

Benthic-pelagic coupling in coastal seas – Modelling macrofaunal biomass and carbon processing in response to organic matter supply[☆]



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ABSTRACT

Benthic macrofauna is an important component linking pelagic and benthic ecosystems, especially in productive coastal areas. 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 imperative to understand the functioning of coastal ecosystems. In this study, we develop a dynamic model of benthic macrofauna to quantify the relationship between organic matter input and benthic macrofaunal biomass in the coastal zone. The model simulates the carbon dynamics of three functional groups of benthic macrofauna and their sediment food sources and is forced by a hydrodynamic-biogeochemical model simulating pelagic physical and biological dynamics. The model reproduces measured time-series of macrofaunal biomass from two coastal sites with contrasting sedimentation in the Baltic Sea in 1993–2005 with comparatively high accuracy, including a major increase at one of the sites dominated by the bivalve *Limecola (Macoma) balthica*. This shift in community composition suggests altered pathways of organic matter degradation: 39% of simulated sedimentation was mineralised by macrofauna in 2005 compared to 10% in 1995. From the early 2000s onward macrofaunal biomass seems to be food-limited, as ca 80% of organic carbon sedimentation was processed by the deposit-feeding macrofauna at both sites. This model is a first step to help quantify the role of macrofauna in marine coastal ecosystem functioning and biogeochemical cycles and build predictive capacity of the effects of anthropogenic stressors, such as eutrophication and climate change, on coastal ecosystems.

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 affects 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 primary productivity compared to the open ocean (Graf, 1992; Kopp et al., 2015). Together, these factors lead to a higher amount of fresh organic matter reaching the seafloor, fuelling the benthic fauna. Benthic macrofauna play a central role in organic matter retention, remineralisation and benthic-pelagic exchange, both directly through ingestion, biomass production, respiration and excretion (Herman et al., 1999; Josefson and Rasmussen, 2000; Middelburg, 2018) and indirectly through bioturbation (Aller,

1982; Meysman et al., 2006; Rhoads, 1974). Benthic macrofauna is also an important food source for demersal fish, including commercially important species such as flatfish and cod (Borg et al., 2014; Hüsey et al., 1997; Link and Garrison, 2002).

The effects of macrofauna on benthic-pelagic processes such as carbon cycling are strongly linked to the community biomass (Snelgrove et al., 2018). Organic matter input is recognised as the most important driver of macrozoobenthic biomass globally (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 and references therein; Weigel et al., 2015). In addition to food availability, physical factors such as salinity,

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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).

Coastal ecosystems around the world are undergoing rapid environmental change (Cloern et al., 2016). Nutrient loading, climate change, and multiple other anthropogenic pressures are affecting the quality and quantity of organic matter inputs and the integrity of sea-floor communities, with potential major repercussions for ecosystem functioning (Gray et al., 2002; Griffiths et al., 2017). This highlights the importance of building predictive capacity to assess the consequences for benthic-pelagic coupling processes.

The Baltic Sea provides a well-studied example of the consequences of eutrophication, including the spread of anoxic zones with consequent loss of benthic fauna, not only in the deeper parts (Carstensen et al., 2014; Conley et al., 2009), but also increasingly in the coastal zone (Conley et al., 2011; Gammal et al., 2017). Conversely, in coastal oxic areas, macrozoobenthic biomasses have increased during the last century (Cederwall and Elmgren, 1990; Karlson et al., 2002). The increase is mostly attributed to increased food availability due to eutrophication-induced increases in primary production and sedimentation (Bonsdorff et al., 1997; Boström et al., 2002; Cederwall and Elmgren, 1980). However, it is hard to ascertain and quantify the causes and effects since historical data on sedimentation are scarce, and thus most studies have inferred a correlation between biomass increase and food availability based on indirect and uncertain indicators, such as primary production or nutrient loads. Additionally, substantial population fluctuations of the bivalve *Limecola (Macoma) balthica*, dominating the benthic community biomass in large parts of the Baltic, have not been clearly linked to indicators of eutrophication (Hewitt et al., 2016; Perus and Bonsdorff, 2004; Rousi et al., 2013; Zettler et al., 2006). Developing models that allow for quantitative exploration of benthic–pelagic coupling is hence imperative and would significantly advance our ability to understand changes in coastal ecosystems.

To generalize and quantify relationships observed in natural ecosystems and to test hypotheses over large temporal and spatial scales, mechanistic modelling is an essential tool (Duarte et al., 2003; Jackson et al., 2000). Here, we present a mechanistic model simulating the carbon flows through functional groups of benthic macrofauna and their sediment food sources. The model is forced by output from a hydrodynamic-biogeochemical model simulating the pelagic physical (e.g. temperature) and biogeochemical (e.g. oxygen and organic matter) dynamics. The benthic model is partly based on a benthic fauna model by Timmermann et al. (2012) which was used to study the interactive effects of hypoxia and nutrient loading on macrofaunal biomass in the open Baltic Sea. We used the new benthic model to simulate macrozoobenthic biomass development in two coastal soft-sediment areas of the Baltic Sea to: (a) quantify the effects of increasing biomass on carbon fluxes, and (b) test the hypothesis that macrozoobenthic communities are food limited in these oxic areas.

2. Materials and methods

2.1. Study area

The Baltic Sea is a geologically young brackish-water basin characterized by latitudinal and water depth gradients in salinity, temperature and species diversity. The benthic communities consist of a mixture of species of marine and limnic origin, generally declining in diversity and biomass with increasing latitude and water depth (Bonsdorff, 2006; Laine, 2003; Rumohr et al., 1996). 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 during winter months results in a strong peak in phytoplankton production in spring followed by a peak in sedimentation. In summer the pelagic recycling of primary production is more efficient and sedimentation generally lower (Heiskanen et al.,

1998; Tamelander et al., 2017).

In this study, we developed a benthic biomass model for a nearshore area in the Gulf of Finland as a representative example of coastal soft-sediment systems. Long-term monitoring of the benthos in Tvärminne Storfjärden (59° 51' N, 23° 16' E) and a long marine research tradition in the area provide a good basis to quantify the benthic-pelagic link in terms of carbon fluxes. As validation, the model was run in a coastal site in the Gotland Basin, and compared against monitoring data from the Askö area (58° 46–50' N, 17° 35–41' E). The two areas represent a similar latitude, water depth, temperature range, salinity regime and species composition, but differ in eutrophication status, allowing for a comparison of the effects of differing amount of organic matter supply to the benthos, which is estimated to be > 1.5 times higher in the Gulf of Finland than in the Baltic Proper (Leipe et al., 2011). The location and main characteristics of the sites are presented in the Supplement (S1).

Zoobenthic monitoring data used in this study consists of 3–5 replicate Van Veen grab samples (0.1 m²) taken yearly in the spring (Tvärminne Storfjärden station XLIV, Askö stations 6001 and 6004) and/or autumn (XLIV). The samples were sieved on a 1 mm mesh and the taxa identified and weighed wet as described in e.g. Rousi et al. (2013). The data are available in national databases (syke.fi/avoindata for Tvärminne and www.smhi.se for Askö).

The soft-sediment macrofauna in these areas is dominated by deposit-feeders including the bivalve *Limecola balthica* and the amphipods *Monoporeia affinis* and *Pontoporeia femorata*. The main invertebrate predator/scavengers are the isopod *Saduria entomon*, the polychaete *Bylgides sarsi* and the priapulid *Halicryptus spinulosus*. The non-native deposit-feeding polychaete genus *Marenzelleria* spp. arrived in the early 1990s, but established large populations only in the late 2000s (Kauppi et al., 2015, this study). Following a period of suspected failure in recruitment, the biomass of *L. balthica* increased drastically during the 1990s in the Gulf of Finland site and settled at a new level in the 2000s. This period was chosen to study the effects of the deposit-feeding community biomass increase on carbon cycling through metabolic processes (ingestion, biomass retention and respiration), and to test the model's ability to reproduce the transient as well as conditions close to steady state in the benthos.

2.2. Model description

The benthic model simulates the flows of carbon through five state variables including three functional groups of fauna and two sediment food banks (Fig. 1). It is partly based on the physiological fauna model presented by Timmermann et al. (2012), but with significant alterations and additions, including a dynamic feedback to detrital food sources, some new formulations and parameterizations of physiological processes, and a different modelling environment (Matlab© v. R2015b). Given these substantive differences, the entire model is presented below with references to the original model (Timmermann et al., 2012) where applicable.

The benthic macrofauna is represented by three functional groups divided by their feeding mode and position in the sediment: surface deposit-feeders, predator/scavengers and *Limecola*, representing the infaunal key species *Limecola balthica*.

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, recruitment, predation and mortality. For each functional group, the biomass dynamics are described by:

$$\begin{aligned} dB_i/dt = & rec_i + B_i \times I_i \times AF_j \times (1 - r_{g,i}) \\ & - B_i \times (r_{b,i} + m_{other,i} + m_{ox,i}) - m_{pred} \end{aligned} \quad (1)$$

where B_i is biomass of the functional group i (in mg C m⁻²), rec_i is

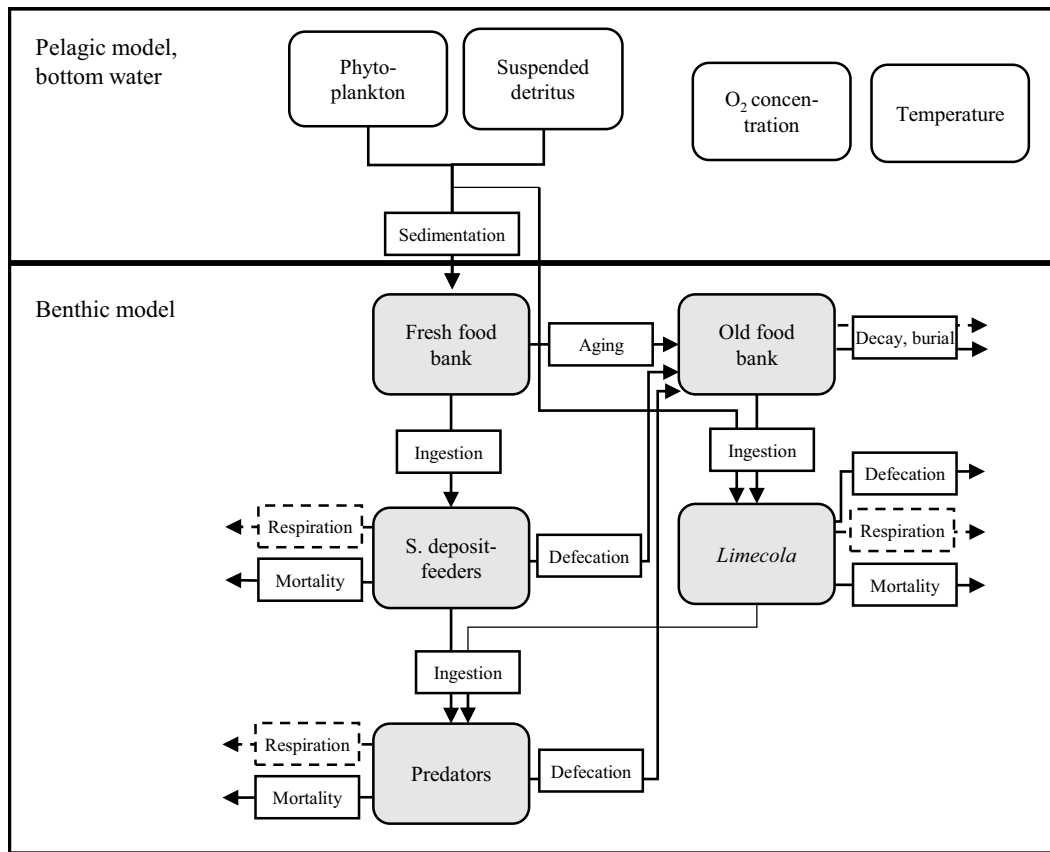


Fig. 1. Conceptual figure of the model processes. Solid and dashed arrows represent organic and inorganic carbon fluxes, respectively. Gray rounded boxes are benthic model state variables, white rounded boxes are forcing variables from the BALTSEM model.

recruitment, 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, $r_{b,i}$ 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.

To avoid permanent extinction of any group, a small biomass increase rate is applied to all groups during one day per year to represent recruitment from other areas:

$$rec_i = \begin{cases} rec_{0,i}, & \text{if day of year} = 241 \\ 0, & \text{else} \end{cases} \quad (2)$$

where rec_i is recruitment and $rec_{0,i}$ is recruitment rate. Ingestion is formulated as a function of maximum ingestion rate and food availability following a type II functional response (Holling, 1966). In the model, surface deposit-feeders eat freshly deposited detritus, while *Limecola* can eat slightly older detritus. The growth of the main surface deposit-feeder *Monoporeia affinis* seems dependent on freshly deposited algal material, while *Limecola 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 Timmermann et al. (2012). Predator/scavengers eat mostly surface deposit feeders (Ankar, 1977; Englund et al., 2008), but can supplement their diet with *Limecola* (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):

$$I_{j,i} = I_{max,i} \times \left(\frac{pr_j \times (F_j - Flim_j)}{K_{m,j} + \sum_{k=1}^n (pr_k \times (F_{kj} - Flim_k))} \right) \quad (3)$$

where $I_{j,i}$ is ingestion rate of the food source F_j , $I_{max,i}$ 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 $K_{m,j}$ 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 surface deposit-feeders and *Limecola* eating only one food source at the time, the formulation can be simplified to:

$$I_i = I_{max,i} \times \left(\frac{F_j}{K_{m,j} + F_j} \right) \quad (4)$$

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 $r_{b,i}$ is a function of biomass, while growth and activity respiration is related to ingestion and described by a single factor $r_{g,i}$ (Tian, 2006).

The predation mortality function m_{pred} equals intake by predator/scavengers (Eq. (3)) for surface deposit-feeders and *Limecola*. The formulation for hypoxia-induced mortality from Timmermann et al. (2012) was used:

$$m_{ox,i} = (1 - m_{0,i}) \times \frac{m_{0,i} \times e^{-K_{ox,i} \times [O_2]}}{1 - m_{0,i} \times e^{-K_{ox,i} \times [O_2]}} \quad (5)$$

Table 1
Parameter values and conversion factors used in the model.

Parameter	Unit		<i>Limnocola (mac)</i>	Surface deposit feeders (<i>depf</i>)	Predator/scavengers (<i>preds</i>)	
I_{max}	Maximum specific ingestion rate	day ⁻¹	0.06 ^b	0.14 ^a	0.09 ^a	
pr	Preference factor of predator for prey	–	0.01 ^e	0.9 ^c		
$Flim$	Lower biomass limit for predation	mg C m ⁻²	30 ^c	30 ^c		
r_b	Basal respiration rate	day ⁻¹	0.003 ^{b,c,d}	0.012 ^a	0.012 ^a	
r_g	Growth and activity respiration factor	–	0.2 ^b	0.2 ^b	0.2 ^{a,b}	
m_0	Anoxic mortality rate	day ⁻¹	0.081 ^a	0.69 ^a	0.069 ^a	
K_{ox}	Sensitivity to hypoxia	(mg O ₂ L ⁻¹) ⁻¹	2.5 ^a	1.5 ^a	2.5 ^a	
m_{other}	Other mortality rate	day ⁻¹	8 × 10 ^{-4e}	1 × 10 ^{-3e}		
rec_0	External recruitment rate	(mg C m ⁻² day) ⁻¹			1 × 10 ^{-5e}	
$wwt:C$	Wet weight to carbon ratio	mg wwt (mg C) ⁻¹	1 ^e	1 ^e	1 ^e	
T_{ref}	Reference temperature	°C	20 ^a	10 ^a	11 ^a	
$Q_{10,ox}$	Q ₁₀ -value for hypoxia-induced mortality	–	2.6 ^a			
Q_{10}	Q ₁₀ -value for all other rates	–	2 ^{a,b,c,d}			
			Suspended organic matter (<i>phyto</i>)	Fresh food bank (<i>fbf</i>)	Old food bank (<i>fbo</i>)	Prey (<i>prey</i>)
AF	Assimilation factor	–	0.8 ^a	0.7 ^a	0.5 ^a	0.7 ^a
K_m	Ingestion half-saturation constant	mg C m ⁻²		3000 ^f	8000 ^f	500 ^f
k	Aging/degradation factor	day ⁻¹	300 ^f	0.05 ^c	0.02 ^c	

^a Timmermann et al. (2012).

^b Ebenhöh et al. (1995).

^c Blackford (1997).

^d Vichi et al. (2004).

^e Further explanations and references in text.

^f Calibrated.

where [O₂] is bottom-water oxygen concentration, $m_{0,i}$ is the mortality rate under anoxic conditions, and $K_{ox,i}$ 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 $m_{other,i}$. Model closure is achieved by quadratic mortality for the predator/scavengers (Fulton et al., 2003).

Growth ($I_{max,i}$) and basal respiration ($r_{b,i}$) rates are dependent on bottom water temperature according to a Q_{10} -formulation (Eq. (6)), while the factor $r_{g,i}$ is assumed to be independent of temperature (Anderson et al., 2017; Tian, 2006).

$$Q(T) = Q_{10}^{\frac{T-T_{ref}}{10}} \quad (6)$$

where $Q(T)$ is the temperature-dependency factor, T is current temperature and T_{ref} is reference temperature. Also mortality ($m_{other,i}$) 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).

To resolve possible food-limitation of the fauna, two sediment food banks are included in the benthic model as state variables. Daily flux of organic matter to the bottom (*sed*) is integrated into a pool of fresh organic carbon in the sediment (*fbf*). Loss terms of the pool are ingestion by deposit-feeders (*depf*) and aging by the factor k_{fbf} . Microbial mineralisation of the fresh food bank is assumed to be negligible in comparison to aging given the short residence time.

$$dfbf/dt = sed - depf \times I_{depf} - fbf \times k_{fbf} \quad (7)$$

The aging detritus enters a pool of older sediment organic carbon (*fbo*) available as food to *Limnocola* only. Also the faeces of deposit-feeders and predator/scavengers (*preds*) adds to the older food bank. Loss terms for the older food bank are ingestion by *Limnocola (mac)* and degradation or burial by the factor k_{fbo} .

$$dfbo/dt = fbf \times k_{fbf} + depf \times I_{depf} \times (1 - AF_{fbf}) + preds \times I_{preds} \times (1 - AF_{prey}) - mac \times I_{mac,fbo} - fbo \times k_{fbo} \quad (8)$$

The degradation and aging factors are temperature-dependent according to Eq. (6) (e.g. Soetaert et al., 1996; Soetaert and Middelburg, 2009). Conceptually, these banks consist of living and dead organic matter including algae, other microbes and meiobenthos.

2.3. Pelagic model

The benthic model was forced by the hydrodynamic-biogeochemical model BALTSEM (Gustafsson, 2003, 2000; Gustafsson et al., 2017; Savchuk et al., 2012), that has been successfully applied and validated to study long-term eutrophication of the Baltic Sea (Gustafsson et al., 2012) as well as seasonal variations (Savchuk et al., 2012). BALTSEM simulates the dynamics of physical circulation and stratification as well as nutrients and plankton dynamics with a vertical resolution of about 1 m. The full organic and inorganic carbon cycles are also included (Gustafsson et al., 2017 and references therein). Outputs from BALTSEM used as forcing in the benthic model were time-series of bottom water concentrations of suspended phytoplankton and detritus, oxygen and temperature as well as organic carbon flux to the bottom, which is formed by sinking detritus and plankton. Similarly, outputs from an earlier version of BALTSEM were successfully used to force the benthos model simulations by Timmermann et al. (2012).

2.4. Simulation settings and initial conditions

The model was run with forcing from BALTSEM at 35 m depth in the Gulf of Finland, corresponding to the Tvärminne Storfjärden XLIV zoobenthic monitoring station. The simulation was started at the lowest recorded biomass 21.9.1993 and run until the end of 2005, when the benthic biomass had stabilised at a new level. The model solver used an

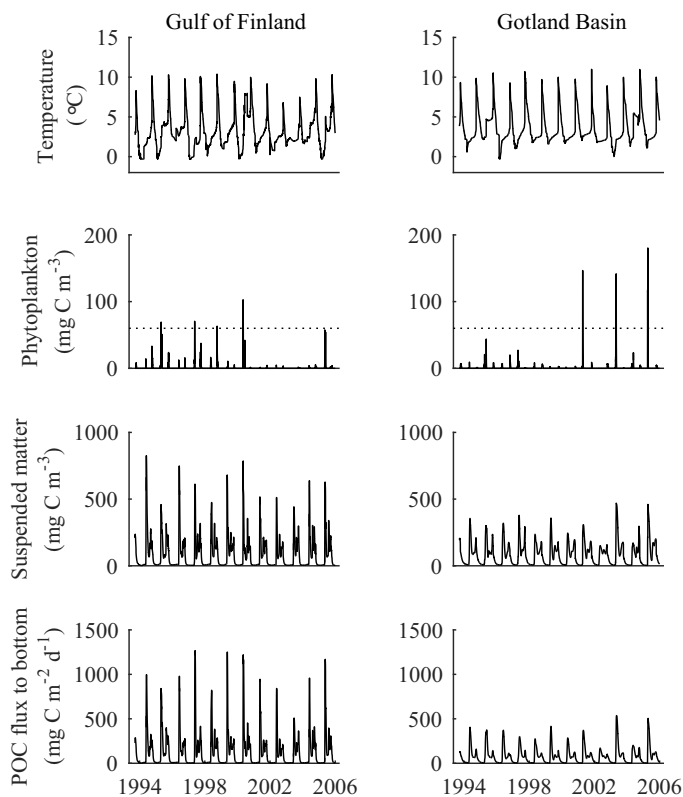


Fig. 2. Forcing time-series for the benthic model runs simulated with BALTSEM 1993–2005. The variables are temperature, phytoplankton (diatoms + flagellates) concentration and suspended organic matter (phytoplankton + detritus) concentration in the bottom water layer as well as organic matter (POC) flux to the bottom. The dotted line marks the switching threshold for suspension-feeding in *Limnocola*.

adaptive time-step of less than one day. Forcing time-series from BALTSEM had a daily resolution. Initial conditions for the functional groups were based on measured wet biomasses that were converted to carbon biomass (Table 1, Timmermann et al., 2012). No measurements on the magnitude of the sediment food banks were available to base the initial values on, instead they were estimated from Eqs. (7) and (8) assuming balance between sedimentation and aging/degradation without benthos present.

2.5. Parameterization and calibration

All model parameters are presented in Table 1. Parameter values for macrofauna were primarily based on Timmermann et al. (2012). To ensure that overall turnover rates were realistic, they were compared against yearly production over mean biomass (P/B) values for macrofauna (> 1 mm) measured in the Baltic Sea, and rate parameters were adjusted accordingly. The ranges of possible parameter values were derived from Timmermann et al. (2012) and a similar functional group-based model, ERSEM, as applied to macrozoobenthos of the North Sea (Blackford, 1997; Butenschön et al., 2016; Ebenhöf et al., 1995) and the Baltic Sea (Vichi et al., 2004).

Limnocola balthica is a long-lived species with a very low P/B of ca. 0.1–0.4 year⁻¹ (Bergh, 1974; Gusev and Jurgens-Markina, 2012; Sarvala 1981 in Kuparinen et al., 1984; Ostrowski, 1987). For the surface deposit-feeders *Monoporeia affinis* and *Pontoporeia femorata* P/B-values of 1.3–1.9 year⁻¹ (Cederwall, 1977; Cederwall and Jermakovs, 1999; Kuparinen et al., 1984; Ostrowski, 1987), and for predator/scavengers (*Saduria entomon*, *Halicryptus spinulosus* and *Bylgides sarsi*) values of 0.9–2 year⁻¹ have been reported (Sarvala 1981 in Kuparinen et al., 1984). Assuming a balance between biomass production and elimination in the latter part of the simulation period, mortality rates were approximated from the P/B-values. The rates of maximum ingestion and respiration for *Limnocola* were reduced to match the low production rates measured in the Baltic Sea.

An average Q_{10} of 2 has been reported by several authors for

Limnocola balthica respiration in the temperature range of 0 to 15 °C, although the variation is large (Hummel et al., 2000; Jansen et al., 2007; van der Veer et al., 2006). For surface deposit-feeders and predators, corresponding values range between 1.7 and 2.3 (Kangas and Lappalainen, 1978; Lehtonen, 1996; Robertson et al., 2001). The standard relationship of $Q_{10} = 2$ was used for all rates within the model temperature range of 0 to 11 °C, except for hypoxia-induced mortality (Timmermann et al., 2012).

The aging of the fresh food bank into the older bank of lower nutritional quality was estimated from the average degradation rate of chlorophyll as a proxy for food quality (Herman et al., 1999), giving a degradation factor (k_{fbf}) of 0.05 day⁻¹. For the older sediment food bank, the loss rate k_{fbo} of 0.02 day⁻¹ represents slow remineralisation (Butenschön et al., 2016) as well as burial below feeding depth.

In a final stage, the model was calibrated against measured biomass development from monitoring in the Tvärminne site by adjusting the ingestion half-saturation constants and fine-tuning mortality rates.

2.6. Model validation

To validate the model, it was run with forcing from BALTSEM at 40 m depth in the Gotland Basin, corresponding to the monitoring stations 6001 and 6004 in the Askö area. All settings and parameter values were kept exactly as in the Gulf of Finland run, except for the initial conditions, which for the fauna were based on measured biomasses in spring 1993–1994 at the two stations.

2.7. Sensitivity analyses

The sensitivity of model dynamics to growth-related parameters was tested by increasing and decreasing maximum ingestion rate ($I_{max,i}$) and basal respiration rate ($r_{b,i}$) for each functional group by 25% while keeping all other model settings as in the original run. Similarly, the sensitivity of model dynamics to the loss rate of food banks was tested by increasing and decreasing the aging/degradation rates k_{fbf} and k_{fbo}

by 25%. Additionally, the effects of *Limecola* on the system were studied by excluding the group from model runs in both sites. The sensitivity analyses are presented in the Supplement (S2).

3. Results

3.1. Pelagic dynamics

The conditions for the benthos as simulated by BALTSEM showed a similar seasonal range in bottom water temperature in the Gulf of Finland site and the Gotland Basin site (hereafter referred to as GoF and GB, respectively) without any clear trend over time during the simulation period (Fig. 2). Simulated oxygen concentrations indicated normoxic conditions at both sites (O_2 concentrations $> 7.7 \text{ mg L}^{-1}$, data not shown).

The concentration of chlorophyll *a* was low at both sites (shown as phytoplankton organic carbon in Fig. 2), and the threshold value for suspension-feeding for *Limecola* was only occasionally reached for short periods in connection to the spring bloom, as illustrated by the dotted line.

The amount of suspended organic matter in the bottom water column and sedimentation were significantly higher in GoF than in GB. The variation both within and between years were also greater in GoF, but neither site showed a consistent trend over time. Mean annual sedimentation was 41 g C m^{-2} (SD ± 5.4) in GoF and 26 g C m^{-2} (± 4.1) in GB. These rates are within the range of measured values for the basins (Leipe et al., 2011; Leppänen, 1988; Tamelander et al., 2017). The annual sedimentation made up between 25% and 48% of primary production; mean annual primary production integrated over the water column was 129 g C m^{-2} (± 29.7) in GoF and 71 g C m^{-2} (± 11.4) in GB.

3.2. Benthic dynamics

The dynamics of the benthic state variables and a comparison to

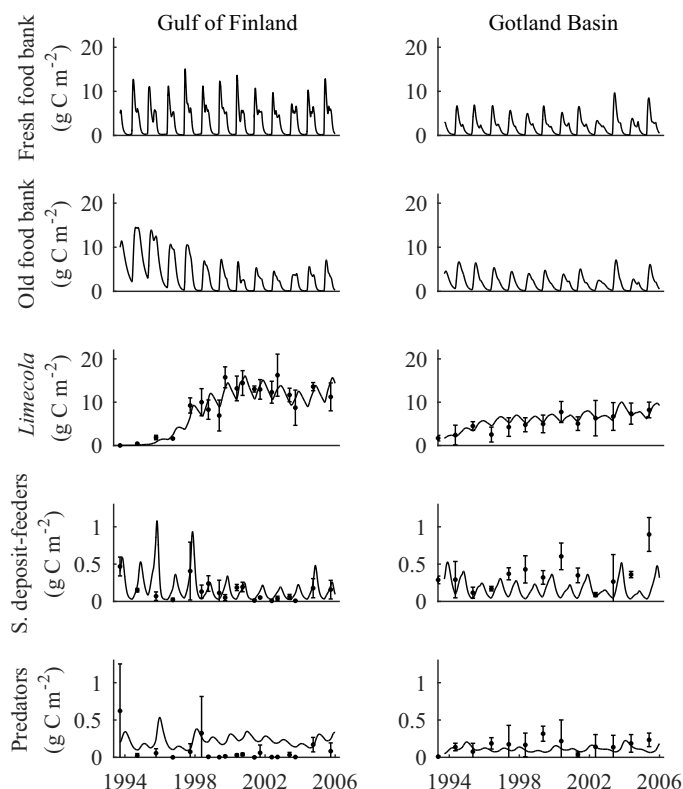


Table 2

Average wet weight and contribution to functional group biomass of macrofauna in monitoring data from the Gulf of Finland (GoF) and Gotland Basin (GB) sites during 1993–2005.

	Gulf of Finland		Gotland Basin	
	g ww m^{-2}	% of group	g ww m^{-2}	% of group
Surface deposit-feeders	1.31		3.49	
<i>Monoporeia affinis</i>	0.80	61%	2.46	70%
<i>Marenzelleria</i> sp.	0.46	35%	0.06	2%
<i>Pontoporeia femorata</i>	0.03	2%	0.98	28%
Other	0.02	2%	0.002	0.1%
Predator/scavengers	0.92		1.72	
<i>Saduria entomon</i>	0.60	65%	0.22	13%
<i>Halicryptus spinulosus</i>	0.21	23%	1.47	85%
<i>Bylgides sarsi</i>	0.09	10%	0.02	1%
<i>Hediste diversicolor</i>	0.03	3%	0.01	1%
<i>Limecola balthica</i>	191.02		74.64	

measured values are presented in Fig. 3. In GoF, monitoring data from XLIV Tvärminne Storfjärden showed an increase of *Limecola balthica* biomass by almost four orders of magnitude during the 1990s, from $0.02 \pm 0.01 \text{ g C m}^{-2}$ in 1993 to $10.00 \pm 3.13 \text{ g C m}^{-2}$ in 1998 (mean \pm SD of replicates), while it thereafter levelled off. In the 2000s, mean *L. balthica* biomass ranged between 9 and 16 g C m^{-2} . The measured *L. balthica* biomass in GB from the Askö area stations was also lowest in 1993 ($1.70 \pm 0.64 \text{ g C m}^{-2}$), but the increase was less extreme and the level in the 2000s was between 5 and 8 g C m^{-2} . Also the simulated *Limecola* biomasses increased towards a level that was higher in GoF due to a higher input of organic matter compared to GB.

The biomass of surface deposit-feeders and predator/scavengers made up $< 1 \text{ g C m}^{-2}$ respectively at both sites. While the same species occurred at both sites, their proportion of functional group biomass differed (Table 2). In GoF year-to-year variations in simulated sedimentation rate were reflected in the freshly deposited detritus food bank and surface deposit-feeder biomass (Figs. 2 and 3). This was partly

Fig. 3. 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 Gotland Basin) are shown for the fauna. Note different scale on y-axes.

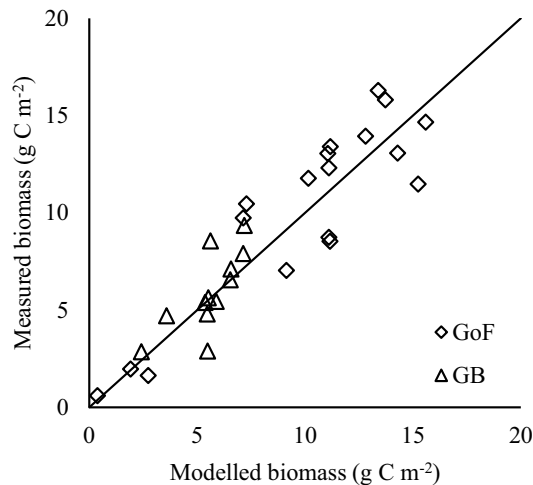


Fig. 4. Comparison of observed (mean of replicates) and modelled total macrozoobenthic biomasses in the Gulf of Finland (GoF, N = 18) and Gotland Basin (GB, N = 12) sites 1994–2005. Diagonal line shows 1:1 ratio.

in agreement with measured biomasses, especially the low biomasses in the years 2001–2004. In the beginning of the simulation period, predator-prey-cycles were strong due to the lack of stabilisation by *Limecola* as an alternative prey for predators, as also seen in the sensitivity analyses (Figs. S2 and S6). The simulated surface deposit-feeder biomass in GB was lower and more constant compared to GoF, following the lower sedimentation rate. Lower prey biomasses were also reflected in lower predator/scavenger biomasses compared to GoF. This was not in agreement with measured biomasses, which were higher than in GoF for both groups (see Section 4.1).

Overall, simulated functional group biomasses were mostly within the standard deviations of measured biomasses, except for an overestimation of predators in GoF and an underestimation of deposit-feeders in GB. A comparison of modelled and measured total macrozoobenthic biomasses is presented in Fig. 4.

3.3. Carbon flows

To explore the effects of the radical increase in macrofaunal biomass on carbon flows in GoF, selected annual carbon flows and stocks were calculated from the model output for two years with contrasting biomasses (Fig. 5). In the low biomass state of 1995, 22% of the sedimented organic carbon was processed by the macrofauna, while in 2005 the corresponding fraction was 80%. 10% of the sedimentation was mineralised through macrofaunal respiration in 1995 and 39% in 2005. In GB, simulated macrozoobenthic biomass increased from 4.7 to 8.4 g C m⁻² between 1995 and 2005, organic carbon processing increased from 59% to 73% and mineralisation from 27% to 35% of sedimentation.

The effect of *Limecola* on its sediment carbon food source can also be seen in Figs. 3 and S6: with low or absent *Limecola* biomass, the older detritus food bank is present around the year, but at higher biomass, the bank is depleted every autumn.

3.4. Model sensitivity to selected parameters

The sensitivity analyses, including variations in parameter values (S2.1) and the elimination of *Limecola* (S2.2), produced quantitative rather than qualitative changes of model dynamics. The time-scale of the increase in *Limecola* was most affected by the maximum ingestion rate $I_{max,mac}$ while $r_{b,mac}$ had the largest effect on biomass in the end of the simulation period. Changes in other parameters had small effects on *Limecola* biomass. Conversely, the amplitude and mean biomass of

surface deposit-feeders increased with both increased food availability (reduced k_{bf} , increased $I_{max,dep}$) and decreased predation pressure. Predator biomass increased in response to increases in either of its prey groups, but responded more strongly to changes in the surface deposit-feeders. Further results of the sensitivity analyses are presented in the Supplement S2.

4. Discussion

We developed a mechanistic model simulating the biomass of benthic macrofauna in response to pelagic physical and biological dynamics in a coastal setting. The model could simulate the overall biomass dynamics of macrofauna at two sites on the west and east coasts of the Baltic Sea over more than a decade, although variations in the groups with small biomass were not as well captured (Figs. 3 and 4). We used the model to explore the hypothesis that macrozoobenthic communities in oxic areas do reach a food-limited state. Indeed, the difference in total biomass between the two study sites in the 2000s seems to be driven by a difference in available food due to different carbon flux to the sediment (Figs. 2 and 3). The carbon budget suggests that up to 80% of annual sedimentation is utilised as food and up to 40% is mineralised by the macrofauna (Fig. 5), further supporting the food-limitation hypothesis and showing the importance of macrofaunal metabolism for organic matter mineralisation. However, the lower biomass in the beginning of the simulation period was not due to food limitation, as discussed in the next section.

4.1. Drivers of soft-sediment communities

The increase in biomass at both sites was mostly due to *Limecola balthica*. This tellinid bivalve dominates the biomass of soft-sediment communities in large parts of the Baltic Sea, and is widely distributed throughout the northern hemisphere (Beukema and Meehan, 1985; Gogina et al., 2016). The growth dynamics of suspension-feeding bivalve populations, including commercially important mussels and oysters, have been extensively quantified (e.g. Ferreira et al., 2018; McKindsey et al., 2006; Saraiva et al., 2017), but much less is known about natural populations of deposit-feeding bivalves, especially in subtidal areas.

At both sites, the model runs show that *Limecola* biomass was food-limited from the end of the 1990s onward, as seen in the depletion of the food banks each year. Considering that simulated sedimentation rates are in the high end of measured values, while the turnover (maximum uptake, respiration and mortality rates) was set rather low compared to similar models, it seems highly probable that the simulated food-limitation reflects the real-world situation.

In addition to food-limitation, it is possible that the GoF population is experiencing density-dependent regulation through limited space. The density of clams (> 1 mm) in GoF in the 2000s is ca. 600–1100 individuals m⁻². The feeding radius of *L. balthica* is 0.2–5 cm (Kamermans and Huitema, 1994; Zwarts et al., 1994), pointing to a possible overlap of feeding areas at these densities. Experiments by Olafsson (1986) showed intraspecific competition among deposit-feeding *L. balthica* in a muddy sand habitat in the southern Baltic Sea at adult densities of 1000 ind. m⁻² and above. In a nearby sandy habitat, where the clams were mostly suspension-feeding, their densities were much lower (average 200–300 ind. m⁻²) and no competition was found. In the Åland archipelago, densities of up to 300,000 ind. m⁻² have been recorded during settling of juveniles, but adult densities were stable at ca 1000 ind. m⁻² (Bonsdorff et al., 1995). Thus, we consider it likely that deposit-feeding *L. balthica* are limited by food and possibly feeding space.

It is unclear what limited the *L. balthica* biomass in the early 1990s and before. A large number of changes in the Baltic Sea ecosystem have been recorded, but none are temporally clearly linked to the biomass variations of *L. balthica* (Hewitt et al., 2016; Rousi et al., 2013). The

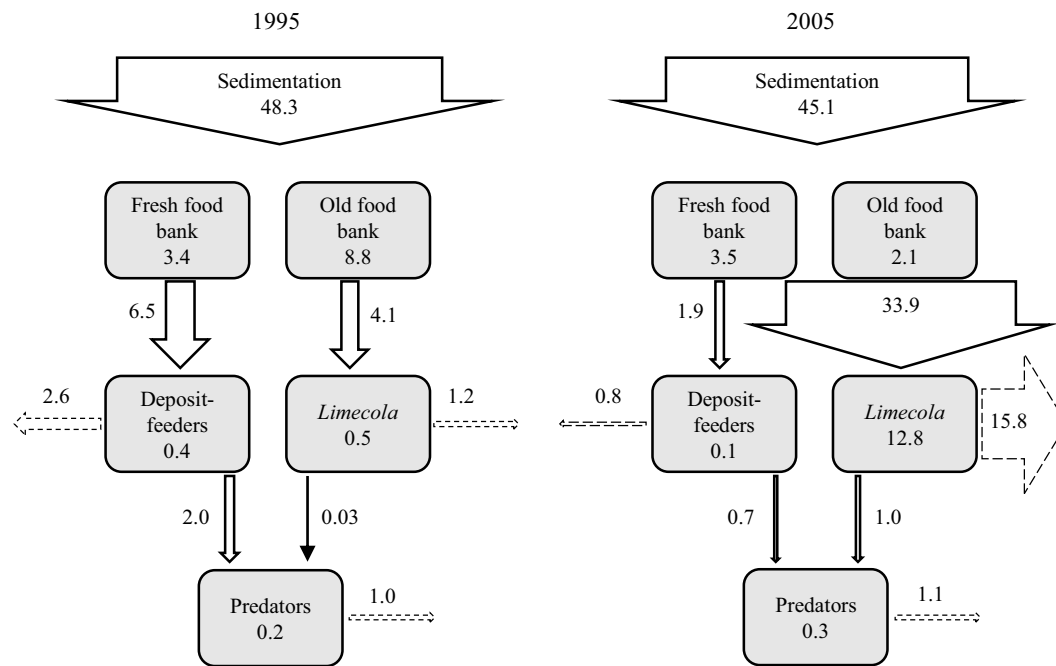


Fig. 5. Modelled flows of organic carbon input to the sediment, ingested organic carbon (solid arrows) and respired CO_2 (dashed arrows) in the benthic food-web in the Gulf of Finland site, illustrating the relative contribution of functional groups of fauna to carbon mineralisation processes between two years with contrasting benthic composition, due to an increase in biomass of *Limecola balthica*. Annual flows and mean stocks are given in g C m^{-2} , arrow widths are proportional to flow size.

amount, timing and species composition of phytoplankton blooms have changed with an increase in summer blooms dominated by cyanobacteria (Kahru et al., 2016; Raateoja et al., 2005; Suikkanen et al., 2007). No increasing trend in sedimentation was seen in the simulation, which is probably due to summer blooms being efficiently recycled in the water column (Tamelander et al., 2017; Vahtera et al., 2007). However, changes in quality of the sedimenting material may be of large importance for the benthos (e.g. Eriksson Wiklund et al., 2008).

Segerstråle (1978) reported a negative correlation between the abundances of *Monoporeia affinis* and *L. balthica* in the Baltic Sea, and Elmgren et al. (1986) showed experimentally that *M. affinis* interferes with newly settled *L. balthica*. In GoF, the increase in *L. balthica* was preceded by a decline in *M. affinis*, which could indicate disturbed recruitment as a limiting factor in the early 1990s. However, there is no clear relationship between *M. affinis* and *L. balthica* in GB, corroborated by an examination of wet weight monitoring data from 21 stations in the Askö region during 1971–2015 ($y = -4.3588x + 105.52$, $R^2 = 0.0317$, $n = 745$, data from www.smhi.se, accessed 2017-08-25).

The surface deposit-feeders are also limited by the fresh organic carbon food source in the model. However, this is dependent on the assumption that this group can only eat fresh detritus. One reason for the underestimation of surface deposit-feeder biomass in the GB site 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 addition to food limitation, predation was an important structuring factor of the surface deposit-feeder group, as seen in the group's sensitivity to changes in predator parameter values (S2.1, Fig. S4).

Strong predator-prey coupling between *S. entomon* and *M. affinis* has been found in the northern Baltic Sea (Englund et al., 2008), but limitation by quantity and quality of organic matter input still seems to be a major driver of the latter (Eriksson Wiklund and Andersson, 2014; Karlson et al., 2011; Lehtonen and Andersin, 1998).

4.2. Effects on the ecosystem

The simulation indicates that macrofauna plays a major role in organic matter cycling directly through their metabolism in these coastal areas. In the latter part of the period, the macrofauna processed the majority of organic carbon sedimentation through their digestive system (80% in GoF and 73% in GB in 2005). More than a third of the sedimented organic matter (39% in GoF and 35% in GB) was mineralised through macrofaunal respiration. On an ecosystem scale, the mineralisation amounted to about a tenth of primary production (9% in GoF and 11% in GB) in 2005. Even though these values contain many sources of uncertainty, they clearly show that the role of macrofaunal metabolism in organic matter degradation is significant.

The radical increase in macrofaunal biomass over a decade in GoF has changed the pathways of carbon in the benthic system. In the low biomass state of 1995 (ca 1 g C m^{-2}) only 10% of sedimentation or 3% of primary production was mineralised through macrofaunal respiration in GoF, leaving the vast majority of organic matter degradation to microbes and meiofauna. The increase also means that about 12 additional g C m^{-2} was bound in the biomass of *Limecola* in GoF in 2005 compared to 1995. This carbon is removed from circulation for an extensive period, as the life span of *L. balthica* can exceed 30 years (Segerstråle, 1960). In GB, lower biomass of *Limecola* and higher biomass of surface deposit-feeders with a life span of 1–3 years implies a higher carbon turnover. Still, simulated retention in *Limecola* biomass compared to annual addition of organic carbon was similar in the two sites (28% in GoF and 24% in GB in 2005).

Our values are comparable to earlier estimates for the Baltic Sea. Ankar (1977) calculated the respiration of a macrofauna stock of 5–6 g C m^{-2} to be 20–24 $\text{g C m}^{-2} \text{ year}^{-1}$ or ca 40% of sedimentation in

the Askö area (i.e. around the GB site). Kuparinen et al. (1984) calculated a carbon budget for a location nearby the GoF site in 1980: a macrofauna stock of 2–4 g C m⁻² ingested ca 30–51% of the sedimentation of 37 g C m⁻² year⁻¹ and respired 22–35%. Elmgren (1984) estimated that a macrofauna stock of 4 g C m⁻² mineralised 16 g C m⁻² year⁻¹ or 34% of annual sedimentation for the whole Baltic Sea. In a more recent study of the Baltic Sea-North Sea transition zone, Hansen and Bendtsen (2013) estimated that benthic macrofauna mineralised almost 60% of annual sedimentation.

L. balthica, although relatively sessile, is an efficient bioturbator, increasing sediment mixing and oxygenation (Viitasalo-Frösén et al., 2009; Volkenborn et al., 2012), which probably enhances the rate of organic matter degradation (Chen et al., 2017; Kristensen, 2001). In shallow intertidal sediments *L. balthica* also causes sediment destabilisation and resuspension (Willows et al., 1998; Wood and Widdows, 2002), but in Baltic Sea muddy sediments it seems to decrease resuspension and turbidity. Both the metabolism and the bioturbation of *L. balthica* seems to increase benthic-pelagic fluxes of inorganic nutrients (Michaud et al., 2006; Norkko et al., 2013; Viitasalo-Frösén et al., 2009) and greenhouse gases (Bonaglia et al., 2017), implying that the recorded biomass increase has had large effects on biochemical cycles and ecosystem functioning.

4.3. Model performance and next steps

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. Overall, the model could simulate the biomass levels of the benthic macrofauna as a function of organic matter input and benthic food-web dynamics, suggesting that the main processes are indeed captured. The skill and generality of the model can also be seen in the ability to reproduce the different biomass dynamics at the two sites without any site-specific tuning of parameters.

It should be noted that the current model setup coupling a large-scale pelagic model to a local benthic system worked well in aphotic, muddy systems dominated by vertical POC fluxes, but the current setup might not be applicable to shallower coastal sites with more complex topography and stronger influence of local variations in substrate and lateral fluxes of organic matter. Indeed, also in the current study the ignored lateral processes of resuspension and sediment focussing add uncertainty to the quantifications of carbon fluxes to the bottom.

The simulation was set to start at the lowest recorded biomass of *Limecola balthica* in the Gulf of Finland site, to see if the radical change could be reproduced by the model. The rate of increase in the 1990s is well captured by the model, suggesting that the reparametrized physiological rates of the *Limecola* functional group are realistic. The sensitivity analysis showed that the maximum ingestion rate $I_{\max,mac}$ has a strong effect on this response rate, while it has virtually no effect on biomass when food-limited (Fig. S2). When food-limited, the magnitude of loss terms such as basal respiration $r_{b,mac}$ affect the level of biomass. In the original model by Timmermann et al. (2012) parameter values were based on measurements of *L. balthica* from an intertidal sand flat in the fully saline north Atlantic. It is likely that *L. balthica* populations in the current study sites have acclimated or adapted to the lower salinity, availability of fresh phytoplankton and more stable conditions by exhibiting lower physiological rates and a longer life-span (e.g. Gusev and Jurgens-Markina, 2012, see Materials and methods), as the Atlantic and Baltic populations have diverged some 2 million years ago (Luttikhuisen et al., 2012; Väinölä and Johannesson, 2017).

Even though the dynamics in the current models were strongly dominated by *Limecola*, the sensitivity analysis showed that the model is able to simulate systems without a dominance of *Limecola* (S1.2, Fig. S6). In the no *Limecola* GoF run, the mass of the other state variables were maintained at the same order of magnitude as the initial

conditions in the GoF standard run. Thus, the model is able to simulate the GoF system both with and without *Limecola*, but not the reason for the low *Limecola* biomass.

To address this main knowledge gap, the ‘missing’ *M. balthica* biomass in the early 1990s and before, possible 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 *Limecola* (Bonsdorff et al., 1995; Elmgren et al., 1986; Segerstråle, 1978), and could also restrain the fluctuations in surface deposit-feeder biomass.

We have developed a model of carbon fluxes through macrofaunal functional groups in soft-sediment communities. The model is very simple and thereby cannot explain some intricate population processes, but it is, however, able to quantify a main benthic-pelagic link, the relationship between primary production, sedimentation and macrofaunal community biomass. As the model performance in reproducing radical changes is fairly good, a next step could include future scenario simulations to unravel how changes in trophic state in combination with ongoing climate change (BACC II Author Team, 2015) might alter the system in the future. For example, would progressive eutrophication result in a decrease of large species such as *M. balthica*, as predicted by classical theory (Pearson and Rosenberg, 1978; Rumohr et al., 1996)?

We also show that macrofauna can process the majority of organic carbon sedimentation in two coastal soft-sediment systems. Thus, our results support the recent calls for inclusion of benthic animals as consumers of organic carbon in biogeochemical models to improve the understanding of sediment diagenetic processes and the global carbon cycle in a changing world (Middelburg, 2018; Snelgrove et al., 2018).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jmarsys.2019.04.003>.

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