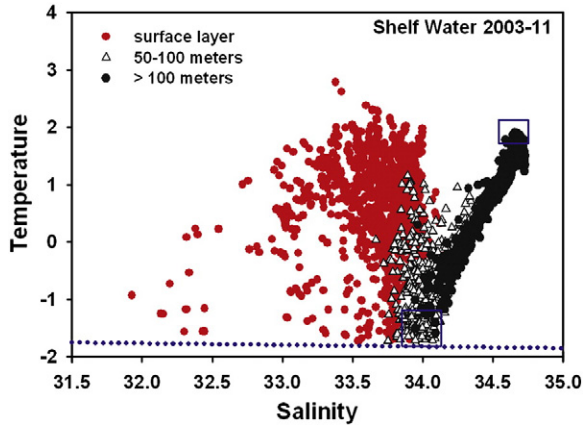


**Fig. 3.** Temperature–salinity (T–S) plot for the Shelf region of the Palmer LTER study area along the western Antarctic Peninsula (see Fig. 1 for location), summer 2003–11. Each symbol is one discrete depth from a CTD cast at a sampling station. The upper and lower blue boxes are Upper Circumpolar Deep Water (UCDW) and Winter Water (WW), respectively. The dotted line is the freezing point of seawater.

### 3.3. Bacterial distributions and relationships

Vertical profiles of bacterial abundance and leucine incorporation rates (Fig. 6; Supplemental Figs. S2, S3) were similar to the profiles of phytoplankton properties. In general the highest values were observed at the surface and declined with depth, mirroring the phytoplankton distributions. There was little year to year variation in the abundance profiles, with the exception of 2007 (up to five times higher than average at all depths) and 2010 (10–50% of mean values). Over all years there were no systematic differences between regions (see below). Peak surface values seldom exceeded $10^{9}$ cells l$^{-1}$. Leucine profiles were more variable, with greater surface (upper 20 m) enhancements and rates exceeding 60 pmol l$^{-1}$ h$^{-1}$ in 6 of 9 years. The highest leucine rates tended to occur in years of late ice retreat (e.g., 2005, Fig. 6A), mirroring PP rates and Chl.

There were no systematic (i.e., across regions and/or years) relationships between leucine incorporation and hydrography, when <20 m samples were pooled across regions (Supplemental Fig. S4), but there were some within-region relationships. For example, leucine rates were inversely related to salinity in the Shelf (Fig. S4C) and Southern regions, and directly related to temperature in Marguerite Bay (Fig. S4A and Table S2). However it is notable there was no universal influence of temperature across regions: equally high rates were found in the Southern region at low temperature (−1 °C) and in Marguerite Bay at high temperatures (>3 °C; Fig. S4B). Temperature effects on leucine incorporation are considered further below.

### 3.4. Chlorophyll and PP relationships with leucine incorporation and bacterial production

Chlorophyll was the most reliable indicator of leucine incorporation rates within and across depths, years and regions. Coefficients of determination ($R^2$) for chlorophyll-leucine regressions (discrete depth samples) over all depths and regions ranged from 28 to 72% for individual years 2003–11 (Table 1). Over all regions and all nine years combined, chlorophyll explained 52% of the discrete-depth variation in leucine incorporation. These Chl–Leucine relationships reflect both within- and between-regional components. Within the Shelf region alone, Chl explained at least 25% of the leucine variability in five of nine years (Supplementary Table S3). The pooled data sets in Fig. 7 show that the overall relationships were partly determined by gradients in Chl and Leu increasing from the Slope through the Shelf regions to Marguerite Bay. Relationships within other regions were not significant in most years, possibly because of lower sample sizes. Regulation of leucine incorporation rates by Chl was also manifested at larger, cross-regional and decadal scales. Water column integrated leucine incorporation rates were significantly related to water column integrated chlorophyll within the Shelf, Ocean and Marguerite Bay regions over all years, but not in the Coastal and Southern regions (Supplementary Table S4). The slopes of the regressions varied between years and regions, indicating different responses of leucine incorporation to Chl accumulation.

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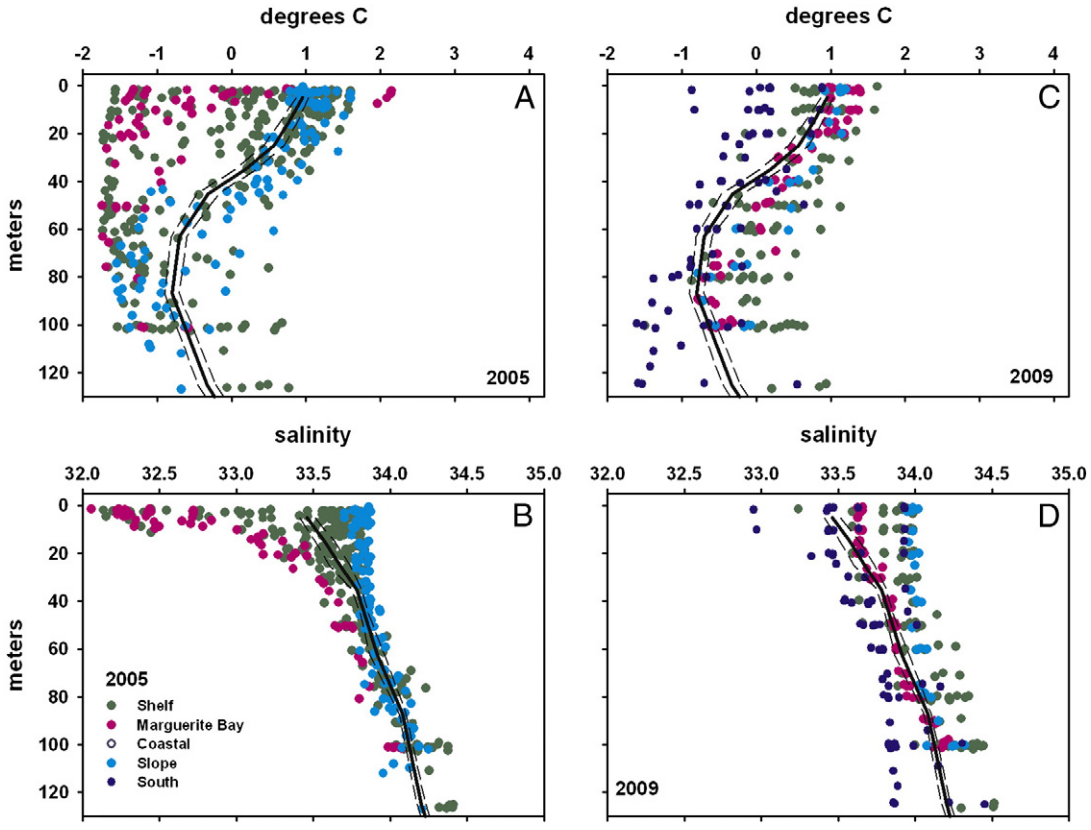


**Fig. 4.** Vertical distribution of temperature (A,C, degrees C) and salinity (B,D) in the Palmer LTER study region in 2005 (late sea ice retreat) and 2009 (early retreat), showing vertical, interannual and regional variability. Regions as in Fig. 1. The lines indicate the 2003–11 mean and 95% confidence intervals.

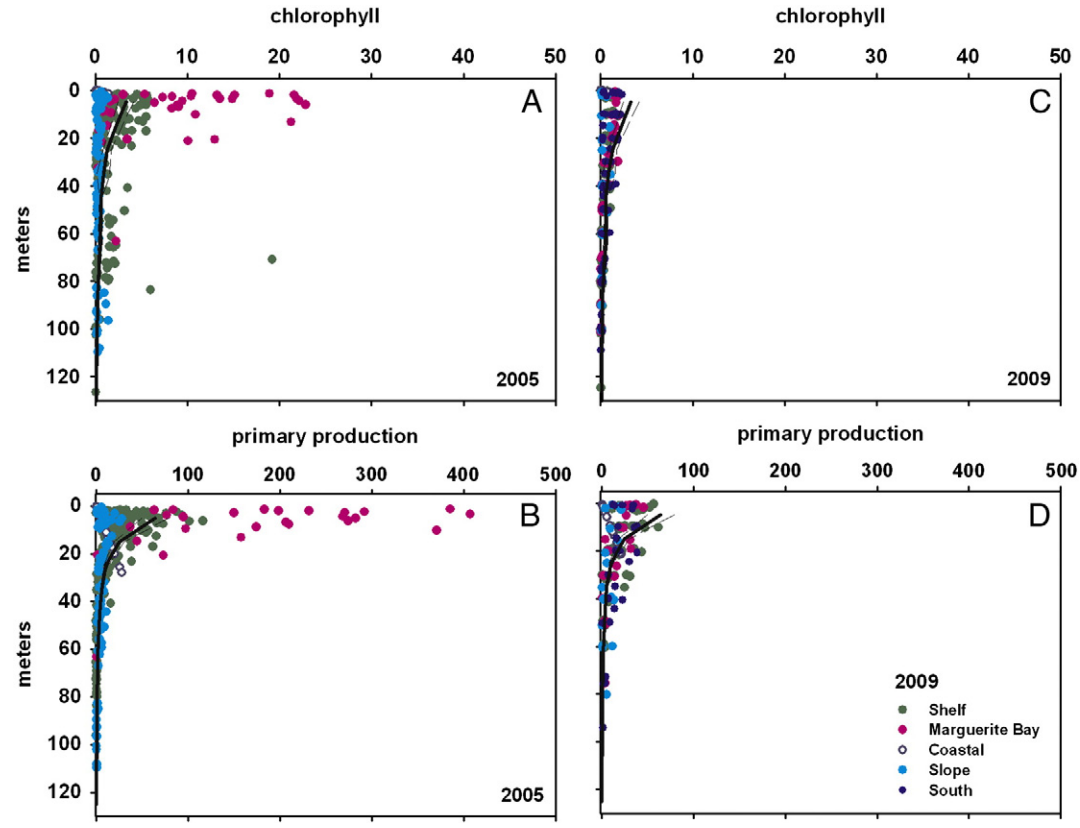


**Fig. 5.** Vertical distribution of chlorophyll (A,C; mg $m^{-3}$) and primary production rates (B,D; mg C $m^{-3}$ $d^{-1}$) in the Palmer LTER study region in 2005 (late sea ice retreat) and 2009 (early retreat), showing vertical, interannual and regional variability. Regions as in Fig. 1. The lines indicate the 2003–11 mean and 95% confidence intervals.

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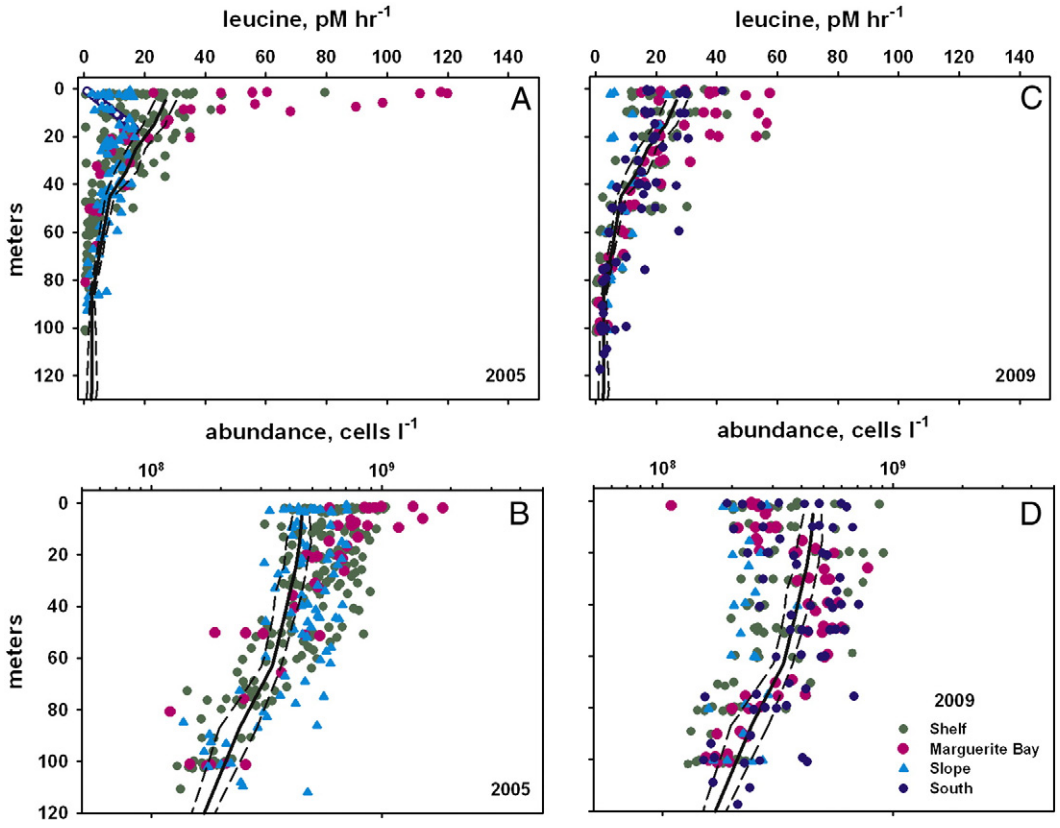


**Fig. 6.** Vertical profiles of $^{3}$H-leucine incorporation rates (A,C; pmol $l^{-1}$ $h^{-1}$) and bacterial abundance (B,D; cells $l^{-1}$) in the Palmer LTER study region in 2005 (late sea ice retreat) and 2009 (early retreat), showing vertical, interannual and regional variability. Regions as in Fig. 1. The lines indicate the 2003–11 mean and 95% confidence intervals.

Discrete-depth leucine incorporation rates were also significantly related to PP (e.g., Fig. 7) across regions and within years (Table 2). Euphotic zone-integrated relationships were significant within the Shelf, Ocean and Marguerite Bay regions (Table S4). The slopes of the *linear* regressions of BP on PP averaged about 1%, suggesting very low ratios of bacterial to primary production rates. The integrated water column values are somewhat higher (~5%). BP:PP ratios are further addressed below.

**Table 1**
Regression statistics for yearly volumetric (discrete depth) chlorophyll–leucine (Chl–Leu) incorporation relationships. All regions are pooled for the annual data sets. Regression equations are Log (Leu) = mLog (Chl) + b. All regressions are significant at $p<0.001$ unless noted. The significance of the regression is given in the $R^2$ column if greater than 0.001. Regressions were calculated for the full water column (e.g., Fig. 7) and for the upper 50 m alone.

| Year/depths | Slope (m) | Intercept (b) | $R^2$ | n |
|---|---|---|---|---|
| 2003 all | 0.82 | 0.75 | 0.61 | 252 |
| 2003 upper 50 | 0.63 | 0.73 | 0.36 | 195 |
| 2004 all | 0.62 | 1.20 | 0.37 | 216 |
| 2004 upper 50 | 0.54 | 1.21 | 0.34 | 193 |
| 2005 all | 0.36 | 1.11 | 0.18 | 212 |
| 2005 upper 50 | 0.38 | 1.18 | 0.28 | 190 |
| 2006 all | 0.56 | 1.05 | 0.43 | 212 |
| 2006 upper 50 | 0.48 | 1.10 | 0.32 | 195 |
| 2007 all | 0.57 | 1.22 | 0.63 | 350 |
| 2007 upper 50 | 0.37 | 1.29 | 0.46 | 251 |
| 2008 all | 0.64 | 1.02 | 0.50 | 323 |
| 2008 upper 50 | 0.64 | 1.10 | 0.49 | 236 |
| 2009 all | 0.78 | 1.34 | 0.72 | 220 |
| 2009 upper 50 | 0.46 | 1.33 | 0.39 | 139 |
| 2010 all | 0.73 | 0.88 | 0.45 | 212 |
| 2010 upper 50 | 0.15 | 1.02 | 0.02 (ns, $p=0.054$) | 142 |
| 2011 all | 0.57 | 1.21 | 0.58 | 251 |
| 2011 upper 50 | 0.45 | 1.32 | 0.40 | 195 |
| All years & depths | 0.67 | 1.08 | 0.52 | 2248 |
| All years, upper 50 | 0.54 | 1.13 | 0.40 | 1737 |

### 3.5. Regional relationships and trends

In spite of interannual variations, there were significant differences in phytoplankton and bacterial stocks and production rates across years and between regions, suggesting clear differences in the regulation of these variables by regional hydrography and ecology. In general, most variables were highest in the Marguerite Bay and Southern regions of the study area (where surface waters were relatively fresher and often colder due to recent or ongoing ice melt), and lowest in the offshore, oceanic region (Fig. 8). Phytoplankton and bacterial properties in the Shelf region were intermediate, greater than the offshore, but less than the Marguerite Bay and Southern areas. There was little variation in total bacterial abundance across regions (see also Fig. S2), with about $5\times10^{8}$ cells $l^{-1}$ in the upper 50 m. The mean regional leucine incorporation rates closely mirrored Chl and PP (Fig. 8). The BP:PP ratio did not differ among regions (ANOVA, $p>0.05$; mean 4%). Time series observations for the well-sampled (over 200 stations) Shelf region also showed similar patterns for the phytoplankton and bacterial properties (Fig. 9). All four properties increased steadily over 2003–06, then were lower, without a discernable trend in 2007–09, and then high again in 2010 (PP) or 2011 (Chl, leucine). The similarity of phytoplankton and bacterial variability in these plots illustrates coupling at cross-regional and decadal scales (Fig. 10).

### 3.6. Role of temperature

Temperature appears to influence BP in some regions or years, but not others. Within the shelf region, there was no relationship in four

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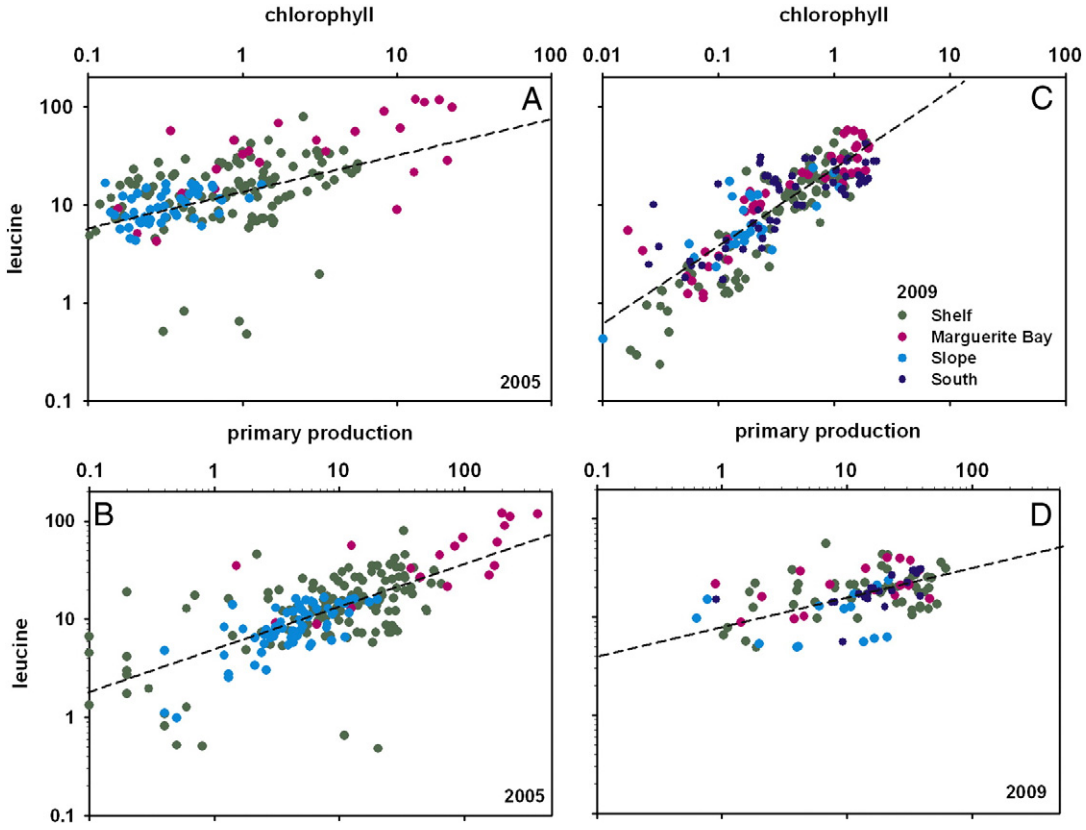


**Fig. 7.** Relationships between discrete depth chlorophyll concentrations (A,C) or PP rates (B,D) with $^{3}$H-leucine incorporation rates in 2005 (late sea ice retreat) and 2009 (early retreat). Regions as in Fig. 1. See Tables 1, 2 for regression statistics.

of the nine years or in all years pooled together (Fig. 11, Table 3). There were significant ($p<0.01$) but weak ($R^2=0.002$–$0.20$) relationships in five years, but the slopes were negative in three years (i.e., rates were higher in colder waters) and positive in two other years (suggesting suppression in colder water). Clearly there was no universal suppression of leucine incorporation rate by cold temperature.

**Table 2**
Regression statistics for yearly volumetric (discrete depth) primary production–leucine (PP–Leu) incorporation and PP–BP relationships. All regions are pooled for the annual data sets. Regression equations for PP–Leu and PP–BP are Log (Leu) = mLog (PP) + b; and BP = mPP + b, respectively. The slope of the *linear* BP regression indicates BP as a fraction of PP. All regressions are significant at $p<0.001$ unless noted.

| Year | Slope (m) | Intercept (b) | $R^2$ | n |
|---|---|---|---|---|
| 2003 PP–Leu | 0.39 | 0.14 | 0.29 | 180 |
| 2003 PP–BP | 0.007 | 0.07 | 0.30 | 180 |
| 2004 PP–Leu | 0.41 | 0.72 | 0.32 | 190 |
| 2004 PP–BP | 0.03 | 0.25 | 0.22 | 190 |
| 2005 PP–Leu | 0.43 | 0.68 | 0.48 | 205 |
| 2005 PP–BP | 0.01 | 0.41 | 0.61 | 205 |
| 2006 PP–Leu | 0.37 | 0.75 | 0.55 | 201 |
| 2006 PP–BP | 0.005 | 0.56 | 0.27 | 201 |
| 2007 PP–Leu | 0.46 | 0.80 | 0.68 | 258 |
| 2007 PP–BP | 0.006 | 0.61 | 0.39 | 258 |
| 2008 PP–Leu | 0.48 | 0.64 | 0.49 | 243 |
| 2008 PP–BP | 0.017 | 0.28 | 0.33 | 243 |
| 2009 PP–Leu | 0.30 | 0.87 | 0.26 | 117 |
| 2009 PP–BP | 0.010 | 0.46 | 0.17 | 117 |
| 2010 PP–Leu | 0.30 | 0.81 | 0.30 | 131 |
| 2010 PP–BP | 0.008 | 0.37 | 0.03, ($p=0.026$) | 131 |
| 2011 PP–Leu | 0.28 | 1.13 | 0.23 | 179 |
| 2011 PP–BP | 0.001 | 1.43 | 0.01, (ns, $p=0.077$) | 179 |
| All years PP–Leu | 0.43 | 0.69 | 0.39 | 1704 |
| All years PP–BP | 0.004 | 0.57 | 0.13 | 1704 |

## 4. Discussion

Discerning the large-scale controls on bacterial variability in marine systems requires sampling over a broad range of time and space scales that is difficult to satisfy. Time series approaches have been undertaken successfully in a number of locations, but typically only one or a few fixed stations are observed repeatedly over longer time spans (e.g., Fuhrman et al., 2006; Li, 2009; Morris et al., 2005). In contrast more geographically extensive studies tend to be limited to a few seasons over one or two years (e.g., Ducklow et al., 2001a; Garrison et al., 2000; Straza et al., 2009). The Long Term Ecological Research program enables an unprecedented examination, in terms of geographic and temporal coverage, of the interrelationships among climate, sea ice, hydrography, plankton ecology, biogeochemical processes and microbial dynamics (Ducklow et al., 2006a; Karl et al., 1996). Here we employ these extended and extensive observations to address the question of bacterial coupling to phytoplankton and sea ice in the marginal sea ice zone of the Antarctic Peninsula. The marked seasonality of Antarctic coastal seas, the intensity of the phytoplankton bloom and the absence of complicating terrestrial inputs of organic matter all make this a uniquely valuable system in which to examine this fundamental question in microbial oceanography. In addition, the Antarctic Peninsula region is warming rapidly (Meredith and King, 2005; Vaughan et al., 2003), driving a range of biological responses (Montes-Hugo et al., 2009; Schofield et al., 2010). The observations reported here establish a baseline for analyzing possible microbial responses in this rapidly-changing ecosystem.

### 4.1. Phytoplankton dynamics and coupling to bacteria

We examine the working hypothesis that large-scale climate forcing of sea ice extent and duration modulates the timing and distribution of phytoplankton blooms (Vernet et al., 2008). In turn, we hypothesize

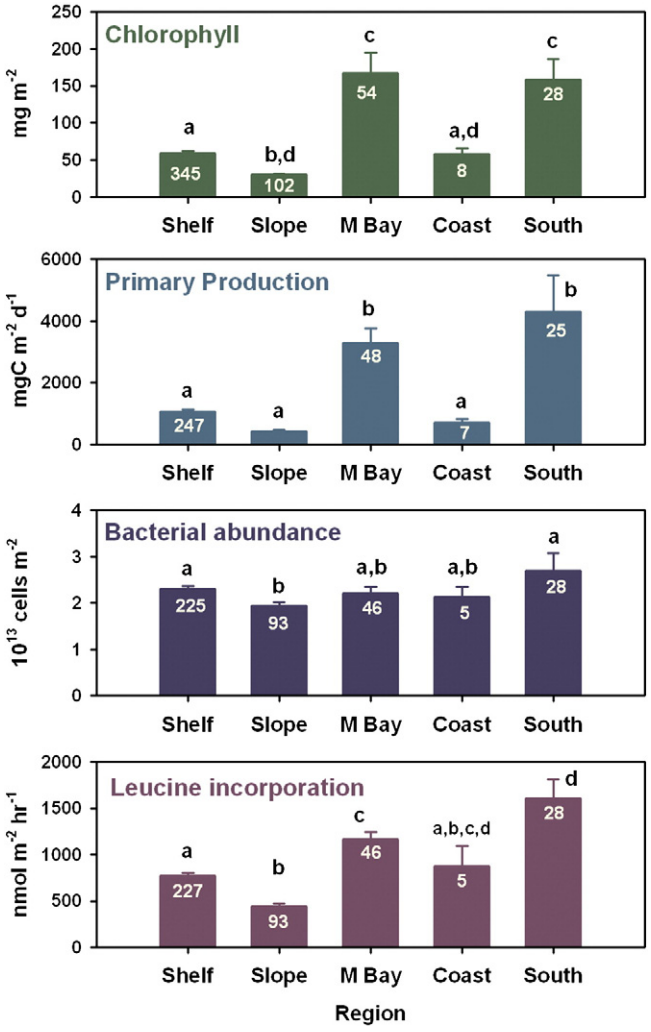


**Fig. 8.** Water column integral chlorophyll and primary production rates (both through euphotic zone to 1% of surface irradiance), bacterial abundance and leucine incorporation rates (both to 50 m). Years 2003–11 pooled for regional comparisons. Regions sharing letters are not significantly different (Tukey Post hoc HSD tests; $p<0.05$). Number of stations is given inside bars.

that regional- and interannual differences in this physical–biological coupling produce a supply of labile organic matter whose variability generates geographic patterns and year-to-year variability in BP. We begin with a brief review of the larger-scale regulation of the phytoplankton bloom by the annual cycle and duration of regional sea ice coverage. Extreme seasonality in Antarctica sets the stage for the spring phytoplankton bloom, historically dominated by diatom production in response to increasing solar irradiance and mixed layer shoaling triggered by melting sea ice (Smith and Nelson, 1985, 1986). Across the region, interannual variations in the magnitude of the bloom are regulated by variations in sea ice extent and the timing of sea ice retreat. In years with a late sea ice retreat, enhanced stratification from melting sea ice leads to shallower mixed layers and higher PP. Vernet et al. (2008) illustrate this relationship with a decade-long analysis of climate variability, sea ice retreat and PP for the PAL LTER study region (200–600 lines), 1995–2006. Updated sea ice retreat anomalies for this region are shown for ice years 2003–2011 in Fig. 12. Sea ice retreat in ice years 2004, 2005 and 2009 (corresponding to Chl and PP in January 2005, 2006 and 2010, respectively) was anomalously late over the shelf and inshore, and Chl and PP in those years were also high (Figs. 9, 10). In contrast, in years with early sea ice retreat (e.g., ice years 2006–08, Fig. 12), Chl and PP are inhibited by high spring winds maintaining deeper mixed layers as indicated by low Chl and PP in January 2007–09 (Fig. 9). At the regional scale, areas with later sea ice retreat (e.g., Marguerite Bay and the South) have higher Chl and PP (Fig. 8).

These patterns do not hold in all years. Sea ice retreat was anomalously early in 2010, but Chl and PP were disproportionately high in January, 2011. Smith et al. (2008) showed that the seasonal progression of the phytoplankton bloom did not necessarily follow the retreating ice edge as the simple model would predict. In particular, they observed that *early* sea ice retreat offshore resulted in *enhanced* blooms in the vicinity of the Southern Antarctic Circumpolar Front Zone, counter to the sea ice/bloom relationship just stated for the shelf region. This offshore bloom was succeeded by inshore blooms in years when the early sea ice retreat offshore was followed by a late retreat inshore of the ACC front. In addition to these effects, the responses of PP to sea ice retreat may be changing. Phytoplankton have responded differently to sea ice decline in different areas of the WAP area since 1978, decreasing in response to sea ice decline in the north, while increasing in response to similar declines in the south (Montes-Hugo et al., 2009). Thus as mentioned above, the early sea ice retreat in 2010 resulted in relatively high PP in January, 2011, particularly in the south, which was once perennially ice covered. Sea ice decline opens new areas of ocean surface to increased irradiance and increasing PP (Peck et al., 2010).

These large-scale processes provide a foundation for exploring regional and interannual variability in regional bacterial processes as well. Inputs of terrestrial organic matter to Antarctic waters are minimal, and the immediate nearshore zone has DOC concentrations typical of the open ocean (40–70 μM, http://oceaninformatics.ucsd.edu/datazoo/data/pallter/datasets; datasets 69,70). Therefore, heterotrophic bacteria in Antarctic shelf waters must ultimately depend on *in situ* PP for organic matter. The question of coupling between phytoplankton and bacterial activity has been studied at several locations around the Antarctic continent (Billen and Becquevort, 1991; Leakey et al., 1996) including the WAP region. In the RACER (Research on Coastal Antarctic Ecosystem Rates) Project, Karl and colleagues (Bird and Karl, 1991, 1999; Karl et al., 1991) investigated microbial processes in waters of the northern Antarctic Peninsula and Drake Passage in summer 1987 and spring 1989. Bacterial activity was not correlated with Chl (as in some of our individual regional or yearly datasets) and did not immediately respond to the spring phytoplankton bloom in the Gerlache Strait. Bacterial biomass was <2% of the total plankton biomass and BP was ~3% of the co-occurring PP. 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 widespread in space and time, and may be expressed more strongly in other seasons.

Morán and colleagues investigated phytoplankton–bacteria coupling experimentally in the same region (Morán and Estrada, 2002; Morán et al., 2001). They identified the flow of recently-synthesized DOC from active phytoplankton (14% of total particulate plus dissolved PP) and its immediate (within hours) incorporation into bacteria as the mechanism of coupling. They showed that the released DOC met the metabolic requirements of bacteria in the same region studied in RACER and concluded that bacteria and phytoplankton were directly coupled. They also determined that BP was a very low fraction (mean $1.5 \pm 0.4\%$) of the total particulate plus dissolved PP, but termed the coupling "strong" nonetheless. That is, the strength of the coupling is indicated by the covariation of bacterial and phytoplankton properties, not the ratio of the production rates.

It follows from these results that leucine incorporation rates should be correlated with PP and Chl, if bacteria are dependent on the recent products of photosynthesis, *sensu* Morán and colleagues. Bacteria may be related to Chl, but not necessarily to simultaneous PP, if organic matter is supplied by other processes such as zooplankton grazing activity (Cole et al., 1982; Ducklow and Carlson, 1992). If the coupling is more remote as suggested by Karl and colleagues, for example if bacteria depend on accumulated semilabile DOC (Ducklow, 2003), BP–Chl relationships might be absent altogether. In our study, leucine

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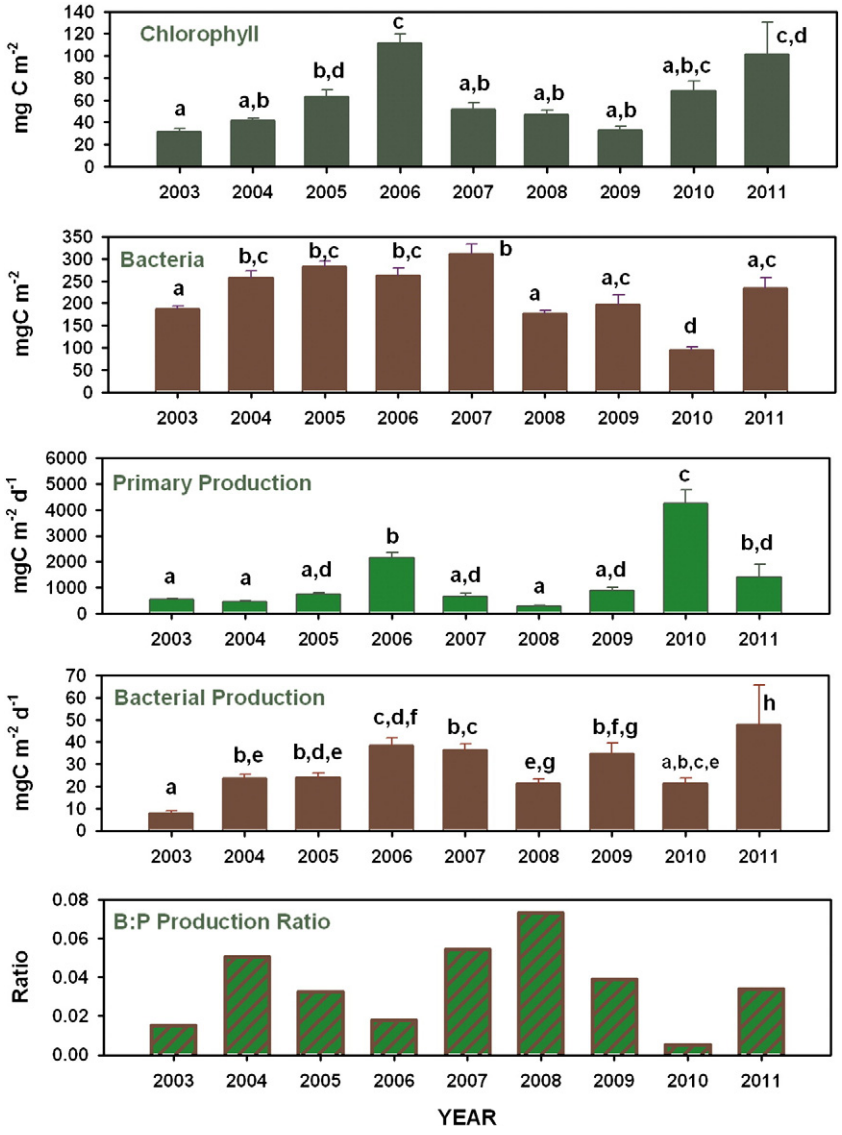


**Fig. 9.** Time series of phytoplankton and bacterial stocks and production rates for the shelf region, 2003–11. See Table S1 for stations sampled in each year. Years sharing letters are not significantly different (Tukey Post hoc HSD tests; $p<0.05$).

incorporation was correlated with both PP and Chl across years, regions and depths. Relationships with Chl were somewhat stronger than with PP. For example, $R^2$ values for Chl–Leucine regressions were usually greater than values for PP–Leucine (Tables 1, 2). Relationships between dissolved primary production (not measured in our study) might have been stronger than particulate primary production (Morán et al., 2009). We interpret the stronger relationships with Chl as indicating greater dependence of BP on DOM supplied from a variety of trophic pathways besides direct release of photosynthetic products from phytoplankton alone. Thus, in regions or years when sea ice retreat triggers large phytoplankton blooms, BP is higher, and *vice-versa*. As with other ecosystem components, sea ice regulates variations in BP via its effects on trophic coupling to food supply.

### 4.2. Multiscale regulation of bacterial production

Here we demonstrate widespread, though variable, phytoplankton–bacterial coupling by relating bacterial leucine incorporation (BP) rates to chlorophyll stocks and PP over a range of time and space scales. Such relationships are well-known in aquatic microbial ecology. Typically the strongest relationships are expressed at the largest scales. That is, bacterial and phytoplankton properties tend to be related most strongly (highest r values) when many studies from different regions and years are pooled together, illustrating the ultimate reliance of bacteria on primary producers in a wide range of aquatic systems (Bird and Kalff, 1984; Cole et al., 1988; Ducklow and Carlson, 1992; Kirchman et al., 2009b; Li et al., 2004). Strong relationships are also commonly observed over full annual cycles, especially in the highly seasonal polar seas, encompassing wide dynamic ranges of bacterial and phytoplankton properties encountered between winter and summer (e.g., Garneau et al., 2008; Pearce et al., 2007).

Relationships at smaller scales, e.g., within seasons and regions or depth intervals, are indicative of mechanistic, process-level couplings and can be more complicated. For example, in the Antarctic Polar Front Zone, Simon et al. (2004) demonstrated a significant correlation between euphotic zone (0–100 m) Chl and integrated leucine incorporation in the underlying mesopelagic zone (100–1000 m), but not with euphotic zone (0–100 m) incorporation rates. However, there was a correlation between BP and PP within the upper layer. These varying mechanisms and degrees of coupling were manifested through relationships among Chl, leucine incorporation and concentrations of dissolved amino acids and carbohydrates (Simon and Rosenstock, 2007). They observed significant relationships on a summer cruise but not in the fall three years later. Their comparisons potentially include

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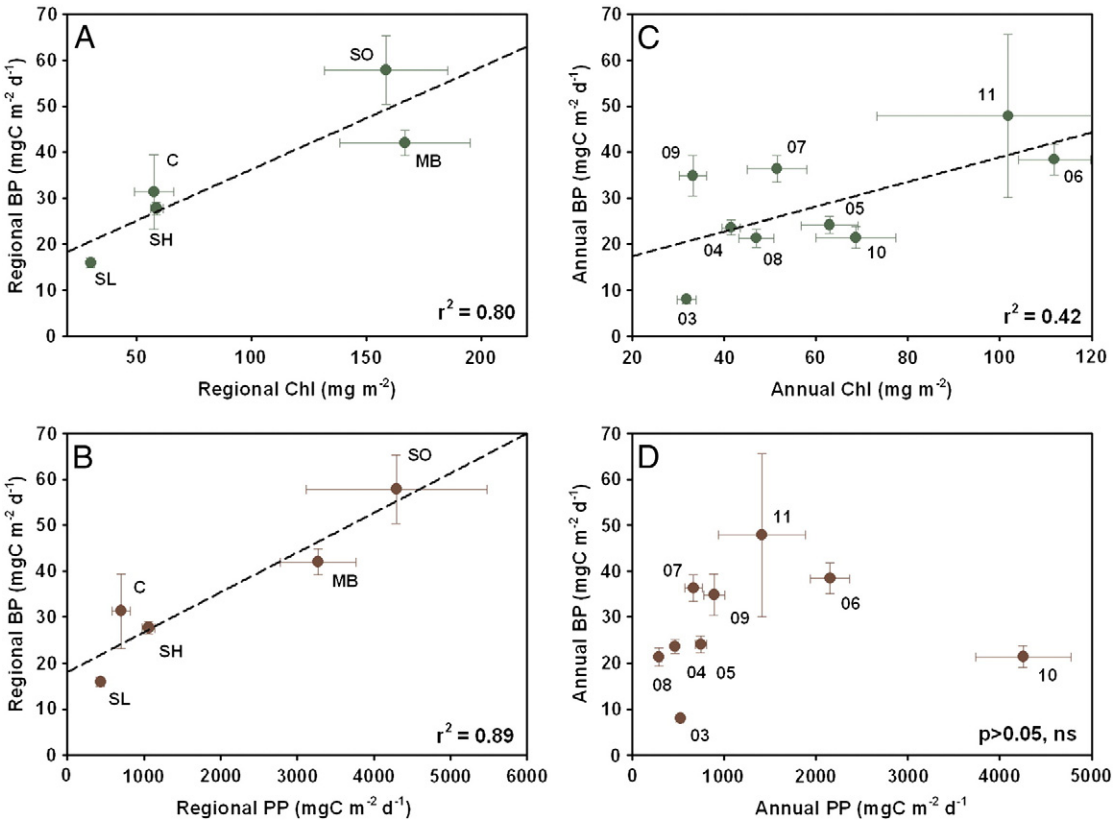


**Fig. 10.** Regional (A,B) and decadal (C,D) scale relationships among chlorophyll, primary and bacterial production rates. See Figs. 8,9 for source data. All years 2003–11 are pooled in each region in panels A, B. Panels C,D are for Shelf region only. Dashed lines and coefficients of determination are given for significant regressions ($p<0.05$). Regions in A,B as in previous figures (SL-slope; Sh-shelf; C-coastal; MB-Marguerite Bay; S-south). Numbers in panels C,D are years.

competing seasonal, regional and interannual sources of variability. Similarly Kirchman et al. (2009a) established correlations between BP and Chl in the western Arctic Ocean (Chuckchi Sea and Canada Basin) in spring–summer 2004 but not in 2002.

In our study, leucine incorporation rates in summer within the shelf region were significantly correlated with Chl in all years except 2011 (Table S3), both in the surface layer (discrete depths 0–20 m) and in the euphotic zone (integrated 0–50 m). Bacterial abundances varied little between years and regions (Figs. 8, S3), and seldom exceeded $1\times10^9$ cells $l^{-1}$. Bird and Karl (1999) suggested that bacterial biomass in the Peninsula region may have been suppressed by heterotrophic nanoplankton grazers. Some support for this idea comes from comparison with the Ross Sea where a large bacterial bloom (up to $3\times10^9$ cells $l^{-1}$) was observed in 1996–97 (Ducklow et al., 2001a) and where the ratio of bacteriovores to bacteria is lower than in the Peninsula region (Ducklow et al., 2006a). In our study, bacterial abundance was relatively stable, suggesting possible grazer control.

The summertime bacterial assemblage in WAP shelf waters results from selective growth of relatively few heterotrophic populations, transforming a high-diversity winter community dominated by chemolithoautotrophs into a lower-diversity, mostly heterotrophic assemblage. Straza et al. (2009) showed that substrate utilization by the summer community was dominated by relatively few taxa of *Gammaproteobacteria*, *Sphingobacteria–Flavobacteria*, and *Alphaproteobacteria*. This pattern was consistent across the shelf and extended throughout the study region.

### 4.3. Role of temperature

The role of cold temperature as a possible suppressant of microbial activity is a classic problem in polar oceanography (Karl, 1993; Karl et al., 1996; Pomeroy and Deibel, 1986). Indeed, on average, both primary and bacterial production rates were lower in the Ross Sea and Western Arctic Ocean than in other warmer, lower latitude regions reviewed by Kirchman et al. (2009b). Kirchman et al. (2009a) found significant relationships between BP and temperature both within and across seasons and years (spring–summer, 2002, 2004) in the western Arctic Ocean, but Garneau et al. (2008), working in nearby Franklin Bay, did not. Simon et al. (1999) demonstrated that temperature regulated bacterial activity differently in different water masses in the Southern Ocean. The ratio of bacterial to primary production (BP:PP) was also lower (~0.05) in the Ross Sea and Western Arctic Ocean, and exhibited a significant correlation with temperatures below 4 °C. In our study BP:PP also averaged about 0.05.

Rivkin et al. (1996) claimed that bacterial production and growth rates were not intrinsically lower in cold oceans. They argued that empirically-derived conversion factors specific to time and location resulted in BP estimates that were the same as in warmer waters. The validity of this argument hinges on conversion factors (CF) having higher values in cold waters; i.e., a fundamentally different relationship between leucine or thymidine incorporation and cellular production at low temperatures. This argument has seldom been critically evaluated. In the Ross Sea Ducklow et al. (1999) found *lower* thymidine CF than the canonical value of $2\times10^{18}$ cells $mol^{-1}$ (Fuhrman and Azam, 1980). The empirically-determined leucine CF was 1.5 kg C $mol^{-1}$, identical to the original value proposed by Simon and Azam (1989). This value was used in Kirchman et al. (2009b) and in the present treatment. Although we used a constant factor, we recognize the possibility that systematic CF variability could change our results (Alonso—Sáez et al., 2008; Kirchman et al., 1982; Morán et al., 2009).

We did not find a consistent relationship between temperature and leucine incorporation (Fig. 11). Although the average leucine incorporation rates tended to be lower in our study area than in warmer locations,

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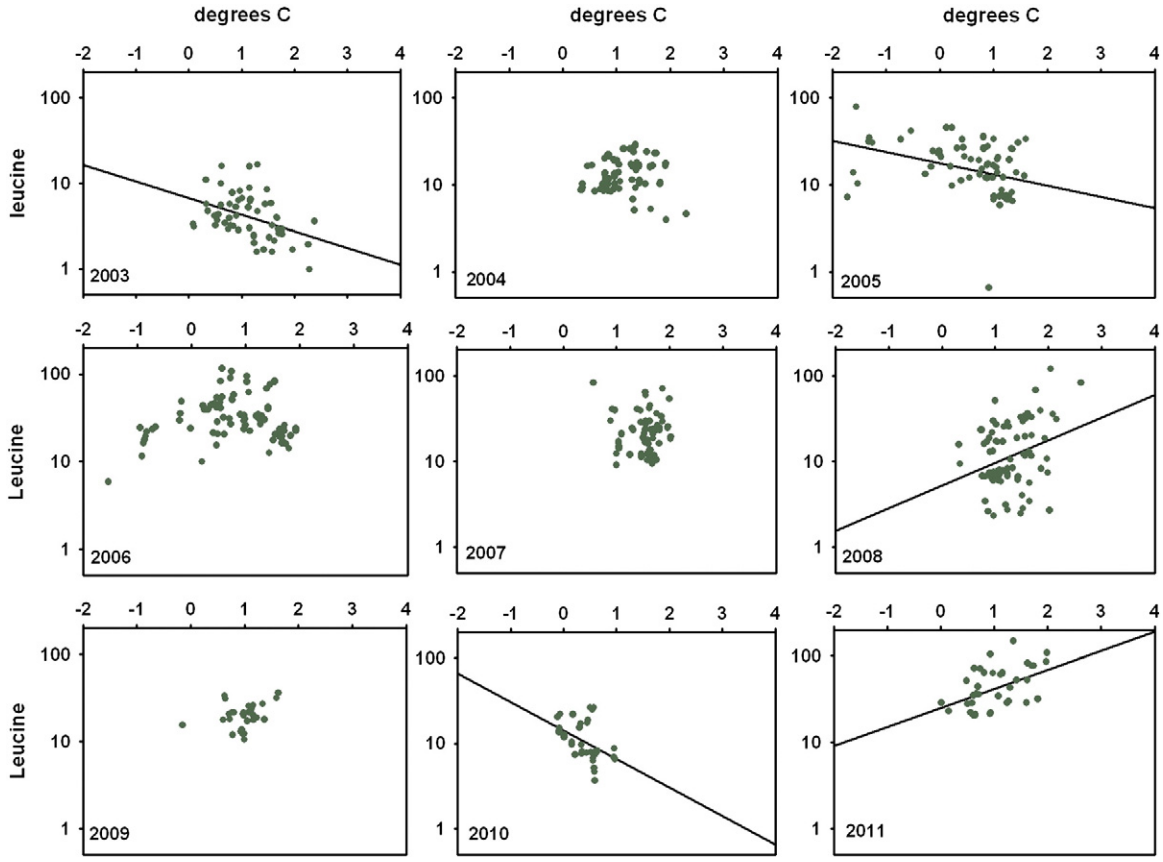


**Fig. 11.** Relationships between discrete depth temperature and $^{3}$H-leucine incorporation rates in the Shelf region for the upper 20 m. Regressions are significant ($p<0.05$) where lines are depicted. See Table 3 for regression statistics.

incorporation rates can attain higher levels comparable to lower latitude systems. Thus in our dataset, the 50-meter integrated BP:PP was 0.1 or greater at 38 of 390 stations. Leucine incorporation rates exceeded 50 pmol $l^{-1}$ $h^{-1}$ in most years (Fig. S3), even in the coldest water (Fig. S4B). These higher rates are no different than peak rates in the Equatorial Pacific Ocean and Arabian Sea, where surface water temperatures exceed 25 °C (Ducklow et al., 2001b; Kirchman et al., 1995).

In their analysis Kirchman et al. (2009b) concluded that low bacterial production in cold polar waters was a consequence of bottom–up factors, mainly the supply of dissolved organic matter (DOM) to bacterial consumers. We found no specific evidence to support the Pomeroy Hypothesis that bacteria are more sensitive to temperature when organic matter concentrations were low (Table 3, Chl<1–2 μg $l^{-1}$). Kirchman et al. (2009b) hypothesized a fundamental difference in how carbon flows to bacteria in polar ecosystems. The result is limitation of BP by labile organic matter availability. Our individual-year regressions for the shelf region (Table S3) support this view.

**Table 3**
Temperature–leucine regression statistics for Shelf region, 2003–11. Discrete-depth (volumetric) relationships for <20 m samples. Regression equations are Log (Int Leu) = m (Temperature) + b. All regressions are significant at $p<0.001$ unless noted (p-value or ns). See also Fig. 11.

| Year/property | Slope | Intercept (b) | $R^2$ | n |
|---|---|---|---|---|
| 2003 Discrete depth (<20) | −0.19 | 0.82 | 0.14 (p = 0.002)[a] | 56 |
| 2004 Discrete depth (<20) | | | p = 0.71, ns | 68 |
| 2005 Discrete depth (<20) | −0.13 | 1.25 | 0.08 (p = 0.008) | 72 |
| 2006 Discrete depth (<20) | | | p = 0.39, ns | 91 |
| 2007 Discrete depth (<20) | | | p = 0.41, ns | 75 |
| 2008 Discrete depth (<20) | 0.26 | 0.72 | 0.07 (p = 0.005) | 85 |
| 2009 Discrete depth (<20) | | | p = 0.72, ns | 30 |
| 2010 Discrete depth (<20) | −0.33 | 1.15 | 0.18 (p = 0.004) | 40 |
| 2011 Discrete depth (<20) | 0.22 | 1.40 | 0.20 (p = 0.003) | 39 |
| All years | | | p = 0.36, ns | 556 |
| All years, Chl<2 | | | p = 0.06, ns | 383 |
| All years, Chl<1 | | | p = 0.9, ns | 239 |

[a] Two measurements with Leucine<0.1 excluded.

### 4.4. Importance of bacterial production and long-term trends

Using a mean bacterial conversion efficiency of 0.15 (Carlson et al., 1999; del Giorgio and Cole, 1998), a BP:PP value of 0.05 implies that about 33% of the primary production flows through bacteria in the Peninsular shelf region. Although this level of PP utilization is lower than other, mostly warmer ocean regions, it still represents a substantial carbon flux in a system once believed to be dominated by larger organisms such as diatoms and krill (Hart, 1934). In more recent times the importance of microbial interactions has been recognized in Antarctic waters, overturning the old diatom-krill-penguin/seal/whale paradigm that once governed most thinking about the region (El-Sayed, 1988; Hewes et al., 1985; Karl et al., 1996).

Climate change appears to be progressively altering foodwebs from north to south along the Antarctic Peninsula, transforming them from diatom-krill-dominated to microbe-dominated systems. The original support for this idea comes from observations of rapid sea ice loss (Stammerjohn et al., 2008a, 2008b), declines of Adélie penguin populations in the north (Ducklow et al., 2006a; Fraser and Ainley, 1986; Smith et al., 1999), shifts in the dominant phytoplankton species from diatoms to cryptophytes (Moline et al., 2004, 2008), and decadal-scale declines in phytoplankton and krill stocks in northern regions (Atkinson et al., 2004; Montes-Hugo et al., 2009).

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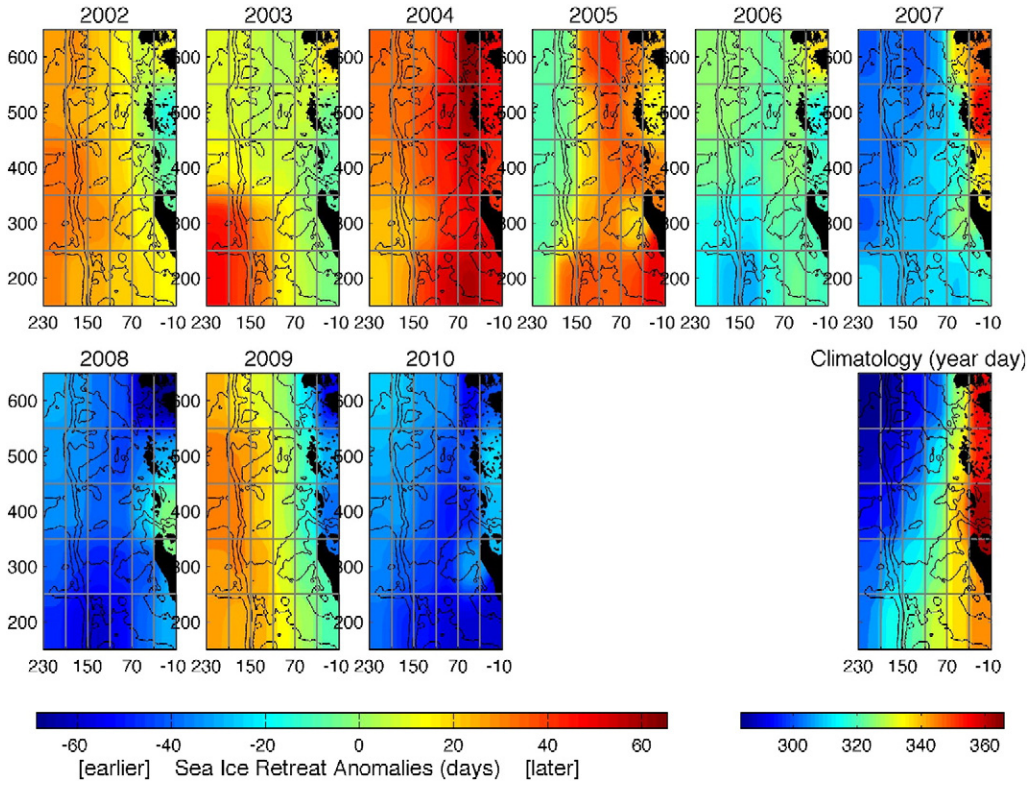


**Fig. 12.** Maps of annual anomalies of the date of sea ice retreat in the PAL study region, 2003–2011 (200–600 lines). Each map shows the anomaly in days relative to the mean date of ice retreat shown in the map at the bottom right corner. Negative anomalies are earlier retreats, positive anomalies are late retreats. In these plots, the year is defined from the March–July ice advance to the following year's Sept–January retreat period. Thus ice year 2002 includes the January 2003 bacterial and other observations, and so on. See Stammerjohn et al. (2008a, 2008b) for details.

Sailley et al. (in review) tested this climate migration hypothesis by incorporating twelve years of Palmer LTER data (1995–2006) into an inverse foodweb model that satisfied various criteria including observational constraints such as primary production, krill biomass and export levels (Stukel and Landry, 2010). The model was used to seek solutions to the complete flow structure of exchanges among organisms each year in northern and southern foodwebs. Their model results estimated that even though BP:PP was lower (1.5–2.8%) than the observations reported here, bacterial DOM utilization and respiration rates were equivalent to krill ingestion and respiration rates across years and throughout the region. Furthermore, by evaluating the trophic indices of Legendre and Rassoulzadegan (1996) with model-generated data, they suggested that the foodwebs of the Antarctic Peninsula region are changing from herbivore-dominated systems with krill and diatoms toward microbial foodwebs dominated by smaller phytoplankton, bacteria and microzooplankton. The apparent trend of increasing bacterial production over time (Fig. 9) is provocative but not significant ($R^2 = 0.41$, $p = 0.06$, $N = 9$). But further warming, sea ice loss and ecosystem change seem inevitable in this region. The effects of climate change on bacterial processes are poorly understood, but rapidly-evolving polar systems seem like the best places to try and understand these important interactions.

## 5. Conclusions

Our results show that as with other trophic levels, variations in bacterial production rates reflect interannual and regional differences in sea ice retreat. Variability in rates of 3H-leucine incorporation were best explained by chlorophyll, and to a lesser extent by PP, suggesting that biomass accumulation and trophic exchange processes such as grazing, detritus turnover and zooplankton excretion all contribute dissolved organic matter to supplement the direct release from phytoplankton. These processes are dependent on the magnitude of phytoplankton blooms which are regulated by the timing of sea ice retreat. These conclusions point out the dependence of bacterial processes on large-scale climate variations and related physical–biological couplings, factors not generally considered in microbial oceanography.

Supplementary materials related to this article can be found online at doi:10.1016/j.jmarsys.2012.03.003.

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