

Benthic communities in relation to wave exposure and spatial positions on sublittoral boulders in the Baltic Sea

Anders Wallin^{1,*}, Susanne Qvarfordt¹, Pia Norling^{1,2}, Hans Kautsky¹

¹Department of Systems Ecology, Stockholm University, 106 91 Stockholm, Sweden

²Norwegian Institute for Water Research (NIVA), 0349 Oslo, Norway

ABSTRACT: Boulders are an important substrate for Baltic Sea benthic communities. Although previous studies have examined benthic species on sublittoral boulders in the Baltic Sea, information on benthic assemblages and how they vary in relation to structuring factors is limited. The aim of the present study was to describe the benthic communities, including both algae and animal taxa, on sublittoral boulders in relation to spatial positions on the boulders (4 levels) and differences in wave exposure (2 levels). The multivariate results, including 29 algae and 25 animal taxa, from the field sampling showed a significant interaction between the 2 main factors. Changes in the biomass of both annual and perennial macroalgae as well as *Mytilus edulis* and *Balanus improvisus*, were found among different positions on wave-exposed boulders, a pattern which was less clear on boulders from sheltered sites, showing that water movement influences small-scale spatial patterns on sublittoral boulders. Apart from water movement, the physical factors substrate slope and light intensity were also associated with the small-scale patterns found in benthic communities. The difference in these factors may influence both settlement and post-settlement processes for both algae and animals, and possible mechanisms leading to the patterns found are discussed.

KEY WORDS: Spatial patterns · Physical factors · Macroalgae · *Mytilus edulis* · *Balanus improvisus*

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

INTRODUCTION

The Baltic Sea has large shallow coastal and archipelago areas dominated by phytobenthic and associated zoobenthic communities (Kautsky & Kautsky 1996). These communities have, in comparison to fully marine environments, a low biodiversity (Ojaveer et al. 2010) and are less structured by biotic interactions, e.g. predation (Kautsky 1981). On a large scale, e.g. within an archipelago, these benthic communities are mainly structured by the physical factors light, water movement and type of substrate (Kautsky & van der Maarel 1990, Eriksson & Bergström 2005). Several factors determine the light reaching the substrate, e.g. the depth, dissolved and suspended matter and the shading by algae and/or boulders, as well as the slope and orientation of the substrate. The substrate type leads to different benthic plant and animal communities (Kautsky 1988, 1989, 1995). The sediment-living animals

and rooted plants are restricted to more fine-grained substrates, whereas most macroalgal species need hard substrate, such as rocks or boulders.

In the Baltic Sea, due to the geology of the area, boulders are a common substrate in shallow sublittoral communities (Waern 1952, Hällfors et al. 1981). Several authors have studied the species distribution on sublittoral boulders in the Baltic Sea. Differences in the distribution of macroalgae on surfaces with different slopes were discussed by Waern (1952) in the Åland Sea. At the Lithuanian coast, the distribution of *Furcellaria lumbricalis* on sublittoral boulders was studied by Bučas et al. (2007). Gilek et al. (2001) studied the spatial pattern of *Mytilus edulis* on sublittoral boulders in a wave-exposed part of the Askö area (northern Baltic proper), and assemblages of macrofauna associated with rocks were investigated in the Gulf of Gdansk by Grzelak & Kuklinski (2010). Furthermore, previous studies indicate a spatial pattern of benthic

*Email: anders@ecology.su.se

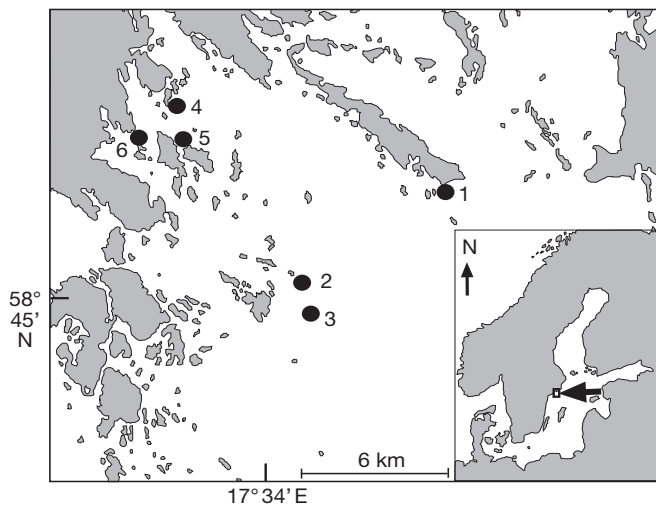


Fig. 1. Map of the Askö area and the 6 sampled sites (1 to 3 are wave-exposed sites; 4 to 6 are sheltered sites)

algae and animals on sublittoral boulders (Kautsky 1989, Gilek et al. 2001), but to our knowledge no study has described the community composition or the small-scale patterns of occurrence for the whole macrobenthic community (including both macroalgae and animals) on sublittoral boulders in the Baltic Sea. The aim of the present study was, therefore, to describe the benthic plant and animal community composition, on a small scale, on sublittoral boulders in the Baltic Sea in relation to different positions on boulders and in relation to different degrees of wave exposure.

MATERIALS AND METHODS

The study was carried out in June 2004 in the Askö area, in the northern Baltic proper (Fig. 1). The salinity in this area is relatively constant at around 7. During the winter months the water-surface temperature is $\sim 0^{\circ}\text{C}$, while in July to August the temperature may exceed 20°C .

On each of 3 wave-exposed (Sites 1 to 3) and 3 sheltered sites (Sites 4 to 6) (Fig. 1) 3 randomly selected boulders were sampled.

All the sites are located in a sparsely populated area. There is no freshwater or sewage water outflow close to any of the sites, and they are homogenous in salinity. The sites were chosen on a marine chart of the area. To determine the degree of wave exposure, a model developed by Isaacs (2004), based on effective fetch, wind direction and wind force, was used. The 3 wave-exposed boulders, which are open to waves from the south (the dominating wind direction), are all homogenous in wave exposure, as are the 3 sheltered sites, all being protected by islands, rocky islets and shallow areas. The sampled boulders were all at 4.5 to 5.8 m depth, and their heights were between 0.7 and 1.1 m. The substrate slope on the boulder sides ranged from 60° to 100° , and the substrate slope on the top of the boulder ranged from 10° to 45° . The samples were collected from the boulder sides facing northward (between the compass directions of 315° and 45°).

Table 1. Taxa found on wave-exposed and sheltered sites. Mean (\pm SE; $n = 9$) biomass (10^{-3} g m^{-2}) is given. nd: not determined (present on boulders, but not weighed)

Phylum/Subphylum/Class/	Exposed	Sheltered
Chlorophyta/.../Chlorophyceae/		
<i>Cladophora glomerata</i>	22.50 \pm 9.97	46.50 \pm 32.04
<i>Cladophora rupestris</i>	0.02 \pm 0.01	0.01 \pm 0.01
<i>Rhizoclonium</i> spp.	0 \pm 0	107.63 \pm 61.27
Chlorophyta/.../Ulvophyceae/		
<i>Ulothrix zonata</i>	0.01 \pm 0.01	0.17 \pm 0.04
<i>Monostroma grevillei</i>	0.05 \pm 0.02	0 \pm 0
<i>Ulva intestinalis</i>	7.37 \pm 4.81	0 \pm 0
<i>Ulva flexuosa</i>	0 \pm 0	0.80 \pm 0.76
<i>Ulva procera</i>	0 \pm 0	14.65 \pm 10.44
Heterokontophyta/.../Phaeophyceae/		
<i>Chorda filum</i>	3.97 \pm 3.97	3.02 \pm 2.11
<i>Dictyosiphon chordarius</i>	0 \pm 0	0.57 \pm 0.57
<i>Dictyosiphon foeniculaceus</i>	29.98 \pm 9.42	10.80 \pm 5.59
<i>Eudesme virescens</i>	618.65 \pm 130.54	0.01 \pm 0.01
<i>Fucus vesiculosus</i>	0.01 \pm 0.01	76.72 \pm 57.77
<i>Pylaiella littoralis/Ectocarpus siliculosus</i>	8697.11 \pm 1614.82	27015.87 \pm 4926.67
<i>Scytosiphon lomentaria</i>	17.04 \pm 11.33	0 \pm 0
<i>Sphacelaria arctica</i>	0.95 \pm 0.58	3744.71 \pm 344.76
<i>Stictyosiphon tortilis</i>	12.36 \pm 5.30	74.30 \pm 19.69
Heterokontophyta/.../Bacillariophyceae/		
Diatoms	nd	nd
Rhodophyta/.../Rhodophyceae/		
<i>Aglaothamnion roseum</i>	0.01 \pm 0.01	15.33 \pm 3.62
<i>Ceramium tenuicorne</i>	18534.46 \pm 4502.52	472.84 \pm 132.15
<i>Ceramium virgatum</i>	2390.82 \pm 1711.71	0.01 \pm 0.01
<i>Coccotylus truncatus</i>	0 \pm 0	3.21 \pm 3.21
<i>Furcellaria lumbricalis</i>	38181.73 \pm 10317.73	5244.15 \pm 1122.09
<i>Hildenbrandia rubra</i>	nd	nd
<i>Phyllophora pseudoceranoides</i>	3538.04 \pm 826.20	113.60 \pm 62.19
<i>Polysiphonia fibrillosa</i>	0 \pm 0	144.21 \pm 53.91
<i>Polysiphonia fucoides</i>	616.33 \pm 286.81	3535.53 \pm 553.78
<i>Rhodochorton purpureum</i>	0.01 \pm 0.01	11.73 \pm 4.67
<i>Rhodomela confervoides</i>	1.90 \pm 1.89	0 \pm 0
Total algal biomass	72673.38 \pm 12600.29	40636.39 \pm 5029.65
Cyanobacteria/.../Cyanophyceae/		
<i>Spirulina</i> spp.	0.09 \pm 0.03	0.03 \pm 0.02

(continued on next page)

Quantitative samples were collected from the 18 boulders using SCUBA diving. On each boulder, a stratified sampling strategy was applied. The boulders were sampled in 4 given positions (levels of boulders): (1) at the lower part (10 to 15 cm above the sea floor) of the boulder side (position 'lower'), (2) at a middle part (25 to 35 cm above the sea floor) of the boulder side (position 'middle'), (3) at the upper 10 to 15 cm of the boulder side (position 'upper') and (4) on the top of the boulder (position 'horizontal').

In each position 3 random samples were taken. This was done using square frames of 7 cm side lengths with a nylon bag (mesh size < 0.5 mm) replacing 1 side. The samples were scraped into the bag using a putty knife. For each sample, the distance to the seafloor and the slope of the substrate were measured using a ruler and a protractor. After the boulders were sampled, duplicate light measurements were performed at every position using a Li-192SA underwater quantum sensor

and a Li1000 data logger. The height, width and depth of the boulder were also measured using a ruler and a depth gauge.

The samples of algae and animals (>1 mm) were frozen and later sorted according to taxa (Table 1). *Mytilus edulis* was sorted into 3 different size classes: small (<5 mm), medium (5 to 10 mm) and large (>10 mm). The different taxa of both the algae and the animals were dried at 60°C to constant dry weight (including shells when present). Before being dried, the numbers of individuals in the 3 size classes of *M. edulis* were also counted.

To obtain a representative sample from each position, the 3 parallel samples on each boulder were pooled. Prior to the multivariate statistical analyses, the data were square-root transformed. This was done in order to lower the difference in biomass between the more and the less dominating taxa, thus obtaining a better analysis of the community composition and its

change instead of an analysis primarily of the most dominating taxa. The data were analysed using the statistical software PRIMER-E 6.1 and PERMANOVA 1.0.2. The effect of the 2 main factors, position (4 levels) and wave exposure (2 levels), on the multivariate matrix of algal and animal biomasses was tested using a 2-way crossed multivariate PERMANOVA test (Anderson et al. 2008) and by using non-metric multidimensional scaling (nMDS). To test the homogeneity in multivariate dispersions among groups, PERMDISP tests were carried out (Anderson et al. 2008). To examine which taxa were most responsible for differences between levels of position and wave exposure, SIMPER tests were carried out (Clarke & Warwick 2001). The differences among positions in the total biomass, subdivided into the categories perennial macroalgae, annual macroalgae, *Balanus improvisus*, *Mytilus edulis* and other animals, were also analysed using nested PERMANOVA tests. Since previous analyses tested the differences between wave-exposed and sheltered sites, separate tests were carried out for these 2 groups.

Table 1 (continued)

Phylum/Subphylum/Class/	Exposed	Sheltered
Annelida/.../Clitellata/		
<i>Piscicola geometra</i>	3.59 ± 3.40	0.01 ± 0.01
Tubificidae spp.	0.96 ± 0.94	0.01 ± 0.01
Annelida/.../Polychaeta/		
<i>Hediste diversicolor</i>	127.55 ± 33.88	4.72 ± 2.72
<i>Byligides sarsi</i>	0 ± 0	8.31 ± 6.10
Arthropoda/Crustacea/Malacostraca/		
<i>Gammarus</i> spp.	2751.53 ± 338.04	587.82 ± 145.77
<i>Idotea</i> spp.	556.91 ± 143.65	82.96 ± 57.12
<i>Jaera albifrons</i> spp.	161.80 ± 36.76	17.06 ± 10.40
<i>Saduria entomon</i>	0.02 ± 0.01	7.56 ± 7.56
<i>Corophium volutator</i>	0.01 ± 0.01	0.01 ± 0.01
<i>Praunus flexuosus</i>	0.01 ± 0.01	0.01 ± 0.01
Arthropoda/Crustacea/Maxillopoda/		
<i>Balanus improvisus</i>	161037.79 ± 22684.14	33716.93 ± 8540.12
Arthropoda/Hexapoda/Insecta/		
<i>Agraylea</i> spp.	0 ± 0	49.70 ± 20.10
Chironomidae spp.	14.83 ± 7.17	47.53 ± 12.72
<i>Phryganea</i> spp.	0 ± 0	749.62 ± 387.73
Bryozoa/.../Gymnolaemata/		
<i>Electra crustulenta</i>	0.89 ± 0.04	0.40 ± 0.07
Cnidaria/Medusozoa/Hydrozoa/		
<i>Cordylophora</i> spp.	263.14 ± 151.69	39.13 ± 27.28
Mollusca/.../Bivalvia/		
<i>Cerastoderma glaucum/</i> <i>Parvicardium hauniense</i>	11185.94 ± 1867.39	3224.30 ± 712.83
<i>Macoma balthica</i>	521.92 ± 374.92	8.50 ± 4.18
<i>Mytilus edulis</i>	208072.41 ± 30202.44	43743.95 ± 4443.72
Mollusca/.../Gastropoda/		
<i>Hydrobia</i> spp.	29897.03 ± 7027.96	59973.17 ± 6455.13
<i>Limapontia capitata</i>	0.19 ± 0.19	0.01 ± 0.01
<i>Radix balthica</i>	128.12 ± 128.12	781.37 ± 544.69
<i>Theodoxus fluviatilis</i>	4294.23 ± 676.03	1293.85 ± 225.40
Nemertea/.../Enopla/		
<i>Cyanophthalma obscura</i>	6.88 ± 2.90	23.92 ± 9.55
Platyhelminthes/Rhabdtophora/Tricladida/		
<i>Dendrocoelum lacteum</i>	14.74 ± 5.97	13.80 ± 9.08
Total animal biomass	419040.47 ± 36410.45	144374.64 ± 11018.68

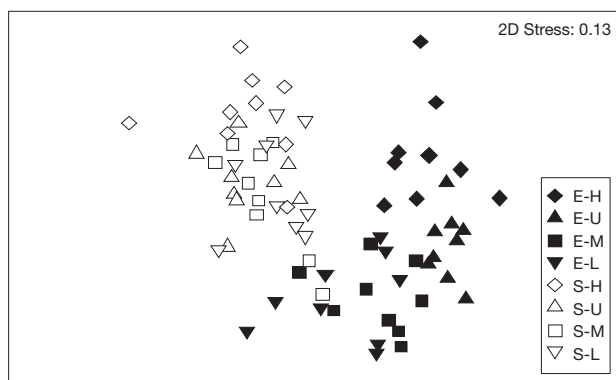


Fig. 2. Comparison (non-metric multidimensional scaling) of the benthic communities in 4 different positions (H: horizontal; U: upper; M: middle; L: lower) at the wave-exposed (E) and sheltered (S) sites

To further test what/which combination of abiotic factor(s) were best associated with the benthic community on the boulders, a stepwise BVSTEP test using Spearman's rank correlation (r_s) method was used (Clarke & Warwick 2001). In this test, the 6 abiotic factors wave exposure (Isaeus 2004), substrate slope, sample depth, relative light extinction, boulder size and geographic orientation were normalised and the Euclidian distance similarity was used. For the biotic data, Bray-Curtis similarity was used in the ordination, the PERMANOVA test and the BVSTEP analysis. The differences in the numbers of individuals of *Mytilus edulis* of different size classes obtained from the different positions on sheltered and wave-exposed boulders were analysed using nested PERMANOVA tests.

RESULTS

A total of 55 taxa were found on boulders, including 29 algal and 25 animal taxa, as well as 1 taxon of colony-forming cyanobacteria (Table 1); 19 of the algae and 22 of the animal taxa were found at both wave-exposed and sheltered sites (Table 1).

The main factors examined, wave exposure and position, had an interactive effect on the biomass of the benthic community of algal and animal taxa on the sublittoral boulders (Fig. 2, Table 2). A small-scale pattern in the benthic community was found on the sublittoral boulders, although the difference among positions depended on wave exposure, being more pronounced on wave-exposed compared to sheltered boulders (Fig. 2, Table 2). At both the wave-exposed and sheltered sites, the benthic community in a horizontal position on the boulders was significantly different from that on the sides of boulders (Fig. 2, Table 2). On the wave-exposed boulders, the community in the upper position was also significantly different from the communities in the middle and lower positions (Fig. 2, Table 2). No difference was found between the middle and lower positions on wave-exposed boulders (Fig. 2, Table 2). On the sheltered boulders, no differences were found among the upper, middle and lower positions (Fig. 2, Table 2). The positions on wave-exposed boulders were all significantly different from the corresponding positions on sheltered boulders (Table 2).

The 2 groups of perennial and annual macroalgae, together with the species *Mytilus edulis* and *Balanus improvisus*, were responsible for most of the differences found between the wave-exposed and sheltered

Table 2. Statistical analyses of the benthic community in different positions on wave-exposed and sheltered boulders. The 2 factors wave exposure (wave exposed and sheltered) and position (horizontal, upper, middle and lower) were tested in a 2-way crossed PERMANOVA test followed by PERMANOVA pairwise tests

PERMANOVA: 2-way crossed		df	F	p	Unique permutations				
Wave exposure		1	51.495	<0.001	9941				
Position		3	7.074	<0.001	9931				
Wave exposure × position		3	3.293	<0.001	9901				
PERMANOVA: pairwise test		Exposed		Sheltered					
Positions	t	p	t	p					
Lower–Middle	0.974	0.414	0.602	0.893					
Lower–Upper	3.159	<0.001	1.207	0.196					
Lower–Horizontal	3.342	<0.001	1.816	0.006					
Middle–Upper	2.989	<0.001	0.874	0.589					
Middle–Horizontal	3.326	<0.001	1.972	0.002					
Upper–Horizontal	2.634	<0.001	1.924	0.005					
PERMANOVA: pairwise test		Horizontal		Upper		Middle		Lower	
Wave exposure	t	p	t	p	t	p	t	p	
Exposed–Sheltered	3.587	0.001	5.725	0.001	3.548	0.001	3.089	0.001	

boulders (SIMPER cumulative dissimilarity = 71.4%). The overall mean biomass of macroalgae was higher on wave-exposed compared to sheltered boulders, and the taxa composition differed. The red algae *Furcellaria lumbricalis* and *Ceramium tenuicorne* dominated at wave-exposed sites, whereas the brown algae *Pyraliella littoralis* (mingled with *Ectocarpus siliculosus*) and *Sphacelaria arctica*, as well as the red alga *Polysiphonia fucoides* dominated the sheltered sites (Table 1). The red algae *Ceramium virgatum* and *Phyllophora pseudoceranoides* were more abundant at the wave-exposed compared to the sheltered sites (Table 1). The brown algae *Fucus vesiculosus* and *Stictyosiphon tortilis* and the red alga *Polysiphonia fibrillosa* were more abundant at the sheltered sites, but, overall, they had a low biomass on the boulders (Table 1). Both *M. edulis* and *B. improvisus* had higher mean biomasses in all the 4 pre-defined positions at wave-exposed sites when compared to sheltered sites (Fig. 3). The remaining animal biomass at both the wave-exposed and sheltered sites was mainly *Hydrobia* spp., *Cerastoderma glaucum/Parvicardium hauniense*, *Theodoxus fluviatilis* and *Gammarus* spp. The mollusc *Hydrobia* spp. had a higher biomass at the sheltered sites, whereas *C. glaucum/P. hauniense*, *T. fluviatilis* and *Gammarus* spp. had higher biomasses at the wave-exposed sites (Table 1). The less abundant taxa *Idothea* spp., *Jaera albifrons* spp. and *Cordylophora* spp. had higher biomass values at the wave-exposed sites (Table 1). At the sheltered sites, the biomasses of the insect larvae Chironomidae spp. and the Trichoptera larvae *Phryganea* spp. were higher when compared to the values at the wave-exposed sites (Table 1).

On the wave-exposed boulders, the annual and perennial macroalgae, as well as the blue mussel *Mytilus edulis*, dominated in the horizontal position (Fig. 3). The differences found between the horizontal and upper positions were characterized by a decrease in the biomass of the perennial macroalgae *Furcellaria*

lumbricalis and *Phyllophora pseudoceranoides* (SIMPER dissimilarity 15%), and of the annual macroalgae *Ceramium tenuicorne* and *Pyraliella littoralis/Ectocarpus siliculosus* (SIMPER dissimilarity 15%) as well as an increase in the biomass of *M. edulis* (SIMPER dissimilarity 22%) and *Balanus improvisus* (SIMPER dissimilarity 17%). A decrease in the biomass of *M. edulis* and the perennial macroalgae *F. lumbricalis/P. pseudoceranoides* and an increase in the biomass of *B. improvisus* contributed most to the difference found between the upper and middle positions (SIMPER dissimilarity—*M. edulis*: 28%; *B. improvisus*: 17%; *F. lumbricalis/P. pseudoceranoides*: 19%). Significantly higher biomasses of *M. edulis* and *B. improvisus* and lower biomass of annual macroalgae were found in the upper compared to the horizontal positions (Fig. 3, Table 3). Significant lower biomasses of *M. edulis* and perennial macroalgae and higher biomass of *B. improvisus* were found at the middle compared to the upper positions (Fig. 3, Table 3). No difference was found between the middle and lower positions (Tables 2 & 3). These 2 positions had the highest *B. improvisus* biomass, both significantly higher compared to the horizontal position (Fig. 3, Table 3). At the middle and lower positions the biomass of annual macroalgae were significantly lower compared to the horizontal position and the biomass of perennial macroalgae significantly lower compared to both the horizontal and upper positions (Fig. 3, Table 3). A higher biomass of other animals (other than *M. edulis* and *B. improvisus*) was found in the horizontal position compared to the upper, middle and lower positions (Fig. 3, Table 3). The highest number of individuals of *M. edulis* from all size classes were found in the horizontal and upper positions (Fig. 4). Small *M. edulis* showed significantly higher numbers in the horizontal and upper positions compared to the lower and middle positions (Fig. 4, Table 4). Although a higher mean number of medium-sized *M. edulis* was found in the horizontal and upper

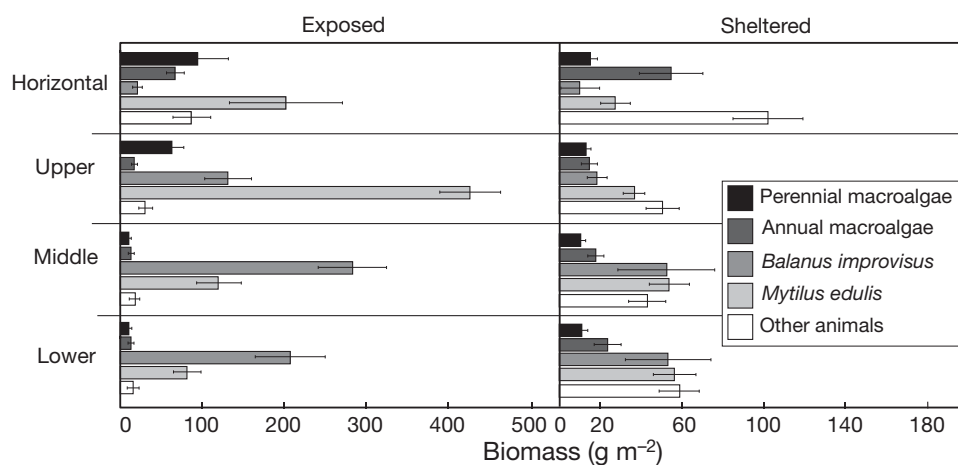


Fig. 3. Comparison of biomass from the 4 sampled positions (horizontal, upper, middle and lower) on boulders from wave-exposed and sheltered sites. Mean (\pm SE; $n = 9$) biomass values (g m^{-2}) of annual macroalgae, perennial macroalgae, *Balanus improvisus*, *Mytilus edulis* and other animals are given. Note scale differences on the x-axes

Table 3. Statistical analyses testing the differences of dominating taxa among 4 positions of wave-exposed and sheltered boulders. The factor position (horizontal, upper, middle and lower) nested in taxa (*Mytilus edulis*, *Balanus improvisus*, annual macroalgae, perennial macroalgae and other animals) was tested in 2 separate PERMANOVA tests followed by PERMANOVA pairwise tests

PERMANOVA: Position (taxa)	Exposed: $F = 12.857$, $df = 15$, $p < 0.001$, unique permutations: 9928												Sheltered: $F = 16.917$, $df = 15$, $p < 0.001$, unique permutations: 9923																	
	Mytilus edulis			Balanus improvisus			Annual macroalgae			Perennial macroalgae			Other animals			Mytilus edulis			Balanus improvisus			Annual macroalgae			Perennial macroalgae			Other animals		
	t	p	t	p	t	p	t	p	t	p	t	p	t	p	t	p	t	p	t	p	t	p	t	p	t	p	t	p		
Lower–Middle	1.138	0.277	1.33	0.202	0.139	0.885	0.020	0.985	0.599	0.555	0.191	0.845	0.054	0.954	0.797	0.435	0.018	0.986	1.175	0.257										
Lower–Upper	8.536	<0.001	1.478	0.162	1.272	0.215	4.981	<0.001	1.850	0.083	1.772	0.095	1.016	0.321	1.270	0.219	0.803	0.425	0.555	0.587										
Lower–Horizontal	1.674	0.123	5.861	<0.001	6.148	<0.001	2.622	0.013	3.892	0.002	2.625	0.020	2.089	0.052	1.886	0.082	1.002	0.327	2.306	0.036										
Middle–Upper	6.584	<0.001	2.963	0.010	1.131	0.273	5.097	<0.001	1.380	0.182	1.558	0.139	1.139	0.281	0.486	0.635	0.853	0.406	0.735	0.474										
Middle–Horizontal	0.902	0.387	8.184	<0.001	6.081	<0.001	2.643	0.012	3.624	0.002	2.448	0.026	2.247	0.040	2.485	0.022	1.041	0.316	3.432	0.004										
Upper–Horizontal	3.194	0.007	4.334	0.001	5.722	<0.001	0.197	0.844	2.628	0.019	1.327	0.203	1.847	0.085	2.819	0.011	0.378	0.724	3.015	0.008										

positions compared to the lower and middle positions, no significant differences were found (Fig. 4, Table 4). Large *M. edulis* had significantly higher numbers in the upper position compared to all other positions (Fig. 4, Table 4). No differences in the numbers of any of the *M. edulis* size classes were found between the middle and lower positions (Fig. 4, Table 4).

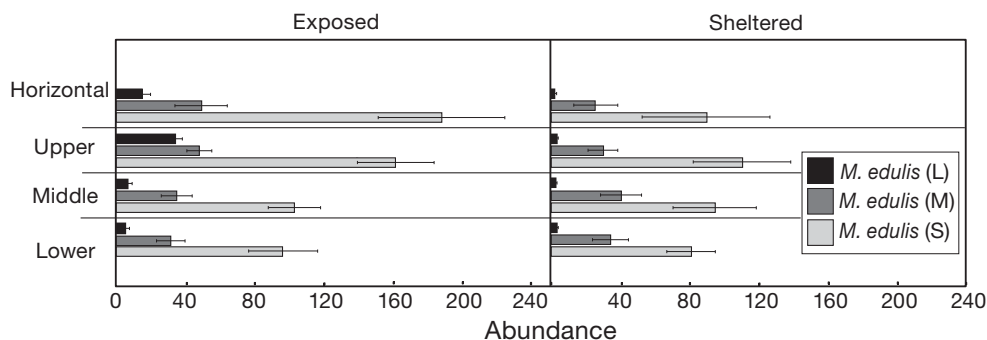
At the sheltered sites, the horizontal position showed a generally higher biomass of annual macroalgae; especially *Ceramium tenuicorne*, *Pylaiella littoralis*/*Ectocarpus siliculosus* and *Polysiphonia fibrillosa* contributed to the differences in biomass compared to the upper, middle and lower positions (SIMPER mean dissimilarity: 15%). The mean biomass values of *Mytilus edulis* and *Balanus improvisus* were lower in the horizontal position compared to the positions on the sides of the boulder, which also contributed to the differences found (SIMPER mean dissimilarity—*M. edulis* 11%, *B. improvisus* 18%). The total biomass of annual macroalgae was significantly higher in the horizontal position compared to both the upper and middle positions (Fig. 3, Table 3). The biomass of *M. edulis* was significantly lower in the horizontal position compared to both the lower and middle positions while a significantly lower biomass of *B. improvisus* was found in the horizontal position compared to the middle position (Fig. 3, Table 3). The other animals (other than *M. edulis* and *B. improvisus*) had a higher combined biomass in the horizontal position compared to the upper, middle and lower positions (Fig. 3, Table 3). No differences in the number of individuals for any of the *M. edulis* size classes were found among positions (Fig. 4, Table 4).

The combination of the 2 abiotic factors wave exposure and substrate slope were found to be best correlated with the benthic community on the boulders (BVSTEP, $r_s = 0.59$, $p = 0.01$). When using only the macroalgae, the combination of the 2 factors wave exposure and light extinction were best correlated to the benthic community on the boulders (BVSTEP, $r_s = 0.56$, $p = 0.001$).

DISCUSSION

In the present study, the algal and animal taxa found on boulders are mainly those species/taxa found in the wave-exposed and sheltered parts of the Askö area (Haage 1975, Wallentinus 1979, Kautsky 1989), those associated with rocks in the Gulf of Gdansk (Grzelak & Kuklinski 2010) and also those found as fouling assemblages on offshore constructions in the central Baltic Sea (Qvarfordt et al. 2006, Wilhelmsson & Malm 2008). Differences in the benthic community between artificial vertical structures and the surrounding natural substrates have been found in studies of bridge pillars and offshore wind turbines, the results of which have

Fig. 4. *Mytilus edulis*. Comparison of the distribution of size classes of *M. edulis* in 4 positions on boulders from wave-exposed and sheltered sites. The numbers of individuals are separated into the size classes: large (L, >10 mm), medium (M, 5 to 10 mm) and small (S, <5 mm). Data are mean (\pm SE; n = 9) numbers of individuals per sample



been discussed in the context of, e.g., the depth, age and orientation of the substrate. Also, substrate structure seems to be an important factor separating community composition between artificial vertical fundaments and the surrounding substrate (Qvarfordt et al. 2006, Wilhelmsson & Malm 2008). The community dominated by *Mytilus edulis*, found on the wave-exposed vertical sides of boulders in the present study, is similar to the 'pier piling communities' that have previously been described on vertical constructions (Davis et al. 1982, Wilhelmsson & Malm 2008), while the communities dominated by both annual and perennial macroalgae, found mainly in horizontal positions, are similar to their surrounding environments (Wilhelmsson & Malm 2008). The present study of benthic communities on sublittoral boulders shows that differences in benthic assemblage on horizontal compared to vertical substrates also occur on significantly smaller scales and that these small-scale patterns on sublittoral substrates are influenced by wave exposure. The substrate structure on the sampled boulders was similar, irrespective of position, indicating that other factors, e.g. light and substrate slope, may explain the observed differences in benthic community composition.

In the study area, sheltered sites are generally located closer to the mainland compared to wave-

exposed sites. Due to logistic constraints, there is a clear geographical segregation between the exposed and the sheltered sites, which could suggest a possible confounding factor with differences in the effect of other abiotic or biological factors. Wave exposure is probably the main factor separating the benthic communities between the wave-exposed and sheltered sites in our study. The sites are homogenous in salinity and water temperature, and there is no freshwater outflow close to any of the sites. Furthermore, anthropogenic activity in the area is probably negligible. The area is very sparsely populated with scattered cabins, and there is no sewage outflow close to any of the sites. However, this geographical segregation was taken into account when the results were interpreted.

The difference in benthic composition between the wave-exposed and sheltered sites suggests that wave-induced water movement may be an important factor determining community composition, as well as the small-scale spatial patterns on the sublittoral boulders. There was a significant difference in the relative dominance of taxa between wave-exposed and sheltered sites. In general, the biomass values of algae, *Mytilus edulis* and *Balanus improvisus* were lower on the sheltered boulders compared to the wave-exposed boulders.

Table 4. *Mytilus edulis*. Statistical analyses testing the differences of 3 size classes of *M. edulis* among 4 positions of wave-exposed and sheltered boulders. The factor position (horizontal, upper, middle and lower) nested in size (large, medium and small) was tested in 2 separate PERMANOVA tests followed by PERMANOVA pairwise tests

PERMANOVA: position (size)		df	F	p	Unique permutations								
Exposed		9	4.078	<0.001	9936								
Sheltered		9	0.360	0.951	9932								
PERMANOVA: pairwise test		Small		Medium		Large		Small		Medium		Large	
Position		t	p	t	p	t	p	t	p	t	p	t	p
Lower-Middle		0.460	0.650	0.418	0.680	0.758	0.462	0.325	0.746	0.337	0.736	0.513	0.608
Lower-Upper		2.324	0.036	1.816	0.089	7.257	<0.001	0.621	0.537	0.391	0.691	0.373	0.705
Lower-Horizontal		2.383	0.027	1.075	0.302	1.840	0.083	0.223	0.840	0.950	0.350	1.388	0.183
Middle-Upper		2.341	0.031	1.445	0.167	7.000	<0.001	0.305	0.763	0.698	0.487	0.116	0.907
Middle-Horizontal		2.316	0.032	0.750	0.464	1.361	0.196	0.431	0.682	1.203	0.234	1.099	0.294
Upper-Horizontal		0.524	0.611	0.308	0.757	3.317	0.005	0.655	0.517	0.588	0.558	1.117	0.278

ders. Since water movement brings in nutrition and takes away waste (Dame 1996), this may influence benthic community composition on the boulders. Furthermore, surface siltation has been found to be stressful to both filter feeders (Seed & Suchanek 1992, Dame 1996) and macroalgae (Wallentinus 1976, Eriksson 2002, Berger et al. 2003). Also, filamentous macroalgae may overgrow and negatively influence the underlying community by shading (Rohde et al. 2008), causing anoxic conditions while decaying (Paalme et al. 2002) and impairing settling, recruitment and early survival of other species (Berger et al. 2003, Råberg et al. 2005, Qvarfordt 2006). Water movement keeps the substrate clean (Kautsky 1988) and more efficiently removes loosely attached macroalgae from the substrate at wave-exposed compared to sheltered locations, and may thereby influence the recruitment and growth of different benthic species.

The biomass of macroalgae in vertical positions was 50% or less compared to that on the horizontal positions. The lower biomass of macroalgae in positions with higher slope may be due to conditions during settlement. In the Askö area, Qvarfordt (2006) found significant differences in settlement comparing different surface slopes with a break-point somewhere between 60° and 90°. However, S. Qvarfordt & H. Kautsky (unpubl. data cited in Qvarfordt 2006) also found that several macroalgal species showed high settlement on vertical surfaces and overhangs and discussed that post-settlement processes must also be of importance. Possibly due to the light conditions, flat and gently sloping surfaces are more favourable environments for macroalgal growth and survival than vertical walls (Witman & Dayton 2001), as a result the biomass of macroalgae on a vertical surface may be only half or less that on a nearby horizontal substrate (Hiscock 1985). Therefore, it is possible that, although the substrate slope on the boulders in the present study is of some importance in the initial settling stage, shading, as a post-settlement process, is important in determining the final macroalgae distribution on the boulders.

Depending on the algal species and the settlement time of the mussel larvae, filamentous macroalgae can have both positive and negative effects on *Mytilus edulis* settlement, as was discussed by Littorin & Gilek (1999a). Blue mussel *M. edulis* larvae prefer to settle in filamentous algae (Bayne 1964). The high biomass of *Ceramium tenuicorne* on the horizontal top of the wave-exposed boulders could be structurally important for *M. edulis* settlement and may contribute to the high number of juvenile mussels found there. In contrast, at the sheltered sites, the lower biomass of *M. edulis* may be caused by the high biomass of loosely attached *Pylaiella littoralis*/*Ectocarpus siliculosus*. Since

P. littoralis detach during the *M. edulis* settling season in June to July (Wallentinus 1979), it could carry newly settled *M. edulis* larvae away from the boulders. Littorin & Gilek (1999a) also found a higher recruitment of *M. edulis* at 50 cm compared to 10 cm above the bottom, and discussed that this might create small-scale variability in *M. edulis* abundance.

Although juvenile *Mytilus edulis* seem to prefer algae when settling, as previously discussed, a high biomass of macroalgae may also have negative effects on mussel distribution, as indicated by the higher number of large mussels in the upper compared to the horizontal position on the wave-exposed boulders. This result may be due to macroalgal overgrowth. S. Qvarfordt & H. Kautsky (unpubl. data cited in Qvarfordt 2006) found that filter feeders in the area readily settled on horizontal surfaces, but they were overgrown by macroalgae. Competition between macroalgae and sessile invertebrates in the brackish Baltic Sea has also been discussed by Kautsky (1988), who observed that macroalgae seemed to be the stronger competitors for space when light conditions were good and the substrate angle low. Similar patterns have also been described previously by other authors (e.g. Witman 1987, Baynes 1999, Witman & Dayton 2001).

Blue mussel *Mytilus edulis* migration after settlement (Littorin & Gilek 1999b) may also contribute to the high biomass of *M. edulis* on the upper sides of wave-exposed boulders. Gilek et al. (2001), who found a similar *M. edulis* pattern on boulders in the area, suggested that mussel movement might be a behaviour associated with finding microhabitats of increased quality. In their study, Gilek et al. (2001) also found an increase in the feeding rate of *M. edulis* with increased height above the bottom. They explained this in part by better feeding conditions away from the bottom due to increased current speed (see also Fréchette et al. 1989). The biomass distribution of *M. edulis* on wave-exposed boulders suggests that the upper part of boulders is the most favourable microhabitat for *M. edulis* growth. This may be due to better feeding conditions and less overgrowth by macroalgae. If so, migration of *M. edulis* from other parts of the boulders to the upper part may contribute to the high biomass of *M. edulis* found there.

The highest biomass of *Balanus improvisus* was found in the lower and middle positions of wave-exposed boulders, where the biomass of other taxa was low. A negative impact on *B. improvisus* from macroalgae, to due, e.g., overgrowth, may explain the lower *B. improvisus* biomass on the parts of boulders with a high biomass of macroalgae. This mechanism has been described elsewhere (e.g. Underwood 1985 and references therein), and, in the Askö area, it was found that, although *B. improvisus* settled on most surfaces, they

were later overgrown by macroalgae on the more horizontal parts (S. Qvarfordt & H. Kautsky unpubl. data cited in Qvarfordt 2006). A competitive relationship, with *Mytilus edulis* being a stronger competitor for space than *B. improvisus*, was observed, e.g., by Harms & Anger (1983) and Dürr & Wahl (2004). The differences in the biomasses of *M. edulis* and *B. improvisus* on the sides of wave-exposed boulders, as found in the present study, may be due to competition for space between the 2 species.

Excluding the barnacle *Balanus improvisus* and the blue mussel *Mytilus edulis*, the taxa *Hydrobia* spp., *Cerastoderma glaucum/Parvicardium hauniense*, *Theodoxus fluviatilis* and *Gammarus* spp. had the highest animal biomass values on both the wave-exposed and sheltered boulders. For the most part, the biomass of mobile invertebrates reflected that of macroalgae; this may be due to the enlarged surface area for settlement and the shelter from predators, as well as the food resources provided by the macroalgae (e.g. Kotta & Orav 2001, Orav-Kotta & Kotta 2004).

In conclusion, the present study shows that the relative position, with differences in substrate slope and light conditions, influences small-scale spatial patterns in benthic community composition, probably through both settlement and post-settlement processes. These results imply that substrate slope should be taken into consideration in the design of benthic monitoring programs and in predictive modelling of species distribution.

Acknowledgements. We thank S. A. Wikström and B. K. Eriksson for valuable comments on the manuscript. We also thank Stockholm Marine Research Centre (SMF) and the staff at Askö Laboratory for the excellent working conditions. Much appreciated comments were also given by 4 anonymous reviewers.

LITERATURE CITED

- Anderson MJ, Gorley RN, Clarke KR (2008) Permanova+ for PRIMER. Guide to software and statistical methods. Primer-E, Plymouth
- Bayne BL (1964) Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *J Anim Ecol* 33:513–523
- Baynes TW (1999) Factors structuring a subtidal encrusting community in the southern Gulf of California. *Bull Mar Sci* 64:419–450
- Berger R, Henriksson E, Kautsky L, Malm T (2003) Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. *Aquat Ecol* 37:1–11
- Bučas M, Daunys D, Olenin S (2007) Overgrowth patterns of the red algae *Furcellaria lumbricalis* at an exposed Baltic Sea coast: the results of a remote underwater video data analysis. *Estuar Coast Shelf Sci* 75:308–316
- Clarke KR, Warwick R (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. Primer-E, Plymouth
- Dame RF (1996) Ecology of marine bivalves: an ecosystem approach. CRC Press, Boca Raton, FL
- Davis N, VanBlaricom GR, Dayton PK (1982) Man-made structures on marine sediments: effects on adjacent benthic communities. *Mar Biol* 70:295–303
- Dürr S, Wahl M (2004) Isolated and combined impacts of blue mussels (*Mytilus edulis*) and barnacles (*Balanus improvisus*) on structure and diversity of a fouling community. *J Exp Mar Biol Ecol* 306:181–195
- Eriksson BK (2002) Long-term changes in macroalgal vegetation on the Swedish coast. PhD thesis, Uppsala University, Uppsala
- Eriksson BK, Bergström L (2005) Local distribution of macroalgae in relation to environmental variables in the northern Baltic proper. *Estuar Coast Shelf Sci* 62: 109–117
- Fréchette M, Butman CA, Geyer WR (1989) The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. *Limnol Oceanogr* 34:19–36
- Gilek M, Littorin B, Saetre P (2001) Spatial patterns of abundance and growth of *Mytilus edulis* on boulders in the northern Baltic Sea proper. *Hydrobiologia* 452:59–68
- Grzelak K, Kuklinski P (2010) Benthic assemblages associated with rocks in a brackish environment of the southern Baltic Sea. *J Mar Biol Assoc UK* 90:115–124
- Haage P (1975) Quantitative investigations of the Baltic *Fucus* belt macrofauna. 2. Quantitative seasonal fluctuations. *Contr Askö Lab* 9:1–88
- Hällfors G, Niemi Å, Ackerfors H, Lassig J, Leppäkoski E (1981) Biological oceanography. In: Voipio A (ed) *The Baltic Sea*. Elsevier, Amsterdam, p 219–274
- Harms J, Anger K (1983) Seasonal, annual, and spatial variation in the development of hard bottom communities. *Helgol Meeresunters* 36:137–150
- Hiscock K (1985) Aspects of the ecology of rocky sublittoral areas. In: Moore PG, Seed R (eds) *The ecology of rocky coasts*. Hodder & Stoughton, London, p 290–328
- Isaacs M (2004) Factors structuring *Fucus* communities at open and complex coastlines in the Baltic Sea. PhD thesis, Stockholm University, Stockholm
- Kautsky N (1981) On the trophic role of blue mussel (*Mytilus edulis* L.) in a Baltic coastal ecosystem and the fate of the organic matter produced by the mussels. *Kiel Meeresforsch, Sonderh* 5:454–461
- Kautsky H (1988) Factors structuring phytobenthic communities in the Baltic Sea. PhD thesis, Stockholm University, Stockholm
- Kautsky H (1989) Quantitative distribution of plant and animal communities of the phytobenthic zone in the Baltic sea. *Contr Askö Lab* 35:1–80
- Kautsky H (1995) Quantitative distribution of sublittoral plant and animal communities along the Baltic Sea gradient. In: Eleftheriou A, Ansell AD, Smith CJ (eds) *The biology and ecology of shallow coastal waters*. Olsen & Olsen, Fredensborg, p 23–31
- Kautsky U, Kautsky H (1996) Coastal production in the Baltic Sea. In: Eleftheriou A, Ansell AD, Smith CJ (eds) *The biology and ecology of shallow coastal waters*. Olsen & Olsen, Fredensborg, p 31–38
- Kautsky H, van der Maarel E (1990) Multivariate approaches to the variation in phytobenthic communities and environmental vectors in the Baltic Sea. *Mar Ecol Prog Ser* 60: 169–184
- Kotta J, Orav H (2001) Role of benthic macroalgae in regulating macrozoobenthic assemblages in the Väinameri (north-eastern Baltic Sea). *Ann Zool Fenn* 38:163–171

- Littorin B, Gilek M (1999a) Vertical patterns in biomass, size structure, growth and recruitment of *Mytilus edulis* in an archipelago area in the northern Baltic Sea proper. *Ophelia* 50:93–112
- Littorin B, Gilek M (1999b) A photographic study of the recolonization of cleared patches in a dense population of *Mytilus edulis* in the northern Baltic proper. *Hydrobiologia* 393:211–219
- Ojaveer H, Jaanus A, MacKenzie BR, Martin G and others (2010) Status of biodiversity in the Baltic Sea. *PLoS ONE* 5: e12467
- Orav-Kotta H, Kotta J (2004) Food and habitat choice of the isopod *Idotea baltica* in the northeastern Baltic Sea. *Hydrobiologia* 514:79–85
- Paalme T, Kukk H, Kotta J, Orav H (2002) *In vitro* and *in situ* decomposition of nuisance macroalgae *Cladophora glomerata* and *Pilayella littoralis*. *Hydrobiologia* 475/476:469–476
- Qvarfordt S (2006) Phytobenthic communities in the Baltic Sea—seasonal patterns in settlement and succession. PhD thesis, Stockholm University, Stockholm
- Qvarfordt S, Kautsky H, Malm T (2006) Development of fouling communities on vertical structures in the Baltic Sea. *Estuar Coast Shelf Sci* 67:618–628
- Råberg S, Berger-Jönsson R, Björn A, Granéli E, Kautsky L (2005) Effects of *Pilayella littoralis* on *Fucus vesiculosus* recruitment: implications for community composition. *Mar Ecol Prog Ser* 289:131–139
- Rohde S, Hiebenthal C, Wahl M, Karez R, Bischof K (2008) Decreased depth distribution of *Fucus vesiculosus* (Phaeophyceae) in the western Baltic: effects of light deficiency and epibionts on growth and photosynthesis. *Eur J Phycol* 43:143–150
- Seed R, Suchanek TH (1992) Population and community ecology of *Mytilus*. In: Gosling E (ed) *The mussel Mytilus: ecology, physiology, genetics and culture*. Elsevier, New York, NY, p 87–169
- Underwood AJ (1985) Physical factors and biological interactions: the necessity and nature of ecological experiments. In: Moore PG, Seed R (eds) *The ecology of rocky coasts*. Hodder & Stoughton, London, p 372–390
- Waern M (1952) Rocky shore algae in the Öregrund archipelago. *Acta Phytogeogr Suec* 30:1–298
- Wallentinus I (1976) Environmental influences on benthic macrovegetation in the Trosa-Askö area, northern Baltic proper. I. Hydrographical and chemical parameters, and the macrophytic communities. *Contr Askö Lab* 15:1–138
- Wallentinus I (1979) Environmental influences on benthic macrovegetation in the Trosa-Askö area, northern Baltic proper. II. The ecology of macroalgae and submersed phanerogams. *Contr Askö Lab* 25:1–210
- Wilhelmsson D, Malm T (2008) Fouling assemblages on offshore wind power plants and adjacent substrata. *Estuar Coast Shelf Sci* 79:459–466
- Witman JD (1987) Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelps and mussels. *Ecol Monogr* 57:167–187
- Witman JD, Dayton PK (2001) Rocky subtidal communities. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer Associates, Sunderland, MA, p 339–366

Editorial responsibility: Riccardo Cattaneo-Vietti, Genova, Italy

Submitted: June 14, 2010; Accepted: February 14, 2011
Proofs received from author(s): April 7, 2011