



Increasing temperatures change pelagic trophodynamics and the balance between pelagic and benthic secondary production in a water column model of the Kattegat

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ABSTRACT

Temperature constrains the various processes in marine ecosystems differently and future climate warming of up to 6 °C will therefore change ecosystem functioning at various trophic levels. This study investigates how increased temperatures would change the present time overall trophic interactions with emphasis on the balance between pelagic primary and secondary productions and between pelagic and benthic secondary productions. A 1D coupled hydrodynamic-biogeochemical model was calibrated against data from a monitoring station in the Kattegat from 2004 to 2006 and validated in a hind-cast study for the period 1994–1996. Climate warming scenarios (+3 and +6 °C) showed that the magnitude and duration of the spring bloom were reduced due to higher grazing impact by heterotrophic plankton. Moreover, sedimentation rate decreased up to 44% due to lower sedimentation of phytodetritus after the spring bloom and higher heterotrophic respiration in the water column. The lower food supply to benthos and enhanced respiration due to higher temperatures reduced the biomass of deposit feeders by 23–66% whereas benthic filter feeders were less affected. The onset of the spring bloom was not changed since it was triggered by the light regime above a permanent halocline at 10–15 m depth. This study showed that climate warming presumably will change the trophodynamics of primary and secondary production and will alter the balance of the ecosystem towards a higher pelagic and a lower benthic secondary production.

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1. Introduction

Climate warming (~0.74 °C) has occurred in most regions of the northern hemisphere over the past century and has been predicted to increase further by 1.1–6.4 °C over the next 100 years according to the Intergovernmental Panel on Climate Change (IPCC, 2007). The temperature of the surface of the oceans will increase correspondingly and thereby influence the marine ecosystems. Temperature constrains the various processes in the marine ecosystems differently and therefore a general warming of the water column will change trophic interactions and ecosystem functioning (Beaugrand and Reid, 2003; Alheit et al., 2005; Hays et al., 2005).

In temperate seas, the seasonal succession of plankton provides one example of how the temperature influences autotrophic and heterotrophic processes differently. The winter–spring blooms of diatoms are triggered by the high nutrient availability and increasing light irradiance and not directly by temperature (Andersson et al., 1994; Iriarte and Purdie, 2004). However, thermal stratification affects bloom development indirectly by reducing the depth of the upper mixed layer and hence the vertical mixing of phytoplankton below the critical depth for photosynthesis (Sverdrup, 1953; Huisman et al., 1999). This can be seen in the western Baltic Sea, where the

spring bloom typically is initiated in March–April after the convective mixing has ceased and thermal stratification starts to establish (Fennel, 1999). However, in the neighbouring Kattegat, the spring bloom is initiated earlier in February–March (Olesen, 1993; Maar et al., 2002) because there is a persistent halocline at about 15 m depth (Andersson and Rydberg, 1988). In this area, the year-to-year variability of the onset of the spring phytoplankton bloom is therefore not related to thermal stratification but depends on the weather conditions that govern the overall light regime in the upper mixed layer such as cloud cover and wind mixing (Iriarte and Purdie, 2004).

In contrast, heterotrophic plankton (bacteria and zooplankton) are strongly dependent on temperature and the typical time-lag between the peak in primary production during the spring bloom and the corresponding response of the zooplankton is expected to be reduced at elevated temperatures (Oviatt, 1994; Keller et al., 1999; Scheffer et al., 2001). Zooplankton could therefore benefit from the increased temperatures due to a faster growth during phytoplankton blooms. This is the case for protozooplankton that have high growth rates and can always respond rapidly to both increasing temperatures and food conditions (Müren et al., 2005; Aberle et al., 2007). In contrast, mesozooplankton, have a lower growth response and for many species it is critical that the timing of the spring bloom matches with the timing of their reproduction otherwise there is the possibility that copepod nauplii will experience food limitation (Sommer et al., 2007; Winder and Schindler, 2004a). Mesocosm experiments with natural sea water

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have shown an increasing capability of protozooplankton and mesozooplankton to control the winter–spring phytoplankton bloom at elevated temperatures (Müren et al., 2005; Aberle et al., 2007; Sommer et al., 2007). The increased temperatures are therefore expected to increase the degree of heterotrophy in the planktonic food web although the composition of the heterotrophic plankton may change with implications for the entire pelagic food web (Müren et al., 2005).

Increasing temperatures could also change the balance between pelagic and benthic secondary production. Sedimentation of phytodetritus after the spring bloom contributes with a significant part of the total annual sedimentary input to the bottom (Wassmann, 1990) and the benthic fauna depends on this input. Sedimentation rate of organic matter during the spring bloom has been shown to decrease due to a higher zooplankton grazing impact and bacterial respiration in the water column if the temperature increases (Keller et al., 1999; Müren et al., 2005). Thus, the total sedimentary input to sustain the benthos may decrease if more material is channelled through the pelagic grazing food chain (Eriksson Wiklund et al., 2009). Higher bottom water temperatures will also increase pelagic microbial remineralisation of the settling particulate organic matter and this effect will be more pronounced the deeper the water column and the longer the sinking material is exposed to pelagic respiration (Hansen and Bendtsen, 2006). Changes in the temperature could probably also change the species composition of the benthos according to their feeding ecology (Coyle et al., 2007). While benthic filter feeders have first access to the sedimenting food and therefore probably will be less affected by a lower food supply, deposit feeders are more likely to experience food limitation (Josefson and Conley, 1997). Altogether, increasing temperatures may alter the functioning of all trophic levels in a cascade from the primary producers to the higher trophic levels such as fish (Alheit et al., 2005).

In order to predict the effects on the marine ecosystem of a warmer climate in the future, it is obviously essential to know how temperature affects the processes at different levels in the marine ecosystem (Winder and Schindler, 2004b; Alheit et al., 2005). In addition to changes occurring at the level of overall trophic interactions, the effect may also be seen at species level where for example species-specific temperature preferences affect the species composition and the species composition may itself shape the ecosystem function as a secondary temperature effect (Smetacek and Cloern, 2008). However, species-specific adaptations and inter-specific competitive ability among organisms sharing the same overall ecological function are in general unknown, but may dampen the overall ecosystem response to climate change. However, we assumed that at the level of functional organism groups (e.g. no species specific competitive responses) the influences of increasing temperatures are more predictable and may in some instances be inferred from patterns observed across climate zone during the present day climate.

The aim of the study was to investigate how increasing temperatures due to climate change would change the present time overall trophic interactions with emphasis on the balance between primary and secondary production and between pelagic and benthic secondary production. By using a coupled hydrodynamic-biogeochemical 1D water column model, we tested the following hypothesis: 1) increased temperatures will increase heterotrophic respiration relatively more than primary production during the winter–spring bloom and thereby reduce the magnitude of the phytoplankton bloom, 2) because more organic matter is respired in the water column, the sedimentary input of organic matter to the benthos will decrease if the climate gets warmer and 3) reduced sedimentary input to the bottom will affect the composition of the benthic fauna.

2. Methods and material

2.1. Study area

The Kattegat is a coastal sea located between northern Denmark and Sweden in the transition zone between the North Sea and the

Baltic Sea (Fig. 1). The hydrography is characterised by a general estuarine circulation sustained by an outflow of brackish water from the Baltic Sea and a transport of high saline water from the North Sea/Skagerrak toward the central Baltic Sea separated by a persistent halocline at 15 m depth (Andersson and Rydberg, 1988). The surface layer is well mixed and the seasonal thermocline largely coincides with the halocline. The flow through the area is mainly forced by differences in sea levels between these two areas, whereas tidal currents are weak. This study focuses on the Southern Kattegat where monitoring data for model calibration and validation were obtained from Gniben Station (56°07'N, 11° 10'E, Fig. 1) with a water depth of 48 m.

The Kattegat is of estuarine character affected by man-introduced eutrophication (Richardson and Heilmann, 1995) and primary production is nitrogen limited during the summer period (Graneli et al., 1990; Richardson and Christoffersen, 1991). However, during the period from 1993 to 2006 the winter surface concentrations of DIN decreased significantly from 9 to 6 mmol m⁻³ (Fig. 2b), and bottom sea water temperatures have increased significantly with about 1.5 °C at the study site (Fig. 2a).

2.2. Model set-up

We applied a coupled model system consisting of the hydrodynamical model COHERENS model ver. 8.4 (Luyten et al., 1999), a pelagic biogeochemical model (Lee et al., 2002), and a one-layer benthic model (Lee et al., 2002). The model was set up in 1D for a 48 m deep water column with a vertical resolution of 1 m and a numerical time step of 300 s and calibrated for the years 2004–2006. The model was forced with hourly meteorological fields of air temperature, wind speed and direction, cloud cover and relative humidity provided by an operational atmospheric model for the considered years (Brandt et al., 2001). We selected a *k*- ϵ turbulent closure scheme without limiting conditions to achieve a more diffusive thermocline according to observations (Fig. 3). The default Total Variance Diminishing (TVD) scheme was selected for vertical movement of scalars. Tidal mixing was included using an amplitude of 0.12 m and a phase of 265° obtained from a nearby station (DMI, 2002). Salinity was included in the model by a relaxation to linear interpolated measurements (Bendtsen et al., 2006) with a timescale of 5 days. Bottom oxygen concentrations are mainly dependent on advection of bottom water from the Skagerrak–Kattegat front (Bendtsen et al., 2009) and were therefore also relaxed to linear interpolated measurements with a timescale of 10 days. This means that bottom oxygen concentration

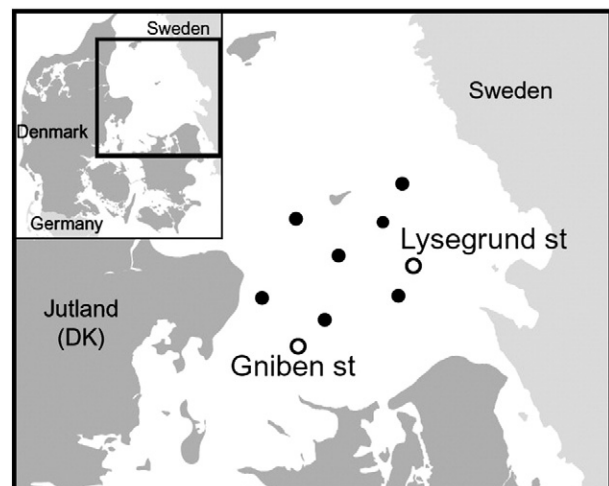


Fig. 1. The Kattegat. The stations for bottom fauna are black and the stations for pelagic variables are white.

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