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PERSPECTIVE

Organic matter export to the seafloor in the Baltic Sea: Drivers of change and future projections

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Abstract The impact of environmental change and anthropogenic stressors on coastal marine systems will strongly depend on changes in the magnitude and composition of organic matter exported from the water column to the seafloor. Knowledge of vertical export in the Baltic Sea is synthesised to illustrate how organic matter deposition will respond to climate warming, climate-related changes in freshwater runoff, and ocean acidification. Pelagic heterotrophic processes are suggested to become more important in a future warmer climate, with negative feedbacks to organic matter deposition to the seafloor. This is an important step towards improved oxygen conditions in the near-bottom layer that will reduce the release of inorganic nutrients from the sediment and hence counteract further eutrophication. The evaluation of these processes in ecosystem models, validated by field observations, will significantly advance the understanding of the system's response to environmental change and will improve the use of such models in management of coastal areas.

Keywords Acidification · Baltic Sea · Climate warming · Eutrophication · Organic matter export · Pelagic food web

INTRODUCTION

The input of organic matter (OM) from the water column to the sediment through sinking of particulate material is a key process connecting pelagic and benthic food webs in freshwater and marine ecosystems. Benthic animal communities below the depth of the euphotic zone are primarily fuelled by this material, which also acts as a driver for remineralisation of carbon and nutrients. OM supply to the seafloor therefore has a structuring effect on the marine food web with strong feedbacks to the magnitude and type of productivity in the system (e.g. Petersen and Curtis 1980; Nixon et al. 2009). Furthermore, the strength of coupling between pelagic and benthic processes determines the trajectory for a system's response to environmental perturbations (Blanchard et al. 2011). Coastal and shelf environments in temperate and polar regions typically reveal a high connectivity between pelagic and benthic food webs due to their shallow depth (e.g. Tamelander et al. 2006; Kopp et al. 2015). These environments are also the part of the ocean most strongly affected by anthropogenic pressures such as nutrient loading and climate warming (Cloern et al. 2016). Eutrophication-related OM deposition to the seafloor in environments with slow water renewal may have adverse effects on ecosystem structure and functioning, with sediment hypoxia constituting a prominent example (Diaz and Rosenberg 2008). OM export and its response to environmental drivers should therefore be an integral part of holistic ecosystem-based management of coastal seas.

The semi-enclosed, brackish Baltic Sea is an example of a shallow system affected by anthropogenic-induced eutrophication (Fleming-Lehtinen et al. 2008) and rapid warming (Belkin 2009) that is also vulnerable to acidification (Havenhand 2012). Hypoxia of near-bottom water is augmented by OM inputs to the seafloor in areas with poor water exchange (Vahtera et al. 2007; Carstensen et al. 2014). Long-term excessive OM loading has contributed to the drastically reduced phosphorus binding capacity of the sediment under anoxic conditions in coastal parts of the Baltic Sea (Lehtoranta et al. 2008). OM export is therefore

an integral part of the eutrophication cycle in the Baltic Sea. Earlier studies of OM export have revealed its regional and seasonal patterns in relation to primary production (Elmgren 1984), phytoplankton dynamics (Heiskanen and Kononen 1994; Tamelander and Heiskanen 2004), pelagic food web structure (Smetacek et al. 1984), and hydrodynamic forcing (Blomqvist and Heiskanen 2001; Tamelander and Heiskanen 2004). The long-term variation in relation to climate change and eutrophication has not been addressed, however. The impacts of environmental drivers (climate warming, acidification) on OM cycling in the pelagic food web and its feedbacks to the benthic system in the Baltic Sea have also not been addressed in recent papers discussing this system (Griffiths et al. 2017).

The lack of consistent historical data on OM export limits the ability to validate models that simulate biogeochemical cycling (Meier et al. 2011) and benthic secondary production (Timmermann et al. 2012). Modellers especially acknowledge the challenge of sedimentary processes for simulating inorganic nutrient dynamics and feedbacks to pelagic primary production (Meier et al. 2011). The dependency of labile OM for sediment chemistry, as shown by Lehtoranta et al. (2009), suggests a pivotal role of pelagic inputs for the sediments' function as a source or sink of nutrients. OM deposition therefore needs to be carefully considered when models are used to evaluate nutrient load reductions by wastewater treatment and agricultural practices under future climate scenarios. This requires a thorough understanding of how the controlling factors respond to environmental drivers.

To advance the understanding of OM cycling in coastal ecosystems, we provide an overview of OM export in the Baltic Sea, discuss how this may change under projected future climate scenarios, and identify knowledge gaps. Although we focus on the Baltic Sea, the processes discussed are relevant to other coastal and estuarine systems affected by the same stressors. OM export and its regulation have typically been considered in the context of the biological carbon pump, applicable to open ocean environments (e.g. Turner 2015). Our synthesis emphasises the role of OM export for ecosystem structure and functioning in shallow coastal areas, which are the systems most commonly targeted by management efforts aimed at improving marine environmental status.

ORGANIC MATTER EXPORT IN THE BALTIC SEA AND INFERRED TEMPORAL TRENDS

Vertical export of OM from the water column to the seafloor has largely been estimated by means of sediment traps in different parts of the Baltic Sea. The estimated annual export varies between 18 and 60 g C m^{-2} year^{-1} (Table 1). OM export rates are highly variable over the season with the highest fluxes typically occurring during or after the spring bloom when new production is high. Summertime OM export may be significant in some years and regions, reaching comparable daily sinking rates as in spring (Gustafsson et al. 2013). The magnitude of summertime export varies more strongly compared to spring exports, however, likely reflecting inter-annual variations in the extent and duration of cyanobacterial blooms and variability in the summer plankton community compared to diatom-dominated spring communities (Simis et al. 2017).

Long-term sediment trap records from the same locations are lacking to address the extent of inter-annual variability in OM export. However, changes in OM deposition can, in some instances, be inferred indirectly from either sediment proxies or from properties of the marine food web. In the Bothnian Sea, reduced OM deposition during a period of decreased primary production was the likely reason for the drastic decline in the abundance of the benthic amphipod *Monoporeia affinis* between 1998 and 2001 (Wiklund and Andersson 2014). In the central Baltic Sea (northern Baltic Proper and Gulf of Finland), OM deposition to the seafloor has likely increased in response to the significant (150%) increase in summer phytoplankton biomass between the 1970s and the early 2000s (Suikkanen et al. 2007; Fleming-Lehtinen et al. 2008). Indirect support is given by the high organic carbon content and high abundances of cyanobacterial pigments in surface sediments in these areas compared to parts of the Baltic Sea where cyanobacteria are less common such as the Bothnian Sea (Leipe et al. 2011; Josefson et al. 2012). The northern Baltic Proper is currently also the sub-basin most strongly affected by near-bottom water hypoxia. The primary reason

Table 1 Annual primary production (PP) and vertical export of particulate organic carbon (POC export) determined by means of sediment traps in different parts of the Baltic Sea. Depth is the bottom depth at the study sites

Region	Depth (m)	PP (g C m^{-2})	POC export (g C m^{-2})
Northern Baltic Sea Bothnian Sea[a]	125	105	18
Central Baltic Sea N Baltic Proper[b]	459	169	50
Gulf of Finland[c]	50	107	38
Southern Baltic Sea Kiel Bight[d]	17	125–175	30–60

[a] Lehtonen and Andersin (1998)

[b] Gustafsson et al. (2013)

[c] Heiskanen and Tallberg (1999)

[d] Smetacek et al. (1984)

for this is the poor exchange of the near-bottom water (Carstensen et al. 2014), but excess deposition of OM below the permanent halocline at ca 70 m depth accelerates the development of hypoxic or anoxic conditions. Sediment trap data from the coastal western Gulf of Finland suggest high inter-annual variation in vertical export during the spring period (Fig. 1).

Documented changes in sediment remineralisation and benthic metabolism in other regions have been largely connected to warming and related changes in water column stability and inorganic nutrients. In Narragansett Bay, winter–spring phytoplankton blooms were delayed and diminished following a shift towards higher water temperature, with negative feedbacks to OM export indicated by reduced sediment nutrient remineralisation (Nixon et al. 2009). Reduced benthic metabolism in the Bering Sea during a decade characterised by increasing sea water temperature and loss of sea ice suggests that the changes in hydrography had negative impacts on primary production and OM export (Grebmeier et al. 2006). The pelagic food web exerts strong control of OM export from the water column (Wassmann 1998), and changes in phytoplankton-derived export therefore further depend on the response of pelagic grazers (microzooplankton and mesozooplankton) and top-down control in the pelagic food web to environmental change. This is particularly evident in oligotrophic systems where natural (climate-controlled) or artificial (experimental) fertilisation stimulates the pelagic food web rather than vertical export of fresh phytoplankton (Thingstad et al. 2005; Forest et al. 2011). Both nutrient inputs

and climate are important for the production and cycling of OM in the water column, and therefore for OM export.

MARINE AND TERRESTRIAL SOURCES OF ORGANIC MATTER

Phytoplankton typically dominates the primary production budget in areas where the total water column depth is greater than the euphotic zone depth and comprises a major source of organic matter to OM exported from the surface layer in most marine systems. However, in coastal areas and semi-enclosed systems such as the Baltic Sea the input from benthic primary production, riverine, and terrestrial sources also contributes to OM deposition and benthic energy intake (Tallberg and Heiskanen 1998; Goñi et al. 2000; Renaud et al. 2015). The total and relative contribution from these sources may change as a result of climate-induced changes in water column stratification, sea ice cover, wind patterns, and freshwater runoff from land.

Future trends in pelagic primary production in the Baltic Sea largely depend on the availability of inorganic nutrients, which again depend on external nutrient inputs and climate (Meier et al. 2011). Under projected climate change and present nutrient loading from land, phytoplankton biomass will increase in the south-western Baltic Sea, in coastal parts of the Gulf of Finland and in the western coastal Baltic proper, while it may decrease in the central open Baltic Proper (Meier et al. 2011). The largest changes in phytoplankton-derived inputs can therefore be expected in these areas (Table 2). However, in a scenario of increased nutrient loading phytoplankton biomass increases in almost the entire southern and central Baltic Sea due to an interaction between nutrient loading and climate (Meier et al. 2011). The Bothnian Bay system is strongly influenced by terrestrial dissolved organic carbon (DOC), which acts as a substrate for heterotrophic bacteria and therefore gives bacteria an advantage over phytoplankton in the competition for inorganic nutrients (Wikner and Andersson 2012). Increased river discharge as a consequence of climate warming (Meier et al. 2011) will likely increase bioavailable terrestrial DOC in the Bothnian Bay system and may hence have a negative feedback to phytoplankton primary production (Wikner and Andersson 2012). These projected changes can be considered to indicate the direction of change or maximum potential increase or decrease in export of pelagic OM.

In coastal areas, particles settled on the sediment surface often become resuspended in the water column during wind-driven mixing. In the Baltic Sea, resuspension is roughly restricted to waters shallower than the permanent halocline at ca 70 m depth. Some of this material may settle again locally, but a variable fraction is also
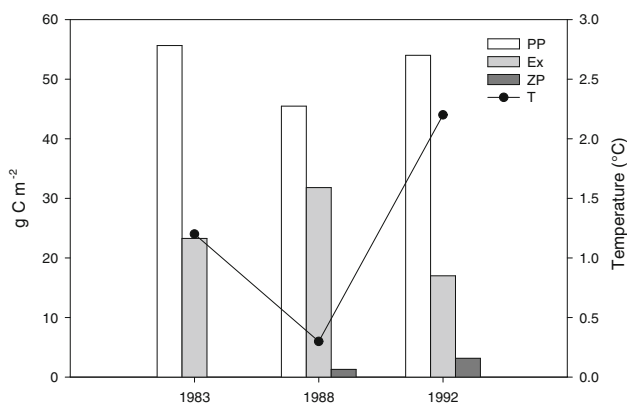

Fig. 1 Phytoplankton primary production (PP), sinking (Ex) and grazing by zooplankton (ZP), and temperature (T, line) during spring in the western Gulf of Finland during the 3 years with available comparable datasets. The 1983 data are from Heiskanen and Leppänen (1995), 1988 data from Lignell et al. (1993), and 1992 data from Heiskanen and Tallberg (1999) and Koski et al. (1999). Zooplankton production was not determined in 1983 (ND). Temperature is the April mean of 0, 5, and 10 m depth, measured on the same three dates in each year. The temperature data were provided by the Finnish Meteorological Institute

Table 2 Impact of environmental drivers on organic matter export, mechanism, direction of change (±), and the region of the Baltic Sea or type of environment where the strongest effect is expected

Driver	Mechanism	Effect	Affected regions
Warming	Increased summer primary production	+	S Baltic Sea, Gulf of Finland, Bothnian Sea, largest increase in coastal areas
	Increased heterotrophy and match between phytoplankton and zooplankton	−	Entire Baltic Sea
Freshwater discharge (warming)	Reduced primary production (light limitation, competition for N and P between bacteria and phytoplankton)	−	N Baltic Sea
	DOM flocculation	+	River outlets, N Baltic Sea
Sea ice loss (warming)	Advanced spring bloom	+	N Baltic
Wind stress	Resuspension in coastal areas	+	Northern Baltic Sea, net input to deep sites below halocline
Nutrient load reductions	Decreased primary production	−	Entire Baltic Sea, largest impact in coastal areas
Acidification	Increased primary production by small cells and increased algal DOM release	− (?)	Entire Baltic Sea

transported offshore and contributes to deposition in deeper areas (Almroth-Rosell et al. 2011). In the Baltic Sea with an average depth of 54 m, resuspension accounts for ca 50% of the deposition of OM to the seafloor as measured by sediment traps (Blomqvist and Larsson 1994). Climate projections for the Baltic Sea predict a future increase in wind stress of the sea surface in response to warming and continued loss of seasonal sea ice (Christensen et al. 2015), which would increase resuspension in coastal areas (Table 2). Model simulations of the effects of climate warming show a future increase in the frequency and magnitude of resuspension events, with the strongest effect in shallow coastal areas <6 m deep (Eilola et al. 2013). As a result, sediment organic carbon content will increase in deep accumulation areas as material resuspended in shallow (<60 m) coastal areas is transported offshore and settles, while in coastal areas sediment organic carbon content will decrease due to enhanced remineralisation (Eilola et al. 2013). Furthermore, increased wave forcing leads to greater detachment of macroalgae from the seafloor in

shallow coastal areas and their dispersal with currents. The quantitative importance of macroalgae detritus for OM deposition in the Baltic Sea is largely unknown, but is conceivably important since the biomass of benthic filamentous algae has increased in response to nutrient loading from land (Bonsdorff et al. 1997).

Freshwater runoff from land is a significant source of dissolved organic matter (DOM) in coastal areas. In the Baltic Sea, the magnitude of this source is dependent on the amount of freshwater discharge and the type of vegetation in the catchment area (Kaartokallio et al. 2016). While DOM does not sink directly, flocculation of DOM into particulate material occurs in salinity transition zones in river mouths where it may sink (Sholkovitz et al. 1978; Asmala et al. 2014). Flocculation of DOM likely introduces particulate matter with high carbon and low nitrogen content to the seafloor in estuarine systems, since the C:N ratio of DOM is higher (around 20 a:a, Hoikkala et al. 2012) compared to that of water column suspended particles (6-8; Tamelander and Heiskanen 2004). Freshwater runoff is projected to increase by 15–22% in the Baltic Sea during the coming century due to increased precipitation over land (Meier et al. 2012). This will likely increase the input of terrestrially derived material in estuarine parts of the northern Baltic Sea where the largest increases in precipitation and runoff are expected to occur (Sonnenborg 2015; Table 2).

IMPACT OF PELAGIC TROPHIC PATHWAYS ON OM EXPORT

Grazing by zooplankton on phytoplankton channels energy from primary production towards the pelagic food web, leading to the retention of phytoplankton biomass in the water column. The trophic coupling between pelagic primary and secondary producers is therefore a key factor determining the magnitude and composition of OM export. This is illustrated by a negative relationship between vertical export and the ratio between pelagic heterotrophic and autotrophic biomass, as seen in the Arctic Ocean (Fig. 2). Remarkably, smaller sinking of particulate organic carbon is observed when heterotrophs dominate the pelagic food web (H:A >1, Fig. 2a). When autotrophic biomass dominate (H:A <1), the "non-grazed" carbon is available for vertical export. The relation of OM export and pelagic heterotroph:autotroph ratio is not known for the Baltic Sea, but it can be expected that the processes are similar, at least in open Baltic Sea waters where the influence of terrestrial OM sources is minimal.

Initiation of the phytoplankton spring bloom is determined by irradiance (Sommer et al. 2012) and is therefore sensitive to changes in water column stability and sea ice
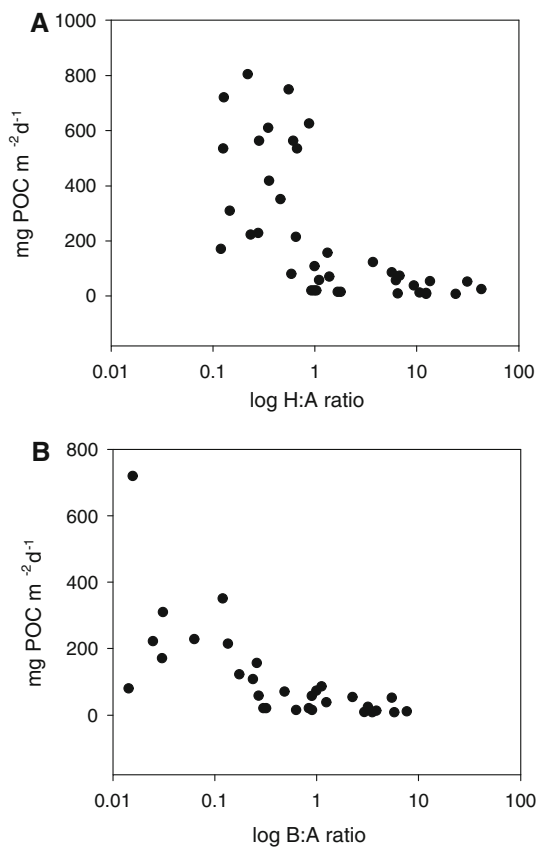
Fig. 2 Relationship between **a** vertical flux of particulate organic carbon (POC) in the Arctic Ocean and the ratio of total pelagic heterotrophic biomass (*H* bacteria, protozoans, and metazoans) to autotrophic biomass (*A* phytoplankton) determined during the course of sediment trap deployments, and **b** POC vertical flux versus the ratio of bacterial biomass (*B*) to phytoplankton. See Appendix S1 for a description of the data

that in turn affect the water column light conditions. These are strongly related to temperature, which therefore has indirect effects on spring bloom phenology. As in polar regions, temperature affects the duration and temporal extent of sea ice cover in the northern Baltic Sea, with profound effects on bloom development (e.g. Ardyna et al. 2014). Many temperate coastal systems affected by warming now experience an earlier onset of spring term primary production (Winder and Sommer 2012), whereas in other areas warming has resulted in a delayed or diminished winter–spring bloom (Nixon et al. 2009). A shift towards earlier, more prolonged spring blooms (but with lower average biomass) has taken place in the central Baltic Sea over the past 20 years (Groetsch et al. 2016; Kahru et al. 2016). In years with extensive sea ice cover, the spring bloom peaks in late April or early May in the western Gulf of Finland, but in more recent years characterised by ice-free winters (Merkouriadi and Leppäranta 2014), the spring bloom peak has been observed in early April (Tamelander and Heiskanen 2004) or late March

(Tamelander, pers. obs.). During the summer period characterised by stratification of the surface layer, temperature has a more direct effect on primary production since cyanobacteria, an important component during the summer months, generally grow faster at higher temperature. In conclusion, the seasonal succession in the phytoplankton community and occurrence of phytoplankton blooms are important factors determining the seasonal pattern in OM export (Tamelander and Heiskanen 2004).

Heterotrophic processes on the other hand are strongly dependent on temperature. In copepods, growth rates are higher and development times are shorter at higher temperature, as seen in e.g. *Acartia clausi* (Leandro et al. 2006). Furthermore, energy demand increases with increasing metabolic maintenance costs (respiration) at higher temperatures. Documented effects of climate warming on zooplankton typically include changes in the distribution, phenology, and community composition (Richardson 2008). In the southern Baltic Sea, the biomass of the dominant copepod species *Acartia* spp. and *Temora longicornis* were higher during the 1990s characterised by higher temperature and predominately positive NAO index compared to the colder period 1960–1980 (Alheit et al. 2005). Copepod biomass in spring has been found to respond positively to mild winters in both southern (Feike et al. 2007) and northern coastal parts of the Baltic Sea (Viitasalo et al. 1995), likely due to increased hatching of eggs and shorter development time at higher temperature, as suggested by Alheit et al. (2005). Temperature also emerges as the main driver for changes in summer zooplankton populations in the northern Baltic Sea, but the responses differ from those observed in spring (Suikkanen et al. 2013). Total zooplankton abundance has decreased since 1979 and rotifers have increased both in total and relative numbers, whereas copepods and cladocerans have decreased (Suikkanen et al. 2013). In the Baltic Sea, salinity also plays an important role for the community composition, with cladocerans and rotifers being favoured by lower salinity and copepods being favoured by higher salinity (Viitasalo et al. 1995; Möllmann et al. 2000). Because salinity changes in the Baltic Sea largely depend on runoff from land (driven by precipitation) and inflow of North Sea water (driven by atmospheric forcing), salinity-related changes in zooplankton communities are subject to climatic forcing.

Changing phenology and community composition of phyto- and zooplankton will likely have a major impact of OM deposition in coastal areas. Model results from the coastal Disko Bay area of western Greenland revealed that increased phytoplankton grazing caused significantly lower vertical export in a warm scenario, in spite of higher primary production (Hansen et al. 2003). Experimental studies in the southern Baltic Sea also show that warming leads

to shorter time lag between phyto- and microzooplankton during spring and increased trophic transfer from phytoplankton to the pelagic food web (Aberle et al. 2012). These observations suggest that climate warming will reduce the amount of pelagic OM available for vertical export due to increased zooplankton grazing (Table 2).

Vertical export is the main loss factor during the Baltic Sea spring bloom due to low overwintering stocks of zooplankton and slow development of heterotrophic biomass at the typically low water temperature during bloom development. For example, as much as 70% of the vernal primary production was found to sink out of the water column during a cold winter–spring with late breakup of the sea ice cover in the western Gulf of Finland (Lignell et al. 1993). However, export was smaller in two warmer years although primary production was comparable in magnitude to the colder year (Fig. 1). Higher growth rate of zooplankton in 1992 and 1983 favoured by the higher temperatures in these years conceivably led to higher grazing losses and smaller export than in the colder year 1988 (Fig. 1). Experimental work on effects of warming on Baltic Sea summer communities also show reduced phytoplankton biomass, which the authors intrepreted as a result of increased grazing (Paul et al. 2015). Filamentous cyanobacteria are an important component of summertime phytoplankton communities, but are considered not to be extensively grazed by mesozooplankton (copepods, cladocerans). However, microzooplankton has been suggested to feed on decaying cyanobacteria, which would channel phytoplankton biomass towards the pelagic food web, thus reducing sinking losses during summer (Engström et al. 2000; Koski et al. 2002).

Sea surface temperature has been projected to increase by 2–3°C in the Baltic Sea by the end of the twenty-first century (Meier 2015). This suggests that the frequency of years with match between auto- and heterotrophic plankton during spring will increase, and that grazing during summer and autumn will increase. Warming will hence increase the retention of OM in the water column through increased energy transfer from primary production to the pelagic food web. Depending on the change in primary production, this could either reduce vertical export (if primary production is unaffected), or shift its composition to more degraded material (if primary production increases but a higher proportion is channelled towards the pelagic food web). Field evidence indicating which process would dominate is not available from the Baltic Sea. However, in the Canadian Arctic, the flux of OM through the pelagic detritus pool was higher during an exceptionally warm year with little sea ice than during a year with normal ice cover (Forest et al. 2011). While gross primary production was higher by 80% in the warmer year, vertical export only increased by 30% (Forest et al. 2010, 2011), which

highlights the importance of pelagic heterotrophic processes for OM cycling under warmer conditions.

Increasing amount of dissolved organic matter (DOM) in coastal waters from terrestrial and freshwater sources may further affect pelagic microbial auto- and heterotrophic production with potential effects on OM export. Elevated DOM was found to stimulate bacterial growth and suppress primary production in the northern Baltic Sea due to increased competition for inorganic nutrients between bacteria and phytoplankton and reduced light levels at elevated DOM concentrations (Wikner and Andersson 2012). Ca 10% of the dissolved organic carbon is bioavailable and degraded in the short term in Finnish rivers draining into the Baltic Sea (12–18 days; Asmala et al. 2013). The net effect of these processes is an increasing importance of microbially mediated carbon flows in the pelagic food web (Wikner and Andersson 2012). OM export will most conceivably decrease in areas where primary production is suppressed by river discharge and a strengthened microbial food web (Table 2). We do not currently have field observations from the Baltic Sea to support this view. However, data from the Arctic Ocean reveal a pattern of higher OM export when phytoplankton dominate the base of the food web compared to situations where bacteria dominate (Fig. 2b). The quality and quantity of DOM and the microbial food web structure in the Arctic Ocean likely differ from those in the Baltic Sea. Yet, the relationship in Fig. 2b illustrates an important functional difference between pelagic food webs based on DOM and bacteria and those based on inorganic nutrients and phytoplankton, relevant to projected changes in DOM loading from rivers in a future warmer Baltic Sea (c.f. Wikner and Andersson 2012).

IMPACT OF ACIDIFICATION ON PELAGIC PROCESSES AND ORGANIC MATTER EXPORT

A large share of the increasing CO_2 concentration in the atmosphere is taken up by the ocean where it reacts with sea water to form a weak acid. The resulting long-term decrease in pH is termed ocean acidification. In some ecosystems, experimental results suggest that higher CO_2 concentration increases primary production, with potential implication for export of OM (Riebesell et al. 2007). However, this is not universal and the effect, if any, of ocean acidification on OM export will, to a large extent, depend on the plankton community composition (Passow and Carlson 2012; Eggers et al. 2014). In a recent mesocosm experiment in the Baltic Sea, increasing the CO_2 concentration during summer conditions with low inorganic nutrients increased the standing stocks of particulate and dissolved organic carbon but did not increase the

particulate export due to small cells and non-sinking forms of carbon (Spilling et al. 2016). If the new phytoplankton biomass does not sink directly or indirectly (e.g. through aggregate formation or in zooplankton faecal pellets), the effect will presumably be a more prevalent microbial loop and stronger OM retention in the water column (Table 2).

For zooplankton, the sensitivity to ocean acidification seems to be species specific, ranging from no effect to negative effects on recruitment (Riebesell and Tortell 2011). This is similar in the Baltic Sea: during a mesocosm experiment, lower pH reduced the size and fitness of *Acartia* sp. (Vehmaa et al. 2016), but had no apparent effect on *Eurytemora affinis* (Almén et al. 2016). Mesocosm studies on summer communities also show that possible acidification effects are overridden by temperature-dependent increase in pelagic heterotrophic carbon demand and consumption of phytoplankton (Paul et al. 2015). The limited knowledge of acidification effects on zooplankton prevents any conclusions on the feedbacks to vertical export. However, the experimental data suggest that acidification will mainly have bottom-up effects on export through the phytoplankton community, whereas top-down effects mediated by zooplankton mainly depend on warming. Acidification effects on whole pelagic communities are also likely to be dampened by the species richness and tropic interactions, as shown in a Baltic Sea mesocosm study (Rosoll et al. 2013).

CONCLUSIONS

Our synthesis illustrates that climate change directly and indirectly affects OM export in the Baltic Sea. Key aspects of the projected warming are increasing terrestrial inputs of DOM and a strengthened role of pelagic heterotrophic processes in OM cycling. In combination with nutrient load reductions, these changes may reduce OM deposition to the seafloor, which will contribute to improved oxygen conditions of the near-bottom water. These are important steps towards reduced inorganic nutrient release from the sediment and will hence counteract further eutrophication. However, in areas where oxygen remains in the near-bottom water (well-mixed coastal areas and parts of the open Baltic Sea unaffected by the permanent halocline), reduced OM export will have a negative feedback to benthic secondary production (Timmermann et al. 2012).

From a management point of view, it is important that ecosystem models realistically capture the mechanisms involved in OM cycling and export, since these processes have feedbacks to the distribution of healthy benthic habitats, benthic secondary production, and biogeochemical cycling in the Baltic Sea. In order to improve such models, more efforts should be directed towards understanding heterotrophic responses to climate warming, e.g. by modelling the production and phenology of different phytoplankton grazers (microzooplankton, mesozooplankton) and bacteria. Field studies are a necessary means to provide validation data, since OM fluxes from mesocosm studies are not extractable to natural conditions. Data on pelagic food web structure, primary and secondary production, and phenology in the contemporary Baltic Sea will be particularly important to support the interpretation of model results and to further shed light on OM deposition in the marine system.

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