Light exposure determines subtidal community assemblages in Corsica, France

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ABSTRACT
Species diversity is directly related to the stability of many marine and terrestrial ecosystems. On shallow rocky reefs, the diversity, community composition and competitive interactions are influenced by abiotic factors such as light exposure, wave action and sedimentation. These processes interact to create and maintain epibiotic assemblages in which algae commonly dominate the topsides of boulders, while invertebrates dominate the undersides ($p<0.0001$). In this study we show that light exposure is inversely correlated to species diversity on rock surfaces at STARESO harbor and is the primary abiotic factor influencing the sessile communities. Wave action and sedimentation did not explain differences in community composition between treatments. We also demonstrate that algae will grow over invertebrate communities if low-lighted areas are exposed to high light intensities. Our results indicate that beyond a certain threshold of light exposure, algae will competitively exclude sessile invertebrates and thereby reduce the epibiotic diversity of rocky reefs.

KEYWORDS: Diversity, Competition, Abiotic, Epibionts, Light, Algae, Invertebrates, Rocky Reef, Mediterranean

INTRODUCTION
Species diversity and composition can have a direct effect on the stability of many marine and terrestrial ecosystems (McCann 2000). The composition of biological communities is influenced by a suite of interacting physical, chemical and biological processes including competition among species (Chambers and Prepas 2006). In the case of competitive exclusion, competition for a shared resource between two or more species can create heterogeneous distributions of organisms in space and time (Hardin 1960; Armstrong and McGhee 1980). This process has been known to reduce diversity when one species excludes another from a particular area (Connell \textit{et al.} 2004). The ability of a species to successfully monopolize a shared resource can be altered by the fluctuation of certain abiotic factors (Dayton 1975; Cronin and Hay 1996; Chambers and Prepas 2006). Hence, changes in these factors may indirectly lead to changes in species diversity by reshaping competitive hierarchies.
Within shallow rocky reefs, sessile organisms such as algae and invertebrates compete for a limited amount of space. The primary abiotic factors influencing the competition between these organisms are light availability, wave action and sedimentation (Irving and Connell 2002). The growth of some algae, especially Chlorophyta, heavily depends on sunlight availability for effective photosynthesis (Raven 1991). Alternately, invertebrates such as sponges may be harmed through overexposure to ultraviolet radiation (Saunders and Connell 2001). Turbulence from waves may negatively affect the growth of algae by directly damaging the thalli and holdfasts of some species (Dayton 1975). Conversely, invertebrate filter feeders such as tunicates require a minimum amount of wave action to capture food particles from seawater (McQuaid and Branch 1985). Sedimentation typically has a negative impact on both algae and invertebrates through shading and clogging filter feeding apparatuses (Airoldi and Cinelli 1997; Irving and Connell 2002). Identifying the relative importance of these interacting physical processes with respect to competition will provide a better understanding of the mechanisms that shape and maintain the diversity of benthic communities.

A common observation within subtidal rocky reefs is that surfaces exposed to high light levels such as the top-sides of boulders are dominated by algal assemblages whereas areas with less light are dominated by sessile invertebrates (Irving and Connell 2002). We quantitatively compared levels of wave action, sedimentation and benthic species diversity in areas of high and low light exposure in nearshore rocky reefs in Calvi, Corsica, France. We also experimentally tested changes in the competitive hierarchy of benthic communities after exposure to high levels of light. These methods allowed us to identify the relative importance of these three physical processes in determining the epibiotic assemblages of rocky reefs in Corsica.

METHODS

Study site

To quantify the effect of differential light exposure on benthic sessile communities, we conducted observational surveys and field experiments at STARESO Research Institute of Oceanography located near Point Revellata, Calvi, Corsica, France (42°34'48.85"N, 8°43'26.89"E). The harbor at STARESO is surrounded by granitic rock walls that shield the harbor from most wind and surf. Sand and gravel comprise most of the substrate in the harbor. Outside of the harbor, the subtidal habitat consists chiefly of large boulders adjacent to Posidonia oceanica meadows at a depth of approximately 8 meters. Observational surveys were completed on SCUBA during October 2012, and took place within 200m north and south of the station harbor at depths up to 15m (Figure 1). To examine the relationship between light availability and community composition on boulders, we employed three focal approaches: 1) light sensor readings; 2) quantitative assessments of benthic community composition at various depths and light exposure
conditions; and 3) an experimental study of the invertebrate community response on inverted boulders.

**FIGURE 1.** Site Map.

*Survey approach*

We evaluated differences in light levels using HOBO photosynthetically available radiation (PAR) sensors. To examine changes in light with depth, we took PAR sensor readings at 1 meter increments from 1 meter to 8 meters deep. PAR, measured in lumens/ft$^2$, was analyzed using HOBO software.

To distinguish between community composition on the tops and bottoms of boulders located at different depths, we placed uniform point contact (UPC) quadrats (50 cm$^2$ area) on the upward facing and downward facing sides of boulders. 30 boulders were randomly selected at each of three depth categories: shallow (3-5 meters), middle (8-10 meters), and deep (13-15 meters). Primary placeholders beneath each of 25 uniform points within the quadrat were identified to the lowest possible taxonomic level.

To further examine the relationship between light availability and community composition, we surveyed two coves south of STARESO harbor. Rates of sedimentation are equal at identical depths for each cove wall because they are both exposed to equal
amounts of run-off. We evaluated differences in light levels using HOBO PAR sensors. Additionally, we placed 25-point UPC quadrats (50cm$^2$) on east and west facing walls to compare community composition. On each wall, we placed four quadrats at 1.5 m depth and recorded the primary placeholders at the 25 points within the quadrat.

In order to determine whether wave action would have a notable effect at our sites, we constructed clod cards out of plaster of Paris and placed them at various locations around our experimental and study sites. Wave action on the undersides of boulders was compared against wave action on the tops of boulders. Wave action was also analyzed at each depth category (3-5m, 8-10m and 13-15m) and on east and west facing canyon walls.

Experimental approach

To examine how invertebrate communities on the bottoms of boulders change in response to increased light, we inverted 12 boulders within the STARESO harbor and examined the change in community composition on the exposed surface. We used photoplot surveys to investigate the change in boulder community composition directly subsequent to flipping and 10 days after exposure to high light. Shade structures constructed from PVC pipe and plastic mesh were erected 10cm over 3 of the flipped boulders to mimic light conditions under boulders. To avoid the confounding effects of invertebrate consumption, fish exclusion cages were erected over 3 of the flipped boulders. The 6 remaining boulders were left exposed. The boulders ranged from 2.7 to 7.4 m in depth. Community composition was analyzed by overlaying 12 random points with Image J (NIH, http://rsb.info.nih.gov/ij) public domain photo analysis software to determine the percent occurrence of each transition (i.e. growth = bare rock to algae, die-off = invertebrate to bare rock) for each boulder before and after the 10-day period of high light exposure.

Statistical analyses

We converted point counts into percent cover for each species and assessed the dissimilarity of species composition between treatments using a Bray-Curtis dissimilarity matrix to create a multidimensional scaling (MDS) plot. Each point on the MDS graph represents a treatment-depth combination. Close proximity between individual points suggests less variance in community composition among factors. We compared the effect of higher light levels and increased depth on community composition dissimilarities using a PERMANOVA. In addition, we ran a similarity percentages (SIMPER) analysis to determine the relative contribution of each species to percentage dissimilarities between depth and treatment.

We converted species abundances into measures of diversity using the Shannon-Wiener diversity index formula (below), where $P_i$ is the proportion of individuals of a species in a community.
We drew species accumulation curves to assess species richness (i.e. number of species compared to the abundance of individuals) using PRIMER software (Clarke and Gorley 2006).

We conducted paired t-tests to assess whether the mean light readings and mean diversity index values that resulted from differential treatments were statistically different from one another. We conducted statistical analysis using JMP with an alpha-level of 0.05 for all tests (JMP, Version 9. SAS Institute Inc., Cary, NC, 1989-2012) and GraphPad Prism (version 6.0 for Macintosh, GraphPad Software, La Jolla California USA, www.graphpad.com). For visualization, we constructed bar graphs with each error bar 1 standard error from the mean.

For flipped boulders, we converted percent data to proportions and then arcsin square-root transformed the values. We used a polynomial contrast of order one to test whether the values for percent occurrence of algal growth are consistent with the a priori hypothesis that the most algal growth will occur on flipped boulders, less on flipped excluded boulders, and least on flipped shaded boulders.

RESULTS

The intensity of light decreased with water depth (Figure 2). There were no significant changes in clod card mass between treatments or depth categories. For this reason, we focused primarily on the effect of depth and consequent light exposure on benthic community diversity.

\[
H' = - \sum_{i=1}^{S} (P_i) * \ln(P_i)
\]

FIGURE 2. Light attenuates at depth.
Light readings on the top-sides and bottom-sides of boulders among all depth categories varied from 2176 lumens/ft\(^2\) to 1 lumens/ft\(^2\). There were significant differences in light exposure between the tops and bottoms of boulders for each depth category (p<0.0001) (Figure 3). In addition, light attenuated significantly between each depth category (p<0.0001) (Figure 3). Light exposure and diversity were inversely related (Figure 3). There was significantly lower diversity on the top-sides of sample boulders when compared to the bottom-sides of boulders among depth categories (p<0.0001).

**FIGURE 3.** Light readings and diversity index for tops and bottoms of boulders at each depth category.

The species accumulation curves showed that not only were treatments significantly different in terms of species density, but that there was also a significant increase in species richness from top-sides to bottom-sides of boulders. The mean and 95% confidence limits for each treatment do not overlap at any point (Figure 4).
Boulder community composition at the species level exhibited a clear ordination pattern, clustering by treatment with the additional effect of interaction between depth and treatment (Figure 5). This pattern was confirmed with a PERMANOVA, which showed a significant interaction effect of light exposure and depth on sample similarities (F= 2.7324, P<0.001). The SIMPER analysis revealed that the 3 most discriminating taxa in each depth*treatment combination accounted for 56.78%, 59.22%, and 61.41% of the dissimilarity at shallow, middle and deep depths respectively. Filamentous green algae was the primary contributor to differences in community composition across treatments for each depth category. Common taxonomic groups for each treatment*depth combination include: encrusting coralline algae, orange sponges and filamentous red algae on the bottom-sides of boulders, and Padina sp. on the top-sides of boulders.
FIGURE 5. Multidimensional scaling plot shows ordination, cluster by treatment with additional interaction effect of depth*treatment.

Light exposure was significantly lower on the east walls of both coves than the west walls (p<0.0001) (Figure 6). Conversely, the east walls of both coves supported more benthic species diversity than the West walls (p<0.0001).

FIGURE 6. Diversity index for each of the coves.

The polynomial contrast test showed that the values for % occurrence of algal growth were consistent with our a priori hypothesis that the most algal growth would occur on flipped boulders, then flipped excluded boulders, then flipped shaded boulders (P=.02) (Figure 7).
DISCUSSION

We surveyed boulders and cove walls with varying treatments to examine the influence of light, wave action and sedimentation on community composition. Our data show that the tops of boulders supported less diverse assemblages of algae, whereas the bottoms of boulders were dominated by a diverse assemblage of invertebrates. Species richness was almost twice as high on the undersides of boulders than the tops of boulders (Figure 4). Light levels were significantly different on the tops and bottoms of boulders at each depth category, which suggests that patchy communities compositions are a result of varying light exposure. The highest diversity index was found on the undersides of boulders at the 13-15m depth category, which was also the depth treatment category with the lowest light exposure. These observations indicate that light exposure and diversity (calculated using the Shannon-Weiner index equation) are inversely correlated.

While we noticed that algae cover on the tops of boulders became sparse with depth, the lack of statistical significance was likely due to the absence of samples representative of depths more than 15m. To further explore the relationship between community composition and light exposure on the tops of boulders, more surveys should be conducted at deeper depths. As different species of algae have different light requirements for recruitment and growth, algal composition will likely differ on boulders.
at varying depths (Pedersen and Snoeijs 2001). Additionally, each algae species has a minimum threshold for light exposure, and algal recruitment or growth will be limited at light levels lower than that threshold (Orfanidis 1992).

Clod cards showed no significant difference in relative wave action between depths, or between the tops and bottoms of boulders. While these results may have appeared erroneous if the study was in a more exposed location, our study site is protected from intense wave action by a north/south peninsula. Wave action at our site could only be generated by a strong storm in the north. Previous research conducted in the Mediterranean supported the notion that light has a greater impact on algal distribution than wave action (Fields and Hubach 2010).

To examine the potential effects of sedimentation on community structure, we conducted benthic surveys on opposite sides of two subtidal rocky coves. Surveys were conducted at identical depth on both sides of the canyon to control for possible effects of sedimentation. On canyons opening to the north, east-facing walls received more light throughout the day than west-facing walls because of the diel path of the sun. The dark (west-facing) wall had a highly diverse invertebrate assemblage as opposed to the lighted (east-facing) wall dominated by algae. As canyons around the point begin to open to the east, adjacent walls are exposed to similar light levels. Due to logistical constraints, we sampled only two coves which were almost identical in aspect. If more coves with varying aspects are sampled, we predict that the assemblages would become more similar as light becomes more uniform across both walls.

To assess if the algal dominance is due to competitive advantage gained by high light, we flipped boulders to expose invertebrate communities to high light. This allowed us to examine the response of invertebrate communities to the light levels typically found on boulder tops. After 10 days of exposure to high light levels, invertebrate communities were bleached and dying. Since pigments act to protect invertebrates from ultraviolet radiation (Karentz et al 1991), prolonged exposure to high light can destroyed pigment and kill sensitive organisms (Wilkinson & Vacelet 1979). In these instances, algae quickly colonized newly available space. In other cases, algae grew over existing invertebrate communities. Algal growth was highest on un-shaded boulders and lowest on shaded boulders. The algal growth on caged boulders was lower than on the un-shaded boulders, but higher than on the shaded boulders. Sarpa salpa, the only observed herbivorous fish at our study site, feeds primarily in Posidonia oceanica beds and rarely on algae growing on boulders (Havelange et al 2008). Therefore, we believe that the cages merely created a partial shade, which is supported by the intermediate algal growth under the cages.

These data support our prediction that light is the primary abiotic factor that allows algae to competitively exclude invertebrates on the topsides of rocks. Certain species of algae are able to take advantage of the high light exposure on the tops of boulders, and can thus dominate these areas. This phenomenon of high diversity in areas
with limited resources (i.e. light) has been observed in many marine and terrestrial systems. For instance, the desolate, resource-depleted interior of Australia has an immensely diverse assemblage of lizards (Pianka 1969). In this case, a lack of resources prevents any one species from dominating, which has resulted in niche partitioning and the subsequent development of specialized adaptations (Morton & James 1988).

At our study site, these microhabitats are directly adjacent to one another, separated only by the location of a single boulder or the angle of a cove wall that allows for differential light exposure. This variation in abiotic factors leads to spatial heterogeneity of metapopulations, which can support a greater diversity of fishes and other species (Eadie & Keast 1984). In this study, we showed how abiotic factors in an area can be used to make predictions about the structure and diversity of benthic communities.
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LITERATURE CITED


