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SHORT NOTE

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Competitive dominance among sessile marine organisms in a high Arctic boulder community

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Abstract In most hard substrate environments, space is a limiting resource for sessile organisms. Competition for space is often high and is a structuring force within the community. In the Beaufort Sea's Boulder Patch, crustose coralline red algae are major space occupiers. This research determined if coralline algae were competitively dominant over other sessile organisms. To test this hypothesis, overgrowth was documented in terms of "winners" and "losers" on the contact borders between different species. Crustose corallines occurred in over 80% of the observed interactions but were only winners in approximately half of them. Most frequently, bryozoans, tunicates, and sponges were superior competitors over crustose corallines, while at the same time these invertebrate groups were among the least abundant space occupiers.

Introduction

Coexistence of species is largely driven by an interacting system of disturbance and competition (Airoldi 2000). While disturbances clear space, competitive success ultimately determines who inhabits the space. Competition for space is a major structuring force in marine benthic communities (Bertness and Leonard 1997). Substrate competition by encrusting marine organisms usually occurs by direct overgrowth at their contact zones (Sebens 1986). These competitive border interactions are commonly evaluated with species being ranked as winners or losers based on their abilities to overgrow the competing taxa. Although losers of interactions are overgrown by winners, this does not always result in death of the overgrown organism (Jompa and McCook 2002). Coralline algae, in particular, can survive while they are overgrown and sometimes even continue to grow (Sebens 1986; Dethier and Steneck 2001). While the outcome of border interactions can vary depending on species, depth, timing, and location, some taxa are typically competitively dominant over others (Nandakumar 1996; Airoldi 2000; Barnes and Dick 2000; Barnes 2002). In temperate and polar waters, ascideans, sponges, and bryozoans have been shown to be strong space competitors (Nandakumar 1996; Maughan and Barnes 2000; Barnes and Kuklinski 2004).

The Boulder Patch is an isolated hard-bottom kelp community surrounded by the soft sediment habitat of the high Arctic Beaufort Sea. Space seems to be a limiting resource as most rock substrate is covered by sessile organisms, usually crustose coralline algae. Based on these observations, we tested whether crustose coralline algae were competitively dominant over other sessile species, and thus excluded or diminished other space occupiers. We included upright and crustose organisms in this analysis as both are space occupiers in this system. Our objectives were to determine (1) if space was limiting, (2) the dominant space occupier, and (3) which taxa were dominant competitors.

Study site

This study was conducted at the Boulder Patch in Stefansson Sound, Beaufort Sea Patch (147°40′W, 70°20′N; see Dunton 1990 for map details). Sediment load is high in this area because of run-off from the Sagavanirktok Delta, but overall sediment accumulation in the benthos is limited due to strong currents (Dunton and Schonberg 2000). Light intensity and duration for the benthic community can be reduced due to water column sediments and the polar winter, respectively (Dunton 1990). Ice scour is relatively low because the area is protected from thicker ice by offshore barrier islands. Water temperatures range from −1.9°C during

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winter to 7°C in summer. The study area was in 6–7 m water depth and contained numerous cobbles and boulders that provided substrate for several invertebrate and macroalgal species. Approximately 148 animal taxa and ten algal species are reported from the area at densities approaching 18,441 individuals/m^2 with a biomass of 283 g/m^2 (Dunton and Schonberg 2000).

Methods

To compare the availability of bare substrate to substrate covered by sessile organisms, percent cover of all sessile organisms or bare rock was estimated in the Boulder Patch in August 2004. Five random point contact surveys (RPCs; Coyer et al. 1999) were conducted along each of eight randomly placed 30 m transects. A RPC is a 1 m bar with a 1.5 m knotted line attached to either end. The line is pulled taught along both sides of the bar and every organism or substrate type that lies directly under each knot is recorded. Ten points are recorded along every RPC bar, each point representing 10% cover. Means of the ten random points on every RPC and subsequent means of all RPCs were used to obtain the average cover for bare rock and the following major taxa: hydroids, bryozoans, sponges, crustose corallines, and red algal holdfasts. Other taxa that were too rare to contribute to the cover estimations included kelp holdfasts, tunicates, spirorbid polychaetes, and soft corals. To determine the major space occupier, coverage of all sessile organisms recorded during the RPCs was compared using a one-way ANOVA and Fisher's PLSD post-hoc test after an arcsin transformation.

To determine which organisms are dominant competitors, overgrowth patterns on Boulder Patch boulders were evaluated in August 2003 and 2004. For this, 157 total boulders were qualitatively examined, on which 449 live interactions were observed (ties and intraspecific interactions were not considered). Erect organisms with small attachments to the rocks were included in the analysis as they still can be important space occupiers, although the base commonly is not the active growing region. For each overlapping border, the overgrown organism was scored "loser" compared to "winner" (the overgrowing organism).

Results

Surveys showed that 60% of the substrate was hard boulders and 40% soft sediments. Of the 60% hard substrate, significant differences were found amongst sessile organism cover (ANOVA, $F_{5,234} = 72.738$, $P \leq 0.0001$, Fig. 1). Only 5.6% of the total hard substrate was bare rock while organisms covered the remaining surface. Crustose coralline algae covered over 60% of the available hard substrate and were significantly more abundant than any other taxon (post hoc Fisher's PLSD, $P \leq 0.0001$). Foliose red algal holdfasts covered approximately 25% of the hard substrate, rendering them significantly more abundant than any invertebrate group or bare rock (PLSD, $P \leq 0.0001$). Hydroids, bryozoans, and sponges covered the remaining hard substrate. No significant differences in percent cover were found among invertebrate groups or between invertebrate groups and bare rock.

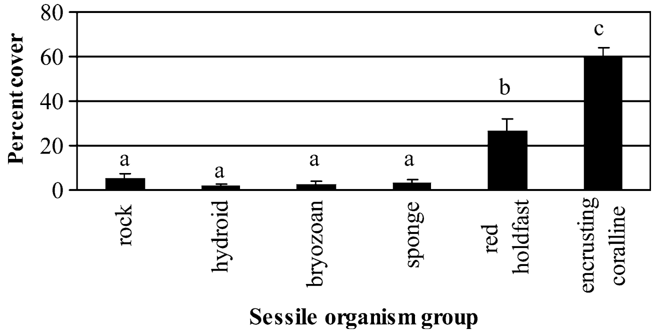

Fig. 1 Mean percent cover (±1 SE) of rock and various sessile organisms at the Boulder Patch, $n = 40$. Results of post hoc test are indicated by *letters* above *bars* with *different letters* representing significant differences at the 99% level

In the observed 449 competitive border interactions, crustose corallines won only over a few groups of sessile organisms (red algal holdfasts, kelp holdfasts, and hydroids) but lost to most others (tunicates, bryozoans, and sponges; Table 1). Overall, tunicates, upright bryozoans, and sponges were the most frequent winners in border interactions. Sponges won all but one (with an upright bryozoan) out of 70 observed interactions. Upright bryozoans won all their 14 border competitions.

Discussion

Although crustose coralline algae were the major space occupiers in this high Arctic ecosystem, they were not the competitive dominants in many of the interactions with other sessile organisms, particularly invertebrates. This is not unusual as overgrowth dominants often do not monopolize space, and in fact, the most abundant species can be mid-ranked to lower ranked competitors (Airoldi 2000; Barnes and Dick 2000). In our study as well as in other areas, sponges and bryozoans are competitive dominants in inter-phyletic encounters, overgrowing most other organism groups (Nandakumar 1996; Maughan and Barnes 2000; Barnes and Kuklinski 2004). Good competitors in other areas also include spirorbids, polychaete tube mats, and erect hydroids (Sebens 1986). Spirorbids and hydroids had mixed results in this study but were not abundant or competitively superior.

The question remains as to why sponges, bryozoans, and tunicates are not the dominant space occupants, if they are competitively dominant over coralline algae? We observed that most interactions occur on the sides of

Table 1 Mean percent ±1 SE of the overgrowth scores in the 449 interactions found on boulders

	Crustose corallines	Foliose red algae	Kelp holdfasts	Tunicates	Encrusting bryozoans	Upright bryozoans	Hydroids	Sponges	Spirorbids	Soft corals
Crustose corallines	n/a									
Foliose red algae	2.0 ± 1.5 (73)	n/a								
Kelp holdfasts	9.7 ± 5.4 (31)	n/a	n/a							
Tunicates	95.2 ± 3.3 (21)	n/a	n/a	n/a						
Encrusting bryozoans	87.6 ± 2.7 (89)	93.3 ± 6.7 (15)	n/a	8.33 ± 8.3 (6)	n/a					
Upright bryozoans	100 ± 0 (13)	n/a	n/a	n/a	100 (1)	n/a				
Hydroids	4.2 ± 2.5 (59)	75.0 ± 25.0 (2)	n/a	0 (2)	0 (7)	n/a	n/a			
Sponges	100(39)	100 (22)	100 (1)	100 (1)	n/a	0 (1)	100 (6)	n/a		
Spirorbids	12.2 ± 4.5 (41)	n/a	n/a	n/a	88.3 ± 11.1 (9)	n/a	n/a	n/a	n/a	
Soft corals	100 (3)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

Vertical organisms on the left correspond to the winners while organisms across the top correspond to losers. *Numbers* in *parentheses* refer to the observed number of interactions. *n/a* refers to no interactions found

boulder sides while the top or up-facing surfaces are dominated by corallines. High macroalgal abundance on up-facing surfaces is common while sessile invertebrates are abundant on down-facing or vertical surfaces (Irving and Connell 2002). This suggests that there are microhabitat differences among surface orientations arising from dissimilar conditions (i.e. sediment and light) on the various substrate orientations. Some invertebrates, especially prostrate forms and filter feeders, may experience high mortality in relation to sedimentation from smothering (Duggins et al. 1990). We suggest that sediment load, which is high in the Boulder Patch, may be lethal to many invertebrates, forcing them toward the vertical sides of boulders. In addition, suspended sediments are likely to decrease light intensity through increased turbidity (Ruffin 1998). While invertebrates thrive on shaded surfaces (Baynes 1999; Glasby 1999), macroalgae typically survive better on up-facing surfaces where light intensity is highest (Irving and Connell 2002), resulting in high algal abundance on top surfaces.

Although coralline algae lost most competitive overgrowth battles in this study, they dominated primary substrate. Corallines can survive overgrowth and may even continue to grow while overgrown (Dethier and Steneck 2001). As such, they have been suggested to maintain their abundance in communities until predation or some other disturbance removes the over-grower (Sebens 1986). While the importance of biological disturbance (grazing) in the Boulder Patch community is under current investigation (B. Konar, unpublished data), physical factors such as sedimentation, low light, and wave action, likely have structuring effects on the epilithic community.

Climate change may influence benthic community structure through an alteration of disturbance regimes. A significant loss of Arctic sea ice is predicted to occur by 2025 (Clarke and Harris 2003), particularly in coastal regions (Morison et al. 2000). We suggest that Arctic nearshore systems such as the Boulder Patch would actually experience more disturbances as a result of climate change. Lack of shore fast-ice cover could result in an increase in wave action and storm surge in these shallow waters. There also could be an increase in sedimentation due to the increase in river discharge caused by melting glaciers, causing further decreasing light levels. This increase in disturbance will probably benefit the crustose coralline community, but be detrimental to most other organisms, likely resulting in communities with fewer species (Barnes and Kuklinski 2004).

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