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PRIMARY RESEARCH PAPER

Spatial pattern of hydrolittoral rock encrusting assemblages along the salinity gradient of the Baltic Sea

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Abstract This study compared the diversity parameters and structures of encrusting assemblages in two habitats situated at two levels of shallow rocky shore: hydrolittoral and littoral along the Baltic Sea system. We investigated the variability and level of distinctiveness of the hydrolittoral encrusting fauna based on species biodiversity and distribution, and compared these features with those of communities inhabiting the adjacent shallow littoral zone (3-m depth). Structural similarities and differences between the encrusting assemblages from adjacent hydrolittoral and littoral zones were studied within 14 locations distributed along the northern coastline of the Baltic Sea. Multivariate analysis indicates that salinity had the greatest influence on the structure of the investigated assemblages. Most of the observed hydrolittoral assemblages contained the same species as the littoral zone. This result indicated a shared common species pool with similar large-scale patterns of species distributions with some variability in the dominating species between zones. The similarity between species composition of the hydrolittoral and littoral assemblages decreased with increase of salinity. Additionally, with higher species richness and the occurrence of marine specialists adapted to hydrolittoral conditions, the role of the rock size in the frequency of species occurrence and assemblage diversity was less significant.

Keywords Rocky coast · Encrusting assemblages · Fauna · Environmental gradients · Baltic Sea

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Introduction

Coastal marine communities are affected by a variety of physical, chemical and biological disturbances (e.g. Bonsdorf & Pearson, 1999; Hänninen & Vuorinen, 2001; Eriksson & Bergström, 2005; Rousi et al., 2011) that modify recruitment conditions, influence species richness, diversity and distribution (Bonsdorff, 2006; Haanes & Gulliksen, 2011).

In marginal marine habitats, such as the intertidal zone, stress is considered to be a structuring factor for benthic community zonation, especially for those sessile organisms sensitive to disturbances (Olenin, 1997; Araujo et al., 2012). Intensified coastal disturbance is associated with tidal basins, particularly where factors such as increased wave action, sea level changes or, in some areas, winter ice formation are observed (Barnes & Arnold, 1999; Araujo et al., 2012). Assemblages of marine organisms in these areas are more susceptible to difficult conditions resulting from increased sedimentation, overturning or scouring (Therriault & Kolasa, 2000; Heaven & Scrosati, 2008). Populations at the boundary of their occurrence, for example those inhabiting the seashore, are typically smaller (Raffaelli & Hawkins, 1996; Guo et al., 2005) and are characterized by a lower abundance compared with populations located deeper in the sea (Sagarin et al., 2006).

Although the Baltic Sea is considered to be a non-tidal basin, seasonal and daily sea level variability can be significant and, over shorter time scales, the sea is affected by meteorological forcing (Johansson et al., 2001; Zaitseva-Pärnaste et al., 2009). These conditions can affect supralittoral or 'hydrolittoral' zone (the latter term being used in this study). As a result of significant hydrodynamic effects, the abiotic and biotic features of this zone are particularly vulnerable to physical disturbance from the constant water mixing (Schumann et al., 2006). Position along the land–sea gradient can directly influence physical and biological processes across the water column, mainly by controlling their intensity and thus influencing community composition (Terlizzi et al., 2007).

The hydrolittoral zone is regularly or occasionally exposed by the action of wind and is separated from littoral habitats below the high water mark (Davies et al., 2004). The hydrolittoral zone of the Baltic Sea constitutes the uppermost part of the submarine coastal slope and is adjacent to the species-rich littoral zone (Olenin, 1997). This area is a very dynamic environment (in terms of waves and currents) and is affected by seasonal temperature and salinity fluctuations (Olenin, 1997). The results from previous studies investigating littoral communities in brackish water bodies suggest that the salinity is a key determinant of community structure and species distribution over the large scale (Bonsdorf & Pearson, 1999; Cognetti & Maltagliati, 2000; Schernewski & Wielgat, 2004; Zetler et al., 2007) and it has been suggested that this is a result of differential tolerances of different species to salinity conditions (Westerbom et al., 2002; Johannesson & André, 2006; Khlebovich & Aladin, 2010). Recent studies investigating the distribution of fauna along the gradient of increasing salinity in the Baltic Sea have shown that the assemblage is transformed from dominated by a few opportunistic species adapted to brackish waters, to communities with a higher number of rare species in the higher salinity North Sea (Telesh et al., 2013).

In this study, we investigate small- and large-scale variability in the structure of encrusting faunal assemblages in the shallow rocky coast of the Baltic Sea. Encrusting fauna is defined here as all sessile animals attached to the sampled rocks. The results of previous studies suggest that the effect of low salinity [leading to a lower number of species, as found in the brackish water littoral zone (see Zettler et al., 2014)], would have a similar effect on hydrolittoral encrusting assemblages. We hypothesize that the large-scale spatial pattern of the structure of hydrolittoral encrusting assemblages (measured in terms of species composition, number and abundance) along the salinity gradient would be similar to large-scale distribution trends found for other Baltic Sea ecological formations (e.g. Bonsdorff, 2006, Telesh et al., 2013).

In temperate fully marine seas, intertidal communities differ substantially from those found in the deeper subtidal range, often containing species that are specialists adapted to the intertidal zone only (Raffaelli & Hawkins, 1996). In contrast, it has been observed that in regions described as more disturbed, including polar areas, the intertidal community often resembles that of the nearby subtidal zone, with these regions typically sharing a common species pool (Kuklinski & Barnes, 2008). However, none of these descriptions particularly relate to the Baltic Sea, a typically brackish environment in which benthic communities are composed of opportunistic species. Therefore, we anticipate that the stressful conditions of the brackish hydrolittoral zone will lead to a lower species diversity of predominately opportunistic organisms and assemblages, as found in the adjacent littoral zone. The higher salinity in the transient environment between the Baltic Sea and North Sea together with Atlantic Ocean-induced waves, tides and sea level changes may lead to an increased difference between hydrolittoral and littoral assemblages, as a result of the appearance of marine species. In this circumstance, intertidal–hydrolittoral specialists from temperate fully marine systems (such as the North Sea) might be expected to contribute to independent hydrolittoral assemblages. The higher frequency of occurrence of encrusting species in the hydrolittoral in higher salinity could be due to random movement of the species originally inhabiting the adjacent littoral environment. This increased probability is likely to be independent of the rock size, which is otherwise a limiting factor for encrusting community development

(Grzelak & Kuklinski, 2010). In this study, the sampling in the hydrolittoral zone was performed concomitantly with sampling in the adjacent littoral zones, allowing a robust comparative analysis between the features of faunal assemblages in both zones along the Baltic Sea coast. To our knowledge, this study is the first investigation of encrusting fauna within the hydrolittoral zone on such a scale in the Baltic Sea.

Materials and methods

Study sites and sampling

To assess the large-scale patterns of the hard-bottom encrusting assemblages structure, we selected 14 locations along the Swedish and Norwegian Baltic Sea rocky shore between Töre (Sweden) (65°53′N, 22°42′E) and Lillesand (Norway) (58°15′N, 08°29′E) (Fig. 1). Locations were labelled chronologically based on their geographical position and sampling order starting from the Bothnian Bay (B01–B05) surveyed in August 2007 through the west coast of Baltic Proper (B06–B09) to the Kattegat and Skagerrak (B10–B14) sampled in October 2007. During the survey, environmental variables such as salinity and temperature were measured. Water salinity ranged from 0.5 in the Bothnian Bay to over 27 in Kattegat and Skagerrak, and the temperature ranged between 13 and 15°C in Bothnian Bay (August) and between 8 and 10°C in the Baltic Proper and Kattegat and Skagerrak (October). These measurements follow the multi-year (10 years) surface temperatures and salinity data [derived for the purpose of this study from the World Ocean Database Select and Search and computed with the use of the Ocean Data View software (Schlitzer, 2015, Germany) (see Fig. 1)].

To compare the structure of encrusting assemblages in the shallow Baltic Sea rocky habitat, rock samples from two marine coastal zones (hydrolittoral and littoral) were collected concomitantly. The Baltic Sea is regarded as non-tidal; however, there are daily mean sea level variations estimated to be between 17 and 18 cm at the Baltic Proper (Suursaar & Kullas, 2006). Stations B11 to B14, located in the area of Skagerrak and Kattegat, are micro-tidal areas with astronomical tidal ranges of 20–30 cm and approximately 40 cm, respectively (Cossellu & Nordberg, 2010). The sea level range in the non-tidal area almost overlaps with the tidal range in the micro-tidal area. Therefore, for the purpose of this study, we used a uniform terminology to describe the two sampling zones across tidal and no tidal areas (hydrolittoral and littoral).

Hydrolittoral samples were collected by hand from the seashore at mean sea level in non-tidal areas and at

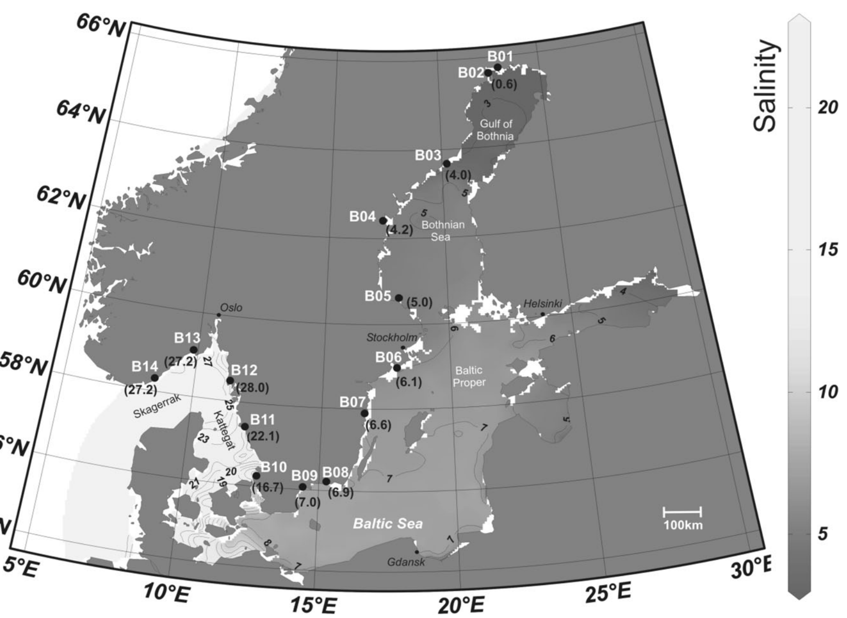


Fig. 1 Map of the study area system with marked sampling locations and salinity in situ values measured at the time of sample collection plotted on multi-year surface salinity data. Multi-year surface salinity data were derived from the World Ocean Database Select and Search and computed with use of the Ocean Data View software

appropriately the extreme low water spring (ELWS) tide level in tidal areas. The mean sea level at non-tidal locations was evaluated by the position of the vegetation line marked by marine and land flora (Kautsky et al., 1986). Rock samples were collected at the same time by SCUBA in the shallow littoral zone from a ~ 3-m depth. At each level of the coastal habitat (hydrolittoral and littoral), three subsamples (separated by approximately 5 m) consisting of rocks of various sizes were collected randomly at each location to obtain examples of the possible rock size variants. The average number of rocks collected per subsample at each location in the hydrolittoral zone varied from 17 to 22, whereas in the littoral zone the number of rocks varied from 33 to 96. The average rock size per subsample varied between locations and ranged from 94 to 332 cm^2 and from 65 to 220 cm^2 in hydrolittoral and littoral zones, respectively. The surface area of each rock was measured with an inelastic net gridded with 2 cm^2, and the percentage cover of fauna and flora on each rock was estimated based on the ratio between covered and bare rock surface. Organisms were identified to the lowest possible taxonomic level, typically to the species level and counted (individuals per m^2). The sampling effort was tested using cumulative plots where the number of observed encrusting species was plotted versus the number of rocks (PRIMER 6^{TM} routine) for the locations within the hydrolittoral and littoral zones. The results from each of the locations were combined for a collective figure (SigmaPlot10.0 software) representing the whole study area.

Data analysis

Faunal data from each subsample were analysed for species richness, abundance (individuals per m^2), the Shannon–Wiener (H′) proportional diversity index (log base 10) and Pielou's evenness index (compare the species abundances in communities). The diversity indices take into account information on both species richness and abundance obtained from measuring the heterogeneity of encrusting assemblages. These results were presented graphically as averaged values (± SE).

The relationship between encrusting assemblages, represented by the total abundance (ind/m^2) and environmental variables, was studied using a canonical correspondence analysis (CCA) with CANOCO software. The analysis was performed on raw abundance data and the untransformed matrix of environmental variables. A selection of variables (salinity, habitat type, wave exposure, mean rock size, temperature, latitude and longitude) was used to best explain the variance of the biological data based on the encrusting species number and abundance. Latitude and longitude were used as covariables. The significance of each variable was estimated in a Monte Carlo test using 999 permutations. For the purpose of the CCA, wave exposure data were obtained for each sampling location. The wave exposure grid covering the Baltic Sea area was constructed from a combined Simplified Wave Model method and the off-shore significant wave height was modelled with MIKE2 using the calculations included in the 2010 AquaBiota report (Wijkmark & Isæus, 2010). According to this source, which reports eight classes of wave exposure levels (from ultra-sheltered to extremely exposed), the wave exposure at our surveyed locations varied over the spatial scale and was rated from sheltered through moderately exposed to exposed, in the Bothnian Bay (locations B01, B02, B04 and B06), central Baltic Sea (locations B03, B05, B07–B10) and Kattegat and Skagerrak (locations B11–B14), respectively. These west-to-east gradients were also accompanied by decreasing tidal amplitude.

The analysis of covariance (ANCOVA) was used to test the effect of salinity and habitat (two levels) on the diversity parameters (species richness, Shannon–Wiener diversity, Pielou's evenness, percent cover of fauna and abundance). Prior to running parametric tests, we tested for homogeneity of variance among samples with Levene's test. For the ANCOVA analysis, we used habitat level as a grouping variable and salinity as a covariate.

To investigate the effect of the increasing salinity gradient within the Baltic system, faunal assemblages from all subsamples collected at the study locations were compared using a resemblance matrix on square-root transformed data based on Bray–Curtis similarity. Non-metric multidimensional scaling (nMDS) was conducted using the PRIMER 6^{TM} package (Plymouth Routines In Multivariate Ecological Research, PRIMER-E Ltd). Differences in community structure between hydrolittoral and littoral were mapped with nMDSs and tested with analysis of similarity (ANOSIM).

To illustrate the relationship between substratum sizes and encrusting assemblages from the hydrolittoral and littoral zones, we segregated the samples according to the rock size into eight groups and compared frequencies of occurrence of encrusting organisms within the different-sized rock groups. To illustrate the probability of species occurrence in relation to rock size range, the frequency of occurrence based on a presence/absence ratio (± standard error) was estimated for a given rock size range (100, 200, 300, 400, 500, 600, 700 and 800 cm^2) for the hydrolittoral zone and compared with the results from the littoral zone. The frequency (mean value ± SE) of species occurrence was plotted against the rock size classes for each location. The assemblage structure differences between habitats based on the species abundance data within the rock size groups as samples were illustrated with nMDS ordination plots and tested with analysis of similarity (ANOSIM).

Results

A total of 24 encrusting taxa were found at 14 sampling locations. At location B01, no encrusting assemblages were recorded in the hydrolittoral and littoral zones and at B02 none were found in the littoral zone; these locations were thus not considered further in this study. For samples collected in the hydrolittoral zone, we identified 21 species (nine bryozoans, six annelids, three barnacles and four other), and for the shallow littoral zone, we identified 24 species (11 bryozoans, six annelids, three barnacles and four other). The complete list of the species and their abundances is presented in Table 1. Accumulation curves for species from locations B02–B10 in the hydrolittoral zone and B03–B09 in the littoral zone (Fig. 2) were asymptotic. For other locations, species accumulation curves showed a continued slight increase.

Spatial patterns of species richness in the hydrolittoral zone resembled those found in the littoral assemblages. At the locations situated between the Bothnia Bay and the Baltic Proper (with the exception of locations B05 and B06), species richness was lower than at locations from B10 to B14 (Fig. 3). The mean abundance of encrusting organisms in hydrolittoral and littoral zones varied through space and varied from only a few individuals per m^2 (location B02) up to over 30,000 (locations B10 and B14). The mean abundance in general was higher at locations with a higher salinity, both in the hydrolittoral and littoral zones. In the brackish Bothnian Bay, Baltic Proper and Kattegat (locations from B03 to B10), the abundance of assemblages from the littoral zone exceeded hydrolittoral assemblages; however, the trend was reversed in the locations with the highest salinity (B11–B14). The results of Pielou's measure of evenness shows that, in general, communities occurring in low salinity (B03–B09) were characterized by higher variation compared to marine communities (B10–B14). However, the values of the evenness index between habitats showed a stronger diversification at locations with low salinity levels and low species number (locations B02–B10), than at locations with higher salinity and species number (locations B11–B14), and the index presented similar values (Fig. 3). Results of analysis of covariance (ANCOVA) showed that the structure of encrusting assemblages varied significantly as a result of salinity change in terms of species richness, abundance, faunal cover and diversity (Table 2). Assemblages differed between habitats (hydrolittoral versus littoral) significantly only in terms of species richness ($F = 23.78$, $P < 0.001$). The canonical correspondence analysis (CCA) showed strong relationship between encrusting assemblages and environmental parameters (Fig. 4). The Monte Carlo permutation test for the first axis was significant ($F = 7.494$, $P = 0.017$). According to the results of the analysis, salinity was the most significant factor affecting assemblage structure ($F = 10.182$, $P = 0.001$). However, there were other factors that had lower but also considerable impacts on overall species composition and community structure. For example, flora coverage ($F = 5.846$, $P = 0.001$), wave exposure ($F = 6.120$, $P = 0.001$), mean rock size ($F = 2.655$, $P = 0.025$) and habitat type ($F = 8.847$, $P = 0.001$) (which was a nominal value) were also statistically significant. Overall, 98.7% of the correlation between species and continuous variables was explained by the first axis of the CCA diagram ($F = 8.762$, $P = 0.001$; Eigenvalues = 2.719; Total inertia = 3.414). Remaining tested variables (temperature and fauna coverage) were not statistically significant and did not appear to have an influence on community structure.

The overall number of species in the hydrolittoral zone was lower than in the littoral and a great majority of the species were found in both habitats (Table 1). Hydrolittoral assemblages in the brackish part of the

Table 1 Encrusting species recorded in hydrolittoral and littoral of the Baltic Sea

Location		B01	B02		B03	
Phylum	Taxa	Hydrolittoral	Hydrolittoral	Littoral	Hydrolittoral	Littoral
Cnidaria	Hydrozoa (Linnaeus, 1758)					
Foraminifera						
Annelida	*Circeis spirillum* (Linnaeus, 1758)					
	Janua pagenstecheri (Quatrefages, 1865)					
	Laeospira corallinae (de Silva & Knight-Jones, 1962)					
	Spirobranchus triqueter (Linnaeus, 1758)					
	Spirorbis spirorbis (Linnaeus, 1758)					
	Spirorbis tridentatus (Levinsen, 1883)					
Arthropoda	*Amphibalanus improvisus* (Darwin, 1854)				20.11 ± 3.56	4.56 ± 6.40
	Semibalanus balanoides					
	(Linnaeus, 1767)					
	Verruca stroemia					
	(O.F. Müller, 1776)					
Bryozoa	*Aetea truncata* (Lamouroux, 1812)					
	Callopora lineata (Linnaeus, 1767)					
	Celleporella hyalina (Linnaeus, 1767)					
	Cribrilina annulata (O.Fabricius, 1780)					
	Cribrilina cryptooecium (Norman, 1903)					
	Cribrilina punctata (Hassall, 1841)					
	Cryptosula pallasiana (Moll, 1803)					
	Einhornia crustulenta (Pallas, 1766)		2.09 ± 3.63			113.94 ± 165.86
	Electra pilosa (Linnaeus, 1767)					
	Escharella immersa (Fleming, 1828)					
	Scrupocellaria reptans (Linnaeus, 1758)					
Mollusca	*Modiolus modiolus* (Linnaeus, 1758)					
	Mytilus (Linnaeus, 1758)					

Table 1 continued

Location		B04		B05		B06	
Phylum	Taxa	Hydrolittoral	Littoral	Hydrolittoral	Littoral	Hydrolittoral	Littoral
Cnidaria	Hydrozoa (Linnaeus, 1758)						
Foraminifera							
Annelida	*Circeis spirillum* (Linnaeus, 1758)						
	Janua pagenstecheri (Quatrefages, 1865)						
	Laeospira corallinae (de Silva & Knight-Jones, 1962)						
	Spirobranchus triqueter (Linnaeus, 1758)						
	Spirorbis spirorbis (Linnaeus, 1758)						
	Spirorbis tridentatus (Levinsen, 1883)						
Arthropoda	*Amphibalanus improvisus* (Darwin, 1854)	13.50 ± 2.09	25.90 ± 7.50	18.36 ± 5.08	142.35 ± 171.20	9.64 ± 3.13	48.34 ± 28.17
	Semibalanus balanoides (Linnaeus, 1767)						
	Verruca stroemia (O.F. Müller, 1776)						
Bryozoa	*Aetea truncata* (Lamouroux, 1812)						
	Callopora lineata (Linnaeus, 1767)						
	Celleporella hyalina (Linnaeus, 1767)						
	Cribrilina annulata (O.Fabricius, 1780)						
	Cribrilina cryptooecium (Norman, 1903)						
	Cribrilina punctata (Hassall, 1841)						
	Cryptosula pallasiana (Moll, 1803)						
	Einhornia crustulenta (Pallas, 1766)		2555.25 ± 1092.34	40.02 ± 29.51	761.74 ± 499.10		1703.94 ± 195.16
	Electra pilosa (Linnaeus, 1767)	10.16 ± 17.59		4.81 ± 8.32		1.09 ± 1.89	
	Escharella immersa (Fleming, 1828)						
	Scrupocellaria reptans (Linnaeus, 1758)						
Mollusca	*Modiolus modiolus* (Linnaeus, 1758)						
	Mytilus (Linnaeus, 1758)				0.58 ± 1.01	5.86 ± 4.05	309.69 ± 95.23

Table 1 continued

Location		B07		B08		B09		B10	
Phylum	Taxa	Hydrolittoral	Littoral	Hydrolittoral	Littoral	Hydrolittoral	Littoral	Hydrolittoral	Littoral
Cnidaria	Hydrozoa (Linnaeus, 1758)								1.30 ± 1.36
Foraminifera									
Annelida	*Circeis spirillum* (Linnaeus, 1758)								
	Janua pagenstecheri (Quatrefages, 1865)								
	Laeospira corallinae (de Silva & Knight-Jones, 1962)								0.60 ± 1.03
	Spirobranchus triqueter (Linnaeus, 1758)								
	Spirorbis spirorbis (Linnaeus, 1758)								2.79 ± 3.84
	Spirorbis tridentatus (Levinsen, 1883)								
Arthropoda	*Amphibalanus improvisus* (Darwin, 1854)		48.14 ±35.57	1.78 ±3.078	0.62 ±1.08		167.28 ±217.85	819.89 ±375.73	26227.41 ±7533.42
	Semibalanus balanoides								
	(Linnaeus, 1767)								
	Verruca stroemia								
	(O.F. Müller, 1776)								
Bryozoa	*Aetea truncata* (Lamouroux, 1812)								0.45 ± 0.78
	Callopora lineata (Linnaeus, 1767)								14.21 ± 13.07
	Celleporella hyalina (Linnaeus, 1767)								
	Cribrilina annulata (O.Fabricius, 1780)								
	Cribrilina cryptooecium (Norman, 1903)								0.90 ± 1.56
	Cribrilina punctata (Hassall, 1841)								
	Cryptosula pallasiana (Moll, 1803)								
	Einhornia crustulenta (Pallas, 1766)		679.24 ± 244.52		367.75 ± 293.60		191.12 ± 179.94		16.18 ± 14.26
	Electra pilosa (Linnaeus, 1767)							69.12 ± 79.67	32.11 ± 27.74
	Escharella immersa (Fleming, 1828)								
	Scrupocellaria reptans (Linnaeus, 1758)								
Mollusca	*Modiolus modiolus* (Linnaeus, 1758)								
	Mytilus (Linnaeus, 1758)	4.74 ± 4.35	484.96 ± 190.4	41.82 ± 40.87	426.53 ± 90.46	206.09 ± 106.38	55.38 ± 65.79	202.85 ± 31.90	2652.46 ± 1446.9

Table 1 continued

Location		B11		B12		B13		B14	
Phylum	Taxa	Hydrolittoral	Littoral	Hydrolittoral	Littoral	Hydrolittoral	Littoral	Hydrolittoral	Littoral
Cnidaria	Hydrozoa (Linnaeus, 1758)	49.58 ± 85.86	41.17 ± 63.93	87.34 ± 89.51	21.63 ± 0.21	3.66 ± 6.34	3.88 ± 0.34	179.40 ± 310.73	0.74 ± 1.29
Foraminifera		125.86 ± 217.99	5.71 ± 2.36	1.42 ± 2.46	200.92 ± 148.97	57.62 ± 97.62	295.38 ± 60.78	63.87 ± 49.66	248.57 ± 189.23
Annelida	*Circeis spirillum* (Linnaeus, 1758)	1.31 ± 2.27							128.07 ± 219.62
	Janua pagenstecheri (Quatrefages, 1865)	702.54 ± 1188.99	216.42 ± 374.85	873.97 ± 1384.30	60.16 ± 31.79	9643.99 ± 15863.01		17709.07 ± 13794.14	427.52 ± 735.22
	Laeospira corallinae (de Silva & Knight-Jones, 1962)	35.38 ± 61.27	12.39 ± 20.06	128.23 ± 209.84	27.08 ± 8.46	7133.42 ± 11067.06	0.35 ± 0.60	3308.64 ± 1645.84	197.39 ± 318.04
	Spirobranchus triqueter (Linnaeus, 1758)		1.16 ± 2.01		38.28 ± 30.58	2.37 ± 4.11	0.35 ± 0.61		5.04 ± 3.40
	Spirorbis spirorbis (Linnaeus, 1758)	116.08 ± 168.16	513.53 ± 392.82	275.36 ± 400.97	541.36 ± 236.15	84.16 ± 54.35	907.99 ± 898.71	2134.99 ± 1930.31	5271.35 ± 5921.17
	Spirorbis tridentatus (Levinsen, 1883)	62.45 ± 94.87	3843.36 ± 4336.96	3263.41 ± 2110.46	793.38 ± 325.29	41.04 ± 40.95	1486.87 ± 1024.16	4630.51 ± 4429.5	11372.41 ± 8370.76
Arthropoda	*Amphibalanus improvisus* (Darwin, 1854)	3444.96 ± 2100.81	80.96 ± 70.74	977.18 ± 640.92	3.18 ± 1.18	105.80 ± 123.39	2.13 ± 2.74	28.22 ± 33.61	0.43 ± 0.74
	Semibalanus balanoides (Linnaeus, 1767)	28.78 ± 49.84	1.37 ± 2.37	14.65 ± 9.3	4.85 ± 8.40	21.37 ± 37.01		73.30 ± 126.96	1.12 ± 1.93
	Verruca stroemia (O.F. Müller, 1776)	1.91 ± 3.30	0.46 ± 0.79	26.24 ± 11.04	22.27 ± 9.09	1.19 ± 2.06	1.65 ± 1.44	119.53 ± 61.37	870.01 ± 1440.36
Bryozoa	*Aetea truncata* (Lamouroux, 1812)		4.26 ± 4.35		131.70 ± 124.11				0.37 ± 0.64
	Callopora lineata (Linnaeus, 1767)	12.87 ± 11.71	89.94 ± 48.84		53.36 ± 84.64	6.41 ± 11.10	38.74 ± 34.06	234.27 ± 275.56	4.26 ± 7.38
	Celleporella hyalina (Linnaeus, 1767)						2.14 ± 2.75	38.88 ± 64.09	1.65 ± 1.97
	Cribrilina annulata (O.Fabricius, 1780)	3.81 ± 6.61	6.92 ± 6.01	26.59 ± 7.34	3205.07 ± 3442.44	3.93 ± 4.13	9.18 ± 5.69	12.97 ± 16.69	79.40 ± 63.32

Table 1 continued

Location		B11		B12		B13		B14	
Phylum	Taxa	Hydrolittoral	Littoral	Hydrolittoral	Littoral	Hydrolittoral	Littoral	Hydrolittoral	Littoral
	Cribrilina cryptooecium (Norman, 1903)		89.37 ± 82.03		58.30 ± 26.25	2.75 ± 4.76	195.54 ± 83.13	211.96 ± 307.18	200.61 ± 212.00
	Cribrilina punctata (Hassall, 1841)	3.81 ± 6.66	37.65 ± 30.08	24.92 ± 28.09	42.41 ± 22.66		29.01 ± 12.68	7.72 ± 13.36	8.52 ± 10.97
	Cryptosula pallasiana (Moll, 1803)	30.27 ± 26.91	22.34 ± 8.90	1020.38 ± 145.23	185.11 ± 83.41	37.55 ± 65.03	98.50 ± 82.38	2469.80 ± 1596.23	200.60 ± 208.99
	Einhornia crustulenta (Pallas, 1766)	1.91 ± 3.30	3.48 ± 6.02						
	Electra pilosa (Linnaeus, 1767)	7.63 ± 13.21	23.86 ± 19.34	46.76 ± 66.69	12.93 ± 8.16		9.39 ± 8.11	3.19 ± 2.94	10.54 ± 10.24
	Escharella immersa (Fleming, 1828)		2.28 ± 2.67		80.50 ± 69.9		9.50 ± 8.26	6.31 ± 10.93	825.82 ± 1358.41
	Scrupocellaria reptans (Linnaeus, 1758)				4.86 ± 1.12				56.79 ± 92.63
Mollusca	*Modiolus modiolus* (Linnaeus, 1758)						319.84 ± 196.32		55.37 ± 54.27
	Mytilus (Linnaeus, 1758)	136.68 ± 20.67	105.36 ± 50.06	51.35 ± 38.17	62.35 ± 29.35	21.77 ± 31.34	321.80 ± 392.37	54.10 ± 80.94	28.51 ± 24.76

Values expressed as mean abundance (indiv./m^2 ± SD), location labels with accordance to Fig. 1

Baltic Sea including Bothnian Bay and Baltic Proper locations (locations B02–B09) were composed of four opportunistic species: *Amphibalanus improvisus* (Darwin, 1854), *Einhornia crustulenta* (Pallas, 1766), *Electra pilosa* (Linnaeus, 1767) and *Mytilus* juv. (Linnaeus, 1758), which were distributed heterogeneously between the locations. Those species, as indicated by the CCA (Fig. 4), show tolerance to low salinity. The hydrolittoral assemblages at the Bothnian Bay and the northern part of Baltic Proper (B02–B06) were dominated mainly by *A. improvisus*. *Mytilus* juv. contributed significantly to assemblage abundance in the Baltic Proper (locations B07–B09) and was an important component of marine encrusting assemblages (locations B10–B14). *E. crustulenta* dominated littoral assemblages and was a rare component of hydrolittoral assemblages (locations B02, B05 and B11 only). Among the species observed in this Baltic Sea region (B04–B06), there was one—*Electra pilosa*—that occurred in the hydrolittoral zone and did not appear in the nearby shallow littoral assemblages. *E. pilosa* also appeared in the marine littoral zone (B11–B14); however, the average numbers in both zones were very low (< 50 individuals per m^2). In the Baltic Sea–North Sea transition (locations B10), both hydrolittoral and littoral assemblages were dominated by *A. improvisus*. This species (*A. improvisus*) was also observed in much lower numbers at locations B11–B14 (Kattegat and Skagerrak) and its abundance was much higher in hydrolittoral compared to littoral. At this part of the studied area (locations B11–B14), assemblages had greater species diversity due to (1) specialized species which were found in the hydrolittoral zone (e.g. *Janua pagenstecheri* (Quatrefages, 1865), *Laeospira corallinae* (de Silva and Knight Jones, 1962), *Semibalanus balanoides* (Linnaeus, 1767) or *Cryptosula pallasiana* (Moll, 1803)) and (2) the high number of species occurring abundantly in the littoral zone (e.g. *Spirorbis spirorbis* (Linnaeus, 1758), *Einhornia crustulenta* or *Escharella immersa* (Fleming, 1828)). Additionally, there were a few species that occurred only in the littoral zone (the bryozoans *Aetea truncata* (Lamouroux, 1812) and *Scrupocellaria reptans* (Linnaeus, 1758) and the mollusc *Modiolus modiolus* (Linnaeus, 1758)). A few species were also found to be specific to the hydrolittoral zone and were present only in very low numbers (Table 1). Hydrolittoral and littoral encrusting assemblages also differed in terms of the

Table 2 The results of the analysis of covariance (ANCOVA) testing the effects of salinity and habitat on the basic community parameters (significant 636 differences are highlighted in bold) where habitat was used as a grouping factor while salinity as covariate

	Degr. of freedom	Species richness				Shannon diversity				Pielou evenness			
		SS	MS	*F*	*P*	SS	MS	*F*	*P*	SS	MS	*F*	*P*
Intercept	1	**1.08**	**1.08**	**13.77**	**<0.001**	0.02	0.02	0.77	0.38	**2.54**	**2.54**	**25.05**	**<0.001**
Salinity	1	**27.55**	**27.55**	**351.41**	**<0.001**	**2.82**	**2.82**	**125.96**	**<0.001**	**0.52**	**0.52**	**5.17**	**0.03**
Habitat	1	**1.86**	**1.86**	**23.78**	**<0.001**	0.07	0.07	3.19	0.08	0.08	0.08	0.77	0.38
Error	75	5.88	0.08			1.68	0.02			7.61	0.10		
Total	77	35.30				4.58				8.22			

	Degr. of freedom	Coverage				Abundance			
		SS	MS	*F*	*P*	SS	MS	*F*	*P*
Intercept	1	25.17	25.17	0.25	0.62	85033346.87	85033346.87	1.05	0.31
Salinity	1	**2391.44**	**2391.44**	**24.00**	**<0.001**	**2301379851.97**	**2301379851.97**	**28.49**	**<0.001**
Habitat	1	212.60	212.60	2.13	0.15	11480841.35	11480841.35	0.14	0.71
Error	75	7473.86	99.65			6057874913.05	80771665.51		
Total	77	10077.90				8370735606.37			

contribution of taxonomic groups to the relative abundance. Samples from the brackish parts of the Baltic Sea (the Bothnian Bay and Baltic Proper) were dominated by arthropods and molluscs. For the corresponding littoral assemblages, there was a greater proportion of bryozoans. In higher salinity (locations B10–B14), serpulid worms contributed significantly to both hydrolittoral and littoral assemblages.

An overall nMDS ordination presenting distribution of all assemblages showed differences in the structure of assemblages between hydrolittoral and littoral zones (Fig. 5). Analysis of similarity (ANOSIM) performed to test the differences in assemblages between habitats showed low but significant separation between hydrolittoral and littoral (Global $R = 0.151$, $P < 0.001$). In detailed comparison, the frequency of fauna occurrence in the littoral samples was higher in most of the rock size classes compared to those in the hydrolittoral samples (Fig. 6). The frequency of occurrence of encrusting organisms equalled 1, regardless of habitat and rock size, in higher salinity (B10–B14). Occurrence of encrusting fauna in relation to rock size differed between hydrolittoral and littoral zones (Fig. 6). In lower salinity, where diversity was low, the negative effect of "small rocks" on frequency of encrusting species occurrence was stronger in the hydrolittoral compared to littoral zone. In general, the probability of finding encrusting fauna increased with the rock size and was higher in littoral zones, where at most of the salinity levels even small rocks had a higher probability of encrustation. Based on the results of the nMDS and ANOSIM performed for each location, the assemblages occurring in hydrolittoral zones were generally different from those of the littoral zones, although the effect of rock size was less significant at locations in the brackish Baltic Sea (location B03–B09) (Fig. 7). Assemblages from the North Sea–Baltic Sea (locations B11–B14) transition zone distinguished between the hydrolittoral and littoral habitats for each of the rock size class. Results of ANOSIM tests for assemblages at given rock size range performed for each location generally showed moderate and high separation between hydrolittoral and littoral assemblages.

Discussion

In this study, we investigated encrusting assemblages inhabiting rocks in the Baltic Sea hydrolittoral zone in comparison to the adjacent littoral zone along a salinity gradient. Comparative measurement of biological parameters describing encrusting assemblages inhabiting the Baltic Sea hydrolittoral and littoral zones (such as species richness, abundance, diversity, percentage cover of fauna) indicated the significant role of local dispersal limitations in encrusting species composition and a strong influence of nearby biotopes.

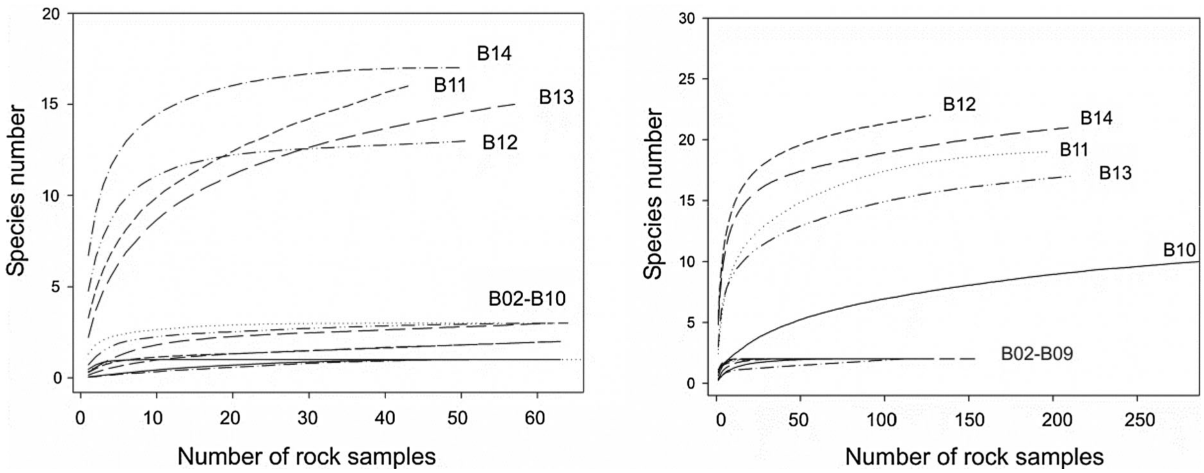
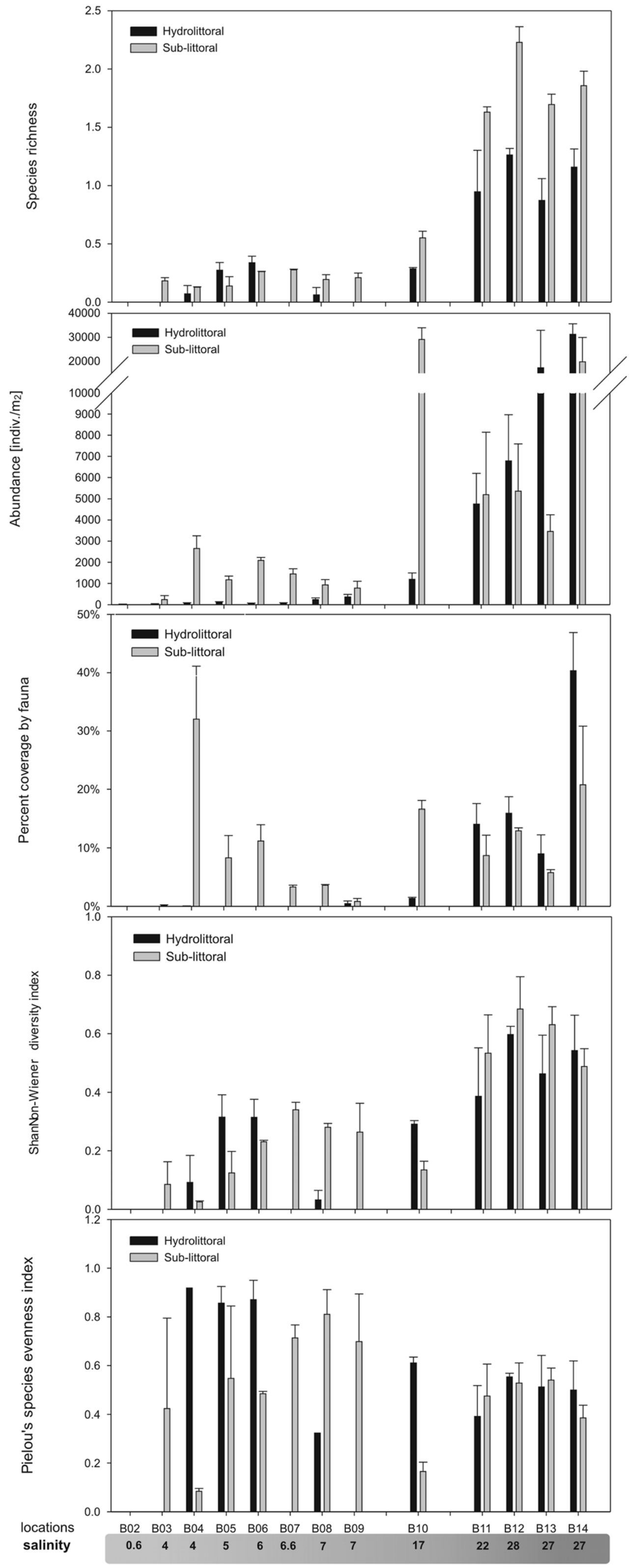


Fig. 2 Species accumulation plots in hydrolittoral (*left*) and littoral (*right*) for the study locations. Location labels are in accordance with Fig. 1

Over the scale of the entire Baltic Sea, spatial species distribution is controlled mainly by the steep salinity gradient (Herkül et al., 2006; Zettler et al., 2014), which, according to the results of this study, is also observed in our data and matched our predictions. Along the gradient of increasing salinity, the spatial trends in the hydrolittoral zone, including species composition and increased diversity of encrusting assemblages, were found to be similar to those reported for other macrobenthic communities from deeper regions of the Baltic Sea (Bonsdorff & Pearson, 1999; Westerbom et al., 2002) and in particular, as this study clearly indicated, the nearby littoral. Similar correlation between the salinity and the species richness and abundance of encrusting assemblages was noted for other taxonomic and functional groups (e.g. Darr et al., 2014; Zettler et al., 2014).

Among the environmental variables we studied (including temperature, mean rock size, wave exposure or percent coverage by fauna), salinity showed the strongest relationship with the large-scale pattern of encrusting assemblages. Low salinity in areas additionally exposed to harsh winter conditions and ice formation appeared to inhibit the development of hydrolittoral communities but favoured species adapted to harsh conditions. The structure of the encrusting assemblages in the brackish environment of the Baltic Sea consisted of four main species: *A. improvisus*, *Mytilus* juv., *Einhornia crustulenta* and *Electra pilosa*. Such homogeneity of species composition was recorded over a large scale along the salinity gradient and was also evident in the values of the Shannon–Wiener and Pielou's indices (Fig. 3). This complementary information indicates that the brackish encrusting assemblages (stations B02 to B09) were generally represented by fewer (although highly abundant) species, in contrast to assemblages recorded from more saline environments (B11 to B14), where communities are more species rich with a few dominant species (with the rest of species considered to be rare in terms of abundance (Fig. 3, Table 1)). Although the structure of the hydrolittoral and littoral assemblages in the brackish environment of the Bothnian Bay and the Baltic Proper remained homogeneous over this large area, hydrolittoral assemblages (in contrast to littoral) were enriched by the episodic appearance of the bryozoan *Electra pilosa*. The most frequent components of the brackish hydrolittoral assemblages, represented by barnacles and mussels (*A. improvisus* and *Mytilus* juv.), have been observed in high biomass on exposed shores of the Baltic Sea (Wallin et al., 2011) and were considered to be the most frequent components of wave-exposed intertidal biotopes in the Northern Atlantic Ocean bioregion (Bartsch & Tittley, 2004). This confirms that *A. improvisus* is well adapted for survival in the highly hydrodynamic coastal rock belt of the Baltic Sea and is one of the dominant species in brackish communities. Similar observations have been made for another barnacle species from the Canadian coast, suggesting

Fig. 3 Comparison of basic diversity parameters: **a** species richness, **b** abundance, **c** percent coverage by fauna, **d**) Shannon–Wenner diversity and **e** evenness index presented as mean values ± standard error between hydrolittoral and littoral assemblages. Location and salinity labels are in accordance with Fig. 1



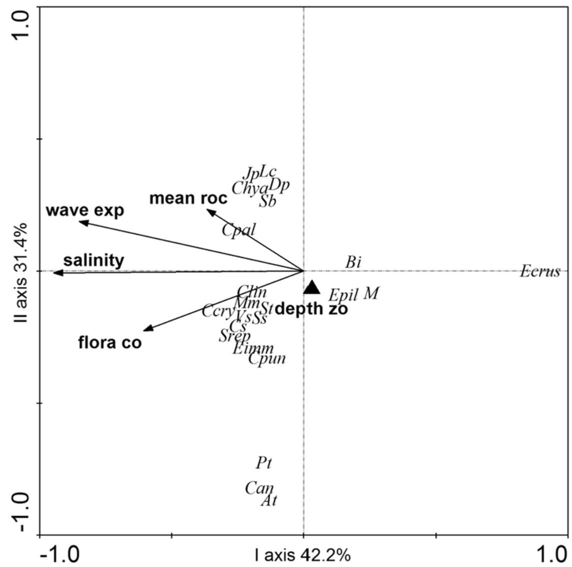


Fig. 4 Canonical correspondence analysis (CCA) plot for all encrusting species from selected environmental variables: salinity, wave exposure (wave exp), mean rock size (mean roc), flora coverage (flora co) (*arrows*) and habitat (depth zo) (*triangular*) represented by nominal value. The percentage of variability explained by the axes is given. Abbreviations regard following taxa: At *Aetea truncata*, Can *Cribrilina annulata*, Pt *Spirobranchus triqueter*, Cpun *Cribrilina punctata*, Eimm *Escharella immersa*, Srep *Scrupocellaria reptans*, Cs *Circeis spirillum*, Ss *Spirorbis spirorbis*, Vs *Verruca stroemia*, Ccry *Cribrilina cryptooecium*, Mm *Modiolus modiolus*, St *Spirorbis tridentatus*, Clin *Callopora lineata*, Epil *Electra pilosa*, M *Mytilus*, Bi *Amphibalanus improvisus*, Ecrus *Einhornia crustulenta*, Cpal *Cryptosula pallasiana*, Sb *Semibalanus balanoides*, Chya *Celleporella hyalina*, Jp *Janua pagenstecheri*, Lc *Laeospira corallinae*, Ds Hydrozoa

that barnacles are better adapted to survive harsh winter ice scour than other species (Heaven & Scrosati, 2008). The lack of adult individuals of *Mytilus* species indicates that some factors (e.g. wave action, salinity and predation) of this zone may prevent this species from reaching maturity. Where the salinity is higher, opportunistic species, especially *Mytilus* juv. are replaced by stenohaline marine species, particularly bryozoans and serpulids (Table 1). As a result of appearance of marine species, including common intertidal taxa (e.g. *L. corallinae, S. balanoides*), we observed increased species diversity in the Baltic Sea–North Sea transition zone (the Sound—location B10) and marine locations, Kattegat and Skagerrak (locations B11–B14), both in the hydrolittoral and littoral encrusting assemblages. In general, there was a lower species richness and abundance in the hydrolittoral assemblages compared with the adjacent littoral zone (Fig. 3), and although there were a few exceptions, these assemblages shared a common species pool, with none of the abundant species were specific to the hydrolittoral zone. Despite sharing species composition similarities, these communities differed in their dominant species; the higher occurrence of *A. improvisus* and *Mytilus* juv. were attributed to hydrolittoral assemblages (except for the marine locations B12–B14), while littoral assemblages were dominated by bryozoans and polychaetes (Table 1). Although the hydrolittoral zone of the Baltic Sea has distinct encrusting faunal assemblages, especially towards more saline water locations, they do not seem to be fully independent and it is possible that they have originated from the adjacent littoral zone.

The species richness and diversity variability across the land–sea gradient has been the subject of a number of studies in tidal basins where the effects of water level elevation on sessile species diversity were compared (e.g. Scrosati et al., 2011). These studies concluded that the structure of sessile assemblages varied in relation to elevation and exposure. In this study, the lower abundance observed in the Baltic Sea hydrolittoral assemblages, and the lower species richness compared to nearby littoral assemblages, appears to be caused by disturbances related to coastal dynamics and the less favourable conditions for community development (Herkül et al., 2006; Balata & Luigi, 2008; Kuklinski & Barnes, 2008; Kuklinski, 2009; Wiklund et al., 2012). Although the Baltic Sea is not tidal, Wiklund et al. (2012) suggested that wave impacts on spring hydrolittoral communities in the Baltic Sea are comparable to those observed in the oceanic areas. Seasonal variability in wave activity, enhanced by increased hydrodynamic forcing during the winter and early spring in the coastal area (Wiklund et al., 2012), leads to a reduction in marine populations by impeding the full development of benthic communities and may be a reason for the distinctive nature of the hydrolittoral communities. A northward gradient of decreasing salinity and changes in climate conditions (e.g. decreasing temperature) may explain the rapid decline in abundance and percentage cover of fauna in the hydrolittoral compared with analogous littoral assemblages elsewhere. Long and extensive ice presence, which, for the northern Baltic Sea, can exceed 150 days annually,

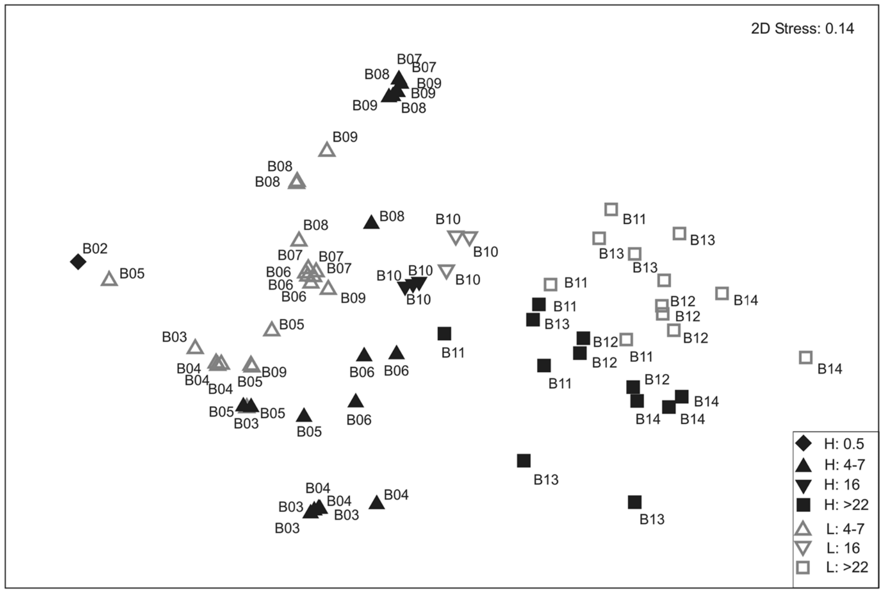


Fig. 5 Comparison (non-metric multidimensional scaling) of the encrusting assemblages in different salinities: 0.5, 4–7, 16 and > 22 at the hydrolittoral (H) and littoral (L). Ordination derived from Bray–Curtis measures based on square-root transformed abundance data for each subsample per sampling location. Location labels are in accordance with Fig. 1

causes severe ice scouring on rocky habitats, especially in the shallowest areas (Scrosati & Heaven, 2007). For hydrolittoral rock encrusting assemblages, this result in seasonal scouring, preventing the formation of multi-year communities and resulting in assemblages composed of young, small organisms. The lack of adult individuals of bivalve *Mytilus* sp. in the hydrolittoral is likely to be caused by such frequent disturbance (Sousa, 1979), explaining low abundance and low percentage coverage by fauna. Additionally, the irregular nature of water level changes also contributes to the scarcity of fauna.

Local heterogeneity can be a result of many factors such as biological adaptations of particular encrusting species (such as the small, hard shell barnacle *A. improvisus* or bryozoan *E. crustulenta*), discontinuous availability of substrate or dynamic coastal conditions. The significant differences between assemblages from hydrolittoral and littoral sites of similar salinity could be due to the contribution of the general sediment characteristics at sampling sites and the way rocks are oriented on the sediment. The properties of the substrate and surrounding sediment can influence flora and fauna occurrence at the hard bottom (Bučas et al., 2007). Comparison of relative frequencies of occurrence of encrusting species in hydrolittoral and littoral samples in relation to the rock size indicated that this was lowest for small rocks in the shallow hydrolittoral. At the same time, it was noticeable that similar-sized rocks in the littoral zone were more frequently overgrown. Multivariate analysis presenting faunal groups according to rock size also illustrated differentiation between assemblages from the two coastal marine habitats and a distinction between hydrolittoral and littoral zones in the western part of the Baltic Sea (Fig. 7). As indicated in a previous study, rock size and its susceptibility to agitation affect epibenthic community development by regulating their abundance and taxonomic diversity (Kuklinski et al., 2005). Small rocks are known to be more sensitive to overturning and scouring as a result of physical disturbance than larger substrates (Gedan et al., 2011), and therefore, a low frequency of species occurrence on this substrate is understandable (this tendency was recorded in our observations). Similar to the previous studies, we observed that a lower percentage of faunal coverage of rock surfaces was recorded within smaller boulders as a result of limitations of space for colonization and higher rate of mortality caused by disturbances, especially when they were surrounded by mobile sediment (Sousa, 1979; Bučas et al., 2007). Similarly to our results (Fig. 6), Grzelak & Kuklinski (2010) found a higher probability of the presence of organisms on large and medium rocks than on small rocks, confirming that in the Baltic Sea coastal habitat larger rocks are more stable and likely to provide a better substrate for community development (Liversage & Kotta, 2015). In higher salinity, where

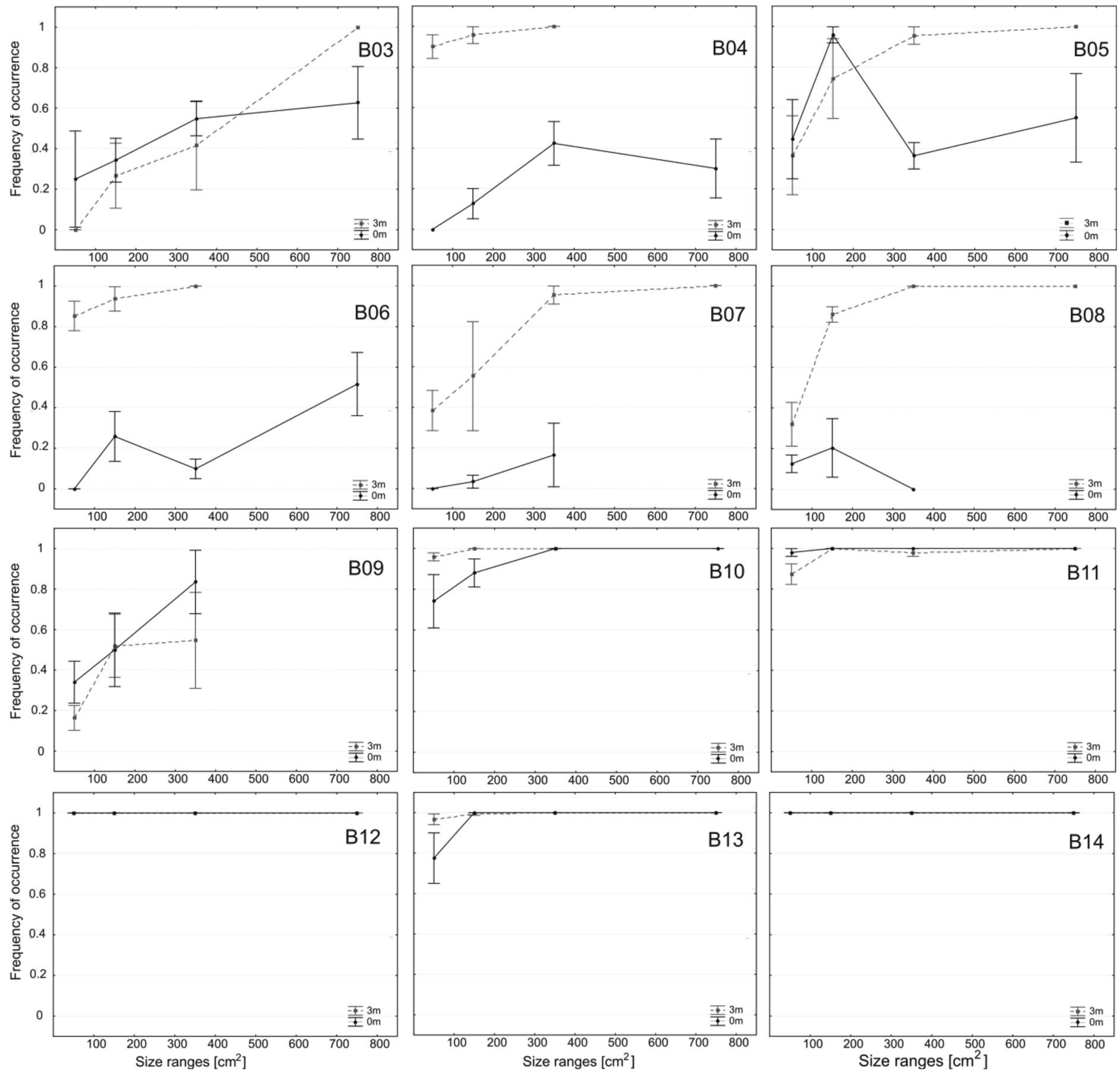


Fig. 6 Frequency (mean values ± standard error) of encrusting fauna occurrence by given rock size classes in the hydrolittoral (marked as 0 m) and littoral (3 m). Location labels are in accordance with Fig. 1

diversity increases, the effect of rock size could be less important as a factor in determining the frequency of occurrence of encrusting species. Higher diversity and the presence of marine intertidal specialists lead to an increased probability of occurrence of encrusting species, even in the dynamic hydrolittoral zone.

In summary, the results of this study indicate that local variability due to periodic or stochastic disturbances can be significant in shaping faunal communities encrusting rock surfaces in the hydrolittoral zone. As salinity increases along the Baltic coast, an increased heterogeneity of assemblages is evident in terms of species richness, abundance and diversity. Multivariate analysis allowed us to distinguish the patterns found in the hydrolittoral zone from those observed in shallow littoral assemblages. The low salinity level observed in the major part of the Baltic Sea system hinders the formation of the types of marine assemblages observed in the higher salinity North Sea region. The structures of hydrolittoral

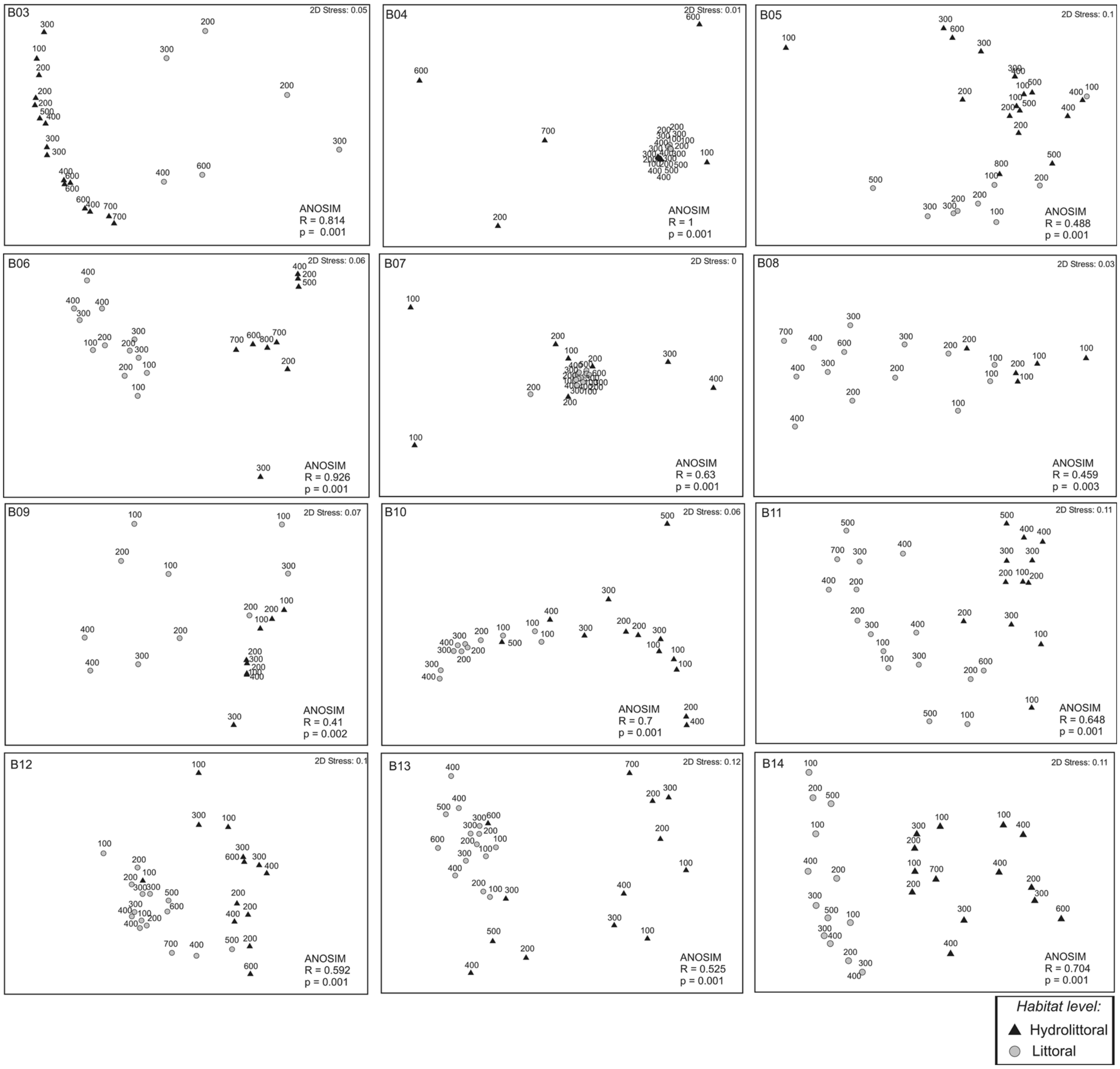


Fig. 7 Multidimensional scaling ordinations showing grouping of encrusting assemblages according to rock size classes (100, 200, 300, 400, 500, 600, 700 and 800 cm^2) and habitat level (hydrolittoral and littoral) for the three subsamples within study location. Locations are labelled in accordance with Fig. 1. Results of ANOSIM test comparing the two habitats are presented for each location

encrusting assemblages within the Baltic Sea differ in terms of their dominant species but seem to be derived from a common species pool with the nearby littoral communities.

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