

Spatial variability in subtidal hard substrate assemblages across horizontal and vertical gradients: a multi-scale approach using seafloor imaging

Kolja Beisiegel^{1,4,*}, Alexander Darr¹, Michael L. Zettler¹, René Friedland²,
Ulf Gräwe³, Mayya Gogina¹

¹Department of Biological Oceanography, Leibniz Institute for Baltic Sea Research Warnemünde, 18119 Rostock, Germany

²Unit Coastal Sea: Management and Planning, Leibniz Institute for Baltic Sea Research Warnemünde, 18119 Rostock, Germany

³Department of Physical Oceanography, Leibniz Institute for Baltic Sea Research Warnemünde, 18119 Rostock, Germany

⁴Present address: BLANO-Geschäftsstelle Meeresschutz, 20539 Hamburg, Germany

ABSTRACT: Knowledge of spatial patterns in subtidal hard substrate assemblages is necessary for the development of effective marine management strategies. However, patterns are intrinsically scale-dependent, and little is known about the relative importance of vertical and horizontal position changes across scales. In the southwestern Baltic Sea, major physicochemical attributes (e.g. salinity, temperature, nutrients) change sharply across different spatial scales. We tested the hypothesis that biological variation generally increases with increasing scales and that horizontal (along-shore) variability becomes at least comparable in magnitude to vertical variation at large scales. An imaging approach was chosen to span a distance of 200 km within which 3 scales (small: a few km; meso: 10s of km; large: 100s of km) along the vertical and horizontal axes were examined and compared. In total, 1800 images were analyzed for species composition and cover. Most biological variability was detected across the large scale, along the horizontal salinity gradient. Species richness decreased with decreasing salinity, and assemblage composition changed significantly. At the meso scale, vertical variation along the bathymetric gradient (10–40 m) appeared to be the dominant pattern. The least variation occurred at the small scale. Vertical zonation and small-scale variation were stronger at higher salinities. The study highlighted horizontal gradients as potential drivers for spatial variability in this system. The multi-scale approach used here was particularly useful for detecting the interactive effects between scales and gaining insights applicable to large-scale management.

KEY WORDS: Spatial scale · Distribution patterns · Hard substrate assemblages · Spatial variability · Vertical zonation · Environmental gradients · Seafloor imaging · Baltic Sea

—Resale or republication not permitted without written consent of the publisher—

1. INTRODUCTION

The spatial distribution of macrobenthic species and assemblages depends on a complex interplay of various environmental and biological factors impacting small to broad spatial scales. Coastal and shelf systems present strong physicochemical gradients, with variation present along the horizontal axis, parallel to the sea surface, but also vertically (with water depth), or at different shore levels (Underwood &

Kennelly 1990, Benedetti-Cecchi 2001, Valdivia et al. 2011, Chappuis et al. 2014). The analysis of spatial patterns of coastal benthic biodiversity has received wide attention, and the consensus is that there is no single natural scale at which ecological phenomena should be studied (Levin 1992, Benedetti-Cecchi 2001, Fraschetti et al. 2005). Many studies report that small-scale processes (10s to 100s of centimeters) are at least as important as large-scale processes in generating patterns in benthic assemblages (Thrush et

*Corresponding author: kolja.beisiegel@mu-niedersachsen.de

al. 1994, Coleman 2002, Fraschetti et al. 2005). In fact, most variation in patterns of abundance was often found at the smallest spatial scale, and variation decreased as the scale of measurement increased (see review by Fraschetti et al. 2005). The few multi-scale assessment studies that included regional to very broad spatial scales (100s to 1000s of kilometers) also found that differences in the structure of benthic assemblages from location to location and from site to site exceeded those at the largest scale (Fraschetti et al. 2005), and strong vertical zonation patterns exceeded large-scale horizontal variation (Chappuis et al. 2014).

Limited studies have examined spatial variation of sessile assemblages on subtidal hard substrate habitats. One of the reasons is that they are more challenging to survey than e.g. intertidal rocky shores. The existing studies focused primarily on understanding meso-scale processes and vertical zonation patterns in subtidal habitats (reviewed by Witman & Dayton 2001), and research has tended to overlook other important sources of spatial variation (Benedetti-Cecchi 2001, Terlizzi et al. 2007). Evidence of large horizontal variability of assemblages on rocky substrates has been available for about 20 yr (Menconi et al. 1999), but the zonation paradigm (referring to vertical variation) is still strong in aquatic ecology, and often remains the only aspect driving a number of new studies and discussions (see also Terlizzi et al. 2007). The few regional-scale studies including hard substrate species and communities below the tides indicated that large-scale oceanographic patterns like spatial heterogeneity in sea surface temperature (Lamy et al. 2018) and chlorophyll *a* concentration (Pinho et al. 2016), as well as the prevailing current regime (Smale 2012) are important drivers for the observed variability in sessile assemblages over 100s of kilometers. Furthermore, differences in sessile community structure along depth gradients were shown to vary interactively with horizontal scales (Terlizzi et al. 2007).

It is important to adopt multi-scale approaches in the analysis of spatial patterns and combine vertical and horizontal gradients to finally obtain basic knowledge of benthic systems that will hopefully help us cope with increased regional and global pressures like climate change and broad-scale habitat loss (Strong & Elliott 2017). Such investigations can provide information that is essential for understanding and managing marine resources over larger scales. Understanding how a species is distributed based on a large-scale gradient such as temperature might help in predicting what might happen broadly

with climate change. Processes at other scales such as competition may influence more localized outcomes. However, until now, such multi-scale studies have rarely been undertaken in subtidal environments, particularly over scales reaching 100s of km.

Traditional subtidal sampling approaches like grab sampling typically provide point observations and are poorly suited for detecting patterns within broad-scale gradients due to logistical reasons (Strong & Elliott 2017). SCUBA techniques, as commonly used for Reef Check (www.reefcheck.org) or the Reef Life Survey (www.reeflifesurvey.com), are able to span large geographical areas, but these are typically limited to water depths of <30 m and are much more difficult to apply in temperate latitudes. Therefore, remote sensing techniques, often covering multiple spatial scales and being particularly informative for processes and properties occurring at larger scales, are of potential value for the assessment of benthic species and assemblages (Strong & Elliott 2017). While aerial photographs and satellite images are commonly used for the investigation of very shallow coastal habitats like seagrass beds and coral reefs (e.g. Mumby et al. 2001), remote underwater imaging surveys are necessary for habitats in the lower infralittoral and circalittoral zone. For benthic species and assemblages below the tides, video and photographic stills of the seabed taken by remote camera platforms may overcome the difficulties of traditional sampling techniques and are less labor-intensive and time-consuming than SCUBA field surveys (Beisiegel et al. 2017). Camera types and lighting systems have significantly evolved in recent years, and numerous specialized software packages for marine image annotation have been developed in the last 2 decades (Durden et al. 2016, Gomes-Pereira et al. 2016, Schoening et al. 2017). Further, by sampling without seabed contact, imaging enables the investigation of benthic habitats with a complex topography and rough terrain like rocky reefs, where grabs, trawls, and dredges are unsuitable (Dumas et al. 2009, Perkins et al. 2016, Beisiegel et al. 2017). Within these reefs, the sessile macrobenthos can be sampled without removal of the fragile and long-lived biota. Thus, especially on hard substrates in temperate subtidal environments, where sampling is typically expensive and severely time-limited by logistics (Van Rein et al. 2009, Beisiegel et al. 2018), imaging may provide the missing data on spatial patterns of epibenthic organisms at various scales.

To our knowledge, this is the first study using high-resolution seafloor imagery for the multi-scale assessment of spatial patterns of subtidal hard sub-

strate species and assemblages in a coastal, brackish system. Given the sharp environmental gradients, primarily in depth and salinity, we tested the hypothesis that spatial variation generally increases with increasing scale and that horizontal variability becomes at least comparable in magnitude to vertical variation at large scales. To test these predictions, samples were taken continuously along a depth gradient of 10–40 m, while 3 spatial scales at which horizontal and vertical variations were compared were chosen as follows: (1) small scale, examining variability within a few kilometers of reef, (2) meso scale, examining variability within a single reef complex (10s of km), and (3) large scale, examining variability between reef complexes (100s of km).

2. MATERIALS AND METHODS

2.1. Study area

Sampling was conducted on hard substrates within the 3 major subtidal reef complexes in the German exclusive economic zone of the Baltic Sea (Fig. 1). The study area spans 200 km from the Kiel Bight in

the west to the Arkona Basin in the east. Overall, the study area is located in the transition area (Ojaveer et al. 2010) between the North Atlantic and the Baltic Proper and is therefore characterized by strong gradients determined by saline, oxygen-rich water inflows from the west and riverine inflows from the east (Ojaveer et al. 2010). While the Baltic Sea is generally a shallow water body (with an average depth of 55 m), the southwestern part is very shallow (with a maximum water depth of 50 m, in the central Arkona Basin). Hard substrates within the 3 complexes (Fig. 1) consist of patches of coarse and mixed sediments with rock outcrops, stones, cobbles, and shell gravel (Diesing & Schwarzer 2006) that are designated as ‘reefs’ under EU Habitats Directive (Annex 1 EU HD; European Commission 1992). Hard substrates were sampled in each reef complex from 10 m, down to the deepest occurring structures found: 29 m at Kadet Trench, 27 m in the Adler Ground, and 36 m in the trench of the Fehmarn Belt (Table 1). The areas of hard substrate within each complex vary significantly in number and extent, ranging from a single continuous reef at Adler Ground (175 km²) to 5 fragmented reef sites with a total of 23 km² at Kadet Trench.

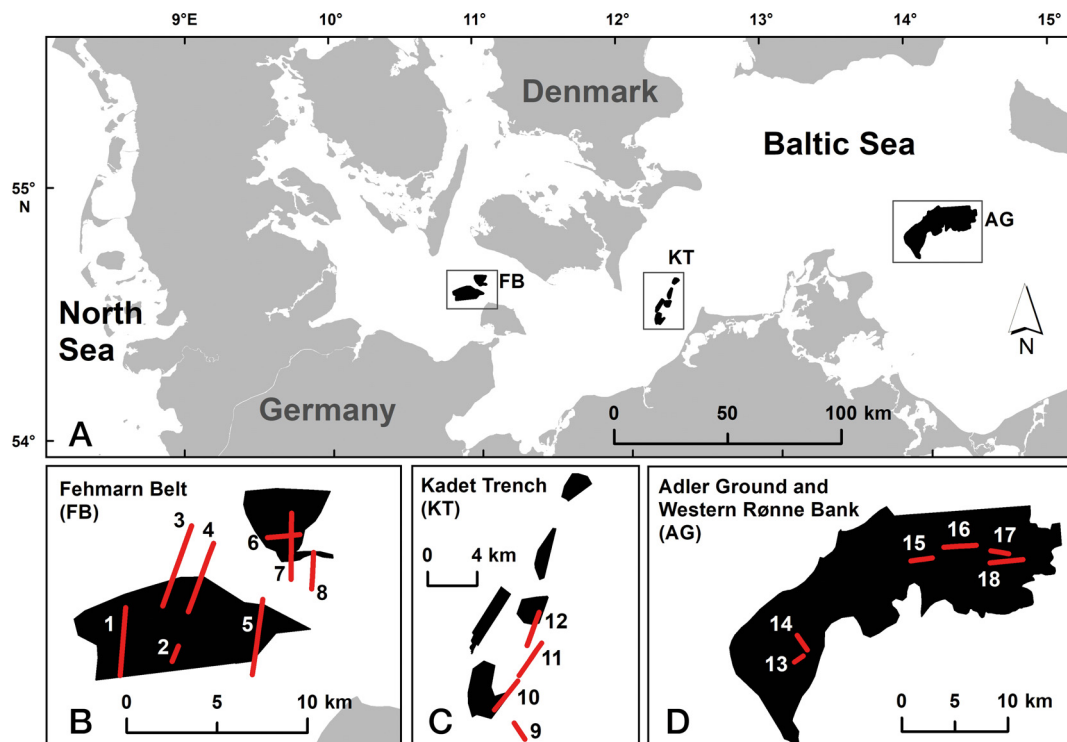


Fig. 1. Study area. (A) Southwestern Baltic Sea, indicating the designated reefs (black areas: Annex 1 EU HD, European Commission 1992) within the 3 major reef complexes ‘Fehmarn Belt’ (FB), ‘Kadet Trench’ (KT), and ‘Adler Ground and Western Rønne Bank’ (AG). (B–D) Detailed locations of the photo transects (1–18) within the 3 complexes. Reefs at KT are situated in an area of heavy marine traffic; therefore, more transects were placed at the inner, coastward reefs

Table 1. Geographical position, length, depth range, and sampling effort for each photo transect within the 3 major reef complexes 'Fehmarn Belt' (FB), 'Kadet Trench' (KT), and 'Adler Ground and Western Rønne Bank' (AG)

Transect	Reef complex	Position (decimal degrees, long., lat.)				Total length (m)	Depth (m)		Number of images	Area analyzed (m ²)
		Start		Stop			Min.	Max.		
1	FB	10.867	54.550	10.872	54.583	3429	15.9	18.3	170	68.0
2	FB	10.911	54.556	10.917	54.564	986	12.6	14.2	51	20.4
3	FB	10.904	54.584	10.931	54.623	4763	16.5	34.9	204	81.6
4	FB	10.926	54.581	10.949	54.614	3845	13.2	27.1	197	78.8
5	FB	10.980	54.548	10.990	54.586	4296	10.0	19.4	62	24.8
6	FB	10.996	54.616	11.023	54.617	1816	11.4	17.9	101	40.4
7	FB	11.015	54.595	11.017	54.628	3712	12.0	35.6	155	62.0
8	FB	11.032	54.590	11.035	54.608	1827	22.8	33.8	49	19.6
9	KT	12.263	54.408	12.251	54.420	1719	15.8	18.8	44	17.6
10	KT	12.227	54.431	12.258	54.451	3677	16.4	28.7	116	46.4
11	KT	12.260	54.455	12.289	54.478	3767	18.8	25.6	41	16.4
12	KT	12.271	54.477	12.288	54.501	2932	18.4	26.5	83	33.2
13	AG	14.024	54.699	14.011	54.695	1408	23.2	24.5	53	21.2
14	AG	14.017	54.717	14.030	54.704	1858	24.7	26.8	70	28.0
15	AG	14.223	54.774	14.191	54.773	3151	17.0	22.2	89	35.6
16	AG	14.289	54.782	14.241	54.783	4774	13.0	21.9	154	61.6
17	AG	14.335	54.773	14.310	54.777	2584	9.7	13.6	44	17.6
18	AG	14.307	54.766	14.356	54.767	4877	12.2	15.5	100	40.0

2.2. Sampling and processing

Seabed images were recorded in June 2016 and August 2017 during 2 expeditions on the German RV 'Elisabeth Mann Borgese.' The study design comprised 18 transects with a total length of 56 km (Fig. 1B–D, Table 1). Transects were situated along the bathymetric gradient, covering hard substrates throughout the entire depth range of each complex. Images were recorded using a downward-facing towed camera system, the Baltic Seafloor Imaging System (BaSIS), as described by Beisiegel et al. (2017, 2018). BaSIS is vertically submerged over the ship's stern to its target altitude of 1 m above the seabed and is towed at a speed of ~0.5 knots along the transects. From earlier deployments, this 1 m altitude has proven to have the best trade-off between area cover, image resolution, illumination, and backscatter in turbid conditions (which often occur in the study area). High-resolution photos (24 megapixels) with a wide-angle camera system (SubCImaging 1Cam Alpha) were taken every 20 s, equivalent to an average distance of approx. 5 m between the seabed images. The average area of the seafloor visible in each image was ~0.8 m², but an exact area was calculated by referencing 4 vertical parallel lasers producing points in each photo. Only the central, well-illuminated area of 0.4 m² in each still was selected for the analysis. The BaSIS mounted sensors included a CTD, while the ship-based GPS was used to determine the camera's position, with consideration of the

offset calculated. Live video feed from additional cameras was used for orientation and piloting. A swell-compensating winch and operator adjustment ensured a constant altitude above the seabed. In total, 56 km of photo transects resulted in >8000 seafloor images. Prior to analysis, the number of photos was reduced in a stepwise approach. First, photos which were out of focus, too far from the seafloor, where reef biota was covered (e.g. by jellyfish, ghost nets), or images with low visibility were discarded. Second, following the 'HELCOM Underwater Biotope and Habitat classification system,' images with <10% cover of hard substratum were treated as soft sediment habitats (HELCOM 2013) and excluded from the analysis. In the final step, 1 image min⁻¹ was selected systematically for analysis in order to avoid overlapping and keep the work load for this broad-scale study feasible. In consequence, 1783 images corresponding to 713 m² of seabed were analyzed (Table 1).

2.3. Biological data

All sessile invertebrates and macroalgae were identified individually to the lowest taxonomic level possible using morphological characteristics. When a reliable identification at the species level was not possible, organisms were classified as higher taxa or 'morphotypes' (used to describe organisms of the same appearance; Table 2). Due to image resolution

Table 2. Taxonomic groups from image-derived cover measurements at the 18 transects, which were used in the multivariate analysis

Lam	Laminariaceae
FiBA	Filamentous annual brown algae
FoRA	Foliose perennial red algae
Furc	<i>Furcellaria lumbricalis</i>
FiRA	Filamentous annual red algae
Chl	<i>Chalinula limbata</i>
Halh	<i>Halichondria paniacea</i>
Halc	<i>Haliclona oculata</i>
Pom	<i>Polymastia boletiformis</i>
ErHyzBrz	Erect colonial hydrozoan and bryozoan
Anem	Sea anemones
Bar	Barnacles
Flu	<i>Flustra foliacea</i>
Myt	<i>Mytilus spp.</i>
Cio	<i>Ciona intestinalis</i>
Dend	<i>Dendrodoa grossularia</i>

and distance to the seafloor, only organisms ≥ 1 cm (in their longest dimension) could be reliably identified. Further, the camera operates perpendicularly to the seafloor and therefore captures organisms on horizontal rather than vertical surfaces. Sessile biota attached to overhangs and vertical walls as well as organisms obscured by larger canopy-forming species could not be observed adequately (see also Beisiegel et al. 2017). Using the software ‘Coral Point Count with Excel extensions’ (CPCe; Kohler & Gill 2006), the organisms beneath 50 randomly-overlaid digital points on each photo were identified. The number of points for each taxon identified in CPCe was standardized to percentage cover of reef (i.e. divided by the number of points with a hard substratum, and multiplied by 100 %). Each single photo was treated as an independent sample in the subsequent analysis.

2.4. Environmental data

Depth information was obtained from the camera-mounted CTD. Slope and rugosity were derived from a bathymetry layer with 50 m resolution obtained from Tauber (2012a) using the ‘Benthic Terrain Modeler’ in ArcGIS (Walbridge et al. 2018); however, as the 2 variables were highly inter-correlated, only slope was included further in the analysis. Other environmental data used as explanatory variables for identified biological patterns included all available modeled continuous coverage data for the study area (Table 3). Salinity, temperature, current speed, oxygen concentration, friction velocity, organic carbon

Table 3. Environmental variables used in multivariate analysis

Depth	Water depth (m)
Slope	Surface slope (°)
SAL	Salinity (psu)
TEMP	Temperature (°C)
CURR	Current speed (m s ⁻¹)
SPEED	Near-bottom current speed (m s ⁻¹)
TAUB	Friction velocity (m s ⁻¹)
O2	Oxygen concentration (mg l ⁻¹)
OC	Organic carbon concentration (mg l ⁻¹)
PAR	Photosynthetically active radiation (W m ⁻²)
Dayshypox	Days per year with oxygen concentration < 2 mg l ⁻¹ (hypoxia)
NH4	Ammonia (μmol m ⁻³)
NO3	Nitrate (μmol m ⁻³)
PO4	Phosphate (μmol m ⁻³)

concentration, photosynthetically active radiation, days per year with oxygen concentration below 2 mg l⁻¹ (hypoxia), and nutrient concentrations (ammonium, nitrate, phosphate) were provided from the General Estuarine Transport Model (GETM; Gräwe et al. 2015), to which the ecosystem model ERGOM was coupled (Radtke et al. 2012, Zettler et al. 2017, Beisiegel et al. 2018). The model simulations covered a period of 7 yr prior to biological sampling (2010–2017). The 10th and 90th percentiles (chosen in order to exclude the effect of outliers and increase statistical robustness) as well as mean values for the bottom water layer were used, with a horizontal resolution of 600 × 600 m. For the multivariate analysis, environmental data were normalized so that each variable had a mean of 0 and a standard deviation of 1.

2.5. Data analysis

Community composition was analyzed using a combination of multivariate techniques (multidimensional scaling [MDS], BEST [BIOENV], analysis of similarity [ANOSIM], similarity percentage [SIMPER], LINKTREE, and distance-based redundancy analysis [dbRDA]) in the program PRIMER v7 (Clarke 1993, Clarke & Gorley 2015). Very rare taxa (<2 % frequency of occurrence across all images) were removed prior to analysis to avoid potential spurious relationships with environmental variables (Clarke & Warwick 2001). Predefined by the multi-scale approach, 3 separate analyses were performed on different spatial scales (small, meso, large).

First, biological resemblance among samples was quantified for the entire study area (large scale) using pairwise Bray-Curtis similarities on square root trans-

formed cover data. Nonmetric MDS analysis was performed to visualize similarities among reef complexes, based either on environmental or on biota cover data. The BIOENV method from the non-parametric BEST routine was applied to identify the environmental variables that best explain the multivariate biotic structure found on the largest spatial scale. Prioritizing depth and salinity, known to be explicitly important drivers of spatial patterns for benthos in the study area (Gogina & Zettler 2010), other highly correlated independent abiotic variables (indicating Pearson correlation $r > 0.90$, $p = 0.05$) were omitted from the analysis (for variables and correlation matrices, see Tables S1–S11 in the Supplement at www.int-res.com/articles/suppl/m633p023_supp.pdf). The pattern was visualized with a dbRDA plot. The best explaining variables were then used in the LINKTREE procedure (a non-parametric version of a decision tree that defines the best splits by maximizing the ANOSIM R statistic between the 2 groups) in order to identify subsets of samples from the biological resemblance matrix that are explained by thresholds in particular environmental variables. Such linkage trees therefore provide abiotic ‘explanations’ for each biotic subdivision of the samples. To avoid over-interpretation, the LINKTREE routine uses an objective stopping rule defined by the SIMPROF test (with 5% significance cut-off level used).

For the second, meso-scale analysis, the dataset was split into the 3 reef complexes (Fehmarn Belt [FB], Kadet Trench [KT], and Adler Ground [AG]; see Fig. 1 and Table 1), and biotic and environmental data from each complex were analyzed separately applying all of the procedures described above. Inter-correlated variables were again omitted using the same criteria. In contrast to the large-scale analysis, salinity was removed from the analysis at the meso scale (within each reef complex), as its variation on the horizontal, longitudinal axis was physiologically irrelevant for the species studied, whereas it indicated significant correlation with other, more relevant, variables that were retained (see Table S1).

For the third, small-scale analysis, the dataset of each complex was fur-

ther split into photic and aphotic zones using modeled local compensation depth (Friedland et al. 2012, Schiele et al. 2015). Depth was removed from the analysis, as it presents only an integrative proxy for a combination of other factors influencing biota distribution, and other more relevant variables were retained (see Table S1).

3. RESULTS

3.1. Large-scale analysis

Analysis on the largest spatial scale showed a clear split between the easternmost reef complex (AG) and the other 2 complexes in the southwestern Baltic Sea. In the MDS ordination of the environmental data (Fig. 2A), AG is clearly separated, indicating that conditions at the easternmost reefs are most dissimilar to the other reef environments. Biota MDS results also indicate that AG assemblages are highly dissimilar to

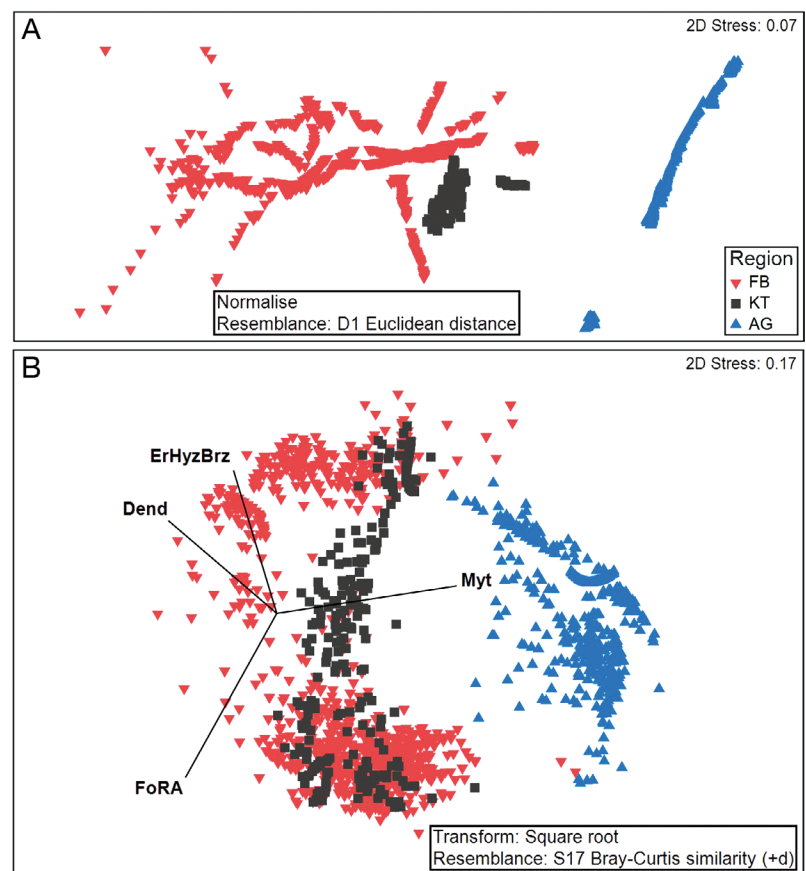


Fig. 2. Multidimensional scaling ordination by reef complex for (A) all environmental variables and (B) mean cover of reef biota. Overlaid vectors show the taxonomic groups (see Table 2) from SIMPER analysis driving the differences. FB: Fehmarn Belt; KT: Kadet Trench; AG: Adler Group

the other reef complexes (Fig. 2B). The environmental variables that best correlated with patterns in biological assemblages were salinity and depth ($R = 0.664$), suggesting that the significant physicochemical, longitudinal gradient strongly affects species composition. Looking closer at these 2 variables, dbRDA ordination clearly demonstrates how biological data are grouped along these 2 factors (Fig. 3). Axis 1 (dbRDA1) is related to salinity, while axis 2 (dbRDA2) is related to depth, explaining 30 and 20% of spatial variation in reef biota, respectively.

Salinity clearly separates the biota of the 3 complexes, whereas depth explains the variation within the respective complexes. The LINKTREE analysis (Fig. 4) revealed that the highest average between-group rank dissimilarity ($B\% = 85$) is found between AG and the other 2 reef complexes (FB and KT), giving a threshold for the first divisive clustering at salinity values <9.3 (>16.2 for the other reefs).

Detailed analysis of biota data shows that the community composition at AG is highly dissimilar to that of FB and KT (ANOSIM: $R = 0.896$, $p < 0.001$) due to the high cover of the epibenthic bivalves *Mytilus* spp., which are lacking at reefs in the 2 western complexes (Fig. 2B). At FB and KT, foliose red algae dominate the reefs, followed by the tunicate *Dendrodoa grossularia* at FB and erect hydrozoan and bryozoan colonies at KT (Fig. 2B). The latter differences in species composition led to significantly dissimilar communities at FB and KT (ANOSIM: $R = 0.045$, $p < 0.001$), although this variation could not be detected on the MDS ordination due to the extreme dissimilarity between AG and the other complexes.

For a more detailed analysis, photic and aphotic zones were separated and compared individually across large spatial scales. Algal community composition at the photic zone of the AG reef complex was highly dissimilar to other algal communities due to the low cover of foliose red algae and high abundances of filamentous annual brown and red algae. The westernmost FB reef complex showed the highest diversity in algal taxonomic units, although the highest cover of algae was found at KT. Despite those distinctions, the FB and KT algal communities did not differ significantly. In contrast, in the aphotic zone, all invertebrate-dominated reef assemblages differed significantly between the complexes, with the highest dissimilarities found between AG and other aphotic reef complexes. *Mytilus* spp. dominated AG, with only a minor cover of erect colonial hydrozoans and bryozo-

ans found there. Epibenthic bivalves were lacking in the aphotic zone of FB and KT, where hard substrate assemblages were dominated by the ascidian *D. grossularia* (FB) and erect hydrozoan and bryozoan colonies (KT). These differences in species composi-

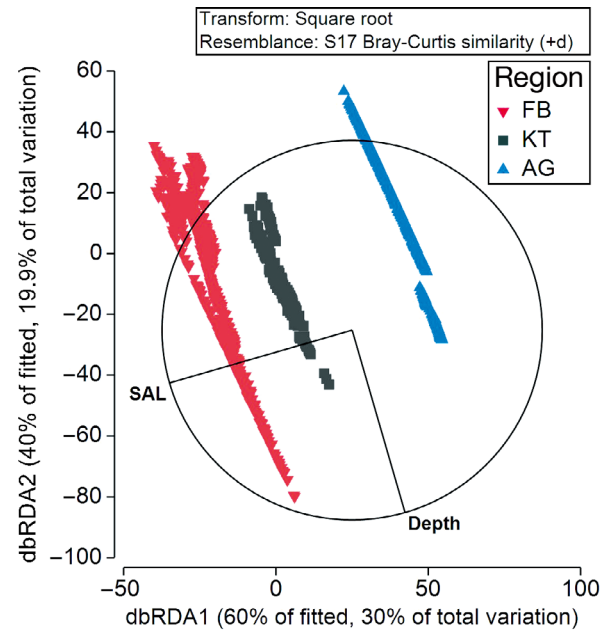


Fig. 3. Distance-based redundancy analysis (dbRDA) ordination plot illustrating the relationship between the 2 by-region BEST environmental variables (salinity and depth) and reef biota cover. FB: Fehmarn Belt; KT: Kadet Trench; AG: Adler Group

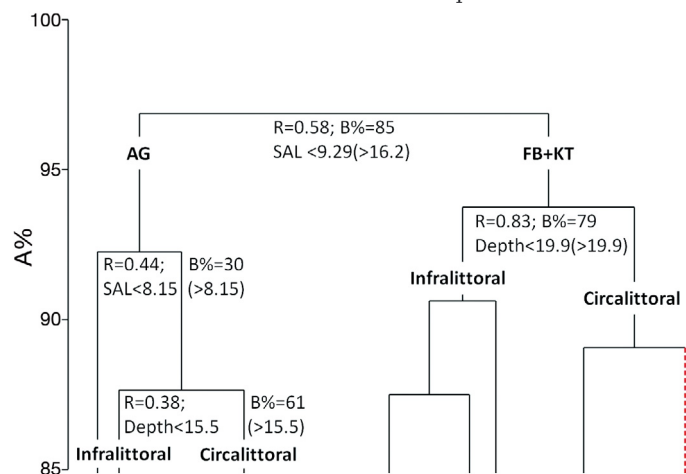


Fig. 4. LINKTREE dendrogram based on biota cover of hard substrate assemblages constrained by the 2 environmental variables driving the large-scale variation according to BEST results (salinity [SAL] in psu and depth in m). y-axis shows equi-stepped binary divisions (A% scale). B% reflects the size of group separation (the magnitude of differences between the subsets of samples formed at each division, in relation to the community structural differences across all samples.) Red dashes denote splits not allowed by SIMPROF test. FB: Fehmarn Belt; KT: Kadet Trench; AG: Adler Group

tion led to significantly dissimilar communities between FB and KT (ANOSIM: $R = 0.271$, $p < 0.001$).

3.2. Meso-scale analysis

Analysis of all environmental variables examined at the meso scale showed a clear split between shallow and deep reef locations within each complex. As already indicated by dbRDA ordination (Fig. 3), depth largely explained the biological variation within each complex. This was also the one variable that best explained biota patterns at this scale according to BIOENV (BEST) results. No combination with any other environmental variable could increase the explanatory power. Samples were split by LINKTREE analysis at threshold depths of 19.9 m at FB and KT, and 15.5 m at AG (Fig. 4).

Detailed analysis of biota data shows that the community composition in the photic zone is highly dissimilar to the aphotic zone within all respective reef complexes (ANOSIM: $p < 0.001$) due to the occurrence of macroalgae. In general, hard substrates in the photic zone had a 23 % higher mean cover of biota. However, variations between the photic and aphotic zones were not evenly distributed across the study area, but were linked to salinity. The largest differences in mean cover between assemblages were found at the easternmost complex, AG (33 %), with the lowest salinities, whereas differences were smallest at the highest salinities in FB (5%; see Table 4). In contrast, compositional differences between photic and aphotic assemblages were more pronounced at higher salinities (FB, average dissimilarity of 89 %), while AG reefs at the lowest salinities were much more similar (47 % dissimilarity). The latter hard substrates showed high cover of the filter-feeding bivalves *Mytilus* spp. along the entire depth gradient, while the other 2 reef complexes showed a clear separation between macroalgae-dominated

photic and invertebrate-dominated aphotic zones (Table 4). Besides the lack of macroalgae, the aphotic zone at FB showed diverse assemblages dominated by *D. grossularia* and erect colonies of hydrozoans and bryozoans with *Haliclona oculata* as the most abundant sponge species. At medium salinities (KT), the aphotic zone was also clearly separated from the photic zone by the lack of algal species and also by the reduced coverage of sponges. Aphotic hard substrata were covered by erect hydrozoan and/or bryozoan colonies (Table 4).

3.3. Small-scale analysis

The highest variability (indicated by lowest values of similarity in Table 4) in hard substrate assemblages at the smallest scale examined was found within the westernmost reef complex (FB). On this scale, however, no single modeled parameter could adequately explain the detected spatial variability. Within the photic zone, FB macroalgae community patterns were best explained by the mean concentration of organic carbon alone ($R = 0.138$), while KT algae communities were structured by mean current speed, mean organic carbon concentration, and slope ($R = 0.285$). In the photic zone of AG dominated by filamentous annual algae, the 90th percentile of nitrate concentration ($R = 0.337$) was the best explanation for the observed structure. Within the aphotic zone, invertebrate community patterns at FB were best explained by mean friction velocity and the 10th percentile of organic carbon concentration ($R = 0.391$), while in KT, reef biota was structured by mean temperature ($R = 0.215$). The bivalve-dominated aphotic zone at AG was best explained by the 90th percentile of oxygen concentration ($R = 0.309$). In general, at higher salinities, aphotic assemblages showed greater small-scale variability, which decreased with decreasing salinities. Consequently, in

Table 4. For each reef complex and each zone within the reef, total taxa richness, mean biota cover, and average Bray-Curtis similarity of the assemblage within the respective area (SIMPER) is given. Characteristic taxa are displayed per zone. FB: Fehmarn Belt, KT: Kadet Trench, AG: Adler Ground. See Table 2 for a list of investigated taxa and abbreviations

Complex	Richness	Cover (%)	Similarity (%)	Zone	Richness	Cover (%)	Similarity (%)	Characteristic taxa
FB	14	60	31	Photic	12	62	54	FoRA, FiRA, Lam
				Aphotic	13	57	38	Dend, ErHyzBrz, Halc
KT	10	68	44	Photic	7	91	70	FoRA, Halh
				Aphotic	10	58	52	ErHyzBrz
AG	7	63	59	Photic	7	78	61	Myt, FiRA, FiBA
				Aphotic	6	45	68	Myt

the easternmost complex (AG) at the lowest salinities, photic assemblages showed a higher spatial variability than in the circalittoral zone.

4. DISCUSSION

Studies which, like ours, cover multiple scales (including large scales) are important for obtaining information required for the spatial planning of a marine reserve network designed to protect representative communities across a region. Also, any understanding of the distribution of individual species is enhanced by an understanding of the links between environmental covariates and prevalence.

Multivariate analysis of both environmental conditions and hard substrate assemblages across multiple scales indicated that horizontal, along-shore variability over a large spatial scale (100s of kilometers) is the dominant spatial pattern in the southwestern Baltic Sea. Vertical variation along the depth gradient acted as a secondary distribution pattern for assemblages, but it was less pronounced and accounted for less variation on the largest scale examined (see also Tables S12 & S13). Strong, horizontal variability occurred along the natural prevailing salinity gradient, separating the 3 reef complexes FB, KT, and AG. These results corroborate previous findings of soft-sediment species distribution patterns in the Baltic Sea, showing that salinity is a major descriptor in species–environment relationships on a large spatial scale (Gogina & Zettler 2010, Ojaveer et al. 2010). The present study, which is based upon extensive seafloor imaging surveys, confirmed that in the studied brackish coastal system, salinity is also the most important factor in determining the distribution of subtidal hard substrate assemblages on large spatial scales. In the past, epibiota on subtidal reefs was generally neglected in large-scale studies due to logistical reasons (Fraschetti et al. 2005). However, our study promotes the assistance of novel technical tools, like high-resolution imaging, in analyzing spatial patterns of sessile hard substrate assemblages over large spatial scales. Obviously, species lists from imaging surveys cannot be compared with laboratory examination of destructive samples (Fraschetti et al. 2001, Beisiegel et al. 2017). Small species might be overlooked or underestimated in density if they are hidden under large, branching forms (e.g. foliose algae). However, the dominant sessile taxa, including important foundation species, were recorded without removal of the fragile and long-lived biota and a quick general estimate of biodiversity over a

large geographic area was provided (Fraschetti et al. 2001, Perkins et al. 2016, Beisiegel et al. 2017).

Comparable data on hard substrate assemblage distribution across 10s of km is scant, and only a few studies have examined variation along the vertical axis simultaneously. Despite the fact that 1 study from the Mediterranean found that vertical variation is the main distribution pattern even on 1000s of km of shoreline (Chappuis et al. 2014), there are indications for the last 20 yr or so, that horizontal and temporal patterns might be at least as important as vertical positioning (Menconi et al. 1999). More recent studies on the variability of intertidal organisms of rocky shores reported some inconsistent results. In particular, in the northwestern Mediterranean, Benedetti-Cecchi (2001) concluded that the degree of univariate vertical and horizontal variability was comparable at very small spatial scale (10s of cm), whereas horizontal variability was generally larger at scales of 100s to 1000s of m. The multivariate structure of assemblages was more variable vertically than horizontally at the scale of 10s of cm, but not at the scale larger than 1000s of m (with the largest regional scale examined constituting 100s of km). On exposed rocky shores in southeastern Australia, Underwood & Chapman (1996) found most small-scale variability in abundances for many species on many shores on scales of centimeters to a few meters, whereas large-scale differences in abundance were found at a horizontal scale of 100s of m alongshore. However, there was little or no additional variation between shores, separated by 10s of km, than was shown among patches of shore separated by 100s of m. Valdivia et al. (2011) compared the variation in community structure across intertidal rocky shore levels of Helgoland Island with independent estimates of horizontal variation measured at scales from 10s of cm to 1000s of m. This study showed that vertical variation was significantly higher than patch- and site-scale horizontal variation, but lower than shore-scale horizontal variation, for both the multivariate structure of assemblages and the abundance of canopy-forming macroalgae. Benedetti-Cecchi (2001) formulated the model that much of the variation occurs across the vertical gradient, unless major physical attributes of the habitat change. This major change in physical attributes, particularly salinity, is the major feature of the southwestern Baltic Sea. Thus, these studies partly confirm our results, which show that horizontal variation can be the dominant pattern on a scale of 100s of km; however, they were all conducted in the intertidal zone, where vertical zonation is likely to produce strong variation due to the harsh environmental stress gradient

related to desiccation, temperature, and irradiance (see review by Fraschetti et al. 2005).

Among the few studies that were conducted over large spatial scales below the tides, Smale (2012) explored horizontal variation of sessile assemblages in Australia, Pinho et al. (2016) investigated macroalgae along Portuguese coasts, and Lamy et al. (2018) examined kelp communities in southern California (USA). All 3 studies confirm our finding that most biological variation in subtidal rocky reefs occurs over broad spatial scales (100s of km) and indicate that large, horizontal oceanographic gradients are the potential driving force. However, none of these studies included a vertical gradient, but rather were confined to 1 depth. Only 1 study has taken into account horizontal and vertical gradients in the subtidal zone: Terlizzi et al. (2007) showed that the largest components of variation occurred at the smallest spatial scale (centimeters to meters). Unfortunately, this scale was not considered in the present study; however, both studies show that variation along the vertical and horizontal axes are highly interactive.

Here, for the first time, we explore the suggested mechanisms that salinity and depth interactively drive the macrobenthic assemblages of hard substrates in a brackish system over 100s of km. Drastic changes in salinity obviously cause the observed large horizontal variability already found at shorter distances than e.g. in the Mediterranean. On one hand, decreasing salinity directly reduces the number of marine sessile species by reaching their lower physiological limit (Table 4). This finding is in accordance with the concept of Remane (1934), who described the hypothetical distribution of benthic invertebrate diversity along a marine–freshwater salinity gradient. The lowest species numbers were predicted at the horohalimum (5–8 psu), and this theory was validated for the macrozoobenthos of the Baltic Sea by Zettler et al. (2014). On the other hand, decreasing salinity indirectly affects organisms by changing their biological interactions. The observed dominance of the epibenthic bivalves *Mytilus* spp. at the easternmost reef complex (AG; Table 4, Fig. 5) can likely be attributed to the lack of their main predators, the common sea star *Asterias rubens*, as well as the dramatically reduced number of sessile competitors for the limited settling areas. In the southwestern Baltic Sea, salinity overrides other factors that usually force large-scale differences (100s of km) in invertebrate community structure, like water temperature and upwelling (Schoch et al. 2006), coastal geomorphology (Schoch & Dethier 1996), variation in grazing and

predation (Rilov & Schiel 2011), and variation in recruitment (Underwood & Chapman 1996).

Some mechanisms and life-history attributes that are partly responsible for the observed large spatial variability may be masked or uncovered by the data available for this case study. Dispersal modes have been shown to affect the spatial distribution of invertebrates, whereby species with planktonic larval stages show more variation on the scale of 10s of km than species with direct development (Johnson et al. 2001). Investigated reef complexes in the southwestern Baltic Sea are physically separated from each other by mud and sand flats (Tauber 2012b, Schiele et al. 2015), and reduced connectivity may also amplify spatial variability for reef epibiota with predominantly larval development. Some variability is likely caused by the strong and prevailing nutrient gradient in the area. Eutrophication (and its consequences) is still one of the major pressures on benthic communities (Ojaveer et al. 2010, Dailianis et al. 2018); however, the longitudinal gradient with higher concentrations of nitrate and phosphorus at the easternmost reefs may also be masked by effects of low salinity. The massive occurrence of opportunistic, annual algae (Fig. 5) and lack of perennial species at the AG reef complex shape significantly different photic communities. This is likely a consequence of drastic nutrient loads fueling fast-growing filamentous brown and red algae like *Pylaiella littoralis*, *Ectocarpus* spp., and *Polysiphonia* spp., which outcompete slow-growing perennial taxa by shading (Duarte 1995, Krause-Jensen et al. 2007).

In contrast to the general picture that suggests only little variability being detected over larger spatial scales (see review by Fraschetti et al. 2005), the present study demonstrated a decrease of variance in several physical and biological variables from large to meso scales. Vertical variation is clearly a consistent pattern on a kilometer scale, albeit less strong compared to spatial variability on a large scale. All 3 investigated reef complexes show significant zonation of sessile epibiota along the depth gradient (Fig. 5). These changes are often explained by the variation of abiotic and biotic variables which covary with depth and may directly affect species and communities (Chappuis et al. 2014). Within all 3 investigated complexes, the strongest vertical variation took place along the natural light gradient. Threshold depths of 20 m at FB and KT, and 16 m at AG (defined by LINKTREE) correspond to the modeled local compensation depth (Friedland et al. 2012, Schiele et al. 2015), spatially separating the macroalgae-dominated photic zone and the invertebrate-

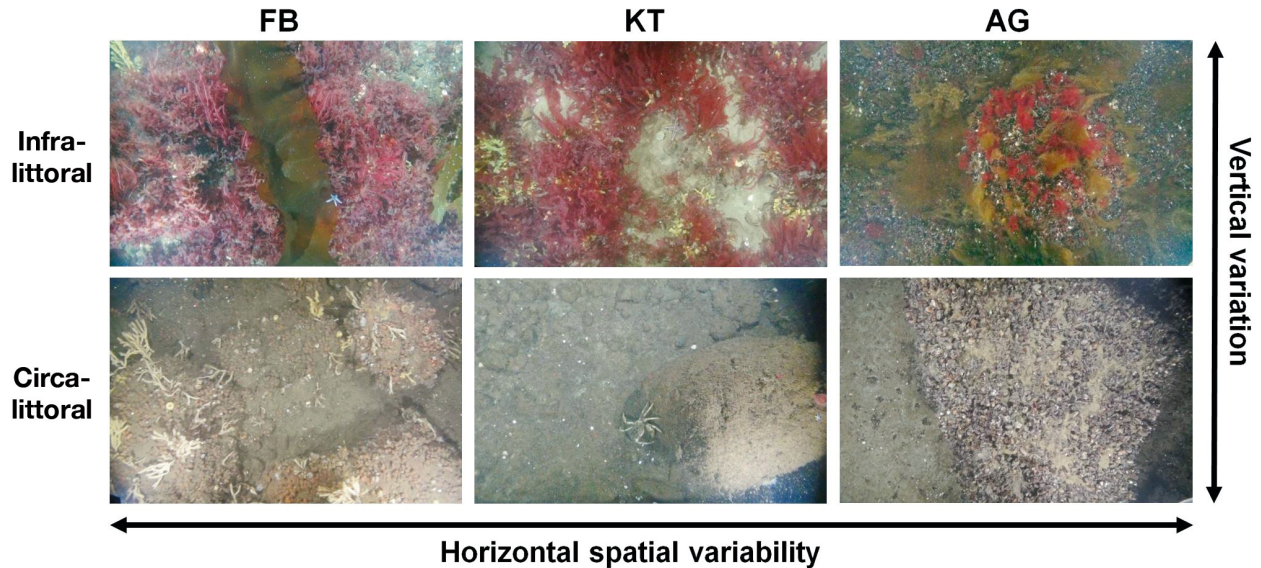


Fig. 5. Images of representative hard substrate assemblages in the infralittoral and circalittoral zone of the 3 major reef complexes in the southwestern Baltic Sea: Fehmarn Belt (FB), Kadet Trench (KT), and Adler Ground and Western Rønne Bank (AG). Horizontal variation along the salinity gradient was the dominant spatial pattern at a large spatial scale (100s of km), while vertical variation along the depth gradient acted as a secondary distribution pattern, dominating the biological variation at meso scales (10s of km)

dominated aphotic zone (Fig. 5). These results are also in accordance with the general division of the rocky subtidal (Witman & Dayton 2001) in the infralittoral zone that extends as deep as there is light for photosynthesis (Golikov & Scarlato 1968, Dayton 1975), and the circalittoral zone, the region below dominated by sessile invertebrates (Hiscock & Mitchell 1980). The general occurrence of macroalgae and invertebrates together in the infralittoral zone also explains the overall higher cover of hard substrate with biota in the well-lit zone. These results are confirmed by other subtidal reef studies in the Baltic Sea, where the highest cover and diversity have been reported for the lower infralittoral zone due to the presence of both multi-layered vegetation and upright sessile fauna (Dahl et al. 2016, Beisiegel et al. 2018). However, a multi-scale assessment revealed that meso-scale vertical variation was not independent of large-scale horizontal variation. At higher salinities, circalittoral communities showed a higher diversity, and cover was generally higher than at lower salinities. These large-scale horizontal differences led to decreased vertical variation with regard to cover at FB and KT. In contrast, the compositional differences along the vertical axis were most pronounced at higher salinities and less defined at the easternmost reef complex, AG. Here, the lack of large seaweed species and dominance of an invertebrate species (blue mussel) in the infralittoral zone

were associated with large-scale salinity patterns. Similarity in species composition between the photic and aphotic zones was increased and vertical variation was significantly lowered at the meso scale.

Spatial variability in hard substrate assemblages further decreased when the scale of analysis decreased from meso to small (a few kilometers). Spatial variability was overall present, but the explanatory power of BEST analysis at the smallest scale was significantly decreased, and abiotic measures were not reliable predictors of variation at the smallest scale, likely due to insufficient horizontal resolution (600 m) of the model data. It is obviously not possible to explain all of the ecological mechanisms accounting for the observed variation with the data at hand. Small-scale variability has been discussed in several papers, and nearly all benthic populations and assemblages (even in habitats considered homogeneous) show a patchy distribution at finer scales (Fraschetti et al. 2005). Studies agree that local biological interactions and small-scale physical processes are pervasive in marine systems (Underwood & Chapman 1996, Legendre et al. 1997, Benedetti-Cecchi 2001, Coleman 2002, Terlizzi et al. 2007). Multi-scale assessment also demonstrated that variability at the small scale was not independent of large-scale horizontal and meso-scale vertical variability. Higher small-scale variability generally found at higher salinities is likely a consequence of en-

hanced species richness. As more taxa have to share limited hard substrates for settlement, heterogeneity increases, especially on small spatial scales. Besides horizontal salinity effects, small-scale variability was also linked to meso-scale patterns as higher spatial variability was detected in the circalittoral zone. A review of a subset of images revealed clear variability in the type and cover of hard substrates. Geological data were not gathered and therefore were not considered as abiotic predictors in this study, but we detected a change from high seabed cover with cobbles and pebbles at shallower reefs to more solitary stones and boulders surrounded by muddy sediments in deeper areas of FB and KT (see also Diesing & Schwarzer 2006). Higher substrate patchiness is likely to also produce higher local variability in epibenthic assemblages and might explain some small-scale differences between infra- and circalittoral assemblages at higher salinities.

5. CONCLUSIONS

For the first time, the use of seafloor imaging enabled us to include underrepresented larger spatial scales (10s to 100s of km) in the assessment of distribution patterns of hard substrate assemblages in less accessible subtidal environments. The results support our hypothesis that in the southwestern Baltic Sea, where major physical attributes change sharply, spatial variation increases with increasing scale, and the importance of horizontal variation exceeds vertical zonation at larger scales. Differences among depths varied interactively across the horizontal scale, possibly due to changes in diversity and species identity along the salinity gradient. Our results indicate that processes that determine sessile species distribution are highly scale-dependent, and even large-scale patterns such as depth (vertical) or salinity (horizontal) alone are not sufficient to predict the abundance and type of sessile assemblage. Only knowledge of the interactive effects, as demonstrated for the 3 scales used in this study, can allow an understanding of ecological heterogeneity. The identification of relevant scales of variation for the highly variable southwestern Baltic Sea should allow for more reliable predictions of human impacts and more effective determination of conservation units. However, to fully understand patterns of distribution in the system, sampling at several spatial and especially temporal scales is required; the latter were completely ignored in this very first multi-spatial scale study and should be assessed in future work.

Acknowledgements. We thank the captain and crew of RV 'Elisabeth Mann Borgese' for their assistance at sea and the staff of the institute's mechanical workshop for their maintenance of the imaging platform. The analysis of seafloor images was performed with the dedicated help of the technical staff of the working group 'Ecology of benthic organisms' at the Leibniz Institute for Baltic Sea Research Warnemünde and support from Celina Burkholz, Lotte Pohl, and Leo Gottschalk. Comments and input by 2 anonymous reviewers greatly improved the clarity and focus of the paper. We are grateful to Irina Steinberg and Anastasia Semenova for correcting the English. This work was supported by the German Federal Agency for Nature Conservation within the project 'Monitoring, assessment and mapping of macrobenthic species and habitats' (support code: 532 02 AWZ), M.G. was also financed by BONUS ECOMAP project (Art 185). Supercomputing power was provided by HLRN (North-German Supercomputing Alliance).

LITERATURE CITED

- ✦ Beisiegel K, Darr A, Gogina M, Zettler ML (2017) Benefits and shortcomings of non-destructive benthic imagery for monitoring hard-bottom habitats. *Mar Pollut Bull* 121: 5–15
- ✦ Beisiegel K, Darr A, Zettler ML, Friedland R, Gräwe U, Gogina M (2018) Understanding the spatial distribution of subtidal reef assemblages in the southern Baltic Sea using towed camera platform imagery. *Estuar Coast Shelf Sci* 207:82–92
- ✦ Benedetti-Cecchi L (2001) Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. *Mar Ecol Prog Ser* 215:79–92
- ✦ Chappuis E, Terradas M, Cefali ME, Mariani S, Ballesteros E (2014) Vertical zonation is the main distribution pattern of littoral assemblages on rocky shores at a regional scale. *Estuar Coast Shelf Sci* 147:113–122
- ✦ Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- Clarke KR, Gorley RN (2015) PRIMER v7: user manual/tutorial. PRIMER-E, Plymouth
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth
- ✦ Coleman MA (2002) Small-scale spatial variability in intertidal and subtidal turfing algal assemblages and the temporal generality of these patterns. *J Exp Mar Biol Ecol* 267:53–74
- Dahl K, Støttrup JG, Stenberg C, Berggreen UC, Jensen JH (2016) Best practice for restoration of stone reefs in Denmark (Codes of Conduct). DCE Tech Rep 91. Aarhus University, Danish Centre for Environment and Energy. <https://dce2.au.dk/pub/TR91.pdf>
- ✦ Dailianis T, Smith CJ, Papadopoulou N, Gerovasileiou V and others (2018) Human activities and resultant pressures on key European marine habitats: an analysis of mapped resources. *Mar Policy* 98:1–10
- Dayton PK (1975) Experimental studies of algal canopy interactions in a sea otter dominated kelp community at Amchitka Island, Alaska. *Fish Bull* 73:230–237
- Diesing M, Schwarzer K (2006) Identification of submarine hard-bottom substrates in the German North Sea and Baltic Sea EEZ with high-resolution acoustic seafloor imaging. In: von Nordheim H, Boedeker D, Krause JC

- (eds) Marine protected areas in the North and Baltic Seas. NATURA 2000 sites in German offshore waters. Springer, Berlin, p 111–125
- ✦ Duarte CM (1995) Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41:87–112
- ✦ Dumas P, Bertaud A, Peignon C, Léopold M, Pelletier D (2009) A 'quick and clean' photographic method for the description of coral reef habitats. *J Exp Mar Biol Ecol* 368:161–168
- ✦ Durden JM, Schoening T, Althaus F, Friedman A and others (2016) Perspectives in visual imaging for marine biology and ecology: from acquisition to understanding. *Oceanogr Mar Biol Annu Rev* 54:1–72
- European Commission (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. <https://eur-lex.europa.eu/eli/dir/1992/43/oj>
- ✦ Frascchetti S, Bianchi CN, Terlizzi A, Fanelli G, Morri C, Boero F (2001) Spatial variability and human disturbance in shallow subtidal hard substrate assemblages: a regional approach. *Mar Ecol Prog Ser* 212:1–12
- ✦ Frascchetti S, Terlizzi A, Benedetti-Cecchi L (2005) Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Mar Ecol Prog Ser* 296:13–29
- ✦ Friedland R, Neumann T, Schernewski G (2012) Climate change and the Baltic Sea action plan: model simulations on the future of the western Baltic Sea. *J Mar Syst* 105–108:175–186
- ✦ Gogina M, Zettler ML (2010) Diversity and distribution of benthic macrofauna in the Baltic Sea. *J Sea Res* 64:313–321
- ✦ Golikov AN, Scarlato OA (1968) Vertical and horizontal distribution of biocoenoses in the upper zones of the Japan and Okhotsk seas and their dependence on the hydrological system. *Sarsia* 34:109–116
- ✦ Gomes-Pereira JN, Auger V, Beisiegel K, Benjamin R and others (2016) Current and future trends in marine image annotation software. *Prog Oceanogr* 149:106–120
- ✦ Gräwe U, Naumann M, Mohrholz V, Burchard H (2015) Anatomizing one of the largest saltwater inflows into the Baltic Sea in December 2014. *J Geophys Res Oceans* 120: 7676–7697
- HELCOM (2013) HELCOM HUB. Technical Report on the HELCOM Underwater Biotope and habitat classification. Balt Sea Environ Proc No 139. www.helcom.fi/Lists/Publications/BSEP139.pdf
- Hiscock K, Mitchell R (1980) The description and classification of sublittoral epibenthic ecosystems. In: Price JH, Irvine DEG, Farnham WF (eds) *The shore environment*, Vol 2. Ecosystems. Systematics Association Special Vol 17. Academic Press, London, p 323–370
- ✦ Johnson MP, Allcock AL, Pye AL, Chambers SJ, Fitton DM (2001) The effects of dispersal mode on the spatial distribution patterns of intertidal molluscs. *J Anim Ecol* 70: 641–649
- ✦ Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Comput Geosci* 32:1259–1269
- ✦ Krause-Jensen D, Middelboe AL, Carstensen J, Dahl K (2007) Spatial patterns of macroalgal abundance in relation to eutrophication. *Mar Biol* 152:25–36
- ✦ Lamy T, Reed DC, Rassweiler A, Siegel DA and others (2018) Scale-specific drivers of kelp forest communities. *Oecologia* 186:217–233
- ✦ Legendre P, Thrush SF, Cummings VJ, Dayton PK and others (1997) Spatial structure of bivalves in a sandflat. *J Exp Mar Biol Ecol* 216:99–128
- ✦ Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- ✦ Menconi M, Benedetti-Cecchi L, Cinelli F (1999) Spatial and temporal variability in the distribution of algae and invertebrates on rocky shores in the northwest Mediterranean. *J Exp Mar Biol Ecol* 233:1–23
- ✦ Mumby PJ, Chisholm JRM, Clark CD, Hedley JD, Jaubert J (2001) Spectrographic imaging. a bird's-eye view of the health of coral reefs. *Nature* 413:36
- ✦ Ojaveer H, Jaanus A, MacKenzie BR, Martin G and others (2010) Status of biodiversity in the Baltic Sea. *PLOS ONE* 5:e12467
- ✦ Perkins NR, Foster SD, Hill NA, Barrett NS (2016) Image subsampling and point scoring approaches for large-scale marine benthic monitoring programs. *Estuar Coast Shelf Sci* 176:36–46
- ✦ Pinho D, Bertocci I, Arenas F, Franco JN and others (2016) Spatial and temporal variation of kelp forests and associated macroalgal assemblages along the Portuguese coast. *Mar Freshw Res* 67:113–122
- ✦ Radtke H, Neumann T, Voss M, Fennel W (2012) Modeling pathways of riverine nitrogen and phosphorus in the Baltic Sea. *J Geophys Res* 117:C09024
- Remane A (1934) *Die Brackwasserfauna*. *Zool Anz* 7:34–74
- ✦ Rilov G, Schiel DR (2011) Community regulation: the relative importance of recruitment and predation intensity of an intertidal community dominant in a seascape context. *PLOS ONE* 6:e23958
- ✦ Schiele KS, Darr A, Zettler ML, Friedland R, Tauber F, von Weber M, Voss J (2015) Biotope map of the German Baltic Sea. *Mar Pollut Bull* 96:127–135
- ✦ Schoch GC, Dethier MN (1996) Scaling up: the statistical linkage between organismal abundance and geomorphology on rocky intertidal shorelines. *J Exp Mar Biol Ecol* 201:37–72
- ✦ Schoch GC, Menge BA, Allison G, Thompson SA, Wood SA (2006) Fifteen degrees of separation: latitudinal gradients of rocky intertidal biota along the California Current. *Limnol Oceanogr* 51:2564–2585
- ✦ Schoening T, Durden J, Preuss I, Branzan Albu A and others (2017) Report on the Marine Imaging Workshop 2017. *Res Ideas Outcomes* 3:e13820
- ✦ Smale DA (2012) Extreme spatial variability in sessile assemblage development in subtidal habitats off southwest Australia (southeast Indian Ocean). *J Exp Mar Biol Ecol* 438:76–83
- ✦ Strong JA, Elliott M (2017) The value of remote sensing techniques in supporting effective extrapolation across multiple marine spatial scales. *Mar Pollut Bull* 116: 405–419
- Tauber F (2012a) Meeresbodenrelief in der deutschen Ostsee (Seabed relief in the German Baltic Sea). Bundesamt für Seeschifffahrt und Hydrographie, Hamburg
- Tauber F (2012b) Meeresbodensedimente in der deutschen Ostsee (Seabed sediments in the German Baltic Sea). Bundesamt für Seeschifffahrt und Hydrographie, Hamburg
- ✦ Terlizzi A, Anderson MJ, Frascchetti S, Benedetti-Cecchi L (2007) Scales of spatial variation in Mediterranean subtidal sessile assemblages at different depths. *Mar Ecol Prog Ser* 332:25–39
- ✦ Thrush SF, Pridmore RD, Hewitt JE (1994) Impacts on soft-

sediment macrofauna: the effects of spatial variation on temporal trends. *Ecol Appl* 4:31–41

- ✦ Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107:212–224
- ✦ Underwood AJ, Kennelly SJ (1990) Ecology of marine algae on rocky shores and subtidal reefs in temperate Australia. *Hydrobiologia* 192:3–20
- ✦ Valdivia N, Scrosati RA, Molis M, Knox AS (2011) Variation in community structure across vertical intertidal stress gradients: How does it compare with horizontal variation at different scales? *PLOS ONE* 6:e24062
- ✦ Van Rein HB, Brown CJ, Quinn R, Breen J (2009) A review of sublittoral monitoring methods in temperate waters: a focus on scale. *Underw Technol* 28:99–113
- ✦ Walbridge S, Slocum N, Pobuda M, Wright DJ (2018) Unified geomorphological analysis workflows with Benthic Terrain Modeler. *Geosciences* 8:94
- Witman JD, Dayton PK (2001) Rocky subtidal communities. In: Bertness MD, Gaines SD, Hay M (eds) *Marine community ecology*. Sinauer Associates, Sunderland, MA, p 339–366
- ✦ Zettler ML, Karlsson A, Kontula T, Gruszka P and others (2014) Biodiversity gradient in the Baltic Sea: a comprehensive inventory of macrozoobenthos data. *Helgol Mar Res* 68:49–57
- ✦ Zettler ML, Friedland R, Gogina M, Darr A (2017) Variation in benthic long-term data of transitional waters: Is interpretation more than speculation? *PLOS ONE* 12: e0175746

Editorial responsibility: Lisandro Benedetti-Cecchi, Pisa, Italy

*Submitted: June 3, 2019; Accepted: October 11, 2019
Proofs received from author(s): December 11, 2019*