Spring development of hydrolittoral rock shore communities on wave-exposed and sheltered sites in the northern Baltic proper

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Abstract

Spring development in the hydrolittoral zone was investigated at five wave-sheltered and five wave-exposed sites on four occasions from late March to late May (every third week). The number of species was higher at the sheltered locations and increased significantly over time. The difference in community structure was significant: over 95% of the Bray-Curtis dissimilarities were due to the biomass of only eleven taxa, and the total Bray-Curtis dissimilarity between exposed and

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sheltered sites was 75%. Macroalgae made up 70–80% of the total biomass and was dominated by filamentous species. In contrast to previous studies, macroalgal biomass was higher at the exposed sites, which may be due to the fact that this was a spring study, unlike previous studies, which were conducted during summer.

1. Introduction

The intertidal zone of rocky shores is a dynamic environment where diversity, distribution, competition and abundance of both algae and animals are driven by the interplay between physical and biological factors (Christofoletti et al. 2011). In the Baltic Sea, this part of the shore is known as the 'hydrolittoral' zone (Wærn 1952). Since tides are negligible in the Baltic Sea (Keruss & Seŋŋikovs 1999), irregular and unpredictable variation in air pressure is the most important force driving water level fluctuations, with a maximum amplitude of approximately 2–4 m, depending on the area (Wallentinus 1976, Suursaar & Sooäär 2007). Wave exposure is an important structuring agent for rocky shore communities. Strong waves induce physical disturbances, particularly during the break-up of sea ice, influence the availability of nutrients to algae, replenish the food supply for sessile animals, alter sedimentation rates, and control the desiccation of intertidal/hydrolittoral organisms (Kraufvelin 2007). Furthermore, wave action can cause detachment of algae, thereby moderating the accumulation of excessive algal biomass (Pihl et al. 1999, Thompson et al. 2002, Barrón et al. 2003, Kraufvelin 2007, Kraufvelin et al. 2010). It has also been stated that macroalgae may induce 'whiplash effects', by which epiphytic algae are removed from their substrate or prevented from settling (Kiirikki 1996, Irwing & Connell 2006, Kraufvelin 2007). In combination with frequent ice-scraping events, irregular and prolonged periods of drought inhibit the recruitment and growth of perennial macroalgal species in the hydrolittoral zone and favour algal vegetation comprising fast-growing filamentous species with ephemeral life cycles (Choo et al. 2005, Kraufvelin et al. 2007).

The composition of the filamentous algal community in the hydrolittoral of the Baltic Sea shows strong seasonal variability in response to both regular seasonal changes and irregular disturbances (Hällfors et al. 1975, Wallentinus 1979, 1991, Borum 1985, Torn et al. 2010). The effects of the irregular disturbances also vary depending on season (Torn et al. 2010). The filamentous brown alga *Pylaiella littoralis* (L.) Kjellman begins to grow in January, and by April–May this species dominates the rocky shores (Wallentinus 1979, Kautsky et al. 1984, Kiirikki & Lehvo 1997, Lotze et al. 1999). The peak in *P. littoralis* biomass is followed by a rapid decrease in early June (Kautsky 1995). The green algae *Cladophora glomerata* (L.) Kütz (Wallentinus 1979, Kraufvelin & Salovius 2004) and *Ulva* spp. (Lotze et al.

1999) replace *P. littoralis* and are dominant throughout the summer. The filamentous red alga *Ceramium tenuicorne* (Kützing) Wærn occurs from the hydrolittoral zone downwards year-round and is a rapid colonizer of empty space (Bäck & Likolammi 2004, Qvarfordt 2006).

The animal subset of hydrolittoral communities appears to follow the same general pattern as found along other oceanic coasts, with a higher abundance of sessile suspension-feeding invertebrates on wave-exposed shores compared to wave-sheltered coasts, including *Balanus improvisus* Darwin and *Mytilus edulis* (L.) (Hällfors et al. 1975, Kautsky 1995, Westerbom et al. 2008). Menge (1976) suggested that this pattern was the result of a higher continuous flow of food particles at more exposed sites, which favours sessile organisms such as barnacles and mussels, whereas mobile invertebrates, like grazers and carnivores, occur in low numbers because of the increased risk of dislodgement. At more sheltered locations organic matter accumulates (Prathep et al. 2003) and sediment particles can be trapped in filamentous algae to a greater extent than in fucoids (Eriksson & Johansson 2003). A greater abundance of detrivores and deposit feeders can therefore be anticipated at more sheltered locations (Johnson 1985, Prathep et al. 2003). Disturbance in the form of wave action, for example, also has implications for richness and diversity, and theory predicts that both these peak at intermediate stress levels since neither consumer pressure nor abiotic stress is too great (Menge & Sutherland 1987, Bruno et al. 2003, Scrosati et al. 2011).

Most published studies investigating the ecology of the hydrolittoral zone in the Baltic Sea proper were published several decades ago (Jansson 1974, Haage 1975, Hällfors et al. 1975, Jansson & Kautsky 1977, Wallentinus 1979) and more recently by Salovius & Kraufvelin (2004). All these studies except the one by Haage (1975) describe summer conditions, with the first observations normally made in May. Furthermore, the studies from the 1970s can best be described as semi-quantitative: they do not meet modern requirements for statistical relevance. To date, there have been no true quantitative studies describing the spring succession of the hydrolittoral fauna in the northern Baltic proper (i.e. from March to June). As the recruitment of most macrofaunal species occurs in spring, this implies a gap in our understanding of the ecology of these habitats. It is unknown whether the abundance and biomass patterns observed on wave-exposed and wave-sheltered sites during the summer months are also valid during spring. Furthermore, to enable the identification of any future changes in the spring ecosystem, it is important to have recent information on species composition, as well as on the abundance, biomass and succession of the flora and fauna.

The aim of this study was to examine the development of community structure (qualitatively and quantitatively) on sheltered and wave-exposed shores during the spring in a part of the northern Baltic proper (Askö, Stockholm archipelago). We hypothesized that biomass and abundance would increase during the sampling period. Further, we assumed that wave action at wave-exposed sites could be considered as moderate disturbance; on the basis of theories underlying the effects of disturbance on biodiversity formulated by Menge & Sutherland (1987), Bruno et al. (2003) and Scrosati et al. (2011), we hypothesized that the biodiversity would be higher at the exposed sites. Our counter-hypothesis was that abundance would be higher on the sheltered sites as a consequence of the greater abundance of detrivores and deposit feeders.

2. Material and methods

2.1. Study area

The study was carried out in the vicinity of the Stockholm University field station at Askö Island (58°49′N, 19°39′E) in the northern Baltic proper. The area is considered to be one of the most undisturbed archipelagos in the northern Baltic proper. There is extensive sheep farming in parts of Askö; otherwise, the island is uninhabited. Houses, barns and corrals are located more than 3 km from our sites, and since there is no watercourse discharging into our study area, nutrient leaching from farmland or sewers is unlikely to have affected our results. The distance between wave-exposed and wave-sheltered sites was less than 100 m; hence, there were no potentially confounding differences in salinity and temperature.

The salinity in the area fluctuates around 6 per mil. The average water temperature is approximately 20°C in summer and may fall to 0°C in winter, when sea ice regularly forms (Voipio 1981). Ice cover in the northern Baltic proper lasts from 20 to 30 days and normally begins to break up in mid-March (Granskog et al. 2006); prolonged periods of low water are common in spring (Chen & Omstedt 2005). The southern shore of Askö is protected from north-easterly to north-westerly winds (Figure 1).

The study was conducted from March to May. The water level was 4–5 cm below the mean water level (MWL) in late March and dropped to 25–27 cm below MWL in early May. At this time the water level began to rise, and by late May, the water level was 13–14 cm above MWL. The water temperature rose from 1°C in late March to 8°C by late May. The maximum wind speed from the south-east, which is the sector most open to the sea, never exceeded 10 m s^{-1} during the sampling period. The salinity was fairly stable over the study period at 6.1–6.5 per mil.
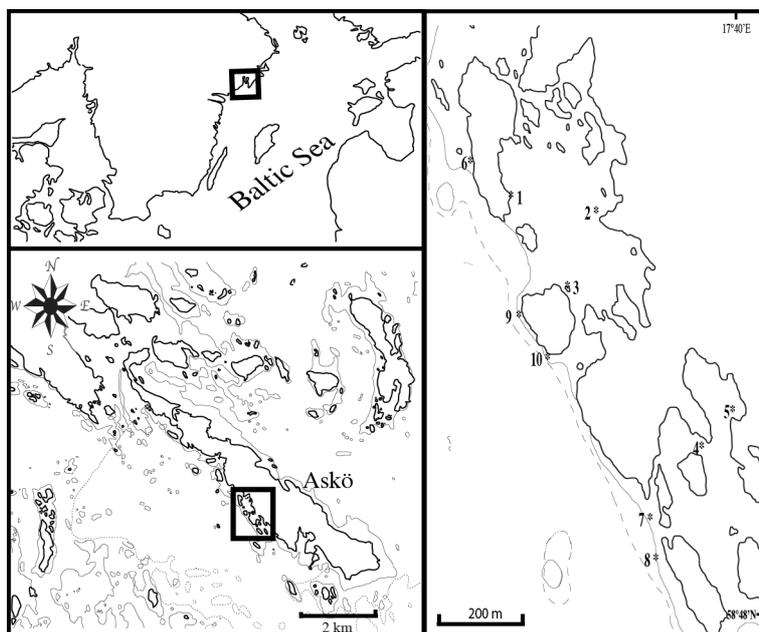
Figure 1. Map of the study area at Askö in the southern archipelago of Stockholm. Coastline contours are shown by thick solid lines. 3 m depth contours are indicated by thin solid lines and 6 m depth contours are indicated by thin dotted lines. The different collection sites are indicated by asterisks and the numbers 1 to 10

2.2. Sampling design

Ten sampling sites were chosen along the rocky shores of the south-western part of Askö Island – five wave-exposed sites and five wave-sheltered sites, all with approximately the same slope of 30° (Figure 1). Wave exposure at the sampling sites was calculated using the formula $L_f = (\sum c_i \cos g_i)/(\sum \cos g_i)$ (Håkansson 1981), where L_f is the maximum local fetch and c_i is the distance in km to the nearest land. L_f was 0–1 at wave-sheltered sites and 45–77 at wave-exposed sites. The distance was measured in 15 directions using deviation angles (g_i: ±6, ±12, ±18, ±24, ±30, ±36 and ±42) from a central radius; this was set in the direction that gave the highest L_f value.

Samples were collected on the hard bottom on four different occasions, in late March, mid-April, early May and late May. The first sampling period (25 and 26 March) occurred one week after the break-up of the ice-cover. Owing to the ice conditions on this occasion, three wave-exposed sites and three wave-sheltered sites were sampled, with four replicates at each site.

In the second (15 and 19 April), third (6 and 7 May) and fourth (25 and 27 May) sampling periods, five wave-sheltered and five wave-exposed sites were chosen, with four replicates at each site. For each wave-exposure range, the sites were selected randomly from a larger set of possible sampling sites.

The samples were collected at a depth of ~ 0.5 m below the MWL. A 0.04 m^2 quadrat (0.2×0.2 m) was placed at random on the rocky bottom. All organisms inside the quadrat were scraped off with a putty knife into a 1 mm mesh bag fixed to one side of the frame (Malm & Isæus 2005). All the samples were stored frozen ($-18°$C) until sorting, when they were sorted to the nearest possible taxa by one single person. The samples were dried to constant weight at 60°C, and the biomass of both algae and fauna, expressed in g, was measured accurate to three decimal points. *Gammarus* and *Idotea* specimens smaller than 4 mm were identified as juvenile *Gammarus* spp. and *Idotea* spp. Three species of the genus *Hydrobia*, namely *Hydrobia ulvae* (Pennant), *H. ventrosa* (Montagu) and *H. neglecta* (Muus), as well as the introduced species *Potamopyrgus antipodarum* (J. E. Gray) were all classified as the family Hydrobiidae. All cockles were classified to the family Cardiidae. Only the macrofauna were included in the study, that is, invertebrates larger than 1 mm (Hartley 1982). Prior to numerical analysis, all data were standardized with respect to biomass and frequency per m^2.

2.3. Statistical analyses

Multivariate analyses were conducted using PRIMER 6™ software on square root transformed data. Differences in community structure between wave exposure and sampling period were tested for by one-way analysis of similarities (ANOSIM) in a two-way crossed design. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis similarities was further used to map samples, and the similarity percentage breakdown procedure (SIMPER) was used to list the species contributing most to the observed dissimilarities between wave-sheltered and wave-exposed locations. The data were further analysed by univariate means using linear mixed models (LMM), which is a generalization of a repeated-measures ANOVA (West et al. 2007). ANOVA is based on the assumption of independent observations, whereas our model was adequately able to deal with correlation structures in the data and also to handle better an unequal number of replicates. This was essential since our design implied that samples were taken repeatedly at given sites, hence data were likely to be correlated even if the samples were taken independently (West et al. 2007). All the results are listed in Appendix. The models included sampling time and exposure, and their interaction, as fixed factors, while site was included as a random effect (the model is shown in the

supplementary material in Appendix). The model allows for correlations between repeated measurements over time within each site. The results of the statistical analyses are presented in Appendix both corrected for multiplicity according to Holm (1979) and uncorrected. Values of p that were initially lower than 0.05, but then became non-significant after the multiplicity correction, will still be brought up as potentially significant in the discussion, which is in accordance with the recommendations by Moran (2003) and practised by e.g. Kraufvelin (2007). We also examined the partial correlations between invertebrates and algae. In these analyses total algal biomass or the biomass of algae divided into four functional groups (filamentous green, filamentous red, filamentous brown and non-filamentous algae) were included as explanatory variables in addition to the factors mentioned above (the model is shown in Appendix). The analyses were performed on the median of the four replicates for each site and sampling time. To avoid increasing the complexity of the model by adding corrections for heterogeneity within the models, the abundance and biomass data were log-transformed prior to the analyses. The validity of the models was examined by residual plots, and the analyses were performed using SAS software ver. 8.2.

3. Results

3.1. General findings

46 taxa, comprising 20 algae and 26 invertebrates, were found to inhabit the hydrolittoral zone in the study area. Complete lists of species and their abundances and biomasses are presented in Tables 1 and 2. The number of species was higher at wave-sheltered locations (LMM, $p < 0.05$, Appendix) and increased over time, measured as the significant difference between the first and the third as well as the fourth sampling (LMM, $p < 0.0001$ in both cases, Appendix), i.e. from late March to early May (Figure 2). The difference in community structure based on biomass differences between the wave-sheltered and wave-exposed shores was significant (two-way crossed ANOSIM R $= 0.64$, $p = 0.001$) (Figure 3). No significant difference in the Shannon diversity index was found between shorelines experiencing different wave exposures, nor did the diversity change significantly over the sampling period (Table 1b, Appendix). The difference in community structure was significant, and over 95% of the Bray-Curtis dissimilarities were due to the biomass of only eleven taxa (SIMPER-analysis, see Tables 1 and 3). The total Bray-Curtis dissimilarity between exposed and sheltered sites was 75%, and the dissimilarities on respective sampling occasions were 61%, 58%,

Table 1. a) Biomass of macroalgae (g dry weight $m^{-2} \pm$ SD) of all taxa found in the hydrolittoral zone of the rocky shores of Askö, spring 2004. Species contributing more than 90% of the Bray-Curtis dissimilarities are in italics; $-=$ absence of species

	Late March		Mid-April		Early May		Late May	
	wave sheltered	wave exposed	wave sheltered	wave exposed	wave sheltered	wave exposed	wave sheltered	wave exposed
1	2	3	4	5	6	7	8	9
Algae								
Acrosiphonia arcta	0.04 ± 0.1	–	–	–	–	–	–	–
Cladophora glomerata	*0.24 ± 0.37*	–	*0.2 ± 0.31*	*0.02 ± 0.08*	*0.42 ± 0.83*	*0.16 ± 0.43*	*4.72 ± 5.61*	*0.97 ± 2.31*
Cladophora rupestris	0.1 ± 0.31	–	0.06 ± 0.24	0.01 ± 0.06	–	–	–	–
Monostroma grevillei	0.03 ± 0.03	0.88 ± 1.09	0.13 ± 0.36	1.36 ± 1.83	0.13 ± 0.22	0.22 ± 0.29	0.01 ± 0.06	0.02
Ulva intestinalis	–	–	–	0.02 ± 0.07	0.02 ± 0.05	–	0.39 ± 1.08	0.01
Ulva spp.	0.07 ± 0.2	0.02 ± 0.03	0.02 ± 0.04	–	–	–	–	–
Urospora penicilliformis	0.01 ± 0.03	1.18 ± 0.76	0.01	0.41 ± 0.44		0.01 ± 0.03	–	–
Chorda filum	–	0.01 ± 0.03	0.01 ± 0.03	0.3 ± 0.41	0.16 ± 0.28	0.83 ± 1.23	0.06 ± 0.14	2.69 ± 5
Dictyosiphon foeniculaceus	–	–	–	–	–	–	0.79 ± 3.14	0.02
Eudesme virescens	–	–	–	–	–	0.01 ± 0.03	0.26 ± 0.57	0.3 ± 0.54
Ectocarpus siliculosus	–	–	*1.76 ± 5.59*	*1.01 ± 4.51*	*13.79 ± 42.14*	–	*8.56 ± 18.11*	*0.7 ± 3.12*
Fucus vesiculosus	*2.38 ± 4.18*	0.01	*3.54 ± 5.56*	*0.06 ± 0.22*	*0.95 ± 1.41*	*1.13 ± 2.95*	*5.61 ± 9.18*	*0.06 ± 0.12*
Pylaiella litoralis	*18.02 ± 12.13*	*6.35 ± 4.62*	*44.84 ± 30.96*	*39.31 ± 32.17*	*47.99 ± 35.95*	*40.57 ± 41.54*	*24.43 ± 28.81*	*25.5 ± 35.32*
Sphacelaria arctica	–	–	0.23 ± 0.65	–	0.44 ± 0.81	–	0.25 ± 0.5	–
Stictyosiphon tortilis	–	0.02 ± 0.05	0.22 ± 0.6	–	0.12 ± 0.3	–	0.27 ± 0.41	0.09 ± 0.23
Ceramium tenuicorne	*1.02 ± 1.01*	*8.54 ± 7.34*	*0.86 ± 1.2*	*18.79 ± 18.21*	*0.92 ± 1.56*	*49.39 ± 49.17*	*0.86 ± 1.28*	*43.43 ± 49.37*
Furcellaria lumbricalis	0.01 ± 0.03	–	–	–	–	–	–	–
Polysiphonia fibrillosa	–	–	–	–	–	–	–	–
Polysiphonia fucoides	0.08 ± 0.23	–	0.02 ± 0.07	–	–	–	0.03 ± 0.11	–
Rivularia atra	1.45 ± 2.95	0.17 ± 0.11	0.96 ± 1.08	0.44 ± 0.46	0.59 ± 0.76	0.51 ± 0.47	1.13 ± 1.93	1.21 ± 1.62
Total biomass $[\mathrm{g\,dw\,m^{-2}}]$	**23.45**	**17.18**	**52.86**	**61.73**	**65.53**	**92.83**	**47.37**	**75.00**
Total number of algae taxa	**12**	**9**	**14**	**11**	**11**	**9**	**14**	**12**

Table 2. Abundance of invertebrates (No m$^{-2}\pm$SD) found in the hydrolittoral zone of the rocky shores of Askö, spring 2004

Animals	Late March		Mid-April		Early May		Late May	
	wave sheltered	wave exposed	wave sheltered	wave exposed	wave sheltered	wave exposed	wave sheltered	wave exposed
Hediste diversicolor	0 ± 0	0 ± 0	4 ± 9	0 ± 0	9 ± 15	5 ± 10	10 ± 17	4 ± 12
Gammarus locusta	0 ± 0	17 ± 39	54 ± 68	189 ± 286	56 ± 62	505 ± 927	25 ± 34	134 ± 99
Gammarus oceanicus	4 ± 14	31 ± 26	4 ± 9	40 ± 53	10 ± 22	44 ± 52	0 ± 0	26 ± 40
Gammarus salinus	23 ± 23	65 ± 114	20 ± 30	89 ± 66	8 ± 14	58 ± 112	36 ± 66	86 ± 46
Gammarus zaddachi	73 ± 75	515 ± 321	53 ± 62	893 ± 589	79 ± 100	2103 ± 1745	58 ± 133	1749 ± 1618
Gammarus spp.	31 ± 47	67 ± 73	183 ± 141	194 ± 199	500 ± 458	1525 ± 1273	939 ± 2229	4261 ± 2545
Idotea baltica	8 ± 22	2 ± 7	13 ± 25	10 ± 19	10 ± 29	71 ± 82	10 ± 24	20 ± 29
Idotea granulosa	0 ± 0	0 ± 0	1 ± 6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Idotea chelipes	2 ± 7	0 ± 0	6 ± 16	4 ± 12	14 ± 31	10 ± 26	21 ± 36	10 ± 19
Idotea juvenile	0 ± 0	0 ± 0	0 ± 0	5 ± 10	3 ± 8	10 ± 22	0 ± 0	0 ± 0
Jaera albifrons	8 ± 29	194 ± 342	31 ± 52	528 ± 712	10 ± 19	1466 ± 1266	30 ± 65	1084 ± 1240
Palaemon adspersus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 6	0 ± 0
Praunus inermis	0 ± 0	0 ± 0	13 ± 21	1 ± 6	11 ± 30	0 ± 0	8 ± 20	0 ± 0
Balanus improvisus	42 ± 67	42 ± 57	29 ± 38	181 ± 241	119 ± 204	399 ± 562	29 ± 60	55 ± 135
Ceratopogonidae	0 ± 0	0 ± 0	41 ± 118	0 ± 0	43 ± 66	1 ± 6	78 ± 101	1 ± 6
Chironomidae	898 ± 840	48 ± 79	3906 ± 2544	1628 ± 1743	3129 ± 1807	5329 ± 3928	1301 ± 1443	959 ± 940
Tricoptera	2 ± 7	0 ± 0	29 ± 79	0 ± 0	11 ± 17	0 ± 0	18 ± 23	0 ± 0
Cardiidae	835 ± 1151	8 ± 16	1000 ± 1293	23 ± 44	625 ± 717	165 ± 260	804 ± 1161	48 ± 114
Macoma baltica	2 ± 7	0 ± 0	20 ± 44	0 ± 0	26 ± 65	1 ± 6	35 ± 60	1 ± 6
Mya arenaria	0 ± 0	0 ± 0	1 ± 6	0 ± 0	4 ± 17	0 ± 0	3 ± 11	0 ± 0
Mytilus edulis	13 ± 23	648 ± 521	53 ± 82	1344 ± 1556	53 ± 97	3416 ± 3628	83 ± 88	4641 ± 6099
Bithynia tentaculata	0 ± 0	0 ± 0	8 ± 24	0 ± 0	11 ± 32	0 ± 0	1 ± 6	0 ± 0
Hydrobiidae	292 ± 674	2 ± 7	2063 ± 2694	36 ± 56	2638 ± 3165	31 ± 56	2401 ± 2357	8 ± 28
Lymnaea stagnialis	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 6	0 ± 0	0 ± 0	0 ± 0
Radix baltica	0 ± 0	0 ± 0	20 ± 72	0 ± 0	3 ± 8	0 ± 0	4 ± 9	0 ± 0
Theodoxus fluviatilis	152 ± 164	96 ± 162	319 ± 273	806 ± 2977	458 ± 416	415 ± 479	596 ± 355	219 ± 374
Total [m$^{-2}\pm$SD]	**2385**	**1735**	**7871**	**5971**	**7831**	**15554**	**6491**	**13306**
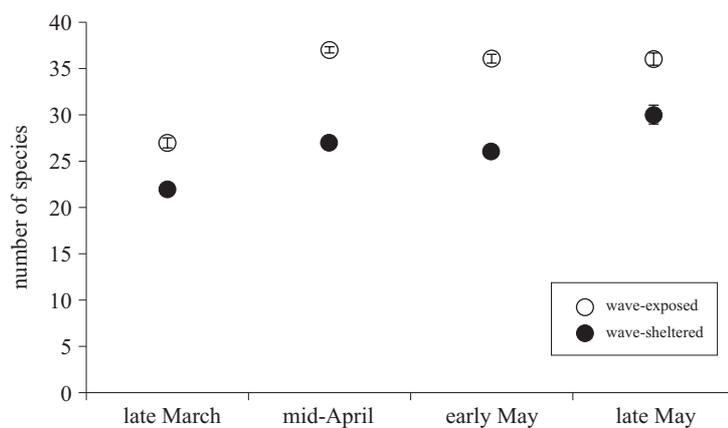
Figure 2. Number of species ($\pm$ SE) at wave-exposed and wave-sheltered sites in the hydrolittoral zone of Askö, spring 2004
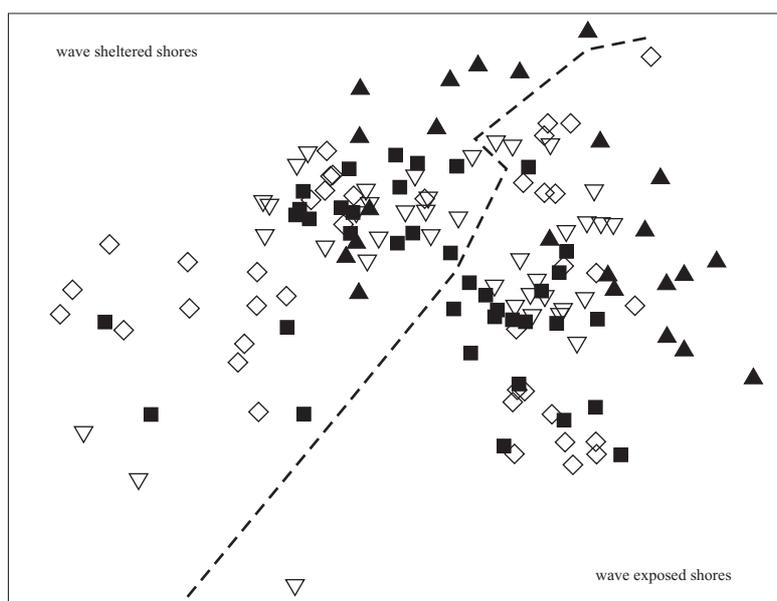
Figure 3. NMDS-plot based on Bray-Curtis similarities of communities in the hydrolittoral zone of Askö, spring 2004. Wave-exposed and wave-sheltered communities are clearly separated as indicated by the hatched line; ▲ indicates communities in late March, ∇ in mid-April, ■ in May and ◇ in late May. Data were square root transformed, and the stress value is 0.18

59%, and 71%, starting with the first sampling. The development of the biomass of the eleven dominant species is shown in Figure 4.
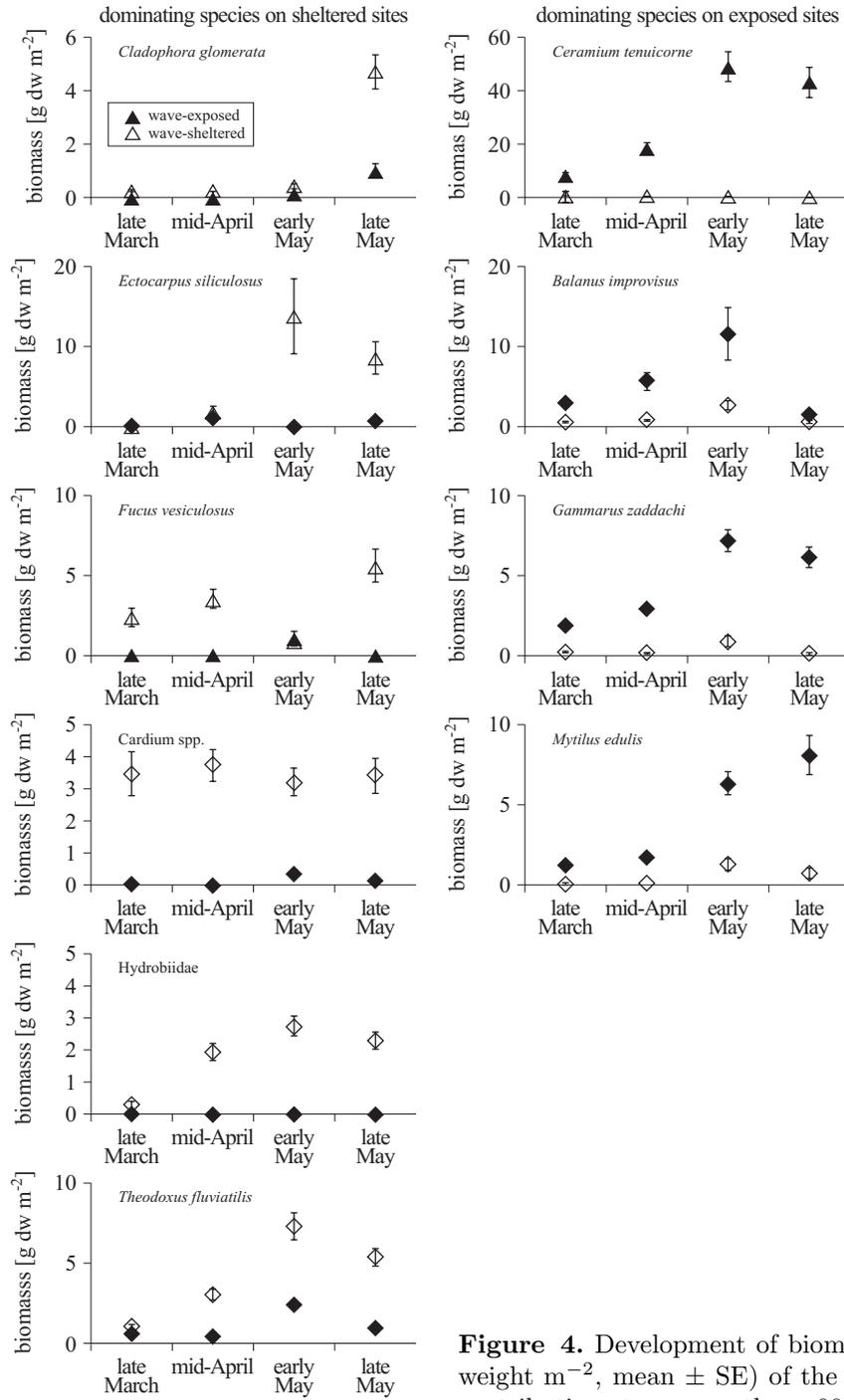
Figure 4. Development of biomass (g dry weight m^{-2}, mean ± SE) of the 10 species contributing to more than 90% of the Bray-Curtis dissimilarities in the community structure on wave-exposed and wave-sheltered sites in the hydrolittoral zone of Askö, spring 2004

Table 3. Differences in community structure between wave exposure and sampling period were tested for by one-way analysis of similarities (ANOSIM) in a two-way crossed design based on biomass data for algae and animals from rocky shores of the island of Askö, northern Baltic Proper, 2004, significance level 0.1%

Sampling dates	R statistics
late March ⇔ mid-April	0.301
late March ⇔ early May	0.559
late March ⇔ late May	0.453
mid-April ⇔ early May	0.103
mid-April ⇔ late May	0.220
early May ⇔ late May	0.157

The total abundance of the macrofauna taxa ranged between 1700 and 15 500 individuals m^{-2}, with the highest numbers being found at the wave-exposed sites on the last two sampling occasions in May (Table 2, Appendix). The number of individuals increased with time until early May at both sheltered and wave-exposed sites measured as the significant difference between the first and third sampling at respective sites ($p < 0.01$ for both, Appendix).

The macroalgae found in the hydrolittoral zone constituted 70–80% of the total biomass on both wave-exposed and wave-sheltered shores. The total biomass of macroalgae increased at both exposed and sheltered sites until it peaked in early May (Figure 5). This was measured as the significant difference between the first and third sampling at the exposed sites (LMM,
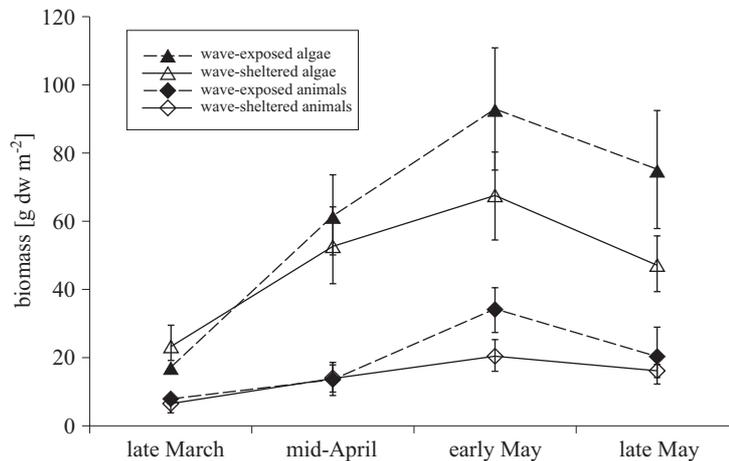

Figure 5. Development of algae and animal biomass (g dry weight m^{-2}, mean ± SE) in the hydrolittoral zone of Askö, spring 2004

$p < 0.0001$, Appendix) and sheltered sites ($p < 0.01$, Appendix). There were no differences in total algal biomass between exposed or sheltered sites on the first two sampling occasions, whereas there were significant differences on the two subsequent sampling occasions ($p < 0.05$ in both cases, Appendix, Figure 5). The total algal biomass at the exposed sites ranged from 17 g dry weight m^{-2} in late March to a maximum of 93 g dry weight m^{-2} in early May, while the average maximum biomass at the wave-sheltered sites was 65 g dry weight m^{-2} (Table 1a). The development of algal biomass was followed by a similar development of faunal biomass (Figure 5, Table 1b), which varied between 6.5 and 34 g dry weight m^{-2}. The ratio between algal biomass and faunal biomass varied between 2.2 and 4.6; we found no effect of sampling or site exposure level on these ratios.

3.2. Algae

Filamentous algae were dominant during the sampling period, and constituted over 85% of the total algal biomass at all times. Each group of red, green, and brown filamentous algae was completely dominated by one species: *Ceramium tenuicorne* dominated the red algae ($> 99\%$), *Pylaiella littoralis* the brown algae ($> 85\%$) and *Cladophora glomerata* the green algae ($> 70\%$). *Chorda filum* (L.) Stackhouse and *Fucus vesiculosus* were of equal importance among the non-filamentous algae. Among all algal species, *P. littoralis* was the single dominant species at the sheltered sites on all four sampling occasions. This species also was dominant on the first two sampling occasions at the exposed sites, with peaks in mid-April and early May (Table 1a, Figure 4). No significant change with time or between exposure levels was seen for *P. littoralis*. The red alga *C. tenuicorne* started to increase in May along the wave-exposed sites, reaching biomasses of up to 49 g dry weight m^{-2} (Table 1a, Figure 4), which were significantly higher than on wave-sheltered shorelines (LMM, $p < 0.01$, Appendix). In May, *C. tenuicorne* accounted for approximately 55% of the standing biomass at the exposed sites and *P. littoralis* for around 40%. Juvenile specimens of perennial brown algae, mainly *F. vesiculosus*, had started to grow in the hydrolittoral zone on the first sampling occasion and increased with time at the exposed sites from 0.02 to 2.75 g dry weight m^{-2}. Growth was more rapid at the sheltered sites and increased from 2.4 to 5.7 g dry weight m^{-2}. The biomass of *F. vesiculosus* was significantly higher along the wave-sheltered than the wave-exposed shores (LMM, $p < 0.05$, Appendix), but the biomass did not change significantly over time.

3.3. Fauna

Significant differences were found in the species composition between exposed and sheltered sites. The gastropods *Bithynia tentaculata* L., *Radix baltica* L. and *Lymnaea stagnalis* L., the bivalve *Mya arenaria* L., the crustaceans *Idotea chelipes* (Pallas) and *Palaemon adspersus* (Rathke), and the insect order Trichoptera were found only at the wave-sheltered sites. The most abundant taxa at the wave-sheltered sites were Hydrobiidae, Cardiidae and Chironomidae. The abundances of these species were significantly higher at the wave-sheltered sites (LMM, $p < 0.001$, $p < 0.001$ and $p < 0.05$ respectively, Appendix). The abundance of gastropods increased over time at the sheltered sites, measured as the significant difference between the first and last sampling (LMM, $p < 0.01$, Appendix), while no change was observed at the exposed sites (Table 2). There were no species that were found only at the wave-exposed sites. The most abundant species at the wave-exposed sites were *Gammarus zaddachi* (Sexton) and *Mytilus edulis*. There was also a significant difference between exposed and sheltered sites for these species (LMM, $p < 0.001$ and $p < 0.01$ respectively). In addition, there was an increase over time of *G. zaddachi* and juvenile gammarids at the exposed sites, measured as the significant difference between the first and last sampling (LMM, $p < 0.01$ and $p < 0.0001$ respectively, Appendix).

In a similar way to algae, the biomass of invertebrates increased significantly over time (LMM, $p < 0.01$, Appendix, Figure 5). The biomass of *G. zaddachi* peaked in early May at the wave-exposed sites, while the biomass was low and constant at the sheltered sites (Table 1b, Figure 4). The biomass was significantly higher at the wave-exposed sites than at the wave-sheltered sites (LMM, $p < 0.001$, Appendix). In contrast, the biomass of Cardiidae and Hydrobiidae were significantly higher at the wave-sheltered sites (LMM, $p < 0.001$, $p < 0.01$, Appendix) (Figure 4). The increase in biomass of all these species (except Cardiidae) was delayed compared to the algal biomass (Figure 4, Table 1a,b). Hydrobiidae only increased in abundance at the wave-sheltered sites ($p < 0.01$, Appendix), while the biomass of Cardiidae showed no significant changes over time (Figure 4).

3.4. Interactions between algae and fauna

Red filamentous algae, in this case 99% *C. tenuicorne*, were positively correlated with the abundance of *M. edulis* (LMM, $p < 0.001$). The isopods *Idotea* spp. were less abundant, but showed a positive correlation with the non-filamentous algae (LMM, $p < 0.05$). No specific correlations were found for brown filamentous algae or green filamentous algae with the abundance of any of the invertebrates.

4. Discussion

After the sea ice broke up in the middle of March, a community dominated by filamentous macroalgae rapidly established itself in the rocky hydrolittoral zone. As expected, because of increased temperature and light and from the life cycles of the organisms, the biomass increased from the first sample collection in March to the last sample collection in May at three of the sheltered sites and at four of the exposed sites. During the same period, the number of taxa increased only slightly. Three species were mainly responsible for the significant changes in algal biomass over time: *Pylaiella littoralis, Ceramium tenuicorne* and *Fucus vesiculosus* (Figure 5). The peak of *P. littoralis* and *C. tenuicorne* occurred in early May, coinciding with the development of increased faunal biomass. In contrast to previous findings in the northern Baltic Sea (e.g. Hällfors et al. 1975, Rönnberg 1975), we found a higher macroalgal biomass at the exposed sites than at the sheltered sites on the last two sampling occasions. This difference could be explained by the fact that the present study was performed during spring and because we focused on the hydrolittoral zone (0–0.5 m under MWD). Other comparable investigations (see Hällfors et al. 1975, Rönnberg 1975, Jansson & Kautsky 1977, Kautsky 1995) started sampling in May and continued sampling through the summer, usually with samples collected below the hydrolittoral zone. In those studies, filamentous algae, including *Cladophora glomerata*, *Dictyosiphon foeniculaceus* (Hudson) Greville and *Ectocarpus siliculosus* (Dillwyn) Lyngbye, were dominant at sheltered sites, whereas these species were present in only low biomasses during our spring study. *C. glomerata* possesses a number of traits that gives it a competitive advantage compared to other algae in shallow areas. It is promoted by higher temperature (Snoeijs & Prentice 1989), it has a superior nutrient and carbon uptake capability (Wallentinus 1984, Choo et al. 2005), as well as a better ability to cope with light stress in the upper littoral zone (Choo et al. 2005). This is probably the main reason for our contrasting results compared to the earlier studies, and the reason why we rejected our hypothesis that biomass would be higher at wave-sheltered sites.

To describe the spring development in greater detail, the first species to exhibit increased biomass was the brown alga *P. littoralis*. The explanation for the successful early establishment of *P. littoralis* is that it reproduces in winter (Kiirikki & Lehvo 1997) and has the ability to grow rapidly at low temperatures (5°C), compared to other competitive filamentous species like *C. glomerata*, *D. foeniculaceus* and *E. siliculosus* (Lotze et al. 1999). The biomass produced by *P. littoralis* was substantially less than that found in the only other quantitative investigation conducted in the spring in the Baltic Sea: Kraufvelin et al. (2007) reported a 2 to 6 times higher biomass

of *P. littoralis.* This difference may be due to the higher nutrient content in the Tvärminne archipelago in southern Finland (Bernes 2005) than in our study area, which could be stimulating annual algal growth (Worm & Lotze 2006). *P. littoralis* appears to be a strong competitor irrespective of wave exposure, since we did not see any differences between the sheltered and exposed sites for this species. This assumption is supported by observations made by Lotze et al. (1999), along with the demonstrated plasticity of this species to different environmental conditions (Müller & Stache 1989). We did not find any specific correlation between *P. littoralis* and any of the macrofaunal species, probably because the alga had a similar biomass across both exposures and on all sampling occasions. In early spring, *Ulva intestinalis* L. has been shown to be superior to *P. littoralis* in occupying space (Lotze et al. 2000), and grazing experiments have shown that *P. littoralis* is preferred by gammarids as a food source over *Ulva, Ceramium, Cladophora, Fucus* and *Furcellaria* (Orav-Kotta et al. 2009). Although contradictory to our results, these findings may still support the results of our study. Among the first faunal species to occur in high numbers was from Hydrobiidae. Being a grazer, it may have indirectly supported the growth of *P. littoralis* rather than the usually common *U. intestinalis,* owing to selective grazing during the establishment period (Lotze et al. 2000), which may also explain the restricted occurrence of *U. intestinalis* in our study. Later in spring when gammarids become more abundant, they may begin to feed on *P. littoralis*, which may partly explain the reduction in the biomass of this alga at this time. The dominance of *P. littoralis* during the early spring and the demonstrated food preference for gammarids (Orav-Kotta et al. 2009) means that *P. littoralis* is a foundation species for food and shelter for the spring macrofauna community.

In contrast to *P. littoralis*, the biomass of *C. tenuicorne* was ten times greater at the wave exposed sites than at the more sheltered sites (30–58% and 3–4% of the total algal biomass respectively), which supports the results of Wærn (1952), Hällfors et al. (1975), Wallentinus (1991) and Bäck & Likolammi (2004). The weak competitive ability of this species at wave-sheltered sites could be due to its slow growth, giving it a competitive disadvantage at these sites compared to more opportunistic species like *C. glomerata* (Korpinen et al. 2007), which can better withstand sedimenting particles (Eriksson & Johansson 2005).

The spring development in our study, expressed as the relationship between the biomass of primary and secondary producers, was lower (2.2 to 4.6) than previously reported summer ratios for the Baltic Sea: from 6 to 61 at an exposed site and from 8 to 296 at a more sheltered site (Hällfors et al. 1975). Our results indicate that a standing crop with a biomass higher

than the faunal biomass by a factor of two to five is sufficient to support the fauna in the spring ecosystem, whereas the high summer (July to August) ratios indicate that a surplus of algal material is available to grazing animals in this part of the Baltic Sea. We assume that there are several possible explanations for these differences between seasons. One could be the lower rate of metabolism at lower temperatures in smaller individuals during spring. Another factor could be that during spring, the diatom bloom in the microphytobenthos plays an important role (Gebersdorf et al. 2005); we did not measure this in the present study.

A significant partial correlation was found between *C. tenuicorne* and *M. edulis.* This may be explained by the settling preference of this bivalve on either other byssus threads or on filamentous algae (Cáceres-Martinez et al. 1994, Hunt et al. 1996). Wallin et al. (2011) found similar results on sublittoral boulders: they suggested that the lack of a correlation with, for example, *P. littoralis* might be due to the detachment of this species during the settling season of the mussels. Another possible explanation could be the microhabitat structure of many red algae (Kraufvelin et al. 2006). Both the biomass and abundance of *M. edulis* were significantly higher at the exposed sites, confirming the structuring effect of wave action (Westerbom et al. 2008), which continuously replenishes food particles for suspension-feeding animals (Leigh et al. 1987). Differences in predation pressure between wave-exposed and wave-sheltered sites are probably not very important at our study sites, since critical predators, such as starfish and crabs, are not found in the northern Baltic Sea.

In the present study, the biomass of *F. vesiculosus* never exceeded 12% of the total algal biomass, which contrasts with previous studies (Kiirikki 1996, Bäck & Ruuskanen 2000). We found a higher biomass of *F. vesiculosus* at sheltered sites compared to wave-exposed sites. The juvenile specimens of *F. vesiculosus* increased in biomass from March to late May, especially at the sheltered sites, and this could be an effect of the more severe ice scraping at the exposed sites, resulting in fewer surviving specimens. Disturbance in the form of ice scraping is often found at natural field sites on cold temperate coasts (Kiirikki & Ruuskanen 1996). Since the settlement of *F. vesiculosus* normally occurs in June (Berger et al. 2003), the small surviving propagules were able to start growing in March, even though the hydrolittoral zone was still covered by ice. Our findings show that *F. vesiculosus* specimens were able to grow in spite of competition with *P. littoralis*: growth was variable, but the maximum biomass was the same as that recorded by Berger et al. (2003). The abundance of Cardiidae, Hydrobiidae and *Theodoxus fluviatilis* L. was high at the sheltered sites, where *F. vesiculosus* was frequently found; these gastropods may favour *Fucus* growth by selective grazing of

the filamentous annual algae (Worm et al. 2001). Furthermore, the high number of filtering species like Cardiidae may reduce suspended matter in the column, which has been shown to be important for the survival of young *Fucus* specimens (Berger et al. 2003). We found endofaunal species like *Mya arenaria* in the hydrolittoral. This species and also *Macoma balthica*, for instance, belong in the sediment but can sometimes be found in other environments. This may be due to active transport of the organism from the sediment (Sorlin 1988, Cummings et al. 1993).

The dominance of *Mythilus edulis* in the abundance was one of the main reasons for rejecting our hypothesis regarding higher diversity at the wave-exposed sites. Koivisto et al. (2011) have shown that the successional stage of the mussels is a strong determinant of faunal abundance: mussel size was positively correlated to faunal abundance and species richness. In the present study young mussels dominated the samples and no positive effect of the presence of mussels on faunal abundance could be observed. A second explanatory factor associated with this result was the higher number of invertebrate species, particularly of freshwater origin, found exclusively at the sheltered sites; this included the gastropods *Bithynia tentaculata*, *Radix baltica* and *Lymnaea stagnalis*, and the insect order Trichoptera. Because of their weight, several species (e.g. *L. stagnalis*) have difficulty in remaining attached to the vegetation at wave-exposed locations. This ability to cling on to vegetation has proved important for the isopod *Idotea balthica* (Pallas), particularly at wave-exposed sites, as this species prefers the narrow thallus of *F. vesiculosus* to the broader thallus of *Fucus serratus* L. (Engkvist et al. 2004). In addition, some of the observed freshwater species are mostly deposit- and detritus-feeders that benefit from the larger amounts of suspended matter being deposited at wave-sheltered sites. All these factors probably increased the diversity at the sheltered sites compared to the exposed sites.

This study is a thorough investigation of the spring hydrolittoral ecology in the Baltic Sea. Appropriately replicated in time and space and covering the spring development, this study can complement other important studies, e.g. Wærn 1952, Haage 1975, Kautsky & van der Maarel 1990, and help to acquire a better understanding of the spring succession of filamentous algae and the associated macrofauna in this region. The results clearly demonstrate the dominance and succession of filamentous algae in the hydrolittoral zone in spring and may explain the fluctuations in several invertebrate species, especially the grazers, which find shelter among the algae. The study indicates that the general experience of wave impact on hydrolittoral communities from oceanic areas is also applicable in the northern Baltic proper, despite its low salinity and the absence of tides.

Acknowledgements

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Appendix

SAS-code main comparisions

```
ODS GRAPHICS On;
proc mixed data=s2 cl covtest;
class sampling exposure sample;
model y = sampling exposure sampling*exposure / s ddfm=kr
residual;
random sample / s;
repeated sampling / subject=sample type=cs;
lsmeans  sampling exposure sampling*exposure / diff;
run; ods graphics off; quit;
```

Results – main comparisons

In the following tables we present the results of the statistical tests. Fixed effects are presented in a table of differences within one factor e.g. differences between specific sampling occasions are presented under differences of least squares means. We have used the following denotations: Sampling 1 = late March, Sampling 2 = mid-April, Sampling 3 = early May, and Sampling 4 = Late May, Exposure 1 = sheltered sites and Exposure 2 = exposed sites. Corrected = Multiplicity corrections according to Holm (1979).

Number of species

Table 1. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	20.1	13.83	< 0.0001
exposure	1	7.86	6.98	< 0.05
samp. × exp.	3	20.1	0.86	ns

Table 2. Differences of least squares means

Effect	Samp.	Exp.	Samp.	Exp.	Estimate	SE	DF	t	p	Corrected
sampling	1		2		−3.70	0.86	20.52	−4.30	< 0.001	significant
sampling	1		3		−5.00	0.86	20.52	−5.81	< 0.0001	significant
sampling	1		4		−5.05	0.86	20.52	−5.87	< 0.0001	significant

Diversity measured as Shannon index

Table 3. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	19.9	0.58	ns
exposure	1	7.56	0.15	ns
samp. × exp.	3	19.9	2.15	ns

Abundance of fauna

Table 4. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	20.4	11.51	0.0001
exposure	1	7.77	0.87	ns
samp. × exp.	3	20.4	1.64	ns

Table 5. Differences of least squares means

Effect	Samp.	Exp.	Samp.	Exp.	Estimate	SE	DF	t	p	Corrected
sampling	1		2		−1.24	0.33	21.46	−3.74	< 0.01	significant
sampling	1		3		−1.88	0.33	21.46	−5.66	< 0.0001	significant
sampling	1		4		−1.59	0.33	21.46	−4.80	< 0.0001	signifiant
exposure		1		2	−0.27	0.29	7.77	−0.93	ns	ns
samp. × exp.	1	1	1	2	−0.10	0.57	27.77	−0.18	ns	ns
samp. × exp.	1	1	2	1	−1.46	0.47	21.46	−3.11	< 0.01	significant
samp. × exp.	1	1	3	1	−1.50	0.47	21.46	−3.19	< 0.01	significant
samp. × exp.	1	1	4	1	−1.42	0.47	21.46	−3.02	< 0.01	significant
samp. × exp.	1	2	2	2	−1.03	0.47	21.46	−2.18	< 0.05	ns
samp. × exp.	1	2	3	2	−2.27	0.47	21.46	−4.82	< 0.0001	significant
samp. × exp.	1	2	4	2	−1.77	0.47	21.46	−3.75	< 0.01	significant
samp. × exp.	2	1	2	2	0.33	0.44	25.29	0.75	ns	ns
samp. × exp.	3	1	3	2	−0.91	0.44	25.30	−2.06	< 0.05	ns
samp. × exp.	4	1	4	2	−0.87034	0.44	25.30	−1.98	0.05	ns

Biomass of algae

Table 6. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	20.4	14.37	< 0.0001
exposure	1	8.01	0.61	ns
samp. × exp.	3	20.4	1.12	ns

Table 7. Differences of least squares means

Effect	Samp.	Exp.	Samp.	Exp.	Estimate	SE	DF	t	p	Corrected
sampling	1		2		−0.95	0.20	21.15	−4.73	< 0.001	significant
sampling	1		3		−1.29	0.20	21.15	−6.44	< 0.0001	significant
sampling	1		4		−1.03	0.20	21.15	−5.13	< 0.0001	significant
exposure		1		2	−0.16	0.21	8.01	−0.78	ns	ns
samp. × exp.	1	1	1	2	0.26	0.36	26.91	0.70	ns	ns
samp. × exp.	1	1	2	1	−0.75	0.28	21.15	−2.66	< 0.05	ns
samp. × exp.	1	1	3	1	−0.98	0.28	21.15	−3.46	< 0.01	significant
samp. × exp.	1	1	4	1	−0.69	0.28	21.15	−2.44	< 0.05	ns
samp. × exp.	1	2	2	2	−1.14	0.28	21.15	−4.03	< 0.001	significant
samp. × exp.	1	2	4	2	−1.36	0.28	21.15	−4.81	< 0.0001	significant
samp. × exp.	2	1	2	2	−0.13	0.28	21.97	−0.45	ns	ns
samp. × exp.	3	1	3	2	−0.81	0.28	21.97	−2.35	< 0.05	ns
samp. × exp.	4	1	4	2	−0.72	0.28	21.97	−2.07	< 0.05	ns

Biomass of fauna

Table 8. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	20.2	5.67	< 0.01
exposure	1	7.62	0.77	ns
samp. × exp.	3	20.2	0.66	ns

Table 9. Differences of least squares means

Effect	Samp.	Exp.	Samp.	Exp.	Estimate	SE	DF	t	p	Corrected
sampling	1		2		−0.85	0.37	21.22	−2.31	< 0.05	ns
sampling	1		3		−1.50	0.37	21.22	−4.07	< 0.001	signifcant
sampling	1		4		−1.05	0.37	21.22	−2.84	< 0.01	significant
exposure		1		2	−0.29	0.33	7.62	−0.88	ns	ns

Algae/fauna ratio

Table 10. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	22.7	1	ns
exposure	1	9.06	0.61	ns
samp. × exp.	3	22.7	0.86	ns

Ceramium tenuicorne

Table 11. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	19.7	0.82	ns
exposure	1	7.21	14.72	0.01
samp. × exp.	3	19.7	0.73	ns

Table 12. Differences of least squares means

Effect	Samp.	Exp.	Samp.	Exp.	Estimate	SE	DF	t	p	Corrected
sampling	1		2		0.15	0.86	20.55	0.18	ns	ns
sampling	1		3		−0.67	0.86	20.55	−0.78	ns	ns
sampling	1		4		0.41	0.86	20.55	−0.48	ns	ns
exposure		1		2	−3.24	0.84	7.21	−3.84	< 0.01	ns
samp. × exp.	1	1	1	2	−2.50	1.52	27.23	−1.65	ns	ns
samp. × exp.	1	1	2	1	0.42	1.21	20.55	0.34	ns	ns
samp. × exp.	1	1	3	1	0.37	1.21	20.55	0.30	ns	ns
samp. × exp.	1	1	3	2	−4.21	1.37	25.80	−3.07	< 0.01	ns
samp. × exp.	1	1	4	1	0.57	1.21	20.55	0.47	ns	ns
samp. × exp.	1	2	2	2	−0.12	1.21	20.55	−0.09	ns	ns
samp. × exp.	1	2	3	2	3.08	1.37	25.80	2.25	< 0.05	ns
samp. × exp.	1	2	4	2	−1.70	1.21	20.55	−2.14	< 0.05	ns
samp. × exp.	2	1	2	2	−3.04	1.20	22.67	−2.54	< 0.05	ns
samp. × exp.	3	1	3	2	−4.57	1.20	22.67	−3.83	< 0.001	significant
samp. × exp.	4	1	4	2	−2.84	1.20	22.67	−2.37	< 0.05	ns

Fucus vesiculosis

Table 13. Test of fixed effects

	Num DF	Den DF	F	P
sampling	3	21.5	2.41	ns
exposure	1	8.6	8.88	< 0.05
samp. × exp.	3	21.5	1.75	ns

Abundance of Hydrobia

Table 14. Test of fixed effects

	Num DF	Den DF	F	P
sampling	3	20.7	1.66	ns
exposure	1	7.91	41.93	< 0.001
samp. × exp.	3	20.7	2.40	ns

Abundance of Chironomidae

Table 15. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	21.7	12.97	< 0.0001
exposure	1	7.9	6.58	< 0.05
samp. $\times$ exp.	3	21.7	3.84	< 0.05

Abundance of Cardiidae

Table 16. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	21.3	0.90	ns
exposure	1	8.62	23.86	< 0.001
samp. $\times$ exp.	3	21.3	0.84	ns

Abundance of Gastropoda

Table 17. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	20.3	3.66	< 0.05
exposure	1	7.92	17.95	< 0.01
samp. $\times$ exp.	3	20.3	0.88	ns

Table 18. Differences of least squares means

Effect	Samp.	Exp.	Samp.	Exp.	Estimate	SE	DF	t	p	Corrected
sampling	1		2		-1.08	0.53	21	-2.04	0.05	ns
sampling	1		3		-1.71	0.53	21	-3.20	< 0.01	ns
sampling	1		4		-1.42	0.53	21	-2.66	< 0.05	ns
exposure		1		2	2.40	0.57	7.92	4.24	< 0.01	significant
samp. $\times$ exp.	1	1	1	2	1.73	0.97	26.8	1.78	ns	ns
samp. $\times$ exp.	1	1	2	1	-1.51	0.75	21.0	-2.00	ns	ns
samp. $\times$ exp.	1	1	3	1	-1.88	0.75	21.0	-2.49	< 0.05	ns
samp. $\times$ exp.	1	1	4	1	-2.17	0.75	21.0	-2.88	< 0.01	ns
samp. $\times$ exp.	1	2	2	2	-0.66	0.75	21.0	-0.88	ns	ns
samp. $\times$ exp.	1	2	3	2	-1.54	0.75	21.0	-2.04	0.05	ns
samp. $\times$ exp.	1	2	4	2	-0.66	0.75	21.0	-0.88	ns	ns
samp. $\times$ exp.	2	1	2	2	2.57	0.77	21.6	3.33	< 0.01	significant
samp. $\times$ exp.	3	1	3	2	2.06	0.77	21.6	2.67	0.05	ns
samp. $\times$ exp.	4	1	4	2	3.23	0.77	21.6	4.18	< 0.001	significant

Abundance of *Gammarus zaddachi*

Table 19. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	19.7	6.75	< 0.01
exposure	1	7.16	29.09	0.001
samp. × exp.	3	19.7	1.77	ns

Table 20. Differences of least squares means

Effect	Samp.	Exp.	Samp.	Exp.	Estimate	SE	DF	t	p	Corrected
sampling	1		2		−0.88	0.41	20.57	−2.12	< 0.05	ns
sampling	1		3		−1.65	0.41	20.57	−3.99	< 0.001	significant
Sampling	1		4		−1.57	0.41	20.57	−3.79	< 0.01	ns
exposure		1		2	−2.14	0.40	7.16	−5.39	< 0.001	significant
samp. × exp.	1	1	1	2	−2.09	0.73	27.36	−2.88	< 0.01	ns
samp. × exp.	1	1	2	1	−1.20	0,58	20.57	−2.04	0.05	ns
samp. × exp.	1	1	3	1	−1.69	0.58	20.57	−2.89	< 0.01	ns
samp. × exp.	1	1	4	1	−1.11	0.58	20.57	−1.89	ns	ns
samp. × exp.	1	2	2	2	−0.55	0.58	20.57	−0.95	ns	ns
samp. × exp.	1	2	3	2	−1.61	0.58	20.57	−2.75	< 0.05	ns
samp. × exp.	1	2	4	2	−2.03	0.58	20.57	−3.47	< 0.01	significant
samp. × exp.	2	1	2	2	−1.45	0.57	23.13	−2.54	< 0.05	ns
samp. × exp.	3	1	3	2	−2.01	0.57	23.13	−3.53	< 0.01	significant
samp. × exp.	4	1	4	2	−3.02	0.57	23.13	−5.30	< 0.0001	significant

Abundance of *Mytilus edulis*

Table 21. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	20.1	1.35	ns
exposure	1	7.52	23.57	< 0.01
samp. × exp.	3	20.1	1.33	ns

Abundance of juvenile *Gammarus* **spp.**

Table 22. Test of fixed effects

	Num DF	Den DF	F	P
sampling	3	21.1	11.44	p < 0.0001
exposure	1	8.18	3.22	ns
samp. × exp.	3	21.1	1.83	ns

Table 23. Differences of least squares means

Effect	Samp.	Exp.	Samp.	Exp.	Estimate	SE	DF	t	p	Corrected
sampling	1		2		−3.38	0.95	22.3	−3.57	< 0.01	ns
sampling	1		3		−4.80	0.95	22.3	−5.07	< 0.0001	significant
sampling	1		4		−5.14	0.95	22.3	−5.43	< 0.0001	ns
exposure		1		2	−1.32	0.73	8.18	−1.79	ns	ns
samp. × exp.	1	1	1	2	−1.03	1.57	28	−0.65	ns	ns
samp. × exp.	1	1	2	1	−4.15	1.34	22.3	−3.10	< 0.01	ns
samp. × exp.	1	1	3	1	−4.55	1.34	22.3	−3.40	< 0.01	significant
samp. × exp.	1	1	4	1	−4.05	1.34	27.8	−5.21	< 0.01	significant
samp. × exp.	1	2	2	2	−2.62	1.34	22.3	−1.96	ns	ns
samp. × exp.	1	2	3	2	−5.05	1.34	22.3	−3.77	< 0.001	significant
samp. × exp.	1	2	4	2	−6.24	1.34	22.3	−4.66	< 0.0001	significant
samp. × exp.	2	1	2	2	0.50	1.19	27.2	0.42	ns	ns
samp. × exp.	3	1	3	2	−1.52	1.20	27.2	−1.27	ns	ns
samp. × exp.	4	1	4	2	−3.22	1.20	27.2	−2.69	< 0.05	ns

Biomass of *Gammarus zaddachi*

Table 24. Test of fixed effects

	Num DF	Den DF	F	P
sampling	3	19.8	2.6	ns
exposure	1	7.52	26.18	0.001
samp. × exp.	3	19.8	1.69	ns

Biomass of Hydrobia

Table 25. Test of fixed effects

	Num DF	Den DF	F	p
sampling	3	20.1	2.59	ns
exposure	1	7.81	30.73	0.0006
samp. × exp.	3	20.1	2.32	ns

SAS-code Partial correlation analyses

```
data s2;
set s1;
rename allt=var;
if part=1 then ly=log(y+0.05);
if part le 2 then ly=log(y+0.002);
else if part=3 then ly=log(y+25);
```

```
else if part=4 then ly=log(y);
lt=log(t_ng+0.05);
lr=log(r_d+0.05);
lg=log(gr_n+0.05);
lb=log(brun+0.05);
run;

proc sort data=s2 out=s2s;
by part var;
run;

proc mixed data=s2s;
by part var;
class var sampling exposure sample;
model ly = sampling exposure sampling*exposure / s ddfm=kr;
random sample;
repeated sampling / subject=sample type=cs;
lsmeans sampling exposure sampling*exposure / diff;
ods output lsmeans=lsmeans1 diffs=diffs1;
run; quit;

proc mixed data=s2s(where=(part=2)) cl covtest;
class var sampling exposure sample;
model ly = lt lr lg lb var var*lt var*lr var*lg var*lb
sampling exposure var*sampling var*exposure
sampling*exposure / s
ddfm=kr;
random sample;
repeated sampling / subject=sample type=cs group=var;
lsmeans var*sampling var*exposure sampling*exposure / diff;
ods output lsmeans=lsmeans2 diffs=diffs2 solutionf=sol2;
run; quit;

proc mixed data=s2s(where=(part=2)) cl covtest;
by var;
class var sampling exposure sample;
model ly = lt lr lg lb sampling exposure sampling*exposure / s
ddfm=kr;
random sample;
repeated sampling / subject=sample type=cs;
lsmeans sampling exposure sampling*exposure / diff;
```

```
ods output lsmeans=lsmeans2b diffs=diffs2b solutionf=sol2b;
run; quit;

proc mixed data=s2s(where=(part=3)) cl covtest;
class var sampling exposure sample;
model ly = lt lr lg lb var var*lt var*lr var*lg var*lb
sampling exposure var*sampling
var*exposure sampling*exposure / s
ddfm=kr;
random sample;
repeated sampling / subject=sample type=vc group=var;
lsmeans var*sampling var*exposure sampling*exposure / diff;
ods output lsmeans=lsmeans3 diffs=diffs3 solutionf=sol3;
run; quit;
```

Results from the partial correlation analyses denoted according to the manuscript

Abundance of *Mytilus edulis*

Table 26. Test of fixed effects

	Num DF	Den DF	F	p
non-filamentous	1	23.9	0.13	ns
red filamentous	1	23.1	14.28	0.001
green filamentous	1	21.4	0	ns
brown filamentous	1	23.8	0.07	ns
sampling	3	18.9	1.84	ns
exposure	1	13.7	2.46	ns
samp. × exp.	3	19.5	0.66	ns

Abundance of *Idothea* spp.

Table 27. Test of fixed effects

	Num DF	Den DF	F	p
non-filamentous	1	16.6	4.69	ns
red filamentous	1	21.7	0.19	0.0049
green filamentous	1	22.8	0	ns
brown filamentous	1	20	0	ns
sampling	3	13.9	6	< 0.01
exposure	1	7.92	1.31	ns
samp. × exp.	3	14.4	4.27	< 0.05