



Spatial pattern indicates an influence of barnacle and ascidian aggregations on the surrounding benthic assemblage

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Abstract

Joint clusters of solitary ascidians *Styela* spp., *Bolthenia echinata* (L.), *Molgula* spp. and barnacles *Balanus crenatus* Bruguiere in the White Sea subtidal often develop on shells or stones partially buried into muddy sediment. To assess the structuring role of these suspension-feeders' aggregations, we examined the spatial patterns of the surrounding infaunal assemblage. Pairs of cores obtained close to clusters (Close ones) and 20–25 cm away from them (Distant ones) were compared, the distance corresponding to the average distance observed between aggregations. These pairs were spatially grouped in replicas (blocks) tens of meters from each other. Out of 10 dominating invertebrate species found around the clusters (84 in total), 5 demonstrated significant difference in density (N) close to aggregations and between them. All the five, including polychaets *Scoloplos armiger* (Muller, Orbiniidae), *Aricidea nolani* (Eliason, Paraonidae), *Heteromastus filiformis* Zachs (Capitellidae), *Chaetozone setosa* Malmgren (Cirratulidae) and undetermined oligochaets, were associated with Close cores. Total abundance of polychaets, oligochaets, crustaceans and bivalves was also different in Close and Distant cores and indicated significant correlations (of either sign) with biomass estimates for barnacles and ascidians in each block. Individual mean body weight (IMW) in pairs of cores was different for 3 of 10 dominants, maldanid polychaets being larger close to clusters, and cirratulids being larger between them. For several taxa the difference, observed in both parameters (N and IMW), significantly varied between the replicas.

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Filter-feeding activity and faeces production are regarded as the main possible factors explaining the effect of barnacles and ascidians presence, since the spatial pattern observed corresponds with feeding types of the infaunal taxa studied. Average distance between the clusters was short enough, which allows us to conclude that the spatial distribution pattern of benthic infaunal species within the research area strongly depends on barnacle and ascidian aggregations mosaic.

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1. Introduction

Patterns revealed in spatial distribution of different species at a range of scales are one of the key aspects of the community structure, intensively studied in various habitats (Keough, 1984; Underwood and Chapman, 1996; Bergström et al., 2002; Hewitt et al., 2002). The nature of these patterns is recognised as a combined effect of environmental variation and biotic interactions. Depending on the scale, the importance of these two factors in structuring a particular system may vary (Zajac et al., 1998). Since the majority of species in diverse assemblages are involved in numerous interactions and the heterogeneity of habitats is also generally high, actual patterns are often complex and hard to interpret (e.g. Findlay, 1982; Cummings et al., 2001). Given no direct data on distances at which strongest interspecific processes flow, one may try to predict them by analysing the spatial variation at different scales (Underwood and Chapman, 1998; Azovsky et al., 2000; Bergström et al., 2002; Hewitt et al., 2002). Vice versa, strong interactions at a known scale result in a corresponding spatial pattern (e.g. Hiddink et al., 2002).

As a rule, such strong biotic interactions are observed between one or more “edificator-species” (Braun-Blanquet and Pavillard, 1930) or “keystone species” (Paine, 1969; Menge et al., 1994), whose activity influences many others, and the rest of taxa. Regular spatial patterns are usually documented for purely epibenthic systems (e.g. Ryland, 1972; Stebbing, 1972; Harvey et al., 1976; Connel and Keough, 1985; Keough, 1986; Lahoinen and Furman, 1986; Young and Gotelli, 1988), much less data is available on soft-bottom assemblages. Specific infauna is found in and around aggregations of mussels (Mattison and Linden, 1983; Tsuchiya and Nishihara, 1985, 1986; Dittman, 1990; Ragnarsson and Raffaelli, 1999) or oysters (Dumbauld, 1997), and polychaets (Woodin, 1974; Luckenbach, 1986; Somaschini, 1993). Large sessile or motile suspension-feeders usually combine the features of predators or competitors for food with habitat-engineering in terms of Jones et al. (1994). This includes predation on motile larvae (Hunt et al., 1987; Hines et al., 1989), suspension-feeding interference (e.g. Peterson, 1982; Okamura, 1988), changing the properties of the sediment (Rosenberg and Loo, 1983; Norkko et al., 2001; Hewitt et al., 2002) and providing specific habitat architecture (e.g. Woodin, 1974; Crooks and Khim, 1999). Thus, we recognise large suspension-feeders as good model objects for spatial-effects studies, in which spatial patterns reflecting strong biotic interactions can be found and quantified.

In the White Sea, barnacles *Balanus crenatus* and several species of ascidians usually form small clusters on shells and stones distributed over a muddy bottom. Both taxa seem

to be the strongest suspension-feeders in soft-bottom communities they are found in. Neither the structure of these epibenthic aggregations, nor their spatial effects on the surrounding fauna have ever been studied. Different species of barnacles and ascidians are regarded as keystone ones in a variety of epibenthic assemblages (McDougall, 1943; Sutherland, 1978; Bros, 1987; Dean and Hurd, 1980; Dean, 1981; Monteiro et al., 2002). Similarly to large filter-feeding bivalves in soft bottoms, they are involved into a wide range of interactions with the surrounding flora and fauna. Predation upon larval stages of other benthic organisms, as well as its spatial consequences, has been studied for both taxa (for cirripeds see Barnes, 1959; Young and Gotelli, 1988; Young and Cameron, 1989; Navarrete and Wieters, 2000; for ascidians see Young, 1989; Osman and Whitlatch, 1995). The effects revealed seem to vary (at least, in barnacles) depending on the potential prey species. Although the very fact of predation has been proved directly, the spatial patterns observed have not always been consistent with those predicted (e.g. Young, 1989).

Competition for food, though seemingly present, has been poorly studied in the taxa under discussion. Some data are only available on intraspecific feeding interference in cirripeds (Pullen and La Barbera, 1991; Lohse, 2002). Apparently, no effect of competition for food either between ascidians or between them and other organisms has ever been quantified. There are also absolutely no direct data on biodeposition in ascidians, as well as in cirripeds. However, according to our personal unpublished observations, when a cluster of these suspension-feeders is placed into an empty dish, the accumulation at least of barnacle faeces (which are characteristic enough to be recognised with certainty) can be noticed. Numerous faeces of this kind were also found in cores during the sorting.

Clumps of barnacles and ascidians are common in the Onega Bay of the White Sea (Grishankov, 1995). Preliminary results indicating that individual aggregations may develop according to a certain temporal pattern (Yakovis, 2002) provides a context for future investigation of corresponding changes in the surrounding infaunal assemblage, once their spatial properties have been described. Our goal was to establish a role for barnacles and ascidians as environmental modifiers in muddy habitats. The predicted effect of aggregations (with each one expected to operate like a huge suspension-feeder) on the surrounding population of sediment was tested at a spatial scale of individual clusters (tens of centimeters from each other) and at the scale of blocks of samples (tens of meters from each other). In first case a factor to be tested was the presence of a nearby aggregation, in second one it was variation of aggregations' density between blocks.

The following consequences of the hypothetical influence of aggregations were expected. Firstly, species positively sensitive to organic matter content should concentrate close to the clusters their abundance increasing with that of barnacles and ascidians. Similarly, biodeposition by bivalves is believed to lead to higher abundances of deposit-feeders (Rosenberg and Loo, 1983; Gray et al., 1990). Secondly, infaunal suspension-feeders that may suffer from competition with clustered barnacles and ascidians should concentrate between the aggregations rather than close to them. Negative correlation is also to be expected between their abundance and that of barnacles and ascidians. Besides the density, the population structure of the infaunal organisms may be affected, the state of which is generally reflected in individual mean weight (IMW, see Hily, 1987).

Observation of spatial patterns that fit the above predictions is not an evidence of a causal relationship. However, it suggests that the latter is highly probable and that the problem is at least worthy of a further experimental check.

2. Methods

2.1. Study site

Samples were collected in July 1999–2002 to the southwest of Solovetskiy Island (Onega Bay, White Sea) 100 m off the shore ($65^{\circ}01'N$, $35^{\circ}41'E$; Fig. 1). The region of Solovetskiy archipelago demonstrates an extreme variety of sea bottom conditions. Epibenthic communities generally predominate there, the fauna being represented mostly by sessile invertebrates (Grishankov, 1995; Grishankov et al., 1997). The research site was a flat zone of muddy bottom at a depth of 11.2–12.5 m. Sea bottom temperature in July was about $8^{\circ}C$, the salinity, according to Grishankov et al. (1997), ranged from 24.4‰ to 27.6‰

2.2. Aggregations of barnacles and ascidians

Each aggregation (cluster) consisted of primary substrate, represented by a shell or a small stone, to which a number of barnacles *B. crenatus* and several smaller epibenthic

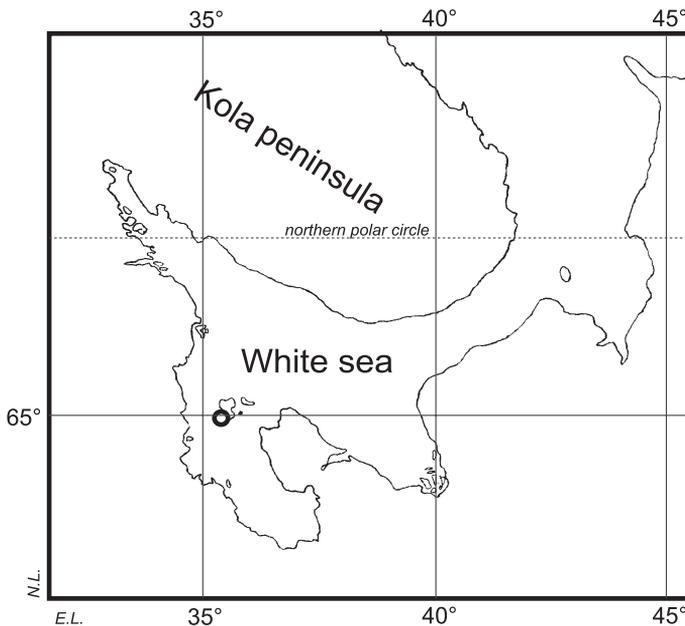


Fig. 1. Sampling area location (encircled).

organisms (bryozoans, red algae) were usually attached. The majority of other sessile organisms were associated with barnacles, including large co-dominating solitary ascidians (*Styela rustica*, *S. coriacea*, *Dendrodoa grossularia*, *Bolthenia echinata*, *Molgula* spp.), as well as bryozoans, sponges and hydroids. Barnacles and ascidians together usually made up more than 90% of biomass and 50% of quantity of all sessile taxa found in clusters. Their relative abundance seemed to change with aggregation age (Yakovis, 2002). The detailed analysis of spatial and temporal patterns within clusters will be covered in one of the next communications. Linear dimensions of the aggregations examined were limited by those of primary substrates and ranged from 3 to 15 cm. According to non-quantified preliminary observations, an average distance between clusters in the research area was comparable to their size and a patch of bare sediment with an area exceeding 1 m² could be hardly found. The clusters seemed to be randomly dispersed and no noticeable patchiness was observed.

2.3. Sampling and laboratory techniques

To estimate the density and individual properties of aggregations of barnacles and ascidians, those were collected by SCUBA divers in 14 square frames 1.44 m² each. Any substrate found on the surface of sediment was examined, regardless of the presence of barnacles and ascidians. We recorded the type of primary substrate and total weight and quantity for solitary ascidians (*S. rustica*, *S. coriacea*, *D. grossularia*, *B. echinata*, *Molgula* spp.—referred to below as “ascidians”) and barnacles (*B. crenatus*) for each aggregation. To determine spatial distribution of benthic species around aggregations we obtained 80 sediment samples in 40 pairs and 14 blocks (replications), each containing 2–12 samples. The block was an area of about 25 m² around a boat limited by the length of the cord the diver was attached to. The largest aggregations (in which the total weight of barnacles and ascidians exceeded 15 g) within this area were selected visually (1–4 per block). Near every such aggregation the diver took a pair of 55 cm² cores, the first one from the pair being situated close to the edge of the aggregation (Close) and the second (Distant), 20–25 cm away (the distance was measured between the centres of cores, Fig. 2). The direction from the

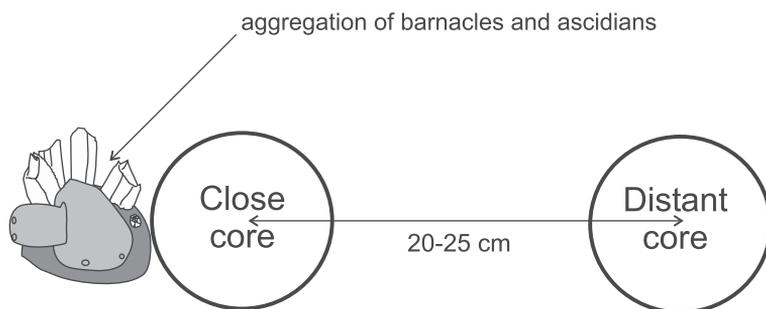


Fig. 2. Sampling scheme.

Close core to the Distant one was always chosen so as to avoid the influence of other aggregations (they were absent at least in the 25 cm range around the Distant core) and was random in relation to the prevailing current direction. The aggregation itself was also collected and examined the same way as those from 1.44 m² frames (see above). Since smaller aggregations generally predominated (see Results), the number of suitable ones varied from block to block, and the number of pairs of cores in a block varied consequently. Pairs of samples within blocks were taken 2–5 m apart from each other. Blocks of samples were randomly distributed over an area of ~2500 m², nine of them (also chosen randomly) containing, in addition to samples of sediment, at least one 1.44 m² frame in which aggregations were counted and collected. Thus, density and biomass (per m²) of barnacles and ascidians, as well as the density of their aggregations, could be estimated for the majority of the blocks. An effect of barnacles and ascidians could be therefore quantified at two spatial scales: as a discrete factor (the presence of an aggregation nearby) at the spatial scale of neighbouring cores and as a continuous factor (the abundance of the dominating epibenthic species) at the spatial scale of blocks.

Sediment from each sample was sieved (0.5 mm mesh diameter used) and sorted. All benthic macrofaunal invertebrates were removed, identified to the lowest taxonomic category possible (generally to the species level), counted and weighted. Individual mean weight (IMW, see Hily, 1987) was calculated for all species in samples where they were found. Taxonomic authorities for all taxa determined may be found in Grishankov et al. (1997).

2.4. Statistical analysis

Calculation of species diversity was based on Shannon–Wiener index. An estimate of average neighbour distance (D) was evaluated from density (N) that could be measured directly, using an original formula, based on random spatial distribution:

$$D = (2/(3^{0.5}N))^{0.5}.$$

Species abundance and IMW (where density was not a zero) in pairs of Close and Distant samples were compared for each species using paired Student t -criteria. For each species and pair of Close and Distant samples, we calculated the difference (dN) between its quantity close to aggregation and far from it:

$$dN_i = N_{\text{close}, i} - N_{\text{distant}, i},$$

where i was the number of sample pairs. Those differences were analysed using ANOVA where Block was a factor (two blocks, each containing only one pair of samples, were excluded). Similarly the dIMW was calculated for each pair. The significance criterion for all tests was $\alpha=0.05$. Means, where given, are \pm S.E. We also performed principal component analysis (PCA; see Gauch, 1982) where densities of 10 most abundant species acted as cases (properties) and samples acted as variables (objects). This multivariate

ordination method was used to test the hypothesis that Close and Distant samples would group separately.

3. Results

The average density of aggregations of barnacles and ascidians was $17.9 \pm 1.9 \text{ m}^{-2}$ and varied from 10.4 to 38.2 m^{-2} from block to block, i.e. an average neighbour distance was $0.26 \pm 0.01 \text{ m}$. The density is distributed normally (Kolmogorov–Smirnov test, $D=0.13$, $p < 0.05$). Thus, no patchiness was found. Most of the clusters sampled (48%) developed on empty shells of *Serripes groenlandicus* (Lamellibranchia), 17% occupied small stones and 22% lacked any primary substrate. These would usually base upon a dead barnacle shell or an ascidian tunic and we considered the primary basis of such aggregations as lost. Clusters demonstrated variation both in biomass of barnacles ($14.56 \pm 1.06 \text{ g}$) and ascidians ($4.82 \pm 0.53 \text{ g}$), smaller ones generally prevailing (Fig. 3).

Out of 84 invertebrate taxa (mostly species or genera) recorded in the sediment samples, 71 occurred in Close samples, 75 in Distant ones, and 62 (74%) were common for samples of both types. The first 10 abundant taxa (referred to below as “dominants”, together they contribute 69% in total abundance, Fig. 4) are 9 polychaete species and undetermined oligochaets. Shannon–Wiener species diversity index was 3.34 for Close samples and 3.27 for Distant ones. Total density of the invertebrates found in those cores was correspondingly 9837 ± 415 and $8418 \pm 303 \text{ m}^{-2}$.

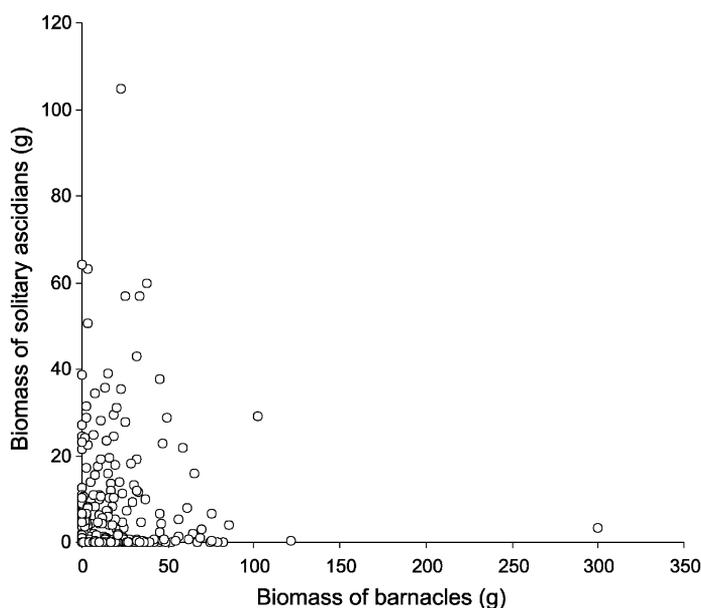


Fig. 3. Biomass of barnacles and ascidians in aggregations.

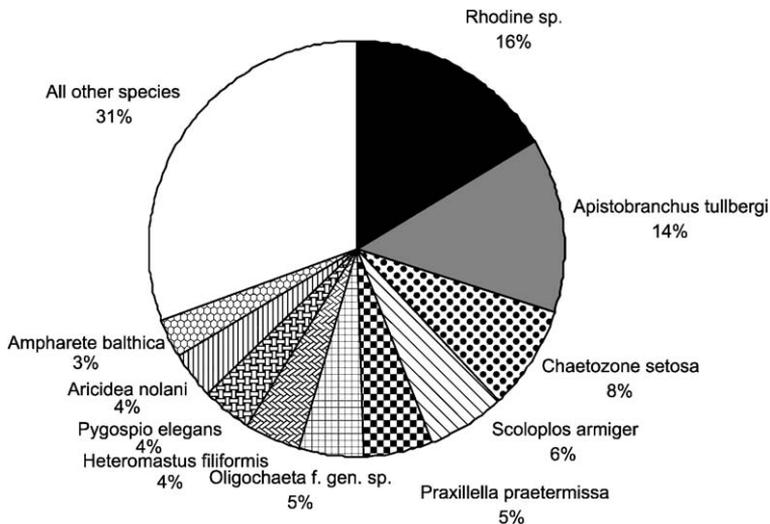


Fig. 4. Contribution of different species in total density of fauna found in cores, regardless of their type.

Fifteen species demonstrate a significant difference between their density in Close and Distant samples; 5 of them belong to dominants (Table 1a). Most of the species for which the difference was observed were more abundant in Close rather than in Distant samples. An opposite trend was found in 2 spionid and 1 sabellid polychaets, in bivalves, including *S. groenlandicus*, and in ophiurans. For 5 species out of the 15, this difference significantly varied between the blocks of samples (Table 1b). Decreasing the taxonomic resolution generally made the results more distinct: polychaets, oligochaets and most crustaceans concentrated in Close samples, whereas bivalves and ophiurans were more abundant in Distant ones (Table 2a). The difference observed significantly varied between blocks in polychaets, oligochaets and molluscs (Table 2b). When polychaets, the most diverse group, were separately analyzed at a family level (Table 3), out of 21 families found, 5 (orbiniids, capitellids, cirratulids, paraonids and terebellids) were associated with Close samples.

Four species, including three dominant ones, demonstrated a significant difference of individual mean weight (IMW) in Close and Distant samples. Maldanid polychaets were larger in Close samples, a cirratulid *Chaetozone setosa* was larger in Distant ones (Table 4a). Among these three, the difference observed significantly varied between the blocks of samples only in *Praxillella praetermissa* (Table 4b).

Fig. 5 presents the results of principal components analysis for Close and Distant samples where densities of 10 dominant species were used as variables. The first of two components, the scatter plot, is based on 25.6% of total variance, the second, 14.8% (40.4% total). Despite overlap, there are clear differences in the whole assemblage. Furthermore, points representing Distant samples receive much less variable scores for the first component than Close ones (i.e. they are more concentrated, Table 5).

Table 1

Summary of analyses comparing (a) the density of most important species in Close and Distant samples (paired Student *t*-test) and (b) the effect of location on the differences between Close and Distant samples (ANOVA on differences)

Species name	(a) Average density $N \pm S.E. (m^{-2})$			(b) Effect of location on the difference in density			
	Close cores	Distant cores	<i>p</i>	MS _{effect}	MS _{error}	<i>F</i> -ratio	<i>p</i>
<i>Scoloplos armiger</i>	691.6 ±61.9	432.3±48.6	***	10.48	8.32	1.26	ns
<i>Apistobranchnus tullbergi</i>	1192.1±124.2	1287.7 ±109.3	ns	22.76	20.94	1.09	ns
<i>Laonice cirrata</i>	4.6±4.6	18.2 ±8.7	*	0.16	0.03	4.94	***
<i>Microspio theeli</i>	0.0±0.0	77.4 ±35.6	*	2.86	1.04	2.76	*
<i>Pygospio elegans</i>	391.3±73.6	332.2±39.0	ns	12.12	4.21	2.88	**
<i>Aricidea nolani</i>	409.5 ±58.9	241.2±38.2	**	8.60	3.72	2.31	*
<i>Chaetozone setosa</i>	928.2 ±133.7	532.4±65.9	**	59.46	14.17	4.20	***
<i>Heteromastus filiformis</i>	445.9 ±50.5	318.5±37.3	*	7.26	5.01	1.45	ns
<i>Praxillella praetermissa</i>	477.8±37.8	464.1±43.2	ns	2.70	2.89	0.93	ns
<i>Rhodine sp.</i>	1578.9±109.3	1419.6±109.5	ns	18.37	24.92	0.74	ns
<i>Laphania boeki</i>	13.7 ±7.7	0.0±0.0	*	0.06	0.08	0.67	ns
<i>Proclea malmgremi</i>	54.6 ±17.5	9.1±6.4	**	0.53	0.41	1.29	ns
<i>Euchone sp.</i>	4.6±4.6	18.2 ±10.9	*	0.08	0.07	1.05	ns
Oligochaeta f. gen. sp.	659.8 ±110.5	250.3±53.6	***	35.45	11.14	3.18	**
Gammaroidea f. gen. sp.	150.2 ±33.2	50.1±15.9	**	1.92	1.73	1.11	ns
<i>Leptognathia sarsi</i>	159.3 ±33.3	91.0±22.6	*	1.37	1.61	0.85	ns
<i>Serripes groenlandicus</i>	0.0±0.0	13.7 ±7.7	*	0.06	0.09	0.65	ns
<i>Macoma calcarea</i>	31.9±11.1	63.7 ±13.9	*	0.57	0.35	1.64	ns
<i>Stegophiura nodosa</i>	0.0±0.0	22.8 ±11.6	*	0.21	0.16	1.29	ns

Species included were either the 10 most abundant (in **bold**) or exhibited significant differences in density. (a) Higher values in pairs of mean density are highlighted in **bold** where the difference is significant. (b) $df=14$, $df_{error}=26$. For each species the variable was calculated as the difference between the density in the core obtained Close to the aggregation of barnacles and ascidians and the density in Distant core. The hypothesis that Block of pairs of cores (random, 12 levels) has no effect on this difference was checked.

ns: not significantly different; * $p<0.05$; ** $p<0.01$; *** $p<0.001$.

Most of the dominant species also demonstrated a significant MS correlation between their density (regardless of the core type, Close or Distant) and the abundance of ascidians and barnacles within the corresponding block (Table 6a). With one exception, significant correlations were positive for all these species. At this scale, polychaets *Scoloplos armiger*, *Heteromastus filiformis* and *Ampharete balthica* showed no sensitivity to the number of aggregations and biomass of keystone species. Negative correlations with all parameters under study (number of clusters, biomass of barnacles, biomass of ascidians) were demonstrated by *P. praetermissa*. Since all the three parameters were strongly correlative (Table 6c), our data are hardly sufficient to assess the contribution of each in density variation of the infaunal species. Nevertheless, *Aricidea nolani* demonstrated an association only with a high abundance of ascidians, whereas *Rhodine sp.* was associated only with a high abundance of barnacles. The same analysis of high order taxa revealed significant correlations between some of those parameters and the abundance of polychaets, oligochaets,

Table 2

Summary of analyses comparing (a) the density of high order taxa in Close and Distant samples (paired Student *t*-test) and (b) the effect of location on the difference between the densities of these taxa in pairs of Close and Distant samples (ANOVA on differences)

Taxa name	(a) Average density $N \pm \text{S.E. (m}^{-2}\text{)}$			(b) Effect of location on the difference in density			
	Close cores	Distant cores	<i>p</i>	MS _{effect}	MS _{error}	<i>F</i> -ratio	<i>p</i>
Priapulida	0±0	5±5	ns	0.0	0.0	1.58	ns
Nemertini	18±9	27±12	ns	0.4	0.2	1.83	ns
Polychaeta	8272±364	7266±264	**	397.5	149.5	2.66	*
Oligochaeta	660±111	250±54	***	35.5	9.0	3.96	***
Amphipoda	182±34	64±17	***	1.9	2.2	0.88	ns
Cumacea	18±9	18±9	ns	0.3	0.2	1.45	ns
Isopoda	27±10	36±13	ns	0.3	0.3	1.02	ns
Tanaidacea	159±33	91±23	*	1.3	1.7	0.76	ns
Gastropoda	27±10	50±18	ns	0.8	0.4	2.17	*
Bivalvia	437±47	555±66	*	10.6	3.9	2.74	*
Ophiuroidea	0±0	23±12	*	0.2	0.2	1.24	ns
Enteropneusta	5±5	5±5	ns	0.0	0.1	0.00	ns

(a) Higher values in pairs of mean densities are highlighted in **bold** where the difference is significant. (b) $df=14$, $df_{\text{error}}=25$. For each taxa the variable was calculated as the difference between the density in the core obtained Close to the aggregation of barnacles and ascidians and the density in Distant core. The hypothesis that Block of pairs of cores (random, 12 levels) has no effect on this difference was checked.

ns: not significantly different; * $p<0.05$; ** $p<0.01$; *** $p<0.001$.

isopods and bivalves (Table 6b). For the first two groups, the dependence observed was positive, for the second two, it was negative.

4. Discussion

The majority of abundant species demonstrated a difference either in medium density or in the individual mean weight between Close and Distant cores. At other levels of taxonomic resolution, this difference was also found in numerous taxa. Correspondingly, PCA ordination of samples indicated the difference in assemblages associated with cores of either type. This result agrees with the one predicted by the hypothesis that aggregations should influence the infauna and affect its spatial distribution. Spatial variation of dN and $dIMW$ in pairs of cores was also significant for many taxa. Furthermore, high significance correlations between the abundance in cores and the density of clusters (as well as biomass of barnacles and ascidians per m^2) were found for most of the dominant infaunal species despite the small sample size. Thus, though non-quantified spatial heterogeneity of a habitat together with biotic interactions not involving barnacles or ascidians and temporal changes in the researched system (which were out of the focus of our present investigation) certainly contribute to the difference between replicas, the latter is also strongly affected by the variation of local density of aggregations.

For high-ordered taxa the results are similar and consistent at both scales studied: mainly detritivorous annelids and crustaceans increase their abundance near individual aggregations (at a scale of $\sim 10^{-1}$ m) and where the density of barnacles and ascidians is

Table 3

Average densities of polychaete families compared in cores sampled Close to aggregations of barnacles and ascidians versus Distant ones (paired Student *t*-test)

Family name	Average density \pm S.E. (m^{-2})		<i>p</i>
	Close cores	Distant cores	
Ampharetidae	318.5 \pm 45.0	263.9 \pm 43.7	ns
Apistobrachidae	1192.1 \pm 124.2	1287.7 \pm 109.3	ns
Orbiniidae	691.6 \pm 61.9	432.3 \pm 48.6	***
Capitellidae	477.8 \pm 52.0	341.3 \pm 38.7	ns
Cirratulidae	1105.7 \pm 144.5	632.5 \pm 64.5	**
Cossuridae	81.9 \pm 24.3	100.1 \pm 33.2	ns
Dorvilleidae	236.6 \pm 38.1	250.3 \pm 35.5	ns
Hesionodae	31.9 \pm 14.4	13.7 \pm 7.7	ns
Lumbrinereidae	36.4 \pm 13.4	63.7 \pm 15.4	ns
Maldanidae	2102.1 \pm 133.1	1956.5 \pm 120.8	ns
Nephtyidae	263.9 \pm 42.2	223.0 \pm 27.3	ns
Oweniidae	41.0 \pm 15.3	36.4 \pm 11.7	ns
Paraonidae	573.3 \pm 59.9	432.3 \pm 49.1	*
Phyllodocidae	31.9 \pm 12.8	59.2 \pm 13.7	ns
Sabellidae	104.7 \pm 27.6	132.0 \pm 24.4	ns
Scalibregmidae	122.9 \pm 27.2	172.9 \pm 31.9	ns
Sigalionidae	104.7 \pm 29.1	127.4 \pm 30.0	ns
Spionidae	536.9 \pm 82.9	568.8 \pm 54.2	ns
Syllidae	18.2 \pm 8.7	22.8 \pm 9.6	ns
Terebellidae	95.6 \pm 20.6	27.3 \pm 10.4	**
Trichobranchidae	54.6 \pm 17.5	68.3 \pm 22.3	ns

Higher values in pairs of means are highlighted in **bold** where the difference is significant.

ns: not significantly different; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 4

Summary of analyses comparing (a) the individual mean weight (IMW) for the 10 dominant species in Close and Distant samples (paired Student *t*-test) and (b) the effect of location on the difference between the IMW of these taxa in pairs of Close and Distant samples (ANOVA on differences)

Species name	(a) IMW \pm S.E. (mg)			(b) Effect of location on the difference in IMW			
	Close cores	Distant cores	<i>p</i>	MS _{effect}	MS _{error}	<i>F</i> -ratio	<i>p</i>
<i>Scoloplos armiger</i>	2.76 \pm 0.33	2.73 \pm 0.33	ns	0.0038	0.0031	1.20	ns
<i>Apistobranchnus tullbergi</i>	1.11 \pm 0.10	1.19 \pm 0.10	ns	0.0025	0.0006	3.86	**
<i>Pygospio elegans</i>	0.67 \pm 0.20	0.57 \pm 0.10	ns	0.0004	0.0014	0.32	ns
<i>Aricidea nolani</i>	0.87 \pm 0.10	0.99 \pm 0.10	ns	0.0008	0.0006	1.28	ns
<i>Chaetozone setosa</i>	1.44 \pm 0.20	2.49 \pm 0.33	**	0.0042	0.0055	0.76	ns
<i>Heteromastus filiformis</i>	1.02 \pm 0.10	1.04 \pm 0.10	ns	0.0008	0.0005	1.62	ns
<i>Praxillella praetermissa</i>	6.15 \pm 0.90	3.79 \pm 0.60	*	0.1166	0.0353	3.30	*
<i>Rhodine sp.</i>	1.43 \pm 0.10	1.12 \pm 0.10	*	0.0006	0.0006	0.94	ns
<i>Ampharete balthica</i>	0.92 \pm 0.10	0.90 \pm 0.10	ns	0.0011	0.0005	2.08	ns
Oligochaeta f. gen. sp.	0.54 \pm 0.10	0.65 \pm 0.10	ns	0.0002	0.0003	0.70	ns

(a) Higher values in pairs of IMW are highlighted in **bold** where the difference is significant. (b) $df = 14$, $df_{error} = 25$. For each species the variable was calculated as the difference between the IMW in the core obtained Close to the aggregation of barnacles and ascidians and the IMW in Distant core. The hypothesis that Block of pairs of cores (random, 12 levels) has no effect on this difference was checked.

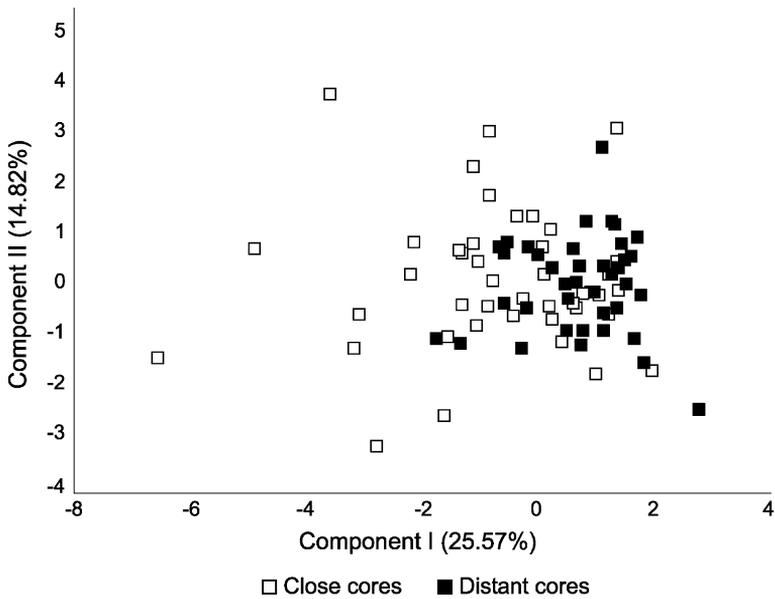


Fig. 5. Principal component analysis: sample scores plot. Cores sampled Close to aggregations (white squares). Distant cores (sampled between the aggregations, black squares). Densities of 10 dominating species were used as variables for the analysis.

higher (at a scale of ~ 10 m). The pattern indicated by suspension-feeding bivalves (like *Serripes* and *Macoma*) was inverse. Isopods, however, demonstrated no association with cores of either type, whereas their number and the abundance of barnacles was negatively correlated. Ophiurans (different species being either omnivorous or suspension-feeders, Roushdy and Hansen, 1960; Feder, 1981) showed no dependence of their density on that of barnacles or ascidians, but concentrated in Distant samples. Correspondence between the feeding types (where the information is available) and spatial associations recorded in this study are summarised in Table 7.

Lower taxa were more diverse than high order ones according to the combinations of effects and scales. Without any exceptions, when indicating an association with

Table 5

Average scores received by Close and Distant samples for the first two principal components (see Fig. 5) and their variance

Core type	Component I		Component II	
	Average score	Variance	Average score	Variance
Close cores	-0.68	3.22	0.04	2.03
Distant cores	0.71	0.91	-0.05	0.94
<i>p</i> (Student <i>t</i> -test)	***		ns	

Student *t*-test is used to compare average scores of PCA components for the cores sampled Close to aggregations of barnacles and ascidiant versus the Distant ones.

ns: not significantly different; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 6

Correlations between (a) densities of 10 dominant infaunal species, (b) densities of high order taxa and the abundance of barnacles and ascidians within a block of samples; correlations between (c) the local abundance of barnacles, the local abundance of ascidians and the density of their aggregations

Taxa name	Pearson <i>r</i> with		
	Density of aggregations (m ⁻²)	Biomass of barnacles (g·m ⁻²)	Biomass of ascidians (g·m ⁻²)
<i>(a)</i>			
<i>Scoloplos armiger</i>	0.12 ns	0.26 ns	0.23 ns
<i>Apistobranchus tullbergi</i>	0.43**	0.44**	0.44**
<i>Pygospio elegans</i>	0.25 ns	0.46**	0.41**
<i>Aricidea nolani</i>	0.15 ns	0.14 ns	0.34*
<i>Chaetozone setosa</i>	0.53***	0.55***	0.50***
<i>Heteromastus filiformis</i>	0.22 ns	0.27 ns	0.26 ns
<i>Praxillella praetermissa</i>	-0.33*	-0.33*	-0.35*
<i>Rhodine</i> sp.	0.01 ns	0.34*	0.05 ns
<i>Ampharete balthica</i>	-0.05 ns	0.23 ns	0.13 ns
Oligochaeta f. gen. sp.	0.29 ns	0.31*	0.27 ns
<i>(b)</i>			
Nemertini	0.02 ns	0.15 ns	0.14 ns
Polychaeta	0.23 ns	0.43**	0.41**
Oligochaeta	0.29 ns	0.31*	0.27 ns
Amphipoda	0.11 ns	0.11 ns	-0.06 ns
Cumacea	-0.03 ns	0.07 ns	0.13 ns
Isopoda	-0.23 ns	-0.35*	-0.23 ns
Tanaidacea	0.06 ns	0.08 ns	-0.12 ns
Gastropoda	0.13 ns	0.21 ns	0.03 ns
Bivalvia	-0.33*	-0.31*	-0.17 ns
Ophiuroidea	0.03 ns	0.11 ns	0.14 ns
<i>(c)</i>			
Density of aggregations	–	0.71***	0.72***
Biomass of barnacles	0.71***	–	0.80***
Biomass of ascidians	0.72***	0.80***	–

Properties of epibenthic fauna (density of the aggregations, biomass of barnacles and ascidians) per area unit were tested for the significance of their correlations with densities of motile fauna from the cores regardless of their type (Close or Distant).

ns: not significantly different; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

samples of either type, deposit-feeding (according to Holte, 1998) polychaets and oligochaets prevailed in Close ones. Alternatively, spionid-like surface deposit feeders (Eckman, 1979), such as *Laonice cirrata* and *Microspio theeli*, were more abundant in Distant cores. Similar patterns found around and under the aggregations of bivalves had been explained (though without any direct evidence) by biodeposition and sediment stability reduction close to them (Rosenberg and Loo, 1983; Brenchley, 1981; Wilson, 1981; Hily, 1987; Dittman, 1990; Gray et al., 1990; Zühlke and Reise, 1994; Ragnarsson and Raffaelli, 1999). For several terebellids (*Laphania boeki* and *Proclea malmgremi*), which are also surface deposit-feeders, an unexpected association with Close clusters was found. However, in terebellids tentacles are much longer than

Table 7
Feeding types and spatial associations of high order taxa found in cores

Taxa name	Feeding type	Association with cores of a certain type	Correlation of density with the abundance of barnacles and/or ascidians
Nemertini	100% ps		
Polychaeta	71% df , 14% sf , 14% ps	c	+
Oligochaeta	100% df	c	+
Amphipoda	Na	c	
Cumacea	100% df		
Isopoda	Na		—
Tanaidacea	100% df (?)	c	
Gastropoda	43% ps , 43% na , 14% hv		
Bivalvia	67% sf , 33% df	d	—
Ophiuroidea	100% ov/sf (?)	d	

The proportion of different feeding types known for local species from high order taxa under study and its correspondence with spatial associations found is listed. The prevailing feeding type is highlighted in **bold**. ps—predators and scavengers; df—deposit feeders; sf—suspension feeders; hv—herbivorous; ov—omnivorous; na—not available for local species; (?)—feeding type only known for several different species from the same taxa as a studied species belongs to; c—significant association with Close cores; d—significant association with Distant cores; +—significant positive correlation; ——significant negative correlation.

in spionids (see Fauchald and Jumars, 1979; Zhadan and Tzetlin, 2002) and their individual feeding zone is consequently larger, which may affect their sensitivity to local instability of the sediment.

Maldanids, the most abundant taxa in the assemblage, demonstrated almost no variance of their abundance between the cores of either type, but the mean weight of individual was increased by 30–60% in Close ones. Furthermore, the two species indicated totally different trends at the spatial scale of blocks of samples: *P. praeterrmissa* was less abundant in blocks with high density of aggregations, whereas the density of *Rhodine* sp. positively correlated with the biomass of barnacles. Lack of data on the biology of both particular maldanid species and maldanids in general does not allow us to offer any convincing explanation of these results. We can only note that both species are extensive tube-builders, the sediment in cores being, to great extent, the matrix made of their tubes. Therefore, in addition to possible interactions with barnacles and ascidians, their abundance can hypothetically be affected by the concentration of particles suitable for their tube-building activity.

Possible larval predation by barnacles or ascidians does not appear to have noticeable effect on the spatial distribution of the infauna. At least, lack of taxa with planktonic development, noted in dense aggregations of bivalves (Dittman, 1990), has not been documented in our study. No other correspondence was noticed, either, between the recruitment mode and distribution of infaunal species. For example, *C. setosa* has a planktonic larva (Wilson, 1991), but is more abundant in Close samples. The majority of other dominating polychaete species under study combine benthic and planktonic types of development (see Wilson, 1991; Morgan et al., 1999; Blake and Arnofsky, 1999; Kruse, 2003). However, benthically recruiting oligochaets were associated with Close cores and planktonically recruiting bivalves, with Distant ones.

The spatial pattern found in *S. groenlandicus* (Lamellibranchia) is of special interest. It is this species that mostly provides aggregations with primary substrates. A decrease in its abundance close to the clusters may reflect a negative feedback in the system, consisting of epibenthic islands dominated by suspension-feeders, and large, also suspension-feeding bivalves, from whose shells these islands originate.

Species composition found in Close cores was more variable than in Distant ones. It is best illustrated by PCA results in Fig. 5. The effect of aggregation's presence is inconstant, which is quite predictable given that clusters vary at least in size and species composition. Further research focused on comparison of spatial patterns associated with aggregations with different properties (e.g. small or large, populated mainly by ascidians or by barnacles) is necessary to quantify this variation. The extent to which spatial distribution of infaunal organisms is affected by epibenthic sessile keystone species may be fairly underestimated in the present study.

Benthic assemblages associated with patchy habitats, where hard and soft substrates mosaic makes direct interactions between sessile epibenthic and motile infaunal organisms possible, are poorly studied. Most data available are on islands of bivalves surrounded by soft sediment (Reise, 1983; Tsuchiya and Nishihara, 1985, 1986; Ragnarsson and Raffaelli, 1999). However, many other invertebrates are also known to form epibenthic clusters or beds: at least polychaetes, cirripedians, phoronids and ascidians (e.g. Brenchley and Tidball, 1980; Johnson, 1990; Pullen and La Barbera, 1991; Thomas, 1994; Monteiro et al., 2002). If particles of hard substrate are available, these organisms may integrate into infaunal assemblage and modify its spatial structure. The system under study is an important example of such a case, where the motile fauna seem to distribute regularly around clustered suspension-feeders, according to the feeding strategies of different taxa. Now that the spatial pattern has been generally described, the research should be conducted in two directions: experiments manipulating aggregations' presence or density and the comparison of assemblages surrounding the clusters of different size and species composition.

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