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Multiple foundation species shape benthic habitat islands

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Abstract Pattern generation by foundation species (FS) is a primary structuring agent in marine and terrestrial communities. Prior research, focused on single-species or guild-dominated habitats, stressed the role of facilitation in maintaining community structure. However, many habitats are developed by multiple FS from different guilds. Competition between these FS may provide an additional agent potentially responsible for spatial and temporal patterns. In the White Sea, epibenthic patches formed by barnacles (*Balanus crenatus*) and solitary ascidians (mainly *Styela* spp. and *Molgula* spp.) on small stones and empty bivalve shells (mainly *Serripes groenlandicus*) produce microhabitats for different sessile taxa. We hypothesized that: (1) several FS would provide habitats for most of other species in the community; (2) different FS promote different assemblages of sessile organisms; (3) the interplay of facilitation and competition best explains observed patterns of abundance and demography in FS; and (4) these interactions shape the whole community, increasing the diversity compared to less heterogeneous patches constituted by single FS. We examined 459 patches and the results generally supported this hypothesis. The number of FS in a patch positively affected species diversity. Most sessile species (72% of individuals) resided on barnacles, ascidians and red algae, except barnacles that dominated the primary substrate. The size structure of barnacles (live individuals and empty shells) and ascidians were interrelated, suggesting long-term patch dynamics whereby ascidians regularly replace barnacles. Following this replacement, we expect consequent changes to the entire dependent assemblage. Evidence for these changes exists in the spatial pattern: most sessile and motile taxa demonstrated significant associations with either FS. Our results indicate that the small-scale patterns observed in patches formed by multiple FS are primarily generated by facilitation of dependent taxa by FS, and facilitation and competition between different FS.

Keywords Facilitation · Competition · Habitat · Barnacles · Ascidians

Introduction

The interplay between predation, competition and facilitation is thought to shape most terrestrial and benthic communities. However, the relative importance of positive and negative interspecific interactions is a subject of the ongoing debate (Bertness and Shumway 1993; Callaway and Walker 1997; Bruno and Bertness 2000). Early authors recognized

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Communicated by Martin Attrill.

Dedicated to E. A. Ninbourg, our late tutor.

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the power of positive interactions in structuring the communities and promoting the successions (Clements 1916). Later, the lack of experimental evidence for positive interactions resulted in ecological theories of communities driven by competition and predation (Connell 1983; Schoener 1983; Menge and Sutherland 1987). Interest in facilitation has resumed during the last two decades, inspired by the growing evidence supporting its structuring role (see Bertness and Callaway 1994). Single foundation species (FS), like a coral or a tree, can determine the entire landscape of other organisms by creating physical habitat structure (bioengineering sensu Jones et al. 1994) of increased complexity and heterogeneity (McCoy and Bell 1991). Communities (at least some) are thus viewed as systems hierarchically organized by reliance principally "on the presence of ... habitat-forming species" (Bruno and Bertness 2000).

Effects of FS can be conditioned by their individual properties, age and size; even the sign of the net effect can be altered depending on these parameters (see Callaway and Walker 1997 for review). At a larger scale, the patch structure, density and population structure of the FS determines the structure of the community (e.g., Tsuchiya 2002; Hewitt et al. 2002). Despite the wide range of the objects studied, the theory relies on investigations performed on pairs of one strong habitat-modifier and one dependent species; in some cases multiple dependent species were considered (see Stachowicz 2001). However, the natural systems frequently are made up of multiple, co-dominating FS like coral reefs and forests. This evident fact is certainly recognized by modern theory (Bruno and Bertness 2000; Stachowicz 2001) but only a limited attempt (Altieri et al. 2007) was made to discuss the possible functional and structural difference between single- and multiple-facilitator dominated communities. Bruno and Bertness (2000) make a distinction between the communities structured by a strong facilitator (like mussel) or a guild thereof (like kelp, corals and seagrasses), but do not further explain the possible difference. They probably use the term "guild" to stress the functional similarity of coexisting facilitators, which is not actually proved. Furthermore, according to the definition (Root 1967; Simberloff and Dayan 1991; Wilson 1999), "guild" only implies similarity in resource usage but not necessarily any similarity in resource provision. Below we argue that multiple coexisting FS may differ in their structuring role (which is important when predicting abundance and diversity patterns) and provide a case from the marine epibenthic community.

Habitats formed by single and multiple FS are common in both terrestrial and marine ecosystems. Mixed forests are dominated by several tree species, which can be definitely attributed to the same guild, but are functionally different enough to support specific ground vegetation composition (Croizer and Boerner 1984; Saetre et al. 1997), epiphytes (Ter Steege and Cornelissen 1989; Callaway et al. 2002) and soil fauna (Scheu et al. 2003). Each tree in mixed stands develops an individual "influence circle" contributing to the mosaic of soil properties (Boettcher Kalisz 1990). In some cases the effect of tree species is weak in relation to geographical and geological variation of the dependent species composition (e.g., Augusto et al. 2003). The positive effect of different nurse-plant species on their beneficiaries can be similar (Valiente-Banuet et al. 1991) or different (Raffaele and Veblen 1998). Architectural properties of coexisting benthic algae affect species composition and abundance of gastropods (Chemello and Milazzo 2002). Experiments with mimics prove that coexisting filamentous and foliose *Sargassum* attract different mobile epifauna (Edgar and Klumpp 2003), but other data show little influence of the seaweed diversity on the diversity of the associated mobile assemblage (Bates and DeWreede 2007).

Coexisting FS, especially those from one guild and with similar resource usage, may exhibit regular replacement sequences (Clements 1916) driven by the temporally shifting balance of competition and facilitation between the key consequent successors (Watt 1947). Cascading effects of several hierarchically facilitated FS were recently proved for the cordgrass bed communities (Altieri et al. 2007), but possible competition between principal facilitators was not examined. To our knowledge, no attempt was made to analyze the patterns in the habitat created by multiple FS considerably varying in their functional similarity but seemingly involved in positive and negative interactions with each other. If coexisting facilitators do support different assemblages of the dependent taxa, the model of hierarchical community design "around" a single FS (Bruno and Bertness 2000) or a sequentially facilitated cascade thereof (Altieri et al. 2007) could be further developed by multiplication of the hierarchies and addition of interactions (not necessarily positive) between the principal facilitators at their tops.

Patches are discrete and internally uniform elements of the landscape. In the soft seabed of Onega Bay in the White Sea, epibenthic patches dominated by barnacles *Balanus crenatus*, several species of solitary ascidians and canopy-forming red algae, often develop on shells and small stones—the only hard substrates available here. These patches also include numerous empty barnacle shells. A number of sessile invertebrates (bryozoans, hydroids, serpulid and spirorbid polychaetes) use the surfaces of the dominants to live on. Most surfaces are covered with silt, potentially increasing space limitation for sessile taxa. Together with a diverse motile fauna inhabiting the cavities between sessile organisms, they form small multi-tier biogenic reefs surrounded by muddy sediment (Yakovis et al. 2004, 2005). Most patches [type II according to Connell and Keough (1985)] occur on empty shells of the quahog

Serripes groenlandicus (Yakovis et al. 2004) and therefore have a clearly defined and experimentally reproducible starting point in time.

We tested several predictions related to the general hypothesis that epibenthic patches are structured by the biogenic effects of multiple FS and their possible interactions (negative or positive):

1. A limited set of biogenic substrates formed by several FS would harbor most other sessile organisms.
2. The coexisting functionally different FS (*Serripes* and *Balanus*) and taxon-guilds of FS (ascidians and red algae) would support considerably different small-scale sessile assemblages; we expected higher variation in the assemblages hosted between taxon-guilds of FS than between species of FS within them.
3. FS also would use the surfaces of each other differentially; their demographies would be interrelated: size structure of barnacles and their dead:live ratio would be affected by the abundance of adult ascidians; size structure of ascidians would differ depending on substrate type. The patterns would suggest replacement sequences explained by the balance of positive and negative interactions between FS.
4. Due to increased habitat heterogeneity we expected higher diversity within the patches with more FS.

Materials and methods

Study area

Two subtidal sites were sampled near Solovetskiy Island, Onega Bay (the White Sea) 100 m offshore and 1,820 m from each other, (65°01.2’N, 35°39.7’E for site 1 and 65°00.7’N, 35°41.7’E for site 2). Sea bottom conditions in the Solovetskiy archipelago are variable, with hard substrates and mixed sediments generally predominating. The benthic macrofauna is represented mostly by sessile invertebrates. The study sites had flat muddy bottoms at depths of 11.2–12.5 m (site 1) and 14.5–15.0 m (site 2). There was no difference in bottom temperature (5–8°C in July) or salinity (24.4–27.6‰) between the two sites [see Yakovis et al. (2005) and references therein].

Sampling and laboratory techniques

Sampling was conducted in July 2001–2005. In 2002–2004 all visible substrates with sessile organisms were collected by SCUBA divers within 16 replicate square frames, 1.00–1.44 m^2, at two sites (ten frames at site 1 and six frames at site 2). We identified and counted all macrobenthic sessile organisms on each of the 323 substrates. Identification was generally performed to species level with the exception of sponges. Motile organisms were also identified and counted but these data were only used to calculate species diversity for each patch. Substrate type was recorded for each individual or colony (see below). Barnacles and their empty shells (hereafter “dead barnacles”) were counted and measured (aperture length accurate to 1 mm). Total wet weight of barnacles in a patch was determined. Solitary ascidians were wet weighed individually to the nearest 0.01 g. Each one was punctured and squeezed slightly on a dry paper towel to remove extra water before weighing. The position of solitary ascidians on barnacle shells was documented as “inner” (inside the orifice, including tergum, scutum and inner surface of other plates) or “outer” (elsewhere outside the orifice).

In addition, barnacles (live and dead) were measured and solitary ascidians were individually weighed in 136 epibenthic patches collected at site 1 in July 2001 (three frames, 1.44 m^2 each) and July 2005 (two frames, 1.00 m^2 each). Substrate type was recorded for each individual. We used these data to increase the sample size in the analyses of substrate associations in barnacles and ascidians of different size. All other analyses were based on the data collected in 2002–2004.

Statistical analysis

Principal substrate types were identified as those with highest total abundances of organisms found on them. To assess the effect of substrate type, we increased the sample size, merging the data for separate epibenthic patches: the abundances of sessile taxa found in one 1.00–1.44 m^2 frame (from five to 55 aggregations) were summarized by substrate type. Each replicate frame was thus represented by seven samples corresponding to the number of different substrate types recognized [absent, primary (Pri), ascidians (A), red algae (R), barnacles (LB), empty barnacle shells (DB) and other]. The Pri type included all objects underlying epibenthic patches (shells and stones). These pooled substrate subsamples of the frames (SSF) were subjected to a non-metric multidimensional scaling (NMDS) ordination (Kruskal and Wish 1978) based on Bray–Curtis dissimilarity. The effects of location and substrate were tested using two-way analysis of similarities (ANOSIM) based on Bray–Curtis dissimilarity on standardized data, followed by the SIMPER procedure (PRIMER-E software package; Clarke 1993) to determine the taxa predominantly responsible for the difference between the assemblages. To compare the assemblages hosted by different FS between and within their taxon-guilds we used ANOSIM and NMDS on SSF pooled separately for four species of solitary ascidians and six species of canopy-forming red algae.

To compare absolute densities of sessile taxa on LB, DB and *Serripes* shells we estimated areas of these solid substrates by wrapping each shell tightly in thin aluminum foil. Extra foil, including that from folds, was removed. The rest was weighed accurate to 1 mg; the surface area was estimated using a previously derived relationship between area and weight (Marsh 1970). Samples of *B. crenatus* and *S. groenlandicus* shells were used to provide regression equations (with $R^2 > 0.85$) to derive areas of their surface from aperture length for barnacles and shell length for *Serripes* (see S1). We only analyzed the surface areas for convex sides of *Serripes* shells since nearly all of them were found lying with this (as a rule, fouled) side up.

The effect of substrate type on abundances of FS was assessed as described above, and also analyzed separately for individual size (for barnacles) or weight (for ascidians) classes. Dead:live ratio is an indirect indicator of mortality commonly used in plant ecology (e.g., Spetich et al. 1999). The ratio depends on mortality and debris preservation, the latter supposed to be similar within a patch for the shells of the same size with the one exception discussed below. To estimate the mortality, dead:live ratios of barnacles were compared pairwise between locations, size classes, microhabitats and patches with different domination type (barnacles or ascidians) using the χ^2 value calculated from 2 × 2 tables.

Log-*e* based Shannon–Wiener species diversity index (H') was calculated for each patch based on abundances of all sessile and mobile taxa without the FS. We used multiple regression to assess the relative effects of total weight and number of FS in a patch on H'.

All mean values are given ±SE unless stated otherwise.

Results

Domination and sources of substrates for sessile organisms

The density of epibenthic patches was significantly higher ($P < 0.001$, Student's *t*-test) at site 1 (20.8 ± 2.3 m^{-2}) than at site 2 (5.9 ± 0.9 m^{-2}). Most (57%) were based on empty shells of *S. groenlandicus* (on average 55.6 ± 0.9 mm long with 12.4 ± 0.3 growth bands). Pri was absent in 20% of the patches. Mean abundance of dominant taxa per patch in terms of numbers of individuals and biomass was as follows: barnacles *B. crenatus* 31.44 ± 2.36 individuals (ind.) and 14.32 ± 1.29 g, solitary ascidians (*Styela* spp., *Molgula* spp. and *Boltenia echinata*) 10.64 ± 0.89 ind. and 3.94 ± 0.51 g, red algae (mostly *Phycodrys rubens* and *Ptilota plumosa*) 0.24 ± 0.04 g. Estimated from length, the total area of the upper surface of *Serripes* shells was 0.031 ± 0.004 m^2 per m^2 of the bottom at site 1 and 0.012 ± 0.001 m^2 per m^2 of the bottom at site 2. Total area of the surfaces provided by live barnacles was 0.098 ± 0.008 and 0.003 ± 0.001 m^2 m^{-2} of the bottom, correspondingly.

Within the patches we recorded 134 sessile macrobenthic taxa (mostly species or genera), 64 of them were bryozoans. Mean number of sessile species per patch was 25.9 ± 1.1. Average Shannon–Wiener species diversity of sessile taxa (without mobile species) in a patch was similar for the two sites (1.78 ± 0.04 for site 1 and 1.87 ± 0.11 for site 2, Student's *t*-test, $P = 0.434$).

Barnacles (either live or dead) were found in 97.0% of all aggregations. Ascidians were found without barnacles in 3.7% of all patches. *B. crenatus* (or its shells) were found without ascidians in 17.6% of patches. In terms of biomass, ascidians dominated in 17.2% of the patches. Ascidian-dominated patches were more frequent at site 2 than at site 1 (34.5% vs. 15.7%, significant at $P < 0.001$, χ^2).

Out of all occurrences of sessile taxa, 98% were associated with one of the five substrate types: LB (34%), Pri (26%, of which 72% were on *Serripes* empty shells), A (19%), R (11%) and DB (8%) (see S2). Not all those substrates were available in each epibenthic patch (see S3) though each of the five was generally as frequent as 70–90%.

The assemblages associated with different FS

The assemblages of sessile organisms associated with major substrate types were different according to NMDS on SSF (Fig. 1), with the largest distance observed between Pri- and R-associated ones. Samples from sites 1 and 2 also grouped separately with a small overlap. Within the taxon-guilds of A and R there was small variation in sessile assemblages associated with individual FS (Fig. 2).

Two-way ANOSIM on SSF revealed similar effects of substrate type and location on the assemblage (substrate type, $R = 0.705$, $P_{\text{same}} = 0.001$; site, $R = 0.766$ $P_{\text{same}} = 0.001$). Pairwise comparisons indicated much less difference between LB- and DB-associated assemblages than between any other pairs of substrates compared ($R = 0.095$, $P_{\text{same}} = 0.065$). The relative effect of substrate type was considerably lower within the sessile assemblages associated with the taxon-guilds A and R analyzed separately (substrate type, $R = 0.170$, $P_{\text{same}} = 0.001$; site, $R = 0.551$ $P_{\text{same}} = 0.001$) for six species of R and (substrate type, $R = 0.252$, $P_{\text{same}} = 0.001$; site, $R = 0.458$, $P_{\text{same}} = 0.001$) for four species of A.

Pri was strongly dominated by *B. crenatus*, whereas all other substrates developed more diverse assemblages (Fig. 3). Solitary ascidians were found on A, LB and DB. Although in terms of numbers of individuals most ascidians were associated with A and LB, the leading substrate in terms of biomass was DB (see below). Red algae predominantly resided on A. Aggregations without Pri were mostly

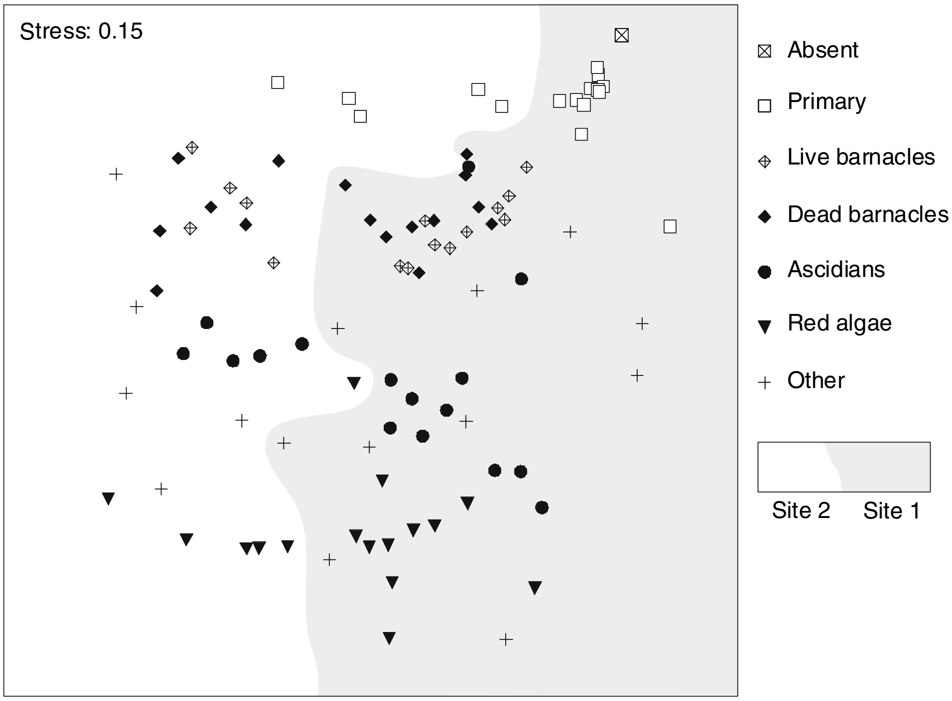

Fig. 1 Non-metric multidimensional scaling (NMDS) ordination of sessile fauna assemblages. Each point represents a pooled sample consisting of sessile taxa found on substrates of a certain type within a 1.00–1.44 m^2 square frame [substrate subsamples of the frames (SSF), see text for details]. Analysis based on standardized abundances and Bray–Curtis dissimilarity

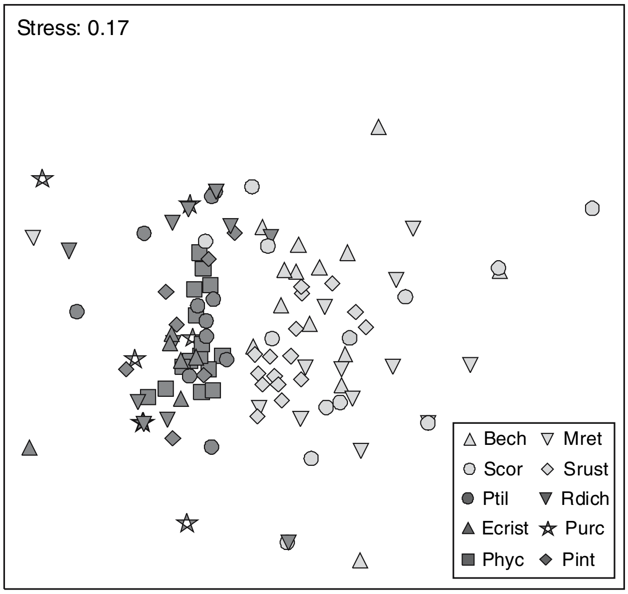

Fig. 2 NMDS ordination of sessile fauna assemblages hosted by different species of ascidians and red algae. Each point represents a pooled sample consisting of sessile taxa found on substrates of a certain type within a 1.00–1.44 m^2 square frame (SSF, see text for details). Analysis based on standardized abundances and Bray–Curtis dissimilarity. Solitary ascidians—*Bech Boltenia echinata*, *Mret Molgula retortiformis*, *Scor Styela coriacea*, *Srust Styela rustica*; red algae—*Ptil Ptilota plumosa*, *Rdich Rhodophyllis dichotoma*, *Ecrist Euthora cristata*, *Purc Polysiphonia urceolata*, *Phyc Phycodrys rubens*, *Pint Phyllophora interrupta*

based on DB. Most frequent associations between epibionts and substrates are summarized in the graph of the epibiosis in Fig. 4.

Epibenthic assemblages associated with three principal solid substrates, *Serripes* and barnacle shells (LB and DB) (together making up 61% of all occurrences of sessile organisms) were compared using absolute densities based on area estimates (Table 1). Out of 20 dominant sessile species, about a half were significantly associated with LB. Most ascidians belonged to this group, with the exception of *Styela rustica*, similarly abundant on LB and DB (but not on *Serripes* shells). *B. crenatus* were associated with *Serripes* shells and (about six times less) with LB. Nearly all the LB-specific taxa had similar small densities on DB and *Serripes* shells.

The absolute density of solitary ascidians, calculated on the basis of area estimates, was significantly higher inside the aperture of live barnacles (1,305 m^{-2}) rather than on the outer surface of the shell (465 m^{-2}) (Student's *t*-test, $P < 0.001$). In total, 21% of ascidians found on live *B. crenatus*, were located inside the aperture (10% on the tergum and scutum and 11% on the inner surface of unmoveable plates). Out of all live barnacles larger than 3 mm (aperture length), 10% had solitary ascidians attached inside their aperture.

Substrate usage and demography of barnacles and solitary ascidians

The smallest barnacles concentrated on live conspecifics and Pri, and to a much lesser degree on dead conspecifics and A. Larger barnacles were more frequent on Pri and were almost never found on A (Fig. 5). The dead:live ratio in *B. crenatus* was about 5 times lower on live

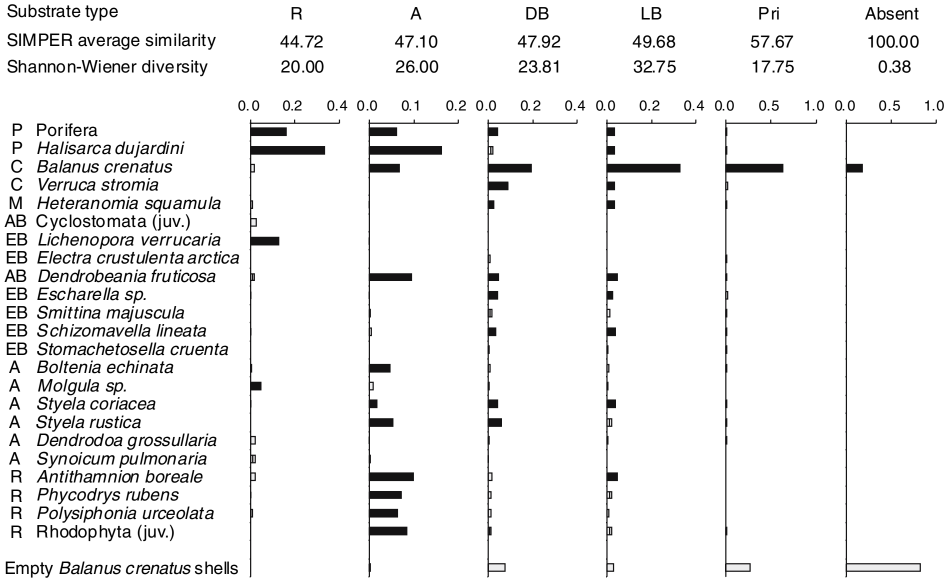

Fig. 3 Relative abundances of dominant sessile taxa on different types of substrate. Species included were among the ten most abundant on at least a single substrate type. *Black bars* mark the species mainly responsible for significant differences between assemblages associated with different substrate types as identified by the SIMPER procedure. Empty barnacle shells were excluded from SIMPER but included in relative abundances calculation. *Pri* Primary substrate, *LB* shells of live barnacles, *DB* empty barnacle shells, *A* solitary ascidians, *R* red algae, *P* Porifera, *C* Cirripedia, *M* Mollusca, *AB* arborescent bryozoans, *EB* encrusting bryozoans

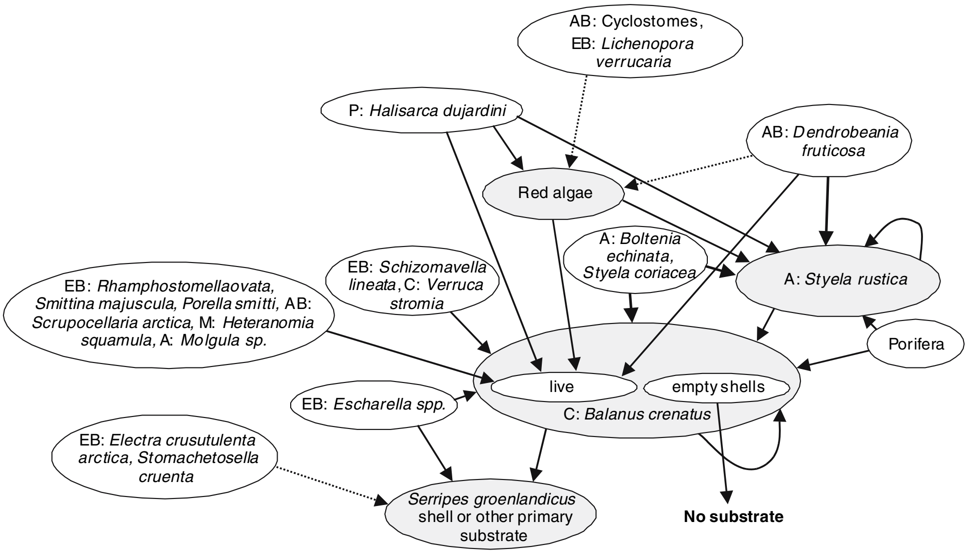

Fig. 4 Graph of the epibiosis based on 50 most frequent associations (*bold arrows*) between epibionts and their substrates. Important sessile taxa (relatively frequent but only on a single substrate type) that formally could not be included in the graph were added manually (*dotted arrows*). For abbreviations see Fig. 3

conspecific individuals (0.08 ± 0.02) than on Pri (0.44 ± 0.05) and on dead conspecifics (0.42 ± 0.06) (significant χ^2, $P < 0.001$ for most size classes, see S4 and S5). Furthermore, it was 4 times higher within the patches where ascidians dominated over barnacles in biomass (1.00 ± 0.20) than within barnacle-dominated ones (0.24 ± 0.02) (significant χ^2, $P < 0.001$ for most size classes, Fig. 6). The location also strongly affected the ratio, but the effect of the abundance of ascidians was nearly the same at both sites accurate to different mean levels (Fig. 6).

The smallest ascidians were found on LB and on other ascidians, whereas large ones occupied shells of DB (Fig. 7). Individual mean weight of *Styela rustica* was significantly (Tukey's honestly significant difference test, $P < 0.001$) higher on DB (2.81 ± 0.23 g) than on A

Table 1 Specific densities of dominant sessile taxa on the substrates, for which area estimates were available. Species included were among the ten most abundant on at least one of the principal substrates [primary, ascidians (*A*), red algae (*R*), live barnacle shells (*LB*), empty barnacle shells (*DB*)]. Only the patches on *Serripes* shells were included in the analysis. Highest densities highlighted in *bold* where the difference was significant. *P* Porifera, *C* Cirripedia, *M* Mollusca, *AB* arborescent bryozoans, *EB* encrusting bryozoans, *n.s.* not significantly different

Taxon species name		Average densities of sessile taxa						Pairwise comparisons between densities (two-tail Student's *t*-test)		
		LB		DB		*Serripes* shells		*Serripes* shells:LB	*Serripes* shells:DB	LB:DB
		n (m^{-2})		n (m^{-2})		n (m^{-2})		*P*	*P*	*P*
P	Porifera	**206.02**	±46.51	52.24	±13.53	57.42	±17.48	**	n.s.	***
P	*Halisarca dujardini*	**128.01**	±23.78	26.59	±8.97	30.12	±8.62	***	n.s.	***
C	*Verruca stromia*	**375.50**	±156.32	90.67	±45.63	9.10	±7.43	*	n.s.	*
AB	*Dendrobeania fruticosa*	**167.24**	±29.77	57.91	±11.34	62.65	±15.13	**	n.s.	***
EB	*Schizomavella lineata*	**137.63**	±28.70	54.52	±12.52	29.74	±8.55	***	n.s.	***
EB	*Smittina majuscula*	43.97	±10.24	16.60	±4.48	29.46	±8.22	n.s.	n.s.	**
AB	*Boltenia echinata*	**56.94**	±16.19	14.44	±4.94	17.69	±8.13	*	n.s.	*
AB	*Molgula* sp.	**24.95**	±6.54	6.26	±2.44	7.45	±4.09	*	n.s.	**
AB	*Styela coriacea*	**213.20**	±36.58	75.89	±13.10	43.42	±17.10	***	n.s.	**
R	*Antithamnion boreale*	**129.26**	±53.65	21.02	±8.20	12.03	±5.88	*	n.s.	*
R	*Phycodrys rubens*	**64.81**	±16.84	16.23	±6.60	3.02	±1.74	***	n.s.	**
R	Rhodophyta f. gen. sp. (juv.)	**81.87**	±29.23	7.56	±3.03	27.40	±13.53	**	n.s.	***
A	*Styela rustica*	**159.11**	±38.87	**114.88**	±14.74	13.94	±6.49	***	***	n.s.
M	*Heteranomia squamula*	**114.52**	±30.28	25.65	±7.47	**88.25**	±24.67	n.s.	*	**
C	*Balanus crenatus*	1124.91	±252.29	224.31	±44.64	**6,798.36**	±1160.88	***	***	***
EB	*Escharella* sp.	82.74	±17.09	44.41	±12.06	**166.32**	±33.35	***	***	**
EB	*Stomachetosella cruenta*	13.14	±3.72	3.19	±1.88	**56.89**	±17.38	*	**	**
EB	*Lichenopora verrucaria*	1.63	±0.61	0.00	±0.00	**15.16**	±6.11	*	*	*
EB	*Electra crustulenta arctica*	4.16	±1.56	4.41	±2.62	**51.76**	±12.44	***	***	n.s.
A	*Dendrodoa grossullaria*	10.27	±4.60	9.83	±4.42	**46.41**	±16.88	*	*	n.s.
A	*Synoicum pulmonaria*	3.35	±1.56	2.05	±1.74	2.29	±1.63	n.s.	n.s.	n.s.
R	*Polysiphonia urceolata*	21.47	±8.54	10.46	±4.01	5.11	±3.78	n.s.	n.s.	n.s.
AB	*Cyclostomata* f. Gen. sp. (juv.)	0.00	±0.00	0.00	±0.00	0.00	±0.00			
	Empty *Balanus crenatus* shells	155.43	±40.21	117.55	±35.53	**3,167.92**	±406.41	***	***	n.s.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

(0.25 ± 0.07 g) and LB (0.73 ± 0.17 g) regardless of the location (ANOVA, see S6).

Species diversity and the number of FS in a patch

Functional richness of the FS measured as the number of their different taxon-guilds in a patch (zero to three: ascidians, barnacles, red algae) affected Shannon–Wiener species diversity of all other taxa ($\beta = 0.34$, $P < 0.001$) more than did the total weight of the FS ($\beta = 0.24$, $P < 0.001$; tolerance = 0.81, $R^2 = 0.24$; multiple regression). Average Log-*e* diversity (calculated including mobile taxa and excluding barnacles, ascidians and red algae) was 2.02 ± 0.10 for purely ascidian, 2.15 ± 0.05 for purely barnacle, and 2.53 ± 0.05 for the co-dominated patches.

Discussion

Assemblages and species diversity associated with different FS

Consistent with predictions, most sessile organisms were attached to biogenic substrates of a few types of FS and epibenthic assemblages differed depending on substrate. Epibenthic fauna often selectively utilize hard substrates due to differential settlement or post-settlement mortality (Dayton 1971). In addition to space, the substrata, when represented by a live animal or algae, may also supply inhabitants with food either directly (Seed and O'Connor 1981) or indirectly by facilitating their feeding activity (Lahoinen and Furman 1986). In our case, the differentiation in epibenthic assem-

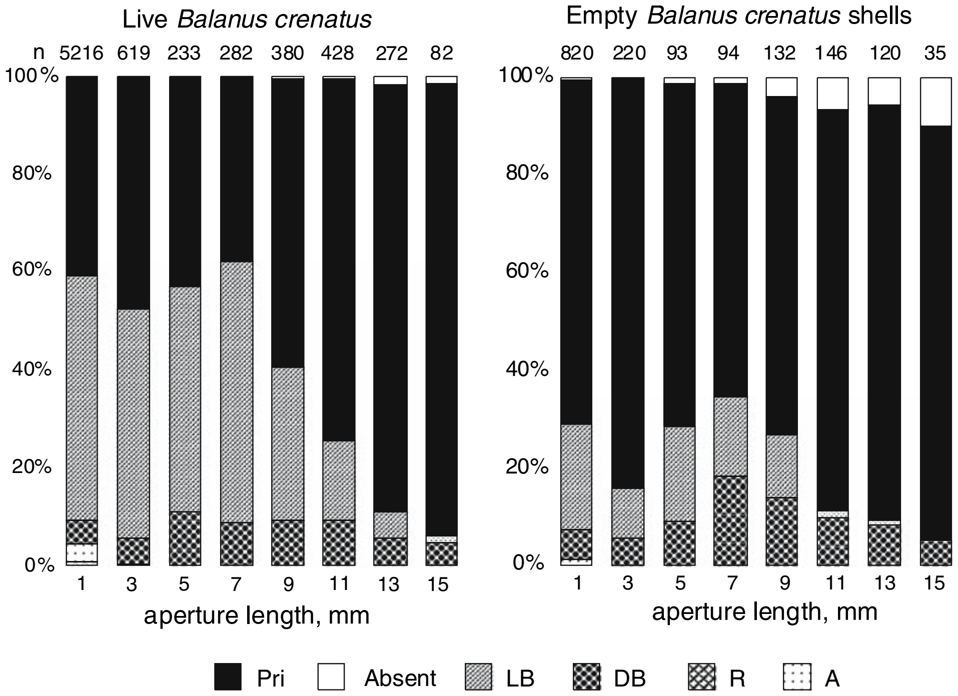

Fig. 5 Distribution of live barnacles and their empty shells by substrate type. Data collected in 2001–2005 were used. For abbreviations see Fig. 3

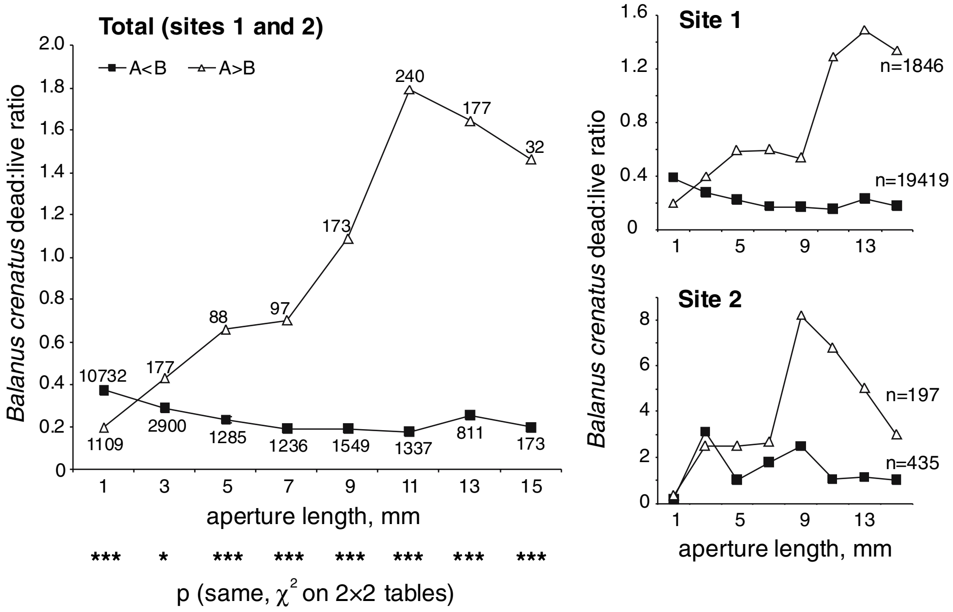

Fig. 6 Dead:live ratio of *B. crenatus* in the patches dominated in terms of biomass by barnacles ($A < B$) and ascidians ($A > B$). Points on the *left-hand plot* are labeled with the sample size (number of individuals) for the corresponding ratio. The, χ^2-test results are shown below this plot comparing dead:live ratios in A < B and B < A patches for each size class. Data collected in 2001–2005 were used. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

blages may result from the interplay of effects of light, sedimentation, hydrodynamics, substrate texture and stability. For instance, bryozoans, which constitute 48% of the sessile species collected, are especially sensitive to substrate flexibility (e.g., Kukliński and Barnes 2005), which considerably varies between hard Pri, LB and DB, semi-solid A and flexible R. Silt, which tended to cover any substrate that was not (like live filter-feeders) self-cleaning, is also a primary factor affecting epibenthic assemblage structure (Maughan 2001; Hinchey et al. 2006). The low species diversity associated with Pri is most likely the result of sedimentation, given that many more species occupy Pri of barnacle aggregations at neighboring sites with lower sedimentation rates (Yakovis 2007). A similar low density of LB-specific taxa on DB and *Serripes* shells (Table 1) suggests their facilitation by living barnacles.

Given the difference in assemblages hosted by each FS it is expected that species diversity is more affected by their number than by the weight (which reflects the size) of the patch. The number of functionally different FS contribute to habitat heterogeneity, which is the basic source of the diversity (Blanchard and Bourget 1999). The functional difference

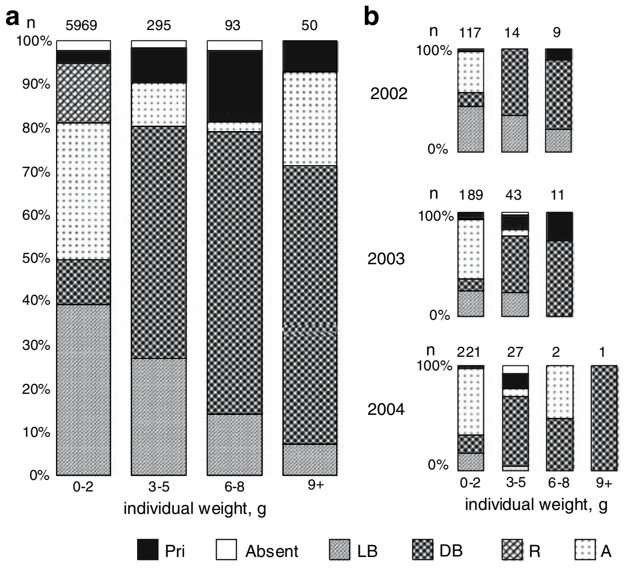

Fig. 7 Distribution of solitary ascidians by substrate type depending on their individual weight, total for all species (2001–2005) (**a**) and for *Styela rustica* by year (2002–2004) (**b**). For abbreviations see Fig. 3

of barnacles, ascidians and red algae, according to their effect on hosted sessile assemblages, is higher than previously observed in coexisting seaweeds (Bates and DeWreede 2007) and trees in mixed stands (e.g., Saetre et al. 1997).

Use of principal substrates by FS and their possible interactions

S. groenlandicus lives below the sediment surface (Siferd and Welch 1992), so that no epibionts colonize its shell until the mollusk dies. Small stones are mainly supplied by melting winter ice (A. B. Tsetlin, personal communication) and so are also initially unfouled. In nearly all the patches studied, barnacles (and never ascidians) exclusively dominated on Pri. Field experiments in which initially clear *Serripes* shells were exposed for 5 years, also indicated barnacles as the primary colonizer (Yakovis et al. 2005). At least three models, or any combination thereof, can explain this pattern: (1) substrate preferences of ascidian larvae, (2) high competitive ability of barnacles (relative to ascidians) on plain or muddy surfaces, (3) the seasonal sequence of recruitment periods for FS.

Ascidians occupy the surfaces previously covered by hydroids, sessile polychaete tubes, and cirripedians rather than bare ones (Dean 1981; Schmidt 1983; Khalaman 2001) and silt is responsible for early post-settlement mortality in several ascidian species (Young and Chia 1984; Hinchey et al. 2006). Silt heavily covered the epibenthic patches studied with the exception of self-cleaning live barnacles, ascidians and algae, potentially affecting the distribution of young ascidians. The roughness of barnacle shells can also decrease predation risks for them (Young and Chia 1984; Walters and Wethey 1991). These processes fit the first and the second model. In accordance with the third model, White Sea barnacles settle for 2 months starting in July (Mileikovsky 1970), whereas *Styela rustica* spawns and settles in September for a week or 2 (Khalaman 2001). Consequently, barnacles gain primary access to any space added to the habitat 11 months out of 12.

According to spatial patterns demonstrated by newly settled barnacles and ascidians (Figs. 4, 6), the surface of live barnacles is their common principal source of free space. This suggests competition for space between FS. Dead:live ratios (S4) indicate that living on conspecifics is likely to give some advantages to barnacles.

In large barnacles dead:live ratios show a higher mortality rate associated with ascidian dominance. The opposite pattern in newly settled barnacles should be attributed to their presence on the surface of ascidians (though without any further positive prospects; Fig. 4) where their empty shells are evidently not preserved at all (Fig. 4). This pattern could be produced by different causal relationships: ascidians may prefer the patches with declining barnacles or increase their mortality by competition.

Overgrowth often negatively affects the basibiont (Wahl 1989; Donovan et al. 2003; O'Connor et al. 2006 and references therein). In addition, direct feeding interference between barnacles and ascidians may occur due to the overlap in their feeding particle spectra (Barnes 1959; Carlisle 1979; Armthworthy et al. 2001). Indirect effects like preferential predation of either fouled (see Enderlein et al. 2003) or clear (see Wahl et al. 1997) individuals are also possible. Barnacles, at the very least, experience the negative effects of the ascidians commonly attached to the inside of their aperture. They compete with ascidians for space providing the preferred substrate both for their recruits and for ascidians. Barnacles and ascidians may consume larvae of each other (Young 1989; Young and Cameron1989), being thus involved in mutual negative adult–larval interactions. Besides, ascidians divert some barnacle larvae from relatively gainful microhabitats to their tunic surface, with no chances of further survival.

Several studies describe the successions where ascidians replace cirripedians (Dean 1981; Hatcher 1998). These surveys do not examine interactions between the taxa discussed, but Butler (1991) reported barnacles as "good recruits to bare substrata but very poor competitors". Other examples provide evidence for epibenthic assemblages where cirripedians persist among key space holders (Bram et al. 2005). Generally, a sequence and outcome of a particular succession is often conditioned by numerous external factors (Sousa 1984; Underwood and Anderson 1994). In the absence of barnacle recruitment, succession may lack a stage where they clearly dominate. Purely ascidian clumps on *Serripes* shells are known from different locations in the

White Sea (E. L. Yakovis, A. V. Artemieva, N. N. Shunatova, M. A. Varfolomeeva, unpublished data).

Conclusion

Similar to mobile taxa (Yakovis et al. 2005), sessile organisms associated with different FS formed rather different assemblages; however, within taxon-guilds of FS the difference in sessile assemblages hosted was relatively small. Species diversity was higher in the patches with more FS. The spatial pattern observed suggests the competitive exclusion of barnacles by ascidians, likely due to the difference in their relative competitive ability on Pri and barnacles.

Habitat modification and associated spatio-temporal patterns are commonly studied on widespread, relatively simple systems consisting of a single FS or a taxon-guild thereof and multiple dependent ones. We suggest the term "1-∞" to describe these systems that are believed to be driven internally by facilitation (Bruno and Bertness 2000). The present survey gives an example of a system that includes multiple coexisting FS from different guilds operating at a comparable spatial scale. We define these systems as "$n-\infty$", a distinction that we believe is warranted given the need to consider competitive interactions. Multiple internal facilitation processes similar to those revealed in $1-\infty$ systems are probably combined here with a few strong interactions among FS. Evidence suggests these interactions may be of either sign (e.g., *Serripes*-facilitated barnacles that both facilitate and compete with ascidians) which expands the model suggested by Altieri et al. (2007) that consider only positive interactions between the coexisting FS. We believe that research on $n-\infty$ patches would considerably improve our progress towards understanding pattern generation and ecosystem functioning.

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