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Primary production and bacterial carbon metabolism around South Shetland Islands in the Southern Ocean

Eva Teira [a,*], Beatriz Mouriño-Carballido [a], Sandra Martínez-García [a,1], Cristina Sobrino [a], Julia Ameneiro [a], Santiago Hernández-León [b], Elsa Vázquez [a]

[a] Departamento Ecoloxía e Bioloxía Animal, Facultade de Ciencias do Mar, Universidade de Vigo, 36200 Vigo, Spain
[b] Institute of Oceanography and Global Change, Universidad de Las Palmas de Gran Canaria, Spain

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ABSTRACT

Phytoplankton and bacterioplankton dynamics were studied around South Shetland Islands (Antarctica) with special emphasis on the Drake Passage region, during austral summer, in order to expand our knowledge on the coupling between the autotrophic and heterotrophic microbial plankton compartments in polar ecosystems. In addition, we directly estimated bacterial growth efficiency in the Drake Passage with the aim of better constraining total bacterial carbon utilization in this important polar ecosystem. Integrated chlorophyll-a concentration (21–86 mg m^{-2}), primary production rates (0.7–19.3 mg C m^{-3} d^{-1}) and mean water-column photochemical efficiency (0.24–0.60) were significantly correlated with Si* tracer ($r^2=0.55$, 0.46 and 0.64, respectively), which indirectly points to iron as the major limiting factor for phytoplankton growth in the area. Bacterial production was considerably low (0.002–0.3 mg C m^{-3} d^{-1}) and was best explained by chlorophyll-a concentration, protein-like fluorescence of dissolved organic matter and temperature ($r^2=0.53$, $p<0.001$). Water temperature appeared to influence bacterial activity when organic substrate availability is high. Bacterial production accounted on average for only 3.9% of co-occurring primary production, which has been frequently interpreted as an indicator of the marked uncoupling between bacteria and phytoplankton in cold waters. However, using the experimentally derived mean bacterial growth efficiency for the photic zone ($6.1\pm1.3\%$) the bacterial carbon demand represented on average $63\pm18\%$ of concomitant primary production, similar to what is found in warmer productive waters. Thus, our study suggests that bacterioplankton and phytoplankton appear to be connected in this polar area.

1. Introduction

The Southern Ocean represents 20% of the global ocean and is a critical sink for excess atmospheric carbon (Sarmiento and Le Quéré, 1996). The annual mean temperature in the Antarctic Peninsula (AP) region has increased 2 °C since 1950, which has translated into a rapid warming of shelf waters west of AP by 0.6 °C (Ducklow et al., 2007). Such rapid changes may lead to higher microbial plankton activity and less energy and organic carbon for supporting higher trophic levels (Kirchman et al., 2009).

The area around South Shetland Islands (SSI) off the northern tip of the Antarctic Peninsula sustains elevated phytoplankton biomass during the austral summer, while high nutrient-low chlorophyll (HNLC) conditions prevail in Drake Passage to the north and in the Bransfield Strait to the south (Hewes, 2009). The Drake Passage Antarctic Surface Water (ASW) mass to the north of the SSI develops a warm and less saline upper mixed layer during the austral summer where phytoplankton growth is limited by low iron concentration (Holm-Hansen and Hewes, 2004). On the other hand, intense mixing of iron-replete Transitional Weddell Water (TWW) appears to cause phytoplankton light limitation in the south of Bransfield Strait (Hewes et al., 2008).

Bacterial consumption of dissolved organic matter represents a critical trophic link that supports higher trophic levels and nutrient regeneration in the ocean (Azam, 1998). Primary production is the ultimate source of most organic material in the sea, and it is estimated that about 50% of primary production is consumed by heterotrophic bacteria in low latitude oceans (Robinson, 2008). By contrast, a much lower percentage of primary production is utilized by bacteria in polar systems (Bird and Karl, 1999; Ducklow, 2000; Morán et al., 2001; Kirchman et al., 2009; Ducklow et al., 2012) which has been considered as indicative of phytoplankton–bacteria uncoupling (Billen and Becquevort, 1991; Karl, 1993). Such low bacterial activity has been ascribed to temperature limitation (Pomeroy and Deibel, 1986), limited dissolved organic matter (DOM) availability (Bird and Karl, 1999), a combination of temperature and DOM regulation (Pomeroy and Wiebe, 2001), or a strong grazing pressure

* Corresponding author. Tel.: +34 986 812591; fax: +34 986 812556.
E-mail address: teira@uvigo.es (E. Teira).
[1] Present address: Department of Oceanography, University of Hawaii, Honolulu, 96822 HI, USA

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(Bird and Karl, 1999; Duarte et al., 2005). However, growing evidence points to questionable higher grazing control in polar waters than elsewhere and to negligible effect of low temperature on bacterial growth in polar oceans (Ducklow et al., 2001, 2012; Kirchman et al., 2009). Therefore, the bacterial metabolism in these perennially cold waters seems to be essentially limited by dissolved organic matter availability.

Although several studies have described phytoplankton biomass distribution around or nearby SSI (Basterretxea and Arístegui, 1999; Kelley et al., 1999; Kawaguchi et al., 2001; Varela et al., 2002; Holm-Hansen and Hewes, 2004; Hewes et al., 2008), only a few have measured primary production rates and/or phytoplankton physiological parameters (Burkholder and Mandelli, 1965; Basterretxea and Arístegui, 1999; Kelley et al., 1999; Lorenzo et al., 2002). On the other hand, there are only a few reports of bacterial production (BP) rates around or nearby SSI (Karl et al., 1991; Kelley et al., 1999; Morán et al., 2001; Pedrós-Alió et al., 2002; Ortega-Retuerta et al., 2008; Manganelli et al., 2009), and to the best of our knowledge none simultaneously reporting BP and bacterial respiration (BR) rates. Only a few papers have directly or indirectly assessed the degree of phytoplankton–bacterioplankton coupling in the region (Mullins and Priddle, 1987; Kelley et al., 1999; Karl et al., 1991; Morán et al., 2001; Ortega-Retuerta et al., 2008), although they do not include much data on autotrophic and heterotrophic microbial plankton production rates in the Drake Passage. Some of the most recent studies in the vicinity of Bransfield strait have concluded a relatively close coupling between phytoplankton and bacteria (Morán et al., 2001; Ortega-Retuerta et al., 2008).

The main objective of our study was to expand our knowledge on phytoplankton and bacterioplankton dynamics and their couplings around SSI, with special emphasis on the Drake Passage region. In addition, we directly estimated bacterial growth efficiency at 3 different stations in the Drake Passage in order to better constrain total bacterial carbon utilization in this important polar ecosystem. As far as we know, these are the first direct estimations of bacterial respiration in the area.

2. Materials and methods

2.1. Study area and sampling

Sampling was carried out during the COUPLING cruise in January 2010 on board the RV Hespérides along 7 transects around the SSI (Fig. 1). At each station vertical profiles of temperature, salinity and in situ fluorescence were obtained using a Conductivity–Temperature–Depth sensor (CTD) Seabird 911plus attached to the rosette, down to the bottom in the coastal and the shelf stations and down to 1000 m in the offshore stations. The depth of the upper mixed layer (UML) was computed as the depth where potential density differed by 0.05 Kg m^{-3} from the mean potential density measured at the surface (Mitchell and Holm-Hansen, 1991). Photosynthetically active radiation (PAR, 400–700 nm) was measured with a Satlantic OCP-100FF radiometer attached to the rosette.

Samples for nutrients and plankton-related variables (size-fractionated chlorophyll-a concentration, dissolved organic matter (DOM) fluorescence and bacterial production) were collected at 5–6 depths (between 5 and 150 m) using 12 l acid-clean Niskin bottles attached to a rosette sampler. Bacterial production rates and DOM fluorescence were measured at 2–3 additional depths (from 200 to 480 m depth) along transect TB (Fig. 1). Primary production was measured at 11 selected stations (station 5, 8, 10, 26, 29, 33, 36, 42, 61, 68, 76) in surface waters and at the deep chlorophyll maximum (DCM) depth.

2.2. Size-fractionated chlorophyll-a concentration

Chlorophyll-a (chla) concentration was determined fluorometrically. 250-mL water samples were sequentially filtered through 0.2, 2 and 20 μm polycarbonate filters and pigments were extracted in 90% acetone at −20 °C overnight. Fluorescence was measured on a Turner TD-700 fluorometer which had been calibrated with pure chlorophyll a.

2.3. Fluorescence of dissolved organic matter

Samples for fluorescence of dissolved organic matter (FDOM) determination were collected into 200 mL acid-cleaned borosilicate bottles and filtered by hand with 100 ml polyethylene syringes with teflon plunger tips through Whatman Puradisc GF/F disposable filter devices (0.45 μm pore size) on polypropylene housing. The filtering system and syringes were previously "washed" with 0.1 N HCl and rinsed with Mili-Q water. In addition, the syringes were rinsed three times with sample. FDOM was measured with a Perkin Elmer LS 55 luminescence spectrometer equipped with a xenon discharge lamp, equivalent to 20 kW for 8 μs duration. Measurements were performed in a 1 cm quartz fluorescence cell.

Discrete excitation/emission (E_x/E_m) pair measurements were performed at peak-T, characteristic of protein-like substances

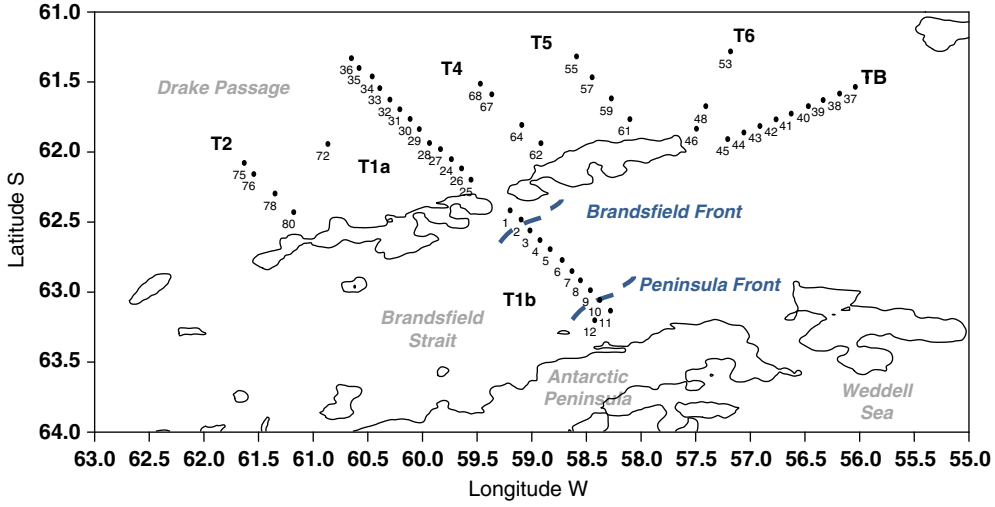

Fig. 1. Map showing stations sampled around the South Shetland Islands (SSI) during the COUPLING cruise. Numbers indicate CTD stations.