Full citation:
Gammal J, Norkko J, Pilditch CA, Norkko A (2017) Coastal hypoxia and the importance of benthic macrofauna communities for ecosystem functioning. Estuaries and Coasts 40:457-468

Coastal hypoxia and the importance of benthic macrofauna communities for ecosystem functioning

Johanna Gammal, Joanna Norkko, Conrad A. Pilditch, Alf Norkko

Johanna Gammal (corresponding author)
Tvärminne Zoological Station, University of Helsinki, J.A. Palménin tie 260, 10900 Hanko, Finland
johanna.gammal@helsinki.fi, phone: +358-294128055, fax: +358-294128049

Joanna Norkko
Tvärminne Zoological Station, University of Helsinki, J.A. Palménin tie 260, 10900 Hanko, Finland

Conrad A. Pilditch
School of Sciences, University of Waikato, Private Bag 3105, Hamilton, New Zealand

Alf Norkko
Tvärminne Zoological Station, University of Helsinki, J.A. Palménin tie 260, 10900 Hanko, Finland
Marine Research Centre, Finnish Environment Institute, PO Box 140, 00251 Helsinki, Finland

Abstract

Coastal ecosystems are important because of the vital ecosystem functions and services they provide, but many are threatened by eutrophication and hypoxia. This results in loss of biodiversity and subsequent changes in ecosystem functioning. Consequently, the need for empirical field studies regarding biodiversity-ecosystem functioning in coastal areas has been emphasized. The present field study quantified the links between benthic macrofaunal communities (abundance, biomass and species richness), sediment oxygen consumption and solute fluxes ($NO_3^- + NO_2^-$, NH_4^+, PO_4^{3-}, SiO_4, Fe, Mn) along a 7.5-km natural gradient of seasonal hypoxia in the coastal northern Baltic Sea. Sampling was done in late August 2010 in the middle archipelago zone of the Hanko peninsula, Finland. As predicted the macrofaunal communities were decimated with increasing hypoxia, and the nutrient transformation processes were changed at the sediment-water interface, with notably higher effluxes of phosphate and ammonium from the sediment. Solute fluxes varied even during normoxia, which implies a high context-dependency, and could be explained by even small variations in environmental variables such as organic matter and C/N-ratios. Importantly, the low diversity benthic macrofaunal communities, which were dominated by *Macoma balthica* and the invasive *Marenzelleria* spp., had a large influence on the solute fluxes, especially under normoxia, but also under hypoxia.

Key words: Benthic macrofauna, ecosystem functioning, nutrient fluxes, hypoxia, coastal zone, Baltic Sea

Introduction

Coastal environments are often heterogeneous, with a complex mosaic of different habitats and conditions that sustain high biodiversity. They are important areas because of the vital ecosystem functions (e.g. primary production and nutrient cycling) and services (e.g. food provision and recreational opportunities) they provide (Levin et al. 2001; Barbier et al. 2011; Snelgrove et al. 2014). The integrity of coastal ecosystems is however under threat, from dredging and construction activities, eutrophication and oxygen deficiency among others that can impair biotic communities and alter ecosystem functions (Levin et al. 2001; Lotze et al. 2006; Conley et al. 2011).

Hypoxia (oxygen concentration < 2 mg l^{-1}) is a pressing threat globally, especially in coastal areas and often results from a combination of nutrient loading and stratification of the water column (Rabalais et al. 2002; Diaz and Rosenberg 2008; Gilbert et al. 2010; Carstensen et al. 2014). The severity of the disturbance can be variable depending on the duration and extent of the reduced oxygen conditions. For example, seasonal and reoccurring hypoxia (due to salinity and temperature stratification of the water column) in coastal waters puts the ecosystems into a cycle of alternating states of disturbance and recovery (Conley et al. 2009). Hypoxia also greatly modifies biogeochemical cycles, for example increasing the flux of phosphorus and bio-available nitrogen from the sediments (Virtasalo et al. 2005; Hietanen and Lukkari 2007; Kemp et al. 2009; Mort et al. 2010). This internal nutrient recycling then re-enforces the production-decomposition cycle that causes hypoxia in a continued vicious circle of eutrophication (Diaz and Rosenberg 1995; Vahtera et al. 2007).

As bottom-water oxygen concentration declines it leads to loss of bottom-living organisms (Diaz and Rosenberg 1995; Norkko and Bonsdorff 1996; Vaquer-Sunyer and Duarte 2008; Villnäs et al. 2012). Hypoxia-induced changes in macrofauna species diversity, size structure and behavior will likely result in altered or impaired ecosystem functioning (Karlson et al. 2007; Norkko et al. 2013; Norkko et al. 2015). For example the rates of activities important to remineralization of organic material at the sediment surface and within the sediment, such as feeding, bioturbation, construction and ventilation of burrows will change (Aller and Aller 1998; Kristensen 2000; Mermillod-Blondin and Rosenberg 2006). These changes are likely to influence the distribution of organic material and oxygen in the sediment (Josefson et al. 2012), which in turn affects the nutrient transformation processes,

such as denitrification and phosphorus retention in the sediment (Glud 2008; Villnäs et al. 2013). To date however real-world quantifications of these changes are scarce and changes in function are often merely inferred from shifts in functional trait diversity or based on results of laboratory experiments with simplified faunal assemblages (e.g. Marinelli and Williams 2003; Ieno et al. 2006; Karlson et al. 2007; Norling et al. 2007). This is problematic because these approaches do not capture the many positive and negative feedbacks in organism-sediment relationships that drive ecosystem function (Braeckman et al. 2014; Snelgrove et al. 2014; Lohrer et al. 2015). As the incidence of coastal hypoxia increases globally (Diaz and Rosenberg 2008; Rabalais et al. 2010; Conley et al. 2011) there is a pressing need to link changes in macrofaunal diversity to ecosystem functions in field settings so that consequences to ecosystem services can be better assessed on larger scales (Snelgrove et al. 2014; Lohrer et al. 2015).

In the open Baltic Sea we have previously demonstrated that the influence of benthic macrofauna diversity on nutrient cycling is reduced as bottom-water oxygen concentrations decline, but that the fauna nevertheless plays a role also under hypoxic conditions (Norkko et al. 2015). However it is not clear whether similar relationships hold in coastal waters where the majority of primary production and nutrient processing takes place (Levin et al. 2001) and the coupling between the sediments and the euphotic layer of the water column is potentially stronger (Welsh 2003; Kristensen et al. 2014).

Our objective was therefore to quantify the links between benthic macrofauna, sediment oxygen consumption and solute fluxes along a natural gradient of seasonal hypoxia in the coastal zone of the northern Baltic Sea. Solute fluxes across the sediment-water interface were used as a direct measure of ecosystem function since they represent mineralization processes within the sediment and the regeneration of nutrients. Since the northern Baltic Sea is a low-biodiversity system with low functional redundancy (Villnäs and Norkko 2011) we predicted that with increasing hypoxia the contribution of macrofauna to ecosystem function would decrease. Exploring these relationships along a gradient of declining oxygen in the field is a useful way of examining the context-dependent effects of hypoxia on natural communities, ecosystem functioning and the biodiversity ecosystem function relationships (Pearson and Rosenberg 1978; Larsen et al. 2005;Villnäs et al. 2012; Norkko et al. 2015).

Methods

Study area and sampling

Hypoxic bottom-water has been observed in many bays and archipelago areas along the Finnish south coast, mostly resulting from eutrophication and upwelling, but also as a result of water column stratification and topography that prevents the circulation and oxygenation of the bottom-water (Vallius 2006). Enclosed bays and sounds with partly deeper areas are thus more prone to seasonal hypoxia than more open areas with swifter currents. The studied area is a complex shallow archipelago with a labyrinth of bays and sounds, and consequently many seasonally hypoxic areas due to strong water column stratification. Macrofaunal communities are dominated by the bivalve *Macoma balthica*, polychaetes *Marenzelleria* spp., gastropods Hydrobiidae, and amphipods *Monoporeia affinis*. To investigate the links between macrofaunal community structure and ecosystem functioning in response to hypoxia we sampled benthic macrofauna and measured sediment oxygen consumption and solute fluxes from 9 sites within a 4 km radius spanning a range of bottom-water oxygen concentrations (0.0–7.7 mg l^{-1}) in the middle archipelago zone of the Hanko Peninsula, western Gulf of Finland (Table 1, see map Appendix 1). The study area was thus small enough to ensure equal background diversity, i.e. the same species pool, at all sites. Sampling was done in late-summer, August 10-24, 2010, to coincide with the peak distribution of seasonal hypoxia, which occurs at some of the sampling sites (in a deeper part of a sound with poor mixing during summer). Hypoxia at these sites generally appears during late-summer when a strong temperature stratification of the water column becomes established and the bottom-water is re-oxygenated in the fall when the water column is mixed again. The exact timing depends on the location and on weather conditions. Three of the sampling sites experienced severe, prolonged seasonal hypoxia (SH1–3), two were classified intermittently hypoxic (IH4–5) due to their close proximity to the deeper anoxic areas even though were normoxic at the time of sampling and the remaining four sites (O1–4) remain normoxic all year around due to their geographically more open locations. Site SH1 is monitored twice per year by Centre for Economic Development, Transport and the Environment in Uusimaa and sites O2 and O3 are monitored by Tvärminne Zoological Station, which provides information of the history of the oxygen conditions and benthic macrofaunal communities in the more open area. Water depths varied between 8–33 m and the salinity at all sites was around 6 (Table 1). Bottom-water temperatures were 7–19°C on the sampling dates. The lower temperatures at the deeper sites were a result of the seasonal thermocline. At the deep sites O1 and O2 temperatures were,

however, higher due to a mixing event. We selected sites with similar sediment properties (Appendix 2) to emphasize the role of the variation in the faunal communities and oxygen concentrations on ecosystem function.

Sediment oxygen consumption and solute flux measurements

Oxygen consumption and solute fluxes across the sediment-water interface were estimated by incubations of intact sediment cores. Cores were collected with a Gemax twincorer (internal diameter 90 mm), using split tubes, where the upper section (30 cm sediment + 10 cm bottom-water; see also Norkko et al. 2015) was sealed and used as a flux chamber. The cores were immediately incubated onboard in darkness and at in situ temperature. The oxygen concentration in the overlying bottom-water did not decrease more than 20% compared to initial values (i.e. in situ concentrations) during the incubations, except for at site SH3 which already had a low oxygen concentration at the start of the incubation (decrease <35% compared to initial values). The core lid contained a Teflon-coated magnetic stirring bar, which provided continuous gentle stirring by an external magnet throughout the 2-h incubation ensuring the overlying water was well mixed, but no sediment was resuspended. Five replicate cores were incubated per site except at sites SH2 and O4 where n = 3. All samples were taken within a few meters at each site.

Water samples for oxygen and solute concentrations (NO_3^- + NO_2^-, NH_4^+, PO_4^{3-}, SiO_4, Fe, Mn) were obtained at the start and the end of incubation and used to calculate solute fluxes (mmol m^{-2} d^{-1}). Each core was incubated once. Dissolved oxygen concentrations (mg l^{-1}) were determined by the Winkler procedure. Water samples for analysis of nutrient, Fe and Mn concentrations were filtered (Whatman GF/F) and then nutrient samples were frozen until analysis, while samples for dissolved Fe and Mn were preserved with HNO_3 before storage at +5°C. Nutrients (NO_3^-, NO_2^-, PO_4^{3-}, SiO_4) were analyzed spectrophotometrically with an autoanalyzer (Lachat QuickChem 8000), NH_4^+ with Genesys UV10, while dissolved Fe and Mn were analyzed with the ICP-OES (Inductively Coupled Plasma-Optical Emission Spectrometry) technique.

Sediment characterization

At each site a core (90-mm diameter) was collected, sliced (0–1, 2–3, 10–11 cm) and frozen for subsequent determination of sediment properties. For the grain size samples, large shell fragments were removed and the samples were treated with hydrogen peroxide (H_2O_2, 6%) to dissolve organic material, then they were sieved (63, 250, 500 µm) and the % dry weight of each fraction measured. Homogenized surface sediment (0–1 cm) was analyzed for organic material (OM) as loss on ignition (3 h at 500°C). Freeze-dried surface sediment samples were analyzed spectrophotometrically for chlorophyll *a* (Chl *a*) and phaeophytin content (PerkinElmer Lambda 650 UV/VIS), and acidified then re-dried (60°C) before analysis of carbon and nitrogen content at the Stable Isotope Facility, UC California, Davis. In order to get a perception of the nutrient concentrations (NO_3^- + NO_2^-, NH_4^+, PO_4^{3-}, SiO_4) in the sediment pore-water one intact core at each site was collected and sliced (0–3 and 10–11 cm). The depth fractions were centrifuged (30 min, 4000 rpm, 4ºC) and the supernatant filtered (Whatman GF/F) and then frozen until analysis as described above for the nutrient samples.

Characterization of macrofaunal communities

All incubation cores were sieved (0.5-mm sieve, contents preserved in 70% ethanol) to quantify the benthic macrofaunal species richness (lowest taxonomic level possible), abundance and biomass by dry weight (48 h at 60°C), as well as individual body size. Box core samples (0.04 m^2, n = 3) were also collected from each site and analyzed to assess whether the smaller incubation cores sufficiently managed to encompass the macrofaunal communities.

Statistical analysis

To describe site differences in the benthic faunal communities (abundance and biomass), we used non-metric multidimensional scaling (nMDS PRIMER 6, Clarke and Gorley 2006), based on the Bray-Curtis similarity index (biomass data $\log_{10}(x+1)$ transformed to down-weigh dominance). Dummy species were included in the analyses (added to all samples with the same value) to enable inclusion of anoxic sites with no fauna (Clarke et al. 2014). Additionally, multivariate one-way analysis of similarities (ANOSIM, PRIMER 6) was used

to determine the significance of differences in community abundance, biomass and the multivariate measure of solute fluxes between all sites, as well as among the normoxic sites (O1–4).

Distance-based linear models (DistLM in PERMANOVA+ for PRIMER 6, Anderson et al. 2008) are in essence a multiple linear regression model performed on multivariate response data in order to determine how much of the variation can be explained by predictor variables. DistLM were used to examine the influence of (A) environmental variables (bottom-water oxygen concentration, depth, salinity, temperature, OM, silt/clay-content, Chl *a*, phaeophytin, Chl *a*/Phaeo-ratio, C/N-ratio) on multivariate macrofaunal community structure (abundance and biomass) and (B) environmental variables and total macrofaunal community abundance, biomass and species richness on ecosystem functioning (fluxes). For all sets of analyses we first examined the relationships including all sites (excluding SH2 due to missing environmental data) along the oxygen gradient and then a subset only including the normoxic sites (O1–4). This division was made in order to examine the relationships during seasonal hypoxic conditions and during normoxic conditions in a coastal ecosystem. Sites IH4 and IH5 were not included in the normoxic sites due to potential effects of intermittent hypoxia due to their close proximity to the anoxic and hypoxic sites. For solute fluxes and macrofauna, the datasets included 3–5 replicates per site, while the environmental variables were represented by one replicate per site. Individual size was included in the initial analyses, but did not improve model fits, so therefore this information is not presented.

A backward-selection and an AIC stopping criterion were used in the DistLM to determine important predictors of the macrofaunal communities. Resemblance matrices for the multivariate community abundance and biomass ($\log_{10}(x+1)$ transformed) were based on Bray-Curtis similarities between samples. Predictors included in the analyses were bottom-water oxygen concentration, depth, temperature and the surface sediment (0–1 cm) OM and C/N-ratio. Highly co-correlated environmental predictor variables were excluded from the analyses (i.e. Pearson's $r > 0.90$; salinity, silt/clay-content, Chl *a*, phaeophytin and Chl *a*/Phaeo-ratio; see Appendix 3).

Distance-based linear models were also used to investigate the role of environmental and biological variables in predicting a multivariate measure of oxygen consumption and solute fluxes. Environmental variables included were bottom-water oxygen

concentration, water depth, and the surface sediment (0–1 cm) OM and C/N-ratio. Biological predictor variables were total macrofaunal community abundance, biomass ($log_{10}(x+1)$ transformed) and number of species from the individual incubation cores. The biological predictors were included in the analyses to account for faunal metabolism and bioturbation effects on the solute fluxes. Highly co-correlated predictor variables were excluded from the analysis (i.e. Pearson's $r > 0.90$; salinity, temperature, silt/clay-content, Chl *a*, Phaeophytin and Chl *a*/Phaeo-ratio; see Appendix 3). Flux data (NO_x, NH_4^+, PO_4^{3-}, SiO_4, Fe, Mn, O_2) were normalized to ensure equal importance of all fluxes (subtract the mean and divide by the standard deviation for each variable) before resemblance matrices based on between sample similarities of Euclidean distances were created. An AIC stopping criterion and forward, rather than backward-selection were used to determine the relative importance of predictors. The marginal test indicate the proportion of the variation the predictor accounts for alone, while the results from the sequential test indicate the proportion added by the predictor to the cumulative total proportion explained.

Results

Environmental variables

All sites had fine muddy sediments dominated by grain sizes smaller than 63 µm (Table 1 and Appendix 2). The OM and Chl *a* content, as well as the Chl *a*/phaeophytin-ratio was negatively correlated with oxygen concentration (Table 1 and Appendix 3). The nutrient concentrations in the bottom- and sediment pore-water followed the same pattern with higher concentrations of phosphate and ammonium at the sites with low or no oxygen (Appendix 4 and 5).

Macrofaunal communities

The site-averaged macrofaunal community abundance and biomass in box core and incubation core samples were highly correlated with $r^2 > 0.98$, $p < 0.001$, with slopes very close to 1 (1.1 and 1.0 respectively). However incubation cores on average contained two less species than the box core samples ($r^2 > 0.82$, $p < 0.001$) which was expected due to

differences in sample area. Consequently we used the macrofauna community data from the incubation cores in all subsequent analyses.

In total 12 species or taxonomical groups of infauna were observed in the incubation core samples (Table 2). No fauna were present at the anoxic sites SH1 and SH2, and at site SH3 only 3 species were present with mean total abundance and biomass of 790 ind. m^{-2} (SD ± 1100) and 0.6 g dwt m^{-2} (SD ± 0.7), respectively. At sites IH4–5 on average 4 species were present in the incubation cores with total abundances ranging from 1000 to 5000 ind. m^{-2} and total biomasses ranging from 1 to 40 g dwt m^{-2}. In comparison, at the oxic sites 5–6 species were generally present with total abundances between 3000–11000 ind. m^{-2} and total biomasses 1–300 g dwt m^{-2} (Table 2 and Appendix 6). The dominant species in terms of abundance were *Marenzelleria* spp. (Polychaeta) and *Macoma balthica* (Bivalvia) (represented on average 44% and 38%, respectively, of total abundance in each core with fauna; Table 2), while biomass was dominated by *M. balthica* (represented on average 90% of total biomass in each core with fauna; Appendix 6). Community structure based on abundance and biomass differed between sites (ANOSIM; abundance R = 0.764, p = 0.001; biomass R = 0.648, p = 0.001) and followed the gradient of oxygen concentration, with for example higher total community abundances and biomasses at the non-hypoxic sites (Fig. 1). Additionally, the macrofaunal communities also differed among the normoxic sites (O1–4, ANOSIM; abundance R = 0.797, p = 0.001; biomass R = 0.362, p = 0.001). There was natural intra-site variability between incubation cores in both abundance and biomass, but biomass variation was especially high at site O3 because of variability in the density of large *M. balthica* (Fig. 1). The shallower site O4 was slightly different in community structure but serves as a valuable comparison to the other sites with normoxic conditions all year around.

The results of the analyses of variations in macrofaunal community structure based on species abundance at all sites (including the hypoxic conditions) showed that all included environmental variables oxygen, depth, temperature, OM and C/N-ratio were important in explaining the structural variation and the predictors could explain a total of 78% (Table 3). Similarly, all the environmental variables could account for a total of 77% of the variation in the species biomass when all sites were included.

At sites with normoxic conditions all year around (O1–4) all the predictor variables, except bottom-water oxygen concentration, were important in explaining the

variation in community abundance and biomass. The predictors could account for a total of 79% and 41% of the variation in abundance and biomass respectively (Table 3).

Ecosystem function

Sediment oxygen consumption and solute fluxes were very variable, even within the relatively small area of this study, with for example generally higher efflux of phosphate and ammonium at sites with low or no oxygen (Table 4). The ranges of fluxes of phosphate and ammonium at the anoxic sites SH1 and SH2 were 2.5–5.9 and 13.0–43.0 mmol m^{-2} d^{-1}, respectively, which is much higher compared to the same flux-ranges at the oxic sites O1–4, which were -0.2–1.7 and 1.4–3.5 mmol m^{-2} d^{-1}, respectively. Both phosphate ($r^2 = 0.677$, $p < 0.001$) and ammonium ($r^2 = 0.811$, $p < 0.001$) fluxes showed a negative linear trend with increasing bottom-water oxygen concentration.

The multivariate solute fluxes differed between all sites (ANOSIM; $R = 0.603$, $p = 0.001$) and even when only considering the multivariate fluxes at the normoxic sites (O1–4) substantial variability was observed (ANOSIM; $R = 0.799$, $p = 0.001$). The multivariate measure of solute fluxes across the sediment-water interface was linked to environmental and biological variables. When considering all sites, from anoxia to normoxia, the most important factors explaining the variability of the fluxes cumulatively were bottom-water oxygen concentration (37%) and macrofaunal abundance (17%), while depth, C/N and OM added 4% each. The community biomass and number of species did not add explanatory power to the model. All included predictor variables in the model explained a total of 66% of the variation (Fig. 2 and Table 5).

Macrofaunal community abundance was selected as the most important predictor variable for the fluxes at the normoxic sites, explaining 37% of the variability, while OM and C/N added 14% and 11%, respectively (Table 5). Bottom-water oxygen concentration added cumulatively 8% and number of species added another 4% but it was not significant. The predictor variables chosen into the model could together explain a total of 72% of the variation in the solute fluxes.

Discussion

By exploring relationships between benthic macrofauna and solute fluxes across environmental gradients, we demonstrate how important components of biodiversity, such as the abundance, biomass and species richness of macrofaunal communities, can have a major contribution to nutrient transformation processes. It is well known that functional diversity affects many ecosystem functions, but there is, however, a lack in knowledge of the context-dependency of these effects and how relationships change across environmental disturbance gradients, such as eutrophication and hypoxia. Theoretical advances in our understanding of marine biodiversity-ecosystem functioning relationship have outpaced verification in the field, and hence the need for empirical field studies, which encompass natural communities, has been emphasized (Snelgrove et al. 2014). Our study aimed to reduce this knowledge gap through exploring the role of in situ benthic macrofaunal communities for nutrient cycling processes at the sediment-water interface, against the backdrop of the changing relationships with the onset of seasonal hypoxia in the coastal zone.

We encompassed the variability in macrofauna communities and nutrient transformation processes along a gradient of declining oxygen concentration in coastal muddy soft-bottom habitats with the same overall regional background diversity. As expected the benthic macrofaunal communities were severely decimated and the processes of the nutrient flow through the coastal ecosystem were markedly changed with the increasing hypoxic disturbance, with for example increased effluxes of nutrients from the sediment (Table 4). Interestingly the results further showed a large variation in the solute fluxes and benthic macrofauna communities even in areas with normoxic conditions within the same type of habitat. Under normoxic conditions even subtle differences in environmental variables such as organic matter and C/N-ratios played an important role in modifying the relationships (Table 5). This implies a high context-dependency of macrofauna-ecosystem functioning relationships, which makes it difficult to predict and generalize the biodiversity ecosystem functioning-patterns, unless a range of environmental variables are accounted for. We could however show that the benthic macrofaunal communities were significantly affecting the ecosystem functioning during normoxic conditions, and also to some extent when hypoxic disturbance influenced the benthos (Table 5). Obviously some of the measured variability could be attributed to sampling artefacts (i.e. cores are never totally undisturbed), but we are confident that the measured differences between sites reflect real differences. The direct effects of the benthic macrofauna on the solute fluxes due to faunal respiration and excretion

should not be ignored. From the total solute fluxes measured in this study we cannot, however, calculate the different contributions since the fluxes include overall sediment metabolism as well as the faunal metabolism. Studies have reported large variability in direct faunal effects, both species intra- and inter-specific variability (Banta et al. 1999; Alves et al. 2010; Sereda and Hudson 2011), but for example one species of *Marenzelleria* has been shown to directly contribute only 8% to the ammonium efflux and 2–4% to the total oxygen consumption (Quintana et al. 2013). Excretion alone was, however, not likely to drive the differences in the measured fluxes in this study since there was not a significant trend of increasing ammonium efflux with increasing abundance or biomass at the normoxic sites, but the direct faunal effects were of course contributing to the fluxes to some extent. In our analyses temperature was excluded due to co-correlation among predictors (abundance at the normoxic sites), but it should be remembered that temperature is an important variable for the mineralization processes at the sediment-water interface and temperature was also an important variable in accounting for the variation in the macrofaunal communities (Table 3). Including temperature in the analyses would, however, not change the main conclusions of this study, since the largest nutrient effluxes were observed at the anoxic/hypoxic and cold sites (i.e. contrary to expectations).

Eutrophication and expanding coastal hypoxia modify the processes and pathways of the nutrient and energy flow through the coastal ecosystem (e.g. Diaz and Rosenberg 1995; Conley et al. 2011). Especially the effluxes of phosphorus (PO_4^{3-}) and bio-available nitrogen (NH_4^+) were large when anoxia and hypoxia occurred, which also mirrored the nutrient concentrations in the pore-water. Thus the declining oxygen conditions at the sea floor resulted in increasing internal nutrient recycling, i.e. decreased absorption of phosphorus and decreased removal of nitrogen, which may lead to further eutrophication and hypoxic problems (Mortimer 1941; Smith and Hollibaugh 1989; Hietanen and Lukkari 2007; Vahtera et al. 2007; Mort et al. 2010). The altered mineralization processes were also implied by the higher OM, Chl *a* content and Chl *a*/phaeophytin-ratio in the surface sediment at the sites with anoxic and hypoxic conditions (Table 1). The organic matter mineralization in an anoxic system is performed by anaerobic processes, which are potentially slower than the aerobic processes, and there are no macrofauna that buries or modifies the organic matter (Bianchi et al. 2000; Sun and Dai 2005; Woulds et al. 2007; Josefson et al. 2012). The accumulation of un-degraded organic material and reduced inorganic metabolites are further causing an

oxygen debt within the sediment, which leads to impaired capacity for buffering and possibility for recovery in anoxic and hypoxic systems (Conley et al. 2007).

This investigation showed, as predicted, that the benthic macrofauna communities had a large influence on solute fluxes (36% of variation) during normoxic conditions. However, when hypoxia and anoxia occurred in the coastal zone the bottom-water oxygen concentration was the most important variable (37% of variation), but the macrofauna still had some influence on the fluxes (17% of variation, Table 5). Similar results have been reported from the open Baltic Sea, where the biodiversity ecosystem function relationships were explored over a large spatial scale (> 1200 km) with natural gradients in macrofaunal diversity and environmental conditions (i.e. oxygen concentration, salinity and nutrient regime, Norkko et al. 2015). The macrofauna was shown to have a large influence on the solute fluxes both under normoxic and hypoxic conditions, but the species important for driving the variation in the fluxes differed.

In this study the macrofaunal community abundance was the most important variable for explaining the solute fluxes and the communities were dominated by two species, the polychaete *Marenzelleria* spp. and the bivalve *Macoma balthica*. It has been suggested that the dominance of a few species with key functions may be more important than species richness for ecosystem functioning, and this might be of particular significance especially in ecosystems like the Baltic Sea with naturally low biodiversity (Chapin III et al. 1997; Josefson et al. 2012; Norkko and Reed et al. 2012; Norkko et al. 2013). Our results showed that the abundance of *Marenzelleria* spp. alone accounted for 32% (total abundance 36%) of the variation in the multivariate solute fluxes at the sites with normoxic conditions and 17% (total abundance 17%) of the variation in the fluxes along the entire oxygen gradient. Consequently, a loss of the dominating species due to hypoxia could have large consequences for the ecosystem functioning (Norkko and Bonsdorff 1996; Levin et al. 2001). Studies have shown that species identity is important (Karlson et al. 2007; Norkko and Reed et al. 2012), and even intra-specific variation can affect ecosystem functionality (e.g. variation in size: Norkko et al. 2013). The invasive polychaete genus *Marenzelleria* spp. has become the numerically dominant member of many benthic communities in the Baltic Sea (Kauppi et al. 2015). In the study area, all three species, *M. viridis*, *M. arctia*, *M. neglecta*, occur (genetic analyses under way, Kauppi pers. comm.).The deep-burrowing characteristic of *Marenzelleria* spp. (Renz and Forster 2013) have in a modelling study been shown to potentially be very important for counteracting internal nutrient recycling, through facilitation

of increased long-term (years) retention of phosphorus in the sediment (Norkko and Reed et al. 2012). Additionally, *Marenzelleria* spp. also buries settling phytodetritus deeper down in the sediment, which slows down decomposition and immediate oxygen consumption at the sediment surface (Josefson et al. 2012). In short-term studies with homogenized sediments, however, the instantaneous phosphorus efflux from the sediments may increase with increasing densities of *Marenzelleria* spp. and subsequent higher rates of bioturbation (Hietanen et al. 2007). Additionally, individual body size of the bivalve species *M. balthica* and *Mya arenaria* may have a major influence on solute fluxes; the biomass of only the large individuals was the most important driver of the variation in oxygen consumption and solute fluxes in a field experiment testing the consequences of changed macrofaunal community size-structure for ecosystem functioning (Norkko et al. 2013). This effect was not, however, observed in this data.

Consequently, an ecosystem might not be dependent on a high number of species but every system needs a sufficient number of individuals of functionally important species or groups in order to preserve efficient ecosystem functioning (Levin et al. 2001; Norkko et al. 2013). Due to hypoxia, however, faunal communities are reduced and many vital functions lost. Additionally, it is most often the long-lived and deep-burrowing individuals that are lost (and recover slowly), and these are often the individuals that contribute the most to ecosystem functioning (Norkko et al. 2013). The feeding and bioturbation activities of the benthic macrofaunal communities produce structure, oxygenate, create microhabitats and influence the rates and pathways of organic matter mineralization in the sediment (Aller and Aller 1998; Kristensen 2000; Lohrer et al. 2004; Mermillod-Blondin and Rosenberg 2006; Josefson et al. 2012). Active macrofauna communities can, for example, influence the immediate oxygen consumption at the sediment surface through burial of organic matter and enhance the redox-conditions, as well as stimulate the re-oxidation of reduced metabolic products through oxygenation of the deeper sediment layers (Kristensen 2000; Josefson et al. 2012). All these processes that are influenced by the benthic macrofauna, affect the nutrient recycling at the sediment-water interface and contribute to the buffering capacity of the coastal ecosystems against nutrient loading and establishment of hypoxia.

A healthy normoxic coastal ecosystem is an important component of the nutrient transformation and retention processes between land and open sea (Levin et al. 2001; Smith et al. 2003). These shallow areas are highly productive and support high biomasses of macrofauna and maintain a plethora of important ecosystem processes, including

mineralization and nutrient recycling. In our study area, the coastal zone is a complex shallow archipelago, with a mosaic of islands and underwater habitats, and is likely to be important in modulating nutrient transport between land and open waters (Bonsdorff et al. 1997; Helminen et al. 1998). The actual efficiency of this coastal nutrient retention remains to be quantified, but it is clear that hypoxia affects this function. Studies from many coastal ecosystems around the world have shown changed biogeochemical processes due to hypoxia. In Chesapeake Bay large areas are affected by seasonal hypoxia (e.g. Kemp et al. 2005). Mass-balance analysis of sources and sinks for total N and P in Chesapeake Bay has strongly implicated that the estuary is an important buffer between land and open sea performing active uptake and transformation of nutrients within the ecosystem (Kemp et al. 1997). The expanding seasonal hypoxia does, however increase effluxes of both phosphate and ammonium in some parts of the Bay during the summer months (e.g. Cowan and Boynton 1996). Similar reports have also come from one of the world's largest hypoxic area situated in the northern Gulf of Mexico (Rabalais et al. 2002). In the summer months during peak distribution of hypoxia/anoxia the benthic macrofaunal communities are heavily reduced and many higher taxa are lost, e.g. bivalves, gastropods and ophiuroids, and the nutrient transformation processes change, with for example decreased denitrification and thus more ammonium recycled to the overlying water column (e.g. Rabalais et al. 2001; Childs et al. 2002). Continued nutrient loading and the expanding hypoxia are thus serious threats to the functioning of the important coastal ecosystems.

Here we were able to show that the benthic faunal communities were important for driving the variation in solute fluxes, especially under normoxic conditions, but also to some extent when influenced by hypoxia. The internal nutrient recycling during hypoxia/anoxia was also very evident, with large effluxes of phosphorus and ammonium at low oxygen concentrations. Further, this study showed that the solute fluxes across the sediment-water interface can be variable under normoxic conditions, even within this relatively restricted area and at sites in similar habitats, which implies that there is large spatial variability of ecosystem functioning in the heterogeneous coastal zones. This presents challenges for marine spatial planning, management and conservation efforts. In order to better understand the complex positive and negative interactions between both biological and environmental components that lead to a multifaceted web of feedbacks for ecosystem functioning, further exploration of the fauna ecosystem function relationships in different habitats and over different temporal scales is needed.

Acknowledgements

This study was funded by Walter and Andrée de Nottbeck Foundation, Svenska studiefonden, the BONUS+ project HYPER (AN), The BONUS COCOA project, which was supported by BONUS (Art 185), funded jointly by the EU and the Academy of Finland (AN), the Sabbatical leave program of the University of Waikato (CAP), and the University of Helsinki (3-year grant to JN). We thank the reviewers for valuable comments on earlier versions of the manuscript. Judi Hewitt provided valuable advice on statistical analyses and Torsten Sjölund and Veijo Kinnunen helped with field sampling, which is gratefully acknowledged.

Conflict of interest: The authors declare that they have no conflict of interest.

References

Aller, R.C., and J.Y. Aller. 1998. The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. *Journal of Marine Research* 56: 905–936.

Alves, J.M., Caliman A., Guariento R.D., Figueiredo-Barros M.P., Carneiro L.S., Farjalla V.F., Bozelli R.L. and Esteves F.A. 2010. Stoichiometry of benthic inverterbrate nutrient recycling: interspecific variation and the role of body mass. *Aquatic Ecology* 44:421–430

Anderson, M.J., R.N. Gorley, and K.R. Clarke. 2008. PERMANOVA+ for PRIMER. Guide to software and statistical methods, 214 pp.

Banta, G.T., M. Holmer, M.H. Jensen, and E. Kristensen. 1999. Effects of two polychaete worms, *Nereis diversicolor* and *Arenicola marina*, on aerobic and anaerobic decomposition in a sandy marine sediment. *Aquatic Microbial Ecology* 19: 189–204.

Barbier, E.B., S.D. Hacker, C. Kennedy, E.W. Koch, A.C. Stier, and B.R. Silliman. 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81: 169–193.

Bianchi, T.S., B. Johansson, and R. Elmgren. 2000. Breakdown of phytoplankton pigments in Baltic sediments: effects of anoxia and loss of deposit-feeding macrofauna. *Journal of Experimental Marine Biology and Ecology* 251: 161–183.

Bonsdorff, E., E.M. Blomqvist, J. Mattila, and A. Norkko. 1997. Coastal eutrophication: causes, consequences and perspectives in the archipelago areas of the northern Baltic Sea. *Estuarine, Coastal and Shelf Science* 44 (Supplement A): 63–72.

Braeckman, U., M.Y. Foshtomi, D. Gansbeke, F. Meysman, K. Soetaert, M. Vincx, and J. Vanaverbeke. 2014. Variable importance of macrofaunal functional biodiversity for biogeochemical cycling in temperate coastal sediments. *Ecosystems* 17: 720–737.

Carstensen, J., D.J. Conley, E. Bonsdorff, B.G. Gustafsson, S. Hietanen, U. Janas, T. Jilbert, A. Maximov, A. Norkko, J. Norkko, D.C. Reed, C.P. Slomp, K. Timmermann, and M. Voss. 2014. Hypoxia in the Baltic Sea: biogeochemical cycles, benthic fauna, and management. *Ambio* 43: 26–36.

Chapin III, F.S., B.H. Walker, R.J. Hobbs, D.U. Hooper, J.H. Lawton, O.E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. *Science* 277: 500–504.

Childs, C.R., N.N. Rabalais, R.E. Turner, and L.M. Proctor. 2002. Sediment denitrification in the Gulf of Mexico zone of hypoxia. *Marine Ecology Progress Series* 240: 285–290.

Clarke, K.R., and R.N. Gorley. 2006. PRIMER v6: User Manual / Tutorial. Plymouth: PRIMER-E.

Clarke, K.R., R.N. Gorley, P.J. Somerfield, and R.M. Warwick. 2014. Change in marine communities: an approach to statistical analysis and interpretation, 3rd edition. PRIMER-E: Plymouth.

Conley, D.J., J. Carstensen, G. Ærtebjerg, P.B. Christensen, T. Dalsgaard, J.L.S. Hansen, and A.B. Josefson. 2007. Long-term changes and impacts of hypoxia in Danish coastal waters. *Ecological Applications* 17: S165–S184.

Conley, D.J., J. Carstensen, R. Vaquer-Sunyer, and C.M. Duarte. 2009. Ecosystem thresholds with hypoxia. *Hydrobiologia* 629: 21–29.

Conley, D.J., J. Carstensen, J. Aigars, P. Axe, E. Bonsdorff, T. Eremina, B.M. Haahti, C. Humborg, P. Jonsson, J. Kotta, C. Lannegren, U. Larsson, A. Maximov, M.R. Medina, E. Lysiak-Pastuszak, N. Remeikaite-Nikiene, J. Walve, S. Wilhelms, and L. Zillen. 2011. Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environmental science & technology* 45: 6777–6783.

Cowan, J.W., and W. Boynton. 1996. Sediment-water oxygen and nutrient exchanges along the longitudinal axis of Chesapeake Bay: Seasonal patterns, controlling factors and ecological significance. *Estuaries* 19: 562–580.

Diaz, R.J., and R. Rosenberg. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology - an Annual Review, Vol 33* 33: 245–303.

Diaz, R.J., and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321: 926–929.

Gilbert, D., N.N. Rabalais, R.J. Diaz, and J. Zhang. 2010. Evidence for greater oxygen decline rates in the coastal ocean than in the open ocean. *Biogeosciences* 7: 2283–2296.

Glud, R.N. 2008. Oxygen dynamics of marine sediments. Marine Biology Research 4: 243–289.

Helminen, H., E. Juntura, J. Koponen, P. Laihonen, and H. Ylinen. 1998. Assessing of long-distance background nutrient loading to the Archipelago Sea, northern Baltic, with a hydrodynamic model. *Environmental Modelling & Software* 13: 511–518.

Hietanen, S., and K. Lukkari. 2007. Effects of short-term anoxia on benthic denitrification, nutrient fluxes and phosphorus forms in coastal Baltic sediment. *Aquatic Microbial Ecology* 49: 293–302.

Hietanen, S., A.O. Laine, and K. Lukkari. 2007. The complex effects of the invasive polychaetes *Marenzelleria* spp. on benthic nutrient dynamics. *Journal of Experimental Marine Biology and Ecology* 352: 89–102.

Ieno, E.N., M. Solan, P. Batty, and G.J. Pierce. 2006. How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. *Marine Ecology Progress Series* 311: 263–271.

Josefson, A.B., J. Norkko, and A. Norkko. 2012. Burial and decomposition of plant pigments in surface sediments of the Baltic Sea: role of oxygen and benthic fauna. *Marine Ecology Progress Series* 455: 33–49.

Karlson, K., E. Bonsdorff, and R. Rosenberg. 2007. The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediments. *Ambio* 36: 161–167.

Kauppi, L., A. Norkko and J. Norkko. 2015. Large-scale species invasion into a low-diversity system: spatial and temporal distribution of the invasive polychaetes *Marenzelleria* spp. in the Baltic Sea. *Biological Invasions* 17:2055–2074

Kemp, W.M., E.M. Smith, M. MarvinDiPasquale, and W.R. Boynton. 1997. Organic carbon balance and net ecosystem metabolism in Chesapeake Bay. *Marine Ecology Progress Series* 150: 229–248.

Kemp, W.M., W.R. Boynton, J.E. Adolf, D.F. Boesch, W.C. Boicourt, G. Brush, J.C. Cornwell, T.R. Fisher, P.M. Glibert, J.D. Hagy, L.W. Harding, E.D. Houde, D.G. Kimmel, W.D. Miller, R.I.E. Newell, M.R. Roman, E.M. Smith, and J.C. Stevenson. 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology Progress Series* 303: 1–29.

Kemp, W.M., J.M. Testa, D.J. Conley, D. Gilbert, and J.D. Hagy. 2009. Temporal responses of coastal hypoxia to nutrient loading and physical controls. *Biogeosciences* 6: 2985–3008.

Kristensen, E. 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia* 426: 1–24.

Kristensen, E., M. Delefosse, C.O. Quintana, M.R. Flindt, and T. Valdemarsen. 2014. Influence of benthic macrofauna community shifts on ecosystem functioning in shallow estuaries. *Frontiers in Marine Science* 1.

Larsen, T.H., N.M. Williams, and C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters* 8: 538–547.

Levin, L.A., D.F. Boesch, A. Covich, C. Dahm, C. Erséus, K.C. Ewel, R.T. Kneib, A. Moldenke, M.A. Palmer, P. Snelgrove, D. Strayer, and J.M. Weslawski. 2001. The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems* 4: 430–451.

Lohrer, A.M., S.F. Thrush, and M.M. Gibbs. 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431: 1092–1095.

Lohrer, A.M., S.F. Thrush, J.E. Hewitt, and C. Kraan. 2015. The up-scaling of ecosystem functions in a heterogeneous world. *Scientific Reports* 5.

Lotze, H.K., H.S. Lenihan, B.J. Bourque, R.H. Bradbury, R.G. Cooke, M.C. Kay, S.M. Kidwell, M.X. Kirby, C.H. Peterson, and J.B.C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312: 1806–1809.

Marinelli, R.L., and T.J. Williams. 2003. Evidence for density-dependent effects of infauna on sediment biogeochemistry and benthic–pelagic coupling in nearshore systems. *Estuarine, Coastal and Shelf Science* 57: 179–192.

Mermillod-Blondin, F., and R. Rosenberg. 2006. Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. *Aquatic Sciences* 68: 434–442.

Mort, H.P., C.P. Slomp, B.G. Gustafsson, and T.J. Andersen. 2010. Phosphorus recycling and burial in Baltic Sea sediments with contrasting redox conditions. *Geochimica et Cosmochimica Acta* 74: 1350–1362.

Mortimer, C.H. 1941. The exchange of dissolved substances between mud and water in lakes. *Journal of Ecology* 29: 280–329.

Norkko A, and E. Bonsdorff. 1996. Rapid zoobenthic community responses to accumulations of drifting algae. *Marine Ecology Progress Series* 131:143–157.

Norkko, J., D.C. Reed, K. Timmermann, A. Norkko, B.G. Gustafsson, E. Bonsdorff, C.P. Slomp, J. Carstensen, and D.J. Conley. 2012. A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biology* 18: 422–434.

Norkko, A., A. Villnäs, J. Norkko, S. Valanko, and C. Pilditch. 2013. Size matters: implications of the loss of large individuals for ecosystem function. *Scientific Reports* 3.

Norkko, J., J. Gammal, J.E. Hewitt, A.B. Josefson, J. Carstensen, and A. Norkko. 2015. Seafloor ecosystem function relationships: in situ patterns of change across gradients of increasing hypoxic stress. *Ecosystems* 18:1424–1439.

Norling, K., R. Rosenberg, S. Hulth, A. Gremare, and E. Bonsdorff. 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology Progress Series* 332: 11–23.

Pearson, T.H., and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology - an Annual Review* 16: 229–311.

Quintana, C.O., E. Kristensen, and T. Valdemarsen. 2013. Impact of the invasive polychaete Marenzelleria viridis on the biogeochemistry of sandy marine sediments. *Biogeochemistry* 115: 95–109.

Rabalais, N.N., L.E. Smith, D.E. Harper, and D. Justic. 2001. Effects of seasonal hypoxia on continental shelf benthos. In *Coastal hypoxia: consequences for living resources and ecosystems*, ed. N.N. Rabalais and R.E. Turner, 211–240. Washington DC: American Geophysical Union.

Rabalais, N.N., R.E. Turner, and W.J. Wiseman. 2002. Gulf of Mexico hypoxia, aka "The dead zone". *Annual Review of Ecology and Systematics* 33: 235–263.

Rabalais, N.N., R.J. Diaz, L.A. Levin, R.E. Turner, D. Gilbert, and J. Zhang. 2010. Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* 7: 585–619.

Renz , J.R. and S. Forster. 2013. Are similar worms different? A comparative tracer study on bioturbation in the three sibling species *Marenzelleria arctia*, *M. viridis*, and *M. neglecta* from the Baltic Sea. *Limnology and Oceanography* 58: 2046–2058.

Sereda, J.M. and J.J. Hudson. 2011. Empirical models for predicting the excretion of nutrients (N and P) by aquatic metazoans: taxonomic differences in rates and element ratios. *Freshwater Biology* 56: 250–263

Smith, S.V., and J.T. Hollibaugh. 1989. Carbon-controlled nitrogen cycling in a marine macrocosm - an ecosystem-scale model for managing cultural eutrophication. *Marine Ecology Progress Series* 52: 103–109.

Smith, S.V., D.P. Swaney, L. Talaue-McManus, J.D. Bartley, P.T. Sandhei, C.J. McLaughlin, V.C. Dupra, C.J. Crossland, R.W. Buddemeier, B.A. Maxwell, and F. Wulff. 2003. Humans, hydrology, and the distribution of inorganic nutrient loading to the ocean. *BioScience* 53: 235–245.

Snelgrove, P.V.R., S.F. Thrush, D.H. Wall, and A. Norkko. 2014. Real world biodiversity-ecosystem functioning: a seafloor perspective. *Trends in Ecology & Evolution* 29: 398–405.

Sun, M.-Y., and J. Dai. 2005. Relative influences of bioturbation and physical mixing on degradation of bloom-derived particulate organic matter: Clue from microcosm experiments. *Marine Chemistr*y 96: 201–218.

Vahtera, E., D.J. Conley, B.G. Gustafsson, H. Kuosa, H. Pitkanen, O.P. Savchuk, T. Tamminen, M. Viitasalo, M. Voss, N. Wasmund, and F. Wulff. 2007. Internal

ecosystem feedbacks enhance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic Sea. *Ambio* 36: 186–194.

Vallius, H. 2006. Permanent seafloor anoxia in coastal basins of the northwestern Gulf of Finland, Baltic Sea. *Ambio* 35: 105–108.

Vaquer-Sunyer, R., and C.M. Duarte. 2008. Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* 105: 15452–15457.

Villnäs, A., and A. Norkko. 2011. Benthic diversity gradients and shifting baselines: implications for assessing environmental status. *Ecological Applications* 21: 2172–2186.

Villnäs, A., J. Norkko, K. Lukkari, J. Hewitt, and A. Norkko. 2012. Consequences of increasing hypoxic disturbance on benthic communities and ecosystem functioning. *PLoS One* 7: e44920.

Villnäs, A., J. Norkko, S. Hietanen, A.B. Josefson, K. Lukkari, and A. Norkko. 2013. The role of recurrent disturbances for ecosystem multifunctionality. *Ecology* 94: 2275–2287.

Virtasalo, J.J., T. Kohonen, I. Vuorinen, and T. Huttula. 2005. Sea bottom anoxia in the Archipelago Sea, northern Baltic Sea - Implications for phosphorus remineralization at the sediment surface. *Marine Geology* 224: 103–122.

Welsh, D.T. 2003. It's a dirty job but someone has to do it: the role of marine benthic macrofauna in organic matter turnover and nutrient recycling to the water column. *Chemistry & Ecology* 19: 321–342.

Woulds, C., G.L. Cowie, L.A. Levin, J.H. Andersson, J.J. Middelburg, S. Vandewiele, P.A. Lamont, K.E. Larkin, A.J. Gooday, S. Schumacher, C. Whitcraft, R.M. Jeffreys, M. Schwartz. 2007. Oxygen as a control on sea floor biological communities and their roles in sedimentary carbon cycling. *Limnology and Oceanography* 52: 1698–1709.

Table 1 Environmental variables at the sea floor at nine sites in the northern Baltic Sea, outside Hanko, Finland, sampled in August 2010. Organic material (OM), chlorophyll a (Chl a), Chl a/phaeophytin-ratio and C/N-ratio values are for surface (0–1 cm) sediment, while the mud content is depth (0–11 cm) averaged. Mean (± SD) macrofaunal community abundance (N), biomass (Bio) and number of species (S)

Site	Coordinates		Depth	T	O_2	OM	Mud content	Chl *a*	Chl *a* /phaeo	C/N	N	Bio	S
	N	E	(m)	(°C)	(mg l^{-1})	(%)	(% < 63µm)	(µg g^{-1} s)			(ind. m^{-2})	(g m^{-2})	
SH1	59˚51.493’	23˚22.475’	25.0	6.7	0.0	19	94	314	0.98	6.9	0 ± 0	0 ± 0	0 ± 0
SH2	59˚51.437’	23˚22.480’	21.5	9.6	0.2	-	-	-	-	-	0 ± 0	0 ± 0	0 ± 0
SH3	59˚51.418’	23˚22.457’	18.5	9.4	4.1	15	92	72	0.42	7.0	786 ± 1072	0.6 ± 0.7	1.4 ± 0.9
IH4	59˚51.397’	23˚22.478’	17.0	13.8	5.8	12	79	26	0.24	7.2	1698 ± 422	25 ± 14	3.2 ± 0.8
IH5	59˚51.357’	23˚22.458’	15.0	18.8	7.0	6.7	79	13	0.23	6.7	3081 ± 1098	22 ± 17	4.0 ± 1.2
O1	59˚51.868’	23˚20.416’	30.0	18.4	5.7	6.6	59	13	0.14	7.0	8928 ± 490	162 ± 73	4.2 ± 1.5
O2	59˚51.331’	23˚15.720’	33.0	18.6	5.9	14	88	25	0.15	7.3	9840 ± 858	117 ± 67	4.0 ± 0.0
O3	59˚51.166’	23˚15.275’	20.5	8.8	6.0	7.6	73	9.8	0.17	7.9	3615 ± 484	73 ± 77	3.0 ± 1.2
O4	59˚50.608’	23˚15.729’	8.5	19.2	7.5	3.6	54	8.4	0.33	8.0	8121 ± 743	21 ± 11	6.7 ± 1.2

Table 2 Mean (± SD) abundance (ind. m-2) of main taxa (n = 5, except at SH2 and O4 n = 3) based on incubation core data. “Others” include species that were only found at one site (Hediste diversicolor, Saduria entomon, Oligochaeta, Valvata sp.) Taxonomic Class: B = Bivalvia, M = Malacostraca, Pr = Priapulida, P = Polychaeta, I = Insecta, G = Gastropoda

Site	*Macoma balthica* B	*Monoporeia affinis* M	*Halicryptus spinulosus* Pr	*Marenzelleria* spp. P	*Bylgides sarsi* P	Chironomidae I	Hydrobiidae G	*Manayunkia aestuarina* P	Others
SH1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
SH2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
SH3	440 ± 560	0 ± 0	0 ± 0	314 ± 545	0 ± 0	31 ± 70	0 ± 0	0 ± 0	0 ± 0
IH4	692 ± 326	0 ± 0	126 ± 132	723 ± 238	0 ± 0	31 ± 70	63 ± 141	0 ± 0	63 ± 141
IH5	1383 ± 375	0 ± 0	283 ± 281	1100 ± 609	0 ± 0	63 ± 86	220 ± 179	31 ± 70	0 ± 0
O1	3238 ± 691	314 ± 314	126 ± 132	4967 ± 615	252 ± 238	0 ± 0	0 ± 0	0 ± 0	31 ± 70
O2	2641 ± 740	597 ± 407	31 ± 70	6319 ± 204	252 ± 141	0 ± 0	0 ± 0	0 ± 0	0 ± 0
O3	1572 ± 333	0 ± 0	94 ± 86	1886 ± 533	31 ± 70	0 ± 0	31 ± 70	0 ± 0	0 ± 0
O4	1886 ± 967	0 ± 0	472 ± 223	3144 ± 1454	52 ± 79	0 ± 0	1310 ± 1067	419 ± 344	140 ± 264

Table 3 Environmental variables affecting macrofaunal community structure (species abundance and biomass based on incubation core replicates) when regarding all sites (SH1–O4) and normoxic sites (O1–4). The results from the marginal tests and the total variation explained of the predicting variables from the sequential tests in the DistLM-analyses with backward-selection are presented. Marginal tests indicate the proportion of the variation the predictor accounts for alone, while the results from the sequential tests indicate the total proportion of the variance accounted for by the predictors in the model

	Abundance		Biomass	
	All sites	Normoxic sites	All sites	Normoxic sites
Oxygen	0.432***		0.455***	
Depth	0.148**	0.400**	0.107*	0.278**
Temp.	0.320***	0.459**	0.450***	0.134
OM	0.351***	0.234**	0.353***	0.097
C/N	0.116**	0.431**	0.106*	0.282***
Total (seq. test)	0.779	0.794	0.767	0.409

*** p=0.0001, **p<0.01, *p<0.05

Table 4 Mean (± SD) sediment oxygen consumption (mg m^{-2} d^{-1}) and solute (mmol m^{-2} d^{-1}) fluxes. Negative values represent a flux into the sediment whereas a positive value represents an efflux (n = 5, except at SH2 and O4 n = 3)

	O_2	NO_x	NH_4^+	PO_4^{3-}	SiO_4	Fe	Mn
SH1	0 ± 0	0.0 ± 0.0	18.8 ± 3.4	2.9 ± 0.3	10.6 ± 5.5	-0.0 ± 0.9	0.0 ± 0.1
SH2	-297 ± 266	-0.1 ± 0.0	27.6 ± 13.1	5.3 ± 0.6	1.1 ± 0.9	-0.3 ± 0.2	0.5 ± 0.1
SH3	-1001 ± 452	-0.1 ± 0.0	6.9 ± 1.3	2.2 ± 0.4	0.3 ± 1.4	0.4 ± 0.1	0.5 ± 0.1
IH4	-598 ± 121	0.1 ± 0.0	2.9 ± 1.4	0.6 ± 0.6	3.4 ± 1.2	0.2 ± 0.2	0.6 ± 0.3
IH5	-1129 ± 392	0.2 ± 0.2	3.4 ± 1.5	0.6 ± 0.1	4.8 ± 1.6	0.7 ± 1.1	0.6 ± 0.3
O1	-1334 ± 287	0.9 ± 0.2	2.9 ± 0.7	0.7 ± 0.1	4.2 ± 0.8	0.1 ± 0.1	2.4 ± 0.4
O2	-1165 ± 238	1.0 ± 0.2	2.7 ± 0.2	1.4 ± 0.3	1.6 ± 1.4	0.2 ± 0.2	1.2 ± 0.1
O3	-737 ± 289	0.1 ± 0.1	2.2 ± 0.6	-0.1 ± 0.1	0.2 ± 0.8	0.3 ± 0.2	0.6 ± 0.2
O4	-1347 ± 398	0.7 ± 0.3	3.1 ± 0.2	0.3 ± 0.1	5.3 ± 2.0	0.2 ± 0.1	0.5 ± 0.1

Table 5 Proportion of the variation in multivariate oxygen and solute fluxes accounted for at (A) all sites and (B) only sites with normoxic conditions. Empty cells means that the predictor was not chosen into the model after accounting for all the other variables. Marginal test indicate the proportion of the variation the predictor accounts for alone, while the results from the sequential test indicate the proportion added by the predictor to the cumulative total proportion explained

	Marginal test	Sequential test	Cumulative proportion explained
(A) All sites			
Oxygen	0.371***	0.371***	0.371
Abundance	0.311***	0.169***	0.540
Depth	0.104**	0.042*	0.582
C/N	0.085*	0.038**	0.621
OM	0.280***	0.038**	0.658
Biomass	0.304***		
Number of species	0.262***		
(B) Normoxic sites			
Abundance	0.362**	0.362**	0.362
OM	0.128	0.135**	0.496
C/N	0.307**	0.111**	0.608
Oxygen	0.125	0.075*	0.682
Number of species	0.135	0.035	0.717
Depth	0.187*		
Biomass	0.138*		

*** p=0.0001, **p<0.01, *p<0.05

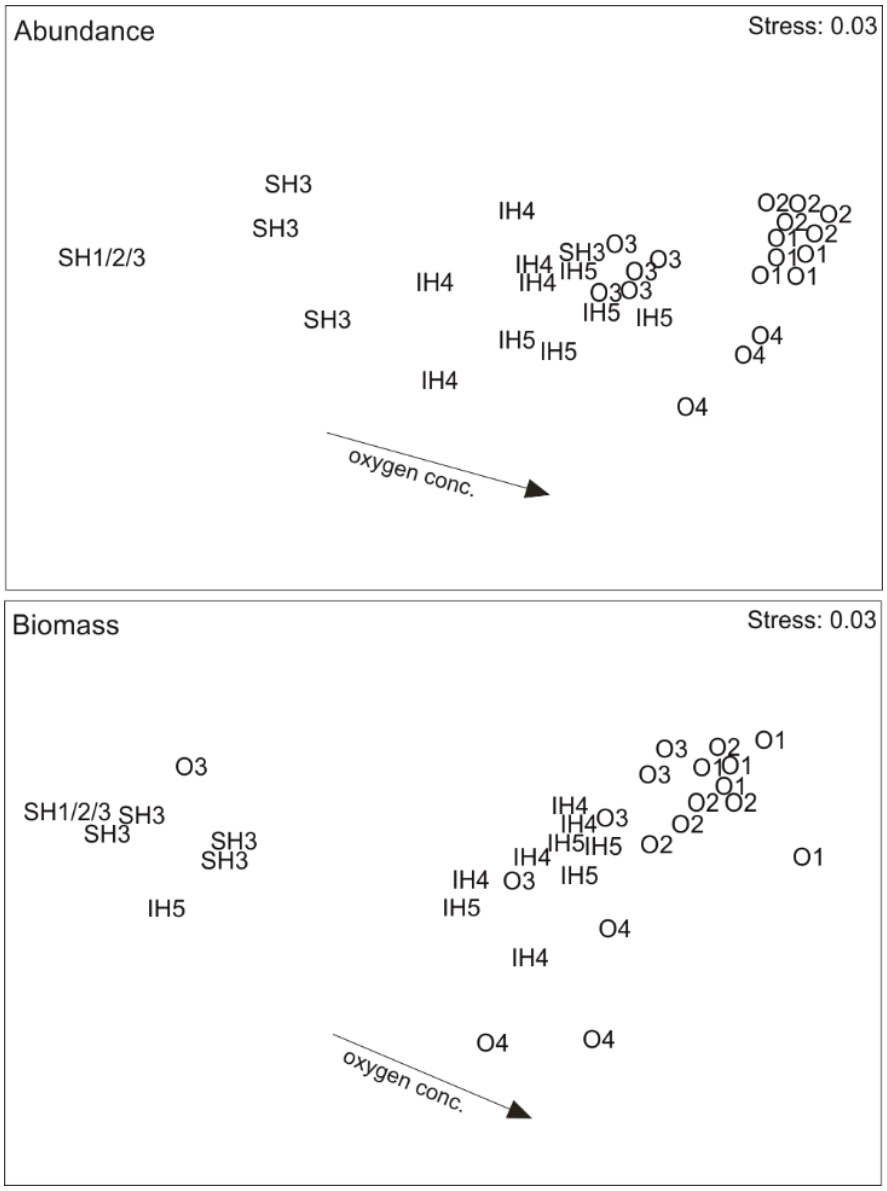


Figure 1 nMDS of macrofaunal community abundance and biomass (log10-transformed) (based on Bray-Curtis similarity) in incubation core samples with a vector overlay of increasing bottom-water oxygen concentration (n = 5, except at SH2 and O4 n = 3). See Table 1 for site characteristics

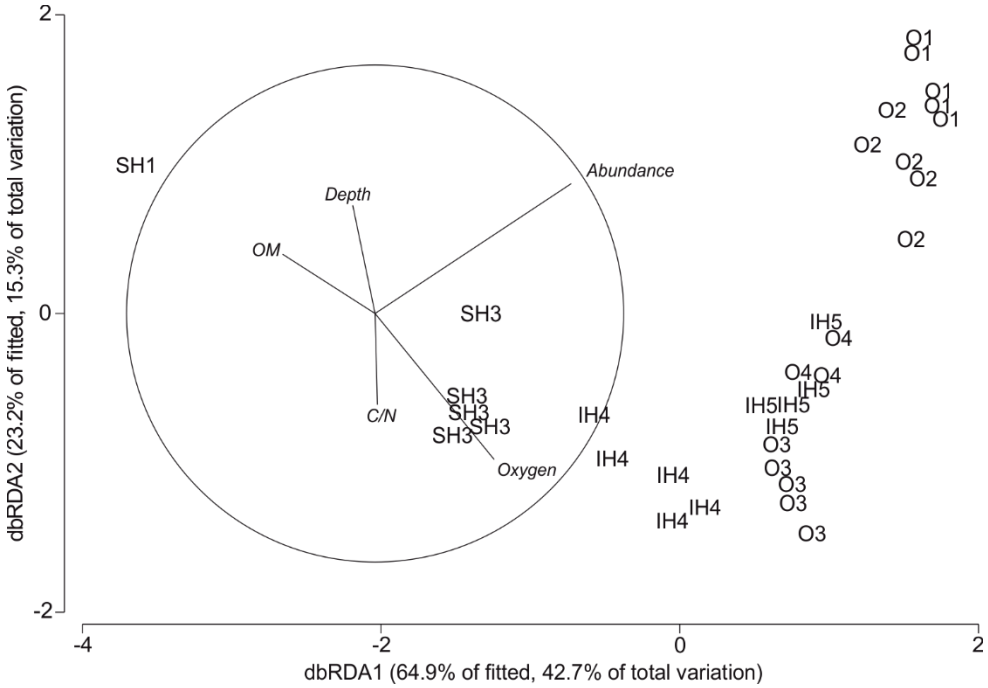
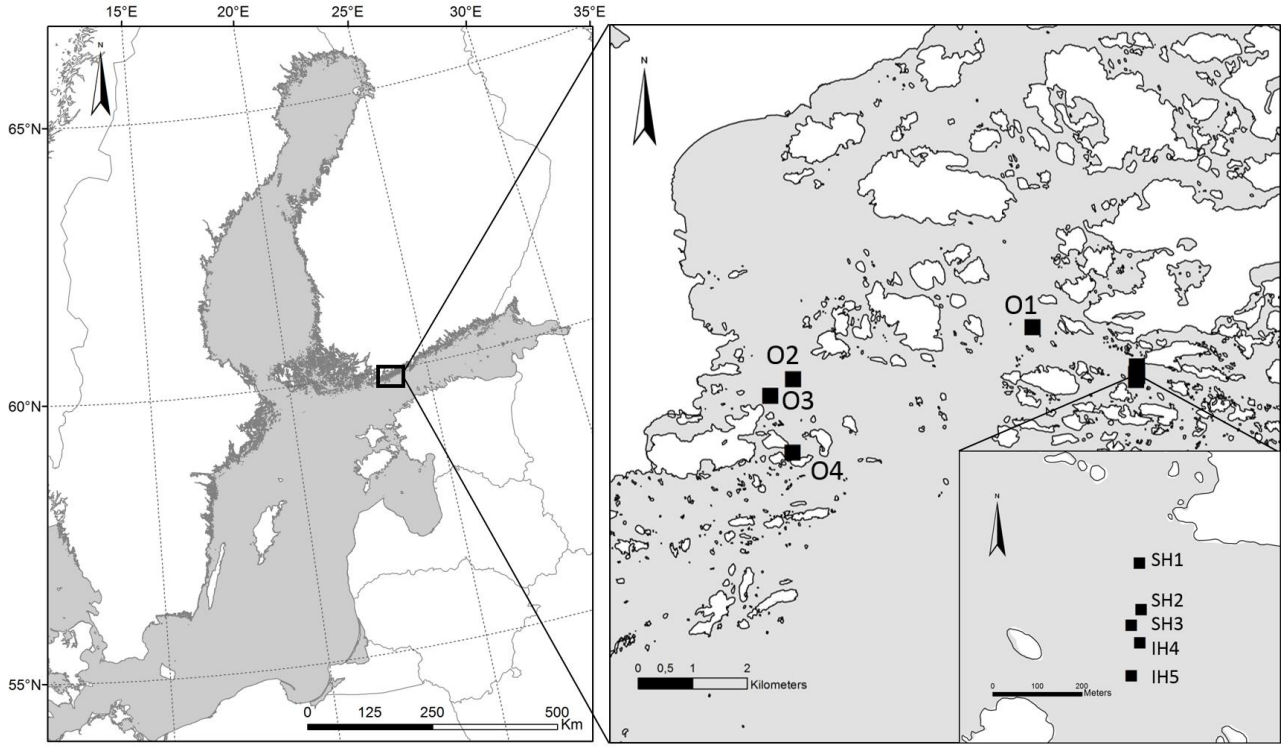


Figure 2 Graphical representation by dbRDA of the relationships between significant predictors (bottom-water oxygen concentration, OM, C/N, depth, macrofaunal community abundance) and Euclidean distances of the multivariate oxygen and nutrient fluxes at all sites (n = 5, except at SH2 and O4 n = 3). The closer samples are to each other, the more similar are their fluxes. The vectors indicate the direction and the importance of the predictors for the fluxes on these two axes

Title: Coastal hypoxia and the importance of benthic macrofauna communities for ecosystem functioning
Journal: Estuaries and Coasts
Authors: Johanna Gammal[1], Joanna Norkko[1], Conrad A. Pilditch[2], Alf Norkko[1, 3]

Corresponding author: J. Gammal (johanna.gammal@helsinki.fi)

[1] Tvärminne Zoological Station, University of Helsinki, J.A. Palménin tie 260, 10900 Hanko, Finland
[2] School of Sciences, University of Waikato, Private Bag 3105, Hamilton, New Zealand
[3] Marine Research Centre, Finnish Environment Institute, PO Box 140, 00251 Helsinki, Finland



Appendix 1 Map of the sampling area and the nine sites in the archipelago east of Hanko peninsula in the western Gulf of Finland (map source: HELCOM)

Appendix 2 Grain size data, depth (0–11 cm) averaged % dry weight of each fraction at the sampling sites

Fraction	SH1	SH2	SH3	IH4	IH5	O1	O2	O3	O4
> 500 µm	0.0	-	0.0	0.0	0.0	2.5	0.0	0.6	2.6
> 250 µm	0.1	-	0.0	0.2	0.1	4.8	0.0	1.5	2.9
> 63 µm	6.0	-	7.8	20.4	21.3	33.5	11.8	24.4	40.8
< 63 µm	93.9	-	92.2	79.4	78.6	59.2	88.2	73.4	53.6

Appendix 3 Pearson correlation coefficients among environmental and biological predictors of multivariate oxygen and nutrient fluxes. The upper right hand side of the matrix is for all sites while the lower left is for the normoxic sites.

	Oxygen	Depth	Salinity	T	OM	Silt /Clay	Chl *a*	Phaeo	Chl *a* /Phaeo	C/N	N	Bio	S
Oxygen		-0.30	-0.23	0.73	-0.84	-0.63	-0.96	-0.94	-0.91	0.40	0.54	0.65	0.80
Depth	-0.86		-0.18	0.05	0.38	0.22	0.18	0.45	-0.04	-0.22	0.44	0.33	-0.16
Salinity	-0.02	-0.35		-0.69	0.16	0.20	0.22	0.07	0.21	0.46	-0.49	-0.19	-0.37
T	0.18	0.24	-0.97		-0.62	-0.55	-0.65	-0.57	-0.65	-0.02	0.75	0.66	0.79
OM	-0.54	0.76	-0.05	0.11		0.89	0.77	0.94	0.70	-0.41	-0.48	-0.57	-0.78
Silt/Clay	-0.46	0.58	0.25	-0.17	0.95		0.57	0.74	0.53	-0.44	-0.57	-0.57	-0.75
Chl *a*	-0.44	0.78	-0.40	0.45	0.94	0.79		0.91	0.97	-0.38	-0.53	-0.66	-0.72
Phaeo	-0.60	0.89	-0.41	0.41	0.92	0.76	0.98		0.83	-0.46	-0.39	-0.55	-0.74
Chl *a* /Phaeo	0.97	-0.91	0.02	0.14	-0.60	-0.51	-0.51	-0.67		-0.33	-0.61	-0.76	-0.68
C/N	0.66	-0.83	0.71	-0.55	-0.33	-0.06	-0.51	-0.65	0.70		0.33	0.29	0.39
N	-0.07	0.46	-0.93	0.94	0.33	0.05	0.63	0.61	-0.09	-0.66		0.76	0.71
Bio	-0.46	0.59	-0.40	0.30	0.31	0.15	0.40	0.48	-0.51	-0.63	0.41		0.65
S	0.64	-0.41	-0.53	0.60	-0.42	-0.53	-0.17	-0.25	0.62	0.04	0.42	-0.02	

Appendix 4 Mean (± SD) bottom-water oxygen (mg l^{-1}) and solute concentrations (µmol l^{-1}) (n = 5, except at SH2 and O4 n = 3)

	SH1	SH2	SH3	IH4	IH5	O1	O2	O3	O4	Detection limits
O2	0.0 ± 0.0	0.2 ± 0.2	4.1 ± 0.1	5.8 ± 0.5	7.0 ± 0.2	5.7 ± 0.1	5.9 ± 0.2	6.0 ± 0.2	7.5 ± 0.1	
NO_x	0.1 ± 0.0	0.1 ± 0.0	0.4 ± 0.0	0.8 ± 0.0	0.4 ± 0.0	0.6 ± 0.1	0.8 ± 0.1	1.4 ± 0.1	0.4 ± 0.1	0.1
NH_4^+	48.3 ± 4.9	20.4 ± 4.5	8.2 ± 0.2	7.8 ± 1.2	3.4 ± 0.2	7.6 ± 0.5	5.9 ± 0.7	6.2 ± 0.5	2.7 ± 0.3	0.25
PO_4^{3-}	7.8 ± 0.3	4.7 ± 1.4	1.9 ± 0.1	1.2 ± 0.2	0.5 ± 0.0	1.0 ± 0.1	0.8 ± 0.2	1.1 ± 0.1	0.2 ± 0.0	0.05
SiO_4	29.5 ± 1.5	18.2 ± 2.0	18.0 ± 0.7	14.5 ± 0.4	11.1 ± 0.4	15.4 ± 0.4	15.2 ± 1.0	15.8 ± 0.7	11.5 ± 0.5	0.5
Fe	3.0 ± 0.1	1.9 ± 0.8	0.4 ± 0.1	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.1	0.3 ± 0.0	0.1 ± 0.0	0.09
Mn	3.1 ± 0.1	3.9 ± 0.1	1.3 ± 0.0	0.7 ± 0.2	0.1 ± 0.0	0.8 ± 0.2	0.8 ± 0.2	1.1 ± 0.1	0.1 ± 0.0	0.04

Appendix 5 Depth resolved pore-water nutrient concentration (µmol l^{-1}) profiles at each site

	Depth (cm)	SH1	SH2	SH3	IH4	IH5	O1	O2	O3	O4
NO_x	0–3	0.1	0	0.2	0.2	0.4	2.8	1.0	0.3	0.6
	10–11	0.9	0.0	0.8	0.5	0.5	0.4	0.3	0.0	0.0
NH_4^+	0–3	636	580	284	102	92	28	32	60	64
	10–11	1812	1229	652	225	279	66	530	198	148
PO_4^{3-}	0–3	108	117	94	12	1.6	1.6	1.6	3.6	3.6
	10–11	201	264	156	76	79	7.9	142	95	48
SiO_4	0–3	448	444	287	76	89	93	84	63	100
	10–11	545	594	471	449	402	193	484	458	431

Appendix 6 Mean (± SD) biomass (g dwt m^{-2}) of main taxa (n = 5, except at SH2 and O4 n = 3) based on incubation core data. "Others" include species that were only found at one site (*Hediste diversicolor*, *Saduria entomon*, Oligochaeta, *Valvata* sp.)

Site	*Macoma balthica*	*Monoporeia affinis*	*Halicryptus spinulosus*	*Marenzelleria* spp.	*Bylgides sarsi*	Chironomidae	Hydrobidae	*Manayunkia aestuarina*	Others
SH1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
SH2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
SH3	0.5 ± 0.6	0 ± 0	0 ± 0	<0.1 ± 0.1	0 ± 0	<0.1 ± <0.1	0 ± 0	0 ± 0	0 ± 0
IH4	24 ± 14	0 ± 0	<0.1 ± <0.1	0.4 ± 0.3	0 ± 0	<0.1 ± <0.1	0.2 ± 0.3	0 ± 0	<0.1 ± <0.1
IH5	22 ± 17	0 ± 0	<0.1 ± <0.1	0.4 ± 0.4	0 ± 0	<0.1 ± <0.1	0.2 ± 0.1	<0.1 ± <0.1	0 ± 0
O1	159 ± 74	0.08 ± 0.08	0.2 ± 0..3	2.5 ± 0.4	<0.1 ± <0.1	0 ± 0	0 ± 0	0 ± 0	0.6 ± 1.4
O2	115 ± 67	0.15 ± 0.09	<0.1 ± <0.1	2.5 ± 0.4	<0.1 ± <0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0
O3	72 ± 76	0 ± 0	<0.1 ± <0.1	0.6 ± 0.1	<0.1 ± <0.1	0 ± 0	<0.1 ± 0.1	0 ± 0	0 ± 0
O4	18 ± 12	0 ± 0	<0.1 ± <0.1	0.9 ± 0.5	<0.1 ± <0.1	0 ± 0	2.1 ± 2.2	<0.1 ± <0.1	0.2 ± 0.3