Journal of Marine Systems 132 (2014) 83–94

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

Regulation of bacterioplankton activity in Fram Strait (Arctic Ocean) during early summer: The role of organic matter supply and temperature

Judith Piontek [a,b,*], Martin Sperling [a,b], Eva-Maria Nöthig [b], Anja Engel [a,b]

[a] GEOMAR Helmholtz Centre for Ocean Research Kiel, 24105 Kiel, Germany
[b] Alfred-Wegener-Institute Helmholtz-Centre for Polar and Marine Research, 27570 Bremerhaven, Germany

ARTICLE INFO

Article history:
Received 13 May 2013
Received in revised form 2 January 2014
Accepted 7 January 2014
Available online 15 January 2014

Keywords:
Arctic Ocean
Bacterial production
Extracellular enzymes
Carbohydrates
Amino acids

ABSTRACT

The bacterial turnover of organic matter was investigated in Fram Strait at 79°N. Both Atlantic Water (AW) inflow and exported Polar Water (PW) were sampled along a transect from Spitsbergen to the eastern Greenland shelf during a late successional stage of the main annual phytoplankton bloom in summer. AW showed higher concentrations of amino acids than PW, while organic matter in PW was enriched in combined carbohydrates. Bacterial growth and degradation activity in AW and PW were related to compositional differences of organic matter. Bacterial production and leucine-aminopeptidase along the transect were significantly correlated with concentrations of amino acids. Activity ratios between the extracellular enzymes β-glucosidase and leucine-aminopeptidase indicate the hydrolysis potential for polysaccharides relative to proteins. Along the transect, these ratios showed a higher hydrolysis potential for polysaccharides relative to proteins in PW than in AW, thus reflecting the differences in organic matter composition between the water masses. Q_{10} values for bacterial production ranged from 2.4 (±0.8) to 6.0 (±6.8), while those for extracellular enzymes showed a broader range of 1.5 (±0.5) to 23.3 (±11.8). Our results show that in addition to low seawater temperature also organic matter availability contributes to the regulation of bacterial growth and enzymatic activity in the Arctic Ocean.

1. Introduction

Field studies and experimental work conducted in the Arctic Ocean during the last two decades demonstrated the presence of responsive bacterial communities with a high potential for metabolic activity (e.g. Thingstad and Martinussen, 1991; Yager et al., 2001). Nevertheless, the heterotrophic carbon turnover mediated by these bacterioplankton communities in Arctic waters is comparatively low. Less than 5% of primary production in the Arctic Ocean is recycled by bacterial production, a share that is significantly lower than in low-latitude oceans (Cota et al., 1996; Kirchman et al., 2009; Rich et al., 1997). In addition, Arctic rivers annually discharge 23–25 Tg of allochthonous organic carbon that is largely refractory to bacterial reworking in the adjacent shelf seas (Meon and Amon, 2004; Saliot et al., 1996).

It has been suggested that low seawater temperatures in the range of −1 to +1 °C have a stronger regulatory effect on bacterial carbon remineralization than on the autotrophic production of organic matter (Pomeroy and Deibel, 1986). A cell-physiological explanation for such observations is a diminished fluidity of the cell membrane and a concomitant decrease in substrate affinity that reduces the sequestration of resources in a very dilute environment (Nedwell, 2000; Nedwell and Rutter, 1994). Also the metabolic theory of ecology predicts that respiration and photosynthesis will increase at different rates with rising temperature (Brown et al., 2004; Gillooly et al., 2001). In fact, recent experimental studies have determined a threshold of 5 °C seawater temperature, beyond which the net community production of Arctic plankton shifts from autotrophic to heterotrophic (Holding et al., 2013; Vaquer-Sunyer et al., 2010). Conversely, similar temperature sensitivities of autotrophic and heterotrophic activities were determined in plankton communities of the Antarctic and the temperate ocean (Li and Dickie, 1987; Robinson and Williams, 1993). Hence, the potential of temperature variability, induced by the distribution of water masses, seasonal development and, on longer time scale, by climate change, to affect the metabolic balance in the Arctic Ocean is currently hard to assess.

There is growing evidence that organic matter concentration and composition are also constraints on bacterial production and growth in polar oceans and might even exceed the influence of low temperature (Kirchman et al., 2009; Thingstad and Martinussen, 1991). Data available to date support the hypothesis that a co-variation of temperature with utilizable organic matter leads to an overestimation of temperature effects, while the impact of carbon limitation on bacterial growth rates in polar oceans is underestimated (Kirchman et al., 2009). Organic matter produced by phytoplankton and ice-algae is a complex mixture that is only poorly characterized by compound-specific chemical analysis. A recent modeling study revealed that the bacterial utilization of labile organic matter alone only poorly explains observations of bacterial biomass and production in the open ocean. Instead, the model suggests

* Corresponding author at: GEOMAR Helmholtz Centre for Ocean Research Kiel, Düsternbrooker Weg 20, 24105 Kiel, Germany. Tel.: +49 431 600 4122.
E-mail address: jpiontek@geomar.de (J. Piontek).

0924-7963/$ – see front matter
http://dx.doi.org/10.1016/j.jmarsys.2014.01.003

that semi-labile compounds contribute up to 40% to the bacterial carbon demand (Luo et al., 2010). In contrast to labile organic matter that is turned over within some hours or days, semi-labile organic matter is re-worked by heterotrophic bacterial activity on time scales of weeks to months. The turnover of this quantitatively important fraction has a high potential to control the export of carbon produced during the productive season to the deeper ocean. Two major chemically characterized components of semi-labile organic matter are combined carbohydrates and amino acids, which both accumulate in seawater during phytoplankton blooms (Engel et al., 2011; Søndergaard et al., 2000). Together these organic polymers can account for 50% of organic carbon in freshly produced particulate organic matter (POM), as well as up to 12% in dissolved organic carbon (DOC) of high molecular weight (Kaiser and Benner, 2009). Sharply decreasing concentrations of carbohydrates and amino acids in the upper few hundred meters of the water column revealed intense microbial utilization of these compounds also in cold marine environments (Amon and Benner, 2003; Davis et al., 2009; Kattner and Becker, 1991; Shen et al., 2012).

This study combines measurements of bacterial activity with chemical analysis of combined carbohydrates and amino acids in seawater samples collected along a natural gradient of salinity, temperature and productivity in the Arctic Ocean. Sampling took place in Fram Strait during a late stage of the main annual phytoplankton bloom. Atlantic Water (AW) and Polar Water (PW) located between Spitsbergen and the Greenland shelf were investigated along a transect at 79°N. The metabolic activity of heterotrophic bacteria was investigated by extracellular enzyme activity and biomass production. Our study aims (i) to characterize bacterial activity and its temperature sensitivity in the different water masses and (ii) to test whether the composition of semi-labile organic matter can act as a significant regulatory factor for bacterial production and enzyme activity in Fram Strait.

2. Material and methods

2.1. Study area and sampling

The study was carried out in the Fram Strait (Arctic Ocean) during the cruise ARK-XXVI/I of RV *Polarstern* in June and July, 2011. The Fram Strait represents the only deep passage for water mass exchange between the Arctic Ocean and the Atlantic Ocean. Here, in- and outflow occur in two current systems: Cold Polar Water (PW) including sea ice, flows south in the East Greenland current (EGC), while warmer Atlantic Water (AW) is transported north in the West Spitsbergen Current (WSC). Surface samples (3–5 m depth) were collected with a rosette sampler equipped with Niskin bottles at 17 stations along a transect from the west coast of Spitsbergen to the shelf of eastern Greenland (9.5°E–10.0°W) at 78.8°N from June, 24th to July, 9th, 2011 (Fig. 1A). Ten stations had ice-coverage of 15–95%. The temperature–salinity diagram separates the samples into three different groups (Fig. 1B). PW of low salinity (30.9–31.4) and temperature (−1.5 to −1.0 °C) was sampled at six stations between 4.0°W and 10.0°W. AW was identified by higher salinity (34.1–35.2) and higher temperature (3.7–6.7 °C) at six stations between 9.5°E and 0.3°W (Schlichtholz and Houssais, 2002). Five samples of intermediate salinity (32.7–33.0) and temperature (−0.6 to 0.5 °C) were collected between 4.7°E and 3.0°W. The origin of these samples is referred to as Mixed Water (MW). MW is used as a pragmatic term to describe water of Atlantic origin that is likely part of the Return Atlantic Current and modified at

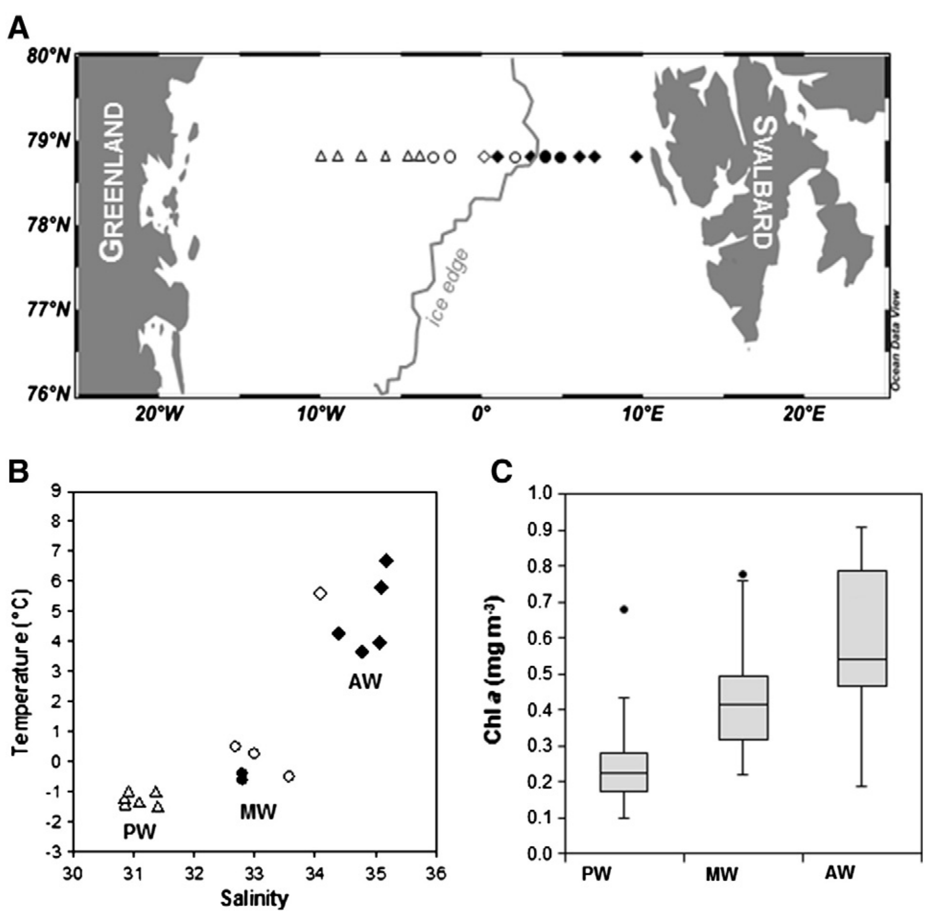

Fig. 1. Field sampling in Fram Strait. (A) Sampling stations along the transect at 78.8°N with (B) temperature–salinity characteristics and (C) chlorophyll *a* concentration of samples collected between June, 24th and July, 9th, 2011. The gray line in diagram A represents the ice edge as derived from satellite data on June, 23rd. Open symbols denote ice covered stations, filled symbols represent ice-free stations (triangles: Polar Water, circles: Mixed Water, diamonds: Atlantic Water).