



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

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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 inter-annual 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 $20 \text{ mg C m}^{-2} \text{ d}^{-1}$ 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.

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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

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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-rossette 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 FACS Calibur 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 ³H-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 ³H-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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