

Benthic assemblages associated with rocks in a brackish environment of the southern Baltic Sea

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*Sandy bottoms, with local patches of rocks, dominate the southern Baltic Sea coast. These rock patches create three-dimensional habitats with additional niches that can support diverse assemblages of organisms. In this study we investigated macrofaunal assemblages associated with the boulder field in the brackish Gulf of Gdansk. Of the 30 recorded taxa three animal species (*Mytilus trossulus*, *Balanus improvisus* and *Electra crustulenta*) together with five species of algae were directly attached to rocks. These engineering organisms provided habitats for a further 22 taxa. Among the fauna directly associated with rocks, barnacles (76%) were the most abundant while among indirectly associated biota, oligochaetes were the dominant group (45%). Rock size and algal biomass explained most variance in macrofaunal structure of the assemblages investigated. There were statistical differences in assemblage structure between two separate localities within the rocky patch, despite environmental homogeneity (salinity, water temperature and structure of sea bottom). These differences in assemblage structure were mostly due to differences in dominance of particular species rather than in species composition. Our results show that rocky patches in an otherwise soft sediment habitat provide additional living space for macrofauna leading to an increase in local biodiversity and organismal abundance.*

Keywords: rocky habitat, associated fauna, biodiversity, macrofauna, Baltic Sea

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INTRODUCTION

One of the main goals of ecology has been to understand patterns in the composition and structure of the benthic assemblages. Recognizing the broad-scale processes and web of interactions among organisms, which operate in heterogeneous habitats, must include an understanding of functioning at smaller spatial scales (Underwood & Chapman, 1998). In many cases, spatial patterns are considered in terms of patches, which are areas of a definite size with species composition differing from that in neighbouring ones (e.g. Wu & Levin, 1994; Yakovis *et al.*, 2005).

Biodiversity and faunal abundance are directly related to the complexity of marine and brackish habitats (e.g. Jones *et al.*, 1994; Attrill *et al.*, 1996; Yakovis *et al.*, 2004, 2008). For example Attrill *et al.* (1996, 1999) recorded the number of supralittoral species in the brackish environment of the Thames Estuary to be positively correlated with habitat complexity. Sandy–muddy sediments with a larger number of plant species, particles such as stones, shells, decayed wood and clay provided additional niches leading to much higher biodiversity than in locations lacking these complex features (Attrill *et al.*, 1996, 1999). In the areas with relatively low diversity (e.g. estuaries and brackish seas) the heterogeneity of the substrate seems to be of prime importance for the sustainability of local ecosystems (Attrill *et al.*, 1996, 1999).

Therefore, documenting ecological patterns of such diversity hot spots is of special need in the light of proper ecosystem management and protection (Attrill *et al.*, 1996, 1999).

Boulder fields assemblages have been the focus of many studies (e.g. Chapman & Underwood, 1996; Chapman, 2002a,b; Cruz Motta *et al.*, 2003; Le Hir & Hily, 2005). With their spatial and temporal variations they constitute heterogeneous habitats conducive to high biodiversity (Chapman, 2002a). Smaller rocks are usually at constant state of recolonization following disturbance caused by overturning. Larger rocks being heavier are harder to overturn and thus offer much more stable substrate and usually support a more abundant biota (Osman, 1977; Wilson, 1987). Together with their sessile inhabitants, boulders can create complex three-dimensional structures and provide additional niches for other organisms. The biotic part of such structures is often composed of animals ('ecosystem engineers') like corals, mussels or algae (e.g. Seed & O'Connor, 1981; Seed, 1996; Kuklinski & Bader, 2007; Yakovis *et al.*, 2008). Such species influence the diversity and abundance of organisms living in these three-dimensional structures and while they may not be involved in direct trophic interactions they can modulate the availability of resources to other species by creating physical complexity (Jones *et al.*, 1994). Even when such three-dimensional structures are separated by only a few metres, they can harbour rather different faunal assemblages due to differences in their complexity (Yakovis *et al.*, 2008).

In this study we investigated rocks and their associated biota in the brackish environment of the Baltic Sea (Gulf of Gdansk). A sandy bottom dominates the coastal zone of the

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Gulf of Gdansk, however, in places large patches of stones and boulders exist. Several studies have indicated that these patch areas support relatively diverse assemblages of organisms (Haque *et al.*, 1997; Osowiecki, 2000; Osowiecki & Żmudziński, 2000; Kruk-Dowgiallo & Szaniawska, 2008; personal observations). HELCOM (1994) Helcom recommendation 15/5: System of coastal and marine Baltic Sea Protected Areas (BSPA) recommended that one of these sites (near Gdynia-Redlowo) should be included in the Baltic Sea Protected Areas. However, it is recognized that rocky areas on sediment enhance diversity and increase its conservation importance (e.g. Attrill *et al.*, 1996); quantitative ecological studies of biota associated with rocks from the area are lacking. The main goal of the present investigation is to fill this gap in our knowledge concerning the rocky habitats of the Gulf of Gdansk where, given its low diversity, such habitats can be considered as local diversity hot spots. In addition to the faunistic aspect of this study, we also investigate some of the factors that influence rock-associated fauna.

MATERIALS AND METHODS

Sampling and laboratory analyses

The Gulf of Gdansk is located in the southern part of the Baltic Sea (Figure 1). It covers an area of 4940 km², with a mean depth of 59 m (Majewski, 1990). Its water is brackish, with an average salinity of 5–8 psu. Furthermore, the fresh

waters of the Vistula River influence coastal waters of the Gulf. Surface temperature varies between 0°C in winter to more than 22°C in summer (Kruk-Dowgiallo & Szaniawska, 2008). The bottom of the Gulf is made up of soft sediments, largely coarse and medium sand with occasional silt deposits. Rocky patches of postglacial origin (pebbles and boulders) occur at several locations, usually near the shore (Majewski, 1990; Osowiecki & Żmudziński, 2000). However, in the majority of cases, such patches are small and very shallow. The boulder field selected for this study is the largest in the bay and is located in the vicinity of Gdynia (Figure 1). It is approximately 3 km long and 0.2 km wide. Within it, boulder patches are separated by bare sand and/or seagrass. Environmental variables, e.g. salinity, water temperature and anthropogenic influences are constant across the study area (Nowacki & Jarosz, 1998).

The study was conducted in spring 2007 in a shallow, coastal zone of the Gulf of Gdansk at a depth of ~3 m. Samples of rocks of various sizes (31 rocks from Station A and 40 rocks from Station B) were collected haphazardly from two randomly chosen locations by SCUBA diving (Figures 1 & 2). Each rock was placed in a separate zip-bag *in situ* by a diver in order to retain all the associated biota. After removing algae (and their associated fauna), each rock was dried and all encrusting fauna were determined to species level and counted. Stone surface area (as a proxy for size) and the percentage coverage of encrusting fauna were estimated using an inflexible net marked in a grid of square centimetres. Fauna indirectly associated with rocks were

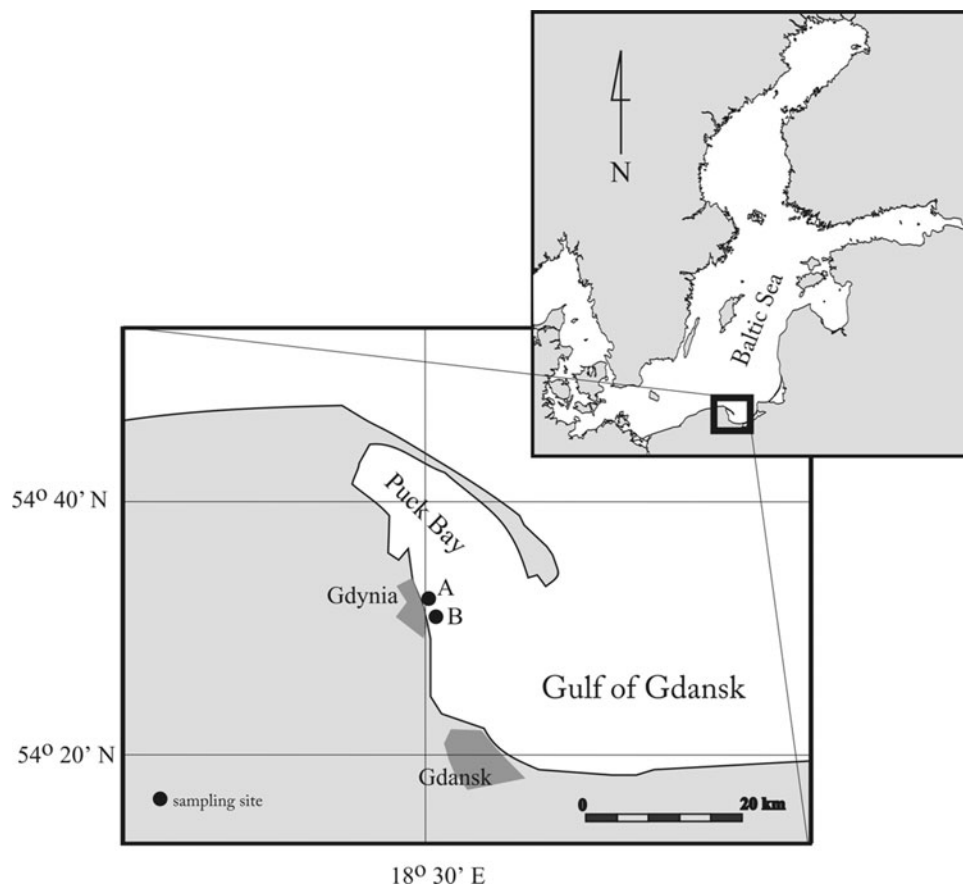


Fig. 1. Study area with sampling locations.

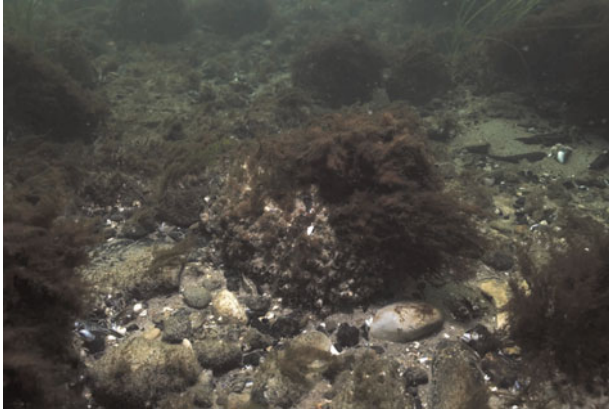


Fig. 2. Rocks *in situ* with their associated biota at study locality.

separated from algae and all macroorganisms (larger than 500 μm) were determined to the lowest taxonomic level, in most cases to species. All individuals were counted and their abundance expressed as individuals per 1 m^2 of rock surface. In the case of the present study each colony of a bryozoan species was considered as one individual.

We explored the influence of substrate stability and heterogeneity on species composition and abundance in rock-associated biota. We used the surface area of the rocks as a proxy for substrate stability. The size of the rock has previously been shown to be directly related to its stability (Osman, 1977). The presence of any three-dimensional structure on a rock increases its complexity by adding extra niches (e.g. Attrill *et al.*, 1996). Because the smoothness of the substrate was negligible, we used the number and dry mass of large engineering species (algae, bivalves and barnacle soft tissue with a shell) present on a given rock as a proxy for substrate heterogeneity. The dry mass of the samples was measured after 24 hours of drying at 60°C to constant weight.

Data analyses

In order to analyse whether samples were saturated with respect to the faunal species pool, species accumulation curves were plotted for both sites. Species accumulation curves describe the number of observed species (S_{obs}) as a function of the number of samples. The non-parametric estimator Chao2 (Chao, 1987) was additionally selected to calculate the theoretical species richness from presence/absence in all the available samples. Richness estimators predict richness, including species not discovered in the sample, from the proportional abundances of species within the total sample (Soberón & Lorente, 1993). The Chao2 estimator provides the least biased estimates of species richness for small numbers of samples and moderate species richness, as is the case for this study. S_{obs} and Chao2 were calculated using the PRIMER package (Clarke & Gorley, 2001).

A series of multivariate techniques were used for statistical analyses of the faunal communities. All analyses were conducted on un-transformed, square- and four-root transformed data, in order to detect the effects of the dominant and rarer species.

To explore the influence of variables, regarded as proxies of substrate heterogeneity and stability (rock size, number of engineering species, percentage coverage, etc.) on faunal

assemblages, a correlation-based principal component analysis (PCA) was used. Prior to the PCA a draftsman plot was produced to detect correlation between variables. Data for PCA analysis were fourth-root transformed and normalized.

To assess simultaneous response in the indirectly rock-associated faunal assemblages between sites and within sites of proxy variables (rock size, algal biomass and abundance of sessile fauna), permutational multivariate analysis of variance (PERMANOVA: Anderson, 2005) was used. PERMANOVA calculates P value using permutations, rather than relying on tabled P value (as traditional ANOVA), which assumes normality. The assumption of normality is difficult to achieve and cannot be properly tested according to ecological data. Analyses were conducted on four-root transformed data, to reduce the influence of highly abundant taxa, using Bray–Curtis dissimilarities. Data for rock-size were divided into three groups: small rocks—all of which were smaller than 100 cm^2 (later indicated in the text as 100), medium rocks—between 100 and 200 cm^2 (indicated as 200); and large—bigger than 200 cm^2 (indicated as >200). A similar division was conducted for algal biomass (algal biomass <0.5 g, between 0.5–1 g, and >1 g) and sessile fauna abundance (density <5, 5–50 and >50). PERMANOVA analysis requires an equal number of observations per treatment. In our case 10 rocks were randomly included in each group. Finally, a second draftsman plot was performed (Pearson correlation coefficients: Clarke & Warwick, 1994) to identify further correlations between mobile species densities, the number of recorded species and proxy variables. Using PRIMER software non-metric multidimensional scaling (nMDS) was performed on the similarity matrices of quantitative data to illustrate patterns in the spatial distribution of the samples in terms of faunal assemblages (associated fauna, sessile fauna and all faunal data) and analysis of similarities (ANOSIM) was performed to test for differences between sites according to different factors (e.g. abundance of structural species and abundance of associated species).

RESULTS

A total of 26,609 faunal organisms from 25 animal taxa were found on 71 rocks totalling 12,450 cm^2 surface area (Station A: 6422 cm^2 and Station B: 6028 cm^2).

The shapes of the species accumulation curves were very similar for both sites (Figure 3A). For site A the curve levelled before all the samples were included, while for site B the accumulation plot was levelling at the end of its curve. The total number of species observed was 23 for Station A and 24 for Station B. The Chao2 estimate of total richness gave mean 24 ($\text{SD} \pm 0.68$) species for Station A and 26 ($\text{SD} \pm 0.97$) species for Station B (Figure 3B). For Station A the points tended to form a curve of asymptotic shape even if a small number of samples were considered. For Station B the shape of the curve was slightly more variable.

Among the fauna there were three species that directly encrusted stones and 23 species indirectly associated with rocks (associated with algae growing on the rocks (Table 1). One individual of *Caprella mutica* Schurin was recorded for the first time in the Bay of Gdansk. The number of species per stone varied from 5 to 17, while their abundance varied from 19 to 926 individuals.

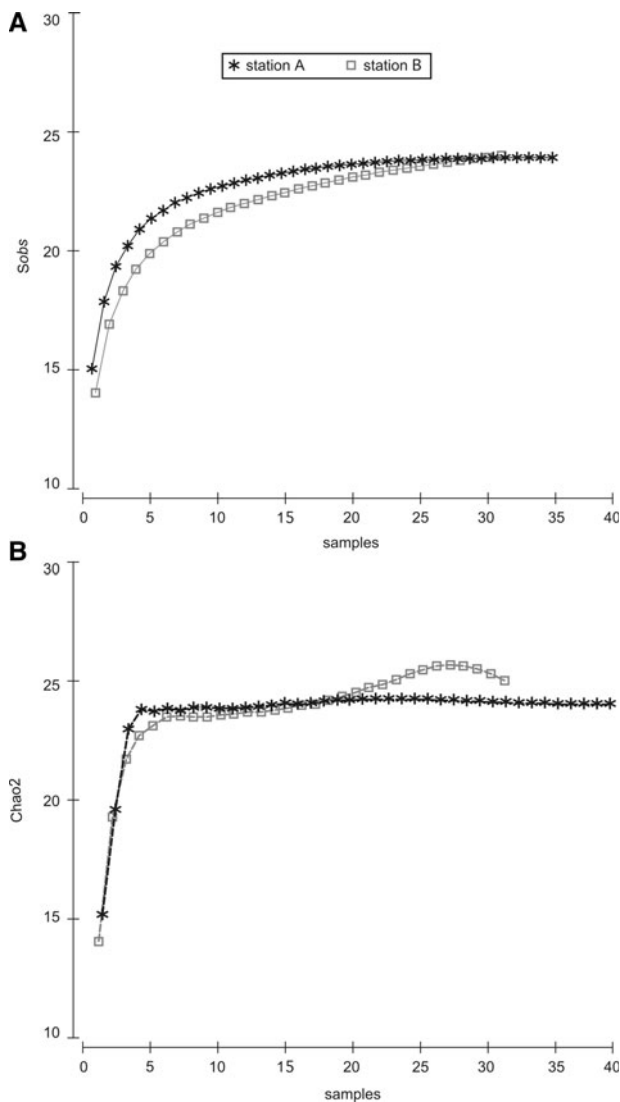


Fig. 3. Species accumulation curves for both investigated locations. Species richness estimated by the total number of all species (S_{obs}) (A) and Chao2 estimators (B).

Three sessile animal species (*Balanus improvisus*, *Mytilus trossulus* and *Electra crustulenta*) were directly attached to the rocks and were present at both locations and on almost all rock size-classes, except for rocks below 100 cm² in surface at site A, where *M. trossulus* was absent (Table 1). The community structure of these sessile species was homogeneous and no differences between sites were recorded (ANOSIM test: $R = 0.056$, $P = 0.32$; Figure 4C). *Balanus improvisus* dominated at each site, both numerically (Station A: 74% and Station B: 77%) and in terms of weight (Station A: 89% and Station B: 65%).

Five species of algae (*Cladophora* sp., *Pilayella littoralis* Linnaeus, *Polysiphonia nigrescens* Hudson, *Ectocarpus confervoides* (Roth) and *Ulva* sp.) were recorded on rocks at both sites. The mean total biomass of algae was not equal between locations. At Station A dry biomass reached 65.1 g·m⁻² (SD ± 58.8) and at Station B 52.0 g·m⁻² (SD ± 30.3). Based on the total data set for animals indirectly associated with rocks, oligochaetes were the most abundant group (45%) followed by crustaceans (27%) and polychaetes

(26%). The most common species was the oligochaete *Nais elinguis* (32% at Station A and 22% at Station B), which was followed by the crustacean *Heterotanais oerstedti* (19%) and second species of oligochaete *Paranais littoralis* (12%) at Station A, and the polychaetes *Pygospio elegans* juv. (21%) and *P. littoralis* (13%) at Station B. The crustacean *Idotea cheilipes* was recorded only at site B, while a clavid hydrozoan was found only at Station A. The mean total abundance of associated fauna was higher at Station A (28085 ind·m⁻²; SD ± 13651) compared to Station B (11916 ind·m⁻²; SD ± 5991). There was a clear difference in the composition of the associated fauna between stations (ANOSIM test: $R = 0.512$, $P = 0.001$; Figure 4B).

In general, the abundance of species indirectly associated with rocks increased with the size of the rock and the algal biomass ($r = 0.64$, $P < 0.001$ and $r = 0.78$, $P < 0.001$ respectively; see also Figure 5). Not all variables for engineering species were correlated with faunal abundance and species number (e.g. *M. trossulus* abundance versus abundance of associated organisms $r = 0.26$, $P > 0.05$; *M. trossulus* mass versus number of associated species $r = 0.36$, $P > 0.05$). Only the number of *B. improvisus* individuals had significantly positive correlation with faunal abundance and species number ($r = 0.78$, $P < 0.001$; $r = 0.82$, $P < 0.001$ respectively).

The total variability explained by PCA was 73.3%. 58.4% variations were explained by the first principal component (PC1), with PC2 explaining 14.9%. The analysis indicated algal biomass, rock size and *B. improvisus* abundance as the primary PC1 variables explaining the variation in data. The remaining variables included in the analysis (percentage coverage, *E. crustulenta* and *M. trossulus* abundance) had minor influence on the observed data variation.

Significant differences in the indirectly rock-associated faunal assemblages between sites and within the site were found. Of the variables which were regarded as proxies for substrate stability and heterogeneity, algal biomass had significant effect on the assemblages within investigated stations (PERMANOVA: $F = 4.91$, $P = 0.015$) and between the sites ($F = 23.86$, $P < 0.0001$). These differences are apparent in the nMDS, however, the three algal biomass classes show some degree of overlap (Figure 6A). Consistent with the PERMANOVA results, rock size and *B. improvisus* abundance were also significant for faunal communities ($F = 5.82$, $P = 0.031$; $F = 3.80$, $P = 0.023$ respectively). Nonetheless, the differences between rock size-classes were smaller for Station B compared with Station A (Figure 6B). For Station A changes with increasing rock size can be seen, even if a PERMANOVA *post-hoc* pairwise test was not significant ($P > 0.05$) for all rock classes. A similar pattern is observed for number of *B. improvisus* individuals (Figure 6C).

DISCUSSION

Local biodiversity

Natural, undisturbed stony seafloors are colonized by an abundance of plants and animals (mostly invertebrates), so they might be regarded as 'living rock'. Furthermore, the spatially complex structures developed by primary structural species provide food and shelter for a rich diversity of dependent species (Wenner *et al.*, 1984) to the extent that even small

Table 1. Mean density values of species abundance (ind·m⁻²) and standard deviation (*italic*) for each rock size-class at investigated stations (B, Bivalvia; Br, Bryozoa; C, Crustacea; G, Gastropoda; H, Hydrozoa; I, Insecta; O, Oligochaeta, P, Polychaeta).

Station	Station A				Station B			
	100	200	>200	All	100	200	>200	ALL
Rock encrusting fauna								
<i>Balanus improvisus</i> (C) Darwin	1409	6403.7	5502.7	3864.5	3916.7	1698.3	3265	2530.8
	± 1453.2	± 3762.3	± 2625.2	± 3105.3	± 5894.3	± 2369.5	± 2203.5	± 3444.6
<i>Electra crustulenta</i> (Br) Pallas	759.3	1302.5	1816.5	1289.4	570.5	786.3	778.2	639.6
	± 553.9	± 1064.5	± 874.8	± 1247.6	± 974.6	± 747.4	± 743.2	± 780.8
<i>Mytilus trossulus</i> (B) Linnaeus		48.1	94.2	56.2	173.7	59.3	70.6	100.4
		± 59.6	± 58.0	± 94.3	± 336.3	± 133.1	± 72.2	± 176.0
Rock indirectly (via algae) associated fauna								
<i>Caprella mutica</i> (C) Schurin						6.4		1.4
						± 16.9		± 8.0
Chironomidea (I) indet.	653.8	705.4	650.1	623.5	103	93.4	82.6	100
	± 655.6	± 777.3	± 643.4	± 542.5	± 113.9	± 117.7	± 87.8	± 125.0
Clavidae (H) indet.	80.8	8.9		17.9				
	± 169.9	± 23.6		± 74.7				
<i>Corophium</i> sp. juv. (C)	264	44.6	46.4	64.6		30.6		7.8
	± 698.4	± 88.6	± 58.2	± 293.2		± 81.0		± 38.6
<i>Corophium lacustre</i> (C) (Vanhoffen)	110.1	79.3	68.3	67.6	397.5	260.7	267.6	291.7
	± 209.0	± 132.8	± 62.2	± 115.3	± 519.1	± 235.8	± 172.8	± 308.5
<i>Corophium multisetosum</i> (C) Stock	109.6	109.9	66.1	92.5	23.8	28.7	17.1	17
	± 124.3	± 85.0	± 85.9	± 120.6	± 63.0	± 54.8	± 33.8	± 41.7
<i>Cyatura carinata</i> (C) (Krøyer)	31.8	60.1	122.5	65	39.3	9.4	85.2	35.8
	± 54.3	± 65.1	± 111.5	± 111.9	± 69.2	± 24.9	± 176.0	± 91.5
<i>Fabricia sabella</i> (P) (Ehrenberg)	2678.2	2528.1	2140.8	2473.3	479.3	752.4	1024.4	708.7
	± 2276.6	± 1263.6	± 444.8	± 1529.7	± 165.6	± 644.8	± 789.0	± 530.5
<i>Gammarus</i> sp. juv. (C)	784.7	586.3	489.4	630.1	1016.8	1098	399.7	864.1
	± 1344.4	± 394.8	± 424.8	± 708.3	± 1286.8	± 1268.1	± 404.5	± 929.2
<i>Gammarus salinus</i> (C) Spooner	206.7	117.8	65.3	157.6	202	284.5	111.6	194.7
	± 271.9	± 175.5	± 40.6	± 221.8	± 200.0	± 518.3	± 112.6	± 286.7
<i>Gammarus zaddachi</i> (C) Sexton			20.8	14.6	31.1	37	4.4	27.1
			± 39.5	± 39.6	± 82.2	± 63.7	± 11.5	± 58.9
<i>Heterochaeta costata</i> (O) Claparède	692.8	345.5	303.6	572.5	1129.3	449.1	503.5	812.5
	± 548.4	± 380.1	± 200.6	± 714.8	± 707.3	± 407.8	± 259.9	± 867.5
<i>Heterotanaïs oerstedti</i> (C) (Krøyer)	3693.4	6973.1	6220.7	5379.2	1702.2	1569.9	1565	1455.6
	± 2995.7	± 3764.5	± 3238.0	± 3819.6	± 2238.2	± 1308.7	± 1507.7	± 1480.6
<i>Hydrobia</i> sp. (G) Hartmann			5.6	8.3		12.3		2.8
			± 14.8	± 35.7		± 32.6		± 15.5
<i>Idotea chelipes</i> (C) (Pallas)					15.5	24.7	4.3	14.8
					± 41.1	± 45.6	± 11.4	± 32.4
Insecta larvae (I)			6.2	5.9			6.4	1.4
			± 16.3	± 31.0			± 16.9	± 8.0
<i>Leptocheirus pilosus</i> (C) Zaddach	988.5	891.5	1014.3	890.9	546.2	317.6	376	356.9
	± 751.3	± 619.3	± 498.5	± 762.6	± 628.6	± 425.7	± 312.3	± 414.2
<i>Lumbricillus lineatus</i> (O) Müller	34.9	96.9	56.3	75	367.8	147.8	277.4	328.2
	± 59.6	± 173.5	± 96.7	± 180.3	± 257.5	± 105.5	± 151.8	± 422.2
<i>Mytilus trossulus</i> (B) Linnaeus		59.6	17.7	35.4	23.8	38.9	46.5	31.3
		± 47.5	± 31.1	± 73.6	± 63.0	± 80.3	± 70.4	± 59.0
<i>Nais elinguis</i> (O) Müller	9871.1	8969.4	6211.2	9003.3	4356.8	2243.3	2039.9	2584.5
	± 5865.1	± 3087.3	± 4710.9	± 4966.5	± 2382.4	± 1072.8	± 888.9	± 1777.2
<i>Nereis diversicolor</i> (P) (Müller)	2284.9	2303.8	1330.7	1818.2	21.6			6.2
	± 4707.5	± 3143.3	± 1411.8	± 2751.5	± 57.3			± 28.0
<i>Paranais litoralis</i> (O) (Müller)	3651.7	4181.8	2624	3363.2	2218.9	1360.7	1379.7	1517.1
	± 2829.9	± 2318.6	± 1699.5	± 2547.5	± 1443.1	± 812.2	± 845.1	± 1102.4
<i>Pygospio elegans</i> juv. (P) (Claparède)	3770.9	2384.3	2077.9	2726.8	5414	2349	1183.9	2555.4
	± 2962.1	± 1823.8	± 2252.8	± 2557.1	± 4485.3	± 2785.4	± 981.5	± 3025.5

or isolated rocky areas surrounded by soft sediment can be considered as oases of biodiversity and productivity at any latitudes.

For the Polish Baltic coastal zone, a lack of baseline information on the biological functioning of nearshore hard

bottom dictates a need for research and monitoring. To our knowledge this study, is the first quantitative investigation of a stony habitat in the Gulf of Gdansk. The only other study that has focused on faunal assemblages on hard bottoms was performed by Andruliewicz *et al.* (2004) at the

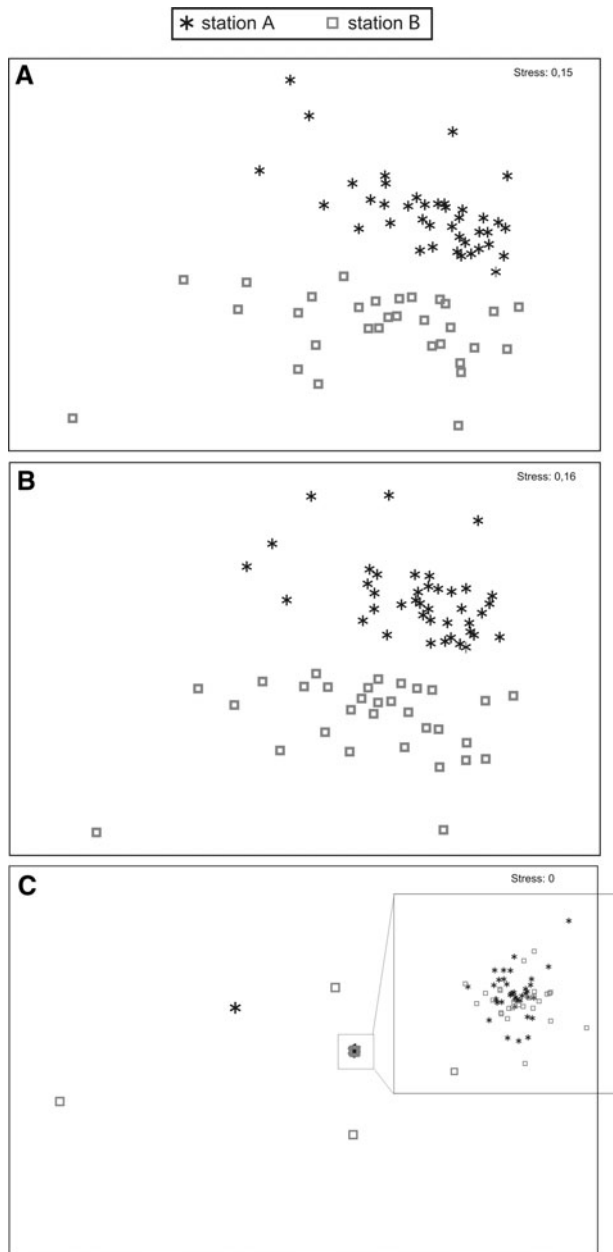


Fig. 4. Non-parametric multidimensional scaling plots based on abundance and composition of all faunal data (A), only fauna indirectly associated with rocks (B) and fauna directly associated with rocks (C).

stony reef (8.5 to 18 m depth) of the Slupsk Bank (open Baltic water). In addition Kotwicki (1996) investigated the fauna associated with algae growing on a shallow sandy bottom, in the inner basin of Puck Bay, part of the Gdansk basin; data from these sources are summarized in Table 2. Andrulowicz *et al.* (2004) recorded 27 faunal taxa, including Turbellaria and Nematoda, which are usually considered to be meiofauna (Table 2) as well as common representatives of cooler and deeper waters such as the isopod *Saduria entomon* and the polychaete *Harmothoe sarsi* (Hagerman & Szaniawska, 1990; Janas *et al.*, 2004). In total, there is only a 48% overlap in species composition between our study and that of Andrulowicz *et al.* (2004) (see Table 2). Kotwicki (1996), who investigated shallower, inshore waters, observed 29 taxa (Table 2). There were several organisms found by Kotwicki

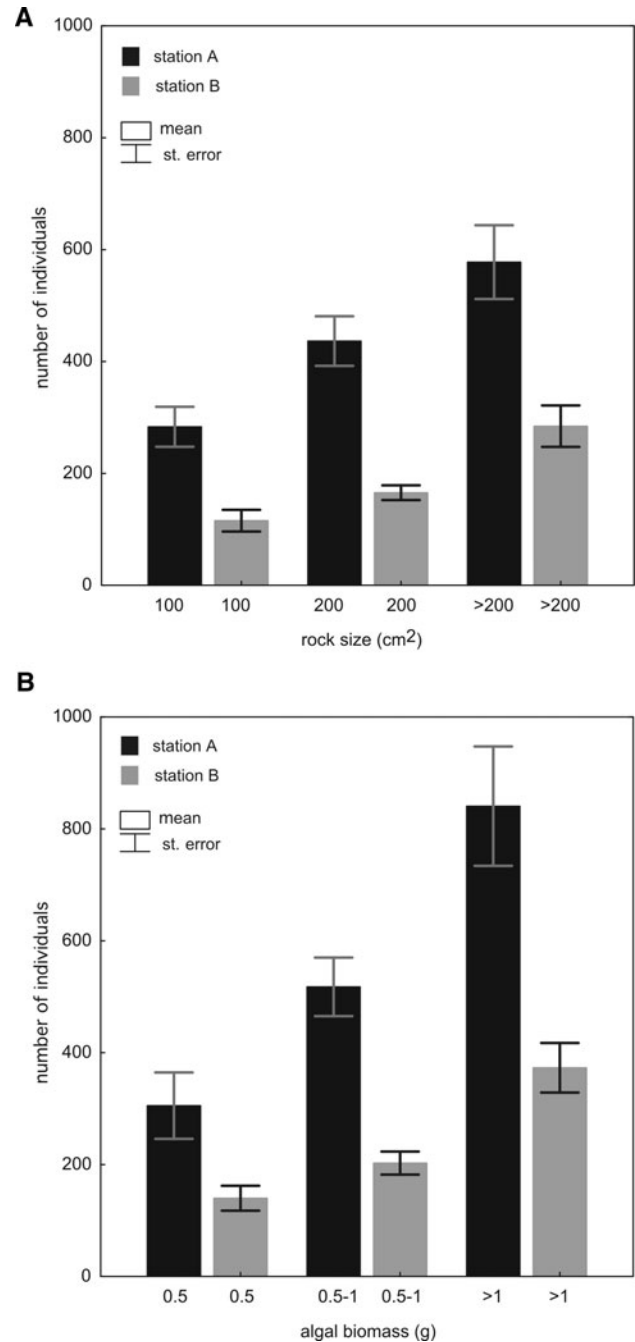


Fig. 5. Mean abundance of indirectly associated fauna at different size rock classes (A) and algal biomass classes (B).

(1996) but not encountered in our study (see Table 2), e.g. the crustacean *Idotea baltica* or the gastropod *Theodoxus fluviatilis*. The most probable factors causing dissimilarities in our results are differences in habitat and sampling methodology. In addition, temporal fluctuations of faunal recruitment may also play an important role, even though sampling was performed in the same season of the year.

Our results, as well as a number of published studies, indicate that rocky habitats increase local biodiversity by attracting different sets of species to those found in nearby soft bottoms (e.g. Yakovis *et al.*, 2004, 2008 and references therein). By introducing extra living space to the area, rocks promote both the abundance and biomass of local macrofauna

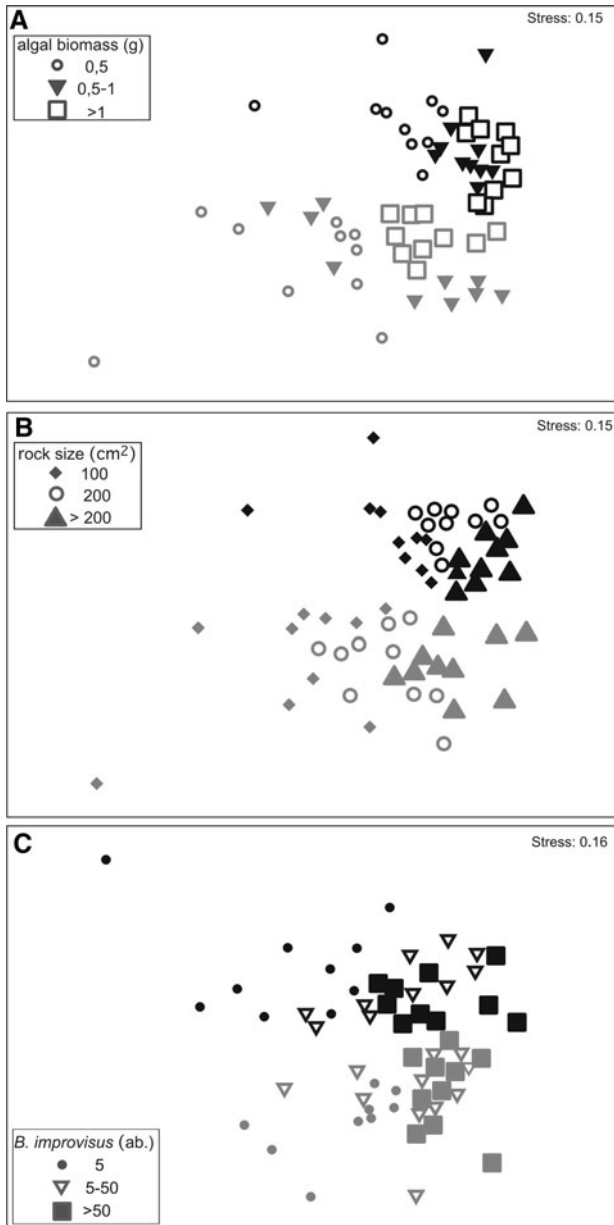


Fig. 6. Non-parametric multidimensional scaling plots showing the effect of the biomass of algae (A), size of the rocks (B), and abundance of barnacles (C) on the faunal assemblages at Station A (black symbols) and at Station B (grey symbols). The stress value indicates that the two-dimensional plots give an adequate representation of the data.

communities. Although the number of species in our study (25) corresponds well with the number of macrofaunal species recorded for adjacent soft bottoms, there was very little overlap in species composition between these two habitats (e.g. Jażdżewski & Konopacka, 1995; Żmudziński, 1996; Kotwicki, 1997).

The abundance of rock-associated macrofauna is above the range reported for the Gulf of Gdansk sandy habitats. The total mean density revealed by this study varied between 10,000 and 23,500 ind·m⁻² of rocks surface area (Table 1), while for earlier studies of sandy habitats it ranged from 0 to 14,000–15,000 ind·m⁻² of sea bottom surface (Haque *et al.*, 1997; Osowiecki & Żmudziński, 2000). A comparison of these data indicates that rocks, and the engineering

species colonizing them, provide much more living space per unit surface area than does a sediment habitat; their fractal dimensions (Gee & Warwick, 1994) are considerably greater. Boulders often offer sheltered living space (Le Hire & Hily, 2005). They influence the benthic boundary layer and reduce environmental disturbance including currents created by wave action, temperature or salinity variation as well as protection from predation (Kraufvelin & Salovius, 2004; Le Hire & Hily, 2005; Norling & Kautsky, 2007). Moreover, they physically trap detritus and faeces from associated fauna, which may also facilitate abundance, via nutrients provision, of these associations (Norling & Kautsky, 2007).

Factors affecting assemblage structure

A detailed examination of the data indicates that structure of faunal assemblages within the patches is driven mostly by differences in the dominance of the associated fauna rather than by species composition, which was similar among the sites, or by structural species (Table 1; Figure 4). Some of the assemblages' patterns could have been driven by organismal biology. All three animal species that were attached to rocks (*M. trossulus*, *B. improvisus* and *E. crustulenta*) produce a large number of planktotrophic larvae (e.g. Bayne, 1964; Brusca & Brusca, 2002). While such larvae give these organisms the potential to colonize over large distances, they are also responsible for highly variable interannual variation in recruitment. It might be suggested that such a life history would lead to homogeneous colonization of the area, which was evident in our data when only these sets of organisms were analysed (Figure 4C). On the other hand, among indirectly rock-associated fauna there are a number of brooders (e.g. *H. oerstedii*, *G. salinus* and *C. multisetosum*), which have limited larval dispersion, often limited to the immediate vicinity of the parent (e.g. Waage-Nielsen *et al.*, 2003; Väinölä *et al.*, 2008). Therefore life strategies can lead to either spatial patchiness (e.g. indirectly rock associated fauna) or homogeneity (e.g. sessile fauna) (Figure 4).

Faunal associations can also be affected by different physical and chemical properties of algae (Parker *et al.*, 2001; Goodsell & Connell, 2008). It was found that quantitative descriptors of algae, such as the ratio of surface area to biomass, can play a role in epifaunal assemblage structure (Parker *et al.*, 2001). Aquatic plants with higher ratios of surface area to biomass are more structurally complex and therefore are capable of supporting more abundant and diverse epifaunal assemblages (Parker *et al.*, 2001). However, other studies have shown that macrobenthic assemblage structure can be related to particular attributes of the habitat, for instance the presence of a given algae species (e.g. Edgar, 1983; Parker *et al.*, 2001; Kraufvelin & Salovius, 2004). Associated faunal assemblages often differ to a large extent among algae species (Edgar, 1983; Parker *et al.*, 2001). In our study, there were five species of filamentous algae associated with rocks. Differences in their relative occurrence, and therefore the level of complexity among locations could lead to numerical differences in the associated fauna. There are a number of studies indicating that an increase in epifaunal abundance, biomass and diversity is directly related to plant quantity (e.g. Attrill *et al.*, 1996; Parker *et al.*, 2001; Christie *et al.*, 2003; Norderhaug *et al.*, 2007).

The size of rocks in the Gulf of Gdansk caused spatial variability in the composition of the associated macrofaunal

Table 2. Checklist of associated macrofaunal species found on the Polish coast (stony and algal habitats): √, present; -, absent; *, sum of abundance of all four recorded species; **, recorded, but considered as meiofauna and not counted.

Class	Species/taxa	References			
		Andrulewicz <i>et al.</i> (2004)	Kotwicki (1996)	Present study	
Mean total abundance (ind·m ⁻²)					
Polychaeta	<i>Nereis diversicolor</i> (Müller)	√	50.7	912.2	
	<i>Streblospio shrubsolei</i> (Buchanan)	-	6.3	-	
	<i>Pygospio elegans</i> (Claparède)	√	26.0	2641.1	
	<i>Fabricia sabella</i> (Ehrenberg)	√	-	1591.0	
	<i>Harmothoe sarsi</i> (Malmgren)	√	-	-	
Oligochaeta	Oligochaeta	√	24.0	9128.2*	
Crustacea	<i>Balanus improvisus</i> Darwin	√	-	3197.2	
	<i>Calliopius laeviusculus</i> (Krøyer)	√	-	-	
	<i>Caprella mutica</i> Schurin	-	-	0.7	
	<i>Crangon crangon</i> (Linnaeus)	-	22.0	-	
	<i>Corophium lacustre</i> (Vanhoffen)	-	-	179.7	
	<i>Corophium multisetosum</i> Stock	-	-	54.8	
	<i>Corophium volutator</i> (Pallas)	-	9.0	-	
	<i>Corophium</i> juv.	-	-	36.2	
	<i>Cyatura carinata</i> (Krøyer)	-	12.3	50.4	
	<i>Gammarus locusta</i> (Linnaeus)	-	6.5	-	
	<i>Gammarus oceanicus</i> Segerstrale	√	4.0	-	
	<i>Gammarus salinus</i> Spooner	√	24.0	176.2	
	<i>Gammarus zaddachi</i> Sexton	√	9.7	20.9	
	<i>Gammarus</i> juv.	-	236.3	747.1	
	<i>Heterotanais oerstedti</i> (Krøyer)	-	-	3417.4	
	<i>Idotea balthica</i> (Pallas)	√	45.8	-	
	<i>Idotea chelipes</i> (Pallas)	-	57.4	7.4	
	<i>Idotea</i> juv.	-	285.3	-	
	<i>Jaera albifrons</i> Leach	√	31.0	-	
	<i>Saduria entomon</i> Linnaeus	√	-	-	
	<i>Spaeroma hookeri</i> Leach	-	65.7	-	
	<i>Leptocheirus pilosus</i> Zaddach	-	46.2	623.9	
	<i>Mysis mixta</i> Liljeborg	√	-	-	
	<i>Neomysis integer</i> (Leach)	-	6.8	-	
	<i>Praunus inermis</i> (Rathke)	√	-	-	
	Gastropoda	<i>Hydrobia</i> sp.	√	6953.9	5.6
		<i>Theodoxus fluviatilis</i> (Linnaeus)	√	301.3	-
<i>Lymnea peregra</i> (Müller)		-	371.9	-	
<i>Embletonia pallida</i> (Alder. Hancock)		√	-	-	
Bivalvia	<i>Mytilus trossulus</i> Linnaeus	√	526.2	33.5	
	<i>Macoma baltica</i> (Linnaeus)	√	6.3	-	
	<i>Cerastoderma glaucum</i> (Poiret)	-	337.2	-	
Others	<i>Mya arenaria</i> Linnaeus	-	66.9	-	
	Chironomidae	-	61.7	361.8	
	Pisces larvae	-	44.2	-	
	Insecta larvae	√	-	3.7	
	Hydrozoa	√	-	9.0	
	Nematoda	√	-	**	
	Turbellaria	√ (2 species)	-	**	
	Hirudinea	√	6.5	-	
Nemertinea	√	-	-		

assemblages (Table 1; Figure 6B); the larger the rock size the higher the number of both species and individuals (Figure 5). These results confirm the findings of a number of earlier studies (e.g. Osman, 1977; Sousa, 1979; Barnes & Kuklinski, 2003) which have shown that the size of rocks is of prime importance for colonization patterns. Most studies revealed a similar pattern to the one recorded here. As rock size increases there is both an increase in availability of surface for colonization and substrate decrease in the probability that it will be overturned by wave action (Wilson, 1987). Increased surface area increases the probability of an

organism settling as well as enabling a larger number of biota to coexist. With increased stability of the substrate there is a greater chance that organisms will achieve reproductive age before the next disturbance occurs (e.g. turnover of the rock caused by storm) (Sousa, 1979). There is also the possibility that rocks might be overturned during the period of larval settlement or immediate post-settlement leading to individuals failing to establish. Moreover, with increased rock size we recorded an increased number of engineering organisms (e.g. barnacles— $r = 0.61$, $P < 0.001$; algae— $r = 0.71$, $P < 0.001$), which may have caused the observed

increase in other macrofaunal individuals. The number of *B. improvisus* individuals and the biomass of algae had significant effect on the associated faunal assemblages (Figure 6). Barnacles and algae enhance the complexity of smooth surfaces of stones (personal observation), which creates additional living space (Yakovis *et al.*, 2005; Norling & Kautsky, 2007).

The results suggest that rock associated macrofauna is influenced by combined effect of rock size and surface complexity created by structural organisms. It appears that factors influencing rock-assemblages at the two locations studied follow similar trends, however, patterns at Station A are slightly easier to detect (Figure 6).

CONCLUSIONS

Boulder fields are important components of coastal ecosystems, particularly in low diversified habitats dominated by sandy bottom as in the brackish waters of the southern Baltic Sea. As indicated above they can be regarded as local diversity hot spots. This study also showed that hard-bottom benthic assemblages are affected by a complex of the factors. Substrate stability and heterogeneity are of prime importance for faunal assemblages associated with rocks. There were statistical differences in assemblages' structure between sites within the rocky patch. Yet the observed differences were mostly due to differences in numerical abundance rather than species composition. Further investigations of boulder patches together with the surrounding sandy habitat are needed to describe interaction between these two habitats more precisely and provide information allowing the determination of the specific functional importance of existing rocky habitats.

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