

## The fate of production in the central Arctic Ocean – top–down regulation by zooplankton expatriates?

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### Abstract

We estimated primary and bacterial production, mineral nutrients, suspended chlorophyll *a* (Chl), particulate organic carbon (POC) and nitrogen (PON), abundance of planktonic organisms, mesozooplankton fecal pellet production, and the vertical flux of organic particles of the central Arctic Ocean (Amundsen basin, 89–88° N) during a 3 week quasi-Lagrangian ice drift experiment at the peak of the productive season (August 2001). A visual estimate of ≈15% ice-free surface, plus numerous melt ponds on ice sheets, supported a planktonic particulate primary production of 50–150 mg C m<sup>-2</sup> d<sup>-1</sup> (mean 93 mg C m<sup>-2</sup> d<sup>-1</sup>, *n* = 7), mostly confined to the upper 10 m of the nutrient replete water column. The surface mixed layer was separated from the rest of the water column by a strong halocline at 20 m depth. Phototrophic biomass was low, generally 0.03–0.3 mg Chl m<sup>-3</sup> in the upper 20 m and <0.02 mg Chl m<sup>-3</sup> below, dominated by various flagellates, dinoflagellates and diatoms. Bacterial abundance (typically 3.7–5.3 × 10<sup>5</sup>, mean 4.1 × 10<sup>5</sup> cells ml<sup>-1</sup> in the upper 20 m and 1.3–3.7 × 10<sup>5</sup>, mean 1.9 × 10<sup>5</sup> cells ml<sup>-1</sup> below) and Chl concentrations were closely correlated (*r* = 0.75). Mineral nutrients (3 μmol NO<sub>3</sub> l<sup>-1</sup>, 0.45 μmol PO<sub>4</sub> l<sup>-1</sup>, 4–5 μmol SiO<sub>4</sub> l<sup>-1</sup>) were probably not limiting the primary production in the upper layer. Suspended POC concentration was ~30–105 (mean 53) mg C m<sup>-3</sup> and PON ~5.4–14.9 (mean 8.2) mg N m<sup>-3</sup> with no clear vertical trend. The vertical flux of POC in the upper 30–100 m water column was ~37–92 (mean 55) mg C m<sup>-2</sup> d<sup>-1</sup> without clear decrease with depth, and was quite similar at the six investigated stations. The mesozooplankton biomass (≈2 g DW m<sup>-2</sup>, mostly in the upper 50 m water column) was dominated by adult females of the large calanoid copepods *Calanus hyperboreus* and *Calanus glacialis* (≈1.6 g DW m<sup>-2</sup>). The grazing of these copepods (estimated via fecal pellet production rates) was ≈15 mg C m<sup>-2</sup> d<sup>-1</sup>, being on the order of 3% and 20% of the expected food-saturated ingestion rates of *C. hyperboreus* and *C. glacialis*, respectively. The stage structure of these copepods, dominated by adult females, and their unsatisfied grazing capacity during peak productive period suggest allochthonous origin of these species from productive

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shelf areas, supported by their long life span and the prevailing surface currents in the Arctic Ocean. We propose that the grazing capacity of the expatriated mesozooplankton population would match the potential seasonal increase of primary production in the future decreased ice perspective, diminishing the likelihood of algal blooms.

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## 1. Introduction

In recent years, the Arctic Ocean (AO) has received considerable scientific interest. Remote sensing has revealed an accelerated decrease in the extent of the Arctic sea-ice (Johannessen et al., 1995). Simulations by coupled global atmosphere–ocean–ice models project decreases of sea ice extent in the range from about 12% to 46% in the Arctic by the end of the 21st century (Walsh and Timlin, 2002). Intercomparisons between general atmospheric circulation models for the Arctic show wide discrepancies in the simulation of Arctic climate (Rinke et al., 1999), possibly due to inadequate parameterization of typical Arctic phenomena or insufficient description of high latitude processes. There are also signs that the production of deep-water in the Nordic Seas is slowing (Bryden et al., 2005; Hansen et al., 2001), which may change the import of Atlantic Water into the AO and influence the ice conditions.

Recent primary production estimates from the AO have revealed a 10-fold increase compared to earlier reports (Gosselin et al., 1997; Sakshaug, 2004; Wheeler et al., 1996), altering our perception of the AO as a biological desert. An extended melt period in the AO will inevitably be reflected in the availability of under-water light followed by increase of primary production. The fate of the increasing primary production will be regulated by the pelagic plankton community as well as by advective transport processes. Conceptual models of the organic carbon flux in the ocean have two essential regulatory components: vertical flux of particulate carbon on one side, counteracted by remineralization processes by pelagic organisms, on the other side. These components partition the primary production into a fraction that is exported into the ocean interior for prolonged periods in the former, and a fraction returned to inorganic form in the surface layer in the latter case. Processes and controls of surface primary production have received considerable attention because of the general belief that productivity has the greatest influence on the ability of the ocean to take up and store carbon (bottom–up type of approach). In contrast, the remineralization side of organic carbon transport (top–down type of approach) has not received the attention it deserves.

Recent investigations emphasize that only a minor fraction of the export production leaving the euphotic zone of Arctic waters (ArW) reaches layers deeper than 200 m (e.g. Noji et al., 1999). The quantitatively important processes of vertical flux regulation in the ArW occur in the uppermost layer, often over very short vertical distances (Wassmann et al., 2003). Detailed investigations of the vertical flux in the Barents Sea (Andreassen and Wassmann, 1998; Olli et al., 2002) and off the shelf of NW Spain (e.g. Olli et al., 2001) revealed that the attenuation of the vertical POC export is largest in the upper 100 m. In tropical waters, planktonic bacteria appear to have the potential to remineralize most of the sinking organic carbon (e.g. Cho and Azam, 1998), while in the cold water ecosystems the importance of bacteria has been questioned (e.g. Pomeroy and Deibel, 1986). However, the summer temperature in the ArW is not very different from temperatures during the spring bloom in temperate waters, which is regularly associated with the annual peak in bacterial activity (Kuosa and Kivi, 1989; Thingstad and Martinussen, 1991). Recent investigations in the North Water polynya (northern Baffin Bay) suggest similar bacterial extracellular enzyme activity at near-0 °C temperatures as compared to temperate waters, and elevated activity associated with sinking particles (Huston and Deming, 2002), emphasizing a role for bacterial decomposition in the vertical flux attenuation in high latitude waters. Furthermore, bacterial production has been found to be comparable to or even exceed the primary production in the central AO (Rich et al., 1997).

In arctic regions mesozooplankton, depending on their composition and abundance, are an important and complex regulator of the fate of primary production (Noji, 1991; Pasternak et al., 2002; Reigstad et al., 2000;

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