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SHORT NOTE

Recolonization of a high latitude hard-bottom nearshore community

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Abstract Early recolonization of sessile organisms and grazer effects on recolonization was examined in a high latitude nearshore rocky environment. A manipulative experiment using cleared boulders and cages was used to determine the time needed for initial recruitment and composition of early recruits. The hypothesis tested was invertebrate grazing is causing slow recolonization. Four years of monitoring cleared boulders resulted in an initial recruitment of primarily barnacles in year 3 on boulders that were caged to exclude grazers. The total percent cover on these boulders after 4 years was less than 2%. Cage control and uncaged boulders showed less recruitment. Uncleared and uncaged control rocks showed insignificant temporal variation. Concurrent observations revealed that macroalgae were reproductive during the study and that space was limiting in this community. This study strongly suggests that perturbations causing removal of hard substrate sessile communities in the Beaufort Sea will result in very slow community recovery.

Keywords Arctic · Recruitment · Grazers · Boulders

Introduction

In temperate marine systems, boulder fields are very dynamic because of physical disturbance (Sousa 1979, 1980; vanTamelen 1987). When a boulder is overturned, the sessile community can be killed in whole or part by a combination of grazing, anoxia, low light levels, or mechanical damage caused by crushing or abrasion (Sousa 1980). Studies in temperate systems have shown that algal communities can recover to previous densities within 1 year of denuding (Foster 1975; Bertness et al. 2004; Milazzo et al. 2004). Many studies on coralline algal recruitment have shown that although their growth is remarkably slow, they will settle and grow to a visible size in a few months (Adey and Vasser 1975; Matsuda 1989; Konar and Foster 1992). In contrast to temperate systems, recruitment in high Arctic systems appears to be much slower (Dunton et al. 1982).

One possible reason for slow recolonization is invertebrate grazing. Many studies have shown that grazers can be very important in structuring communities (Wilson et al. 1999; Konar 2000; Jenkins et al. 2005, and many others). In the coastal high Arctic of the Beaufort Sea, motile herbivorous, omnivorous, and carnivorous invertebrates such as chitons, snails, seastars, and polychaetes are common (Dunton et al. 1982) but the influence they have on community structure is unknown.

The goals of this high latitude study were to (1) determine the length of time needed for initial recruitment onto a cleared natural substrate and (2) determine the taxonomic composition of the early recruits. The null hypothesis tested was that the exclusion of grazers would have no significant impact on recruitment of sessile organisms onto cleared natural substrates. Concurrent with this recruitment study, two community surveys were performed. The first survey determined if macroalgae were reproductive during this study and able to send out propagules and the second survey determined if substrate was limiting.

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Typically substrate is a limiting factor for hard-bottom benthic communities. Hence when substrate is limiting, recruitment is usually rapid.

Study site

This study was conducted at the Boulder Patch in Stefansson Sound, Beaufort Sea (147°40′W, 70°20′N; see Dunton 1990 for map details). Here, sedimentation can be high because of run-off from the Sagavanirktok Delta, but overall sediment accumulation on the substrate is limited due to strong currents (Dunton and Schonberg 2000). Light intensity and duration to the benthos can be reduced due to water column sediments and the polar winter, respectively (Dunton 1990). Ice scour is relatively low because offshore barrier islands provide protection against large icebergs. 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 10 algal species cover nearly all exposed substrate at densities approaching 18,441 individuals/m^2 with an average biomass of 283 g/m^2 (Dunton and Schonberg 2000). During this study, foliose algae covered approximately 24.5 ± 3.6 SE of the substrate. The primary herbivores encountered were the chitons *Amicula* spp. (6.4 ± 2.1 SE per 0.25 m^2) and *Ischnochiton* sp (12.8 ± 2.09 SE per 0.25 m^2). Seastars and the gastropod *Margarites* sp. were also occasionally seen at the study site.

Methods

To address the goals and hypothesis of this study, 54 boulders (approximately 30–40 cm in diameter and 10–20 cm tall) from the study site were brought to the surface and cleared of all sessile organisms. All boulders were left in air for 5 days to kill any remaining seed bank and then assigned to one of three treatments: (1) caged, (2) uncaged, and (3) cage controls. Although no controls were conducted to determine if 5 days was sufficient to kill the seed banks, the lack of growth after 3 years implies that seed banks did not contribute to recovery. The cages that were deployed were 45 cm on a side, 30 cm tall, with a 1 cm mesh size and constructed of stainless steel mesh coated with a non-toxic antifouling compound (copper paint) to inhibit sessile invertebrate and algal growth. It is believed that the antifouling compound did not negatively affect recruitment as uncaged boulders had less growth than caged boulders. It did appear that the cages were successful in excluding grazers as grazers were never seen inside cages during the study. Uncaged rocks were deployed to monitor natural recruitment. Cage controls (cages with holes cut into them so that grazers had access to the boulders) controlled for artifacts produced by the cages themselves. Six replicates of each treatment were randomly placed in situ at one of three sites within the Boulder Patch in August 2002. All boulders (cleared and uncleared) were at least 2 m away from each other. As a control for natural changes in the community, six non-cleared boulders were randomly chosen and monitored in each area, totaling 18. Boulders were examined each summer from 2003 to 2006 to determine percent cover of sessile organisms. To determine if there was significant light reduction due to cage shading, light measurements were taken within and adjacent to cages with a Li-Cor Model LI-185A Quantum Light Meter with spherical sensor in 2004 on three separate days.

To determine if the dominant alga by biomass, *Laminaria solidungula*, was reproductive at the study site in 2004, 13 random 5 × 2 m swaths were surveyed. All *L. solidungula* along each swath were enumerated and reproductive status was recorded. To determine hard substrate space availability at the study site, surveys were conducted in 2004 for percent cover of sessile organisms on boulders. Along eight randomly placed transects, five 1-m long random point contact bars (Coyer et al. 1999) were randomly placed. These bars had a string attached at each end, with five knots along each length. Knots randomly placed on the line were pulled tight away from the bar and placed on the substrate and the identity of the alga or invertebrate was recorded. If no organisms were present at the knot, the type of substratum was noted. By moving the string from one side of the bar to the other, ten points were sampled per area.

Results

There were no significant differences among sites for any variables so data were combined for final analyses. Community composition on the control, uncleared boulders did not significantly vary over time (repeated-measures ANOVA, $F_{4,72} = 1.622$, $P = 0.2$, Fig. 1). The majority of uncleared boulders were covered with encrusting coralline algae, foliose algae, and sessile invertebrates, while very little (a mean of 2% or less) was bare. Foliose algae were primarily the red alga *Phycodrys rubens*, averaging 17.4% ± 2.5 SE and *Coccotylus truncatus (*formally *Phyllophora truncata*), averaging 10% ± 2.2 SE over the 5 year period. Other

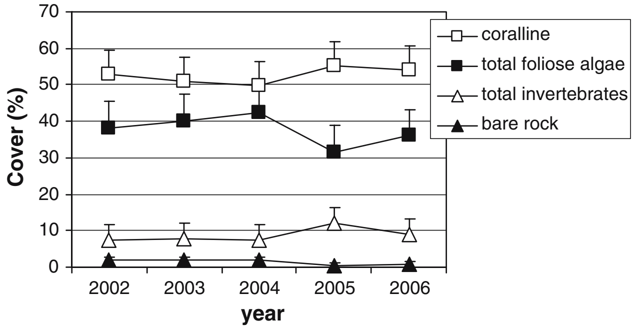

Fig. 1 Mean percent cover (+1 SE) of bare rock, encrusting algae, total foliose algae and total invertebrates on uncleared boulders from 2002, 2003, 2004, 2005, and 2006

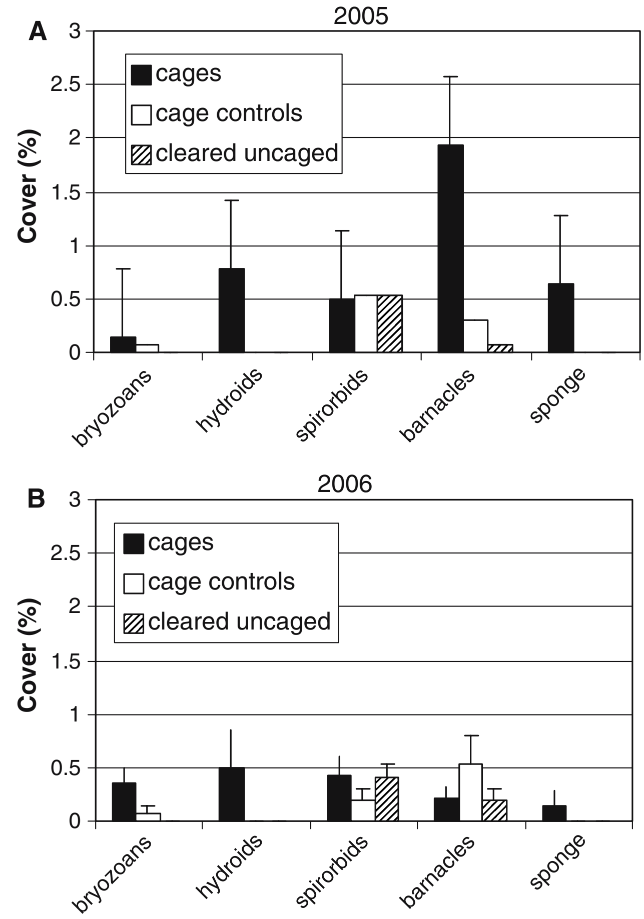

Fig. 2 Mean percent cover (±1 SE) of bryozoans, hydroids, spirorbids, barnacles, encrusting corallines and sponges on cleared boulders in the various treatments in 2005 (**a**) and 2006 (**b**)

foliose red algae included *Dilsea integra* (5.8% ± 1.0 SE), *Odonthalia dentata* (2.8% ± 0.9 SE), and *Rhodomela* spp. (1.2% ± 0.4 SE).

While there was very little bare rock on the uncleared control boulders, the new substrate provided by the cleared boulders remained open for the majority of this study. As such, no recruitment of sessile organisms was seen during the first 2 years (2002 and 2003) after the cleared boulders of all treatments were placed in situ. In the third year (2005), small (typically less than 0.5 cm) bryozoans, hydroids, spirorbids, barnacles, and encrusting corallines began to appear on many of the rocks (Fig. 2a). Interestingly, there was significantly more recruitment on cleared rocks held in cages than on cleared rocks held in open cages or left uncaged (ANOVA, $F_{2,39} = 10.848$, $P = 0.0002$). In year 4 (2006), there was still more recruitment in the caged versus uncaged rocks (ANOVA, $F_{2,41} = 4.461$, $P = 0.02$; Fig. 2b), however, overall recruitment was less than the previous year. In 2005, 98.1% ± 0.4 of the rock was bare while 99.1% ± 0.2 was bare in 2006. There was a significant reduction in light due to cages (ANOVA, $F_{2,6} = 12.924$, $P = 0.0067$), however, there was no significant light difference between cages and cage controls. This suggests that differences found between results occurring within caged boulders and cage control boulders were not due to a lighting effect.

Surveys showed that macroalgae were reproductive during this study. Forty percent of the 361 *L. solidungula* individuals that were checked for reproductive status in 2004 were found with reproductive sori. *L. solidungula* also were observed to be reproductive in all other years. Likewise, casual observations found cystocarpic *C. truncatus* in all years. Surveys also showed that substrate was limiting with only 5.6% ± 2.1 bare hard substrate. The primary cover on boulders was encrusting coralline algae (59.7% ± 4.4).

Discussion

Although grazing may have impacts on community structure and recruitment in high latitudes, effects are much less obvious than in temperate systems. In temperate areas, grazers such as urchins, can completely eliminate all foliose macroalgae and sessile invertebrates leaving a “barren ground”, or encrusting coralline monoculture (Harrold and Reed 1985; Scheibling 1986; Konar and Estes 2003, and many others). In this study, recolonization was so slow that the grazers role in the initial recruitment is minor. Although significant differences were found between grazer excluded boulders and controls, the overall difference was less than 1% of the total area cleared. This very small difference implies that although results are significantly different; they are probably not ecologically different. Other factors, such as sedimentation or reduced light may play a much bigger role in initial recruitment but would not explain the differences between cages and cage controls as has been seen elsewhere (Connell 2005). A longer-term experiment is needed to determine the potential impact of grazers in this system.

The most noteworthy result of this study was the extremely slow recolonization rate. As typical for many macroalgal systems, surveys in this study suggest that available substrate in the Boulder Patch was a limiting resource as very little bare rock (never exceeding about 10%) was found during the community surveys. This implies that there is competition for space. In a subtidal clearing experiment in California, it took only a few weeks for coralline recruits to be visible to the naked eye (Konar and Foster 1992). In Kachemak Bay, Alaska, subtidal recruits began to settle on cleared rocks after just two months (N. Harman and B. Konar, unpublished data). Typically, 1–2 years after clearing, bare areas cannot be distinguished from control areas (Foster 1975; Konar and Foster 1992; Konar and Estes 2003). At the current recruitment rate in this high arctic environment, it might take 10+ years for full recovery if sessile communities are completely removed. The reasons for this incredibly slow recruitment are unknown. Also, the actual time needed for a full recovery is unknown; however, the time estimate for recovery may be much shorter if vegetative regrowth was possible.

Another interesting result of this study is that the composition of the epilithic community in the Boulder Patch is very stable as no significant temporal variation was noted in uncleared control boulders. Within this community, the dominant organisms are the encrusting corallines (by percent cover; this study) and the red and brown macroalgae (by biomass; Dunton et al. 1982). Interestingly, no foliose red or brown macroalgal individuals recruited to any cleared rock in the first 3 years of monitoring. Typically, exclusion of grazers causes an increase in foliose macroalgae (Belliveau and Paul 2002). Along with the lack of foliose macroalgal recruitment, encrusting coralline recruitment also was very limited, found only on one caged boulder in year 3. In other temperate region studies, algal organisms, particularly encrusting corallines, have been amongst the first to colonize open space and do so relatively quickly (Konar and Foster 1992; Airoldi 2000). While the reproductive status of the corallines was not assessed during this study, the dominant brown macroalga, *L. solidungula*, was observed to be reproductive during all years (personal observation). In 2004, approximately 40% of the plants were reproductive. Reproductive maturity of one red alga, *C. truncatus*, was observed in multiple years as many of these plants contained cystocarpic material (personal observation). The reasons why these reproductive macroalgae were not recruiting onto the cleared areas are unknown and can only be speculated. Obviously the results indicate a supply-side recruitment limitation; however the reasons for the limitation are unknown. It is known that macroalgae have recruitment "windows" where specific conditions are needed for sexual propagules to establish, whereas vegetative propagation is much more constant and predictable (Deysher and Dean 1986; Airoldi 2000). In this study, boulders were completely cleared and were not touching other boulders so vegetative regrowth was not possible. Perhaps much of the recovery of disturbed sessile communities that occurs in this system is accomplished through regrowth and not recruitment. Boulder Patch sessile organisms do compete for space through vegetative growth as seen by overlapping borders of existing organisms (Konar and Iken 2005). The rate of regrowth and subsequent recovery from disturbances are unknown and require further study.

A surprising result of this study was that barnacles were among the first to recruit on the cleared boulders (especially in the cages). This is contrary to another study that found that barnacles recruited less inside cages than outside, which was speculated to have been caused by reduced light and water motion (Schmidt and Warner 1984). In the Boulder Patch, community surveys based on percent cover and surveys of uncleared control rocks never resulted in notable barnacle presence. In fact, invertebrates actually appear to play a minor role (typically less than 10%) as far as space occupation. One potential reason for the presence of barnacles on cleared rocks but not in the community surveys is that the barnacles that were found were extremely small, typically less that 2 mm. Organisms this small would be missed during in situ community surveys because of the overwhelming dominance of other organisms. Perhaps multiple very small (but reproductive) barnacles inhabit the community, but rarely grow to significant size. Another potential reason for the lack of barnacle recruits in the community surveys could be due to grazers consuming them before they reach a notable size.

The time needed for a full recovery and the reasons for the slow recovery require more study and are imperative knowledge needed to understand community dynamics in this high arctic rocky system. This insight will be a valuable polar extension of the current ecological understanding of boulder field dynamics and will be useful in management plans to protect this sensnsitive habitat. This study strongly suggests that any perturbations causing scouring of hard substrate in the Beaufort Sea will result in very slow community recovery.

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