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RESEARCH REVIEW

The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world

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Abstract

Benthic–pelagic coupling is manifested as the exchange of energy, mass, or nutrients between benthic and pelagic habitats. It plays a prominent role in aquatic ecosystems, and it is crucial to functions from nutrient cycling to energy transfer in food webs. Coastal and estuarine ecosystem structure and function are strongly affected by anthropogenic pressures; however, there are large gaps in our understanding of the responses of inorganic nutrient and organic matter fluxes between benthic habitats and the water column. We illustrate the varied nature of physical and biological benthic–pelagic coupling processes and their potential sensitivity to three anthropogenic pressures – climate change, nutrient loading, and fishing – using the Baltic Sea as a case study and summarize current knowledge on the exchange of inorganic nutrients and organic material between habitats. Traditionally measured benthic–pelagic coupling processes (e.g., nutrient exchange and sedimentation of organic material) are to some extent quantifiable, but the magnitude and variability of biological processes are rarely assessed, preventing quantitative comparisons. Changing oxygen conditions will continue to have widespread effects on the processes that govern inorganic and organic matter exchange among habitats while climate change and nutrient load reductions may have large effects on organic matter sedimentation. Many biological processes (predation, bioturbation) are expected to be sensitive to anthropogenic drivers, but the outcomes for ecosystem function are largely unknown. We emphasize how improved empirical and experimental understanding of benthic–pelagic coupling processes and their variability are necessary to inform models that can quantify the feedbacks among processes and ecosystem responses to a changing world.

Keywords: benthic, climate change, ecosystem dynamics, ecosystem function, fishing, nutrient loading, pelagic

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Introduction

Coastal and estuarine ecosystems are hot spots of environmental variability, biogeochemical transformations, and biological interactions, where dynamic exchanges of energy, mass, and nutrients occur between benthic and pelagic habitats via diverse pathways. Consequently, they are among the world's most productive ecosystems (Nixon, 1988; Berger *et al.*, 1989; Costanza

et al., 1995) that provide important ecosystem services, such as food provision and water filtration (Agardy *et al.*, 2005; Granek *et al.*, 2010). These transitional ecosystems between land and sea are often densely populated and experience multiple anthropogenic pressures including climate change, nutrient loading, and fishing (Lotze *et al.*, 2006; Halpern *et al.*, 2008; Cloern *et al.*, 2016).

The implementation of effective management strategies that mitigate or adapt to human-driven changes in these ecosystems requires a better understanding of how anthropogenic pressures can cause changes in

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ecosystem structure and function. Essential ecosystem functions, such as production and energy transfer in food webs, biogeochemical cycling, and provisioning of fish nursery areas (Granek *et al.*, 2010; Seitz *et al.*, 2014), are supported by multiple and interacting benthic–pelagic coupling processes (e.g., Chauvand *et al.*, 2000). We define benthic–pelagic coupling as those processes which connect the bottom substrate and the water column habitats through the exchange of mass, energy, and nutrients. However, the compartmentalization of these ecosystems into their benthic and pelagic components in empirical studies and models often limits our understanding of the scope and strength of interactions between these habitats, their role in maintaining ecosystem function, and their sensitivity to future change.

The traditional view of benthic–pelagic coupling has focused on the deposition of nonliving organic material to benthic habitats (Hargrave, 1973; Suess, 1980; Smetacek, 1985; Graf, 1992), bioresuspension (Graf & Rosenberg, 1997), and the release of inorganic nutrients from the sediments (Raffaelli *et al.*, 2003). These fluxes have been quantified in a variety of ecosystems (e.g., Duineveld *et al.*, 2000; Smith *et al.*, 2006), including the seasonal variation and spatial heterogeneity of these fluxes. Substantial limitations remain, however, in our quantitative predictive capacity of flux occurrence and magnitude and in our ability to generalize among ecosystems. Efforts are increasing to describe and understand the diversity of processes that couple benthic and pelagic habitats, especially those mediated by living organisms (Marcus & Boero, 1998; Schindler & Scheuerell, 2002; Raffaelli *et al.*, 2003; Baustian *et al.*, 2014). These include pelagic predation on benthic fauna, ontogenetic shifts in habitat use, reproductive (life-cycle) fluxes, diel and seasonal migrations, nutrient-cycling effects of benthic bioturbation and bioirrigation, and filter-feeding by benthic organisms. For many of these processes, however, the limited knowledge of their rates and importance impedes our ability to do quantitative syntheses.

Anthropogenic pressures regulate benthic–pelagic coupling directly and indirectly through their effects on the physical (e.g., salinity, oxygen, temperature) and biological (e.g., species, communities, functional traits) components of ecosystems. In coastal and estuarine ecosystems, climate change, nutrient loading, and fishing have been shown to have direct effects on benthic–pelagic coupling with clear consequences for ecosystem function. For example, increased water temperatures in Narragansett Bay (USA) have caused shifts in the timing and a decrease in the magnitude of phytoplankton blooms. This has decreased the deposition of organic material to the benthos and ultimately reduced

inorganic nutrient release from the sediment (Fulweiler & Nixon, 2009; Nixon *et al.*, 2009). Additionally, the loss of oyster reefs in Chesapeake Bay (USA) initiated by overfishing resulted in a decline of water filtration capacity by nearly 200-fold in the last century leading to increased phytoplankton production and declines in water clarity and quality (Kemp *et al.*, 2005). In contrast, the successful establishment of an invasive filter-feeding clam in San Francisco Bay (USA) has resulted in an increased flow of energy into the benthic habitat while depriving pelagic pathways of phytoplankton production (Cloern & Jassby, 2012). Importantly, and despite the above examples, it is still more common to investigate the response of a specific species or community to anthropogenic pressures than to investigate the effects of anthropogenic pressures on processes that couple benthic and pelagic habitats. This strongly limits our ability to assess ecosystem resilience, that is, the ability of an ecosystem to retain its structure and function when exposed to pressures. Advancing the knowledge of how habitat coupling processes respond to anthropogenic pressures will significantly improve our ability to predict ecosystem responses to environmental change and to implement the appropriate management actions to maintain or reach healthy ecosystems.

We use the Baltic Sea as a case study to illustrate how benthic–pelagic coupling shapes coastal and estuarine ecosystems and to evaluate the sensitivity of coupling processes to three anthropogenic pressures: climate change, nutrient loading, and fishing. The high-latitude position of the Baltic Sea (associated with higher rates of warming, for example, Belkin, 2009; Rutgersson *et al.*, 2014) and its large catchment area populated with over 85 million people expose this ecosystem to multiple regional and global anthropogenic pressures that are expected to continue to impact its overall function and health (Elmgren *et al.*, 2015). We examine two categories of benthic–pelagic coupling processes, those that control inorganic nutrient fluxes and those that control organic material fluxes. Within these two categories, we identify key physical and biological processes and review their potential responses to the three anthropogenic pressures listed above. We also identify knowledge gaps and conclude with recommendations about how to address them in coastal and estuarine ecosystems worldwide through observational, experimental, and modeling approaches.

The Baltic Sea

The Baltic Sea is one of the largest brackish water bodies in the world with a geographically stable salinity gradient (surface salinity 1–25; Fig. 1a; Table 1) providing comparisons of benthic–pelagic coupling across the

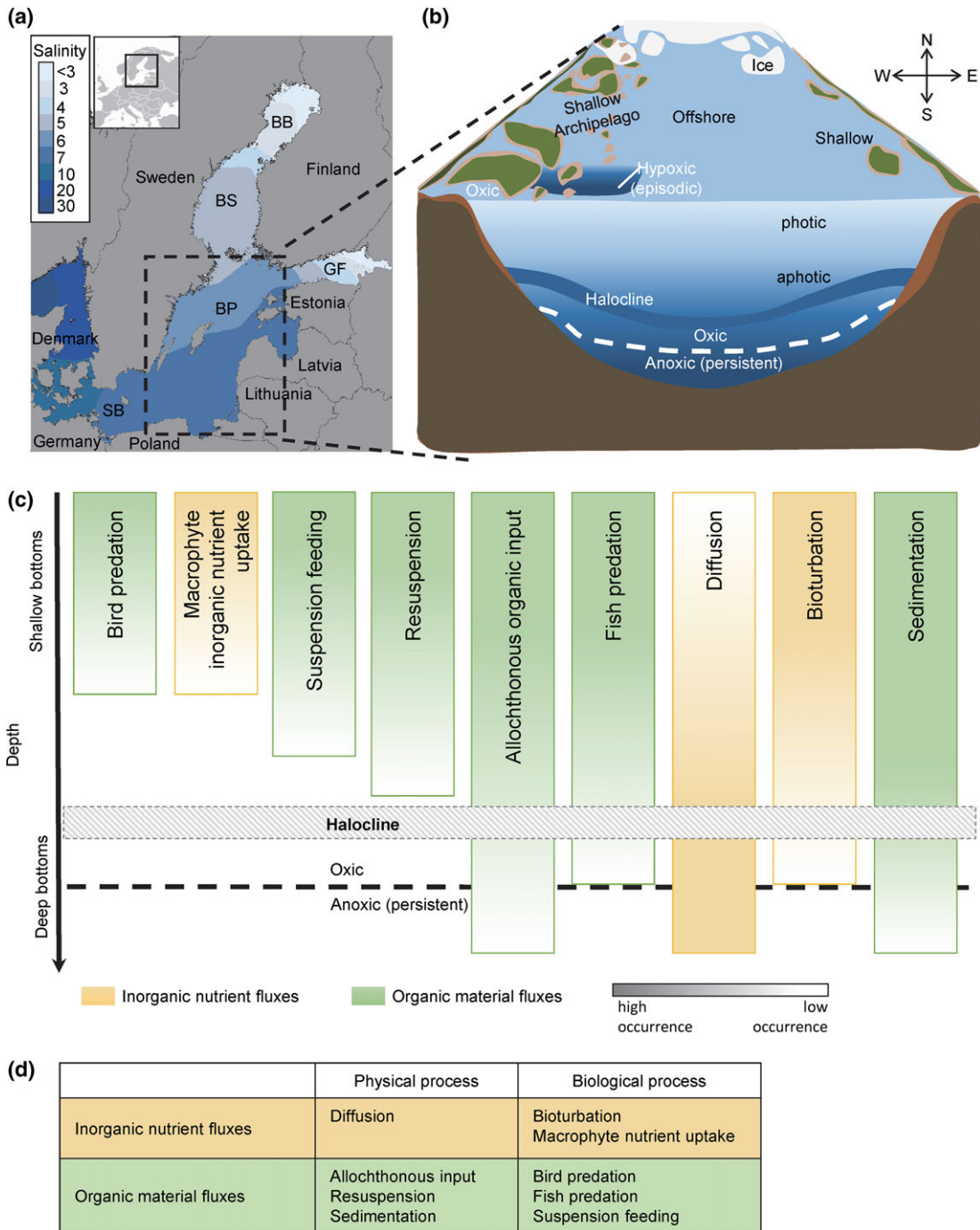


Fig. 1 Map and conceptual visualization of Baltic Sea gradients and benthic–pelagic coupling processes. (a) Baltic Sea salinity gradient and basins: Bothnian Bay (BB), Bothnian Sea (BS), Gulf of Finland (GF), Baltic Proper (BP), and Southern Baltic Sea (SB). (b) A cross section of the Baltic Proper and abiotic gradients. In shallow, coastal areas, there is episodic hypoxia while north to south, there is a strong climatic gradient including the northern areas having winter sea ice cover. Offshore is a semipermanent halocline at ~70 m depth and persistent anoxia in deep areas. (c) Benthic–pelagic coupling processes are represented by the vertical bars. These processes occur at the sediment–water interface, and the y-axis shows the range of bottom depths at which each process occurs. The shading indicates the magnitude of the occurrence (dark = high, light = low) at each bottom depth. The bars are colored by flux type (inorganic or organic). Note that latitudinal gradients in coupling processes are not depicted in (c). (d) The table categorizes benthic–pelagic coupling processes by their role in either the flux of inorganic nutrients or organic material and by whether it is a physical or a biological process.

Table 1 Abiotic and biotic characteristics of major Baltic Sea regions. Data are provided by a specific monitoring station or for the basin as a whole. Shallow and deep station classifications are relative to the maximum depth of each basin. The percent shallow water surface area was defined as the surface area where 1% of available light penetrates to the seafloor relative to the total surface area. The mean regional macrofaunal species diversity is the average richness across stations (>40 m depth) in each basin per year; shown here are the reference values for each basin. The number of benthic invertebrate species and the percent invasive benthic invertebrate species are based upon species presence in each basin including all depths

Depth	Bothnian Bay		Bothnian Sea		Gulf of Finland		Baltic Proper		Southern/Western Baltic		Data source
	Shallow (68 m) CVI	Deep (108 m) BO3	Shallow (104 m) F18	Deep (125 m) SR5	Shallow (47 m) GOF2	Deep (70 m) GOF6	Shallow (63 m) EGB1	Deep (81 m) LF2	Shallow (47 m) BY2	Deep (90 m) BY5	
<i>Abiotic characteristics</i>											
Salinity	3.2	3.8	6.1	6.5	7.2	9.0	7.8	9.4	15.6	15.9	Norkko <i>et al.</i> (2015)
Oxygen (ml l ⁻¹)	8.5	8.6	5.2	5.2	3.4	0.9	4.9	0.0	5.2	0.0	Norkko <i>et al.</i> (2015)
Temperature (°C) mean (min – max)	3.7 (–0.4 to 21.2)	6.0 (–0.4 to 21.4)	4.0 (–0.4 to 21.0)	6.5 (–0.4 to 21.0)	5.7 (–0.5 to 22.9)	7.4 (–0.5 to 24.4)	6.2 (–0.6 to 23.2)	8.3 (–0.7 to 24.1)	9.4 (–1.0 to 22.7)	9.5 (–1.0 to 23.9)	Kotta <i>et al.</i> (2014)
Ice period (days) mean (min – max)	23.5 (16.8–35.2)	30.3 (17.8–43.4)	9.4 (4.3–15.9)	13.1 (8.8–18.5)	17.6 (6.4–50.1)	28.7 (10.6–54.5)	2.6 (0.1–8.7)	4.2 (0.3–8.2)	14.4 (7.3–24.8)	11.2 (2.9–30.3)	Armstrong & Knowles (2010)
% Surface area of shallow waters	29	11	11	13	13	15	69	69	69	69	Based on Helcom data portal GIS layers
<i>Biological characteristics</i>											
Mean regional macrofauna species diversity (1 mm sieve)	2.1	3.3	3.3	5.3	5.3	5.3	5.3	5.3	8.8–14.6	8.8–14.6	Villnäs & Norkko (2011)
Number of benthic invertebrate species	132	147	147	482	482	482	53–164	53–164	300–1028	300–1028	HELCOM (2012)
% invasive benthic invertebrate species	9	8	8	4	4	4	10–30	10–30	2–8	2–8	HELCOM (2012), Baltic Sea Alien Species Database (2010)

entire salinity range from marine to almost-freshwater conditions. Temperature and ice cover also show a north (colder/longer) to south (warmer/shorter) latitudinal gradient (Leppäranta & Myrberg, 2009; Table 1; Fig. 1b) as well as strong seasonal dynamics. The Baltic Sea is relatively shallow with an average depth of 54 m. Mixing and resuspension continue to occur at water depths greater than the photic zone (max. depth ~20 m), but a semipermanent halocline at ~70 m prevents full water column mixing in the Baltic Proper and Gulf of Finland (Fig. 1b). Deep-water oxygen conditions vary by basin (Table 1), but large areas of the central Baltic Sea, as well as the Gulf of Finland, are permanently hypoxic (Carstensen *et al.*, 2014). North–south abiotic gradients are associated with gradients in biological diversity (species richness increases with increasing salinity, Table 1) and phenology.

Air temperature in the Baltic Sea region has increased more rapidly than the global average since the 1870s (BACC II Author Team, 2015), ice season length and ice thickness have declined (Merkouriadi & Leppäranta, 2014), and, since the 1980s, the Baltic Sea is the world's fastest warming large marine ecosystem (net sea surface temperature change of 1.35 °C (1982–2006), Belkin, 2009). The Baltic Sea has been highly impacted by eutrophication throughout the 20th century (Andersen *et al.*, 2015), although the decrease in external nutrient loads since 1980 (1990–2006 decline of 45% total phosphorus, 28% total nitrogen (not normalized for river flow); HELCOM, 2011), has led to local improvements in coastal zones (Elmgren *et al.*, 2015). Fishing pressure along the coast varies in space and time, but is generally moderate. Both recreational and commercial fishery sectors mainly target the same predatory and (often) benthivorous fish species. There are two dominant offshore fisheries: the commercial cod fishery, which is concentrated in the southern and more saline areas, and the mixed fishery for sprat and herring (ICES, 2014).

Future projections of anthropogenic pressures

With continued climate change, the Baltic Sea is projected to become more strongly stratified (Hordoir & Meier, 2011) but with dampened north–south gradients in temperature and salinity (BACC II Author Team, 2015). Climate change projections suggest a continued warming, with summer surface water temperature increasing from 2 °C (south) to 4 °C (north) by the end of this century (BACC II Author Team, 2015). Projections for future salinity are uncertain because Baltic Sea salinity responds both to precipitation in the catchment area (runoff) and saltwater inflows from the North Sea. However, most studies

project declines in both surface and bottom salinities with the largest declines in surface salinity in the more saline (south and west) regions due to both increased runoff and decreasing inflows (BACC II Author Team, 2015).

External nutrient loads have been a major cause of Baltic Sea eutrophication, but the recovery of the ecosystem is governed by internal nutrient recycling (Vahtera *et al.*, 2007). With adherence to the Baltic Sea Action Plan, an international agreement that includes nutrient load reduction targets (HELCOM Ministerial Meeting, 2007), reduction in nitrogen and phosphorus (target reduction from 1997 to 2003 levels is 18.3% of total nitrogen and 42% of total phosphorus) would eventually result in decreased eutrophication under present climate conditions. However, climate change scenarios indicate that increased precipitation and runoff in combination with changes in water column stratification may offset the effects of reduced nutrient input (Meier *et al.*, 2012).

Fishing pressure has the greatest potential for quick adaptation to changes in ecosystem state due to its short response time. The internationally managed commercial fisheries are subject to annual management decisions, while there is less regulation of recreational and small-scale coastal fisheries. Socioeconomic drivers have a strong influence on fishery management decisions, and long-term projections of future changes in fishing pressure are therefore highly uncertain (Lade *et al.*, 2015).

Sensitivity of benthic–pelagic coupling to anthropogenic pressures

A wide range of benthic–pelagic coupling processes control the flow of inorganic nutrients and organic material in the Baltic Sea (Fig. 1c). In the following section, we discuss key physical and biological processes (e.g., diffusion, sedimentation, predation) in view of their current and projected responses to anthropogenic pressures (Fig. 1d). A subset of these processes has been measured in multiple Baltic Sea basins, which we summarize in Table 2.

Inorganic nutrient exchange

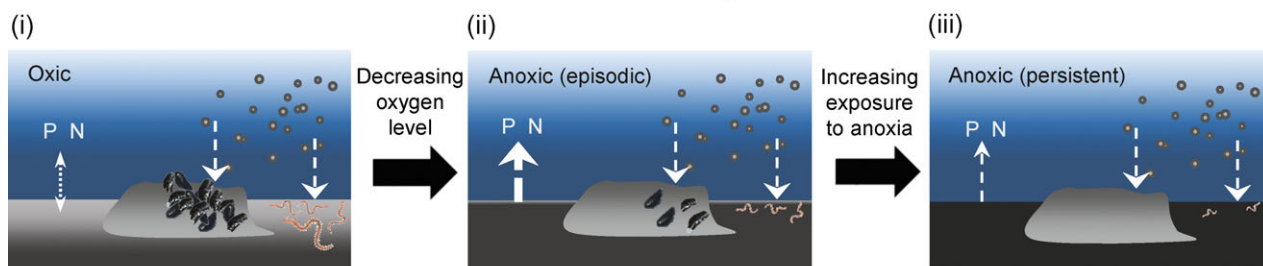
Oxygen is the overriding environmental regulator of inorganic nutrient fluxes across the sediment–water interface (Conley *et al.*, 2009; Carstensen *et al.*, 2014; Norkko *et al.*, 2015) because it determines the extent to which diffusion and bioturbation govern these fluxes. Oxygen also determines flux rates and directionality while responding to climate and nutrient conditions (Fig. 2a). The focus here is on fluxes of nitrogen and

Table 2 Measurements of inorganic nutrient fluxes and organic material exchange between benthic and pelagic habitats in the Baltic Sea. Data are provided by a specific monitoring station or for the basin as a whole. Processes with comparable data have been included here. These comparisons exclude very shallow habitats where processes are highly variable and locally influenced. For inorganic nutrient flux measurements, a positive flux value equals a flux out of the sediment

Depth Station Name	Bothnian Bay			Bothnian Sea			Gulf of Finland			Baltic Proper			Southern/Western Baltic			Data source
	Shallow (68 m) CVI	Deep (108 m) BO3	Shallow (104 m) F18	Deep (125 m) SR5	Shallow (47 m) GOF2	Deep (70 m) GOF6	Shallow (63 m) EGB1	Deep (81 m) LF2	Shallow (47 m) BY2	Deep (90 m) BY5						
<i>Inorganic nutrient fluxes</i>																
NO ₃ ⁻ (μmol m ⁻² day ⁻¹)	151 ± 70	217 ± 69	-43 ± 141	-205 ± 83	-626 ± 229	-1125 ± 99	111 ± 56	26 ± 3	200 ± 34	-811 ± 290				Norkko <i>et al.</i> (2015)		
NO ₂ ⁻ (μmol m ⁻² day ⁻¹)	1 ± 10	8 ± 41	-12 ± 20	-14 ± 32	-16 ± 5	54 ± 21	-6 ± 17	-7 ± 6	9 ± 17	-1 ± 26				Norkko <i>et al.</i> (2015)		
NH ₄ ⁺ (μmol m ⁻² day ⁻¹)	32 ± 18	-10 ± 39	195 ± 87	-68 ± 87	890 ± 916	4554 ± 881	133 ± 70	3005 ± 1130	-12 ± 153	1522 ± 514				Norkko <i>et al.</i> (2015)		
PO ₄ ³⁻ (μmol m ⁻² day ⁻¹)	2 ± 24	33 ± 10	124 ± 113	38 ± 16	297 ± 395	2795 ± 1066	-263 ± 58	457 ± 236	38 ± 25	361 ± 220				Norkko <i>et al.</i> (2015)		
Bioturbation depth (arPD, cm)	9.6	9.3	13.1	10.9	7.5	0.0	7.3	0.0	8.5	1.1				Norkko <i>et al.</i> (2015)		
<i>Organic material fluxes</i>																
Pigments top 1 cm of sediment (μg cm ⁻³)	0.97 ± 0.16															
Total pigments	0.04 ± 0.02															
Chlorophyll a	0.97 ± 0.16															
Sediment accumulation rate (g dry wt m ⁻² yr ⁻¹)	290.00	910.00	5935.00	1160.00	970.00	1261.00	NA	680.00	400.00	NA	9.55 ± 4.06	2.52 ± 1.77	5.98 ± 3.06	0.81 ± 0.38	Josefson <i>et al.</i> (2012)	
Sedimentation of organic matter (g C m ⁻² yr ⁻¹)	20*	NA	NA	198.4 [†]	9.4-34 [‡]	38 [§]	NA	6.13 [¶] -50.1 ^{**}	50-65 ^{††}	NA	NA	NA	NA	NA	Josefson <i>et al.</i> (2012)	
% benthos in diet, 20-30 cm cod ^{‡‡}	NA	NA	NA	NA	NA	NA	80-95 (except 45 in 1976-79) ^{††}	60-95 ^{***}	80.80	NA	NA	NA	NA	NA	Josefson <i>et al.</i> (2012)	
% benthos in diet, >30 cm cod ^{‡‡}	NA	NA	NA	NA	NA	NA	50-95 ^{††}	10-65 ^{***}	25.20	NA	NA	NA	NA	NA	Josefson <i>et al.</i> (2012)	
% benthos in herring diet ^{§§}	NA	NA	NA	NA	NA	NA	~5 benthos, 30-55 mysids	NA	NA	NA	NA	NA	NA	NA	Josefson <i>et al.</i> (2012)	

* Estimated from annual primary production assuming export efficiency (e-ratio). Depth not specified; † Sediment trap at 80 m (max depth 125 m); ‡ Sediment trap at 15 m (max depth 38 m) and sediment trap at 20 m (max depth 36 m); § Sediment trap at 20 m (max depth 50 m); ¶ Sediment trap at 140 m (max depth c. 200 m); ** Sediment trap at 40 m (max depth 459 m); †† Sediment trap at 15 or 18 m (max depth 20 m); ††† May not reflect current pelagic prey availability, size class >30 cm may include sizes consuming large quantities of benthic prey and the largest individuals that eat primarily fish; §§ Annual average, not depth specific, modeling result.

(a) Response of benthic–pelagic coupling due to changing oxygen scenarios over time (nutrient loading and climate conditions held constant at current conditions).



(b) Response of benthic–pelagic coupling under future nutrient load reductions and projected climate change scenarios (oxic conditions held constant).

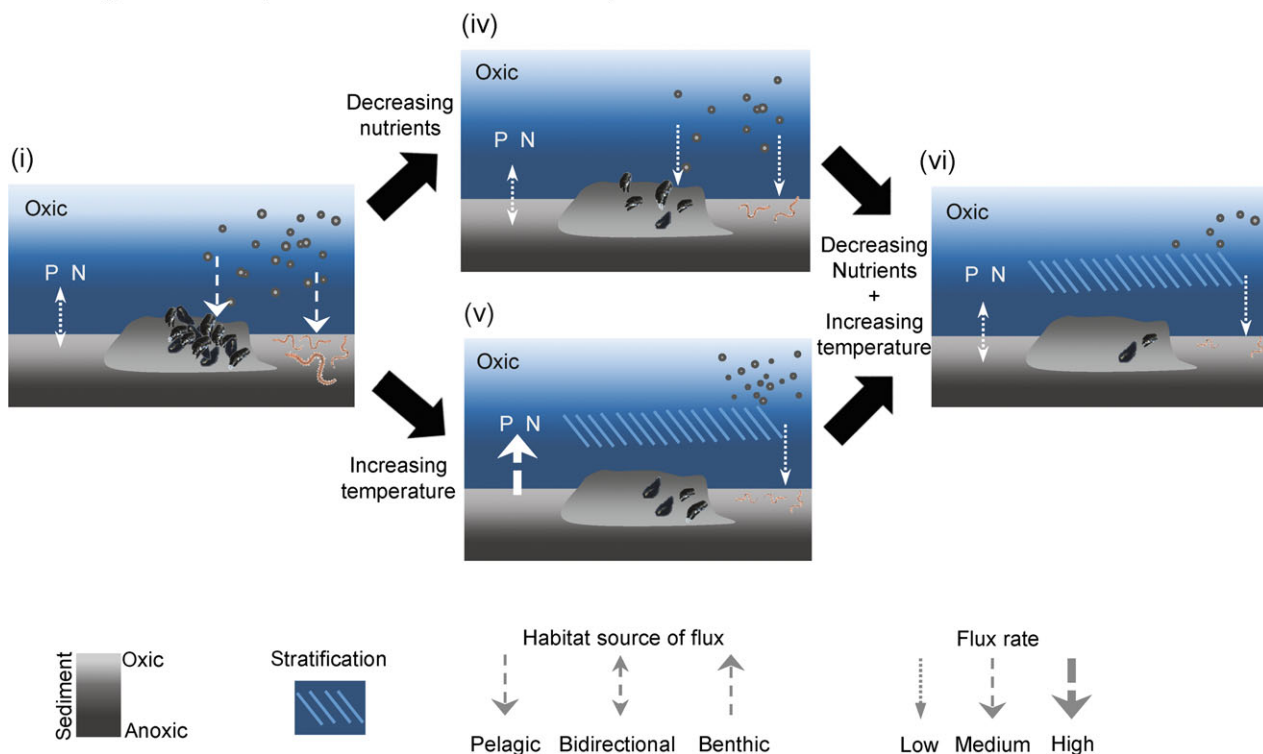


Fig. 2 Changes in inorganic nutrient flux and organic material flux during exposure to different pressures at a single location. (a) Response of benthic–pelagic coupling due to changing oxygen scenarios over time (nutrient loading and climate conditions held constant at current conditions). (i) Flux of inorganic nutrients and organic material in oxygenated waters inhabited by benthic fauna. (ii) Episodic anoxia stimulates and increases fluxes of inorganic nitrogen and phosphorus from the sediment to the water column. Fewer benthic species can survive in anoxic conditions. (iii) Persistent anoxia leads to a decrease in nitrogen and phosphorus fluxes from the sediment, while organic material degradation decreases and burial increases. Only resistant meiofauna can survive in persistent anoxic conditions. (b) Response of benthic–pelagic coupling to scenarios of future nutrient load reductions and projected climate change (oxic conditions held constant). (i) Same as in (a). (iv) Reduced nutrient loading lowers primary production, which decreases organic material sedimentation. This decreases the abundance and size of benthic fauna. (v) Increased water temperature stimulates fluxes of inorganic nutrients from the sediments to the water column. Decreased salinity, combined with increased temperature, strengthens stratification and reduces the amount of organic material reaching the sediments and benthic organisms. These abiotic conditions decrease mussel biomass. (vi) The combined effects of nutrient load reduction and projected climate change reduce benthic fauna, but no net change in inorganic nutrient flux from the sediment is expected as these pressure changes offset one another.

phosphorus, elements that are of particular importance for biological production in aquatic ecosystems (e.g., Baltic Sea estimates of flux rates in Table 2).

Physical processes. Diffusive exchange—The direction of nutrient fluxes varies with oxygen conditions, from a balanced nitrogen and phosphorus exchange in oxic

conditions, to a slow sedimentary efflux during permanent anoxia (Fig. 2a). In the deep basins of the central Baltic Sea, exchange processes are dominated by slow, molecular diffusion (Figs 1c and 2a). These basins have been almost permanently anoxic since the 1990s, due to high external inputs of nutrients, increased sedimentation, and semipermanent water stagnation (Hansson & Andersson, 2014; Vahtera *et al.*, 2007; Fig. 2a). The projected strengthening of stratification, due to climate change, will decrease mixing and increase the extent of anoxia in deep waters of the Baltic Sea (Meier *et al.*, 2011; Table 3). This could expand the hypoxic/anoxic area to currently oxygenated benthic sediments triggering stronger fluxes of inorganic nutrients (especially phosphorus) from benthic habitats to the water column (Eilola *et al.*, 2014; Fig. 2a; Table 3). Warmer temperatures could also exacerbate fluxes of inorganic nutrients as rates of organic material degradation processes (i.e., aerobic respiration and denitrification) are temperature sensitive (Bonaglia *et al.*, 2014a; Table 3). If external nutrient load reductions are achieved according to the Baltic Sea Action Plan (HELCOM Ministerial Meeting, 2007), the resulting decrease in the areal extent of anoxia could lower the release of inorganic nitrogen and phosphorus from the sediment (e.g., reduce internal recycling, Bonaglia *et al.*, 2013, 2014a; Viktorsson *et al.*, 2013).

Biological processes. Bioturbation—Meio- and macrofauna inhabiting benthic habitats have a direct effect on inorganic nutrient fluxes between the sediment and the water column. In the oxygenated areas of the Baltic Sea (Carstensen *et al.*, 2014), they enhance inorganic nutrient fluxes by advective fluid flow and bioturbation (Aller & Aller, 1992; Elmgren, 1978; Figs 1c and 2a). The presence of meiofauna can double nutrient fluxes while macrofauna can enhance nutrient fluxes by a factor of 2 to 10 because of enhanced physical exchange and physiological factors (Aller & Aller, 1992; Nascimento *et al.*, 2012; Bonaglia *et al.*, 2014b). Morphological traits of macrofauna, such as size, may influence the nutrient flux more than species richness, community composition, or abundance, as larger and older individuals have a disproportionately large effect on oxygen and nutrient fluxes (Norkko *et al.*, 2013). Overall, the net direction of the inorganic nutrient flux due to bioturbation can vary substantially because of organism geometry, density, or bioturbation mode. For example, surface-mixing amphipods such as *M. affinis* stimulate denitrification rates (Karlson *et al.*, 2005, 2007a) while deep-burrowing, bioirrigating polychaetes have minimal effect on this process (Kristensen *et al.*, 2011; Bonaglia *et al.*, 2013). In addition, bioturbation effects are not

uniform across nutrients; for example, bioturbation by deep-burrowing polychaetes has been shown to strongly enhance sediment phosphorus retention (Norkko *et al.*, 2012), while on the other hand increasing the fluxes of dissolved nitrogen to the water column (Bonaglia *et al.*, 2013; Ekeröth *et al.*, 2016).

Current and projected abiotic conditions of the Baltic Sea suggest an ongoing reduction of macrofaunal abundance due to more common hypoxic events in shallow coastal areas (Conley *et al.*, 2011). Macrofaunal abundance decreases will consequently lower the enhancement effects of bioturbation on inorganic nutrient flux (Cederwall & Elmgren, 1990; Karlson *et al.*, 2002; Villnäs *et al.*, 2012; Fig. 2a). In addition, the importance of bioturbation also declines with decreasing salinity, mirroring the decline of native macrobenthic species abundance and diversity (Bonsdorff, 2006; Kautsky & Kautsky, 2000; Table 1). Projected decreased salinity and increased temperature, in conjunction with increased hypoxia, could further reduce native benthic fauna bioturbation capacity (Fig. 2b).

Invasive species can provide new functional traits to communities, and this may enhance the resilience of bioturbation capacity in the Baltic Sea. For example, the three invasive species of the polychaete genus *Marenzelleria* burrow and irrigate deeper than most native species and have a broad tolerance to salinity, oxygen, and even sulfidic conditions (Maximov *et al.*, 2015). Since the mid-1980s, they have spread throughout the Baltic Sea to become a dominant member of the benthic macrofaunal community (Kauppi *et al.*, 2015). *Marenzelleria* bioturbation can enhance phosphorus retention and ammonium regeneration in sediments (Norkko *et al.*, 2012; Bonaglia *et al.*, 2013). However, a recent mesocosm study suggests that these effects on inorganic nutrient fluxes are species specific and might be different for the three different *Marenzelleria* species (Renz & Forster, 2014).

Macrophyte inorganic nutrient uptake—Aquatic macrophytes, microphytobenthos, macroalgae, and their epibionts take up inorganic nutrients from the water column and are important in shallow coastal zones where light is sufficient to sustain benthic primary production (Fig. 1c). As the Baltic Sea becomes fresher, a transition from macroalgal-dominated coastal ecosystems toward nonvegetated areas or habitats dominated by vascular plants is expected (Kotta *et al.*, 2014). The loss of perennial macroalgae (Kotta & Möller, 2014) would reduce the uptake of pelagic nutrients by benthic primary producers, resulting in increased phytoplankton production (Smith *et al.*, 2006) and potentially pelagic fish yields (Kotta *et al.*, 2004).

Table 3 Summary of mechanisms by which anthropogenic pressures affect benthic–pelagic coupling responses and the projected direction of the response. Details are provided in the relevant paper sections. Upward arrows (↑) indicate an increase or positive response while downward arrows (↓) indicate a decrease or negative response. ‘No change’ is written when no process response is expected despite mechanism for change while ‘NA’ applied where no mechanism for change is identified. Question marks (?) indicate an unknown response. Direct effects are indicated in bold font and indirect effects in plain font. Color indicates an inorganic nutrient (yellow) or organic material (green) flux

		Climate change	Nutrient loading		Fishing	
		↑ Temperature ↓ Salinity ↑ Precipitation ↓ Ice cover	↓	↑	↓	↑
Bird predation	Mechanism	Distribution & intensity; Decrease quality of food resource	Decreased prey availability with less phytoplankton production (less organic material sedimentation)	Decreased water clarity decreases prey visibility	NA	NA
	Response	↓; ↓	↓	↓		
Suspension feeding	Mechanism	Bivalve decline; Invasive species increase	Decreased food availability with less primary production	Increased food availability (if no hypoxia)	Decreased bottom-trawling reduces mortality	Increased bottom-trawling increases mortality
	Response	↓; ↑	↓	↑	↑	↑
Macrophyte inorganic nutrient uptake	Mechanism	Shift from perennial (macroalgae) to annual (plants) composition	Nutrients less available; Increased water clarity results in more light available	Nutrients more available; Decreased water clarity results in less light available	NA	NA
	Response	↓	↓; ↑	↑; ↓		
Resuspension	Mechanism	Ice cover loss increases wave-induced bottom stress	Less organic material produced by phytoplankton	More organic material produced by phytoplankton	Depends on fishing gear/type	Depends on fishing gear/type
	Response	↑	↑	↑		
Allochthonous organic input	Mechanism	Increased precipitation leads to increased runoff	NA	NA	NA	NA
	Response	↑				
Fish predation	Mechanism	Coastal fish and benthic community composition change; Cod declines; Changes in phenology	Decreased prey availability with less phytoplankton production (less organic material sedimentation); Predator community change	Increased prey availability in shallow oxic areas; Decreased prey availability in hypoxic areas	Increased abundance (if benthic-feeding fish targeted)	Decreased abundance (if benthic-feeding fish targeted)
	Response	?; ↓; ?	↓; ?	↑; ↓	↑	↓
Diffusion	Mechanism	Temperature affects rates; Stratification affects O₂	Reduced anoxic areas	Increase in anoxic areas	NA	NA
	Response	↑ rates; Depends on nutrient	Depends on nutrient	Depends on nutrient		
Bioturbation	Mechanism	Species composition change; Stratification affects O₂	Reduced anoxic areas	Increase in anoxic areas	NA	NA
	Response	No change or ↑; ↓	↑	↓		
Sedimentation	Mechanism	Phenology & composition change	Reduced production	Increased production	NA	NA
	Response	↓ (quality), ?(timing)	↓	↑		

Organic material fluxes

Phytoplankton production fuels benthic secondary production through sedimentation of organic matter. In turn, the benthic organisms provide additional food sources for pelagic fish and birds, supporting and stabilizing pelagic dynamics (Rooney & McCann, 2012). The physical and biological processes transferring organic material between benthic and pelagic habitats have variable responses to changes in anthropogenic pressures and exhibit complex feedbacks among each other.

Physical-dominated processes. Sedimentation—Phytoplankton production is the largest source of particulate organic material sinking to the benthos at the basin scale (Fig. 1c; Table 2). Sedimentation is temporally and spatially variable and regulated by climate and nutrient conditions, which can be seen in the decrease of phytoplankton production from south to north (Table 2; Bonsdorff & Pearson, 1999) due to the shorter productive season and lower inorganic nutrient concentrations at higher latitudes. Reduction in nutrient loading would in the long run decrease the pelagic to benthic organic material flux by reducing phytoplankton production and sedimentation in offshore regions (Fig. 2b; Table 3). In these regions, benthic primary production is limited because the bottom depth is greater than the euphotic zone. Thus, the benthos is dependent on the sinking organic material and offshore benthic productivity may eventually be significantly affected by decreased nutrient loads.

The projections of further climate-induced winter ice cover declines and increased temperatures (BACC II Author Team, 2015) may alter the timing, duration, and quantity of organic material transfer to the benthos in all basins of the Baltic Sea (Table 3). For example, the initiation of the spring bloom has shifted earlier in the central Baltic Sea during the past 20 years (Kahru *et al.*, 2015) and models have projected earlier blooms in the future due to decreased ice cover (Eilola *et al.*, 2013). High-latitude regions of the Baltic Sea (Bothnian Sea, Bothnian Bay), however, will continue to be light-limited by long winters and higher concentrations of humic substances than other Baltic Sea basins. The consequences of these changes in phytoplankton phenology for benthic communities are largely unknown as they are also affected by the ability of both pelagic (zooplankton) and benthic consumers to adjust to such shifts.

There is clear spatial and temporal variation of organic material sedimentation already affecting resource availability to benthic consumers. This is due to strong seasonality, spatial variation in seasonality,

smaller-scale oceanographic processes, and a coastal-to-offshore gradient in phytoplankton productivity. Across the Baltic Sea, the spring bloom accounts for the largest flux of matter from the pelagic habitat to benthic communities. The late summer blooms (and autumn in the south-central regions) provide a secondary input to the benthos, albeit less regular in occurrence and magnitude than during spring (Gustafsson *et al.*, 2013) and of lower nutritional quality (Nascimento *et al.*, 2009). Phytoplankton production also decreases from the open sea to the coast, as water transparency decreases with increasing sediment resuspension and dissolved and particulate organic material input from land (Olafsson & Elmgren, 1997; Tallberg & Heiskanen, 1998; Gustafsson *et al.*, 2013). Substantial recovery from eutrophication would not only reduce phytoplankton production (as mentioned above) but also increase water transparency, favoring benthic primary production in shallow regions. In turn, community dominance could change from phytoplankton to macroalgae and seagrasses (Riemann *et al.*, 2015) as well as benthic microalgae production and this benthic production would result in feedbacks to inorganic nutrient cycling (see Macrophyte inorganic nutrient uptake).

Resuspension—Resuspension of sedimentary material commonly occurs in the Baltic Sea due to the shallow average depth of the water column (Fig. 1c). Sinking particles due to resuspension account for >50% of the total sinking material in shallow (<50 m) coastal areas (Blomqvist & Larsson, 1994; Heiskanen, 1998), and this source often dominates the diet of benthic suspension feeders, as opposed to the traditional view that phytoplankton are their primary food source (Lauringson *et al.*, 2014). In deeper waters, mixing is prevented by the permanent halocline at ~70 m depth and resuspension is low. Despite no active resuspension in deep water, deep benthic habitats receive resuspended materials through advection offshore of organic material resuspended in shallow waters (c.f. Eilola *et al.*, 2013).

Resuspension is sensitive to both projected climate change and the use of bottom trawl gear (Table 3). For example, reduced ice cover during spring has already increased wave-induced bottom stress (BACC II Author Team, 2015) and a potential consequence is increased resuspension of organic material during spring (Eilola *et al.*, 2013). Furthermore, bottom-trawling increases resuspension and can cause long-term impacts on nutrient fluxes (Olsgard *et al.*, 2008), as well as on benthic fauna abundance, biomass, and community structure (Rumohr & Krost, 1991; Hinz *et al.*, 2009). Trawling has a large spatial footprint (Korpinen *et al.*, 2013), but any fishing-related effects in the future on resuspension

will depend on future gear use (e.g., extent of trawl use) and fishing intensity.

Allochthonous organic material inputs—Organic material from terrestrial sources and riverine primary and secondary production contributes substantially to organic material deposition in the nearshore environment (Tallberg & Heiskanen, 1998; Malmqvist *et al.*, 2001) (Fig. 1c). High levels of colored dissolved organic material can, however, also reduce phytoplankton production by decreasing light availability (Wikner & Andersson, 2012), thus dampening the autochthonous pelagic flux of high-quality organic material to the benthos. River flow and precipitation events control allochthonous inputs and lead to strong seasonal patterns, but these dynamics differ across the Baltic Sea region (Reader *et al.*, 2014).

The extent of the benthos response to either increased allochthonous organic matter inputs or to indirect effects of dampened phytoplankton production due to projected increase in precipitation and earlier peak river discharge (BACC II Author Team, 2015) is still unclear. While increased freshwater runoff may increase the deposition of organic material in nearshore and coastal sediments (Table 3), this would lower the quality of the food available to the marine food web because terrestrial organic material typically has lower nitrogen content compared to autochthonous sources (Grebmeier *et al.*, 1988). In salinity-transition zones, increased flocculation of dissolved organic material occurring with increased freshwater runoff would also introduce low-nitrogen-content organic material due to the higher carbon:nitrogen ratio in dissolved vs. particulate organic material (c.f. Asmala *et al.*, 2013; Tamelander & Heiskanen, 2004).

Biological processes. A wide array of biological processes that are inherently linked to species-specific life-history traits and phenology contribute to shaping the exchange between benthic and pelagic habitats (Baustian *et al.*, 2014). These processes are spatially and temporally highly variable and sensitive to human pressures. The Baltic Sea is a relatively species-poor ecosystem (Elmgren & Hill, 1997; Bonsdorff & Pearson, 1999; Villnäs & Norkko, 2011), but its food webs are sufficiently complex to highlight the challenge of evaluating the sensitivity of biologically mediated benthic–pelagic coupling to anthropogenic pressures (Yletyinen *et al.*, 2016). Disentangling the relative effects of different pressures on species-mediated energy transfer between benthic and pelagic habitats is challenging – especially due to limited understanding of the factors regulating the timing and magnitude of trophic interactions. We focus on two trophic processes (suspension

feeding and predation) to describe our current understanding of their role in benthic–pelagic coupling. While processes such as diel migrations and reproductive (life-cycle) fluxes (Marcus & Boero, 1998; Baustian *et al.*, 2014) may result in large exchange of organic material, these processes are poorly quantified from the perspective of energy transfer between Baltic Sea benthic and pelagic habitats (but see Katajisto *et al.*, 1998) and are not discussed here.

Suspension feeding—Suspension feeding by benthic macrofauna in the Baltic Sea, especially by bivalves (Elmgren, 1984), transfers organic materials from the pelagic zone to the benthos. In addition to secondary production (somatic growth), the deposition of feces from benthic consumers constitutes a significant organic input to the sediment which is locally important, particularly in areas shallower than 30 m dominated by blue mussels (Kautsky & Evans, 1987; Fig. 1c).

The filtering function of benthic macrofauna decreases sharply when moving toward the less saline northern basins (Elmgren, 1984). This results from the decreasing diversity and biomass of suspension feeders with decreasing salinity in both soft-bottom (Bonsdorff & Pearson, 1999) and hard-bottom areas (blue mussels, Westerbom *et al.*, 2008). Projected changes in nutrients and salinity could have negative effects on the distribution and productivity of mussels (Kotta *et al.*, 2015) and diminish their role in benthic–pelagic exchange (Fig. 2b; Table 3). For example, decreased nutrient loading by humans would lessen the sedimentation of organic material and reduce mussel stock growth (Riemann *et al.*, 2015; Fig. 2b). The persistence of suspension-feeding traits in benthic communities may be supported by invasive species despite decreasing salinity (Table 3). Very dense populations of the invasive mussel *Dreissena polymorpha* now occur in the low-saline regions of the Baltic Sea and perform the same suspension-feeding function as marine-origin bivalves (Lauringson *et al.*, 2007). Alternatively, the loss of filter-feeding functions from benthic communities may also occur due to invasive species. The predatory round goby (*Negobius melanostomus*), for example, can decimate local populations of suspension-feeding mussels (Ojaveer & Kotta, 2015).

Fish predation—Most fish species in the Baltic Sea feed on benthic invertebrates during at least part of their life cycle (Casini *et al.*, 2004; Hüsey *et al.*, 1997; Snickars *et al.*, 2015; see Table 2 for cod and herring), yet the patterns and relative importance of benthic–pelagic coupling by fish predation are often poorly understood or quantified. This is because predation strength depends on population abundances, which vary

considerably over time and space (e.g., stickleback, Bergström *et al.*, 2015; herring, Casini *et al.*, 2011), and the spatial and temporal dynamics of predation also depend upon fish life histories (spawning and feeding migrations, ontogenetic diet shifts). The relative importance of pelagic and benthic prey sources will also depend on prey availability, and therefore, changes in prey composition and biomass may alter trophic coupling pathways.

Coastal benthic invertebrate and fish communities in the Baltic Sea have already experienced substantial changes in species composition, abundance, and biomass since the early 1970s (Olsson *et al.*, 2013; Weigel *et al.*, 2015), increasingly due to climate impacts (Snickars *et al.*, 2015). There has been a decrease in coastal abundances of fish species of marine origin that prefer colder waters (i.e., herring, cod and sculpins), and an increase in freshwater species and those favored by warmer waters (i.e., perch and cyprinid fishes, Olsson *et al.*, 2012), with concurrent changes in their benthic invertebrate prey (Olsson *et al.*, 2013; Weigel *et al.*, 2015). With increased warming and decreasing salinity of the Baltic Sea, the future coastal fish communities are expected to mainly be comprised of benthic-feeding fish species of freshwater origin. Despite the changing composition of invertebrate macrozoobenthos and fish communities, it is unknown whether this will also alter the magnitude of predation on the benthos. Future oxygen conditions will also govern predator–prey relationships, and hypoxic vs. anoxic conditions could have different effects. Hypoxia is more likely to result in species composition shifts in the benthic community while anoxia results in dead zones with no prey (Karlson *et al.*, 2002; Villnäs *et al.*, 2012).

The Eastern Baltic cod, a commercially important fish species, preys mainly on benthic invertebrates during juvenile life stages (Hüssy *et al.*, 1997; Table 2) and pelagic fish prey as adults in addition to larger benthic invertebrates. Cod populations, and therefore their predation pressure on the benthos, are sensitive to both climate and fisheries management. Under reduced salinity and continued spread of hypoxic and anoxic waters, some model projections show continued decline of the Eastern Baltic cod stock despite reductions in fishing mortality (Lindegren *et al.*, 2010; Gårdmark *et al.*, 2013). Alternatively, under favorable environmental conditions, the cod population size may increase substantially if management decisions and the actual exploitation adhere to current fishery management plans (Niiranen *et al.*, 2013). However, scenario projections vary greatly across different models depending on which species' interactions each model accounts for (Gårdmark *et al.*, 2013). Modeling studies demonstrate the importance of ontogenetic shifts from

benthic to pelagic predation by cod for feedbacks between the structure and dynamics of fish communities and their prey (van Leeuwen *et al.*, 2013, 2014), thereby determining the extent of ontogenetic benthic–pelagic coupling. These feedbacks increase the difficulty of quantifying current and future benthic–pelagic coupling through cod predation.

The consequences of changing cod predation for benthic–pelagic coupling will vary spatially. In the southwestern Baltic Sea, greater taxonomical and functional diversity in the benthos and fish community (Törnroos *et al.*, 2015; Pécuchet *et al.*, 2016) may uphold benthic–pelagic coupling despite reduced cod predation due to compensatory increases in functionally similar gadoid and flatfish species (Lindegren *et al.*, 2012; Sparrevohn *et al.*, 2013). In contrast, the less saline southeastern Baltic Sea has fewer benthic-feeding fish species, mainly flounder and gobies besides cod (Ojaveer & Kotta, 2015), which may not compensate for decreased cod predation.

Bird predation—The Baltic Sea is a favored habitat for benthivorous sea ducks (Skov *et al.*, 2011), which consume large quantities of bivalves (Nilsson, 1980; Stempniewicz & Meissner, 1999). Bivalves can also be an important prey for populations of generalist bird species (e.g., gulls Garthe & Scherp, 2003). Bird predation on benthos takes place mainly in the shallow and transition zones (Bonsdorff *et al.*, 1990), as greater depth limits the accessibility of benthic resources to diving birds (down to 25 m, Skov *et al.*, 2011; Fig. 1c). Predation magnitude is mainly determined by bird abundance, so trends in breeding success and survival may affect the strength of coupling over time while seabird migration patterns and phenology lead to strong seasonal variation. Some benthivorous species remain in the Baltic Sea year-round, but migrate within the region, while others only overwinter there. The spatial dynamics and intensity of coupling varies during the overwintering period, as birds gather in contracted areas during arrival/departure but then disperse throughout shallow coastal waters and offshore banks (Skov *et al.*, 2011).

Climate change is expected to influence waterbird phenology and distribution (Guillemain *et al.*, 2013; Lehikoinen *et al.*, 2013), increasing the duration and intensity of benthic predation in the northeastern Baltic Sea while decreasing their presence in the southern and western part of the area (Table 3). Decreasing salinity is likely to shift the occurrence, size, and densities of mussel beds (as discussed above, Kotta *et al.*, 2015; Fig. 2b) in turn affecting the availability and quality of benthic prey and bird consumers. In addition, exposure to increasing temperatures can reduce the meat-to-shell

ratio in overwintering mussels which decreases their quality as food for birds (Waldeck & Larsson, 2013). Bottom-up factors may also limit bird predation on the benthos as a negative response of mussel growth to decreased nutrient loading reduces bird prey availability (Laursen & Møller, 2014).

Summary and outlook

Our review highlights the importance of an integrated, whole-system perspective for understanding how estuarine and coastal ecosystems will respond to anthropogenic drivers through their effects on benthic–pelagic coupling. We identify key processes that define the type and level of interdependency between benthic and pelagic habitats in coastal and estuarine environments. Based on our Baltic Sea example, the most significant processes can be divided into three groups: nutrient release from sediments, sedimentation, and biological processes, which include pelagic consumer predation on benthic fauna and the response of community function to changes in composition. These processes all respond to widespread human impacts on the environment (climate change, nutrient loading, and fishing) and are not independent of one another. Historical and ongoing changes of the Baltic Sea ecosystem contribute to our general understanding of many of the world's coastal and estuarine ecosystems facing increasing pressures from these impacts (Cloern *et al.*, 2016). Our review focused on the most likely effects on benthic–pelagic coupling processes from projected anthropogenic pressures, and below we highlight the role of oxygen, interactive effects of climate change and nutrient load reductions, and key uncertainties for biological processes. We then provide our recommendations on how we can improve our quantification of benthic–pelagic coupling processes in any ecosystem such that the feedbacks among processes can be better understood.

Oxygen concentration is a main driver of inorganic nutrient and organic material exchange between benthic and pelagic habitats particularly affecting nutrient release and biological communities (Table 3). The extent of low-oxygen areas in the Baltic Sea is controlled by water exchange, climate, and eutrophication. Oxygen directly regulates the flux of inorganic nutrients and the potential for biological activity to contribute to bidirectional inorganic nutrient fluxes (Norkko *et al.*, 2015). There is great uncertainty related to the nature and magnitude of inorganic nutrient cycling in the future due to the complexity of internal feedbacks that may contribute to maintaining the Baltic Sea in a state of hypoxia/anoxia, despite major nutrient load reduction. Oxygen availability also governs the

spatial and temporal dynamics of the biological interactions that lead to organic material exchange. During hypoxia or anoxia, the flow of organic material from the benthos to pelagic consumers decreases. Given the widespread increase in reports of hypoxia in coastal ecosystems since the 1960s (Diaz & Rosenberg, 2008; Conley *et al.*, 2011), changing oxygen conditions will affect benthic–pelagic coupling globally.

Climate change impacts, in combination with management actions to reduce nutrient loading, suggest that organic fluxes from pelagic primary producers to benthic habitats (sedimentation) will decrease in the future due to shifts in phytoplankton composition, phenology, and physiology. This combined response may also be expected in other systems with similar management goals to reduce eutrophication. Although organic matter sedimentation is likely to decline, the transfer of this organic matter between habitats through biological pathways remains uncertain in the Baltic Sea and responses are likely system specific, based upon the unique properties of pelagic and benthic communities. The interdependency of these processes results in a large degree of uncertainty in the ultimate, systemwide effects. Moreover, sinking of particulate material is rarely covered by monitoring programs and improving this knowledge base will improve our ability to draw conclusions on its response to environmental change.

Biologically mediated couplings (bioturbation, suspension feeding, and predation) respond to the interactive effects of anthropogenic pressures acting through multiple pathways (Table 3), and their sensitivity depends on the functional traits in the community. The continued increase in species invasions globally (Hulme, 2009; Walther *et al.*, 2009) will influence the biological processes of habitat coupling in multiple ways sustaining, increasing, or reducing current coupling (e.g., Norkko *et al.*, 2012) as well as potentially introducing new coupling pathways (e.g., as seen in San Francisco Bay, Cloern & Jassby, 2012). Overall, biological processes coupling habitats have greater unpredictability in their responses and are more difficult to quantify than other processes.

Recommendations

An important step forward is the quantification of inorganic nutrients and organic material exchange between the two habitats, which will improve our understanding and the predictability of these processes. Quantifying these fluxes and their sensitivity to anthropogenic pressures at different spatial and temporal scales (e.g., Fig. 2) requires the following: (1) coherent spatiotemporal measurements of rates across ecosystem components; (2) experimental studies that explicitly evaluate the

benthic–pelagic coupling to multiple pressures and linkages among processes; and (3) ecosystem models incorporating benthic–pelagic coupling processes.

Coherent spatiotemporal measurements—A coordinated and comprehensive monitoring of ecosystems across benthic and pelagic habitats is needed to fill our knowledge gaps. The temporal and spatial scatter of observations, methodological differences between studies, and regional bias of observations (e.g., specific species or habitats) complicate the assessment of specific fluxes or comparisons among processes. Strong seasonal dynamics likely shape many benthic–pelagic coupling processes, but, overall, these dynamics are poorly captured by current monitoring. First, measuring processes in a common currency using a standardized methodology (sampling frequencies, incubation periods) is essential. Second, depending on the process under consideration, there are often observations of either biomass or rates but both are necessary for a more integrative understanding of benthic–pelagic coupling in ecosystems. For example, sedimentation rates of organic material are measured (Table 2) but benthic biomass, not secondary production rates, is typically monitored. Improving our observational extent and consistency will allow us to track the relative responses of the coupling processes to anthropogenic stress and evaluate ecosystem change.

Experimental studies—In addition, experimental studies specifically targeting the interactive effects of various pressures on benthic–pelagic processes would enhance our mechanistic understanding. For example, building upon experiments that quantify species density (Karlson *et al.*, 2007b) or functional group (Michaud *et al.*, 2006; Bonaglia *et al.*, 2014b) effects on sediment–water solute exchange and carbon mineralization would help to evaluate the consequences of projected changes in temperature and oxygen. While mechanistic laboratory studies are important for exploring specific processes, the emphasis should be put on resolving our real-world understanding of how particular processes and pressures may be modulated by environmental drivers. Hence, embedding experimental work along environmental gradients may be particularly powerful for resolving the context dependency of patterns in benthic–pelagic coupling (Snelgrove *et al.*, 2014; Norkko *et al.*, 2015). Designing experiments to be valid at the seascape level would also ensure that results are applicable to ecosystem modeling efforts.

Ecosystem models—Ecosystem models are needed to explore the sensitivity of ecosystem structure and function to projected future anthropogenic pressures. Models allow the exploration of complex feedback loops

between biological and physical processes that are challenging to measure (e.g., as described in Fig. 2), as well as the sensitivity of benthic–pelagic coupling processes to synergistic changes in anthropogenic pressures. The development of ecosystem models including hydrology, biogeochemical cycles, and some components of biological system (e.g., phytoplankton groups) is highly advanced for the Baltic Sea (e.g., BALTSEM model, Savchuck *et al.*, 2012). The BALTSEM model already provides inputs to benthic trait models for assessing eutrophication effects (Timmermann *et al.*, 2012) and to food web models (e.g., Niiranen *et al.*, 2012). Integrating feedbacks from biological responses to the abiotic dynamics and vice versa in these types of models would allow for an assessment that ranks the most important feedbacks and sensitivities, providing grounds to evaluate the consequences of multiple pressures throughout complex ecosystems now and in the future. The parameterization and validation of these coupled models require both the coherent spatiotemporal measurements and experimental approaches discussed above.

Outlook

Common management goals for many of the world's coastal–estuarine ecosystems are to improve their ecological status and to protect or enhance their provision of ecosystem services. However, management advice and ecological targets are often based upon the current compartmentalization of benthic and pelagic habitats. Management indicators, such as used for the European Water Framework Directive (WFD; Directive 2000/60/EC) and Marine Strategy Framework Directive (MSFD; EU Directive 2008/56/EC), often describe the status of pelagic or benthic habitats separately, and there are few attempts to combine indicators across habitats (Dimitriou *et al.*, 2015) despite this being the overarching goal in some of these directives (e.g., the MSFD).

Human activities alter important benthic–pelagic linkages and disrupt the flow of ecosystem services in coastal and estuarine ecosystems. In many coastal–estuarine systems, eutrophication and climate change continue to affect the physical and biological processes that cycle nutrients between benthic and pelagic habitats. Simultaneously, food web dynamics are responsive to direct physical habitat changes, predator–prey feedbacks, and fishing. Consequently, understanding the interdependency between benthic and pelagic communities in specific ecosystems, such as the Baltic Sea, can be instrumental for projecting their future trajectories, status, and contribution to ecosystem services. To maintain the function of coastal and estuarine ecosystems and to safeguard the services they deliver under future

anthropogenic change, we need to ensure that the inorganic and organic exchange between pelagic and benthic habitats is understood, monitored, modeled, and included in management frameworks.

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References

- Agardy T, Alder J, Dayton P *et al.* (2005) Coastal Systems. In: *Ecosystems and Human Well-Being: Current State and Trends* (eds Hassan R, Scholes R, Ash N), pp. 513–549. Island Press, Washington, D.C.
- Aller RC, Aller JY (1992) Meiofauna and solute transport in marine muds. *Limnology and Oceanography*, **37**, 1018–1033.
- Andersen JH, Carstensen J, Conley DJ *et al.* (2015) Long-term temporal and spatial trends in eutrophication status of the Baltic Sea. *Biological Reviews*, **91**, 135–149.
- Armstrong RL, Knowles K (2010) *ISLSCP II Global Sea Ice Concentration*. Oak Ridge National Laboratory Distributed Active Archive Center, ISLSCP Initiative II Collection, Oakridge, TN.
- Asmala E, Autio R, Kaartokallio H, Pitkanen L, Stedmon CA, Thomas DN (2013) Bioavailability of riverine dissolved organic matter in three Baltic Sea estuaries and the effect of catchment land use. *Biogeosciences*, **10**, 6969–6986.
- BACC II Author Team (2015) *Second Assessment of Climate Change for the Baltic Sea Basin*. Springer International Publishing, Switzerland.
- Baltic Sea Alien Species Database (2010) http://www.corpi.ku.it/nemo/balt_reg.html. Accessed December 15, 2016.
- Baustian MM, Hansen GJA, de Kluijver A *et al.* (2014) Linking the bottom to the top in aquatic ecosystems: mechanisms and stressors of benthic–pelagic coupling. In: *Eco-DAS X Symposium Proceedings* (ed Kemp PF), pp. 25–47. Association for the Sciences of Limnology and Oceanography.
- Belkin IM (2009) Rapid warming of Large Marine Ecosystems. *Progress in Oceanography*, **51**, 207–213.
- Berger WH, Smetacek VS, Wefer G (eds) (1989) *Productivity of the Ocean: Present and Past*. Report of the Dahlem Workshop on Productivity of the Ocean: Present and Past, Berlin 1988, Berlin.
- Bergström U, Olsson J, Casini M, Eriksson BK, Fredriksson R, Wennhage H, Appelberg M (2015) Stickleback increase in the Baltic Sea – A thorny issue for coastal predatory fish. *Estuarine, Coastal and Shelf Science*, **163**(Part B), 134–142.
- Blomqvist S, Larsson U (1994) Detrital bedrock elements as tracers of settling resuspended particulate matter in a coastal area of the Baltic Sea. *Limnology and Oceanography*, **39**, 880–896.
- Bonaglia S, Bartoli M, Gunnarsson JS *et al.* (2013) Effect of reoxygenation and *Marenzelleria* spp. bioturbation on Baltic Sea sediment metabolism. *Marine Ecology Progress Series*, **482**, 43–55.
- Bonaglia S, Deutsch B, Bartoli M, Marchant HK, Bruchert V (2014a) Seasonal oxygen, nitrogen and phosphorus benthic cycling along an impacted Baltic Sea estuary: regulation and spatial patterns. *Biogeochemistry*, **119**, 139–160.
- Bonaglia S, Nascimento FJA, Bartoli M, Klawonn I, Bruchert V (2014b) Meiofauna increases bacterial denitrification in marine sediments. *Nature Communications*, **5**, 5133–5141.
- Bonsdorff E (2006) Zoobenthic diversity-gradients in the Baltic Sea: Continuous post-glacial succession in a stressed ecosystem. *Journal of Experimental Marine Biology and Ecology*, **330**, 383–391.
- Bonsdorff E, Pearson TH (1999) Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: A functional-group approach. *Australian Journal of Ecology*, **24**, 312–326.
- Bonsdorff E, Blomqvist EM, Pearson TH (1990) Zoobenthos, fish and birds in a brackish archipelago area - trophic interactions in time and space. In: *Trophic Relationships in the Marine Environment* (eds Barnes M, Gibson RN), pp. 389–403. Aberdeen University Press, Aberdeen.
- Carstensen J, Andersen JH, Gustafsson BG, Conley DJ (2014) Deoxygenation of the Baltic Sea during the last century. *Proceedings of the National Academy of Sciences*, **111**, 5628–5633.
- Casini M, Cardinale M, Arrhenius F (2004) Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. *ICES Journal of Marine Science*, **61**, 1267–1277.
- Casini M, Kornilovs G, Cardinale M *et al.* (2011) Spatial and temporal density dependence regulates the condition of central Baltic Sea clupeids: compelling evidence using an extensive international acoustic survey. *Population Ecology*, **53**, 511–523.
- Cederwall H, Elmgren R (1990) Biological effects of eutrophication in the Baltic Sea, particularly the coastal zone. *Ambio*, **19**, 109–112.
- Chauvand L, Jean F, Ragueneau O, Thouzeau G (2000) Long-term variation of the Bay of Brest ecosystem: benthic–pelagic coupling revisited. *Marine Ecology Progress Series*, **200**, 35–48.
- Cloern JE, Jassby AD (2012) Drivers of change in estuarine-coastal ecosystems: Discoveries from four decades of study in San Francisco Bay. *Reviews of Geophysics*, **50**.
- Cloern JE, Abreu PC, Carstensen J *et al.* (2016) Human activities and climate variability drive fast-paced change across the world's estuarine-coastal ecosystems. *Global Change Biology*, **22**, 513–529.
- Conley DJ, Paerl HW, Howarth RW *et al.* (2009) Controlling eutrophication: Nitrogen and phosphorus. *Science*, **323**, 1014–1015.
- Conley DJ, Carstensen J, Aigars J *et al.* (2011) Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environmental Science & Technology*, **45**, 6777–6783.
- Costanza R, Kemp M, Boynton W (1995) Scale and biodiversity in coastal and estuarine ecosystems. In: *Biodiversity Loss: Economic and Ecological Issues* (eds Perrings C, Maler K-G, Folke C, Holling CS, Jansson B-O), pp. 84–126. Cambridge University Press, Cambridge.
- Diaz RJ, Rosenberg R (2008) Spreading Dead Zones and Consequences for Marine Ecosystems. *Science*, **321**, 926–929.
- Dimitriou PD, Papageorgiou N, Arvanitidis C *et al.* (2015) One step forward: Benthic pelagic coupling and indicators for environmental status. *PLoS ONE*, **10**, e0141071.
- Directive 2000/60/EC (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy (Water Framework Directive).
- Duineveld GCA, Tselepides A, Witbaard R *et al.* (2000) Benthic–pelagic coupling in the oligotrophic Cretan sea. *Progress in Oceanography*, **46**, 457–480.
- Eilola K, Martensson S, Meier HEM (2013) Modeling the impact of reduced sea ice cover in future climate on the Baltic Sea biogeochemistry. *Geophysical Research Letters*, **40**, 149–154.
- Eilola K, Almröth-Rosell E, Meier HEM (2014) Impact of saltwater inflows on phosphorus cycling and eutrophication in the Baltic Sea: a 3D model study.
- Ekeröth N, Blomqvist S, Hall POJ (2016) Nutrient fluxes from reduced Baltic Sea sediment: effects of oxygenation and macrobenthos. *Marine Ecology Progress Series*, **544**, 77–92.
- Elmgren R (1978) Structure and dynamics of Baltic benthos communities, with particular reference to the relationship between macro- and meiofauna. *Kieler Meeresforschungen, Sonderheft*, 1–22.
- Elmgren R (1984) Trophic dynamics in the enclosed, brackish Baltic Sea. *Rapports et Procès-verbaux des Réunions, Conseil international pour l'Exploration de la Mer*, **183**, 153–179.
- Elmgren R, Hill C (1997) Ecosystem function at low biodiversity - the Baltic example. In: *Marine Biodiversity: Patterns and Processes* (eds Ormond RFG, Gage JD, Angel MV), pp. 319–336. Cambridge University Press, Cambridge.
- Elmgren R, Blenckner T, Andersson A (2015) Baltic Sea management: successes and failures. *Ambio*, **44**, S335–S344.
- EU Directive 2008/56/EC (2008) Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action

- in the field of marine environmental policy (Marine Strategy Framework Directive).
- Fulweiler RW, Nixon SW (2009) Responses of benthic-pelagic coupling to climate change in a temperate estuary. *Hydrobiologia*, **629**, 147–156.
- Gårdmark A, Lindegren M, Neuenfeldt S *et al.* (2013) Biological ensemble modeling to evaluate potential futures of living marine resources. *Ecological Applications*, **23**, 742–754.
- Garthe S, Scherp B (2003) Utilization of discards and offal from commercial fisheries by seabirds in the Baltic Sea. *ICES Journal of Marine Science*, **60**, 980–989.
- Graf G (1992) Benthic-pelagic coupling - a benthic view. *Oceanography and Marine Biology*, **30**, 149–190.
- Graf G, Rosenberg R (1997) Bioresuspension and biodeposition: a review. *Journal of Marine Systems*, **11**, 269–278.
- Granek EF, Polasky S, Kappel CV *et al.* (2010) Ecosystem services as a common language for coastal ecosystem-based management. *Conservation Biology*, **24**, 207–216.
- Grebmeier JM, McRoy CP, Feder HM (1988) Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. 1. Food-supply source and benthic biomass. *Marine Ecology Progress Series*, **48**, 57–67.
- Guillemain M, Poysa H, Fox AD *et al.* (2013) Effects of climate change on European ducks: what do we know and what do we need to know? *Wildlife Biology*, **19**, 404–419.
- Gustafsson O, Gelting J, Andersson P, Larsson U, Roos P (2013) An assessment of upper ocean carbon and nitrogen export fluxes on the boreal continental shelf: A 3-year study in the open Baltic Sea comparing sediment traps, Th-234 proxy, nutrient, and oxygen budgets. *Limnology and Oceanography-Methods*, **11**, 495–510.
- Halpern BS, Walbridge S, Selkoe KA *et al.* (2008) A global map of human impact on marine ecosystems. *Science*, **319**, 948–952.
- Hansson M, Andersson L (2014) Oxygen survey in the Baltic Sea 2014 - Extent of anoxia and hypoxia, 1960–2014. In: *Report Oceanography*. Swedish Meteorological and Hydrological Institute, Norrköping, Sweden.
- Hargrave BT (1973) Coupling carbon flow through some pelagic and benthic communities. *Journal of the Fisheries Research Board of Canada*, **30**, 1317–1326.
- Heiskanen AS (1998) Factors governing sedimentation and pelagic nutrient cycles in the northern Baltic Sea. Unpublished PhD Thesis University of Helsinki, Helsinki, Finland.
- Heiskanen AS, Tallberg P (1999) Sedimentation and particulate nutrient dynamics along a coastal gradient from a fjord-like bay to the open sea. *Hydrobiologia*, **393**, 127–140.
- HELCOM (2011) The Fifth Baltic Sea Pollution Load Compilation (PLC-5). In: *Baltic Sea Environ. Proc. No. 128*. Baltic Marine Environment Protection Commission – Helsinki Commission, Helsinki, Finland.
- HELCOM (2012) Checklist of Baltic Sea macro-species. In: *Baltic Sea Environment Proceedings*. Helsinki Commission, Helsinki, Finland.
- HELCOM Ministerial Meeting (2007) *HELCOM Baltic Sea Action Plan*. HELCOM Ministerial Meeting, Krakow, Poland.
- Hinz H, Prieto V, Kaiser MJ (2009) Trawl disturbance on benthic communities: chronic effects and experimental predictions. *Ecological Applications*, **19**, 761–773.
- Hordoir R, Meier HEM (2011) Effect of climate change on the thermal stratification of the Baltic sea: a sensitivity experiment. *Climate Dynamics*, **38**, 1703–1713.
- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, **46**, 10–18.
- Hüssy K, St. John MA, Bottcher U (1997) Food resource utilization by juvenile Baltic cod *Gadus morhua*: a mechanism potentially influencing recruitment success at the demersal juvenile stage? *Marine Ecology Progress Series*, **155**, 199–208.
- ICES (2014) Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 3–10 April 2014. (ed 2014/Acom IC), Copenhagen, Denmark, ICES.
- Josefson AB, Norkko J, Norkko A (2012) Burial and decomposition of plant pigments in surface sediments of the Baltic Sea: role of oxygen and benthic fauna. *Marine Ecology Progress Series*, **455**, 33–49.
- Kahru M, Elmgren R, Savchuk OP (2015) Changing seasonality of the Baltic Sea. *Biogeosciences Discuss*, **12**, 18855–18882.
- Karlson K, Rosenberg R, Bonsdorff E (2002) Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic waters - A review. *Oceanography and Marine Biology*, **40**, 427–489.
- Karlson K, Hulth S, Ringdahl K, Rosenberg R (2005) Experimental recolonisation of Baltic Sea reduced sediments: survival of benthic macrofauna and effects on nutrient cycling. *Marine Ecology Progress Series*, **294**, 35–49.
- Karlson K, Bonsdorff E, Rosenberg R (2007a) The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediments. *Ambio*, **36**, 161–167.
- Karlson K, Hulth S, Rosenberg R (2007b) Density of *Monoporeia affinis* and biogeochemistry in Baltic Sea sediments. *Journal of Experimental Marine Biology and Ecology*, **344**, 123–135.
- Katajisto T, Viitasalo M, Koski M (1998) Seasonal occurrence and hatching of calanoid eggs in sediments of the northern Baltic Sea. *Marine Ecology Progress Series*, **163**, 133–143.
- Kauppi L, Norkko A, Norkko J (2015) Large-scale species invasion into a low-diversity system: spatial and temporal distribution of the invasive polychaetes *Marenzelleria* spp. in the Baltic Sea. *Biological Invasions*, **17**, 2055–2074.
- Kautsky N, Evans S (1987) Role of biodeposition by *Mytilus-edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. *Marine Ecology Progress Series*, **38**, 201–212.
- Kautsky L, Kautsky N (2000) The Baltic Sea, including Bothnian Sea and Bothnian Bay. In: *Seas at the Millennium: An Environmental Evaluation* (ed. Sheppard CRC), pp. 122–133. Pergamon, Amsterdam.
- Kemp WM, Boynton WR, Adolf JE *et al.* (2005) Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology Progress Series*, **303**, 1–29.
- Korpinen S, Meidinger M, Laamanen M (2013) Cumulative impacts on seabed habitats: An indicator for assessments of good environmental status. *Marine Pollution Bulletin*, **74**, 311–319.
- Kotta JK, Möller T (2014) Linking nutrient loading, local abiotic variables, richness and biomasses of macrophytes, and associated invertebrate species in the north-eastern Baltic Sea. *Estonian Journal of Ecology*, **63**, 145–167.
- Kotta J, Simm M, Kotta I, Kanošina I, Kallaste K, Raid T (2004) Factors controlling long-term changes of the eutrophicated ecosystem of Parnu Bay, Gulf of Riga. *Hydrobiologia*, **514**, 259–268.
- Kotta J, Möller T, Orav-Kotta H, Pärnoja M (2014) Realized niche width of a brackish water submerged aquatic vegetation under current environmental conditions and projected influences of climate change. *Marine Environmental Research*, **102**, 88–101.
- Kotta J, Oganjan K, Lauringson V *et al.* (2015) Establishing functional relationships between abiotic environment, macrophyte coverage, resource gradients and the distribution of *Mytilus trossulus* in a brackish non-tidal environment. *PLoS ONE*, **10**, e0136949.
- Kristensen E, Hansen T, Delefosse M, Banta G, Quintana C (2011) Contrasting effects of the polychaetes *Marenzelleria viridis* and *Nereis diversicolor* on benthic metabolism and solute transport in sand coastal sediment. *Marine Ecology Progress Series*, **425**, 125–139.
- Lade SJ, Niiranen S, Hentati-Sundberg J *et al.* (2015) An empirical model of the Baltic Sea reveals the importance of social dynamics for ecological regime shifts. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 11120–11125.
- Lauringson V, Mälton E, Kotta J, Kangur K, Orav-Kotta H, Kotta I (2007) Environmental factors influencing the biodeposition of the suspension feeding bivalve *Dreissena polymorpha* (Pallas): comparison of brackish and freshwater populations. *Estuarine Coastal and Shelf Science*, **75**, 459–467.
- Lauringson V, Kotta J, Orav-Kotta H, Kaljurand K (2014) Diet of mussels *Mytilus trossulus* and *Dreissena polymorpha* in a brackish nontidal environment. *Marine Ecology - an Evolutionary Perspective*, **35**, 56–66.
- Laursen K, Möller AP (2014) Long-term changes in nutrients and mussel stocks are related to numbers of breeding eiders *Somateria mollissima* at a large Baltic colony. *PLoS ONE*, **9**, e95851.
- van Leeuwen A, Huss M, Gardmark A *et al.* (2013) Predators with multiple ontogenetic niche shifts have limited potential for population growth and top-down control of their prey. *American Naturalist*, **182**, 53–66.
- van Leeuwen A, Huss M, Gardmark A, de Roos AM (2014) Ontogenetic specialism in predators with multiple niche shifts prevents predator population recovery and establishment. *Ecology*, **95**, 2409–2422.
- Lehikoinen A, Jaatinen K, Vahatalo AV *et al.* (2013) Rapid climate driven shifts in wintering distributions of three common waterbird species. *Global Change Biology*, **19**, 2071–2081.
- Lehtonen KK, Andersin AB (1998) Population dynamics, response to sedimentation and role in benthic metabolism of the amphipod *Monoporeia affinis* in an open-sea area of the northern Baltic Sea. *Marine Ecology Progress Series*, **168**, 71–85.
- Leppäranta M, Myrberg K (2009) *Physical Oceanography of the Baltic Sea*. Praxis Publishing Ltd, Chichester.
- Lindegren M, Mollmann C, Nielsen A, Brander K, MacKenzie BR, Stenseth NC (2010) Ecological forecasting under climate change: the case of Baltic cod. *Proceedings of the Royal Society B-Biological Sciences*, **277**, 2121–2130.
- Lindegren M, Blenckner T, Stenseth NC (2012) Nutrient reduction and climate change cause a potential shift from pelagic to benthic pathways in a eutrophic marine ecosystem. *Global Change Biology*, **18**, 3491–3503.
- Lotze HK, Lenihan HS, Bourque BJ *et al.* (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, **312**, 1806–1809.
- Malmqvist B, Wotton RS, Zhang YX (2001) Suspension feeders transform massive amounts of seston in large northern rivers. *Oikos*, **92**, 35–43.

- Marcus NH, Boero F (1998) Minireview: the importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnology and Oceanography*, **43**, 763–768.
- Maximov A, Bonsdorff E, Eremina T, Kauppi L, Norkko A, Norkko J (2015) Context-dependent consequences of *Marenzelleria* spp. (Spionidae: Polychaeta) invasion for nutrient cycling in the Northern Baltic Sea. *Oceanologia*, **57**, 342–348.
- Meier HEM, Andersson HC, Eilola K *et al.* (2011) Hypoxia in future climates: a model ensemble study for the Baltic Sea. *Geophysical Research Letters*, **38**.
- Meier HEM, Andersson HC, Arheimer B *et al.* (2012) Comparing reconstructed past variations and future projections of the Baltic Sea ecosystem—first results from multi-model ensemble simulations. *Environmental Research Letters*, **7**.
- Merkouriadi I, Leppäranta M (2014) Long-term analysis of hydrography and sea-ice data in Tvärminne, Gulf of Finland, Baltic Sea. *Climatic Change*, **124**, 849–859.
- Michaud E, Desrosiers G, Mermillod-Blondin F, Sundby B, Stora G (2006) The functional group approach to bioturbation: II. The effects of the Macoma balthica community on fluxes of nutrients and dissolved organic carbon across the sediment–water interface. *Journal of Experimental Marine Biology and Ecology*, **337**, 178–189.
- Nascimento FJA, Karlson AML, Näslund J, Gorokhova E (2009) Settling cyanobacterial blooms do not improve growth conditions for soft bottom meiofauna. *Journal of Experimental Marine Biology and Ecology*, **368**, 138–146.
- Nascimento FJA, Naslund J, Elmgren R (2012) Meiofauna enhances organic matter mineralization in soft sediment ecosystems. *Limnology and Oceanography*, **57**, 338–346.
- Niiranen S, Blenckner T, Hjerne O, Tomczak MT (2012) Uncertainties in a Baltic Sea food-web model reveal challenges for future projections. *Ambio*, **41**, 613–625.
- Niiranen S, Yletyinen J, Tomczak MT *et al.* (2013) Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. *Global Change Biology*, **19**, 3327–3342.
- Nilsson L (1980) Winter diving duck populations and available food resources in the Baltic. *Wildfowl*, **31**, 131–143.
- Nixon SW (1988) Physical energy inputs and the comparative ecology of lake and marine ecosystems. *Limnology and Oceanography*, **33**, 1005–1025.
- Nixon SW, Fulweiler RW, Buckley BA, Granger SL, Nowicki BL, Henry KM (2009) The impact of changing climate on phenology, productivity, and benthic-pelagic coupling in Narragansett Bay. *Estuarine Coastal and Shelf Science*, **82**, 1–18.
- Norkko J, Reed DC, Timmermann K *et al.* (2012) A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biology*, **18**, 422–434.
- Norkko A, Villnas A, Norkko J, Valanko S, Pilditch C (2013) Size matters: implications of the loss of large individuals for ecosystem function. *Scientific Reports*, **3**, 2646–2652.
- Norkko J, Gammal J, Hewitt J, Josefson A, Carstensen J, Norkko A (2015) Seafloor ecosystem function relationships: In situ patterns of change across gradients of increasing hypoxic stress. *Ecosystems*, **18**, 1424–1439.
- Ojaveer H, Kotta J (2015) Ecosystem impacts of the widespread non-indigenous species in the Baltic Sea: literature survey evidences major limitations in knowledge. *Hydrobiologia*, **750**, 171–185.
- Olafsson E, Elmgren R (1997) Seasonal dynamics of sublittoral meiobenthos in relation to phytoplankton sedimentation in the Baltic Sea. *Estuarine Coastal and Shelf Science*, **45**, 149–164.
- Olsgard F, Schaanning MT, Widdicombe S, Kendall MA, Austen MC (2008) Effects of bottom trawling on ecosystem functioning. *Journal of Experimental Marine Biology and Ecology*, **366**, 123–133.
- Olsson J, Bergstrom L, Gardmark A (2012) Abiotic drivers of coastal fish community change during four decades in the Baltic Sea. *Ices Journal of Marine Science*, **69**, 961–970.
- Olsson J, Bergstrom L, Gardmark A (2013) Top-down regulation, climate and multi-decadal changes in coastal zoobenthos communities in two Baltic Sea areas. *PLoS ONE*, **8**, e64767.
- Pécuchet L, Törnroos A, Lindegren M (2016) Patterns and drivers of fish community assembly in a large marine ecosystem. *Marine Ecology Progress Series*, **546**, 239–248.
- Raffaelli D, Bell E, Weithoff G *et al.* (2003) The ups and downs of benthic ecology: considerations of scale, heterogeneity and surveillance for benthic-pelagic coupling. *Journal of Experimental Marine Biology and Ecology*, **285**, 191–203.
- Reader HE, Stedmon CA, Kritzbeg ES (2014) Seasonal contribution of terrestrial organic matter and biological oxygen demand to the Baltic Sea from three contrasting river catchments. *Biogeosciences*, **11**, 3409–3419.
- Renz JR, Forster S (2014) Effects of bioirrigation by the three sibling species of *Marenzelleria* spp. on solute fluxes and porewater nutrient profiles. *Marine Ecology Progress Series*, **505**, 145–159.
- Riemann B, Carstensen J, Dahl K *et al.* (2015) Recovery of Danish coastal ecosystems after reductions in nutrient loading: a holistic ecosystem approach. *Estuaries and Coasts*, **39**, 82–97.
- Rooney N, McCann KS (2012) Integrating food web diversity, structure and stability. *Trends in Ecology & Evolution*, **27**, 40–46.
- Rumohr H, Krost P (1991) Experimental evidence of damage to benthos by bottom trawling, with special reference to *Arctica islandica*. *Helgoländer Meeresuntersuchungen*, **33**, 340–345.
- Rutgersson A, Jaagus J, Schenk F, Stendel M (2014) Observed changes and variability of atmospheric parameters in the Baltic Sea region during the last 200 years. *Climate Research*, **61**, 177–190.
- Savchuck OP, Gustafsson BG, Muller-Karulis B (2012) BALTSEM- a marine model for decision support within the Baltic Sea Region. In: Technical Report No. 7. Baltic Nest Institute, Stockholm, Sweden.
- Schindler DE, Scheuerell MD (2002) Habitat coupling in lake ecosystems. *Oikos*, **98**, 177–189.
- Seitz RD, Wennhage H, Bergstrom U, Lipcius RN, Ysebaert T (2014) Ecological value of coastal habitats for commercially and ecologically important species. *Ices Journal of Marine Science*, **71**, 648–665.
- Skov H, Heinänen S, Žydelis R *et al.* (2011) Waterbird populations and pressures in the Baltic Sea. In: TemaNord 2011:550. Nordic Council of Ministers, Copenhagen, Denmark.
- Smetacek V (1980) Annual cycle of sedimentation in relation to plankton ecology in western Kiel Bight. *Ophelia*, **65**–76.
- Smetacek VS (1985) Role of sinking in diatom life-history cycles - ecological, evolutionary and geological significance. *Marine Biology*, **84**, 239–251.
- Smith CR, Mincks S, DeMaster DJ (2006) A synthesis of benthic-pelagic coupling on the Antarctic shelf: Food banks, ecosystem inertia and global climate change. *Deep-Sea Research Part II-Topical Studies in Oceanography*, **53**, 875–894.
- Snelgrove PVR, Thrush SF, Wall DH, Norkko A (2014) Real world biodiversity-ecosystem functioning: a seafloor perspective. *Trends in Ecology & Evolution*, **29**, 398–405.
- Snickars M, Weigel B, Bonsdorff E (2015) Impact of eutrophication and climate change on fish and zoobenthos in coastal waters of the Baltic Sea. *Marine Biology*, **162**, 141–151.
- Sparrevohn CR, Lindegren M, Mackenzie BR (2013) Climate-induced response of commercially important flatfish species during the 20th century. *Fisheries Oceanography*, **22**, 400–408.
- Stempniewicz L, Meissner W (1999) Assessment of the zoobenthos biomass consumed yearly by diving ducks in the Gulf of Gdansk (southern Baltic Sea). *Ornis Svecica*, **9**, 143–154.
- Suess E (1980) Particulate organic-carbon flux in the oceans - surface productivity and oxygen utilization. *Nature*, **288**, 260–263.
- Tallberg P, Heiskanen AS (1998) Species-specific phytoplankton sedimentation in relation to primary production along an inshore-offshore gradient in the Baltic Sea. *Journal of Plankton Research*, **20**, 2053–2070.
- Tamelaender T, Heiskanen AS (2004) Effects of spring bloom phytoplankton dynamics and hydrography on the composition of settling material in the coastal northern Baltic Sea. *Journal of Marine Systems*, **52**, 217–234.
- Timmermann K, Norkko J, Janas U, Norkko A, Gustafsson BG, Bonsdorff E (2012) Modelling macrofaunal biomass in relation to hypoxia and nutrient loading. *Journal of Marine Systems*, **105**, 60–69.
- Tomczak MT, Niiranen S, Hjerne O, Blenckner T (2012) Ecosystem flow dynamics in the Baltic Proper—Using a multi-trophic dataset as a basis for food-web modelling. *Ecological Modelling*, **230**, 123–147.
- Törnroos A, Bonsdorff E, Bremner J, Blomqvist M, Josefson AB, Garcia C, Warzocha J (2015) Marine benthic ecological functioning over decreasing taxonomic richness. *Journal of Sea Research*, **98**, 49–56.
- Uzars D (1994) Feeding of cod (*Gadus morhua callarias* L.) in the central Baltic in relation to environmental changes. In: *Cod and Climate Change - Proceedings of a Symposium* (eds Jakobsson J, Athorsson OS, Beverton RJH, Björnsson B, Daan N, Frank KT, Meincke J, Rothschild B, Sundby S, Tilseth S), pp. 612–623. ICES, Copenhagen.
- Vahtera E, Conley DJ, Gustafsson BG *et al.* (2007) Internal ecosystem feedbacks enhance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic Sea. *Ambio*, **36**, 186–194.
- Viktorsson L, Ekeröth N, Nilsson M, Kononets M, Hall POJ (2013) Phosphorus recycling in sediments of the central Baltic Sea. *Biogeosciences*, **10**, 3901–3916.
- Villnäs A, Norkko A (2011) Benthic diversity gradients and shifting baselines: implications for assessing environmental status. *Ecological Applications*, **21**, 2172–2186.
- Villnäs A, Norkko J, Lukkari K, Hewitt J, Norkko A (2012) Consequences of increasing hypoxic disturbance on benthic communities and ecosystem functioning. *PLoS ONE*, **7**, Copenhagen.

- Waldeck P, Larsson K (2013) Effects of winter water temperature on mass loss in Baltic blue mussels: Implications for foraging sea ducks. *Journal of Experimental Marine Biology and Ecology*, **444**, 24–30.
- Walther GR, Roques A, Hulme PE *et al.* (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution*, **24**, 686–693.
- Weber W, Damm U (1991) Investigations on cod stomachs in the western Baltic 1981–1989. ICES C.M. 1991/J:23.
- Weigel B, Andersson HC, Meier HEM, Blenckner T, Snickars M, Bonsdorff E (2015) Long-term progression and drivers of coastal zoobenthos in a changing system. *Marine Ecology Progress Series*, **528**, 141–159.
- Westerbom M, Mustonen O, Kilpi M (2008) Distribution of a marginal population of *Mytilus edulis*: responses to biotic and abiotic processes at different spatial scales. *Marine Biology*, **153**, 1153–1164.
- Wikner J, Andersson A (2012) Increased freshwater discharge shifts the trophic balance in the coastal zone of the northern Baltic Sea. *Global Change Biology*, **18**, 2509–2519.
- Yletyinen J, Bodin Ö, Weigel B, Nordström MC, Bonsdorff E, Blenckner T (2016) Regime shifts in marine communities: a complex systems perspective on food web dynamics. *Proceedings of the Royal Society B-Biological Sciences*, **283**.