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SHADING FACILITATES SESSILE INVERTEBRATE DOMINANCE IN THE ROCKY SUBTIDAL GULF OF MAINE

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Abstract. Dramatic shifts in community composition occur between vertical and horizontal rocky surfaces in subtidal environments worldwide, yet the forces mediating this transition are poorly understood. Vertical rock walls are often covered by lush, diverse communities of sessile suspension-feeding invertebrates, while adjacent horizontal substrates are dominated by algae, or corals in the tropics. Multiple factors, including light, sedimentation, water flow, and predation have been proposed to explain this pattern, but experimental tests of these hypotheses are lacking. We manipulated light level and predation to test whether variation in these mechanisms could be responsible for the shift in composition of sessile communities between vertical and horizontal surfaces in the rocky subtidal Gulf of Maine. Shaded horizontally oriented granite plots were dominated by invertebrates (e.g., ascidians, barnacles, bryozoans) after 25 months. Unshaded plots were dominated by macroalgae, which was virtually absent in shaded plots. Exclusion of grazers with cages had no effect on percent cover of invertebrates or algae. Preferential settlement of invertebrate larvae to shaded plots, due to larval behaviors such as negative phototaxis, did not seem to play a role. Shading likely affects post-settlement mortality of invertebrates by alleviating competition for space with algae, although greater abundance of micropredators in algal-dominated communities could also be important. Communities on shaded plots lacked many taxa present on natural wall communities, likely due to greater disturbance on horizontal substrates and/or lack of sufficient time for colonization of these taxa. These results suggest that light plays a key role in controlling the structure, composition, and function of shallow subtidal communities.

Key words: ascidians; experimental; Gulf of Maine; physical factors; rock walls; sessile invertebrate; subtidal; zonation.

Introduction

Spatial heterogeneity is an inherent feature of natural landscapes. It has been well studied theoretically and empirically and influences a wide variety of ecological and evolutionary processes and patterns, including species coexistence and diversity, species persistence, metapopulation and patch dynamics, and ecosystem function (reviewed in Levin 1992, Hutchings et al. 2000). The response of organisms to spatial heterogeneity depends on their environmental requirements, physiological tolerances (fundamental niche), biotic interactions (realized niche, Hutchinson 1959), dispersal (Pulliam 2000, Snyder and Chesson 2003), and on the nature and scale of the heterogeneity. Investigating ecological processes influenced by or driving small-scale spatial heterogeneity can reveal processes shaping larger-scale, including biogeographic and evolutionary, patterns (e.g., Baack et al. 2006). For example, abiotic spatial heterogeneity can drive positive correlations between native and invader diversity on large scales (Davies et al. 2005), and knowledge of species' responses to such heterogeneity can be used to predict invasion potential (Peterson 2003). Many correlational studies have related species distributions and diversity to abiotic heterogeneity (reviewed in Hutchings et al. 2000), but experimental studies of the mechanisms driving these patterns are rare (but see, e.g., Crain et al. 2004, Baack et al. 2006).

Understanding the forces that create and maintain heterogeneity is especially important now because anthropogenic influences are rapidly altering landscapes, often fundamentally changing environmental heterogeneity. These forces include habitat fragmentation and destruction through human land use (Tilman et al. 1994), and widespread biotic invasions that homogenize communities (Olden and Poff 2004). In marine subtidal ecosystems, bottom trawling for fish and invertebrates may homogenize complex physical habitats, reducing coral forests, for example, to flat bottom (Watling and Norse 1998). Similarly, dredging to accommodate watercraft (Newell et al. 1998), shoreline fortification, beach renourishment (Peterson and Estes 2001), and beach grooming (Dugan et al. 2003) may eliminate natural patterns of physical and biological heterogeneity

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and alter the structure and function of these communities.

Communities on adjacent vertical and horizontal surfaces in the shallow subtidal often strongly differ, creating considerable spatial heterogeneity coupled to topography. Vertical rock walls are typically covered with dense, diverse communities of suspension-feeding sessile invertebrates, especially ascidians, sponges, bryozoans, and cnidarians, while nearby horizontal rock surfaces are dominated by algae in temperate seas or corals in the tropics (reviewed in Witman and Dayton 2001, Miller 2005). Horizontal–vertical differences also exist in the intertidal, where some invertebrates are restricted to vertical surfaces (Palumbi 1985, McFadden and Hochberg 2003), and on land, where communities on cliff faces differ dramatically from those on horizontal substrates (Larson et al. 2000:79–172). We know little about the forces shaping the differences between subtidal communities on horizontal and vertical surfaces. The processes commonly invoked to explain them include (1) shading (e.g., Witman and Cooper 1983, Sebens 1986*a*, Gili and Coma 1998), (2) physical disturbance, (3) predation, particularly by omnivorous sea urchins (Witman and Cooper 1983, Sebens 1986*a*), (4) sedimentation (Irving and Connell 2002), and (5) water flow, food, and larval flux (Leichter and Witman 1997, Gili and Coma 1998). Similar processes may also explain the larger-scale pattern of increasing sessile invertebrate abundance with depth (Young 1982, Witman and Dayton 2001).

Vertical-horizontal community differences have been attributed to the above processes because they often differ with substrate angle. Horizontal substrates receive direct sunlight favorable for algal growth, which may allow algae to outcompete sessile invertebrates for space (Dayton 1973, Witman 1987, Coyer et al. 1993), and inhibit invertebrate recruitment (Young and Chia 1984, Coyer et al. 1993, Raimondi and Morse 2000). Selection of shaded substrates, such as vertical walls, by photonegative invertebrate larvae may be an adaptive response to higher survival rates on these surfaces, making light an indicator of favorable habitat, and reinforcing vertical-horizontal community differences (e.g., Witman and Cooper 1983, Young and Chia 1984). Scouring of horizontal surfaces by sediment and rock transported by storm-generated waves is a major source of disturbance to benthic communities (reviewed in Witman and Dayton 2001); walls may be literally raised above much of this stress. Urchin grazing greatly influences benthic communities worldwide (Witman and Dayton 2001) and, in the Gulf of Maine, urchins can locally eliminate sessile invertebrates (Sebens 1986*a*, Briscoe and Sebens 1988). Urchin grazing may be reduced on walls if they have difficulty traversing them (Sebens 1986*a*), and urchins are less abundant on walls than horizontal substrates in the Gulf of Maine (Miller 2005). Sedimentation can profoundly affect benthic community structure (e.g., Airoldi 1998), and exploiting vertical surfaces may allow sessile invertebrates to easily shed sediment that would otherwise clog their feeding and respiratory structures. Water flow delivers food to benthic suspension feeders, influences gas and material exchange, and delivers pelagic larvae to the benthos. Bottom currents are modified by topography, and obstructions such as walls and pinnacles often accelerate flows, potentially allowing suspension-feeding invertebrates to dominate sessile communities (Wildish and Kristmanson 1997). Most of these processes can be affected by anthropogenic activities. Identifying factors responsible for vertical-horizontal differences may help to minimize the impact of human disturbance on the structure and function of subtidal communities.

We experimentally evaluate the importance of two of the processes most often cited as responsible for these strong spatial patterns, light and predation, in the Gulf of Maine. We test whether (1) predation or (2) shading limit invertebrate abundance and diversity on horizontal hard substrates. We also ask whether nonnative sessile invertebrates respond to these factors similarly to native species.

METHODS

Experiments were conducted at two sites: Shag Rocks, off East Point, Nahant, Massachusetts (42°24′42″ N, 70°54′24″ W), and Thrumcap, near Pemaquid Point, Maine (43°49′3″ N, 69°33′11″ W). Both are wave-exposed granitic rock ledges, 10–12 m deep at mean low tide. Shag Rocks is described in detail by Sebens (1986*a*, *b*); it is a large expanse of relatively flat solid rock bottom, with nearby vertical walls ~2–4 m high. Thrumcap is similar to the site described in Ojeda and Dearborn (1989), also with expanses of flat rock and walls ~1–2 m high. Horizontal rock at both sites was dominated by crustose coralline algae and macroalgae, particularly *Chondrus crispus, Polysiphonia* spp., *Desmarestia viridis, Bonnemaisonia hamifera*, and at Thrumcap, *Laminaria longicruris*. Experiments were conducted on horizontally oriented roughly surfaced granite slabs (bare space) ~45 × 35 cm, 5 cm thick, purchased from a stoneworks. Treatments were (1) predation, with three levels (reduced predation, procedural control, and full control), (2) light, also with three levels (shade, procedural control, and full control), and (3) location, with two levels (near a rock wall [1–3 m], a source of sessile-invertebrate larvae, vs. away from the wall [4–6 m]). These treatments were orthogonally combined to yield 18 treatment combinations, each with three replicates (54 total units/site). Predators were excluded using cages of 1-cm stiff translucent nylon mesh, which was small enough to block access of the urchin *Strongylocentrotus droebachiensis*. Two-sided cages (sides randomly chosen) were used as procedural controls for effects of mesh other than reduced predation, especially hydrodynamic effects. Shaded slabs had dark gray-tinted Plexiglas roofs (61 × 61 cm) over them. Procedural controls for shades, which might reduce sedimentation and cause hydrodynamic artifacts, had transparent Plexiglas roofs. Cages, shades, and their procedural controls were built on 1.2-cm aluminum angle frames 30 × 22.5 × 10 cm high. Frames were fastened to the granite slabs using underwater epoxy putty (A-788 Splash Zone Compound; Kop-Coat, Rockaway, New Jersey, USA). The slabs were epoxied to the solid rock bottom such that they were essentially contiguous with the bottom, separated by at least 1 m, and randomly located with respect to treatment.

Relative mass transfer, a function of water movement, was measured on control plots and under shaded, caged structures (orthogonal treatments were structure, with two levels [shade + cage vs. control, $n = 4$ treatments/level], and location, with two levels [close to vs. away from rock walls] at Shag Rocks on four deployments of ~2–3 weeks each using blocks of dental plaster (Thompson and Glenn 1994). Water flow near the bottom under a caged shade treatment and a control plot was measured directly on one occasion (8 October 2003) at Shag Rocks at mid-tide using a Sontek 10-Mhz Acoustic Doppler Velocimeter (ADV; Sontek, San Diego, California, USA). The ADV was mounted on a lead-weighted cradle for stability and the probe positioned ~5 cm above the bottom. Flow was measured at 10 hz for >5 minutes at each location, filtered appropriately, and the absolute values of the X, Y, and Z velocities summed to yield total flow velocity. Light (photosynthetically active radiation [PAR], 400–700 nm) was measured under Plexiglas and mesh roofs and on open unshaded bottom in situ at Shag Rocks using a light meter with spherical sensor (LI-193SA; LI-COR, Lincoln, Nebraska, USA) near midday on four clear sunny days during the study (23 May 2003, 14 June 2003, 10 July 2003, 7 September 2003). If algal canopy was present, light was recorded above the canopy.

Sessile communities on the slabs were monitored by photographing a 280-cm^2 (20 × 14 cm) area in the center of each slab using a Nikonos underwater camera with 28 mm lens and close-up kit (Nikonos, Tokyo, Japan), 2 Nikonos strobes, and 50 ASA Velvia slide film (Fuji, Tokyo, Japan). A second photo was taken if algal canopy obscured the substrate, with algae pushed aside. The experiment was deployed in October 2001, and communities on the slabs were monitored approximately once every other month over the next two years. The cages and Plexiglas roofs were cleaned monthly to once every two weeks or more frequently from May to October of each year, and approximately monthly November through April, when fouling was slower and weather more severe. Small urchins and other grazers, as well as trapped debris, were removed from cages if present. The Plexiglas roofs were replaced after one year. Urchins were counted five times at Shag Rocks (August 2001, May 2002, July 2002, June 2003, September 2003) and three times at Thrumcap (October 2001, August 2002, August 2003), by haphazard placement of a 1-m^2 quadrat (n = 8 quadrats/date). The data presented here were collected in November 2003 after 25 months of community development.

To estimate percent cover of invertebrates, algae, and other space occupiers, slides were projected on a screen with 400 randomly positioned dots; sessile organisms under each dot were identified to the lowest possible taxonomic resolution. Algal canopy was also recorded, along with the substrate below if visible. Algae were often not identifiable to species in photos, and for analysis were grouped as macroalgae (including filamentous algae), crustose coralline algae, or *Peysonnelia* sp. (a soft red crustose alga). Networks of tubes and consolidated sediment constructed by amphipods and polychaetes were categorized as tube complex, following Sebens (1986*a*). Abiotic categories included bare rock and loose sediment. Data for natural wall communities were measured as above for 0.25-m^2 photographed quadrats ($n = 10$ quadrats/site), using 100 random dots per slide.

To determine whether larval photonegativity and location relative to the wall influenced the experimental communities, recruitment was measured at Shag Rocks once every two weeks during a two-month period (four deployments) from June through August 2003. Slate tiles (10 × 10 cm) were bolted on the slabs outside the photographed area (but well within the influence of the shades) to minimize impact on the experimental area. Treatments were light, with three levels (shade, control, and procedural control [transparent Plexiglas lid]), and location, with two levels (close to and away from the wall). Tiles were carefully collected and kept in flowing seawater until analysis, within 24 hours under a dissecting microscope. Recruits were identified to the highest possible taxonomic resolution and grouped into major taxa for analysis.

The experiment was analyzed using factorial ANOVA, with site as a random factor, and three fixed factors: location, predation level, and light level. Proportional cover data was transformed to logits, $\ln(p/[p - 1])$, where p is the proportion, to homogenize variances (Ramsey and Schafer 2001). Response variables were cover of sessile invertebrates and macroalgae, and sessile invertebrate species richness, in separate analyses. Two plots at each site were destroyed by storms; the mean of the other two identical replicates was used for each of these, and the missing replicates subtracted from the residual degrees of freedom, in the ANOVAs to retain the benefits of a balanced design (Underwood 1997), although outcomes of tests did not differ if these replicates were omitted completely. Recruitment data were analyzed using ANOVA, with deployment time as a random factor, light (shade, control, procedural control) and location (close to wall vs. away from wall) as fixed factors, and invertebrate recruits and algal recruits as response variables. JMP statistical software (Mac version 5.0.1a, SAS Institute, Cary, North Carolina, USA) was used for all analyses. Planned linear contrasts on significant main effects were calculated by first testing procedural controls against full controls to determine whether significant experimental artifacts were present before testing for treatment effects against the pooled MS for controls plus procedural controls. Tukey's honestly significant difference (hsd) test was used for all unplanned multiple comparisons. We explored how the species composition of shaded and unshaded plots compared to natural wall communities with canonical analysis of principal coordinates (CAP), using a permutation test of significance of differences between groups, and the "leave-one-out" approach to estimate goodness of fit of the groups. Correlation coefficients of the canonical axes with the original taxonomic categories were used to identify the species most influencing the ordination pattern (Anderson and Robinson 2003, Anderson and Willis 2003).

RESULTS

Effects of light and predation on sessile communities

The dominant result of the experiment was the dramatic effect of light on invertebrate cover and species richness (Table 1) after 25 months of community development. Sessile invertebrates were much more abundant (Table 1, Fig. 1a) and diverse (Table 1, Fig. 1c) on shaded plots. All interaction terms including site were pooled in the analyses, using the criteria described by Underwood (1997). Site significantly affected invertebrate cover ($F_{1,89} = 7.3$, $P = 0.008$).

Macroalgae was virtually excluded from shaded plots (Fig. 1b). The heteroscedasticity of these light treatment data, caused by many zero and near-zero values, precluded the use of ANOVA. The treatment effect, however, is clear. The other treatments were analyzed with ANOVA, and no other factor significantly affected macroalgae cover (Table 1).

Sessile invertebrate community structure

Although nearby walls at Shag Rocks are often dominated by colonial ascidians (especially *Aplidium glabrum*), encrusting sponges, and bryozoans (Sebens 1986*a*, *b*, Miller 2005), the invertebrate communities under the experimental shades were dominated by the solitary ascidian *Molgula citrina*, with lesser abundances of other taxa, all of which were also common on nearby rock walls (Table 2). *Didemnum* sp., a cryptogenic colonial ascidian, (Bullard et al. 2007) was the most abundant species on shaded and unshaded plots at Thrumcap, and *M. citrina* was the second most abundant species (Table 2). CAP analysis showed that assemblages on control plots, shaded plots, and wall plots were significantly different (Fig. 2, $P = 0.0001$ from 9999 permutations). Correlations of the canonical axes with the original species data showed that domination by macroalgae largely separated the unshaded plots from shaded and wall plots. Shaded plots were separated from wall plots by dominance of *M. citrina*, and by the lack of several species associated with walls, mostly ascidians (Fig. 2). Leave-one-out analysis of the groups (unshaded plots, shaded plots, and wall plots) showed high classification accuracy, 87.9% overall. Shaded and unshaded plots, respectively, were misclassified as the other two groups with approximately equal frequency, while wall plots were only misclassified as shaded plots (Table 3).

TABLE 1. Results of ANOVAs on light × predation experiment.

Source	df	SS	*F*	*P*
Invertebrate cover				
Site	1, 85	27.86	7.31	<0.01
Location	1, 85	8.31	2.18	0.14
Site × location†	1, 0.5	5.88	3.18	0.49
Light	2, 85	170.59	22.37	<0.0001
CN vs. TL	1, 85	1.20	0.52	0.47
S vs. average (C and TL)	1, 85	168.60	44.21	<0.0001
Site × light†	2, 1.6	18.56	2.43	0.33
Location × light	2, 85	13.55	1.78	0.17
Site × location × light†	2, 4	2.37	0.46	0.66
Predation	2, 85	3.86	0.51	0.60
Location × predation	2, 85	22.11	2.90	0.06
Site × location × predation†	2, 4	6.44	1.26	0.37
Light × predation	4, 85	19.95	1.31	0.27
Site × light × predation†	4, 4	20.74	2.03	0.27
Location × light × predation	4, 85	2.55	0.17	0.95
Site × location × light × predation†	4, 72	10.21	0.69	0.60
Residual	85	339.37		
Macroalgae cover				
Site	1, 1.1	8.92	0.54	0.59
Location	1, 1	2.49	0.16	0.76
Site × location	1, 2	15.79	5.61	0.14
Predation	2, 2	16.31	2.29	0.30
Site × predation	2, 2	7.14	1.27	0.44
Location × predation	2, 2	9.19	1.63	0.38
Site × location × predation	2, 92	5.63	0.17	0.84
Residual	92	1613.8		
Invertebrate species richness				
Site	1, 85	0.02	0.08	0.78
Location	1, 85	0.33	1.22	0.27
Site × location†	1, 0.6	1.29	3.46	0.43
Light	2, 85	14.60	26.77	<0.0001
CN vs. TL	1, 85	14.60	53.52	0.92
S vs. average (C and TL)	1, 85	168.60	44.21	<0.0001
Site × light†	2, 0.8	1.60	1.77	0.50
Location × light	2, 85	1.07	1.95	0.15
Site × location × light†	2, 4	1.32	2.14	0.23
Predation	2, 85	0.91	1.67	0.19
Location × predation	2, 85	0.37	0.67	0.51
Site × location × predation†	2, 4	0.04	0.06	0.94
Light × predation	4, 85	2.44	2.24	0.07
Site × light × predation†	4, 4	0.40	0.32	0.85
Location × light × predation	4, 85	1.35	1.23	0.30
Site × location × light × predation†	4, 72	1.24	1.27	0.29
Residual	85	339.37		

Notes: Response variables were logit-transformed (cover data) or log-transformed (richness) (see *Methods*). Treatments are site (random, two levels: Thrumcap [TC] vs. Shag Rocks [SR]), location (fixed, two levels: near wall [NW] vs. away from wall [AW]), light (fixed, three levels: control, transparent lid, shade [CN, TL, S]), and predation (fixed, three levels: control, partial cage, and cage [CN, PC, C]). Light treatment for algae analysis is omitted due to heteroscedasticity of the data that remained after transformation.

† Terms pooled.

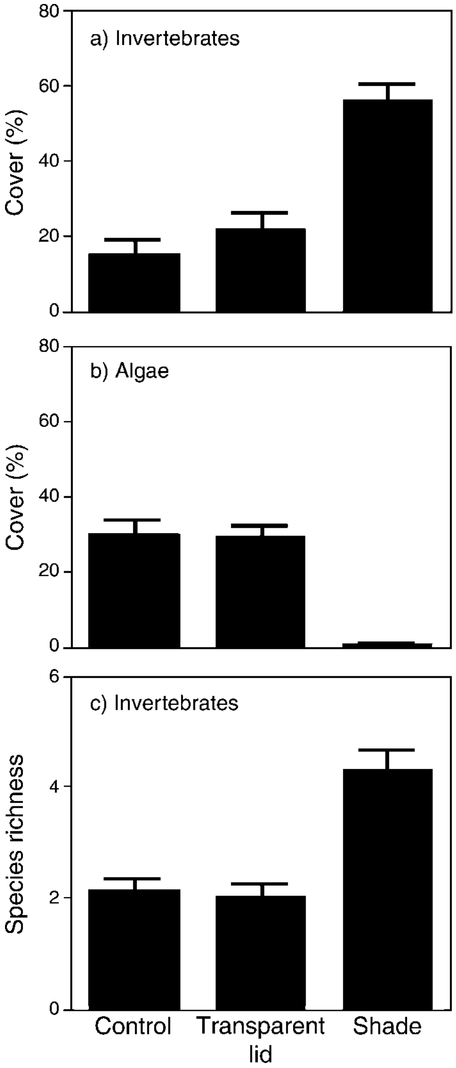

FIG. 1. Percent cover of (a) sessile invertebrates and (b) algae and (c) species richness of sessile invertebrates under the three light treatment levels. Error bars are one standard error. Heteroscedasticity of the algae data prevented ANOVA analysis; nevertheless, it is clear that shading virtually eliminated algae.

Recruitment

Light did not have a significant effect on total invertebrate recruitment at Shag Rocks on the two-week time scale examined (ANOVA, $F_{2,36} = 1.01$, $P = 0.37$), but location did, (ANOVA, $F_{2,36} = 12.90$, $P < 0.01$), with tiles near a rock wall receiving more recruits (Table 4). The major taxa settling were *Spirorbis* sp. ($n = 1800$), bryozoa ($n = 345$), ascidians ($n = 48$), and *Tubularia crocea* ($n = 174$). Taxon-specific analysis showed a significant effect of location only on *Spirorbis* (ANOVA, $F_{2,36} = 3.99$, $P = 0.05$), with other taxa showing no significant relationships with any factor (analyses not shown). Macroalgal recruitment was significantly related to both light (ANOVA, $P = 0.01$), and location (ANOVA, $P = 0.04$, Table 4). Macroalgal recruits were less abundant under shades, and near a wall (Table 4).

Mass transfer and flow

Dissolution rates of plaster blocks at Shag Rocks did not differ inside shaded cages compared to controls (ANOVA, $P = 0.98$), but tended to be greater close to the rock wall, although the difference was not significant (ANOVA, $P = 0.08$). Mean flow velocity measured with the ADV at Shag Rocks did not differ between flat rock bottom and under caged/shaded experimental structures (*t* test, $P = 0.97$, $n = 5$ minutes/treatment). Flow at mid-tide ~5 cm from bottom averaged 13.9 ± 0.2 cm/s (mean ± SE), with most flow horizontal to the bottom. The tidal range on the day of measurement was 2.73 m, close to the mean of 2.76 m. Seas were mild, with wave-height maxima ~0.5 m, and no noticeable surge on bottom at 10 m (tide and wave data from Boston Light Buoy, U.S. National Data Buoy 44013, ~19 km from Shag Rocks).

Light measurements

Mean PAR on open bottom at 10 m depth near midday on four clear sunny days was 47.25 ± 1.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($n = 16$ readings). Walls had mean PAR levels 28.9% ± 3% ($n = 16$ readings, range 12.8–46.9%) of PAR on open bottom. The tinted Plexiglas reduced PAR to mean 23.1% ± 0.9% ($n = 16$ readings) of PAR

TABLE 2. Invertebrate taxa recorded in communities on shaded and unshaded plots, listed in descending order of percent cover (mean ± SE).

Taxon	Shaded	Ambient
Shag Rocks[†]		
Molgula citrina	55.63 ± 5.1	9.78 ± 1.7
Aplidium glabrum	1.37 ± 0.7	0.25 ± 0.1
Semibalanus balanoides	1.22 ± 0.4	0.15 ± 0.1
Spirorbis spp.	1.03 ± 0.6	0.21 ± 0.1
Encrusting bryozoa	0.99 ± 0.4	<0.01
Dendrodoa carnea	0.29 ± 0.1	0.06 ± 0.04
Anomia simplex	0.12 ± 0.1	0.03 ± 0.03
Molgula manhattensis	0.10 ± 0.1	0.01 ± 0.01
Botrylloides violaceus	0.04 ± 0.04	<0.01
Erect bryozoa	0.04 ± 0.03	0.01 ± 0.01
Tubularia sp.	0.03 ± 0.03	<0.01
Mytilus edulis	0.01 ± 0.01	<0.01
Botryllus schlosseri	0.01 ± 0.01	np
Thrumcap[‡]		
Didemnum sp.	29.00 ± 9.1	10.51 ± 6.5
Molgula citrina	11.60 ± 2.2	5.41 ± 1.0
Encrusting bryozoa	2.65 ± 0.9	0.29 ± 0.3
Botrylloides violaceus	2.61 ± 1.5	2.03 ± 1.5
Semibalanus balanoides	2.46 ± 1.3	0.12 ± 0.1
Spirobis sp.	2.25 ± 0.8	0.41 ± 0.3
Botryllus schlosseri	1.06 ± 0.6	np
Anomia sp.	0.82 ± 0.4	<0.01
Membranipora membranacea	0.59 ± 0.6	0.15 ± 0.1
Dendrodoa carnea	0.04 ± 0.03	np

Note: Entries of "np" indicate "not present."

[†] At this site there were 17 shaded plots, 18 unshaded plots.

[‡] At this site there were 18 shaded plots, 17 unshaded plots.

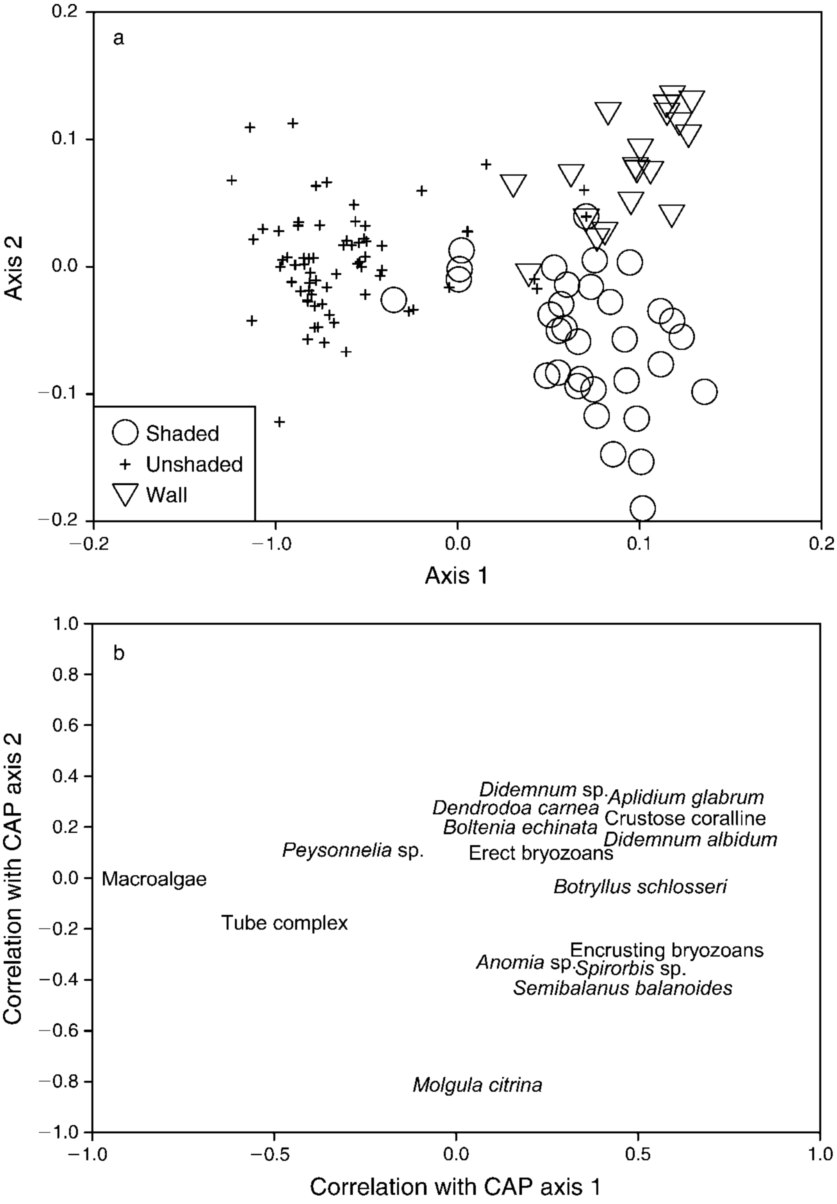

FIG. 2. (a) Canonical analysis of principal coordinates (CAP) ordination of species assemblages on shaded and unshaded experimental plots and on natural wall communities at the two sites using Bray-Curtis dissimilarities of $\log(x + 1)$-transformed percent cover data. (b) Correlations between the CAP axes and the original taxonomic variables, excluding species with correlation coefficients <0.2. Points are located at center of text.

on open bottom. Clear Plexiglas and mesh roofs did not significantly reduce PAR levels underneath them when compared to open unshaded bottom (t tests, mean PAR under clear Plexiglas, 43.67 ± 2.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $n = 9$ readings, $P = 0.3$; under mesh 47.57 ± 1.6 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $n = 6$ readings, $P = 0.9$).

Urchin density

Mean urchin densities at the two sites were similar throughout the study (Shag Rocks 1.36 ± 0.4 urchins/m^2, $n = 40$ quadrats; Thrumcap 1.58 ± 0.6 urchins/m^2, $n = 24$ quadrats).

TABLE 3. Leave-one-out allocation of plots to groups (shaded and unshaded experimental plots, natural wall plots) in canonical analysis of principal coordinates (CAP) analysis.

	No. plots				Correct
Group	Shaded	Unshaded	Wall	Total	(%)
Shaded	27	4	4	35	77.1
Unshaded	2	64	3	69	92.8
Wall	2	0	18	20	90.0

Note: Total misclassification error was 12.1%; classifications were correct in 87.9% of cases.

TABLE 4. Results of ANOVA on recruitment data.

Source	df	SS	*F*	*P*
Invertebrates				
Location	1	7.07	10.71	<0.01
Light	2	1.12	0.85	0.43
Location × light	2	3.78	2.86	0.07
Residual	39	25.75		
Macroalgae				
Location	1	8.25	7.26	0.04
Light	2	15.45	6.80	0.01
C vs. TL	1	2.07	1.82	0.19
S vs. average (C and TL)	1	13.39	11.78	0.001
Location × light	2	2.45	1.08	0.35
Residual	39	44.30		

Notes: Fixed factors are location (two levels: near wall [NW] vs. away from wall [AW]) and light (three levels: control, transparent lid, shade [C, TL, S]). Recruitment of invertebrates and algae was standardized as no. recruits/day, and log-transformed to homogenize variances. The random factor time of deployment ($n = 4$ time periods) was pooled after determining that its effect was insignificant ($P > 0.25$).

DISCUSSION

Many factors may vary between vertical walls and horizontal substrates, including water flow (Leichter and Witman 1997, Gili and Coma 1998), sedimentation (Irving and Connell 2002), physical disturbance, and predation (Witman and Cooper 1983, Sebens 1986*a*); nevertheless, our results show that shading alone can shift sessile subtidal communities to invertebrate dominance. Macroalgae were virtually eliminated from shaded plots that had light levels similar to vertical walls (Fig. 1b). At these low light levels many shallow-water algal species are below or near their compensation point, where photosynthetic production balances respiration (e.g., Lobban and Harrison 1994). The structure and composition of communities under different light regimes may be driven by differential settlement of invertebrates on walls, and/or differential post-settlement mortality.

Differential settlement of invertebrates on vertical walls (and shaded experimental plots) may be mediated by negative phototaxis. Many late-stage sessile invertebrate larvae exhibit negative phototaxis, which enable larvae to choose cryptic refugia for settlement (reviewed in Thorson 1964, Young and Chia 1984). If larvae strongly preferred to settle on shaded plots, and avoided unshaded plots, the experimental results could reflect recruitment. However, invertebrate recruitment was not significantly associated with light level treatment on the short-term (two-week) recruitment tiles at Shag Rocks, suggesting that post-settlement mortality may have been more important than larval phototaxis in shaping the communities that developed on our plots. Short-term recruitment was measured for only two summer months, so some species were probably under-sampled, including the solitary ascidian *Mogula citrina*, which was the dominant space holder in shaded plots (Table 2). Unfortunately, identification to species was not possible for the recruits; however, the ascidians that did settle showed no preference for the shaded plots.

If differential settlement was not responsible for the higher invertebrate cover under shades, then what might cause post-settlement mortality of invertebrates on horizontal substrates? Physical factors such as light level may directly influence the distribution of organisms through physiological effects, or indirectly influence biological interactions. Ultraviolet light can kill invertebrate settlers in shallow tropical waters (Jokiel 1980), but does not typically penetrate below 8 m in the Gulf of Maine (Lesser et al. 2001). Moreover, the transparent Plexiglas lids used as procedural controls for the light treatment block most UV, and invertebrate cover under them was not statistically different from the full controls. The most likely indirect effect of light is overgrowth of recruits or inhibition of invertebrate recruitment by algae. Overgrowth by microalgae was a significant source of mortality for recruits for six species of subtidal solitary ascidians in the San Juan Islands (Young and Chia 1984), and turfing algae on horizontal surfaces in the Gulf of California inhibited invertebrate recruitment and outcompeted them for space (Baynes 1999). Macroalgae can overgrow and kill subtidal invertebrates (e.g., mussels [Witman 1987], soft coral [Coyer et al. 1993], coral [Raimondi and Morse 2000]), but in general this phenomenon is poorly documented and understood. Other possible indirect effects of light include increases in small grazers, e.g., amphipods (Duffy and Hay 2000), or changes in flow, in plots with algae present.

Species richness of invertebrates was also enhanced on shaded plots by a factor of two (Fig. 1c). Since richness and abundance varied in the same direction, the lower richness in unshaded plots could be due to controls on abundance (sampling effect). However, survey data shows much higher asymptotic richness on shaded natural wall communities compared to horizontal algal-dominated substrate (Miller 2005), suggesting that shading, or other factors associated with substrate angle, enhance sessile invertebrate richness.

Predation

Predation had no significant effect on invertebrate or algal cover. This result was somewhat surprising, considering previous experiments (Sebens 1986*a*; K. Sebens, *unpublished manuscript*) that found significant sessile invertebrate growth only inside shaded urchin-exclusion cages, and heavy algal growth only inside unshaded cages. This difference was most likely due to the high urchin densities around Sebens's experiments (K. Sebens, *personal communication*). High urchin densities in the Gulf of Maine (GOM) create typical low diversity "barrens" dominated by encrusting coralline algae, and eventually urchin herds can exclude invertebrates even from vertical walls (Sebens 1986*a*). Coralline algae, not invertebrates, probably dominate barrens because urchins consume invertebrates, especially when macroalgae is scarce (Sebens 1986*a*, Briscoe and Sebens 1988, Simoncini and Miller 2007). After a boom in the 1980s, thought to be caused by overfishing their predators, urchin densities have declined in the GOM due to commercial harvesting (Harris and Tyrell 2001), and low densities (<5 urchins/m^2) are common, particularly in the southern half of the GOM (Grabowski et al. 2005, Miller 2005). At the same time, disease-induced urchin mortality precipitated declines off the coast of Nova Scotia in the northern GOM (Brady and Scheibling 2006). Although the urchin densities we observed were low, urchins were frequently observed on the plots. Other predators, including cunner (*Tautoglabrus adspersus*), crabs (*Cancer irroratus* and *C. borealis*), and winter flounder (*Pseudopleuronectes americanus*), were abundant at the site, and are known predators on sessile invertebrates (Edwards et al. 1982, Osman and Whitlatch 2004). Vertical walls have been viewed as a refuge from predation for invertebrate communities (e.g., Witman and Cooper 1983, Sebens 1986*a*), and predation plays a minor role in structuring established wall communities in some cases (Sebens 1986*a*, Vance 1988). Our results suggest that at these sites in the GOM, predators play a relatively minor role in the establishment of invertebrate communities on rock walls, although selective predation on competitive dominants may facilitate species coexistence on walls (Sebens 1986*b*, Miller 2005).

Predation on newly settled recruits by micropredators, e.g., small invertebrates, that could move through the cage mesh cannot be discounted, and could have controlled invertebrates in both the caged and uncaged plots (see, e.g., Osman and Whitlatch 2004, Stachowicz and Whitlatch 2005). Micropredators (or "mesograzers") such as small crustaceans and gastropods are generally most abundant in macroalgae (e.g., Stachowicz and Whitlatch 2005), and this was true at our study sites; thus, these animals could have influenced the differences between unshaded plots with abundant macroalgae and shaded plots.

Walls vs. shaded plots

Why do communities in experimental plots differ in composition from those on ambient walls? One key factor may be the impact of disturbance. For example, *A. glabrum* was present in experimental plots (mostly shaded ones), but never dominated as it did on walls (Fig. 2). This was likely due to sedimentation, but rather than the vertical rain of sediment often described, the sediment that most heavily impacted these shallow communities was transported across the bottom by periodic storm-generated waves, mostly during winter. This process is often referred to as sediment scouring, but can also simply bury invertebrates under layers of floc or sand, and this was observed frequently at both study sites, particularly in winter. Solitary ascidians like *M. citrina* are relatively resistant to sedimentation compared to colonial forms (e.g., Jackson 1977). Because walls are raised above the bottom, they may act as a refuge from much of this disturbance (Witman and Cooper 1983, Sebens 1986*a*, Vance 1988). Sebens (1986*a*) observed very low levels of disturbance on rock walls at Nahant, even after large winter storms generated waves of >5 m height.

An alternative explanation for the lack of some common invertebrate taxa, such as sponges, on the experimental plots is that the experiment was not long enough for poor dispersing species to colonize these somewhat isolated patches (Connell and Keough 1985). *M. citrina* and *Spirorbis* sp. are good colonizers of open space on walls (Sebens 1986*b*), as is *Semibalanus balanoides* (R. J. Miller, *unpublished data*). *Dendrodoa carnea* and encrusting bryozoans, both of which colonized the shaded experiments extensively, despite not occupying much space, are intermediate in their colonization ability (Sebens 1986*b*). *Aplidium glabrum*, a dominant competitor, took at least two years to reinvade cleared patches on walls (Sebens 1986*b*). Sponges can take years to recolonize cleared areas (Sebens 1986*b*, Hill et al. 2004), and 27 months may have been insufficient for them to colonize the experimental patches. Nevertheless, species with intermediate colonization abilities effectively colonized the shaded experiments, and *A. glabrum* also recruited into the patches, but failed to occupy large amounts of space as it often does on vertical walls.

Invasive species

Our experiments suggest that successful invaders are not regulated by the same factors as native species. The invasive colonial ascidian *Botrylloides violaceus* colonized one plot at Shag Rocks, but was more common at Thrumcap, where neither it nor the cryptogenic *Didemnum* sp. was affected by light level. This may help explain the relative abundance of these species on horizontal substrates compared to native colonial ascidians (Miller 2005; R. J. Miller and R. J. Etter, *unpublished manuscript*). Abundance of nonnative ascidians may be negatively correlated with species richness of native sessile invertebrates (Stachowicz et al. 2003) and experimental work has shown that temporally complementary patterns in abundance of native species can exclude invasive ascidians (Stachowicz et al. 1999). If, as this study suggests, light does not restrict the distribution of these nonnative ascidians as it does native sessile invertebrates, then this may facilitate the spread of these species and partly explain why they have been so successful in the GOM and elsewhere (see Bullard et al. 2007, Simoncini and Miller 2007).

Subtidal rock wall communities are influenced by competition, predation, and water flow (references given in last paragraph). However, our results indicate that in the Gulf of Maine, light, via its effect on algae, may be the most important factor limiting invertebrates to vertical walls. Shading probably alleviates competition for space with algae, and may also reduce predation on recruits by algal-associated micropredators. Disturbance from sedimentation and storm scour might also mediate post-settlement mortality of invertebrates on horizontal rock. Local recruitment probably plays an important role in perpetuating rock-wall communities (Graham and Sebens 1996, Smith and Witman 1999), and in their recovery after intense urchin grazing, which can be very slow (Hill et al. 2004). Local dispersal can promote species coexistence under conditions of permanent spatial heterogeneity (Snyder and Chesson 2003), such as is provided by vertical walls, and limitation of dispersal distance to facilitate settlement into favorable adult habitat, rather than location of new habitats, may be the primary function of larval photonegativity in sessile invertebrates.

Light availability and competition with algae may be the strongest factor limiting nonzooxanthellate sessile invertebrates largely to shaded habitats such as walls, caves, undersides of rubble, and rocky interstices in shallow water. Other subtidal experiments have shown that shading increases sessile invertebrate abundance and negatively affects algae in kelp forests (Reed et al. 2006), on pilings (Glasby 1999), and on artificial settlement plates (Irving and Connell 2002). Hermatypic corals dominate horizontal hard substrates in low-nutrient, high-grazing tropical seas, where algal growth is limited (Knowlton and Jackson 2001). There is little evidence for direct negative effects of nutrients on corals (Atkinson et al. 1995), and algal-coral competition, mediated largely by herbivory, shapes modern coral reef communities (e.g., McCook et al. 2001). Overfished reefs are typically shifted to an alternate community state dominated by fleshy macroalgae (Hughes et al. 2003). A few invertebrate taxa can dominate swaths of horizontal substrate in temperate subtidal and intertidal zones: mussel beds are resistant to urchin grazing, and harbor other small grazers that can prevent algal overgrowth (Witman 1987), as do beds of the large intertidal tunicate, *Pyura praeputialis* (Paine and Suchanek 1983), and colonies of the temperate subtidal coral *Oculina* (Stachowicz and Hay 1999). Some invertebrates, particularly certain sponges, can be abundant on horizontal surfaces in the temperate subtidal (Ayling 1981, Knott et al. 2004), but this seems to occur where algae is sparse due to heavy urchin grazing or other factors (Ayling 1981). Removal of grazers often results in suppression of recruitment and algal overgrowth of intertidal barnacles (e.g., Dunmore and Schiel 2003) and sponges (Palumbi 1985). Below the photic zone, sessile invertebrates are often abundant on horizontal substrate (depth emergence [Young 1982]).

There is no question that environmental heterogeneity is critical to the structure, function, invasibility and dynamics of communities (e.g., Snyder and Chesson 2004, Davies et al. 2005, Seabloom et al. 2005), but we often lack a clear understanding of the forces that generate and maintain it. In some cases the forces are well known. For example, in many systems disturbance, such as fire in terrestrial ecosystems, or wave energy in near-shore coastal communities, creates heterogeneity as a spatiotemporal mosaic of patches in various stages of recovery. In most cases, particularly those involving physical heterogeneity, the underlying mechanisms are not well understood. In the subtidal, the community differences between vertical and horizontal surfaces might be attributed to topographic complexity, but based on our findings are due to differences in light, and the subsequent impact that has on the interactions between sessile faunal and floristic space occupiers. This distinction is critical because if light levels are homogenized in coastal ecosystems due to changes in water quality (increased nutrient loading from near-shore anthropogenic activities), ice cover, or other factors, heterogeneity will decrease and subtidal communities would become more homogeneous even without changes in topographic complexity. Mitigating such changes and predicting how communities might respond requires a clear distinction between proximate and ultimate forces, which is often lacking (see Dayton 1973). Understanding the precise underlying mechanisms that shape the nature and scale of heterogeneity is vital for maintaining its key role in ecosystem processes (Snyder and Chesson 2004) and potentially controlling invasion success (Melbourne et al. 2007).

Sessile invertebrates generally can dominate horizontally oriented hard substrate only where competing algae are absent, due to low light levels or heavy grazing that does not affect the animals. Vertical surfaces are probably dominated by invertebrates because low light levels prevent algae from usurping space. These patterns suggest that mediation of plant–animal competition for space by light level and grazing is a fundamental determinant of spatial heterogeneity in community structure on hard substrates in modern shallow seas.

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