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Influence of allochthonous dissolved organic matter on pelagic basal production in a northerly estuary

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ABSTRACT

Phytoplankton and heterotrophic bacteria are key groups at the base of aquatic food webs. In estuaries receiving riverine water with a high content of coloured allochthonous dissolved organic matter (ADOM), phytoplankton primary production may be reduced, while bacterial production is favoured. We tested this hypothesis by performing a field study in a northerly estuary receiving nutrient-poor, ADOM-rich riverine water, and analyzing results using multivariate statistics. Throughout the productive season, and especially during the spring river flush, the production and growth rate of heterotrophic bacteria were stimulated by the riverine inflow of dissolved organic carbon (DOC). In contrast, primary production and photosynthetic efficiency (i.e. phytoplankton growth rate) were negatively affected by DOC. Primary production related positively to phosphorus, which is the limiting nutrient in the area. In the upper estuary where DOC concentrations were the highest, the heterotrophic bacterial production constituted almost 100% of the basal production (sum of primary and bacterial production) during spring, while during summer the primary and bacterial production were approximately equal. Our study shows that riverine DOC had a strong negative influence on coastal phytoplankton production, likely due to light attenuation. On the other hand DOC showed a positive influence on bacterial production since it represents a supplementary food source. Thus, in boreal regions where climate change will cause increased river inflow to coastal waters, the balance between phytoplankton and bacterial production is likely to be changed, favouring bacteria. The pelagic food web structure and overall productivity will in turn be altered.

1. Introduction

Phytoplankton and heterotrophic bacteria are key groups at the base of the food web as both assimilate dissolved nutrients and constitute a link between the chemical environment and the food web (e.g. Azam et al., 1983). Their production regulates the energy and nutrients that can be channelled through the food web and thus the production potential of intermediate and higher trophic levels, such as mesozooplankton and fish (e.g. Lefébure et al., 2013; Degerman et al., 2018). However, phytoplankton-based pathways are in many cases more efficient than bacteria-based pathways (e.g. Berglund et al., 2007; Degerman et al., 2018), and therefore environmental conditions leading to a dominance of heterotrophic bacterial production may result in lower food web efficiency and lower top-trophic level production (Berglund et al., 2007; Eriksson-Wiklund et al., 2009; Dahlgren et al., 2011). The fact that bacteria in general also represent a less nutritious resource than phytoplankton for grazers amplifies this issue (Klein Breteler et al., 2004; Dahlgren et al., 2011). It is therefore important to elucidate how environmental changes affect the balance between primary and bacterial production.

Model simulations indicate that climate change will not only

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cause elevated temperature in high latitude coastal areas but also affect the hydrology (IPCC, 2013). For example, in the northern Baltic Sea the surface water temperature is expected to increase ~4 °C by 2100, along with a ~30% increase in regional precipitation (Meier, 2006; Omstedt et al., 2012; Andersson et al., 2015). This will be accompanied with an increase in run-off of allochthonous dissolved organic matter (ADOM) from the surrounding terrestrial systems, and consequently of dissolved organic carbon (DOC) (e.g. Stepanauskas et al., 2002; Andersson et al., 2013). Previous studies indicate that phytoplankton might be disfavoured owing to the brown colour of ADOM, while heterotrophic bacteria might be favoured as they can use ADOM as a carbon food source (Andersson et al., 2015; Harvey et al., 2015). In line with this, Wikner and Andersson (2012) showed a negative correlation between the freshwater inflow to the northern Baltic Sea (Gulf of Bothnia) and primary production, and Figueroa et al. (2016) found a negative correlation between DOC concentration and primary production and a positive correlation with bacterial production in a northerly boreal estuary. However, these relationships may have alternative explanations, as for example the dilution of organisms by river discharge. Hence, to get a deeper understanding of the ecological effects of ADOM, it is critical to analyse the relationships between DOC concentrations, photosynthetic efficiency and bacterial growth rate.

ADOM is an environmental stressor in coastal systems, and is likely to affect the food web structure and ecological function of the ecosystem. By promoting bacterial production and disfavouring primary production, additional internal trophic levels will be required to facilitate trophic transfer in a food web predominantly based on smaller organisms. This will increase the energy losses throughout the food web since at each trophic level 70–90% of the energy is lost due to respiration, excretion and sloppy feeding (Straile, 1997). Thus, even if the food web length is only slightly increased, the production of higher trophic levels can be substantially decreased (Berglund et al., 2007). Additionally, bacteria are in general of reduced nutritional quality compared to eukaryotic phytoplankton, commonly lacking important lipids and fatty acids that are vital for grazers (Larsson et al., 2000), and having relatively low carbon: nitrogen: phosphorus ratios (C:N:P-ratio 50:10:1, e.g. Fagerbakke et al., 1996, Cotner et al., 2010). On the other hand eukaryotes conform to the Redfield ratio (106:16:1) and are nutritionally more suitable. Consequently, environmental drivers that turn the base of the food web from phytoplankton to bacterial dominance may induce a poorer physiological state of the grazers (e.g. poor fatty acid content), the effects of which propagate upwards through the food web, also affecting higher trophic levels.

The aim of this study was to find out how inflows of ADOM affect the bacterial and primary production as well as the photosynthetic efficiency and specific growth rate of bacteria in high latitude coastal areas receiving river water from nutrient poor catchment areas dominated by coniferous forests and mires and loads of phosphorus from offshore areas during winter-spring, thus having a pronounced nutrient cycle. We chose the Öre estuary, northern Baltic Sea, as the study system. The Baltic Sea is a brackish semi-enclosed sea where salinity, nutrients and production decrease gradually towards the north. The most limiting nutrient for primary production shifts from nitrogen in the south to phosphorus in the north (Graneli et al., 1990; Tamminen and Andersen, 2007). Both phytoplankton and bacteria have been shown to be phosphorus limited in the actual study area (Andersson et al., 1996; Zweifel et al., 1993). Furthermore, the study region is strongly influenced by ADOM-rich and nutrient-poor river discharge (Skoog et al., 2011). We hypothesized that: (1) primary production and photosynthetic efficiency in the upper estuary would be hampered by coloured DOC, while in the lower estuary primary production and photosynthetic efficiency would be governed by phosphorus concentration, and (2) bacterial production and bacterial growth rate would benefit from DOC in the upper estuary due to the large influence of river borne ADOM in this area of the estuary.

2. Material and methods

The study was performed in the Öre estuary, northern Baltic Sea (Fig. 1). Nineteen stations, radiating from the river to the open sea, were sampled on nine occasions, from May to August 2010 (Suppl. Table 1). The bottom depth in the estuary varies from 5 m at the river mouth (station 2) to 34 m offshore (station 18). The bottom depth at the stations situated on the eastern part of the sampling grid is deeper than at stations located along coast (e.g. stations 5, 8, 12 or 16).

At each sampling occasion, water for all analysis was collected at a depth of 1 m using a Ruttner sampler, and *in situ* temperature and Secchi depth were recorded (the Secchi disk was not deployed at station 1). For primary and bacterial production estimates water was additionally collected at 3 and 5 m depth, though due to their shallow nature water was only collected at 1 m depth at station 1, and at 1 and 3 m at station 2. Primary production samples were incubated *in situ* (at 1, 3 and 5 m) and other water samples were immediately transported to the laboratory for analysis. Data on river water discharge were obtained from the Swedish Meteorological and Hydrological Institute (SMHI). Surface incident PAR (Photosynthetically Available Radiation) was recorded from May to August at the Umeå Marine Sciences Center (located 7–10 km from the sampling area) with a Licor LI-193 spherical quantum sensor.

2.1. Physicochemical variables

Maximum light (PAR) at the air-water interface was calculated based on the surface PAR measurements, solar declination, solar elevation and Fresnel's equation (Kirk, 2011). PAR at 1 and 5 m depth, and the penetration depth of 1 and 0.1% PAR were calculated based on the PAR at the air-water interface and the Secchi depth (Kirk, 2011).

Conductivity and pH were measured using a Mettler Toledo probe at 25 °C and recalculated to *in situ* values using the method of Fofonoff and Millard (1983). Salinity was calculated from conductivity as practical salinity units.

Total phosphorus (TP) and total nitrogen (TN) were measured in unfiltered water samples using a Braan and Luebbe TRAACS 800 autoanalyzer, according to standard analytical methods (Grasshoff et al., 1983). Unfiltered samples for humic substances were measured with a Perkin Elmer LS 30 fluorometer at 350/450 excitation/emission wavelengths. Calibration standards were prepared from quinine dihydrogen sulfate dehydrate in 0.05M sulfuric acid (Hoge et al., 1993; Wedborg et al., 1994), and sulfuric acid (0.05M) was used as a blank. Dissolved organic carbon (DOC) analyses were carried out on 0.22 μm filtered (Supor Membrane Syringe Filter, non-pyrogenic; Acrodisc®) and acidified (8 mM HCl final concentration) water samples on a Shimadzu TOC-5000 instrument.

The absorbance of coloured dissolved organic matter (CDOM) was measured on water samples filtered through 0.22 μm polycarbonate membrane filters and stored in amber glass bottles in the dark at 4 °C until analysis. Absorbance values were recorded from 300 to 850 nm with a Shimadzu UVPC-2501 scanning spectrophotometer, using ultrapure water as a blank. The absorbance was corrected for the average reading between 700 and 750 nm according to D'Sa et al. (1999) and the absorption coefficient at 440 nm ($g_{(440)}$) was calculated according Kirk (2011).

Total suspended particulate matter (SPM) was measured using the gravimetric method described by Strickland and Parsons