Journal of Marine Systems 130 (2014) 160–166

Contents lists available at ScienceDirect

Journal of Marine Systems

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

Different temperature adaptation in Arctic and Atlantic heterotrophic bacteria in the Barents Sea Polar Front region

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ARTICLE INFO

Article history:
Received 20 February 2012
Received in revised form 23 August 2012
Accepted 18 September 2012
Available online 3 October 2012

Keywords:
Barents Sea
Polar Front
Satellite chlorophyll
Primary production
Bacterial production
TOC

ABSTRACT

In the northern Barents Sea, at and around the Polar Front, carbon cycle variables were investigated during 2 weeks in late summer of 2007. Arctic Water primary production in the experimental period averaged 50 mmol C m^{-2} day^{-1}, as estimated from satellite sensed chlorophyll. In Atlantic waters, which appeared to just have passed the culmination of a late summer bloom, primary production was 125 mmol C m^{-2} day^{-1}. Total organic carbon (TOC) averaged 82.4 μM C in the mixed layer, and the values showed a gradient with highest values to the southeast and lowest to the northwest. The distribution of TOC was not related to the distribution of Atlantic and Arctic waters, although the highest values were found in Atlantic Water. Integrated bacterial production in the mixed layer, as estimated from thymidine incorporation rates, averaged 6.3% of primary production. In Atlantic Water, over the depth of the mixed layer, bacterial production rate averaged 0.40 mmol C m^{-3} day^{-1}, which was 6.6 times the average in Arctic Water and 2.3 times the average in the front regions. Below 30 m depth, bacterial production rates were generally higher in the Arctic Water than in the Atlantic Water. Moreover, when production rates of bacteria were compared according to temperature, the rates in Arctic Water were systematically higher than the rates in Atlantic Water. This difference implies that the heterotrophic bacteria from the Arctic have adapted towards higher growth efficiency than the bacteria in Atlantic Water.

1. Introduction

The Barents Sea contains rich commercial fishing grounds and the fish resources and hydrographic aspects have been investigated for many years (Loeng and Drinkwater, 2007). On the other hand, the lower trophic levels of the food web have received comparatively less attention, although clearly the higher levels depend on primary production and a functional microbial food web at high latitudes just as elsewhere (De Laender et al., 2010; Rivkin and Legendre, 2002). Primary production in Barents Sea has been estimated to be around 20–80 g C m^{-2} in the Arctic waters and 80–200 g C m^{-2} in the Atlantic waters (Sakshaug et al., 2009). There is strong seasonality with peak production in the spring. Highest production tends to occur on the shallow, primarily tidally well-mixed regions such as around Bear Island and on Spitsbergenbanken. Few studies have investigated production in the vicinity of the Barents Sea Polar Front that separates the warm, high saline Atlantic waters from the cold, lower saline Arctic waters. In this paper we investigate both bacteria and phytoplankton production, as well as the total organic carbon (TOC) in the Barents Sea, in the vicinity of the Polar Front.

The Barents Sea circulation is dominated by the movement of two water masses. Warm, high saline Atlantic Water enters through the western entrance to the Barents Sea between Norway and Bjørnøya and exits to the east along Novaya Zemlya, through the St. Anna Trough and into the Arctic Ocean (Loeng, 1991). On route it is modified through atmospheric cooling and mixing with surrounding waters. Cold, low saline Arctic Water enters the Barents Sea from the north and flows southwards exiting south of Spitsbergen. Sea ice forms in the northern and eastern Barents Sea during autumn and winter, and brine formation during freezing contributes to dense water formation (Årthun et al., 2011). Conversely, in these regions, melting of sea ice in spring and summer produces freshwater that contributes to large areas with intense vertical density stratification and a shallow mixed layer (Årthun et al., 2011; Loeng and Drinkwater, 2007). The boundary between Atlantic and Arctic water masses forms the Polar Front that is tied to the topography in the western Barents Sea (Fer and Drinkwater, 2014–this issue; Johannessen and Foster, 1978).

Enhanced primary production is often a feature associated with oceanic fronts. For example, this has been observed in fronts associated with eddies and is caused by upwelling of nutrient rich water from below the photic zone (Godø et al., 2012; Lochte and Pfannkuche, 1987; Nelson et al., 1989). Shelf/slope and tidal fronts, also exhibit circulation features that result in increased nutrient concentrations in the surface layers, which leads to enhanced primary production (Belkin et al., 2009; Loder and Platt, 1985; Le Fèvre, 1986). However,

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http://dx.doi.org/10.1016/j.jmarsys.2012.09.007

the Polar Front in the Barents Sea does not produce upwelling or secondary circulations because of weak horizontal density gradients, a result of density compensation from the hydrographic properties of the two water masses (Fer and Drinkwater, 2014–this issue; Våge et al., 2014–this issue). While claims exist that primary production is enhanced along the front (e.g. von Quillfeldt, 2007), recent modeling and field studies have suggested no evidence of increased primary production at the Barents Sea Polar Front (Erga et al., 2014–this issue; Fer and Drinkwater, 2014–this issue; Reigstad et al., 2011). However, the observational studies are based on short duration field studies and few previous studies have examined satellite derived data in detail.

Early bacterial studies showed that their biomass and the percentage of active bacteria increased from south to north in the Barents Sea along a summer transect that crossed the Polar Front (Howard-Jones et al., 2002). In the Arctic waters of the northern Barents Sea, both the abundances and production rates of bacteria are similar to those found in temperate regions (Sturluson et al., 2008; Thingstad and Martinussen, 1991). Live staining of bacteria has shown that the spectrum of high and low activity bacteria, as detected by fluorescent probes, also were comparable to results from other more southern regions (Tammert et al., 2008). High grazing rates by microzooplankton on phytoplankton in the Barents Sea provide a large flux of organic material as substrate for bacterial production during summer (Verity et al., 2002). Generally normal bacterial production rates, along with a healthy microbial loop, have been demonstrated in many other cold regions investigated (Levinsen and Nielsen, 2002; Rich et al., 1997; Sherr and Sherr, 2003).

Determining the dynamics and fluxes in the organic carbon cycle are important for evaluating and modeling the carbon cycle both in the context of fisheries management, and as factors interacting with the total inorganic carbon content thereby influencing processes such as ocean acidification. In the present study we first use primary production and biomass estimates from satellite imagery to investigate the possibility of increased primary production at the Polar Front through the spring and summer period. Second, we examine microbial variables in the vicinity of the Barents Sea Polar Front, focusing on differences among Arctic Water, Atlantic Water, and the Polar Front region. Using frequent sampling across the Front we quantify gradients and differences in bacterial activity and biomass, and the amount of organic matter.

2. Material and methods

SeaWiFS chlorophyll data were downloaded from the NASA ocean color website as level 3, 8-day binned, 9×9 km resolution arrays. Estimates of net primary production based on of the Vertically Generalized Production Model (Behrenfeld and Falkowski, 1997) were downloaded from http://www.science.oregonstate.edu/ocean.productivity/standard.product.php. As an approximate estimate of primary production at the stations sampled (see below), we used the primary production value from the 9×9 km bin containing the station position. A match in the time of sampling and of the satellite observation was not possible because of periodic cloud cover and heavy fog. Therefore, the average signal from the whole period investigated was used at all stations. At 8 stations were the three time-bins from the period contained data, the average standard deviation was 13.5% of the mean. The number of stations with one and two data points was 23 and 9, respectively. To investigate whether there is higher phytoplankton biomass at the Front, the distribution of maximal surface chlorophyll concentrations were mapped for each geographical bin over the whole growing season (April to October) for 2007, along with day of the year of the maximum.

Seawater samples were collected from the RV Jan Mayen as part of the International Polar Year (IPY) project, Norwegian component of the Ecosystem Studies of Subarctic and Arctic Regions (NESSAR) in the Barents Sea from July 27 to August 19 of 2007. Vertical profiles of temperature and salinity were measured using a Sea Bird CTD (Conductivity–Temperature–Depth) probe mounted on a General Oceanic Rosette upon which 5-liter Niskin water bottles were attached. The CTD temperature sensor was calibrated before the cruise, and the salinity was calibrated by analyzing the samples collected routinely from the water bottles at the deepest sampling level on each cast. These analyses were conducted using a Guildline 8400 AutoSal with IAPSO Standard Seawater as a reference.

Bacterial production was measured by the ^{3}H-[methyl]-thymidine method (Fuhrman and Azam, 1980, 1982). Tritiated thymidine with a specific activity 3.1 TBq mmol^{-1} (Du Pont New England Nuclear, USA) was added to a final concentration of 12 nM. Samples were incubated in 10 ml Nunc minisorb tubes in the dark for 50 to 60 min. Care was taken to incubate the thymidine incorporation experiments close to the in situ temperature, using a thermostated gradient with 12 preselected temperatures from −2 °C to 8 °C, with three replicate incubation sites for each temperature (Børsheim, 2000). Samples were collected at each station from the depths at which the observed temperature most closely matched those of the preselected temperatures. These were typically within 0.2 °C of the preselected temperatures, and usually closer. For each station investigated 5 depths were selected. The incubations were stopped by filtering using 0.2 μm pore size Nuclepore filters, followed by washing the filter 3 times with 3 ml ice cold TCA (Børsheim, 1990). Radioactivity was quantified using Ultima Gold XR (Perkin Elmer) and a Packard Tri Carb scintillation counter. Bacterial production was calculated assuming a yield of 0.023 μg C (pmol thymidine)$^{-1}$, corresponding to a thymidine to cell production conversion factor of 2.0 10^{18} bacterial cells per mole of incorporated thymidine and an average cell biomass of 11.5 fg C cell^{-1} (Ducklow and Carlson, 1992).

Samples for Total Organic Carbon (TOC) were collected in 40 ml Supelco vials, preserved with 60 μl 85% phosphoric acid, stored refrigerated in the dark, and analyzed within 2 months after sampling. TOC was measured with the high temperature catalytic combustion technique (Suzuki et al., 1992), using an Apollo 9000 Total Organic Carbon (TOC) Analyzer™ (Teledyne Tekmar, Ohio, USA), following the procedure outlined in Børsheim (2000).

Total bacterial consumption of organic material was calculated using a growth yield of 0.3 as in a comparable earlier study (Børsheim, 2000). Assuming that winter TOC largely represent recalcitrant material, transient TOC was calculated as the difference of observed TOC and winter average, and turnover time of the transient TOC was calculated using this pool size and the bacterial consumption rate (Børsheim, 2000).

Integrated values from profiles were calculated using trapezoid interpolation between each depth sampled.

3. Results

3.1. Satellite sensed chlorophyll and primary production

Fig. 1A shows the distribution of surface maximal chlorophyll concentration estimated from the time series of satellite observations through the growing season of 2007. Also shown are four areas selected to represent typical waters included in the investigation. Southeast of Hopen, Arctic water extended for about 150 km towards the Hopen Trench (region 1). Within this area there were intermediate to high surface maximal chlorophyll values in the south and the north, and low surface maximal values in between. About 200 km southeast of Hopen, a ribbon of high surface maximal values stretched in the northeast direction from 74.5°N to above 77.5°N. This lies over the slope between Spitsbergenbanken and the Hopen Trench and is where the Polar Front is normally situated (Loeng, 1991). It contained some Arctic water and that part of the Polar Front sampled during the present investigation (region 2 on Fig. 1A). Further to the southeast in the Hopen Trench, which constitutes an area with bottom depths >300 m, the waters mostly exhibited lower surface maximal chlorophyll values but with some patches of very high values (region 3 on Fig. 1A). On Storbanken (region 4) the surface maximal values were low in the west and increased eastwards.