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QUANTIFYING BIOMASS AND CARBON PROCESSING OF BENTHIC FAUNA IN A COASTAL SEA — PAST, PRESENT AND FUTURE

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ISBN 978-951-51-5628-0 (PRINT)
ISBN 978-951-51-5629-7 (ONLINE)
ISSN 2342-5423 (PRINT)
ISSN 2342-5431 (ONLINE)
http://ethesis.helsinki.fi

HELSINKI 2020
Dissertationes Schola Doctoralis Scientiae Circumiectalis, Alimentariae, Biologicae

ISBN 978-951-51-5628-0 (print)
ISBN 978-951-51-5629-7 (online)
ISSN 2342-5423 (print)
ISSN 2342-5431 (online)

Hansaprint
Helsinki 2020
Benthic macrofauna is an important component linking pelagic and benthic ecosystems, especially in productive coastal seas. Through their metabolism and behaviour, benthic animals affect biogeochemical fluxes between the sediment and water column. Mechanistic models that quantify these benthic-pelagic links are crucial for understanding the functioning of coastal ecosystems and their responses to anthropogenic pressures, such as climate change and eutrophication. In this thesis the flows of carbon through functional groups of benthic macrofauna and their sediment food sources were explored using a new mechanistic model, called the Benthic Macrofauna model. The model was coupled to the hydrodynamic-biogeochemical BALTSEM model and used to simulate past, present and future biomass and metabolic carbon processing of aphotic soft-sediment communities of macrofauna in the Baltic Sea. The aims of this thesis were to identify the main drivers of macrofaunal biomass and community composition and to quantify the effects of environmental change on macrofaunal communities and their contribution to benthic carbon processing.

Sedimentation of particulate organic carbon as a food source was identified as a main driver of macrofaunal biomass in two coastal areas as well as in the four largest basins of the Baltic Sea. Together with results of a food-web model of the central Baltic Sea, these results indicate that eutrophication has led to increased biomass in most parts of the ecosystem through increased productivity and sedimentation, except where counteracted by associated expanding hypoxia. Hypoxia has severe local effects on community biomass and composition, but on the scale of the Baltic Sea, biomass gains in oxic areas seem to exceed biomass losses due to hypoxia during past eutrophication. Increasing the bottom water temperature had a relatively small negative effect on community biomass in comparison to the other tested drivers, but the indirect effect of increasing surface water temperature through intensification of pelagic recycling and reduction of organic matter input to the sediment was substantial.

Macrofaunal metabolism can contribute substantially to benthic carbon and nutrient processing, especially in shallow, productive coastal areas where biomass is primarily food-limited. For example, in a coastal area of the Gulf of Finland in the early 2000s, the benthic macrofauna was estimated to process up to 80% of simulated carbon input through ingestion and mineralize 40% through respiration. On the scale of the Baltic Sea, the benthic macrofauna was estimated to mineralize about 20% of organic carbon input to the sediments. These results together with a literature review suggest that the role of benthic macrofauna needs to be considered in models of coastal and global carbon and nutrient cycling.
Simulations combining changes in climate and nutrient loads resulted in large reductions in benthic macrofaunal biomass and carbon processing capacity by the end of the 21st century if nutrient loads to the Baltic Sea are reduced according to the Baltic Sea Action Plan, but also if loads are kept at present levels. With increased nutrient loads, climate change counteracted the effects of increased productivity, also leading to a decrease in organic matter sedimentation, macrofaunal biomass and carbon processing capacity in the second half of the century.

This thesis shows that benthic responses to environmental change are nonlinear and partly decoupled from pelagic responses and indicates that benthic-pelagic coupling might become weaker in the future in a warmer and less eutrophic sea.

Keywords: benthic macrofauna; numerical modelling; carbon cycle; Baltic Sea; *Limecola balthica*; sensitivity analysis; climate change; eutrophication
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LIST OF ORIGINAL PUBLICATIONS

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1 INTRODUCTION

Benthic-pelagic coupling is a crucial link in the functioning of marine ecosystems. The exchange of mass and energy between benthic and pelagic habitats is an important part of biogeochemical cycles and food-web dynamics, ultimately shaping ecosystem services provided to humankind (Costanza et al., 1997; Griffiths et al., 2017). The coupling between benthic and pelagic systems is especially strong in coastal areas, due to shallowness of the water column and high productivity compared to the open ocean (Graf, 1992; Kopp et al., 2015). Together, these factors lead to more organic matter reaching the seafloor than in the open ocean. This organic matter is either used as food by benthic animals, mineralized by microbes, or buried in the sediments. Mineralization by microbes and animals returns inorganic nutrients to the pelagic system, where they are readily available for new primary production.

Benthic macrofauna plays a central role in benthic-pelagic coupling processes in coastal seas (Fig. 1). Benthic animals contribute to organic matter processing and benthic-pelagic fluxes of nutrients, carbon and oxygen both directly through their metabolism and indirectly through bioturbation. By reworking the sediments and flushing their burrows, they bring oxygen into the sediments, stimulate microbial processes and can increase both resuspension and burial of organic matter (Graf and Rosenberg, 1997; Kristensen et al., 2012). Suspension-feeding fauna increases sedimentation fluxes by ingesting organic matter in the water column and depositing it on the seafloor (Graf and Rosenberg, 1997). In addition, nutrients and carbon are retained in biomass and transformed between organic and inorganic forms through metabolic processes, including release of CO₂ through respiration and excretion of inorganic nutrients (Herman et al., 1999; Josefson and Rasmussen, 2000; Middelburg, 2018). Benthic macrofauna is also an important food source for other animals, such as the commercially important flatfish, cod and herring in the Baltic Sea (Borg et al., 2014; Hüssy et al., 1997; Karlson et al., 2019).

Coastal ecosystems around the world are undergoing rapid environmental change due to multiple anthropogenic pressures (Cloern et al., 2016; Halpern et al., 2008). Excessive nutrient loading has led to eutrophication and associated hypoxia which have deteriorated coastal seas and continue to pose a major threat to marine ecosystems globally (Breitburg et al., 2018; Cloern, 2001; Gray et al., 2002). Climate change affects the life-histories and distributions of marine species, and is recognized as a major driver of food-web reorganizations (Cloern et al., 2016; Poloczanska et al., 2013). Together, these changes are affecting the quality and quantity of organic matter inputs to the seafloor with potential major repercussions for the integrity of benthic communities (Gray et al., 2002; Griffiths et al., 2017). Unravelling the effects of these and other interacting drivers on benthic macrofauna is imperative for
proper ecosystem management to ensure the future functioning of marine ecosystems and the provisioning of ecosystem services (Atkins et al., 2011; Cloern et al., 2016).

Figure 1  Major processes related to vegetation and fauna controlling benthic biogeochemical fluxes. White arrows: solute fluxes, black arrows: particulate fluxes. Primary production: nutrient and CO₂ uptake and oxygen release (1), enhanced sedimentation and sediment stabilization by vegetation (2), uptake/filtration of food (3), egestion/biodeposition of faeces (4), nutrient excretion and respiration (5), and bioturbation, including bioirrigation (6) and mixing of sediments (7). Illustration by J Lokranz/Azote (study IV).

1.1 DRIVERS OF BENTHIC COMMUNITY BIOMASS

The effects of macrofauna on benthic-pelagic processes such as carbon cycling are strongly linked to the community biomass (Snelgrove et al., 2018). Globally, organic matter input to the seafloor is recognised as the most important driver of macrozoobenthic biomass and abundance (Dayton and Oliver, 1977; Pearson and Rosenberg, 1987; Rowe et al., 1974). The often observed decline in macrozoobenthic biomass with water depth correlates well with decreasing quantity and quality of organic matter as food originating from primary production in the photic zone (Dauwe et al., 1998; Duineveld et al., 1997; Grebmeier et al., 1988; Johnson et al., 2007). However, the evidence of food-limitation in shallow coastal systems is conflicting (Josefson and Rasmussen, 2000; Weigel et al., 2015). In addition to food availability, physical factors such as salinity, temperature and oxygen concentration, and biotic interactions such as predation and competition influence benthic community structure and biomass (Bertness et al., 2001; Diaz and Rosenberg, 2008; Heip et al., 1995).
It has been suggested that a stable supply of sediment organic carbon over evolutionary time-scales leads to specialisation of deposit-feeding species and thereby food limitation, while evolutionarily young communities and/or communities experiencing strong fluctuations in physical conditions and food supply (which is often the case in coastal systems) would not become food-limited (Levinton, 1972; Sanders, 1968). Another reason for the lack of evidence of food limitation in some coastal areas may be that data on actual organic matter supply to the sediments is scarce, and most studies use correlations between benthic biomass and indirect and uncertain indicators of organic matter supply, such as measures of primary production or nutrient loads. The relationship between primary production and export production, i.e. the amount of organic matter sinking out of the photic zone, is non-linear and interannual variations can be large (Tamander et al., 2017). Therefore, to unravel the major drivers of benthic biomass in a particular system, a good mechanistic understanding of the system, including processes determining organic matter supply to the benthos, is needed.

1.2 MECHANISTIC MODELLING AS A TOOL TO STUDY MASS BALANCE

Mechanistic process-based models can be used to simulate the functioning of a system over time by a set of mathematical equations. One common application of these kinds of models is to study the mass or energy flows in ecological systems. The focus of such models vary in scale from individuals (Kooijman, 2000) to food-webs (Christensen and Walters, 2004; Timmermann et al., 2012) and entire ecosystems (Butenschöhn et al., 2016; Fulton, 2010; Fulton et al., 2011). Common to all these models is the concept of mass balance: the dynamics of a state variable is expressed as the difference between source and sink fluxes. The energy or mass budget defining the growth of an individual animal can be expressed as a function of food uptake on the source side, and egestion, excretion and respiration on the sink side (Brey, 2001). The mass budget of populations or entire food-webs is the sum of individual mass budgets and the additional population-level processes of reproduction, mortality and migration. Importantly, these concepts can also be used to link biomass production and metabolism of benthic fauna to biogeochemical fluxes and transformations of carbon (C), nitrogen (N) and phosphorus (P) in the ecosystem (Fig. 2).

Mechanistic models are useful to generalize and quantify relationships observed in natural systems and to test hypotheses over spatial and temporal scales that are difficult or impossible to study with empirical methods (Duarte et al., 2003; Jackson et al., 2000). For example, to gain insight into possible future states of marine ecosystems in response to environmental change and/or management actions, there is a need to consider effects of multiple drivers on several components simultaneously. For logistical reasons, the
number of drivers and levels that can be included in empirical tests are limited by costs in terms of time and resources (Boyd et al., 2018). Process-based ecological models are powerful and cost-effective tools to conduct such tests (Christensen and Walters, 2004; Coll et al., 2015; Seidl, 2017). Additionally, such models can be used to study the relative importance of direct (e.g. physiological) and indirect (e.g. food-web mediated) effects on ecosystem components (Blackford, 2002; Condie et al., 2012; Fulton et al., 2004a).

That said, mechanistic models are associated with large uncertainties, especially when used to describe complex ecological systems over large temporal and spatial scales. A model is always a simplification of reality and must balance the competing goals of generality (i.e. applicable to a variety of systems or situations without specific tuning), precision (i.e. able to reproduce observations in detail) and realism (i.e. can describe the detailed dynamics of a real system) (Ganju et al., 2016; Levins, 1966). There are many ways to manage uncertainty in model results, for example by testing the sensitivity of model results to changes in uncertain parameters or by using multiple models to study the same question (Eilola et al., 2011; Fulton, 2010; Uusitalo et al., 2016). Obviously, the better a system is studied through empirical research and monitoring, the more precise and realistic models can be built of that system.

**Figure 2**  Biomass source and sink processes of a typical benthic animal with links to C, N, P and O cycles. POM: particulate organic matter; DIN, DIP: Dissolved inorganic N and P, respectively; DOC: Dissolved organic carbon. Illustration from study IV.

### 1.3 THE BALTIC SEA

The Baltic Sea is a semi-enclosed coastal sea in northern Europe, characterized by latitudinal and water depth gradients in salinity, temperature and species diversity (Fig. 3). Due to its location and hydrography, it is heavily affected by multiple anthropogenic pressures, such as nutrient loading, climate change
Introduction

and overfishing (Belkin, 2009; Carstensen et al., 2014; Elmgren, 1989; Karlson et al., 2002).

Due to a limited connection to the ocean and large runoff area, the salinity of the Baltic Sea is low, ranging from nearly freshwater in the northern Bothnian Bay and eastern Gulf of Finland to 25-30 psu in the transitional Skagerrak-Kattegat area in the southwest. Salinity also increases towards the bottom with a permanent halocline in the deep parts of the Baltic Proper and Gulf of Finland. The current brackish-water stage of the Baltic Sea has only lasted for about 8000 years, which is a very short time for evolutionary adaptation to brackish conditions. The salinity range of 5 to 7 psu, covering a large part of the sea, poses severe physiological stress to most macroscopic species of both marine and freshwater origin, as noted already by Remane (1934). Consequently the number of species occurring in the Baltic Sea is low and the food-webs are dominated by a few key species (Elmgren, 1984; Snoeijs-Leijonmalm, 2017).

Figure 3 Map of the Baltic Sea with bathymetry and position of the study areas: Tvärminne Storfjärden (A, study I), Askö area (B, studies I & II), and the four basins of model implementation in study III: Baltic Proper (BP), Gulf of Finland (GoF), Bothnian Sea (BS) and Bothnian Bay (BB). Macrofauna biomass sampling points used in study III are shown as black diamonds.

Strong seasonal variations in temperature and light conditions drive primary production and sedimentation patterns (Kahru et al., 1991; Schneider et al., 2017). The accumulation of nutrients (primarily nitrogen and phosphorus) during winter months result in a peak in phytoplankton...
production dominated by diatoms in spring followed by a peak in sedimentation of organic matter. In summer and autumn, the phytoplankton community is generally dominated by flagellates and, when bioavailable nitrogen is depleted from the water, by nitrogen-fixing cyanobacteria. The pelagic recycling of primary production is more efficient and sedimentation generally lower than in the spring (Heiskanen et al., 1998; Tamelander et al., 2017).

The timing and composition of plankton blooms varies along the north-south gradient of increasing water temperatures and decreasing ice cover. During the last decades, the Baltic Sea has been one of the fastest warming marine ecosystems in the world (Belkin, 2009), with associated changes in timing and composition of phytoplankton blooms (Kahru et al., 2016; Suikkanen et al., 2007).

Since the 1950s, increased anthropogenic nutrient inputs has led to eutrophication of most of the Baltic Sea, with strongest effects in the south and east, while the Bothnian Bay still remains oligotrophic (Gustafsson et al., 2012). Eutrophication has increased primary production, providing additional food for zooplankton and planktivorous fish in the pelagic food web (Eero et al., 2016), as well as for benthic communities though increased sedimentation of organic matter (Cederwall and Elmgren, 1980; Karlson et al., 2002). However, associated increased oxygen consumption has led to spreading hypoxia and anoxia both in the open Baltic Proper and in coastal areas where topography, salinity and temperature stratification limit water renewal (Carstensen et al., 2014; Conley et al., 2009, 2011; Gammal et al., 2017).

The gradients in environmental conditions, such as productivity, salinity, temperature and oxygen, determine the large-scale distribution of benthic fauna, shaping communities that generally decline in diversity and biomass with increasing latitude and water depth (Bonsdorff, 2006; Bonsdorff and Pearson, 1999; Carman and Cederwall, 2001; Laine, 2003; Remane, 1934; Rumohr et al., 1996; Snoeij-Leijonmalm et al., 2017; Villnäs and Norkko, 2011). Gogina et al. (2016) defined 10 major macrozoobenthic communities in the Baltic Sea and found that soft-sediment communities characterized by the facultative suspension/deposit-feeding bivalve *Limecola balthica* (formerly *Macoma balthica*), the surface deposit-feeding amphipod *Monoporeia affinis* and the deposit-feeding non-indigenous polychaete species complex *Marenzelleria* spp., cover the major part of the seafloor. In addition, the omnivorous isopod *Saduria entomon*, the polychaete *Bylgides sarsi* and the priapulid *Halicryptus spinulosus* are key predators in the soft-sediment communities. These communities are very simple in terms of functional complexity, but species and functional diversity increases markedly towards the entrance of the Baltic Sea and in shallow coastal areas with a complex mosaic of small-scale habitats due to local variations in e.g. exposure and substrate (Bonsdorff and Pearson, 1999; Villnäs and Norkko, 2011). Environmental conditions do not only set limits to species’ occurrence ranges, but also influence their physiology and population dynamics within the range.
For example, some bivalves show decreased size and growth rate but increased longevity in the Baltic Sea, compared their relatives in the Atlantic and Pacific Oceans (Kautsky, 1982; Segerstråle, 1960; Snoeijs-Leijonmalm, 2017).

The effects of decreasing oxygen concentrations on growth and survival differ among marine groups, with demersal fish and crustaceans generally showing high sensitivity while bivalves (such as *L. balthica*) can survive extended periods of complete anoxia by closing their valves (Gray et al., 2002). In the Baltic Sea, the common amphipods *M. affinis* and *Pontoporeia femorata* are highly sensitive to hypoxia while *S. entomon* is among the most tolerant (Timmermann et al., 2012). Hypoxia also has negative impacts on reproductive conditions for demersal fish, such as cod (MacKenzie et al., 2000; Margonski et al., 2010). The balance between biomass gained and lost in the benthos due to these two opposing effects of eutrophication, i.e. increased food availability and hypoxia, remains poorly quantified (Diaz and Rosenberg, 2008; Karlson et al., 2002).

Temperature affects most physiological rates across the whole food web, with varying effects on different species and their interactions (Brander, 2010; Pörtner and Farrell, 2008). Temperature generally increases growth and productivity of zooplankton and planktivorous herring and sprat (Bartolino et al., 2014; Hakala et al., 2003; Margonski et al., 2010; Tamelander et al., 2017). On the other hand, Rousi et al. (2013) found a negative correlation between rising temperatures and several common species of macrofauna, including the glacial relicts *M. affinis* and *S. entomon*. Glacial relicts are species that immigrated soon after the end of the last glaciation and are generally considered cold-adapted and stenothermic (Hahtela, 1990; Segerstråle, 1950, 1962). Beukema et al. (2009) found negative effects of warming on the growth, reproduction and survival of *L. balthica* in the Wadden Sea, suggesting that warming might affect also Baltic populations in the future. Increasing temperature also increases the sensitivity of benthic groups to hypoxia (Vaquer-Sunyer and Duarte, 2011). Furthermore, rising temperatures speed up the microbial degradation of organic matter, consuming oxygen and reducing food availability for benthic macrofauna.

The extended history of multiple perturbations together with a long monitoring and research tradition of the relatively simple ecosystems, makes the Baltic Sea an ideal site for studying the effects of multiple stressors and the possible future states of coastal systems worldwide (Reusch et al., 2018). The Baltic Sea area is also a prime example of advanced cross-border collaboration to manage the various environmental problems. Intergovernmental agreements such as the Helsinki Convention (1974) and the Baltic Sea Action Plan (2007) have contributed to a reduction in nutrient loads to the sea since the peak loads around 1980 (Gustafsson et al., 2012). The science-based management has made extensive use of mechanistic modelling e.g. to set quantitative targets for nutrient load reductions and ecological status of the sea (e.g. HELCOM, 2013), but the models used so far do not include benthic fauna.
2 AIMS OF THE THESIS

In this thesis, a mechanistic model simulating the carbon flows through functional groups of benthic macrofauna and their sediment food sources was developed (the Benthic Macrofauna model, BM). The model was coupled to the existing hydrodynamic-biogeochemical BALTSEM model simulating the physical (e.g. temperature) and biogeochemical (e.g. oxygen and organic matter) dynamics of the Baltic Sea and used to simulate macrozoobenthic biomass development in soft sediment areas of the Baltic Sea with the main aims to:

1. Identify the main drivers of macrofaunal biomass and community composition in the Baltic Sea (studies I, II & III)

2. Test the hypothesis that macrozoobenthic communities are food limited in two oxic coastal areas (study I).

3. Quantify the effects of changing nutrient loads and climate on macrofaunal biomass and community composition (studies II & III).

4. Quantify the effects of changing macrofaunal biomass and community composition on benthic carbon fluxes (studies I & III)

Additionally, study IV investigates the present capabilities to model how the biomass and metabolism of benthic fauna drive nutrient and carbon processing in the coastal zone and how such models can be utilized to understand changes in the benthos and associated nutrient and carbon fluxes in coastal areas under environmental change.
3 MATERIALS AND METHODS

3.1 STUDY AREAS

The areas of model implementation in studies I, II and III are shown in Fig. 3. The Benthic Macrofauna model (BM) was initially developed to represent Tvärminne Storfjärden (59° 51' N, 23° 16' E) in the western Gulf of Finland (Study I). As validation, the model was run at 40 m depth in the Baltic Proper, and compared against zoobenthic monitoring data from the Askö area (58° 46-50' N, 17° 35-41' E). The two areas represent coastal soft-sediment benthic communities with a similar latitude, water depth (30-40 m), temperature range (Tvärminne 4.78±3.91, Askö 4.01±2.13), salinity regime (Tvärminne 6.24±0.64 psu, Askö 6.83±0.36 psu) and species composition, but differ in eutrophication status, allowing for a comparison of the effects of differing amounts of organic matter supply to the benthos. (See study I supplement S1 for details.)

In study II, the model implementation in the Baltic Proper site was used and compared to results from a food-web model representing the Baltic Proper and the Bornholm Basin. In study III, the model was extended to cover the major part of the Baltic Sea including the Baltic Proper, Gulf of Finland, Bothnian Sea and Bothnian Bay (see introduction for a general description of the Baltic Sea).

3.2 ZOOBENTHIC BIOMASS DATA

Observations of macrozoobenthic biomass included in the national databases of Sweden (www.sharkweb.smhi.se) and Finland (www.syke.fi/avointieto) as well as unpublished data collected by the research vessel Aranda were used for calibration and validation purposes in studies I and III. Only quantitative soft-sediment samples taken with a Van Veen grab (ca 0.1 m²), sieved on a 1 mm mesh and weighed wet as described e.g. in Rousi et al. (2013) were used. In study III, all data sampled between 1990 and 2012 following the above criteria was used. Additionally, a geographical selection excluding areas defined as archipelago, embayment or river-dominated according to the Water Framework Directive was made, as the BALTSEM model cannot represent these complex coast-near areas properly. The final dataset consisted of 4750 observations (Fig. 3). In study I, zoobenthic monitoring data from 1995-2005 consisting of 3-5 replicate samples taken yearly in the spring and/or autumn at Tvärminne Storfjärden station XLIV and Askö stations 6001 and 6004 were used. In both studies, the data was aggregated into the three functional groups represented in the BM model: L. balthica, surface deposit-feeders and predator/scavengers.
3.3 THE BENTHIC MACROFAUNA MODEL (BM)

The Benthic Macrofauna model (BM) developed in this thesis simulates the flows of carbon through functional groups of macrofauna and their sediment food sources (Fig. 4). The model is partly based on the physiological macrofauna model presented by Timmerman et al. (2012), and the basic concepts and formulations are also inspired by the benthic biology module in the European Region Seas Ecosystem Model ERSEM (Baretta et al., 1995; Blackford, 1997; Butenschön et al., 2016; Ebenhöh et al., 1995).

The model includes five state variables: three functional groups of benthic macrofauna and two sediment food banks. The functional groups are based on feeding mode and position in the sediment: surface deposit-feeders (hereafter ‘deposit-feeders’), predator/scavengers (hereafter ‘predators’) and the infaunal key species *L. balthica*. The groups are identified in the equations by the lower indices depf, preds and mac, respectively (Table 1).

![Figure 4](conceptual_figure.png)

**Figure 4** Conceptual figure of model processes. Solid and dashed arrows represent organic and inorganic carbon fluxes, respectively. Grey rounded boxes are benthic model state variables, white rounded boxes are forcing variables from the BALTSEM model.

The biomass dynamics of the functional groups share the same processes but with different parameterizations, based on the standard organism concept.
(Baretta et al., 1995; Butenschön et al., 2016). The processes are ingestion, assimilation, respiration, predation and mortality. For each functional group, the biomass dynamics are described by:

\[ \frac{dB_i}{dt} = B_i \times I_i \times AF_j \times \left(1 - r_{g,i}\right) - B_i \times \left(r_{b,i} + m_{other,i} + m_{ox,i}\right) - m_{pred} \]

where \( B_i \) is biomass density of the functional group \( i \) (in mg C m\(^{-2}\)), \( I_i \) is ingestion rate, \( AF_j \) is an assimilation factor of the food source \( j \), \( r_{g,i} \) is growth- and activity-related respiration rate, \( r_{b,i} \) is basal respiration rate, \( m_{ox,i} \) is hypoxia-induced mortality rate, \( m_{pred} \) is predation within the benthos and \( m_{other,i} \) is the rate of all other mortality. For clarity, temperature-dependencies are not shown in the equations, but explained separately below.

Ingestion is formulated as a function of maximum ingestion rate and food availability following a type II functional response (Holling, 1966). In the model, deposit-feeders eat freshly deposited detritus, while \( L. balthica \) can eat slightly older detritus. The growth of the main deposit-feeder \( M. affinis \) seems dependent on freshly deposited algal material, while \( L. balthica \) can grow also when only older more refractory sediment is available (Karlson et al., 2011; Lehtonen and Andersin, 1998; Pekkarinen, 1983). In muddy sediments \( L. balthica \) is mainly a deposit-feeder (Olafsson, 1986), but can switch to suspension-feeding when chlorophyll levels in the water column are high (Hummel, 1985; Lin and Hines, 1994). This is formulated as a switch from deposit- to suspension-feeding on phytoplankton and detritus in the bottom water column when chlorophyll \( a \) content of the water exceeds 2 mg m\(^{-3}\), as in Timmerman et al. (2012). Predators eat mostly deposit feeders (Ankar, 1977; Englund et al., 2008), but can supplement their diet with \( L. balthica \) (Bonsdorff et al., 1995; Ejdung and Bonsdorff, 1992). Intra-guild predation or other potential food sources, such as semi-pelagic mysid shrimp, carcasses and detritus, were not included in the model.

The ingestion of multiple food sources is formulated according to recommendations by Tian (2006):

\[ I_{j,i} = I_{max,i} \times \left( \frac{pr_j \times (F_j - Flim_j)}{K_{nj,j} + \sum_{k=1}^{n} (pr_k \times (F_k - Flim_k))} \right) \]

where \( I_{j,i} \) is ingestion rate of the food source \( F_j \) by group \( i \), \( I_{max,i} \) is the maximum specific ingestion rate, \( pr_j \) is a preference factor for the food source, \( Flim_j \) is a lower limit for feeding on the food source and \( K_{nj,j} \) is the half-saturation constant of the functional response. The total ingestion rate \( I_i \) of group \( i \) is the sum of \( I_{j,i} \) over all food sources. For deposit-feeders and \( L. balthica \) eating only one food source at the time, the formulation can be simplified to:
Note that the maximum specific ingestion rate of \( L. \text{balthica} \) depends on if it is suspension- or deposit-feeding (Table 1). Additionally, ingestion stops at anoxia (bottom-water \( O_2 \) concentration = 0) for all groups (Timmermann et al., 2012).

The part of the ingested carbon that is assimilated is determined by the assimilation factor \( AF_j \), reflecting the quality of the food source (Table 1). The rest is released as faeces.

Respiratory loss of carbon due to basal metabolism \( rb,i \) is a function of biomass, while growth and activity respiration \( rg,i \) is related to ingestion (Tian, 2006).

The predation mortality function \( m_{\text{pred}} \) equals intake by predators (Eq. 2) for deposit-feeders and \( L. \text{balthica} \). The formulation for hypoxia-induced mortality from Timmerman et al. (2012) was used:

\[
(4) \quad m_{\text{ox},i} = (1 - m_{0,i}) \times \frac{m_{0,i} \times e^{-K_{\text{ox},i} \times [O_2]}}{1 - m_{0,i} \times e^{-K_{\text{ox},i} \times [O_2]}}
\]

where \([O_2]\) is bottom-water oxygen concentration, \( m_{0,i} \) is the mortality rate under anoxic conditions, and \( K_{\text{ox},i} \) describes how fast the mortality rate approaches 0 with increasing oxygen concentrations.

Other mortality, including predation not resolved in the model and natural mortality, is represented by the mortality constant \( m_{\text{other},i} \). Model closure is achieved by quadratic mortality for the predators, i.e. other mortality is formulated as \( m_{\text{other,preds}} \times B_{\text{preds}}^2 \) (Fulton et al., 2003). In study I, other mortality was linear for the two other groups, but in study III deposit-feeder mortality was changed to quadratic to account for missing predation pressure in areas where the predator group had a very low biomass or went extinct.

Growth \( (I_{\text{max},i}) \) and basal respiration \( (rb,i) \) rates are dependent on bottom water temperature according to a \( Q_{10} \)-formulation (Eq. 5), while the factor \( rg,i \) is assumed to be independent of temperature (Anderson et al., 2017; Tian, 2006). Hypoxia-induced mortality increases steeply with increasing temperature (Timmerman et al., 2012). Also other mortality \( (m_{\text{other},i}) \) is assumed to be temperature-dependent, as e.g. predation by demersal fish seems to be highest in warm summer months (Mattila and Bonsdorff, 1988).

\[
(5) \quad Q(T) = Q_{10} \left( \frac{T - T_{\text{ref}}}{10} \right)
\]

where \( Q(T) \) is the temperature-dependency factor, \( T \) is current temperature and \( T_{\text{ref}} \) is reference temperature.

To resolve possible food-limitation of the fauna, two sediment food banks are included in the benthic model as state variables. Daily sedimentation flux

\[
I_i = I_{\text{max},i} \times \left( \frac{F_i}{K_{m,i} + F_i} \right)
\]
of organic matter (sed) is integrated into a pool of fresh organic carbon in the sediment (fbf). Loss terms of the pool are ingestion by deposit-feeders and aging by the factor $k_{fbf}$.

\begin{equation}
\frac{dfbf}{dt} = sed - B_{depf} \times l_{depf} - fbf \times k_{fbf}
\end{equation}

The aging detritus enters a pool of older sediment organic carbon (fbo) available as food to L. balthica only. Also the faeces of deposit-feeders and predators adds to the older food bank. Loss terms for the older food bank are ingestion by L. balthica and degradation or burial by the factor $k_{fbo}$.

\begin{equation}
\frac{dfbo}{dt} = fbf \times k_{fbf} + B_{depf} \times l_{depf} \times (1 - AF_{fbf}) \\
+ B_{preds} \times l_{preds} \times (1 - AF_{prey}) - B_{mac} \times l_{mac,fbo} - fbo \times k_{fbo}
\end{equation}

The degradation and aging factors are temperature-dependent according to Eq. 5 (Soetaert et al., 1996; Soetaert and Middelburg, 2009). Conceptually, these banks consist of live and dead organic matter including algae, other microbes and meio-benthos.

To allow recolonization after an extinction event (e.g. temporary anoxia), the sink terms are set to zero when the biomass of a functional group falls below 0.001 mg C m$^{-2}$ (study III). In studies I and II, a recruitment term adding 1 mg C m$^{-2}$ to each group once per year was used for the same reason.

3.3.1 PARAMETERIZATION OF THE BM MODEL

Parameter values for macrofauna were primarily based on Timmerman et al. (2012). To ensure that overall turnover rates were realistic, they were compared with yearly production over mean biomass (P/B) values for the dominating species of macrofauna measured in the Baltic Sea, and rate parameters were adjusted accordingly. In a final stage, the model was calibrated against observed biomass development in the Tvärminne site by adjusting the ingestion half-saturation constants and fine-tuning mortality rates (study I). In study III, some of the parameters were adjusted to improve model performance over the different basins (but using the same values in all basins, i.e. no basin-specific tuning was done). All parameters are shown in Table 1.
Table 1. Parameter values for the BM model as applied in study III. Values used in studies I and II are shown in parentheses in those cases where they differ from study III. SPOM: suspended particulate organic matter.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Unit</th>
<th>Limecola baltica (mac)</th>
<th>Deposit-feeders (depf)</th>
<th>Predators (preds)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$pr$</td>
<td>-</td>
<td>0.01</td>
<td>0.9</td>
<td></td>
</tr>
<tr>
<td>$Flim$</td>
<td>mg C m$^{-2}$</td>
<td>30</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>$r_b$</td>
<td>day$^{-1}$</td>
<td>0.005 (0.003)</td>
<td>0.012</td>
<td>0.012</td>
</tr>
<tr>
<td>$r_g$</td>
<td>-</td>
<td>0.2</td>
<td>0.15 (0.2)</td>
<td>0.2</td>
</tr>
<tr>
<td>$m_o$</td>
<td>day$^{-1}$</td>
<td>0.081</td>
<td>0.69</td>
<td>0.069</td>
</tr>
<tr>
<td>$K_{ox}$</td>
<td>(mg O$_2$ L$^{-1}$$^{-1}$)</td>
<td>2.5</td>
<td>1.5</td>
<td>2.5</td>
</tr>
<tr>
<td>$m_{other}$</td>
<td>day$^{-1}$</td>
<td>1×10$^{-3}$ (1×10$^{-3}$)</td>
<td>1×10$^{-3}$ (1×10$^{-3}$)</td>
<td></td>
</tr>
<tr>
<td>$wwt:C$</td>
<td>(mg C m$^{-3}$ day$^{-1}$)</td>
<td>20</td>
<td>1×10$^{-5}$</td>
<td>1×10$^{-5}$</td>
</tr>
<tr>
<td>$T_{ref}$</td>
<td>°C</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$Q_{10, ox}$</td>
<td>-</td>
<td>2.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$Q_{10}$</td>
<td>-</td>
<td>2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

3.3.2 COUPLING TO THE BALTSEM MODEL

The pelagic conditions needed to drive the BM model were simulated with the hydrodynamic-biogeochemical Baltic Sea Long-term Large-scale Eutrophication Model BALTSEM (Gustafsson, 2000, 2003; Gustafsson et al., 2017; Savchuk et al., 2012). The BALTSEM model simulates physical transport and chemical transformations of nutrients and carbon in the Baltic Sea in response to climatic conditions and nutrient inputs from rivers, point sources and atmospheric deposition. The model has been successfully applied and validated to study long-term historical eutrophication of the Baltic Sea (Gustafsson et al., 2012) as well as seasonal variations (Savchuk et al., 2012) and future scenarios (Meier et al., 2012; Murray et al., 2019). It has also been applied as a decision support tool, e.g. to calculate maximum allowable inputs of nutrients to the Baltic Sea for the riparian countries in the Baltic Sea Action Plan (HELCOM, 2013).

BALTSEM divides the sea into 13 basins with a variable vertical resolution in the water column averaging about 1 m. Sediments are represented as a single layer every depth meter. The hydrodynamic model (Gustafsson, 2000, 2003) simulates water exchange, vertical mixing and stratification and the resulting water temperature and salinity distribution. The biogeochemical
model (Gustafsson et al., 2017; Savchuk et al., 2012) describes the dynamics of dissolved forms of N, P, C, Si and O as well as particulate organic matter, including three functional groups of primary producers (diatoms, nitrogen-fixing cyanobacteria and ‘other’, consisting mostly of flagellates), one group of heterotrophs, and detritus of terrestrial and marine origin.

In study I, the two models were coupled offline, i.e. the BALTSEM model was run first and resulting time-series of organic matter sedimentation rates and bottom water concentrations of suspended phytoplankton and detritus, oxygen and temperature for a specific depth in a specific basin were then used as forcing in the benthic model. In study III, the models were coupled online by adding the BM model code into BALTSEM. This means that BM dynamics were calculated for every 1 m depth segment in all basins for each time-step in BALTSEM. However, coupling was only one way, i.e. the BM model did not affect the BALTSEM model in the current setup but worked in parallel to BALTSEM sediment dynamics.

3.4 HISTORICAL SIMULATIONS IN TWO COASTAL AREAS (STUDY I)

The aims of study I were to develop the BM model to simulate macrozoobenthic biomass development in two coastal soft-sediment areas of the Baltic Sea to: (1) quantify the effects of increasing biomass on carbon fluxes, and (2) test the hypothesis that macrozoobenthic communities are food limited in these oxic areas.

Following a period of suspected failure in recruitment, the biomass of \textit{L. balthica} increased drastically during the 1990s and reached a new, higher level in the 2000s in Tvärminne Storfjärden. This period (1993-2005) was chosen to study the effects of the increase on carbon cycling, and to test the model’s ability to reproduce transient conditions as well as conditions close to steady state in the benthos. The model was run with forcing from BALTSEM at 35 m depth in the Gulf of Finland, corresponding to the Tvärminne Storfjärden XLIV monitoring station. To validate the model, it was run with forcing from BALTSEM at 40 m depth in the Baltic Proper, corresponding to the monitoring stations 6001 and 6004 in the Askö area. All settings and parameter values were kept exactly as in the original run, except for the forcing and initial conditions, which were based on measured wet biomasses in the respective locations.

To test the sensitivity of model dynamics to parameterisations, the model was run with 25% increased and decreased values for parameters related to growth ($I_{\text{max},i}$ and $r_{b,i}$) and food-bank degradation ($k_{fbf}$ and $k_{fbo}$). Additionally, the effects of \textit{L. balthica} on the system were studied by excluding the group from model runs.
The aims of study II were to systematically analyse the effects of two major environmental drivers, nutrient loading and climate, on the biomass and community composition of benthic macrofauna and pelagic and demersal fish. We aimed to identify the most important environmental drivers, potential non-linear responses in the ecosystem, and to explore possible interactive effects between multiple drivers. We used two different models, the BM model as implemented in the Baltic Proper site and an Ecosim with Ecosim (EwE) food-web model of the central Baltic Sea (Bauer et al., 2018, 2019). The two models complement each other in terms of spatial and temporal scales and level of abstraction. The EwE model focuses on the ecosystem scale and describes food web interactions in both benthic and pelagic compartments of the central Baltic Sea, while the BM model focuses on local macrozoobenthos in the area and uses a physiologically more detailed, mechanistic description of the system.

The EwE model of the offshore central Baltic Sea (including the Baltic Proper and the Bornholm Basin) represents the ecosystem as 21 living functional groups and one detritus group encompassing all trophic levels from phytoplankton to grey seals, including the four commercially most important fish species (cod, flounder, herring and sprat). Macrozoobenthos groups in EwE are S. entomon, two bivalve groups (L. balthica and Mytilus sp.), and ‘other macrobenthos’, consisting of oligochoaetes, polychaetes (e.g. Bylgides sarsi), and amphipods. The effects of environmental drivers in EwE are implemented as a time series of multipliers applied on certain model parameters related to primary production, egg production or consumption rates (Table 2). These forcing time series were derived from time series of environmental drivers in an earlier model version (Niiranen et al., 2013; Tomczak et al., 2012). Representing environmental forcing as linear multipliers on certain rates is a major difference to the more mechanistic BM, where forcing is applied as time series of absolute values of a given environmental variable.

Both models were run under systematically varied forcing representing primary productivity, oxygen conditions and water temperature in all possible combinations, over a range representative of expected changes during the 21st century (Table 2). Subsequently, we calculated the biomass change of key functional groups compared to the baseline run representing the early 2000s. In EwE simulations were run for 400 yearly time steps under constant forcing. In BM forcing was repeated as an identical seasonal cycle every year for 100 years, using daily time steps.
Materials and methods

Table 2. Studied environmental drivers, corresponding forcing and groups directly affected by the forcing in the two models used in study II. Range means the tested range of forcing compared to baseline conditions in the early 2000s.

<table>
<thead>
<tr>
<th>Environmental driver</th>
<th>EwE model Range</th>
<th>Directly affected groups (forcing type)</th>
<th>BM model Range</th>
<th>Directly affected groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Productivity</td>
<td>Maximum P/B ratio of phytoplankton; P/B</td>
<td>0.5 - 2 Phytoplankton (primary production)</td>
<td>0.5 - 2 Fresh food bank</td>
<td></td>
</tr>
<tr>
<td>Water temperature</td>
<td>August surface temperature; TSurf</td>
<td>0.5 - 2 Herring, sprat (egg production)</td>
<td>0.5 - 2 L. balthica, deposit-feeders, predators</td>
<td></td>
</tr>
<tr>
<td>Oxygen conditions</td>
<td>Cod reproductive volume; CodRV</td>
<td>0 - 10 Cod (egg production)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Extent of oxic areas; OxAr</td>
<td>0.75 - 1.5 Cod, S. entomon, Mytilus sp., L. balthica, Other macrobenthos, Mysids (consumption)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1The volume of water with salinity >11 psu and oxygen concentration >2 mL L⁻¹

3.6 BENTHIC RESPONSES TO NUTRIENT LOAD AND CLIMATE SCENARIOS (STUDY III)

The main aims of study III were to simulate the combined effects of changing nutrient loads and climate on biomass and metabolic carbon processing of benthic macrofauna in the Baltic Sea in the near past and during the 21st century. In contrast to the systematic approach in study II, here we used combined scenarios of nutrient loading and climate change (Table 3). Another major difference to studies I and II is that the area of model implementation was extended from local coastal sites to the four largest basins of the Baltic Sea (Fig. 3).

As a baseline, the model was run 1961-2012, forced with historical nutrient loads and actual weather conditions as described in Gustafsson et al. (2012, 2017). To test model performance, the results of this baseline simulation were compared to observations using a cost function $CF = \frac{|M-D|}{SD}$ where $M$ is model mean, $D$ is mean of observations and $SD$ is the standard deviation of observations (Eilola et al., 2011).

All scenarios start with historical nutrient loads for 1961-2012. After that a constant seasonal cycle of nutrient inputs was used 2013-2098, representing three different nutrient load scenarios. The ‘best case’ scenario follows the maximum allowable inputs according to the Baltic Sea Action Plan (BSAP).
The ‘worst case’ was calculated as the monthly mean nutrient loads of 1980-1990 (HIGH), i.e. the highest recorded historical loads (Gustafsson et al., 2012). The most recent measured loads available, i.e. the mean loads of 2012-2014 were used as a reference load scenario (REF).

Atmospheric and river runoff model forcing for the climate change scenarios were obtained from a dynamic downscaling of four different global climate change simulations global climate simulations for the Baltic Sea (Meier et al., 2014 and references therein). Additionally, to be able to separate the effects of climate change and nutrient loads, the model was run with 11 variations of ‘current climate’, representing non-climate change statistical forcing data (described in detail in study III).

The nutrient loads and climate scenarios were combined independently, giving 12 combinations of changing nutrient loads and climate and 33 combinations of changing nutrient loads with current climate.

Table 3. Summary of the nutrient load and climate simulations used in study III.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Time frame</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nutrient loads</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline</td>
<td>Historical nutrient load compilation</td>
<td>1961-2012</td>
</tr>
<tr>
<td>BSAP</td>
<td>Nutrient loads following the Baltic Sea Action Plan</td>
<td>2013-2098</td>
</tr>
<tr>
<td>REF</td>
<td>Monthly mean loads 2012-2014</td>
<td>2013-2098</td>
</tr>
<tr>
<td>HIGH</td>
<td>Monthly mean loads 1980-1990</td>
<td>2013-2098</td>
</tr>
<tr>
<td>Climate</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline</td>
<td>Actual weather, river runoff and boundary conditions</td>
<td>1961-2012</td>
</tr>
<tr>
<td>RE_A1B_1</td>
<td>RCAO-ECHAM5 realisation 1, emission scenario A1B</td>
<td>1961-2098</td>
</tr>
<tr>
<td>RE_A1B_3</td>
<td>RCAO-ECHAM5 realisation 3, emission scenario A1B</td>
<td>1961-2098</td>
</tr>
<tr>
<td>RH_A1B_1</td>
<td>RCAO-HadCM3 realisation 1, emission scenario A1B</td>
<td>1961-2098</td>
</tr>
<tr>
<td>RE_A2_1</td>
<td>RCAO-ECHAM5, realisation 1, emission scenario A2</td>
<td>1961-2098</td>
</tr>
<tr>
<td>Current climate</td>
<td>Statistical forcing</td>
<td>1961-2098</td>
</tr>
</tbody>
</table>
4 RESULTS AND DISCUSSION

4.1 HISTORICAL SIMULATIONS IN TWO COASTAL AREAS AND EVIDENCE OF FOOD LIMITATION (STUDY I)

In study I, the conditions for the benthos as simulated by BALTSEM 1994-2005 were similar at the two studied sites (Gulf of Finland 35 m, GoF and Baltic Proper 40 m, BP) in terms of temperature range, concentrations of oxygen (normoxic at both sites, data not shown) and concentrations of phytoplankton, which rarely reached the threshold for suspension-feeding by *L. balthica* (Fig. 5). The organic carbon (POC) input to the sediment was higher in GoF (41±5.4 g C m⁻² y⁻¹) than in BP (26±4.1 g C m⁻² y⁻¹). None of the forcing variables showed clear trends over time.

![Figure 5](image_url)  
*Figure 5*  Forcing time-series for the benthic model runs simulated with BALTSEM 1993-2005. The variables are temperature, phytoplankton (diatoms + flagellates) concentration and suspended organic matter (phytoplankton + detritus) concentration in the bottom water layer as well as organic matter (POC) flux to the bottom. The dotted line marks the switching threshold for suspension-feeding in *L. balthica*. 
The development of the BM state variables is shown in Fig. 6 together with a comparison to observations for the macrofauna. Simulated functional group biomasses were mostly within one standard deviation of observed biomasses, except for an overestimation of predators in GoF and an underestimation of deposit-feeders in BP.

Figure 6  Simulated time-development of sediment food banks and functional groups of macrofauna at two locations in 1993-2005. Means ±1 SD of measured biomass from corresponding monitoring station (left: XLIV in the Gulf of Finland; right: 6001 and 6004 in the Baltic Proper) are shown for the fauna. Note different scale on y-axes.

The biomass of *L. balthica* increased in the 1990ies and reached a new level in the 2000s at both sites, but the increase was steeper and the final biomass higher in GoF than in BP. The higher biomass of *L. balthica* in the 2000s in GoF compared to BP reflected the higher POC input, supporting the hypothesis of food-limitation. Further evidence for food-limitation was that the older food bank was depleted each year after the initial increase in biomass. Considering that simulated sedimentation rates are near the high end of measured values (Leipe et al., 2011; Leppänen, 1988; Tamelander et al.,
Results and discussion

2017), while parameters for macrofauna turnover (maximum uptake, respiration and mortality rates) were set rather low compared to similar models, it seems highly probable that the simulated food-limitation reflects the real-world situation. However, in the beginning of the period the biomass was limited by something other than food supply. This limitation was not explained by the model, but is probably related to recruitment as small individuals were absent from the population (L. Kauppi, pers. comm.).

Inter- and intra-annual variations in simulated POC flux to the sediment were reflected in the freshly deposited detritus food banks and surface deposit-feeder biomass, showing that also this group was limited primarily by food availability in the model. However, this is dependent on the assumption that this group can only eat very fresh detritus. The biomass fluctuations were only partly in agreement with observations and the biomass level was generally underestimated in the model validation site (BP), indicating that this assumption was not correctly formulated. One reason might be the inclusion of *Pontoporeia femorata* in the group. *P. femorata* is known to feed on older sediment, especially when combined with surface-feeding species, and would probably be best represented as a subsurface deposit-feeder (Hill and Elmgren, 1987; Karlson et al., 2011). In addition, the feeding habits of *Marenzelleria* spp. are unclear. *Marenzelleria arctica*, probably the only species of the genus occurring at the study sites (Blank et al., 2008; Kauppi et al., 2018), is generally classified as a surface deposit-feeder, but the isotopic niche differs from that of *L. balthica*, *M. affinis* and *P. femorata* (Karlson et al., 2015). However, it is not known if this is due to different food sources or different fractionation of isotopes in the body. In study III when the model was extended to a larger area, the decay rate of the fresh food bank had to be reduced, increasing the food availability to the deposit-feeder group, to avoid their extinction in more oligotrophic conditions.

In addition to food limitation, predation was an important structuring factor of the deposit-feeder group, as seen in the group’s sensitivity to changes in predator parameter values (supplement S2 of study I). In the beginning of the simulation period in GoF, predator-prey-cycles were strong due to the lack of stabilisation by *L. balthica* as an alternative prey for predators (Fig. 6), as also seen in the sensitivity analyses when *L. balthica* biomass was reduced or excluded.

4.2 TEMPERATURE, FOOD AND HYPOXIA AS DRIVERS OF COMMUNITY BIOMASS AND STRUCTURE (STUDY II)

The systematic sensitivity analyses of the EwE and BM models showed the same main results, indicating that increased primary productivity leads to biomass increase in all parts of the system, but is counteracted by expanding hypoxia. Effects of temperature were complex, but generally small compared
to the other drivers. The models showed several interactive effects of the studied drivers, both synergistic and antagonistic. In many cases these effects were indirect and modified by food web interactions. Here, I restrict the discussion to the main results relevant to the benthos. For further results and discussion, the reader is referred to study II including supplements.

Productivity was the strongest driver of community biomass, having a positive effect on most groups. In EwE, all groups but herring showed a clear positive response to increases in phytoplankton production (P/B, Fig. 7). In BM, two out of three groups (L. balthica and predators) showed a positive response to increased sedimentation of organic matter (Sed, Figs. 8, 9). The other two groups (herring in EwE and deposit-feeders in BM) showed weak responses to productivity. Thus, the food-limitation found in study I turned out to be the main driver of both benthic and pelagic community biomass in this study as well.

The effects of oxygen conditions, measured as extent of oxic areas (EwE), cod reproductive volume (EwE) or oxygen concentration (BM) forcing, were mostly nonlinear. A strong negative effect of low oxygen concentrations (O2Conc) on all benthic groups was evident in BM, but biomasses saturated quickly as concentrations increased (Fig. 10). The form of the response was group-specific with L. balthica being least sensitive to hypoxia. Reduced O2Conc affected predators both directly through mortality and indirectly through reduction in prey biomass, leading to a higher sensitivity than would be predicted from hypoxia mortality rates alone (see Table 1).

In EwE, temperature (TSurf) directly affected only pelagic fish (Table 2), but it also had an indirect effect on benthos though a trophic cascade. TSurf had a positive effect on juvenile sprat which feeds on zooplankton, thereby freeing phytoplankton from predation pressure, and increased phytoplankton increased L. balthica biomass through increased detritus production. In BM, where temperature effects were included on most processes, increased bottom water temperature (TBot) counteracted the positive effects of sedimentation on L. balthica and predators as seen in the decreased slope of biomass response to sedimentation (Fig. 8).

Despite the differences in model formulation, both models showed relatively small overall effects of temperature in comparison to the other drivers. It might be that some important temperature effects are not captured by either model, e.g. on species distributions, phenology or body sizes (Birchenough et al., 2015; Poloczanska et al., 2013; Sommer et al., 2012; Thomas and Bacher, 2018). However, it has also been argued that estuarine areas with strong seasonality and low diversity like the Baltic Sea should harbour organisms with large tolerance ranges to environmental drivers such as temperature (Jernelöv and Rosenberg, 1976). Some of the species included in the models (M. affinis, Mysis relicta, S. entomon) are glacial relics that are considered to be cold-adapted (Segerstråle, 1962), but there is surprisingly little data supporting this. For example, a stable population of M. affinis has been found in a shallow site with temperatures around 20 °C in summer. There
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the growth rate was higher compared to deep areas and sexual maturity was reached within a year in contrast to the more common two years (Segerstråle, 1978b). For S. entomon, osmoregulation experiments and frequent observations at 15-20 °C indicate that it can survive much higher temperatures than the range studied here (Borecka et al., 2016; Haahtela, 1990).

Figure 7  Change in biomass of cod (A), flounder (B), herring (C), sprat (D), Limecola balthica (E), 'other macrobenthos' (F) and Saduria entomon (G) as a function of relative changes in P/B and OxAr, where 1 denotes baseline forcing. Biomass change is relative to baseline equilibrium value. Error bars show the variability in biomass change due to varying TSurf and CodRV. Horizontal line indicates no change. Results from simulations with CodRV = 0, resulting in 0 cod biomass, are excluded from the figure. Forcing abbreviations are explained in Table 2.

Figure 8  Change in biomass of deposit-feeders (A), Limecola balthica (B) and predators (C) as a function of relative changes in Sed and TBot, where 1 denotes baseline forcing. Biomass change is relative to baseline equilibrium value. Error bars show the variability in biomass change due to varying O2Conc. Horizontal line indicates no change. Forcing abbreviations are explained in Table 2.
Figure 9  Change in biomass of deposit-feeders (A), *Limecola balthica* (B) and predators (C) as a function of relative changes in Sed and O2Conc, where 1 denotes baseline forcing. Biomass change is relative to baseline equilibrium value. Error bars show the variability in biomass change due to varying TBot. Horizontal line indicates no change. Forcing abbreviations are explained in Table 2.

Figure 10  Change in biomass of deposit-feeders (A), *Limecola balthica* (B) and predators (C) as a function of relative changes in O2Conc and TBot, where 1 denotes baseline forcing. Biomass change is relative to baseline equilibrium value. Error bars show the variability in biomass change due to varying Sed. Horizontal line indicates no change. Forcing abbreviations are explained in Table 2.

One example of complex interactions between direct and indirect effects of all forcing types is the response of deposit-feeders in BM. Low food availability (i.e., low Sed), in combination with high temperature and/or low oxygen concentration led to severely reduced biomass or even extinction (Figs. 8, 9). This means that the ability to survive in increased temperatures and/or reduced oxygen concentrations was greatly reduced by food shortage.

However, at forcing combinations outside this ‘lethal space’, the response to Sed and O2Conc was slightly negative. These counterintuitive results can be explained by indirect effects through the food web. Sedimentation had a positive effect on the food availability for *L. balthica*, which represents the majority of benthic biomass. Increased biomass of *L. balthica* was one of the main drivers of predators, which in turn asserted an increased predation pressure on deposit-feeders. This is a phenomenon known as ‘apparent competition’, where two prey biomasses are negatively related due to a shared predator (Holt, 1977; Holt and Lawton, 1994). Looking back at study I, the
apparent competition can be seen also there as negative correlation between 
*L. balthica* and deposit-feeder biomass (Fig. 6, supplement S2 to study I). 
Tight predator-prey coupling between *S. entomon* and the deposit-feeder *M. affinis* has been recorded in the northern Baltic Sea where *L. balthica* was 
absent (Englund et al., 2008; Englund and Leonardsson, 2008; Sparrevik and 
Leonardsson, 1999). In an area with few amphipods present, *S. entomon* 
preyed actively upon *L. balthica* (Ejdung and Bonsdorff, 1992), but to our 
knowledge there are no studies that included both prey types that could have 
revealed apparent competition in the lab or field.

A comparison of these results to EwE revealed that the choice of system 
boundaries is important for model outcome. In EwE, the benthic predator *S. 
entomon* did not show a similar strong response to increased productivity as 
in BM. This was at least partly due to a stabilizing effect of predation by cod. 
Cod strongly benefited from increased primary productivity through increased 
availability of one of its main prey, sprat. Thus, under high productivity cod 
caused high predation mortality on *S. entomon*, counteracting the positive 
effect of increased prey availability for *S. entomon*. In BM, predation on 
benthic predators is included as a closure term, and is therefore less dynamic 
than in EwE that explicitly models the dynamics of the top predator (cod) 
feeding on both predatory benthos and pelagic prey. Thus, EwE showed an 
apparent competition effect between sprat and *S. entomon*, mediated by cod 
predation, which was missing from BM.

Both models predicted a change in benthic community composition 
towards a stronger dominance of *L. balthica* with increased productivity. An 
uneven community composition could decrease the functional diversity 
contributing to efficient nutrient recycling as well as decrease the resilience 
of the benthic community to further environmental perturbations (Villnäs et al., 
2013). Changes in the community composition of macrofauna and fish could 
also have large effects on the magnitude of fish predation on benthos and 
therefore on the biomass flows from the benthic to the pelagic food web, with 
important consequences on marine ecosystem functioning (Griffiths et al., 
2017).

### 4.3 EXTENSION OF BM TO THE BALTIC SEA SCALE 
(STUDY III)

The zoobenthic biomass data analysed in study III (Fig. 3) shows that the soft-
sediment systems in the four basins of model implementation are dominated 
by a limited number of species and functional groups, just like the two sites in 
study I. *L. balthica* made up most of the macrofaunal biomass in the Baltic 
Proper and Gulf of Finland, and about half of the biomass in the Bothnian Sea, 
but was almost absent from the Bothnian Bay (Fig. 11).
According to cost function values, the simulated distribution of total macrofaunal biomass was in good agreement with field data, except at 30-70 m in the Gulf of Finland, where *L. balthica* biomass was overestimated (Figs. 12, 13A, D). The simulated biomass of *L. balthica* seems representative for the western Gulf of Finland, for which the model was originally developed (study I), but the observed biomasses decreased towards the east of the basin for unknown reasons.

The model-data agreement for depth profiles of deposit-feeders and predators were in the good range in all basins according to the cost function (Fig. 13B, C), but it should be noted that the large spread of observational data allows for substantial differences in the means. For example, the higher mean biomasses of both groups observed in the Bothnian Sea compared to adjacent basins were not present in the model. This might be due to an underestimation of productivity and/or sedimentation in the basin by BALTSEM (Savchuk et al., 2012). It is also possible that there is a difference in food quality due to different phytoplankton community composition in the different basins, which is not captured by the current model formulations.

Overall, the model’s skill in reproducing observed total macrofaunal biomass was satisfactory especially in areas dominated by *L. balthica*, although the groups with smaller biomass were not as well captured. We believe the model performance is adequate for the purposes it was used for, but recognize a need for refinement to improve performance in the future, especially if the model would be used for more diverse areas along the coasts and in the SW Baltic Sea.
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Figure 12  Comparison of modelled (black bars) and observed (grey bars) biomass densities of total macrofauna in the four basins of model implementation in study III: Baltic Proper (A), Gulf of Finland (B), Bothnian Sea (C) and Bothnian Bay (D). Bars show means for the depth stratum over the period 1990-2012, error bars show ±SD. Estimates presented by Carman & Cederwall (2001) are also shown for comparison (white bars), but note that the time period (ca 1970-2000) and basin delineations are different in these data.

![Figure 12](image)

Figure 13  Vertical profiles of cost function values for biomass of Limecola balthica (A), deposit-feeders (B), predators (C) and total macrofauna (D) in the four basins on model implementation: Baltic Proper (BP), Gulf of Finland (GoF), Bothnian Sea (BS) and Bothnian Bay (BB). Cost function (CF) values indicate model-data agreement (Eilola et al. 2011): good 0≤CF<1, reasonable 1≤CF<2, poor CF≥2.

![Figure 13](image)
4.4 BIOMASS DEVELOPMENT IN CLIMATE AND NUTRIENT LOAD SCENARIOS (STUDY III)

4.4.1 BASELINE SIMULATION 1970-2012

In the baseline simulation with historical nutrient loads and climate, macrofaunal biomass in the model area increased 52% from 478 to 727 kilotonnes C between 1970 and 2012, with a peak of 956 kton C in 1995 (Fig. 14A), following a similar pattern in simulated POC input to the sediments (Fig. 14D). The peak biomass also coincided with the minimum extent of hypoxic areas (Fig. 14B). The increasing biomass trend was seen in all basins except the Bothnian Bay, where biomass remained low compared to the other basins and no consistent trend was found. Sea surface temperature increased between 0.8°C and 1.4°C in the different basins in 1970-2012 (Fig. 14C). Modelled primary production increased 91% and POC input to the sediments 31% during the same period, indicating that pelagic recycling intensified and the proportion of primary production exported to the seafloor decreased (Fig. 14B, D).

Figure 14  Simulated macrofaunal biomass (A) and forces driving biomass development: annual primary production (B, primary y-axis), annual mean extent of hypoxic areas (<2ml O₂ l⁻¹; B, secondary y-axis), annual mean sea surface temperature (SST) (C), and annual POC input to the sediment (D). All graphs show data from the baseline simulation in the model area 1970-2012.
4.4.2 SCENARIOS

The simulated development of forces driving macrofaunal biomass in three nutrient load scenarios with and without climate change are shown in Fig. 15 and the resulting development of macrofaunal biomass in Fig. 16.

In the scenarios with nutrient load reductions according to the Baltic Sea Action Plan (BSAP) and recent loads (REF), primary production and POC input to the sediments decreased over the 21st century (Fig. 15A-D). Despite improved oxygen conditions at the seafloor (Fig. 15E, F), the total macrofaunal biomass also decreased in these two load scenarios (Fig. 16). Ensemble mean change in biomass from the present (mean of 1990-2012) to the end of the century (mean of 2096-2098) was larger with climate change (BSAP -84%, REF -66%) than without (BSAP -69%, REF -44%).

Figure 15  Simulated annual mean primary production (A, B), POC input to the sediments (C, D), and extent of hypoxic areas (<2ml O₂ l⁻¹; E, F) at present (1990-2012) and under three nutrient load scenarios at mid-century (2033-2055) and end of the century (2076-2098) in the model area. Results are shown as ensemble means ±SD of 4 climate change simulations (left column) and of 11 current climate simulations (right column).
Even though recovery trajectories from eutrophication do not necessarily mirror the past changes (Duarte, 2009), the large decrease in biomass with reduced loads and improved oxygenation of the seafloor implies that during past eutrophication, the biomass gained in oxic areas far exceeded that lost due to hypoxia.

In the HIGH load scenario under climate change, primary production increased 77% between present and the end of the century (Fig 15A), but POC input to the sediments increased only until mid-century (+18%), and then decreased giving almost no net change by the end of the century (Fig. 15C). Biomasses also increased until mid-century (+25%), but then decreased, giving an overall decrease of -12% by the end of the century (Fig. 16A). In the HIGH scenario with current climate (Fig. 16B), primary production, POC input and biomasses continued to increase towards the end of the century (+33% and +45%, respectively).

In contrast to results from study II, climate change turned out to be a major driver of macrofaunal biomass. The larger decrease in biomass in climate change scenarios compared to current climate scenarios can be explained by the combined effects of increased metabolism and reduced input of organic matter as food, due to more efficient pelagic recycling of organic matter with increased water temperatures. These effects can be seen both in the scenarios and in the historical period. Thus, this study showed that warming may reduce macrofaunal biomass considerably, but the main mechanism is the intensification of pelagic cycling indirectly affecting the benthos through reduced POC export to the sediments, a mechanism that was not included in study II.

These results are in line with observations of a shift in phytoplankton bloom maxima from spring to summer since the 1970s, indicating a larger proportion of cyanobacteria, which do not sink as quickly as the diatoms that dominate the spring bloom (Kahru et al., 2016; Suikkanen et al., 2007). Both observations and experimental work suggest that increasing temperatures...
increase zooplankton growth rates, metabolic demands and grazing rates on phytoplankton, which leads to decreased sedimentation (Tamelaender et al., 2017 and references therein). Also Maar and Hansen (2011) found negative effects of warming on sedimentation and deposit-feeder biomass in a simulation study of the North Sea-Baltic Sea transition zone.

4.5 CARBON FLOWS IN THE BENTHIC FOOD-WEBS (STUDIES I & III)

To quantify the effects of macrofauna on benthic carbon flows and mineralisation, selected carbon fluxes and stocks were calculated for different time periods in studies I and III. In study I, the drastic increase in biomass between 1995 and 2005 in the Gulf of Finland site changed the pathways of carbon processing (Fig. 17). In the low biomass state of 1995, 22% of simulated POC input to the sediment was processed by the macrofauna through ingestion, while in 2005 the corresponding fraction was 80%. 10% of POC input was mineralized through macrofaunal respiration in 1995 and 39% in 2005. In the Baltic Proper site, macrofaunal biomass increased from 4.7 to 8.4 g C m⁻² and mineralisation of POC input from 27% to 35% between 1995 and 2005.

Figure 17  Modelled carbon flows in the benthic food-web in the Gulf of Finland site in two years with contrasting community composition due to an increase in biomass of Limecola balthica (study I). Annual flows of organic carbon (POC) input to the sediment, ingested POC (solid arrows) and respired CO₂ (dashed arrows) and mean stocks (grey boxes) are given in g C m⁻², arrow widths are proportional to flow size. Redrawn from study I.
Up-scaled to the major part of the Baltic Sea in study III, a mean macrofaunal stock of 2.7 g C m$^{-2}$ ingested 11 g C m$^{-2}$ or 42% of POC input and mineralized 5 g C m$^{-2}$ or 19% in the baseline simulation 1990-2012 (Fig. 18A). The simulated mineralisation of POC input by macrofaunal respiration is in the low end of earlier estimates from the Baltic Sea of 22-40% (Ankar, 1977; Elmgren, 1984; Kuparinen et al., 1984), probably due to the low respiration rate assigned to the major biomass component *L. balthica*. Globally, estimates of macrofaunal respiration scatter considerably from negligible up to 50-70% of total benthic mineralisation (Glud, 2008; Wenzhofer et al., 2002) with a median of 15-20% in estuaries estimated by Herman et al. (1999).

The current BM model only considers a sub-set of benthic carbon processing. The model focuses on macrofauna and its sediment food sources, while the full benthic and pelagic carbon cycling is resolved in parallel in the BALTSEM model. A two-way coupling of the biogeochemical processes in BALTSEM and BM including bacterial and meiofaunal mineralisation as well as mixing and burial processes would allow more detailed calculations of system-level carbon budgets, but is left for future model development. Keeping these limitations in mind, the model results give a first estimate of the role of macrofauna in carbon cycling processes today and in the future.

The scenario simulations indicate that with increasing nutrient loads and POC input, the role of macrofaunal metabolism in carbon processing would not change substantially (mineralizing 19-20% of POC input, Fig. 18D, E), but with decreasing nutrient loads according to BSAP only about a tenth of POC input would be mineralized by macrofaunal respiration (Fig 18B, C). Thus, even though POC input seems to be the main driver of macrofaunal biomass and metabolic carbon processing, the relationships are not linear. Additionally, although warming increases metabolism, the overall effect of climate change was reduced metabolic carbon processing due to reduced biomass.

In conclusion, the two studies indicate that the role of macrofaunal respiration in organic matter mineralisation can be significant, especially in productive areas where biomass is primarily limited by food availability (as exemplified in the two coastal areas in 2005, Fig. 17). However, in a warmer and more oligotrophic future, the role of macrofaunal respiration in benthic-pelagic coupling of the carbon cycle will probably decrease.
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**Figure 18** Input of organic carbon (POC) to the sediment and fluxes of ingested POC (solid arrows) and respired CO2 (dashed arrows) by the benthic macrofauna at present (A) and at the end of the century under two nutrient load scenarios: BSAP (B, C) and HIGH (D, E) combined with climate change (left) and current climate (right). Stocks (g C m\(^{-2}\)) and fluxes (g C m\(^{-2}\) year\(^{-1}\)) are ensemble means in the model area of study III, arrow widths are proportional to flux size.
In study IV, the focus was extended from the direct effects of benthic fauna on carbon processing in the Baltic Sea to the direct and indirect effects of fauna on carbon and nutrient fluxes in coastal areas in general. The study summarizes existing approaches of different complexity for modelling processes related to benthic fauna that affect benthic carbon and nutrient fluxes (Table 4). Figs. 1 and 2 (see introduction) illustrate the main processes discussed. The types of models discussed include models of biomass and metabolism, reactive-transport models of sediment biogeochemistry, and ecosystem models.

### Table 4. Summary of the main approaches to model benthic faunal processes affecting carbon and nutrient fluxes discussed in study IV.

<table>
<thead>
<tr>
<th>Type of effects</th>
<th>Processes</th>
<th>Major process formulations</th>
<th>Example reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effects of biomass production and metabolism</td>
<td>Uptake/filtration, egestion/biodeposition, nutrient excretion, respiration, biomass production, nutrient retention in biomass</td>
<td>Faunal metabolism implicit part of organic matter decay rate</td>
<td>Soetaert &amp; Middleburg, 2009</td>
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<tr>
<td></td>
<td></td>
<td>Biomass/physiological model of fauna</td>
<td>Fulton et al., 2004a</td>
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<tr>
<td></td>
<td></td>
<td>Simple biomass formulation, derived fluxes</td>
<td>Ebenhöh et al., 1995</td>
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<td></td>
<td></td>
<td>Physiological detail, functional groups, explicit fluxes</td>
<td>Spillman et al., 2008</td>
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<td></td>
<td></td>
<td>Physiological detail, structured population, explicit fluxes</td>
<td>Maar et al., 2009</td>
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<td></td>
<td>Physiological detail, structured individuals, explicit fluxes</td>
<td></td>
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<tr>
<td>Physical effects</td>
<td>Bioturbation</td>
<td>Biodiffusion ($D_b$) constant over time</td>
<td>Rooze et al., 2016</td>
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<td></td>
<td></td>
<td>Decreasing with depth</td>
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<td></td>
<td></td>
<td>Biodiffusion ($D_b$) dynamic function of:</td>
<td>Wang et al., 2003</td>
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<td></td>
<td></td>
<td>Proxies for faunal activity: oxygen concentration, POC flux</td>
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<td>Biomass of fauna</td>
<td>Ebenhöh et al., 1995</td>
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<tr>
<td></td>
<td></td>
<td>Uptake rate of carbon by fauna</td>
<td>Blackford, 1997</td>
</tr>
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<td></td>
<td>Bioirrigation, expressed by</td>
<td>A series of evenly distributed and closely packed hollow cylinders of equal length</td>
<td>Aller, 1982</td>
</tr>
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<td></td>
<td></td>
<td>The exchange rate between bottom water and porewater at a certain depth ($\alpha_a$)</td>
<td>Boudreau, 1984</td>
</tr>
<tr>
<td></td>
<td>Bioresuspension</td>
<td>Related to abundance of fauna</td>
<td>Wood and Widdows, 2002</td>
</tr>
<tr>
<td></td>
<td>Related to metabolic rate of fauna</td>
<td>Cozzoli et al., 2019</td>
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</table>
Benthic animals process organic matter by ingesting particulate organic matter (POM) and transforming it to inorganic components that are respired and excreted (Fig. 2). Organic matter is also incorporated in the biomass, transferred in the food web through predation and reproduction, and released back to the inanimate POM pool by egestion of faeces and mortality. There is a multitude of models of different complexity simulating these processes. The simplest models describe biomass of benthic fauna as a function of growth rate, mortality rate and environmental constraints, similar to conventional zooplankton formulations in pelagic biogeochemical models (e.g. Fulton et al., 2004a; Kim and Montagna, 2009; Murray and Parslow, 1999).

While these kinds of models may include carbon and nutrient fluxes out of the organisms (cf. Fig. 2) as derived variables, a more detailed and mechanistic approach is to model the metabolic fluxes explicitly. These models range in complexity from functional group-type models, such as the BM model presented in thesis and the ERSEM model (Butenschön et al., 2016; Ebenhöh et al., 1995), to structured population models that often focus on size classes or life stages of a single population (e.g. Cranford et al., 2007; Grant et al., 2008; Spillman et al., 2008), to models focussing on energy dynamics on the sub-individual level, such as Dynamic Energy Budget models (e.g. Maar et al., 2009; Saraiva et al., 2017).

In models of sediment biogeochemistry, the important role of fauna as bioturbators has long been recognized (Aller, 1980; Boudreau, 1984). In reactive-transport models for simulating distributions of solutes and solids over time and depth in sediments, the effects of fauna are commonly implemented as a biodiffusion coefficient that enhances the rate of molecular diffusion (Reed et al., 2011; Rooze et al., 2016; Wheatcroft et al., 1990). Similarly, the effects of bioirrigation, i.e. the increased exchange of water between the sediment surface and a certain depth due to flushing of animal burrows, is generally related to a bioirrigation coefficient (Boudreau, 1984; Emerson et al., 1984; Norkko et al., 2012). As the animals performing these activities are rarely explicitly included in these models, the effects can be expressed as function of different proxies for the abundance and activity of fauna (Boudreau, 1998; Reed et al., 2011; Wang et al., 2003, see Table 4). However, in coastal areas where the fauna is highly dynamic over time, we see a need to include the dynamics of faunal biomass and activities explicitly in order to properly constrain their effects on biogeochemical fluxes.

Additionally, the effects of faunal metabolism on organic matter degradation in sediments are generally ignored or implicitly included in a first-order decay rate (e.g. Soetaert et al., 2000; Soetaert and Middelburg, 2009). As indicated by the results of this thesis as well as several other studies, there are cases where faunal metabolism has a substantial effect on degradation of carbon (Elmgren, 1984; Hansen and Bendtsen, 2013; Herman et al., 1999) and nitrogen (Kristensen, 1984; Magni et al., 2000; Prins and Smaal, 1994), which has led to recent calls for inclusion of these processes in mechanistic models (Middelburg, 2018; Snelgrove et al., 2018).
Ecosystem models are ideal tools for combining and scaling up the different effects of benthic fauna on benthic and pelagic biogeochemical cycles. These models can also be used to study the effects of environmental change on the joint dynamics of biological, chemical and physical processes in an ecosystem. There is a growing number of model studies coupling benthic fauna and biogeochemistry, although so far, the primary focus has been on coupling bivalve models to pelagic processes, while the coupling of benthic biogeochemistry to biology is less mature. The coupled bivalve models have been used to explore the often substantial effects of grazing, excretion and biodeposition by suspension feeding bivalves on phytoplankton production and nutrient budgets in coastal areas (Cerco and Noel, 2007; Maar et al., 2009; Mussap and Zavatarelli, 2017; Rasmussen et al., 2009; Saraiva et al., 2017; Triantafyllou et al., 2000).

Many ecosystem models simplify the sediments to a reactive boundary layer, but there are also some models coupling benthic biogeochemistry to a dynamic description of benthic fauna. For example, the ERSEM model links the biodiffusion coefficient to the biomass of functional groups (Ebenhöh et al., 1995) or to their uptake rate as an indicator of activity (Blackford, 1997; Butenschön et al., 2016). The former approach has been adopted by a range of other ecosystem models (Audzijonyte et al., 2017; Fulton et al., 2004b, 2004a; Sohma et al., 2001, 2004, 2008, 2018; Vichi, 2002), but may not be detailed enough to account for the great variability in biogenic reworking rates measured between coastal areas (Bernard et al., 2019; Boudreau, 1994; Middelburg et al., 1997; Tromp et al., 1995), and even between replicates at the same site (Morys et al., 2016).

Despite decades of bioturbation research, there is still a lack of mechanistic understanding of all the complex processes that determine the presence and activities of bioturbating organisms in natural settings, and of the diverse effects of bioturbation on physical, chemical and biological processes in the sediment, especially in heterogeneous coastal areas (but see Bernard et al., 2019). Thus, major challenges remain in integrating models of benthic fauna and their effects on biogeochemical fluxes. These are related both to the technical difficulties of combining processes working on diverse spatial and temporal scales, and to a limited understanding of the diverse mechanisms that determine coupled benthic-pelagic processes in dynamic coastal systems.

To overcome this difficulty, we propose that future model development should concentrate on well-studied coastal systems where process understanding and data availability are good. The Baltic Sea is an obvious candidate (see introduction). Additionally, increased interdisciplinary collaboration and understanding between e.g. benthic ecologists and biogeochemical modellers is a prerequisite for planning experiments and monitoring that support modelling efforts and vice versa.

In conclusion, although numerical models can cover a large number of processes in a system, a full mechanistic description of the ecosystem dynamics will never be possible; therefore, it is important to clearly delineate
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the scope of the model with its purpose in terms of scales and complexity. Major challenges and research priorities identified in study IV are (1) to couple the dynamics of zoobenthic biomass and metabolism to sediment reactive-transport in models, (2) to test and validate model formulations against real-world data to better incorporate the context-dependency of processes in heterogeneous coastal areas, and (3) to capture the role of stochastic events.
In this thesis a new tool for simulating macrozoobenthic biomass and metabolism in response to organic matter input and environmental conditions (temperature, oxygen concentrations) was developed. Despite its apparent simplicity, the model works fairly well on the community level over a range of soft-sediment areas differing in environmental conditions in the Baltic Sea.

The model was used to explore the main drivers of macrofaunal biomass and community composition in the Baltic Sea. POC flux to the bottom as a food source was identified as a main driver of macrozoobenthic community biomass (studies I, II & III), adhering to long-standing theory (Dayton and Oliver, 1977; Pearson and Rosenberg, 1987; Rowe et al., 1974), but the ecosystem-level simulations show that this relationship is not a simple function of primary productivity and depth.

The results of study II confirm extensive research showing that hypoxia is an important driver that can diminish biomass and alter community composition of the benthos, which in extension has major implications for benthivorous fish (Diaz and Rosenberg, 1995; Norkko et al., 2015; Villnäs et al., 2013). However, the quantification on the Baltic Sea scale suggests that biomass gains in oxic areas far exceed the biomass lost due to hypoxia during past eutrophication (study III).

Bottom water temperature had a relatively small effect on community biomass (study II), but the indirect effects of increasing surface temperature through intensification of pelagic recycling and reduction of organic matter input to the sediment were substantial (study III). These results support studies showing a shift in timing, composition and predation pressure on phytoplankton blooms with climate warming (Kahru et al., 2016; Suikkanen et al., 2007; Tamelander et al., 2017).

Deposit-feeders were strongly driven by predation pressure in the model simulations. Even though there is some support for tight predator-prey coupling in the Baltic Sea (Englund et al., 2008; Englund and Leonardsson, 2008; Sparrevik and Leonardsson, 1999), these results are probably also artefacts of the simple model formulations excluding pelagic predators, as shown by the comparison to the EwE food-web model (study II). This demonstrates the importance of managing model uncertainty by using complementary (modelling) approaches. The non-linear responses to multiple drivers caused by complex interactions of direct effects on e.g. physiology and effects mediated trough the food-web (studies II & III) also illustrates the need to consider the joint impacts of direct and indirect effects on individual components to understand the system-level responses to multiple perturbations (Crain et al., 2008; Fulton et al., 2004a).
The simulated carbon flows suggest that the contribution of macrofaunal respiration to organic matter mineralisation can be substantial, especially in coastal productive areas where biomass is primarily limited by food availability. These results support the recent calls to include macrofaunal metabolism in biogeochemical models to elucidate the role of marine sediments in global cycling of carbon and nutrients, especially in the light of global change (study IV, Middelburg, 2018; Snelgrove et al., 2018).

Taken together, the results of this thesis suggest that the future nutrient load reductions prompted by political agreements combined with increasing sea temperatures will probably decrease macrozoobenthic biomass and carbon processing drastically, leading to weakened benthic-pelagic coupling.

One main function of mechanistic modelling is to synthesize existing knowledge into quantitative relationships explaining the most important processes determining the state of a study system (Seidl, 2017). Another important task is to identify gaps in current knowledge. The model results suggest that food availability sets an upper limit to the biomass that can be achieved, but there seem to be additional constraints resulting in the ‘missing’ biomass of *L. balthica* in the Tvärminne site in the early 1990s and in the eastern Gulf of Finland in general.

To address this knowledge gap, possible model developments would be inclusion of size structure and a more detailed description of reproductive processes. This would allow exploration of hypotheses related to the recruitment and survival of juveniles as a population bottleneck for *L. balthica* (Bonsdorff et al., 1995; Elmgren et al., 1986; Segerstråle, 1978a), and could also dampen the simulated fluctuations in surface deposit-feeder biomass. Additionally, changes in reproductive phenology in response to climate change may have major effects on future benthic communities (Poloczanska et al., 2013; Thomas and Bacher, 2018).

Other paths for future developments of the model include a two-way coupling of the BM to the physical and biogeochemical processes of the BALTSEM model, and an extension of the model to include the more diverse south-western parts and coastal areas of the Baltic Sea. The latter would require inclusion of additional groups such as deep-burrowing deposit-feeders and epifaunal suspension-feeders (e.g. *Mytilus* sp.). Additionally, there are potentially important drivers of change that could be included in future model versions such as salinity, acidification and species invasions (Cloern et al., 2016; Crain et al., 2008; Holopainen et al., 2016; Norkko et al., 2012).

In more general terms, the major challenges for the future are not just technical inclusion of more processes and groups in the model, but related to the mechanistic understanding of heterogeneous coastal areas, where a complex mosaic of habitats and small-scale variations in abiotic conditions create an intricate pattern of diverse and productive communities of benthic vegetation and fauna (e.g. Rodil et al., 2019). The role of benthic fauna in ecosystem functioning, such as biogeochemical cycling, is influenced by the functional traits of individuals (Mermillod-Blondin et al., 2005; Norkko et al., 2012).
2013) and the environmental context they occur in (Bernard et al., 2019; Braeckman et al., 2014; Gammal et al., 2019; Joensuu et al., 2018), but the understanding of the diverse mechanisms underpinning these effects is far from complete.

To increase the understanding of coastal ecosystem functioning under multiple anthropogenic pressures, there is a need to combine different experimental and modelling approaches, balancing the competing goals of generality, precision and realism (Levins, 1966), from well-controlled lab experiments to more realistic in-situ studies of natural communities to ecosystem modelling of possible future states of the sea. This thesis is a first step towards including benthic fauna in a coastal sea ecosystem model to support efficient management of the sea under environmental change.
I am grateful to my supervisors Bo Gustafsson and Alf Norkko. It has been extremely rewarding to work with two great minds from completely different fields. Together, you have given me a broad scientific basis that has helped me bridge the gap between the mind-set of a field ecologist and that of a modeller. This process has taken a substantial amount of time, giving me a very slow start, and I want to thank you for believing in me and supporting me along the way. Also, I think one of the greatest achievements of my thesis is that it has brought the two of you closer together to understand and even adopt each other’s perspectives. I do hope our fruitful work together will continue.

I would like to thank my co-authors Barbara Bauer, Erik Gustafsson, Christoph Humborg, Bärbel Müller-Karulis, Karen Timmerman, Oleg Savchuk and Xiaole Sun for your substantial input to different parts of this thesis, without you this thesis would not exist. Additionally, I want to thank my roommates and postdoctoral mentors Xiaole and Barbara for your support in all parts of the scientific process, both practical and intellectual. Christoph, I thank you for regularly checking in on how I was doing and for involving me in the broader network of scientists at the Baltic Sea Centre and the Baltic Fellows. And not least for the cosmic salvation of paper IV. Oleg, thank you for always taking the time to sit down and answer my questions and discuss the inner workings of the Baltic Sea. Bo, Bärbel and Erik, thank you for all the help with BALTSEM and for making me part of your team.

For taking the time to read and evaluate my work, I thank the thesis advisors Anna Kuparinen and Monica Quinones Windner and pre-examiners Ragnar Elmgren and Jorma Kuparinen. Ragnar, warm thanks for your detailed comments that significantly improved this thesis.

I thank Laura Kauppi and Caroline Raymond for help with managing zoobenthos data and for interesting discussions about the secret lives of the animals, such as ‘why does Monoporeia swim?’ and ‘what makes Macoma spawn?’. I also want to show my gratitude to generations of researchers doing the gritty work of collecting zoobenthic and environmental data around the Baltic Sea and managing it in databases. Your work is a strong foundation for this thesis.

To all the people at the Baltic Sea Centre who have made my last four years fun, interesting and productive, thank you! Sandra Åberg and Stina Nieminen, thank you for taking care of me as one of your own. Erik Smedberg and Carl Rolff, thank you for all the laughter.

Big thanks to the staff at Tvärminne Zoological Station and the Benthic Ecology Team for making me feel welcome and part of the group whenever I visited Tvärminne. Thanks especially to Anna Villnäs for reading and improving my manuscript and for your sincere interest in my work, and to Anna and Camilla Gustafsson for fun collaborations. Tobias Tamelander,
thank you for providing your unpublished data. Joanna Norkko, thank you for your hospitality and friendliness. Johanna Gammal, thanks for the PhD peer support.

Collaborating across several fields of social and natural sciences is challenging. A big thanks to the BOUNUS BalticAPP team for showing respect and understanding toward each other’s disciplines. Thank you Kari Hyytiäinen for successfully steering the ship. Thank you, Markus Meier, for making a whole lecture about what some biologist called Eva would need for her PhD. Thanks also to the BONUS COCOA team, especially Elin Almroth-Rosell, Moa Edman, Tatjana Eremina, Jacob Carstensen, Joanna Norkko and Artūras Razinkovas-Baziukas for your ideas and input to earlier versions of the review.

This work was supported financially by the EU, the Academy of Finland and the Swedish Research Council Formas through BONUS, the joint Baltic Sea research and development programme (Art 185) and by the Swedish Agency for Marine and Water Management through their grant 1:11—Measures for marine and water environment.

Last but not least I want to thank family and friends who have reminded me that there is life outside the PhD. To all the people at the SU Zoology department, thanks for all the nice discussions at Friday pubs. I am really privileged to feel at home in three places, i.e. the BSC, TZS and Zootis. Chris, Christina, Jason, Lovisa, Peter and Naomi, thank you for expanding my perspectives on science, life and puzzle dungeons. Philipp, you have always had the ability to respectfully put my problems into perspective. We make a good team in life.
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