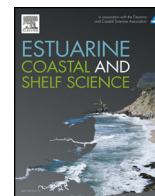




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Long-term records of hard-bottom communities in the southwestern Baltic Sea reveal the decline of a foundation species



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ARTICLE INFO

Keywords:

Abiotic factors
Baseline-studies
Benthos
Community composition
Foundation species
Mytilus edulis
Baltic Sea

ABSTRACT

Ecological processes modulate ecosystem functioning and services. Foundation species are those exerting intense control on such processes as both their existence and loss have profound implications on the structure of ecological communities. For the distinction between random fluctuations and directional regime shifts in community composition, long-term records are of strategic need. In this study we present the monitoring of benthic hard-bottom communities over 11 years along seven stations in the SW Baltic Sea. Regional differences were found between the communities of Kiel and Lübeck bights, with the former area displaying signs of regime shift. The decline and near disappearance of the foundational species *Mytilus edulis* from settlement panels deployed in Kiel Bight correlated with three environmental variables: sea surface temperature, water current speed and chlorophyll *a* concentration. Thus, low spring temperatures, in some cases reinforced by local maxima of chlorophyll *a*, correlated with reduced recruitment of *Mytilus*. Moreover, regional differences of larval dispersal and population connectivity could explain the rapid recovery after disturbance of the mussel populations in Lübeck Bight in contrast to Kiel Bight. Our findings underscore the relevance of long-term monitoring programmes to detect the interactive impacts of global climatic and regional environmental drivers.

1. Introduction

The health of marine ecosystems relies on the maintenance of ecological processes. These processes depend on the structure of ecological communities, which affect ecosystem functioning (Duarte et al., 2018). Certain species have disproportional influence on the structure of communities and the functioning of ecosystems (Loreau et al., 2001). Such species are considered foundation species (Dayton, 1972). Foundation species usually occupy low trophic levels, occur in high abundances and provide habitat to many other species (Ellison et al., 2005; Maggi et al., 2009). Seagrasses, canopy-forming macrophytes or mussels are examples of foundation species in marine systems (Jenkins et al., 1999; Altieri and Witman, 2006; Hughes et al., 2009).

The decrease of foundation species can be critical for ecological communities and may initiate regime shifts. Folke et al. (2004) described regime shifts as transformations of ecological systems and the services they provide. They occur under the effect of perturbations that exceed the ecosystem resilience, which is defined as the capacity of the system to return to the pre-disturbance state (DeAngelis, 1980). The trajectories followed by a regime shift depend on the functions that

species provide (Elmqvist et al., 2003). The understanding of ecosystem dynamics requires a functional approach, where groups of species are categorized into functional groups based on their traits. The analysis of changes in these internally homogenous (in terms of traits) groups of species provides mechanistic insights of how ecosystems processes react to disturbances (Mouillot et al., 2013). For example, the classification in functional groups permits defining whether functionally redundant species within the community could replace lost foundation species (Folke et al., 2004).

The Baltic Sea is a young, semi-enclosed and highly dynamic shelf sea (Snoeijs-Leijonmalm et al., 2017). Its natural characteristics of shallow water depth and low exchange with the North Atlantic have facilitated pronounced impacts of multiple, human-mediated stressors (eutrophication, warming, oxygen depletion, acidification), leading to present-day conditions that are expected for the future in other coastal regions (Reusch et al., 2018). Baltic species are consequently subjected to various press and pulse stressors of natural and anthropogenic nature. As the rate of long-term climate changes as well as the number of extreme events are projected to further increase in the future (Belkin, 2009), Baltic species, which are often already close to their limits of

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<https://doi.org/10.1016/j.ecss.2019.02.029>

Received 27 September 2018; Received in revised form 7 February 2019; Accepted 9 February 2019

Available online 13 February 2019

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physiological - especially osmotic - tolerance, could be particularly sensitive to shifting environmental conditions associated with global change. However, the pronounced abiotic variability of the shallow and land-bound Baltic could also act as a selection pressure towards more tolerant genotypes (Pansch et al., 2014). This uncertainty regarding the future development of Baltic ecosystems underlines the need of biological and environmental long-term records. Monitoring efforts should be dedicated to distinguish regime shifts from stochastic variability (Magurran et al., 2010; Wahl et al., 2013). The Baltic Sea has already experienced regime shifts in the past. For instance, the decline of cod stocks and the resulting increase in sprat abundance (Österblom et al., 2007). Another example is the decrease in depth distribution of the bladder wrack (*Fucus vesiculosus*) leading to habitat losses and simultaneous increase of ephemeral macroalgae (Torn et al., 2006; Wikström and Kautsky, 2007). In both cases biological and environmental long-term records were crucial to detect regime shifts within ecological communities (e.g. Alheit et al., 2005).

Coastal hard-bottom communities establishing on Scandinavian granite boulders dating from the last ice-age are among the most productive and species-rich habitats in the Baltic Sea (Kautsky and Kautsky, 2000). Typically, assemblages of around 60 sessile taxa evenly distributed among macroalgae and animal species (mainly filter feeders) can be found (Wahl et al., 2013). Here, we present the results of a long-term monitoring on standardized hard-bottom communities (identical age, depth and inclination, artificial substrata) in shallow coastal waters of the southwestern (SW) Baltic Sea. The aim of the study is to describe dynamics in community composition with a yearly resolution and discriminate between stochastic and directional structural changes. A further goal is modelling the role of environmental variables to identify which processes possibly shaped the benthic assemblages.

2. Materials & methods

2.1. Study area

Seven stations along the SW Baltic coast were selected for an annual monitoring of hard-bottom communities between 2005 and 2015. The

stations numbered from NW to SE were approximately evenly spaced along the coasts of Kiel Bight (1–4) and Lübeck Bight (5–7) (Fig. 1). Stations 1, 3 and 7 are mainly dominated by seagrass meadows whereas stations 2, 5 and 6 are characterized by boulder fields covered with macroalgae and, sometimes, large and dense mussel beds (6). Only station 4 is characterized by sandy grounds without macrophytes.

2.2. Monitoring

At each station, eight concrete slabs (50 × 50 cm) equipped with two vertical threaded stainless steel bars were deployed at 3 m depth. These constructions served as the basis for horizontally oriented settlement panels (PVC, 12 × 12 cm), which were fixed on the steel bars 30 cm above the seafloor (Fig. S1). Prior to their deployment, the panels were roughened with sand paper (grade 60) in order to facilitate the settlement of benthic organisms. The use of fixed sampling stations and standardized settlement substrate kept spatial and methodological variability at minimum. Every September, panels were exchanged for new ones, thus, all collected communities were 12 months old and in the same seasonal stage. The panels were deployed and retrieved by SCUBA divers, who carefully transferred each panel individually into a zipper bag. Directly after collection, the communities were fixed with buffered formaldehyde to a final concentration of 4%. Collected panels were analysed in the laboratory for sessile species composition to the lowest possible taxonomic level and the relative coverage (%) was estimated to the nearest 5%. In case organisms were exceeding the margins of the panel or settled and grew in multiple layers, the coverage of a single species could exceed 100%.

2.3. Biological data processing

In the analyses of the collected communities only the upward facing side of panels was considered, since they best represent communities of the boulder surfaces. Moreover, only sessile and hemi-sessile taxa (e.g. *Corophium* sp.) were taken into account, since motile organisms were not sampled quantitatively. Taxa which never exceeded 10% coverage on any panel were considered very rare and excluded from the analyses.

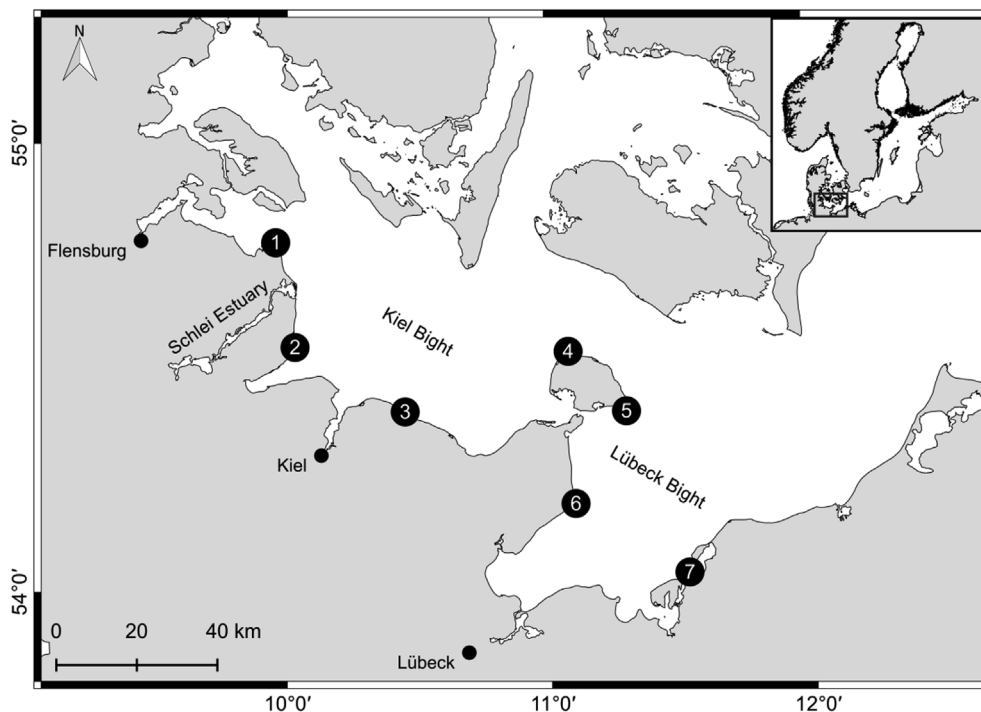


Fig. 1. Geographical position of the seven monitoring stations along the SW Baltic coast.

Table 1

Traits used to categorize each genus into a functional group. Functional groups were constructed by a four letter combination of traits presented.

Adult body size	Growth form	Trophic type	Modularity
S < 1 mm	E encrusting	A autotroph	S solitary
M 1–10 mm	M massive	P predator	C colonial
L 10–100 mm	B bushy	S suspension feeder	
XL 100–1000 mm	F filamentous	D deposit feeder	
XXL > 1000 mm		G grazer	

The coverage of taxa was averaged over all replicates in a given year and station. Since some taxa could not be resolved below the genus, all analyses were performed at this level. Besides taxonomic structure, the functional composition of the assemblages on the settlement panels was examined. This allowed us to assess if taxonomic variations were followed by changes in the functional composition of the communities. Functional groups were defined based on the functional traits proposed by Wahl et al. (2009), assigning a four letters code to each genus. All genera containing multiple species had functionally equivalent species. Functional groups were categorized according to adult body size, growth form, trophic type and modularity (Table 1). Genera that share the same traits were grouped together on the basis of their ecological role in the community (Bremner et al., 2006; Wahl et al., 2009).

2.4. Environmental variables

Data for sea surface temperature (SST), sea surface salinity (SSS), current direction and current speed were extracted for each monitoring station from the Kiel Baltic Sea Ice-Ocean Model (BSIOM, Lehmann and Hinrichsen, 2000). A detailed description of the model system specifications can be found in Lehmann et al. (2014) and Stuckas et al. (2017). The BSIOM also provides a database of three-dimensional velocity fields, in order to calculate Lagrangian drift routes. The three-dimensional trajectories of the simulated drifting particles (resembling planktonic larvae and propagules of benthic organisms) were determined using a 4th order Runge-Kutta scheme (Hinrichsen et al., 1997). The particles were released every five days from 1 July to 30 August within the period 2005–2015. At each release date (13 per year) 175 particles were seeded on a regular spaced grid around the sampling stations. To obtain the origins of the drifted particles that had settled at the sampling stations, their drift was back calculated for a period of 40 days, after being released into the simulated flow fields at sea surface. The back calculation was done by reversing the temporal sequence of the three-dimensional flow fields followed by inverting the sign of the horizontal components of the velocity vector (Hinrichsen et al., 1997). Finally, the spatial extension of the particle release areas was determined by calculating the dispersal kernels after Edwards et al. (2007).

Chlorophyll *a* concentrations (Chl *a*) for all stations were derived from the Baltic Sea biogeochemical reanalysis product (Axell et al., 2018) provided by Copernicus Marine Environment Monitoring Service

Table 2

Environmental variables used in the Generalized Additive Mixed Model (GAMM) for describing changes in *Mytilus* coverage during the period 2005–2010. Mean, maximum (Max) and minimum (Min) values for months April–June (size of dispersal kernels: July–August) from 2005 to 2010 are given.

Variable	Unit	Mean	Min	Max	Source
Sea surface temperature (SST)	°C	11.3	2.0	20.8	Three-dimensional coupled sea ice-ocean model of the Baltic Sea (BSIOM, see Lehmann et al. (2014) and Stuckas et al. (2017) for further information)
Sea surface salinity (SSS)		14.2	8.4	21.1	
Current speed	cm·s ⁻¹	2.5	0.1	7.0	Lagrangian drift routes based on BSIOM
Current direction	°	145.9			
Size of dispersal kernels	km ²	893.3	349.4	2662.6	
Chlorophyll <i>a</i> concentration (Chl <i>a</i>)	mg·m ⁻³	5.6	1.9	10.6	Baltic Sea biogeochemical reanalysis (see Axell et al., 2018 for further information; data downloaded at: http://marine.copernicus.eu). Values extracted for a depth of 1.5 m

(<http://marine.copernicus.eu>). The reanalysis product is based on the coupled physical-biogeochemical model system NEMO-SCOBI (Nucleus for European Modelling of the Ocean - Swedish Coastal and Ocean Biogeochemical model). The data were extracted for a depth of 1.5 m.

2.5. Statistical analysis

Functional redundancy was quantified by the relationship between taxonomic and functional richness using the statistical software R (Version 3.4.2; R Core Team, 2017). The projected function was based on the total number of genera and functional groups recorded for every station and year. The temporal trends of average community compositions (genera and functional groups) at the different stations were examined using non-metric multidimensional scaling (nMDS) plots based on Bray-Curtis dissimilarities between consecutive years. Stress values quantified for each nMDS to which extend dissimilarities are preserved. The obtained resemblance matrices were further employed to test for directional shifts (seriations) in community compositions for each station, using the RELATE function of the PRIMER 7.0 software package (9999 permutations; Clarke and Gorley, 2015). Afterwards, genera and functional groups responsible for observed dissimilarities over time were identified using the SIMPER routine (PRIMER 7.0). Mean coverages of those genera and functional groups with a cumulative contribution to community similarity of 75% were plotted over time for each station. Locally weighted scatter-plot smoother (LOESS) functions with a span of 0.6 were applied.

The decreasing coverage of *Mytilus* after 2009 was found to drive observed changes in the community structure (see section 3.2). Therefore, we specifically compared the coverage of *Mytilus* before (2005–2009) and after (2010–2015) the decline and between Kiel and Lübeck bights using a Generalized Linear Mixed Model (GLMM, see details in Table S2). The GLMM was implemented using the lme4 package (Version 1.1–14; Bates et al., 2015). To further outline the driving forces responsible for changes in 2005–2010, the *Mytilus* coverage of all stations was modelled as a function of relevant environmental variables using a Generalized Additive Mixed Model (GAMM). Mean SST, SSS, current speed and direction, and Chl *a* for the period April to June (spawning season of *Mytilus* sp.; Kautsky, 1982; Stuckas et al., 2017) as well as the size of modelled larval dispersal kernels, were included in the model (Table 2). The selection of these environmental variables was based on their importance for life-history processes of *Mytilus*: water temperature and salinity as well as Chl *a* concentrations are known to mainly affect body-mass and reproductive output of juvenile and adult mussel individuals (Kautsky, 1982; Young et al., 1996; Honkoop and Beukema, 1997), whereas current conditions are important for larval transport and early stage survival (Folmer et al., 2014). The GAMM was implemented using the gamm4 package (Version 0.2–5; Wood and Scheipl, 2017). Since the aim of this analysis was to identify potential drivers of *Mytilus* decline, the model was only applied for the time period during which the decline was observed (2005–2010). The model did not consider the full sampling period (2005–2015) to avoid introducing a bias. Indeed, after 2010 the

coverage of *Mytilus* in the Kiel Bight was low and stable while the environmental variables were fluctuating.

The GAMM was specified based on a gamma distribution with a log-link function. All environmental variables were included as smooth terms using penalized cubic regression splines restricted to up to three degrees of freedom. To adjust the within station variability, the station identity was included as random factor. Starting from the full model (including all considered environmental predictors), sub-models were generated in a stepwise procedure. Predictors were eliminated until the model that included all significant variables and the lowest Akaike's Information Criterion (AIC) was reached. The adequacy of all adjusted models was evaluated by inspecting the plots of residuals.

3. Results

3.1. Structure of the communities

A total of 32 genera from 9 different phyla was recorded. The phyla with highest genera richness were Rhodophyta (11), Chlorophyta (6) and Ochrophyta (4). The genera were classified into 10 different functional groups (i.e. unique combinations of four functional traits; see Tables 1 and S1). Functional groups including the trait “autotroph” grouped most of the genera (21), followed by those including the trait “suspension feeding” (11) (Table S1). There were slightly more genera and functional groups in Kiel Bight (stations 1–4) than in Lübeck Bight (stations 5–7) (Table 3). Functional richness increased non-linearly with taxonomic richness ($p < 0.001$, Fig. 2), based on comparison of AIC calculated for a non-linear (AIC = 200.4) and a linear regression (AIC = 227.5).

3.2. Community dynamics

Interannual recruitment dynamics showed regional differences between stations in Kiel and Lübeck bights. The sessile communities of stations 1, 3 and 4 (Kiel Bight) directionally shifted from an initial configuration in the years 2005–2008 towards a new composition in 2010–2015, as observed in the nMDS plots and confirmed by the RELATE analysis (Fig. 3A,C,D; Figs. S2A,C,D). At these three stations, dissimilarities between community structures were observed among years. Station 2 differs from the other three stations by showing a mixture of directional (e.g. in 2007–2008, Fig. 3B) and cyclic trajectories (e.g. 2011–2013, Fig. 3B). Community trajectories of the Lübeck Bight stations appear to be more compact and seemed to move around a core community configuration over the entire monitoring period (Fig. 3E–G; Figs. S2E–G). These trends were less pronounced at station 5 compared to stations 6 and 7. At station 7, differences from the initial community composition were only observed in three years of the entire monitoring (2006, 2013 and 2015; Fig. 3G; Fig. S2G). According to the RELATE analysis, the stations of Lübeck Bight showed no significant seriation patterns (Fig. 3E–G; Figs. S2E–G).

The SIMPER analysis showed a decreasing number of genera and functional groups contributing to structural differences among years

Table 3

Total number of recorded genera and functional groups in each station for the period 2005–2015. Genera and functional groups that contributed up to a cumulative cut-off value of $\geq 75\%$ (SIMPER analysis) to the observed dissimilarities are listed. Numbers in brackets indicate relative contribution of either genera or functional groups to differences in similarity expressed as percentages. See codes for functional groups in Table 1.

Station	Genera richness	Functional richness	Relevant genera	Relevant functional groups
1	25	10	<i>Mytilus</i> (31), <i>Polysiphonia</i> (15), <i>Ceramium</i> (14), <i>Balanus</i> (11), <i>Aglaothamnion</i> (9)	MMSS (38), MFAS (29), LFAS (24)
2	25	10	<i>Mytilus</i> (27), <i>Polysiphonia</i> (23), <i>Ceramium</i> (21), <i>Corophium</i> (8)	MFAS (36), MMSS (26), SMSS (18)
3	27	10	<i>Mytilus</i> (32), <i>Polysiphonia</i> (20), <i>Ceramium</i> (15), <i>Balanus</i> (12)	MFAS (37), MMSS (36), LFAS (17)
4	23	8	<i>Polysiphonia</i> (47), <i>Mytilus</i> (26), <i>Balanus</i> (8)	LFAS (42), MMSS (35)
5	19	9	<i>Mytilus</i> (61), <i>Balanus</i> (11), <i>Polysiphonia</i> (8)	MMSS (70), MFAS (16)
6	17	8	<i>Mytilus</i> (83)	MMSS (89)
7	21	9	<i>Mytilus</i> (81)	MMSS (74), MESC (15)

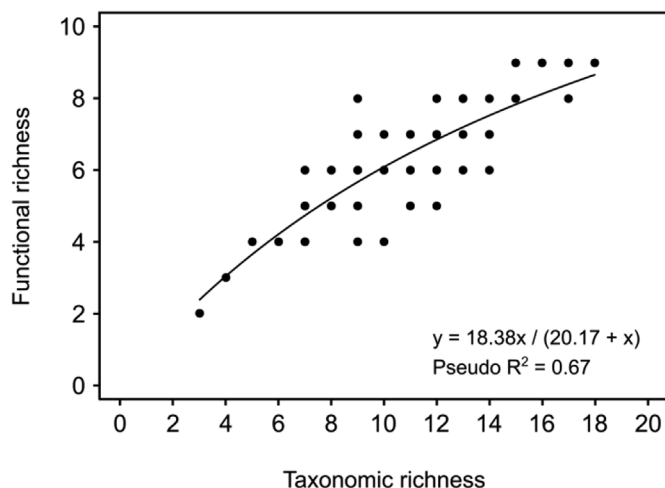


Fig. 2. Relationship between taxonomic and functional richness based on total counts of genera and functional groups per station and year. All parameters of the non-linear regression were significant ($p < 0.05$).

from station 1, with four genera being mainly responsible for dissimilarities, to station 7, exhibiting only one genus as the discriminating taxon (considering a cut-off at 75% similarity) (Table 3). This decrease in the number of discriminating genera went along with a gradual shift from trophically mixed communities (with autotrophs and heterotrophs) towards communities dominated by heterotrophs. Noticeably, the genus *Mytilus* and the functional group MMSS (medium body size, massive growth form, suspension feeder and solitary) appeared to be a relevant discriminating genus/functional group, respectively, at all seven stations (Table 3).

The temporal dynamics of genera and functional groups identified by SIMPER showed for most of the stations that *Mytilus* or the functional group MMSS (containing *Balanus*, *Mytilus*, *Spirorbis*) attained the highest coverages among all genera or functional groups (Fig. 4; Fig. S3). Comparable values for other genera and functional groups were reached in single years only, e.g., *Balanus* and *Corophium* or SMSS and MFAS (Fig. 4D,B; Figs. S3B and E). Diverging temporal trends can be observed for stations of Kiel (Fig. 4A–D) and Lübeck (Fig. 4E–G) bights. The main compositional differences of communities between the bights are driven by the coverage of *Mytilus* (taxonomic) and MMSS (functional). Since the functional group MMSS is dominated by the contribution of *Mytilus*, temporal trends based on taxonomic and functional data were very similar. Coverages in Lübeck Bight were subject to fluctuations with declines followed by recovery phases, particularly in station 6. In Kiel Bight, in contrast, the coverages decreased dramatically in the period 2006–2009 and remained low in the following years. The applied GLMM confirmed the differential developments of *Mytilus* coverage between Kiel and Lübeck bights (Table S2).

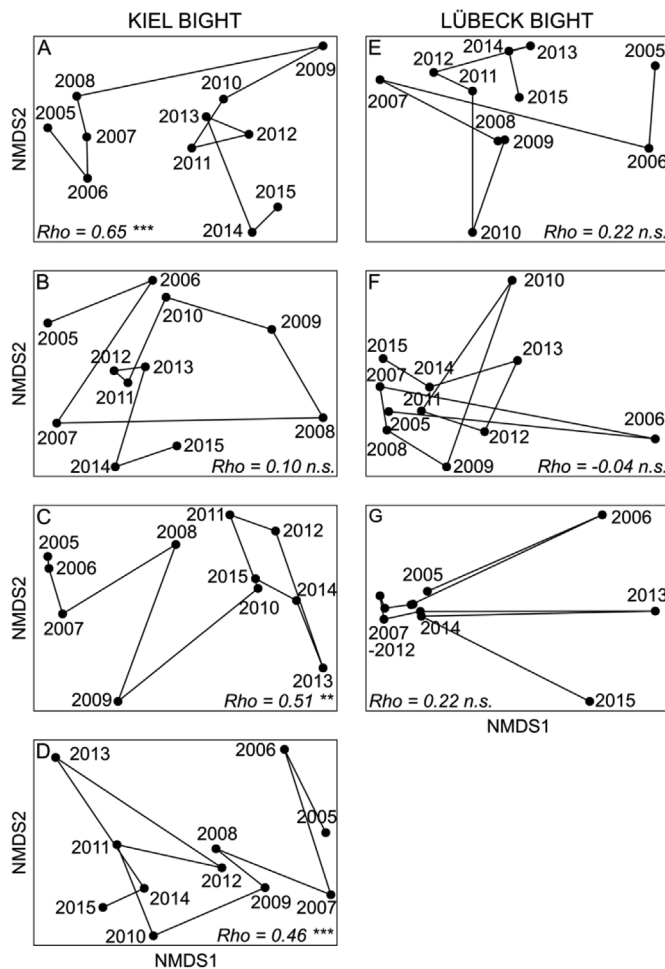


Fig. 3. nMDS trajectories based on Bray-Curtis dissimilarities in taxonomic composition between consecutive years for the seven monitoring stations. For all plots stress was ≤ 0.11 . Correlation coefficient (Rho) and significance levels (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n. s. = not significant) of the RELATE analysis are given. Charts are ordered from station 1 (A) to 7 (G).

3.3. Modelled larval dispersal kernels

The back-calculated origins of simulated, drifting larvae for the period 2005–2015 (*Mytilus* decline) showed site-specific differences in terms of size and orientation of the dispersal kernels (Fig. 5). In general, the dispersal kernels in Kiel Bight were larger than those in Lübeck Bight. With a kernel size of 2662 km², the larvae at the highly exposed station 4 (Kiel Bight) have the largest potential area of origin. Furthermore, at this station the origin of larvae is highly variable and with low overlap between consecutive years, showing higher heterogeneity than all other stations. In contrast, source areas of larvae at stations 6 and 7 (Lübeck Bight) show only little differences between years. Largest dispersal kernels were found for the sites of Kiel Bight. Noticeably, the origins of larvae settling at stations 1 and 2 did not include the stations themselves.

3.4. Potential drivers of *Mytilus* coverage

The final GAMM retained three of the six originally included variables (SST, current speed and Chl *a* concentration, AIC = 392.8) and fixed effects explained 32% of the deviance (Table 4). According to the model, and in the scale of the link function, the coverage of *Mytilus* increases linearly with increasing SST and decreases with increasing current speed. Modelled *Mytilus* coverages stay similar between 3 and 6 mg Chl *a* · m⁻³, but drastically decrease at higher Chl *a*

concentrations (Fig. 6).

4. Discussion

The present study on hard-bottom communities along the SW Baltic Sea revealed temporal community shifts on a regional scale. Different trends in the coverage of the foundational species *Mytilus edulis* entailed contrasting community developments between Kiel and Lübeck bights. In Kiel Bight but not in Lübeck Bight, a strong decline in *Mytilus* coverages since 2006 was associated with substantial re-structuring of the communities. Sea surface temperature, Chl *a* and current speed correlated with the observed structural changes. Taxonomic and functional shifts were similar. This can be explained by: (1) low taxonomic diversity in the functional group MMSS (only three genera included, Tables 1 and 2) strong dominance of *Mytilus* within this functional group. Therefore, any reference to *Mytilus* in the present discussion is also representative for the functional group MMSS.

The communities in this monitoring effort were reset every year by replacing the settlement panels. Thus, the community structure found in month 12 results from reproduction dynamics in neighbouring communities (or in the panel community for short-generation species or asexually reproducing ones), settlement, survival and growth. In the case of the foundational mussels, the dependence of their reproduction on water temperature has been subject to several studies. Mild winter temperatures may lower the reproduction of *Mytilus*, since energy expenses for maintenance and growth are rising in a season when plankton biomass is low (Honkoop and Beukema, 1997). In addition, its predators (e.g. crabs and sea stars) can be more active at elevated temperatures in winter (Young et al., 1996). However, our results suggest differently. We found that higher mean spring temperatures (usually coupled with mild winters, Fig. S4) could have favoured the recruitment of mussels. On the other hand, colder years (after 2007, see Fig. 4; Fig. S4) seemed to promote a decline in mussel coverages. We suggest that during the study period, winter temperatures were not high enough to cause any detrimental effects to the mussel populations. The beneficial effect of elevated temperatures reported for young mussels (up to 20 °C; Hiebenthal et al., 2013) could have outweighed the putatively negative influence of a mild winter and caused the observed patterns, e.g. in 2007 (Fig. 4). Although elevated temperatures were beneficial for the populations in both studied bights, dynamics observed after decline phases were different. The assemblages in Lübeck Bight recovered to their initial state in the years following a decrease in coverage (e.g. station 6 in 2009, Fig. 4F). The populations in Kiel Bight were instead compromised after 2009, thus underlining the existence of further factors determining *Mytilus* coverage.

While SST mainly varied among years, current speed and Chl *a* differed among regions. Indeed, the current speed depends at a local to regional scale on geomorphology and wind regime. As Kiel Bight is a largely open system, the offshore transport of mussel larvae is potentially favoured. Lübeck Bight, in contrast, is a geomorphologically more enclosed system (except for station 5) and, consequently, the mussel beds in Lübeck Bight are better connected to each other. Thus, a “rescue effect” (*sensu* Brown and Kodric-Brown, 1977) resulting from high connectivity between mussel beds in Lübeck Bight could explain the rapid recolonization by *Mytilus* after lower SST in 2009 and 2010. For instance, the mussels from station 6 are likely to supply larvae to station 5, which exhibits mostly unfavourable current conditions for the settlement of its own larvae (i.e. currents directed to the east with mean speeds up to 6 cm s⁻¹). Therefore, the large mussel beds of station 6 may serve as a source of larvae for station 5, i.e. the sink habitat (Sorte et al., 2017). Further evidence is provided by the back-calculated origins of drifting particles reaching the stations. The dispersal kernels of the stations in Lübeck Bight strongly overlap among years, especially those of station 6, which overlap with the two remaining stations in the bight (stations 5 and 7, Fig. 5). In contrast, the dispersal kernels of the stations in Kiel Bight display low mutual overlap. Stations 1 and 2 fully

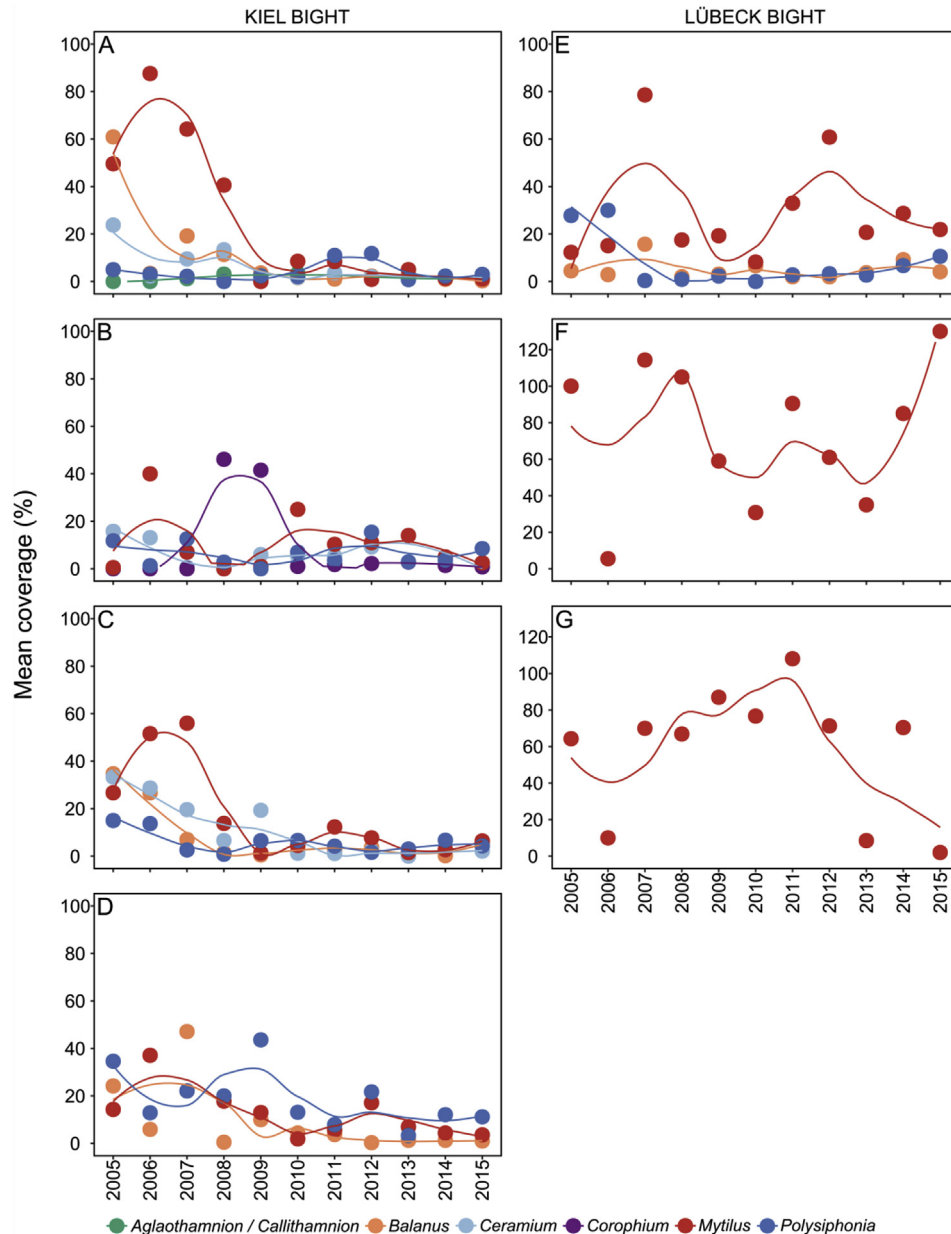


Fig. 4. Mean coverage (%) of genera identified by SIMPER. The genera visualized are those exhibiting a cumulative contribution in similarity of 75% over the monitoring period 2005–2015. Curves from LOESS smooth functions (span = 0.6) are given to highlight temporal dynamics. Please note different scaling of y-axis among plots. Charts are ordered from station 1 (A) to 7 (G).

rely on recruitment from outside, as demonstrated by the kernels. The strong dependency of coastal *Mytilus* populations on ocean currents has been reported in several studies for different mussel species (*M. edulis*, *M. galloprovincialis*) and their respective hybrids (McQuaid and Phillips, 2000; Gilg and Hilbisch, 2003; Folmer et al., 2014). In these studies, based on genetic analyses the authors suggest larval dispersal distances of 30–50 km (McQuaid and Phillips, 2000; Gilg and Hilbisch, 2003; Stuckas et al., 2017). This relatively short larval transport distance underpins the importance of the connectivity between *Mytilus* patches to recolonize certain areas from source habitats after a disturbance (Carson et al., 2011). The lower connectivity of the populations in Kiel Bight compared to Lübeck Bight should be further corroborated by knowledge about the spatial extensions of *Mytilus* populations.

The relationship between *Mytilus* coverage and phytoplankton availability (as measured by Chl *a*) suggests a decline in coverage at mean concentrations higher than $\sim 6 \text{ mg Chl } a \cdot \text{m}^{-3}$. Pascoe et al. (2009) found that the filtration rates of *Mytilus edulis* were reduced

when Chl *a* concentration exceeded $\sim 6 \text{ mg m}^{-3}$ for only 2 h. At stations 1 and 2, which showed generally higher primary productivity than the other stations (Fig. S4), Chl *a* concentrations (averaged for spring) reached values up to 8.3 and 7.7 mg m^{-3} , respectively. Such high primary production could be explained by the proximity of stations 1 and 2 to the Schlei Estuary (Fig. 1). The 43 km long inlet has been described as hypertrophic, exhibiting annual mean Chl *a* concentrations between 5.5 and 87.8 mg m^{-3} (outermost to innermost measurement stations; Gocke et al., 2003). Therefore, the influence of the Schlei water body (in providing great amounts of phytoplankton) could represent a local factor shaping the coverage of *Mytilus* in addition to regional (current regime) and global (SST) drivers.

A decline of *Mytilus* in Kiel Bight can have severe ecological consequences. Functional redundancy was found to be low in the studied communities (Fig. 2), i.e. declines in few or single species could be accompanied by the loss of entire functional groups. The functional group MMSS only includes *Mytilus* and two other genera (*Balanus* and

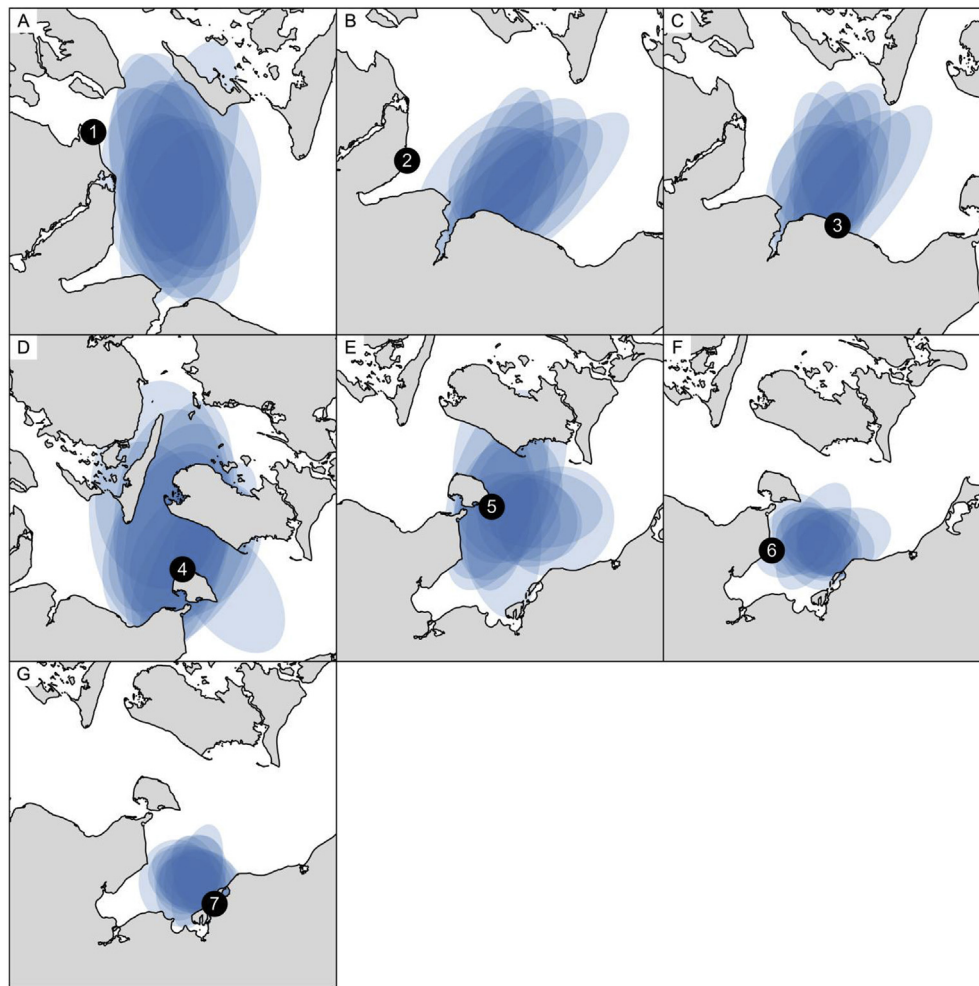


Fig. 5. Dispersal kernels representing back-calculated origins of virtually released, passively moving particles resembling larvae of benthic organisms for the period 2005–2015. Overlap of dispersal kernels is indicated by darker shadings. In the single plots, the number and position of the respective monitoring station is presented.

Table 4

Modelling process of fixed effects for the Generalized Additive Mixed Models (GAMM) describing the influence of sea surface temperature (SST), sea surface salinity (SSS), chlorophyll *a* concentration (Chl *a*), current conditions (current speed, current direction) and size of modelled larval dispersal kernels (dispersal) on the coverage of *Mytilus*. Models are presented in R syntax and the degrees of freedom are given for the single smooth terms (s). The Akaike's information criterion (AIC) is shown for each model. All terms of the last and best model were significant ($p < 0.05$).

Model expression	AIC
s (SST, 1) + s (Chl.a, 2.53) + s (SSS, 2.69) + s (current speed, 1) + s (current direction, 1) + s (dispersal, 1)	402.9
s (SST, 1) + s (Chl.a, 2.54) + s (SSS, 2.70) + s (current speed, 1) + s (dispersal, 1)	398.9
s (SST, 1) + s (Chl.a, 2.55) + s (SSS, 2.70) + s (current speed, 1)	394.9
s (SST, 1) + s (Chl.a, 2.65) + s (current speed, 1)	392.8

Spirorbis, Table S1). However, there is no guarantee that the functional role of *Mytilus* could be sustained after its disappearance, since the functional grouping used here is describing only categorical but not continuous traits of the taxa. Compared to its functional counterparts (e.g. *Balanus* and *Spirorbis*), *Mytilus* bears unique characteristics. Indeed, the blue mussel is considered as an important foundation species in the Baltic Sea (Larsson et al., 2017). It modifies and creates highly diverse habitats, enhancing the number of niches for benthic flora and fauna, which rely on the provision of a three dimensional matrix as

shelter or secondary hard substrate (Norling and Kautsky, 2008; Díaz et al., 2015). Filtering vast amounts of water and creating large bio-masses, *Mytilus* is furthermore important in removing particulate material from the water and cycling nutrients and organic matter, thereby creating a link between pelagic and benthic food webs (Kautsky and Evans, 1987) as well as counteracting eutrophication (Lindahl et al., 2005). The mussels serve as a food resource for several species like the commercially important fish species flounder (*Platichthys flesus*) and cod (*Gadus morhua*), as well as for benthic predators, such as sea stars and shore crabs (Kautsky, 1981). Hence, *Mytilus* interacts with various species and its loss would trigger a chain of reactions leading to changes in community structure and ecosystem functioning (Sorte et al., 2017). Examples of such cascading effects and their consequences on ecosystem services have been reported for the decline of various foundation species, e.g. seagrasses, oysters, corals and kelps (Pandolfi et al., 2003; Hughes et al., 2009; Beck et al., 2011; Krumhansl et al., 2016). Nevertheless, the role of blue mussels as providers of ecosystem services in the Baltic Sea is controversial. Subtidal *Mytilus* populations replaced *Fucus* habitats and promoted the settlement of filamentous red algae in the coast of Sweden (Rönnbäck et al., 2007). The present monitoring further corroborates the negative impact of *Mytilus* on the diversity of sessile taxa. All stations where *Mytilus* coverages decreased showed higher average counts in genera, while lowest biodiversity was recorded in presence of a very dense mussel bed (station 6; Table 3). Our findings suggest space competition as the key mechanism behind the dominance of *Mytilus* over other hard-substrate sessile species (Dürr and

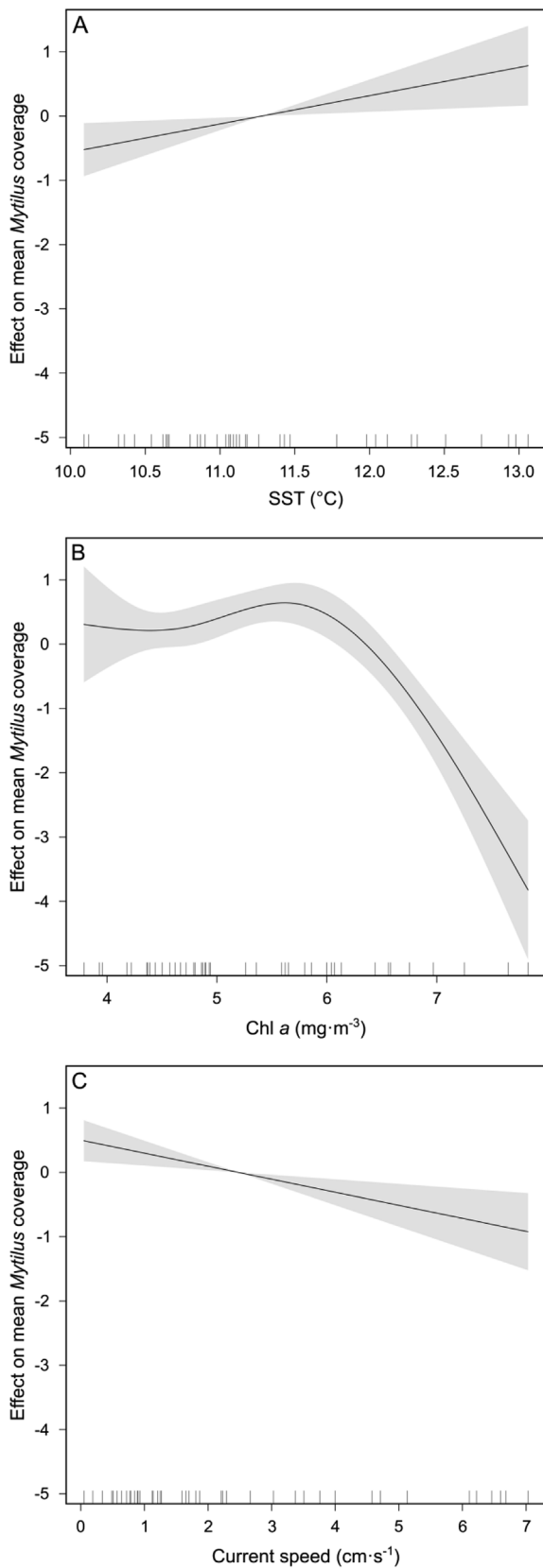


Fig. 6. Generalized Additive Mixed Model (GAMM) relating environmental variables with *Mytilus* coverage. Mean partial effects of SST (mean sea surface temperature in spring; A), Chl *a* (mean chlorophyll *a* concentration in spring; B) and current speed (C) are presented as solid lines. Confidence intervals (95%) are shown as shaded areas. Note that the y-axis is centred and expressed in the scale of the link function (details in section 2.4). The marks on the x-axis show the distribution of the data for each predictor.

Wahl, 2004). Even though *Mytilus* were overly abundant at stations 6 and 7, the respective communities differed in genera richness. Station 7 is located in proximity of a seagrass meadow on muddy substrate with low density of blue mussels (repeated pers. observ.). Such habitat diversity lowered the recruitment of mussels, relaxing the competition for space and allowing more sessile genera to settle. Although the previous examples illustrate how *Mytilus* impairs the biodiversity of sessile communities, mussel beds can also have positive effects on biodiversity as they attract mobile species by providing shelter and organic matter (Norling and Kautsky, 2007). The diverging nature of *Mytilus* interactions shows that its role in supporting ecosystem processes is non-univocal. Predictions on the consequences due to alterations in *Mytilus* coverage are strongly context-dependent and regulated by factors like interacting species and habitat type.

A decline of *Mytilus* can be accompanied by recolonization of perennial macrophytes (Rönnbäck et al., 2007). Germlings of perennial macrophytes (e.g. *F. vesiculosus*) were found on the panels, but they never reached a coverage $\geq 10\%$ (threshold in the analysis) within one year. Thus, tendencies of taxa benefiting of the decline in mussel coverage were visible but not considered in the analysis. Other members of the community responded to the decrease of *Mytilus* abundance. For example, the coverage of filamentous algae (e.g. *Polysiphonia* at station 4) and small filter feeders (e.g. *Corophium* at station 2) peaked shortly after 2006 (Fig. 4B,D). The changes of these taxa come along with the increase in coverage of large and medium autotrophic (LFAS, MFAS, e.g. stations 1, 3, 4) and small filter feeders (SMSS, e.g. station 2) functional groups over a short period (Fig. S3).

The long-term records of hard-bottom communities from the SW Baltic coast revealed trends of alterations in taxonomic and functional structure. The regional decline of the blue mussel was potentially driven by the combination of global, regional and local factors. Years of low temperatures, together with local maxima in phytoplankton biomass, likely impaired the recruitment of *Mytilus*. Poorly connected habitats could have further hampered the recolonization from source populations. Our study shows that the decline of *Mytilus* has pervasive consequences on hard-bottom communities, confirming the role of a foundation species in structuring ecosystems (Hawkins et al., 2009). Local habitat distribution maps of foundation species are often outdated (e.g. *Fucus* spp.; Vogt and Schramm, 1991), hidden in internal reports and grey literature or display coarse resolution, if not completely missing. This is particularly problematic in the context of legislation for the management of marine ecosystems (e.g. Oceans Act for USA, Canada and Australia; Marine Strategy Framework Directive for Europe). Hence, more than ever fine scale monitoring is needed to define the baseline conditions of ecosystems and detect signs of human impacts at different temporal and spatial scales (Pereira and Cooper, 2006). Attempts covering multi-annual trends and including local variabilities like the present study can be very valuable as they help to interpret community dynamics.

Acknowledgements

MF acknowledges the financial support by the State Agency for Agriculture, Environment and Rural Areas of Schleswig-Holstein (LLUR; reference number: 0608.451426). FRB acknowledges the financial support by the German Academic Exchange Service through the project Doctoral Programmes in Germany 2015/16 (57129429). This study has been conducted using E.U. Copernicus Marine Service Information. We thank the research diving team of the Benthic Ecology working group at GEOMAR for 11 years of field work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2019.02.029>.

Declarations of interest

None.

Contributions

MW initiated the long-term monitoring and was involved in the annual samplings. RS analysed all settlement panels for taxonomic composition of the communities. MF wrote the manuscript and performed the data analyses. FRB was involved in data analyses and did the statistical modelling. HHH calculated dispersal kernels for *Mytilus* larvae. AL provided environmental data used in the modelling process. All co-authors significantly contributed to the writing process of the manuscript.

Role of funding source

The funding source had no involvement in study design, collection, analysis and interpretation of data as well as in writing the report or the decision to submit the article.

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