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Modelling macrofaunal biomass in relation to hypoxia and nutrient loading

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ABSTRACT

Nutrient loading of aquatic ecosystems results in more food for benthic macrofaunal communities but also increases the risk of hypoxia, resulting in a reduction or complete loss of benthic biomass. This study investigates the interaction between eutrophication, hypoxia and benthic biomass with emphasis on the balance between gains and loss of benthic biomass due to changes in nutrient loadings. A physiological fauna model with 5 functional groups was linked to a 3D coupled hydrodynamic–ecological Baltic Sea model. Model results revealed that benthic biomass increased between 0 and 700% after re-oxygenating bottom waters. Nutrient reduction scenarios indicated improved oxygen concentrations in bottom waters and decreased sedimentation of organic matter up to 40% after a nutrient load reduction following the Baltic Sea Action Plan. The lower food supply to benthos reduced the macrofaunal biomass up to 35% especially in areas not currently affected by hypoxia, whereas benthic biomass increased up to 200% in areas affected by eutrophication-induced hypoxia. The expected changes in benthic biomass resulting from nutrient load reductions and subsequent reduced hypoxia may not only increase the food supply for benthivorous fish, but also significantly affect the biogeochemical functioning of the ecosystem.

1. Introduction

Benthic fauna plays major roles in the cycling of organic matter (Aller and Aller, 1998; Berner, 1980; Rhoads, 1974) and as providers of food for higher trophic levels, including benthivorous fish, such as the commercially important cod (Gruszka and Wiecaszek, 2011; Salvanes et al., 1992). Furthermore, benthos is used as one of the most important indicators for the assessment of environmental status (HELCOM, 2009a, 2009b; Villnäs and Norkko, 2011). Food availability is central for the structure and function of benthic communities, and primary production is an important factor limiting benthic biomass (Herman et al., 1999; Pearson and Rosenberg, 1978). Marine benthic communities are, however, seriously threatened by the global exponential spread of eutrophication-induced hypoxia ($[O_2]<2\ mg\ L^{-1}$) (Diaz and Rosenberg, 2008; Rabalais et al., 2010). Eutrophication and hypoxia affect benthic communities in complex ways, with generally increasing biomasses at early stages of nutrient loading and organic enrichment (i.e., increased food availability), followed by community impoverishment or complete loss when hypoxia and anoxia develop (Cederwall and Elmgren, 1980, 1990; Pearson and Rosenberg, 1978). The complex interactions between eutrophication, hypoxia and benthic fauna have implications for the functioning and productivity of these systems, but quantitatively predicting these effects is difficult, given the non-linear nature of the phenomenon.

The hypoxic zones of the Baltic Sea are among the largest in the world (Conley et al., 2009; Karlson et al., 2002). Differences in the flux of organic matter to the bottom waters and the strong south–north salinity and temperature gradients, which characterise the Baltic Sea, naturally influence the growth and condition of benthic fauna and set the limit for benthic species and functional diversity (Bonsdorff and Pearson, 1999; Rumohr et al., 1996; Villnäs and Norkko, 2011). Nevertheless, bottom-water hypoxia is currently the main factor structuring the benthic communities in the Baltic Proper and Gulf of Finland, resulting in severely impoverished benthic communities (Conley et al., 2009; Karlson et al., 2002; Villnäs and Norkko, 2011). Early signs of eutrophication did include increasing benthic biomass above the halocline, as observed for example in shallower areas not affected by hypoxia (Cederwall and Elmgren, 1980, 1990). Karlson et al. (2002), however, estimated that the benthic biomass missing in the Baltic due to hypoxia/anoxia could be up to 3 million tons. Although this lost biomass is partly compensated for in other areas of the Baltic, the importance of this spatial displacement is poorly understood. Further, such estimates are difficult to use for prediction of future scenarios or modelling of the impact of, for example, changes in nutrient loading from land as a result of different management options.

Physiology-based fauna models provide an efficient and ecologically useful tool to assess the relative importance of the different

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environmental factors (e.g., salinity, temperature, hypoxia, organic matter) known to influence the growth and biomass of benthic fauna, and these models can be used to quantify the consequences of changes in, e.g., oxygen concentrations for the benthic biomass. Understanding (and being able to quantify it on a system-wide scale) the balance between nutrient loading and hypoxia on one the hand, and the gains and losses of benthic biomass on the other hand, is particularly important for prediction of benthic productivity and ecosystem recovery after reductions in nutrient loading.

Although detailed fauna models like Dynamic Energy Budget and Scope for Growth models may provide a very precise estimate of growth and biomass for specific and often commercially interesting species (Bourles et al., 2009; Kitazawa et al., 2008), these models are not suitable for modelling entire complex benthic communities. Instead, benthic communities are often modelled using functional groups and not species as modelling units/state variables (Blackford, 1997; Maar and Hansen, 2011; Triantafyllou et al., 2000). Effects of changes in, e.g., nutrient loading and hypoxia will occur at species level, where for example species-specific hypoxia tolerance affects species composition and potentially ecosystem functioning. However, species-specific adaptation and interspecific competition are largely unknown and we assume that changes are more predictable at the functional group level.

The aim of the present study was to assess how increased oxygen concentrations and reduced input of organic matter to the benthos, as a result of decreased nutrient loadings, would influence benthic productivity and biomass. The physiological fauna model developed and applied in this study contained five functional groups characterised by differences in food source and hypoxia tolerance. The model was forced with environmental data from the BALTSEM model (Eilola et al., 2011; Gustafsson, 2003; Savchuk, 2002) and validated for six different areas of the Baltic Sea, representing different background diversities and histories of eutrophication. In our analysis, we focussed on the interaction between food availability and oxygen conditions, and the model was used to test the following hypotheses: 1) increased oxygen concentrations will increase benthic productivity and biomass, especially in the Baltic Proper, and 2) decreased eutrophication will increase benthic biomass in areas controlled by hypoxia, whereas the biomass will decrease in areas less affected by hypoxia.

2. Methods

2.1. General description of benthic fauna in the open sea areas of the Baltic Sea

Abundances and biomasses of benthic communities in the open Baltic Sea are highly variable, both spatially and temporally (HELCOM, 2009a; Laine et al., 1997, 2007; Villnäs and Norkko, 2011). The Baltic Sea is characterised by a strong south–north gradient in salinity, where bottom-water salinity decreases from around 14–18 in the Arkona Basin to 3–4 in the innermost reaches of the Gulf of Finland and the Gulf of Bothnia. This salinity gradient determines the background benthic diversity and the maximum number of taxa in specific sea areas (Bonsdorff, 2006; Bonsdorff and Pearson, 1999; Villnäs and Norkko, 2011), and the species composition is a mix of species of marine, brackish water and limnic origin (Remane, 1934).

Species diversity decreases inward from the Arkona Basin and in most of the Baltic Sea, benthic communities are dominated by only a few species. A key species is the facultative suspension/deposit-feeding bivalve *Macoma balthica*, while other important species include the deposit-feeding amphipods *Monoporeia affinis* and *Pontoporeia femorata*, the omnivorous (predator/scavenger) isopod *Saduria entomon* and the deposit-feeding polychaetes *Bylgides sarsi* (also predatory) and *Scoloplos armiger*. Over the last two decades the deposit-feeding invasive spionid polychaete *Marenzelleria* spp. has spread throughout the Baltic since it was first observed in the 1980s (Bick and Burkhardt, 1989) and is now established as one of the dominant taxa in benthic communities in the northern Baltic Sea (Leppakoski et al., 2002).

Six benthic monitoring sites were selected for model validation purposes (Fig. 1). The selected sites were evenly distributed in the open Baltic Sea and were chosen to represent some of the variation in salinity, water depth, benthic diversity and oxygen conditions characterising the Baltic Sea.

2.2. Model formulation

The benthic fauna model detailed here is conceptually similar to the fauna model developed for the North Sea by Ebenhoh et al. (1995) and Blackford (1997) but the model structure and parameterizations were modified to simulate the benthic fauna in the Baltic Sea. The present version of the model contains five main functional groups: Suspension feeders, Surface deposit feeders, Subsurface deposit feeders, Predators/scavengers and the *Macoma* group capable of both suspension and deposit feeding (Table 1). Each of the functional groups is represented by a state variable describing the biomass (mg C m^{-2}) and all groups share the same set of physiological processes (Fig. 2) but differ in the parameterization of these processes and in food source. The processes included are food uptake and assimilation, basal, growth and stress related respiration, oxygen induced mortality, and predation. Furthermore, recruitment is included.

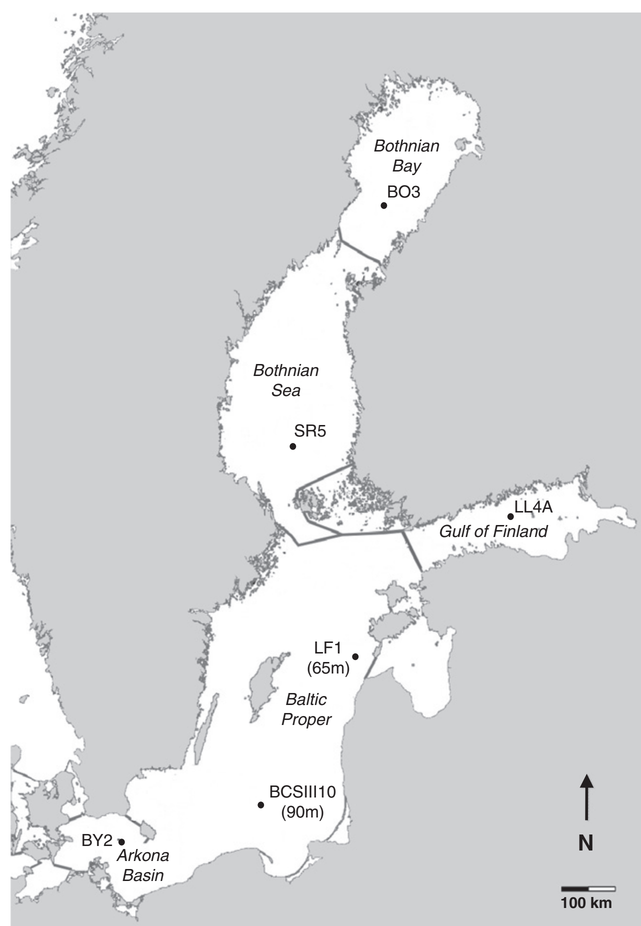

Fig. 1. Map of the Baltic Sea with the selected benthic monitoring sites used for model validation and scenarios (site names are from the Finnish monitoring programme).