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Patches of barnacles and ascidians in soft bottoms: Associated motile fauna in relation to the surrounding assemblage

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Abstract

Epibenthic patches dominated by barnacles *Balanus crenatus* Bruguiere and solitary ascidians *Styela* spp., *Bolthenia echinata* (L.) and *Molgula* spp. in the White Sea shallow subtidal develop on bivalve shells and small stones surrounded with muddy sand. The space between barnacles and ascidians is filled with muddy sediment inhabited by motile taxa. We hypothesized that (i) epibenthic patches and unstructured sediment would attract different motile fauna and (ii) motile fauna of the patches would be affected by local abundances of epibenthic foundation species. Most dominant motile species demonstrated a significant difference in abundance between the two microhabitats. In contrast to the fauna of the sediment, species composition observed in aggregations of barnacles and ascidians was stable across different locations. In the field experiment initially clear bivalve shells after 5 years of exposure developed barnacle clusters with motile fauna similar to that observed in natural aggregations. Amphipods, isopods and bivalves, capitellid polychaets, *Cirratulus cirratus* (Müller) and *Pholoe minuta* Fabricius (Polychaeta) dominated in the sediment inside epibenthic patches. The proportion of capitellids, known to be sensitive to organic enrichment, was much higher within the patches than outside. The abundances of motile taxa found in aggregations were mostly determined by the number of barnacles of different size and of their empty shells, the biomass of ascidians, and the effect of location. Different dominant species demonstrated sensitivity to different parameters.

Physical structure of the habitat, provided by barnacles and ascidians, as well as their biodeposition activity are regarded as the main factors structuring the motile fauna in the community studied. The spatial pattern observed seems to imply a range of pattern-generating biogenic processes, similar to those previously revealed in patches of filter-feeding bivalves, tube-building worms and seagrass.

Keywords: Ascidians; Barnacles; Infauna; Interactions; Patch structure; Spatial pattern; Temporal pattern

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For creatures your size I offer
a free choice of habitat
W. H. Auden, "A New Year Greeting"

1. Introduction

Discrete regular spatial patterns, observed in terrestrial or marine benthic communities, are usually described in terms of "patches", areas of a certain size with species composition differing from that outside (Paine and Levin, 1981; Connell and Keough, 1985; Sousa, 1984; Wu and Levin, 1994). These "islands" originate from spatially localised processes and events that result in substantial alteration of one or more of the ecological resources available. Often such a resource is space itself. Patches that develop where empty space is added to an existing habitat may utilise areas cleared by natural or artificial disturbance (Type I patches) or those provided by settling and growing environment-modifiers (Type II patches) (Connell and Keough, 1985; Sousa, 1984). Relatively large sessile organisms, as habitat engineers (Jones et al., 1994), usually harbor many smaller ones (e.g. Monteiro et al., 2002; Tsuchiya, 2002). Discreteness of their bodies or aggregations (or colonies) results in corresponding discrete spatial pattern of the assemblage.

Quantification of spatial structure in sea bottom communities is recognised as a necessary step towards understanding underlying processes (Underwood et al., 2000; Bergström et al., 2002). Due to their remarkable spatial effect, patches of suspension-feeding bivalves were studied most extensively. Aggregated mussels were proved to modify species diversity and composition, the latter being mainly affected by age structure of the molluscs and their patch size (Tsuchiya and Nishihira, 1985, 1986; Tsuchiya, 2002). Biodeposition and specific alteration of physical structure of habitat have been regarded as the main processes affecting the spatial structure (Crooks and Khim, 1999; Tsuchiya, 2002). Other benthic keystone species studied in respect to community structure associated with their patches are ascidians (Monteiro et al., 2002), tube-building worms (Woodin, 1974; Khaitov et al., 1999; Zühlke, 2001; Bolam and Fernandes, 2002) and seagrass (Bell and Westoby, 1986; Edgar and Robinson, 1992; Bowden et al., 2001; Lee et al., 2001). The spatial effects observed were mainly explained by specific physical properties of the patches formed by these organisms. Thus, patchy structure in benthic communities has been studied on a limited number of objects.

Though barnacles and ascidians are known as keystone species in different subtidal and intertidal habitats (McDougall, 1943; Sutherland, 1978; Dean and Hurd, 1980; Dean, 1981; Bros, 1987; Monteiro et al., 2002; Yakovis et al., 2004), the structure of their joint patches surrounded with soft sediment has never been investigated. The main reason is that most barnacle and ascidian species inhabit hard substrates and are generally infrequent in soft bottoms. However, in the White Sea subtidal barnacles *Balanus crenatus* are often found on relatively small shells or stones, with up to several tens of individuals per substrate. The clusters described usually bear also solitary ascidians from the genera *Styela*, *Molgula* and *Dendrodoa* attached to barnacle shells and to each other. The communities associated with coexisting barnacle clusters and ascidian clumps form an important part of the Onega Bay (the White Sea) ecosystems (Grishankov, 1995; Yakovis, 2002). Numerous empty barnacle shells also appear to be an essential component of these aggregations, providing surface for live cirripedians, ascidians and other empty barnacle shells. The space between barnacles and ascidians is filled with muddy sediment inhabited by motile taxa; the surrounding bottom is also covered with muddy sand. As a result, these islands are Type II patches in relation to the surrounding soft bottom assemblage. Our previous communication reported the density of such patches at study sites near the Solovetsky Islands ranging from 10 to 40 per m^2. The macroinvertebrate assemblage associated with the sediment between the aggregations is spatially structured itself, species abundances depending on the distance to the nearest epibenthic patch and on their density (Yakovis et al., 2004).

In the present study we describe the fauna associated with aggregations (clusters) of barnacles and ascidians in relation to that of the surrounding sediment. The hypothesis tested was that species composition of motile taxa found inside the patches studied would be affected by physical parameters of the aggregation (e.g. the proportion of barnacles and ascidians, their size structure) rather than by the sample's location and characteristics of the surrounding fauna. Aggregations sampled at different sites were compared to cores of bare sediment from the same sites.

The effects of location and patch type on species abundance were assessed. Clusters with different abundance of barnacles (living and dead) and ascidians were also compared to estimate the contribution of different epibenthic keystone taxa to the variation of the associated fauna. In addition, we examined the motile fauna of aggregations that developed on empty shells artificially added to the habitat (hereafter "experimentally reared"or "experimental"). We used *Serripes groenlandicus* (Bruguiere) (Lamellibranchia) shells, since they had been recorded as substrates for most natural clusters (Yakovis et al., 2004). Taking into account their probable origin from local *Serripes* population, it was assumed that natural aggregations generally develop on initially clear shells. This may happen only after the death of molluscs that normally reside under the sediment surface. Experimentally reared clusters were expected to attract a motile fauna similar to that found in natural ones, which should prove the causal nature of the effects revealed in observations. Another objective was to trace the development of the epibenthic patches under study (at least at initial stages, since the whole "life term" was unknown). Regular and consistent temporal pattern, if any, should be a further evidence of a relatively high integration level of the system under study as well as other similar marine benthic assemblages.

2. Methods

2.1. Study site

Sampling was carried out in July 2000–2004 near Solovetskiy Island (Onega Bay, White Sea) at two sites separated by 1820 m, 100 m off the shore (65°01.2′N, 35°39.7′E for Site 1 and 65°00.7′N,35°41.7′E for Site 2; Fig. 1). Though the whole region of the Solovetskiy archipelago demonstrates an extreme variety of sea bottom conditions, the area selected for this particular study was a flat muddy bottom at a depth of 11.2–12.5 m (Site 1) and 14.5–15.0 m (Site 2). Sea bottom temperature in July was about 8 °C at both sites. The salinity was not measured, but previous investigations (Grishankov et al., 1997) had reported the range of 24.4‰ to 27.6‰. On both sites the sediment was muddy sand, more mud being observed at Site 2. The experiment on the development of aggregations on

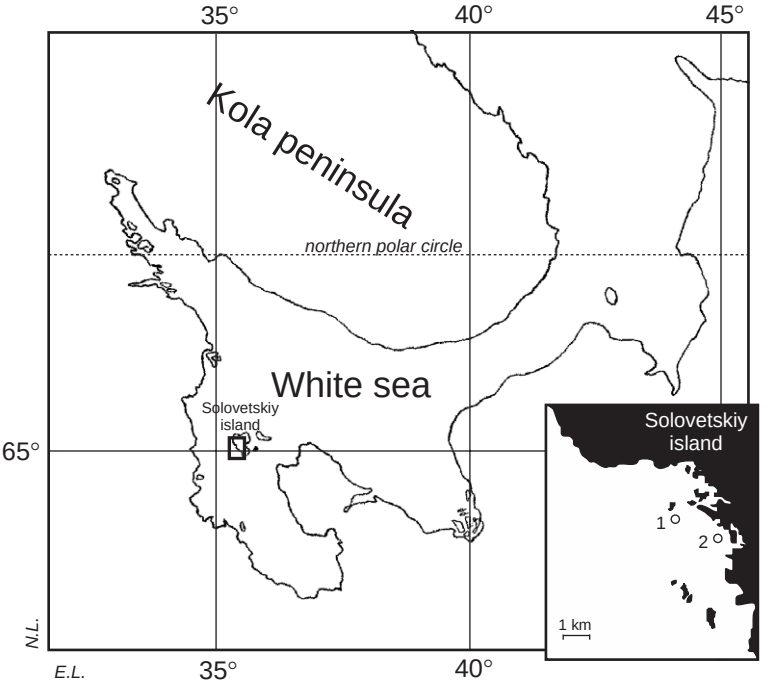

Fig. 1. Sampling sites location (1 and 2, encircled).

empty shells was conducted for 6 years from July 1998 to July 2004 at Site 1.

2.2. Sampling and laboratory techniques

Samples of two types, sediment cores and aggregations of barnacles and ascidians, were collected by SCUBA divers in 18 square frames (replicates) 1.2×1.2 m each. Any substrate found on the sediment surface was examined, regardless of the presence of barnacles and ascidians. We recorded the type of primary substrate and total weight and number of solitary ascidians (*Styela rustica* (L.), *Styela coriacea* (Alder et Hancock), *Dendrodoa grossularia* (Beneden), *Bolthenia echinata* (L.), *Molgula* spp.—referred to below as "ascidians") and barnacles (*B. crenatus*) for each aggregation. Barnacles as well as their empty shells were individually measured (aperture carino-rostral length accurate to 1 mm) and ascidians were individually weighed accurate to 0.01 g. All the sediment found in the aggregation was extracted (to do that, the latter usually had to be carefully destroyed). This sediment and its inhabitants together with the rest of the motile macrofauna found in the aggregation (on the shell and ascidian surfaces, in crevices, etc.) was examined as one sample (hereafter "A-samples"). In addition, 55 cm^2 cores of bare sediment (hereafter "S-samples") were obtained among the epibenthic patches (2–8 samples per replicate, depending on the amount of aggregations and technical conditions). In total, 12 replicates (containing 295 aggregations and 60 cores) were sampled at Site 1 and 6 replicates (containing 47 aggregations and 38 cores) were sampled at Site 2. The disproportion of the data available for the two sites is associated with low visibility and density of aggregations, which, together with sediment properties, made sampling at Site 2 much more difficult than at Site 1.

Sediment from each sample was sieved (0.5 mm mesh diameter) and sorted. All benthic macrofaunal invertebrates were removed, identified to the lowest taxonomic category possible (generally to the species level), counted and weighed.

2.3. Experiments

We used clear *S. groenlandicus* shells attached to small concrete blocks as substrates for experimentally reared aggregations, these shells being the most common substrate for the aggregations collected during the sampling. Blocks were positioned on the bottom at Site 1, buried in sediment so that their upper sides with substrates were left open. Substrates were added every July since 1998 and partially removed for investigation every July since 1999, so that 61 shells were totally exposed for 1–5 years. Experiments were conducted until 2004 and are still being continued. The number of shells examined in relation to the exposure term is given in Table 1. The substrates collected were examined following the procedure similar to that applied to natural aggregations (see above). To compare the faunal changes on experimental substrates to those in the surrounding habitat, the sediment near substrates was sampled with a 0.025 m^2 Petersen grab, 4–10 samples each year. Faunal states in natural aggregations of barnacles and ascidians sampled at Site 1 in 1998–2004 were also used as a reference for the experiment.

2.4. Statistical analysis

2.4.1. General notes

Unless stated otherwise, the abundance measure used was the number of individuals per sample. Since the sampling area representing aggregations could not be fixed, the abundance of each species was standardised by the total abundance of all species in a sample (hereafter referred to as "relative abundance"). The resulting proportions were subjected to angular transformation (Sokal and Rohlf, 1995) in order to normalise their distribution for further use in parametric analyses.

The significance criterion for all tests was $\alpha = 0.05$. Means, where given, are ± 1 S.E.

2.4.2. Aggregations and bare sediment

A-samples and S-samples were subjected together to type III sum of squares two-factor multivariate ANOVA with Site as a random effect, and Microha-

Table 1
Number of substrates (*Serripes* shells) exposed during the field experiment (1998–2004) in relation to exposure term

Exposure term (years)	1	2	3	4	5
Number of substrates examined	10	13	10	12	16

bitat (A-sample or S-sample) as a fixed one. The variables were the transformed abundances of 20 taxa with the largest average standardised densities. Variances were checked for homogeneity using Cochran *C* statistics, and for those species where they were found to be heterogeneous regardless of the transformations performed, Pearson correlations between variances and means were tested for the significant difference from zero. In case of the absence of a significant correlation the data were assumed to meet assumptions of ANOVA (Statsoft, Inc., 1995). Since in many cases this correlation was present, a non-parametric ANOVA (Kruskall–Wallis) was additionally performed. The same variables were analysed with PCA [principal component analysis, see Gauch, 1982] to examine whether the grouping pattern observed for samples would separate those from different sites and microhabitats. To test the effect of microhabitat on the whole assemblage, ANOSIM based on Bray–Curtis dissimilarity measure was applied to relative abundances of motile taxa using PAST software package (Ryan et al., 1995; Hammer et al., 2001). The ANOSIM *R* statistic was used as a dissimilarity measure to compare the effect of location on A- and S-samples (Clarke, 1993; Anderson and Underwood, 1997).

2.4.3. Aggregations with different characteristics

According to the effect on their shape, size and physical structure, the main quantitative characters of the epibenthic patches were considered to be the abundances of ascidians, living barnacles and their empty shells (hereafter "dead barnacles"). We used total numbers of living and dead barnacles (LB and DB) and numbers of those with the aperture length exceeding 9 mm ($LB_{>9\ mm}$ and $DB_{>9\ mm}$ correspondingly). The threshold of 9 mm was selected to separate "large" individuals, since this size had been the median one for the *B. crenatus* measured in this study. Total weight of ascidians (A) was used as their abundance measure. The same measure was not used for barnacles because it is not applicable to their empty shells. Pearson correlation matrix was calculated for the five parameters selected.

Standardised (as described above) angular transformed abundances of motile fauna found in aggregations were analysed for 10 dominant species using type III sum of squares GLM. Site was a random discrete effect, whereas characteristics of the sessile fauna of aggregations (A, LB, DB, $LB_{>9\ mm}$ and $DB_{>9\ mm}$ were gradual effects. Assumptions of the analyses were checked as described above for ANOVA.

2.4.4. Experimentally reared aggregations

Student's *t*-test was used to compare parameters of the sessile fauna for natural and artificial epibenthic clusters. Experimental aggregations were compared with natural ones and with sediment cores using the ANOSIM *R* statistic as a dissimilarity measure. The hypothesis tested was that initially empty *Serripes* shells exposed for 4–5 years would develop a motile fauna more similar to that of natural epibenthic patches rather than to the fauna of the surrounding sediment. ANOSIM on Bray–Curtis dissimilarity measure was applied to relative abundance data for all motile taxa. Mean relative densities of motile species found in natural microhabitats and on experimental substrates were compared using Mann–Whitney *U*-test. Pearson correlation coefficients with year or exposition term were used to compare long-term changes in species abundances on experimental substrates and in natural microhabitats.

3. Results

3.1. Aggregations and bare sediment

Out of 168 motile species totally recorded in A- and S-samples, 152 were found in aggregations and 89 in bare sediment, so that 44.6% of the species list was common for both microhabitats. Shannon–Wiener species diversity index was 2.19 for A-samples and 1.97 for S-samples. Average number of motile species per sample was significantly lower (Student's *t*-test, $p<0.001$) in A- than in S-samples (12.1 ± 0.4 and 18.6 ± 0.5, correspondingly). Numerous polychaete worms, undetermined isopods and amphipods were the most abundant taxa.

It can be clearly seen on PCA plot (Fig. 2) that the assemblage of motile taxa associated with aggregations of barnacles and ascidians was entirely different from that sampled around the patches. Aggregations grouped together regardless of their experimental or natural origin and of their location. Conversely, cores

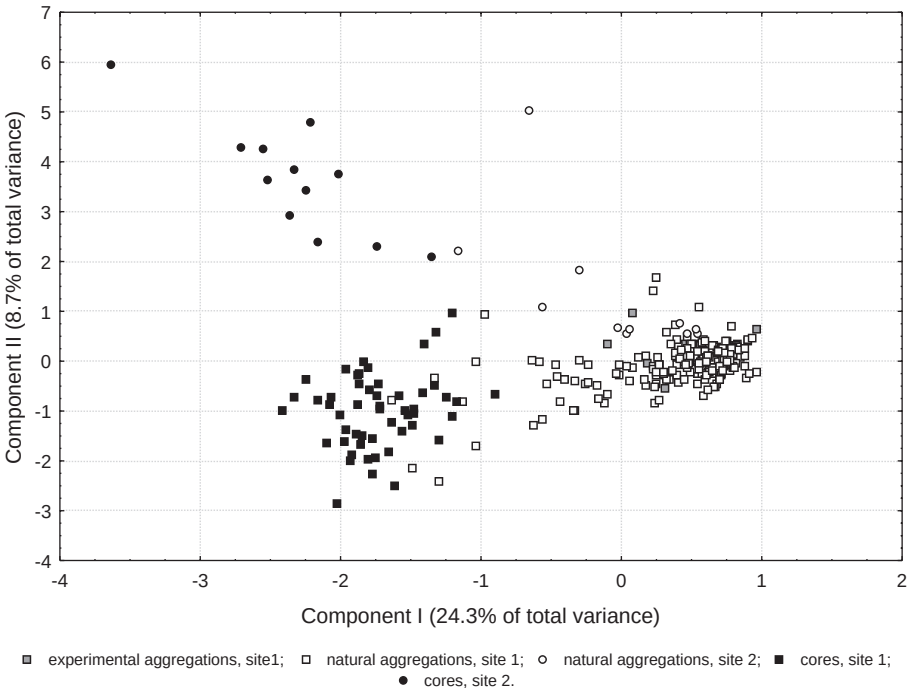

Fig. 2. Principal component analysis: sample scores plot. Densities of 20 dominant species were used as variables.

of bare sediment from different sites grouped separately. The first of the first two principal components, being responsible for 24.3% of total variance, separated samples according to the microhabitat type. Along the second one (8.7% of total variance) S-samples were separated according to the Site where

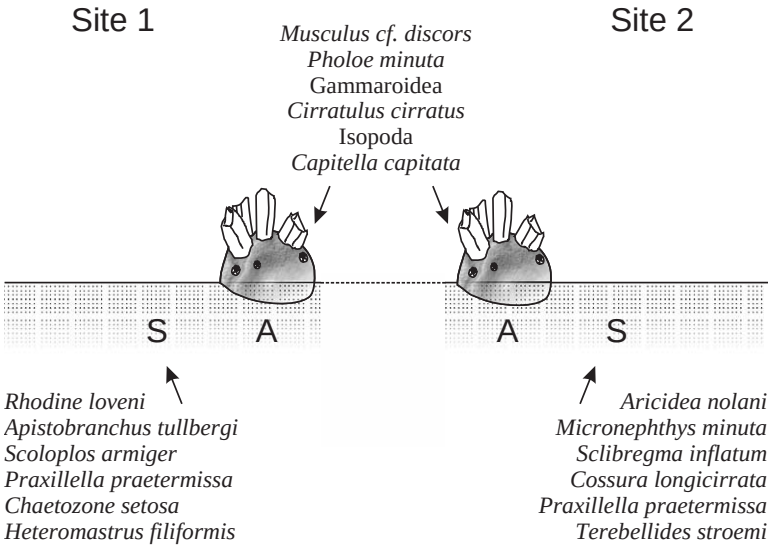

Fig. 3. Species composition of motile benthic fauna found at two sites and different microhabitats (in bare sediment [S] and in association with aggregations of barnacles and ascidians [A]). Fauna of the aggregations was similar at both sites (see text for details). Species are listed in order of their decreasing abundance.

Table 2
Summary of analyses comparing angular transformed relative densities of the 20 dominant motile taxa at different sites and microhabitats (aggregations of barnacles and ascidians vs. cores of bare sediment)

Source of variation	Site (random, 2 levels, *df*=1)							Microhabitat (fixed, aggregation/bare sediment, 2 levels, *df*=1)							Site × Microhabitat (random, *df*=1)			Residual (*df*=335)
Species name	Means		ANOVA			Kruskal–Wallis		Means		ANOVA			Kruskal–Wallis		ANOVA			ANOVA
	S1	S2	MS	*F*	*p*	*H*	*p*	A	BS	MS	*F*	*p*	*H*	*p*	MS	*F*	*p*	MS
Pholoe minuta Fabricius	**0.47**	0.22	0.86	14.5	***	43	***	**0.47**	0.08	4.30	72.7	***	85	***	0.05	0.8	ns	0.06
Sphaerosyllis erinaceus Claparede	0.03	0.04	0.00	0.6	ns	0	ns	**0.05**	0.00	0.08	12.23	***	14	***	0.00	0.1	ns	0.01
Micronephthys minuta (Theel)	0.02	**0.27**	2.19	242.3	***	111	***	0.06	0.27	0.83	91.4	***	61	***	0.17	18.3	***	0.01
Polycirrus medusa Grube	0.03	**0.06**	0.04	6.5	*	5	*	**0.05**	0.01	0.08	13.3	***	9	**	0.02	3.1	ns	0.01
Apistobranchus tullbergi (Theel)	0.07	0.07	0.24	34.8	***	2	ns	0.02	**0.22**	1.55	221.7	***	87	***	0.29	41.9	***	0.01
Pygospio elegans Claparede	**0.08**	0.00	0.23	21.2	***	29	***	0.05	0.05	0.01	0.6	ns	0	ns	0.01	0.5	ns	0.01
Scoloplos armiger (Müller)	0.08	0.13	0.01	0.9	ns	8	**	0.05	**0.25**	1.35	143.3	***	85	***	0.07	7.7	**	0.01
Aricidea nolani (Eliason)	0.03	**0.20**	0.94	155.5	***	69	***	0.03	**0.28**	1.61	267.2	***	102	***	0.17	27.9	***	0.01
Chaetozone setosa Malmgren	0.03	**0.09**	0.03	7.1	**	15	***	0.02	**0.16**	0.64	147.7	***	88	***	0.00	1.1	ns	0.01
Cirratulus cirratus (Müller)	0.16	0.15	0.02	0.6	ns	1	ns	**0.20**	0.00	1.59	54.7	***	52	***	0.01	0.3	ns	0.03
Heteromastus filiformis Zachs	0.07	0.11	0.00	0.0	ns	7	**	0.06	**0.17**	0.37	28.3	***	33	***	0.01	0.9	ns	0.01
Capitella capitata (Fabricius)	0.10	0.07	0.00	0.3	ns	3	ns	**0.11**	0.01	0.36	23.7	***	26	***	0.00	0.0	ns	0.02
Praxillella praetermissa Malmgren	0.06	0.12	0.02	3.2	ns	18	***	0.04	**0.22**	1.01	133.4	***	93	***	0.00	0.3	ns	0.01
Rhodine loveni Malmgren	**0.11**	0.03	1.83	232.7	***	9	**	0.04	**0.24**	2.09	265.1	***	50	***	1.35	171.5	***	0.01
Scalibregma inflatum Rathke	0.03	**0.11**	0.20	32.8	***	26	***	0.01	**0.19**	0.96	159.0	***	101	***	0.12	19.8	***	0.01
Isopoda	0.09	0.06	0.01	0.7	ns	3	ns	**0.10**	0.02	0.22	14.1	***	19	***	0.00	0.2	ns	0.02
Gammaroidea	0.18	0.13	0.00	0.1	ns	3	ns	**0.20**	0.03	1.02	31.5	***	34	***	0.00	0.4	ns	0.03
Crenella decussata (Montagu)	0.05	**0.14**	0.31	30.9	***	32	***	0.03	**0.13**	0.18	18.3	***	24	***	0.03	2.7	ns	0.01
Musculus cf. *discors* (L.)	0.43	0.29	0.02	0.2	ns	8	**	**0.49**	0.00	8.30	108.6	***	79	***	0.01	0.1	ns	0.08
Hiatella arctica (L.)	0.05	0.02	0.00	0.5	ns	6	*	**0.05**	0.00	0.08	10.9	**	17	***	0.00	0.5	ns	0.01

Average angular transformed standardised numbers of individuals per sample (core or aggregation): S1—at Site 1, S2—at Site 2, A—in aggregations, BS—in bare sediment. Higher means are highlighted in bold where both the effect and Tukey HSD post-hoc test for means are significant ($p<0.05$). Since in most cases variances were not homogeneous, non-parametric ANOVA (Kruskall–Wallis) results were added. ns: not significantly different; *$p<0.05$; **$p<0.01$; ***$p<0.001$.

they had been obtained. Each of the resulting three groups of samples (A-samples, S-samples from Site 1 and S-samples from Site 2) was characterised by a specific composition of dominant taxa (Fig. 3).

Different sources of the abundance variation were analysed in multivariate ANOVA. The results are summarised in Table 2. Microhabitat type had a significant effect on the abundance of 19 out of 20 dominant species, 9 and 10 being more abundant, correspondingly, in aggregations and in bare sediment. For 6 species this effect was different depending on the location (a significant interaction Site × Microhabitat was found). Seven out of the 10 dominant species that demonstrated a significant variation of their abundance depending on location were associated with bare sediment, only 2 were aggregation-specific. The results of non-parametric ANOVA were the same as above for the effect of microhabitat type and very similar for the effect of location (Table 2). The dissimilarity between the two sites as indicated by ANOSIM R statistic based on relative abundance data for all species was higher in S-samples ($R=0.52$) than in A-samples ($R=0.19$). Larger difference ($R=0.85$) was observed between A- and S-samples from both sites. In all cases the dissimilarity was significant ($p<0.001$).

3.2. Aggregations with different characteristics

The main noticeable variation in aggregations studied was that of their size (and weight) and composition of the key sessile taxa, barnacles and ascidians. Average total weight of clusters without primary substrates was 44.9 ± 4.0 g, ranging from 1 to 490 g. Barnacles and ascidians dominated in biomass. There was high positive correlation between the number of large dead barnacles and the weight of ascidians (Table 3).

The results of GLM analysis with Site and parameters of the aggregations (A, LB, DB, $LB_{>9\ mm}$ and $DB_{>9\ mm}$) as effects are summarised in Table 4. Effect of location was significant for all the dominant aggregation-specific motile species. For all but one of them one or more parameters of aggregations also had significant effect on the abundance. Amphipods, isopods and *Musculus* (Lamellibranchia) were associated with high abundances of ascidians, the amount of dead barnacles, although correlated with ascidian biomass (see above), had either no effect on them or a negative one. Most other species demonstrated association with high numbers of large living barnacles and no association with small or dead ones. *Cirratulus cirratus* (Polychaeta) density was significantly affected by the amount of large barnacles, both living and dead.

Table 3
Correlations between the main characters of epibenthic fauna in natural aggregetions of barnacles and ascidians

	A	LB	DB	$LB_{>9\ mm}$
LB	**−0.15**			
DB	−0.03	**0.30**		
$LB_{>9\ mm}$	0.02	**0.55**	**0.26**	
$DB_{>9mm}$	**0.45**	−0.01	**0.22**	**0.23**

A—biomass of solitary ascidians; LB—number of living *Balanus crenatus*; DB—number of *B. crenatus* empty shells; $LB_{>9\ mm}$—number of living *B. crenatus* with the aperture length exceeding 9 mm; $DB_{>9\ mm}$—number of empty *B. crenatus* shells with the aperture length exceeding 9 mm. Data in cells are highlighted in bold if the correlation is significant at $p<0.05$ level.

3.3. Experimentally reared aggregations

Changes in the epibenthic flora and fauna found on experimental substrates in relation to the exposure term are summarised in Fig. 4. *Serripes* shells exposed for 5 years had developed *B. crenatus* clusters, with total covers and abundances demonstrating no significant difference from those observed in natural aggregations based on the same substrate type. Ascidians found in experimental clusters, though, were infrequent and small. The numbers of empty barnacle shells as well as the maximal barnacle sizes were also low (Table 5).

As mentioned above, experimental and natural aggregations grouped together on PCA plot based on densities of 20 dominant motile species (Fig. 2). ANOSIM R statistic based on relative abundance data for all species indicated low similarity between sediment cores and aggregations, both experimental and natural ($R=0.93$ and 0.85, correspondingly), in relation to the similarity observed between aggregations of different origin ($R=0.32$). The difference was significant in all the three cases ($p<0.001$). The longer the exposure term was, the less difference was found in motile 1 fauna between experimental and natural aggregations: the number of common dominant species out of the first 10 increased and ANOSIM R decreased (Table 6). Though several species of those abundant on experimental substrates significantly

Table 4
Abundance of dominant aggregation-specific taxa analysed with GLM: parameters of aggregations and sampling site location as effects

Source of variation		A	LB	DB	$LB_{>9\ mm}$	$DB_{>9\ mm}$	Site	Residual
Gradual (G)/discrete (D)		G	G	G	G	G	D	
Fixed (F)/random (R)		F	F	F	F	F	R	
Species name	*df*	1	1	1	1	1	2	387
Pholoe minuta	*R*	−0.07	0.09	−0.03	0.09	−0.03		
	MS	0.11	0.06	0.12	0.08	0.01	11.11	0.07
	F	1.60	0.83	1.77	1.20	0.17	**158.13**	
	p	ns	ns	ns	ns	ns	***	
Capitella capitata	R	0.10	0.21	0.07	**0.30**	0.13		
	MS	0.06	0.05	0.01	**0.36**	0.01	**0.39**	0.02
	F	2.71	2.39	0.43	**16.84**	0.42	**18.23**	
	p	ns	ns	ns	***	ns	***	
Cirratulus cirratus	*R*	0.05	0.12	0.10	**0.24**	**0.25**		
	MS	0.03	0.00	0.00	**0.31**	**0.49**	**1.36**	0.03
	F	0.88	0.01	0.03	**9.29**	**14.79**	**40.59**	
	p	ns	ns	ns	**	***	***	
Polycirrus medusa	*R*	0.06	0.17	0.18	**0.27**	0.17		
	MS	0.00	0.01	0.03	**0.12**	0.00	**0.15**	0.01
	F	0.27	0.60	3.17	**12.45**	0.47	**15.02**	
	p	ns	ns	ns	***	ns	***	
Pygospio elegans	*R*	−0.07	0.02	−0.01	**0.12**	0.00		
	MS	0.07	0.05	0.02	**0.19**	0.01	**1.21**	0.03
	F	2.66	1.84	0.61	**7.25**	0.49	**45.39**	
	p	ns	ns	ns	**	ns	***	
Isopoda	*R*	**0.12**	0.06	**−0.08**	0.08	0.03		
	MS	**0.13**	0.03	**0.10**	0.03	0.00	**0.79**	0.02
	F	**5.59**	1.47	**4.18**	1.25	0.10	**34.57**	
	p	*	ns	*	ns	ns	***	
Gammaroidea	*R*	**0.33**	0.04	0.00	0.06	0.16		
	MS	**1.48**	0.09	0.00	0.00	0.00	**1.37**	0.04
	F	**37.89**	2.35	0.13	0.00	0.04	**35.07**	
	p	***	ns	ns	ns	ns	***	
Hiatella arctica	*R*	−0.02	0.06	0.05	**0.15**	0.02		
	MS	0.01	0.01	0.00	**0.21**	0.00	**0.67**	0.03
	F	0.18	0.32	0.02	**6.36**	0.02	**20.06**	
	p	ns	ns	ns	*	ns	***	
Musculus cf. *discors*	*R*	**0.20**	−0.03	**−0.12**	−0.08	0.03		
	MS	**1.62**	0.19	**0.43**	0.23	0.02	**16.50**	0.11
	F	**14.88**	1.74	**3.89**	2.07	0.21	**151.20**	
	p	***	ns	*	ns	ns	***	

Pearson correlation coefficients (R) are added to the results for gradual effects.
Codes for effects: A—biomass of solitary ascidians; LB—number of living *Balanus crenatus*; DB—number of *B. crenatus* empty shells; $LB_{>9\ mm}$—number of living *B. crenatus* with the aperture length exceeding 9 mm; $DB_{>9\ mm}$—number of empty *B. crenatus* shells with the aperture length exceeding 9 mm; Site—the location of the sampling site (2 levels). Data in cells are highlighted in bold if the effect is significant. Variables are angular transformed standardised numbers of individuals per aggregation.
ns: not significantly different; *$p<0.05$; **$p<0.01$; ***$p<0.001$.

changed their mean density in the surrounding sediment and in natural aggregations during 1998–2004, only *Pholoe minuta* (Polychaeta) and isopods increased their abundance both on experimental substrates and in the surrounding sediment (Table 6).

During the 5 years of exposure all dominant motile taxa increased their abundance on *Serripes* shells, with the only exception of amphipods (Fig. 5). Substrates exposed for 2 years were inhabited mostly by amphipods (61% of all individuals) and *Musculus* cf.

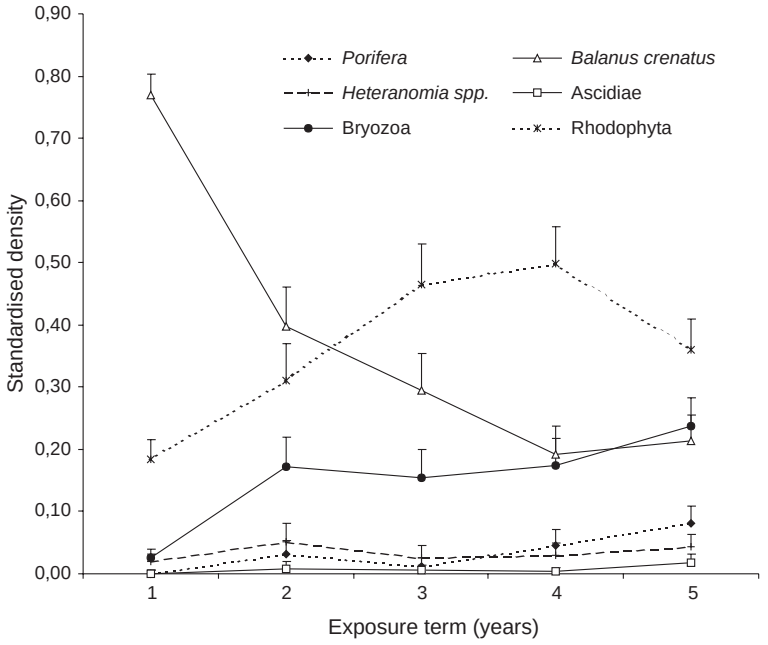

Fig. 4. Changes in abundance of dominant sessile taxa found on experimental substrates in relation to the exposure term. Means +1 S.E. are plotted and −1 S.E. marks are omitted for clarity.

discors (17%); the latter (24%) dominated on substrates exposed for 5 years together with amphipods (12%) and *Capitella capitata* (Fabricius) (9%).

Table 5
Average characters of sessile fauna observed in natural aggregations of barnacles and ascidians and in 5-year-old experimentally reared ones

Parameter	Natural aggregations	Experimental substrates exposed for 5 years	*p*
A	5.37 ± 0.58	0.05 ± 0.03	***
LB	28.38 ± 1.70	20.33 ± 4.55	ns
DB	10.22 ± 1.01	3.08 ± 0.62	***
$LB_{>9\ mm}$	5.73 ± 0.53	5.58 ± 1.83	ns
$DB_{>9\ mm}$	1.59 ± 0.12	0.17 ± 0.11	***
$LB_{<4\ mm}$	14.79 ± 1.22	12.08 ± 3.38	ns
Total cover	0.45 ± 0.02	0.48 ± 0.07	ns

A—biomass of solitary ascidians, g per aggregation; LB—number of living *Balanus crenatus* per aggregation; DB—number of *B. crenatus* empty shells per aggregation; $LB_{>9\ mm}$—number of living *B. crenatus* with the aperture length exceeding 9 mm, per aggregation; $DB_{>9\ mm}$—number of empty *B. crenatus* shells with the aperture length exceeding 9 mm, per aggregation; $LB_{<4\ mm}$—number of living *B. crenatus* with the aperture length less than 4 mm, per aggregation.

4. Discussion

Barnacles and solitary ascidians are known as keystone species in various rocky shore communities (McDougall, 1943; Sutherland, 1978; Dean and Hurd, 1980; Dean, 1981; Bros, 1987; Monteiro et al., 2002). When found in muddy habitats on relatively small substrates like stones or shells, they act as Type II patch providers (Connell and Keough, 1985; Sousa, 1984) in relation to the surrounding sediment.

We observed a strong difference in motile fauna between epibenthic patches and patches of bare sediment, which is in accordance with the hypothesis that aggregations of barnacles and ascidians would attract specific taxa, as it had been previously proved for patches of aggregated bivalves (Tsuchiya and Nishihira, 1985; 1986; Tsuchiya, 2002), tube-building worms (Woodin, 1974; Khaitov et al., 1999; Zühlke, 2001; Bolam and Fernandes, 2002) and seagrass (Bell and Westoby, 1986; Edgar and Robinson, 1992; Bowden et al., 2001; Lee et al., 2001). The effect of microhabitat determines the distribution of all but one dominant motile species. Spatial variation is high in samples of bare sediment, the fauna found

Table 6
Motile fauna and its temporal changes compared in experimental aggregations (EA) and natural microhabitats (S and NA) at Site 1

Species name	Bare sediment (S)		Natural aggregations (NA)		Experimental aggregations (EA)						*U*-tests: experimental aggregations and natural microhabitats			Changes 1998 –2004 and 1+–5+
	Mean, %	*R* with year 1998 –2004	Mean, %	*R* with year 1998 –2004	Mean, %					*R* with expsure term	5+ vs. S	5+ vs. NA	5+ vs. NA_B	
					1+	2+	3+	4+	5+					
Pholoe minuta	1	0.63***	17	0.42***	0	3	8	7	6	0.36*	453 ns	250***	48***	S↑ NA↑ EA↑
Sphaerosyllis erinaceus	0	−0.11 ns	1	−0.09*	0	0	2	0	0	0.05 ns	473 ns	804 ns	176 ns	NA↓
Micronephthys minuta	2	0.07 ns	0	−0.10*	0	0	0	0	0	0.15 ns	140***	979 ns	210 ns	NA↓
Polycirrus medusa	0	−0.15 ns	2	−0.24***	0	0	3	1	1	0.19 ns	442 ns	981 ns	209 ns	NA↓
Apistobranchus tullbergi	7	0.20*	2	−0.19***	0	0	0	0	1	0.21 ns	62***	979 ns	215 ns	S↑ NA↓
Pygospio elegans	3	0.04 ns	3	−0.07ns	0	0	0	2	4	0.27 ns	334*	971 ns	211 ns	
Scoloplos armiger	9	−0.25**	1	−0.10*	0	0	0	0	0	0.05 ns	24***	752 ns	176 ns	S↓ NA↓
Aricidea nolani	4	−0.05 ns	0	−0.13**						–	112***	920 ns	192 ns	NA↓
Chaetozone setosa	9	−0.40***	1	−0.23***						–	56***	880 ns	192 ns	S↓ NA↓
Cirratulus cirratus	0	−0.23**	6	−0.02 ns	0	0	1	2	2	0.42*	256**	757 ns	167 ns	S↓ EA↑
Heteromastus filiformis	5	0.10 ns	2	−0.06 ns	0	0	2	3	1	0.23 ns	215***	991 ns	213 ns	
Capitella capitata	0	−0.27***	3	−0.08 ns	0	0	9	7	9	0.41*	225***	689*	127*	S↓ EA↑
Praxillella praetermissa	5	0.17*	1	−0.13**	0	0	1	0	0	−0.05 ns	8***	840 ns	184 ns	S↑ NA↓
Rhodine loveni	11	0.63***	2	−0.12**						–	0***	760 ns	184 ns	S↑ NA↓
Scalibregma inflatum	1	0.16 ns	0	−0.12***	0	0	1	1	1	0.14 ns	294*	916 ns	198 ns	NA↓
Isopoda	0	0.38***	3	0.06 ns	0	9	1	13	6	0.35*	246**	639*	152 ns	S↑ EA↑
Gammaroidea	1	0.40***	6	0.09*	0	61	17	17	12	0.12 ns	295*	884 ns	200 ns	S↑ NA↑
Crenella decussata	1	0.14 ns	1	0.08 ns	0	0	0	0	0	0.05 ns	152***	800 ns	184 ns	
Musculus cf discors	0	0.07 ns	26	0.27***	0	17	37	25	24	0.41*	148***	879 ns	157 ns	NA↑ EA↑
Hiatella arctica	0	−0.20***	3	−0.19***	0	2	0	2	5	0.35*	221***	660*	142 ns	S↓ NA↓ EA↑
Number of common dominant species with NA					0	5	4	7	8	0.91*				
ANOSIM *R* with NA					–	0.40		0.33						

Species included were 20 dominant motile ones, taxa specific for natural aggregations of barnacles and ascidians (see Table 2) highlighted in bold.

Bare sediment: Mean relative densities of motile taxa in 0.025 m^2 Petersen grab samples of the unstructured sediment at Site 1. *R* with year: Pearson correlation between the relative density and sampling year (*R*, *p*).

Natural aggregations: Mean relative densities of 20 dominant motile taxa in all patches of barnacles and ascidains sampled at Site 1. *R* with year: Pearson correlation between the relative density and sampling year (*R*, *p*).

Experimental aggregations: Mean relative densities of motile taxa on initially clear *Serripes groenlandicus* shells exposed for 1–5 years (1+–5+). ANOSIM *R* dissimilarity measure with natural aggregations: samples for exposure terms 2–3 and 4–5 years were merged to increase the sample size. Number of common dominant species indicates the number of species, out of the 10 most abundant ones, common for experimental (1+–5+) and natural aggregations.

U-tests: Mean relative densities of motile taxa on experimental substrates (5+) were compared to those in sediment cores (2003–2004, Site 1), in all natural aggregations (NA) and in natural aggregations based on *Serripes* shells dominated by barnacles (NA_B) from the same site (*U*, *p*).

S↑ (S↓), NA↑ (NA↓), EA↑ (EA↓)—linear trends summarised for relative abundance changes in bare sediment, natural aggregations and experimental aggregations, correspondingly, based on the sign and significant difference from zero of Pearson *R*. ns: not significantly different; *$p<0.05$; **$p<0.01$; ***$p<0.001$.

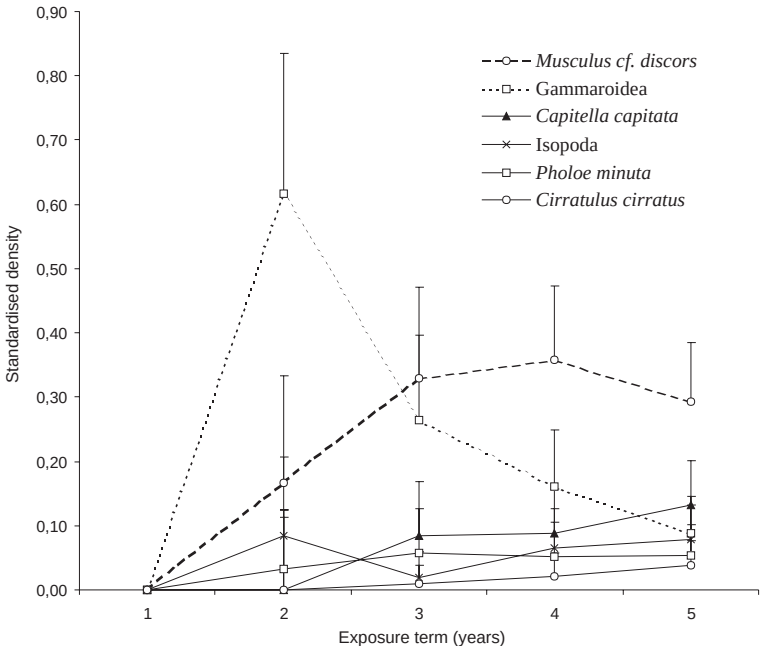

Fig. 5. Changes in abundance of dominant motile taxa found on experimental substrates in relation to the exposure term. Means +1 S.E. are plotted and −1 S.E. marks are omitted for clarity.

in them being to a great extent site-specific. In contrast, species composition and relative abundance of different motile taxa observed in aggregations were much less spatially variable. This is indicated both by the results of ANOSIM, the effect of location being higher for S-samples, and by PCA ordination, where aggregations grouped together whereas cores of bare sediment grouped separately by sampling site.

As shown by GLM results (Table 4), species composition of the aggregation-specific motile fauna, though dependent on location, is almost equally affected by parameters of sessile fauna. Previous research on dense assemblages of benthic keystone species suggests that there are two main processes leading to attraction or avoidance of these patches by motile taxa. They are (1) feeding mediated interactions (including biodeposition and predation on larvae) and (2) the effect of modified physical structure of habitat (Woodin, 1974; Rosenberg and Loo, 1983; Hunt et al., 1987; Hines et al., 1989; Crooks and Khim, 1999; Norkko et al., 2001; Hewitt et al., 2002). The latter primarily implies increasing the habitat complexity, known as direct and indirect modifier of species diversity and composition (see Raffaelli and Hawkins, 1996; Langellotto and Denno, 2004). In our case, any of those processes might have been expected for both barnacles and ascidians. However, we suggest that shells remaining from dead barnacles are directly contributing only to the second one. Comparison of the effects of the abundance of living and dead barnacles on motile fauna may help assessing the relative importance of the two processes.

The observed effect of barnacle abundance on motile fauna depended on the size of the cirripedians. Total numbers of living barnacles (LB) and of empty shells (DB), in contrast to the numbers of those larger than 9 mm ($LB_{>9\ mm}$ and $DB_{>9\ mm}$), generally reflect the amount of small cirripeds in aggregations. No correlation found between the first two parameters and the abundance of the motile fauna seems to indicate none or little influence of young barnacles on aggregations' inhabitants.

Effects of large living barnacles and of their empty shells are different, the latter only being significant for one abundant species. This species, the polychaete *C. cirratus*, is often found in subtidal muddy habitats with cavity-loaded matrix, such as algal holdfasts (Tzetlin et al., 1997; Norderhaug et al., 2002; our unpublished

data). Modification of the habitat physical structure seems to be of less importance for associated mobile organisms in barnacle clusters than it has been observed in aggregations of other benthic habitat engineers (Woodin, 1974; Crooks and Khim, 1999). Furthermore, sessile fauna, particularly bivalves and ascidians, unlike the motile one studied, had previously demonstrated similar dependence both on barnacle shell mimics and on living barnacles (Dean, 1981). Most of aggregation-specific motile taxa are positively sensitive to the abundance of either ascidians or large living barnacles.

Being opportunistic, capitellid polychaets are mostly found in organically enriched habitats (Hily, 1987; Rossi, 2003) including those where the source of the enrichment is excretion by larger suspension-feeders (Mattison and Linden, 1983). Positive correlation between their abundance and that of living barnacles appears to reflect the effect of biodeposition. The presence of this effect is also supported by the results of motile fauna comparison close to and between the patches of barnacles and ascidians (Yakovis et al., 2004): capitellids were significantly more abundant and had a greater individual mean weight close to the patches. Though the same mechanism may account for the spatial pattern revealed in several other aggregation-specific polychaete species, it is probably inapplicable to the filter-feeding bivalve *Hiatella arctica*. Known as an inhabitant of cavities in hard substrate (e.g., Cocito et al., 2000; Gaymer and Himmelman, 2002), this species could be expected to prefer empty shells because they provide an appropriate space for adult molluscs. In fact, according to our non-quantified observations, adult *Hiatella* occupy large empty shells quite often. Thus, the effect of living barnacles observed may reflect the distribution of prevailing smaller bivalve individuals that fit into crevices between the shells of living cirripedians.

Association between different nest-building mytilids (including *Musculus*) and solitary ascidians was reported from various habitats and locations (Bertrand, 1971). Younger individuals are usually harbored by ascidian tunics' texture depressions. Older ones often lose mobility, being overgrown by the tunic and embedded in its matrix with only siphonal end left outside. The nature of this association (mutualistic, commensal or parasitic) is unknown.

Barnacles (both living and dead) in aggregations are much less fouled by red algae than ascidians (Yakovis, 2002). We suggest that epibenthic crustaceans (amphipods and isopods) are attracted to ascidians by their extensive macroalgal cover (see Gunnill, 1982; Norderhaug et al., 2002; Norderhaug, 2004).

According to our preliminary results (Yakovis, 2002), clumps of solitary ascidians seem to develop in barnacle aggregations under study only after the latter exceed a certain age and size. At least, ascidians were almost never found either on primary substrates of the clusters or on the shells of young barnacles (they were associated with the shells of living or dead large barnacles and with conspecific individuals). Thus, it may be expected that experimentally reared aggregations would lack the ascidian population for several years. Similar sequence of keystone species replacement on hard substrata was documented by Dean (1981), who observed ascidians' expansion only at the patches previously occupied by barnacles and hydroids. It was suggested that the settlement and population growth in ascidians had been facilitated by physical structure of the habitat provided by earlier arrivals. The results of our experiments may therefore reflect temporal changes during the "pre-ascidian" period of aggregations' development. Data of observations support the hypothesis that the motile fauna of epibenthic patches is specific and stable because of the influence of both barnacles and ascidians. Similarity found in motile species composition and proportional abundance of dominant taxa between the substrates initially lacking motile fauna after 5 years of exposure and natural aggregations gives a strong evidence for the structuring role of at least the barnacle population. The main difference observed between natural aggregations and 5-year-old experimental ones was that there was more of *C. capitata* and less of *P. minuta* in the experiment (Table 6). Increased abundance of *Capitella* is not unexpected, given that experimental aggregations were dominated by barnacles, indicating their positive effect on this worm (Table 4). Spatially variable (Table 4) abundance of *Pholoe* within aggregations cannot be explained in terms of effects revealed in the present study.

It is probable that, beginning with an empty shell of dead *Serripes* or a stone left by the melting spring ice, the epibenthic patch dominated by barnacles and ascidians passes a succession of specific consequent

changes. The primary goal of our further research is to determine the order of its stages and to reveal the temporal pattern of the community under study. We expect the succession of both motile and sessile components of the assemblage constituted by barnacles and ascidians to be traced in several years, when the long-term experiment started in 1998 has been completed. The present data support the conclusion that the motile fauna is strongly dependent on the sessile one and differs from that of the surrounding sediment. Taking into account the previously confirmed distant spatial effect of the aggregations of barnacles and ascidians (Yakovis et al., 2004), we regard the system investigated as an important example of regularly structured (both in space and in time) marine benthic community, which expands the range of potential objects for the research of pattern-generating biogenic processes.

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