Effects of reef physical structure on development of benthic reef community: a large-scale artificial reef experiment

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ABSTRACT: Much present knowledge about the role of physical factors in structuring reef communities is based on correlative data and small-scale experiments. The construction of a 9 ha artificial reef off southern California allowed a novel opportunity to experimentally examine at a realistic scale how the physical attributes of a reef (i.e. the amount, type, orientation, and physical location of hard substrate) are correlated with the colonization and subsequent development of sessile biota in a giant kelp *Macrocystis pyrifera* forest. The percent cover and slope of hard substrate were significantly related to the abundance and species richness of both understory algae and sessile invertebrates. The abundance and richness of colonizing algae were significantly related to location (i.e. proximity to the nearest natural reef), while that of sessile invertebrates was not. The type of hard substrate (quarry rock vs. concrete rubble) was unrelated to the abundance and diversity of either algae or invertebrates at any time during the 5 yr study. Physical attributes collectively explained between 16 and 40% of the variation in the abundance and diversity of the benthic community, depending on the taxon and time period examined. Variations explained by physical factors were greater in the first year during initial colonization than after 5 yr, when giant kelp was fully established. The construction of the artificial reef was akin to a large disturbance that created free space. Our findings suggest that physical attributes of reef structure may play a key role in structuring reef communities following a disturbance, but their importance diminishes over time as ecological interactions involving established reef organisms become increasingly important.

KEY WORDS: Artificial reef · Colonization · Competition · Disturbance · Dispersal · Kelp forest · Understory algae · Sessile invertebrates

INTRODUCTION

Shallow subtidal reefs provide critical habitat for a diverse array of marine plants and animals and support some of the most productive communities in the world (Mann 2000, Bertness et al. 2001). Physical characteristics are thought to play a major role in accounting for the high degree of spatial variation observed in the biological structure and dynamics of shallow reef communities (Dayton 1985, Sorokin 1993, Guidetti et al. 2004, Toohey & Kendrick 2008, Santos et al. 2010, Teixeira-Neves et al. 2015). For example, light, temperature, nutrients, and water motion typically co-vary with depth, and depth-related variation in species composition and abundance has long been known to be among the most consistent and conspicuous features of shallow reef communities worldwide (Kitching 1941, Goreau 1959, Schiel & Foster 1986).

Unlike calcium carbonate reefs formed in the tropics by hermatypic corals, reefs in temperate seas typically consist of non-living geomorphic materials that vary in composition. Different rock types have different material properties that affect their susceptibility

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to erosion, breakage, and penetration from boring organisms (Connell & Keough 1985). These properties, along with variation in the bottom coverage, topographic relief (including differences between the relative amounts of horizontal vs. vertical and upward- vs. downward-facing surfaces), and smaller-scale substrate rugosity can profoundly influence the abundance and species composition of reef-dwelling biota (Ebeling & Hixon 1991, Connell 2001, Guidetti et al. 2004, Miller & Etter 2008).

Reef communities may also differ in ways that are associated with their physical location. For example, differences in wave exposure have been implicated as a major source of variation in the structure and dynamics of a diverse array of shallow reef communities (Connell & Keough 1985, Witman 1987, 1992, Phillips et al. 1997, Wernberg & Connell 2008). Populations of reef-dwelling species depend greatly on surrounding waters and neighboring reefs for food and propagule subsidies (Bray 1981, Genin et al. 2002, Kritzer & Sale 2006). Variation in currents and proximity to adjacent reefs can alter the supply of these subsidies, and have a major influence on rates of recruitment and growth of reef organisms (Gaines & Roughgarden 1987, Cowen & Sponaugle 2009, Watson et al. 2010). Such effects may be most evident in passive suspension feeders that depend on water motion to deliver food (Eckman & Duggins 1991, Sebens et al. 2003, Arkema 2009) and in species with limited dispersal that depend on nearby populations as sources for recruitment (Gaines & Bertness 1992, Reed et al. 2000, Shanks et al. 2003).

Because it is difficult to manipulate many physical properties, our knowledge of how the physical attributes of a reef affect the biological structure of the community that it supports is based largely on comparative studies (e.g. Pequegnat 1964, Carr 1991, Patton et al. 1994, Santos et al. 2011) and small-scale manipulative experiments (e.g. Kennelly 1983, 1989, Connell & Jones 1991, Glasby 1999, Toohey 2007, Miller & Etter 2008). A major limitation of such comparative studies is that they are correlative and unable to isolate the effects of physical properties such as rock type, substrate coverage, or bottom topography from other confounding variables associated with location, depth, or historical effects. Artificial reefs have the potential to address this problem because they can be constructed in ways that allow the physical properties of a reef to be rigorously evaluated using a manipulative field experimental approach. Unfortunately, few artificial reefs have been designed as carefully controlled experiments (Bohnsack & Sutherland 1985). Those that

have, typically involved very small, easily manipulated reefs (e.g. Foster 1975a, Hixon & Brostoff 1985, Carr 1989, Hixon & Beets 1993), which may be a poor model for many processes that occur on larger natural reefs (Forrester et al. 2008).

We present results from a large-scale, replicated artificial reef experiment that investigated the effects of reef material type, bottom coverage, orientation, and proximity to a neighboring natural reef on the colonization and development of sessile invertebrate and understory algal assemblages inhabiting kelp forest communities off southern California. This study is unique in that it involves a manipulative field experiment conducted on a spatial scale (~9 ha) comparable to many natural reefs. We examined these effects during the initial colonization stage, when distance to the nearest propagule source is likely to be most important, and after a period of 5 yr, when established populations of sessile invertebrates and macroalgae are capable of serving as a local source of new recruits (Kritzer & Sale 2006). Because sessile invertebrates are considered to have a greater capacity for propagule dispersal than macroalgae (e.g. Reed et al. 2000, Kinlan et al. 2005, Shanks 2009), we predicted that their colonization would be less influenced by distance from a neighboring reef than understory algae, and that these differences for understory algae would diminish over time as local populations became established. Our ability to isolate the effects of purely structural attributes from proximity to propagule sources allowed us to experimentally test this prediction. Finally, contemporaneous studies on the artificial reef showed that the colonization and subsequent establishment of giant kelp *Macrocystis pyrifera*, the foundation species in this system, varied strongly with location and time (Reed et al. 2004, 2006a), which in turn influenced the benthic biota (Arkema et al. 2009). Results from these studies provided novel insight into how ecological interactions and physical attributes interact to shape the structure of subtidal reef communities through their influence on colonization and subsequent community development.

MATERIALS AND METHODS

Study area

Wheeler North Reef is part of a comprehensive mitigation project intended to compensate for the loss of giant kelp forest habitat caused by the operation of a coastal power plant in southern California (Reed et al.

2006a,b). The project consists of a 10 ha experimental phase (hereinafter referred to as the San Clemente Artificial Reef or SCAR) to test the efficacy of different reef designs in fulfilling the mitigation requirements, and a subsequent mitigation phase that used knowledge gained during the experimental phase to design and construct a 60+ ha artificial reef to compensate for the kelp forest habitat damaged by the operations of the power plant. The 5 yr experimental phase isolated various substrate and location effects in a stratified block design, thus providing a unique opportunity to experimentally examine the ecological consequences of a reef's physical attributes.

SCAR is located approximately 1 km offshore of the city of San Clemente, CA, USA (Fig. 1). It was constructed in the summer of 1999 and consists of 56 modules clustered at 7 locations (8 modules per location) spaced relatively evenly along 3.5 km of coastline and encompassing an area of approximately 144 ha. Each artificial reef module was roughly 40 × 40 m in size and all were constructed to form low-lying reefs (<1 m tall) that mimicked natural reefs in the region. Four of the 8 modules at each location were constructed from quarried granite boulders and 4 from recycled concrete rubble. These 2 types of materials were chosen because (1) they are the materials most preferred by the agency responsible for managing artificial reefs in California (Lewis & McKee 1989), (2) they are commonly used to construct artificial reefs worldwide (Mather 2006), and (3) little information exists on their relative effectiveness in supporting reef biota (Wilson et al. 1990). By design, the amount of quarry rock and concrete rubble used to build the modules was systematically varied to produce a wide range in the bottom coverage of hard substrate (~30–90%) on modules of the 2 reef types at each location (Reed et al. 2006a). The rock and concrete used to build the low-relief artificial reef had dimensions similar to the boulders that form the natural low-relief reefs nearby SCAR (Table 1; Reed et al. 2006a). Such low-relief reefs are common worldwide (e.g. Harman et al. 2003, Guidetti et al. 2004, Jordan et al. 2005).

Modules at each location were located at similar depths (13–16 m) along a relatively straight coastline. The most obvious difference among locations was their proximity to the nearest natural reef, San Mateo, located 0.5 km south of the southernmost location at SCAR (Fig. 1). Data collected on wave climate during studies to determine the placement of the artificial reef showed no significant differences in swell direction, swell period, or significant wave height among locations at San Mateo and SCAR (Dean et al. 1994). Thus, location effects attributed to distance from San Mateo were most likely not confounded by differences in wave climate. However, since distance from the natural reef was not replicated, it is possible that other factors related to distance may have been present but undetected in our design.
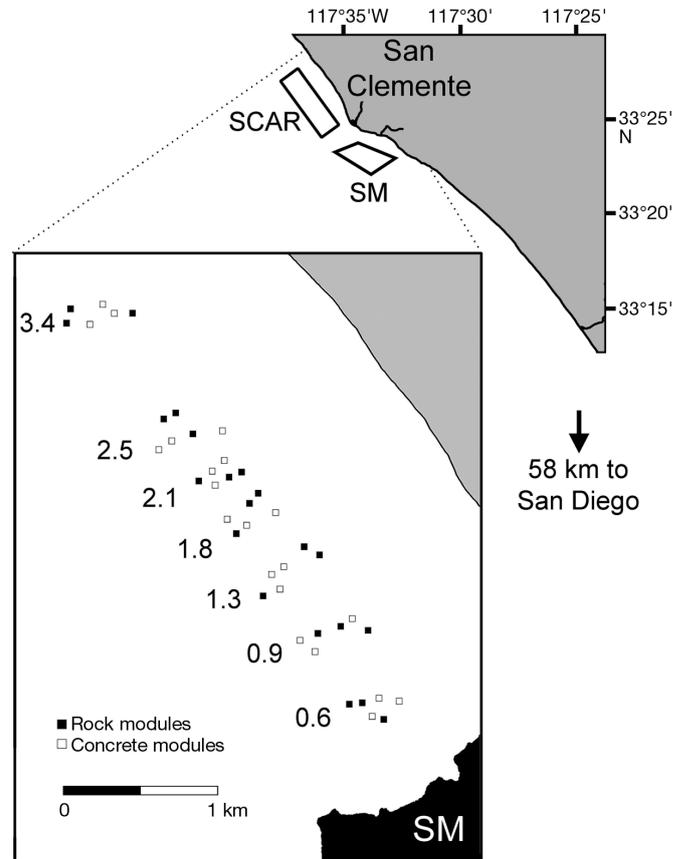

Fig. 1. San Clemente Artificial Reef (SCAR) and the natural reef at San Mateo (SM). Inset: locations of the 7 clusters of 6 modules, with the numbers representing the distance (km) between the northern edge of SM and the center of each cluster. The 42 modules are composed of either quarried granite boulders (rock) or concrete

Table 1. Average dimensions of hard substrate materials (concrete or rock) on the San Clemente Artificial Reef (SCAR) and 2 nearby natural reefs, the San Mateo kelp reef ~0.5 km to the south and the Barn kelp reef ~12.5 km to the south. Data are mean ± SD

Reef	Substrate type	Length (m)	Width (m)	Height (m)
SCAR	Concrete	0.84 ± 0.39	0.58 ± 0.27	0.33 ± 0.20
SCAR	Rock	0.62 ± 0.20	0.46 ± 0.15	0.36 ± 0.16
San Mateo	Rock	0.69 ± 0.29	0.56 ± 0.18	0.29 ± 0.13
Barn	Rock	1.11 ± 0.52	0.81 ± 0.38	0.28 ± 0.12

Sampling design

The benthic assemblages of algae and sessile invertebrates and physical characteristics of the reef substrate were sampled at 42 of the 56 artificial reef modules once per year in the summer in 3 fixed 1 × 1 m quadrats uniformly distributed on each of two 40 m transects, resulting in 6 quadrats sampled per module per year (see Fig. 1 for the location of the 42 modules included in this study). The reef characteristics considered were percent of bottom covered by hard substrate, type of hard substrate (i.e. rock vs. concrete), slope of hard substrate, and distance from the nearest natural reef. The first 3 characteristics influence reef biota via physical processes, while distance from the nearest natural reef can affect reef biota by both biological (e.g. due to proximity to propagule source) as well as physical (e.g. location effects) mechanisms. Abundances of sessile invertebrates, understory algae, and the percent cover of hard substrate were measured as percent cover of the bottom in each quadrat. Percent cover was estimated by noting the identity and vertical position along an imaginary line extending ~25 cm above the bottom of all organisms and the type of bottom substrate under 20 uniformly placed points within each quadrat, resulting in a grid with a 20 cm inter-point spacing. This method can produce estimates of the combined percent cover of all biota that exceed 100 %; however, the maximum percent cover possible for any single species cannot exceed 100 %. We tested the adequacy of this point density by comparing estimates of total average cover of the biota (understory algae and sessile invertebrates combined) from subsampled points ranging from 5 to 20 and found no significant differences in either the mean ($F_{3,164} < 0.0001$, p = 0.9999) or variance ($F_{3,164} = 0.99$, p = 0.97) in the percent cover of understory algae and sessile invertebrates as a function of point density.

Substrate slope was measured in 1 of 4 categories ranging from horizontal to vertical (0°–15°, 15°–45°, 45°–75°, and 75°–90°) at each of the 20 uniform points in each quadrat. The average of the midpoints of the categories of these measurements yielded a continuous index of the slope of the bottom substrate of each quadrat.

Statistical analyses

The effects of reef design and distance from the nearest natural reef on the benthic community of understory algae (i.e. those species growing beneath the floating canopy of the giant kelp *Macrocystis pyrifera*) and sessile invertebrates were examined 1 and 5 yr following the construction of SCAR. Data from the first year (2000) were used to characterize colonization; data from the fifth year (2004) represented the structure of a more developed community. Four response variables pertaining to the percent cover and species richness (measured as the number of species per 1 m^2 quadrat) of sessile invertebrates and understory algae were analyzed separately for each of the 2 time periods. Linear regression analysis was used to detect the presence of temporal trends in the mean value of each response variable as a function of distance from San Mateo, the natural reef closest to SCAR (n = 7 distances). Distances for each of the 7 sampling locations were calculated from the northern edge of San Mateo to the center of the sampling location. Preliminary analyses showed significant variation among modules over and above variation among quadrats. Therefore, module means were used as the unit of replication.

A mixed-model ANCOVA was used to examine the significance of independent variables in explaining variation in the response variables (n = 42 module means). For this analysis, the type of hard substrate was considered a categorical variable, and substrate slope, percent cover of hard substrate, and distance from the natural reef were used as covariates. In addition to determining the significance of each independent variable, sequential analyses were done to determine the percentage of the variation observed in each response variable explained by each independent variable. For each combination of response variable and year (2000 or 2004), we first ran a model that included interactions between the covariates and type of hard substrate (full model) to test the assumption of homogeneity of interactions and slopes.

Significance levels of all highest-order interactions were greater than 0.10; consequently, all interaction terms involving the covariates were dropped, resulting in a reduced model (see Quinn & Keough 2002). We also tested for and found no significant multi-collinearity using tolerance estimates and condition indices (Quinn & Keough 2002), simplifying estimates of the percentage of total variation contributed by each independent variable. Contributions of each independent variable to the total variability of a given dependent variable followed Quinn & Keough (2002) by first fitting the reduced model without interactions (1st stage model). The factor with the smallest *F*-value was dropped, the model run again (2nd stage model), and the coefficient of determina-

tion recorded. The difference between the 1st and 2nd stage models was the estimated contribution of the removed factor to the overall model fit. This procedure was repeated until contributions of all of the independent variables were complete.

To test the prediction that the effects of dispersal potential diminish over time, we examined temporal trends of spatial variation (i.e. variation among locations at different distances from the nearest natural reef) in the percent cover of algae and sessile invertebrates for all 5 yr of the experiment. These analyses required us to remove location-specific differences in percent cover not attributed to distance from the nearest source of propagules (i.e. the natural reef at San Mateo). This was done for each taxonomic group (understory algae or sessile invertebrate) using the method employed by Reed et al. (2000), which involved dividing the percent cover of each taxonomic group for a given year and location (i.e. distance from San Mateo) by its mean percent cover at that location calculated over all years of the 5 yr period. This procedure resulted in an annual standardized percent cover for each taxon by location combination that had an overall mean (averaged over the 5 yr, 2000–2004) equal to 1, and was independent of location-specific differences in absolute percent cover. We assessed whether this procedure controlled for spatial autocorrelation by calculating Moran's I on the transformed data (Moran 1950). This index ranges from −1 to +1 (strong negative and positive spatial autocorrelation, respectively). Because Moran's I was very slightly negative (∼−0.02) in all cases, we concluded that spatial autocorrelation did not bias our results. Differences in temporal trends in the mean and spatial variation in the standardized coverages of algae and sessile invertebrates were compared using ANCOVA. As in Reed et al. (2000), spatial variation was measured as the coefficient of variation in standardized percent cover calculated among locations (i.e. the 7 groups of modules located at different distances from San Mateo). We also conducted ANCOVAs with frond density of giant kelp as a covariate and taxon (understory algae or sessile invertebrates) as a categorical factor to examine the extent to which the adjusted mean and spatial variability of the percent cover of understory algae and sessile invertebrates varied as a function of giant kelp abundance.

In addition to these univariate analyses, several multivariate analyses were done using the software packages PRIMER-E (Clarke & Gorley 2006) and PERMANOVA+ for PRIMER (Anderson et al. 2008) to more closely examine the roles played by individual species. These included multidimensional scaling

(MDS), a permutation-based analysis of variance (PERMANOVA+) to test for differences in the multivariate clusters of understory algae and sessile invertebrates between 2000 and 2004, and an analysis (SIMPER) that decomposed the contributions of individual species leading to dissimilarities (Bray-Curtis) between years.

RESULTS

Decomposing the effects of reef structure

The type of hard substrate (quarried granite boulders vs. concrete rubble) explained little of the observed variation in the percent cover and species richness of understory algae or sessile invertebrates at any time during the study (Fig. 2). In the case of understory algae, the percent cover of hard substrate explained significant amounts of variation in percent cover and richness in 2000 (39 and 19%, respectively), but not in 2004 (0 and 0.3%, respectively). Substrate slope explained less variation in algal per-
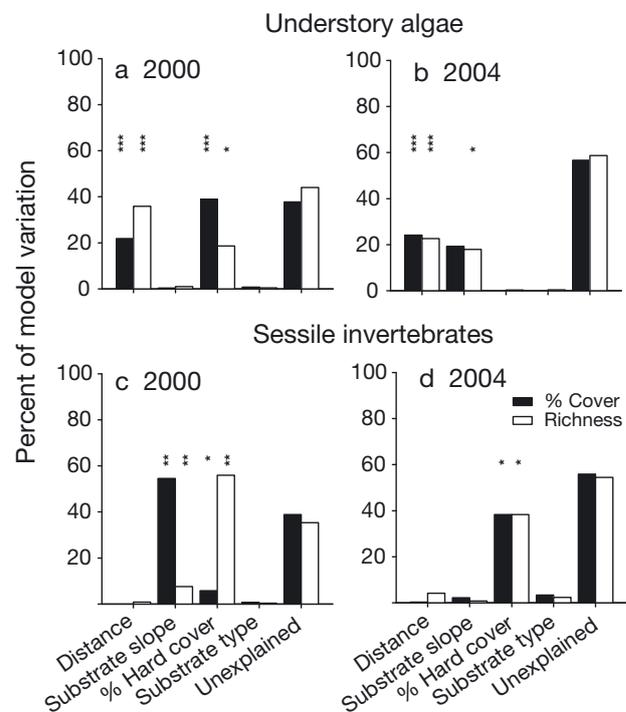

Fig. 2. Percent of variation explained by type of hard substrate (i.e. quarry rock or rubble concrete), percent cover of hard substrate, slope of the substrate, distance from the nearest natural reef, and unexplained error for the percent cover and species richness of: understory algae in (a) 2000 and (b) 2004; and sessile invertebrates in (c) 2000 and (d) 2004. *p < 0.05, **p < 0.01, ***p < 0.001

cent cover in 2000 than in 2004 (0.3 vs. 19%), and less variation in species richness in 2000 than in 2004 (1 vs. 18%; Fig. 2a,b). The relationship between distance from San Mateo and the percent cover and species richness of understory algae differed between 2000 and 2004 (Fig. 3). During the initial colonization of SCAR (i.e. 2000), the percent cover and species richness of understory algae were negatively correlated with distance (Fig. 3a,c), but uncorrelated with distance in 2004 (Fig. 3b,d).

The percent cover and species richness of sessile invertebrates were positively correlated with substrate slope, which explained more variation in 2000 than in 2004 for both percent cover (54 vs. 2%) and species richness (8 vs. 0.2%; Fig. 2c,d). The percent cover and species richness of sessile invertebrates were positively correlated with the percent cover of hard substrate. The percent cover of hard substrate explained less variability in invertebrate percent cover in 2000 than in 2004 (6 vs. 38%), but more of the variability in invertebrate richness in 2000 than in 2004 (56 vs. 38%). Unlike the understory algae, distance from San Mateo explained little of the variation

in the percent cover and species richness of sessile invertebrates in 2000 (0.1 and 0.8%, respectively) or 2004 (0.3 and 4.2%, respectively), suggesting that the colonization and subsequent development of sessile invertebrates on the artificial reef was less dependent on a nearby source of propagules than that of understory algae.

A combination of physical characteristics and the distance from the nearest natural reef explained more variation in both the percent cover and species richness of understory algae and sessile invertebrates in 2000 at the beginning of the study (56–65%) than in 2004 at the end of the study (41–46%).

Temporal changes in abundance and spatial variability

There were complementary changes in the percent cover and species richness of algae and sessile invertebrates between 2000 and 2004. The percent cover and species richness of understory algae decreased by 85 and 75%, respectively from 2000 to 2004 (Fig. 4a; cover: $t_{82} = -8.89$, p < 0.0001; richness: $t_{82} = -9.73$, p < 0.0001). By contrast, the percent cover and species richness of sessile invertebrates increased by 49 and 86%, respectively (Fig. 4b; cover: $t_{82} = 5.75$, p < 0.0001; richness: $t_{82} = 10.11$, p < 0.0001).

Results of MDS were consistent with results of the univariate analyses. Both the understory algal and sessile invertebrate assemblages showed distinct and statistically significant differences between 2000 and 2004 (Fig. 5a,b, Table 2). SIMPER analyses revealed that changes in the algal assemblage between 2000 and 2004 were due primarily to decreases in the most abundant species of red algae and in filamentous brown algae (Table 3). Changes in sessile inverte-
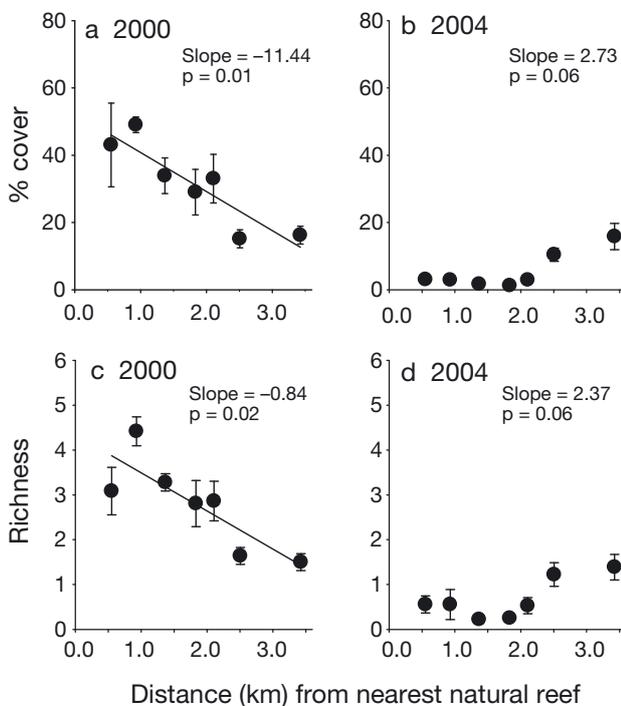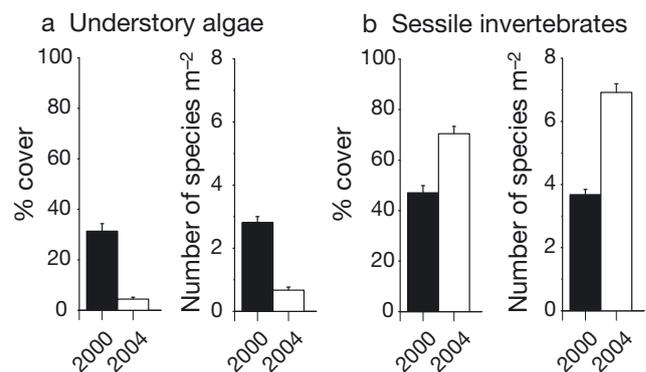

Fig. 3. Relationship between distance from San Mateo and percent cover in (a) 2000 and (b) 2004 and species richness in (c) 2000 and (d) 2004 for understory algae. Data are means (±1 SE, n = 6) for each combination of distance, dependent variable, and year. For sessile invertebrates, neither percent cover nor species richness were significantly related to distance from San Mateo in 2000 and 2004

Fig. 4. Mean (±1 SE) of percent cover and species richness in 2000 and 2004 for (a) understory algae and (b) sessile invertebrates

Table 2. PERMANOVAs comparing understory algal and sessile invertebrate assemblages between 2000 and 2004

Source	df	MS	Pseudo-F	p(perm)
Understory algae				
Year	1	45568	39.9	0.001
Residual	82	1141.8		
Total	83			
Sessile invertebrates				
Year	1	58422	66.4	0.001
Residual	83	880		
Total	84			

brates between 2000 and 2004 were driven by declines in an early colonizing solitary ascidian, *Chelyosoma productum*, and fine filamentous hydroids and increases in the cover of encrusting sponges, colonial ascidians, and the solitary tube-building polychaete, *Diopatra ornata* (Table 4).

The mean standardized percent cover of understory algae averaged over all locations declined dramatically over time, while that of sessile invertebrates increased slightly (Fig. 6a; $F_{1,6}$ =15.6, p = 0.008 for taxon × year interaction). Patterns of variation in the standardized percent cover of understory algae and sessile invertebrates observed over time were remarkably similar to those observed in relation to the density of giant kelp fronds (Fig. 6b; $F_{1,6}$ = 42.6, p < 0.001 for taxon × kelp interaction). Spatial variability among locations in percent cover showed the opposite pattern, increasing substantially over time for understory algae and decreasing for sessile invertebrates, but not significantly so (Fig. 6c; $F_{1,6}$ = 2.83, p = 0.14 for taxon × year interaction). As was the case for the standardized percent cover, a similar pattern
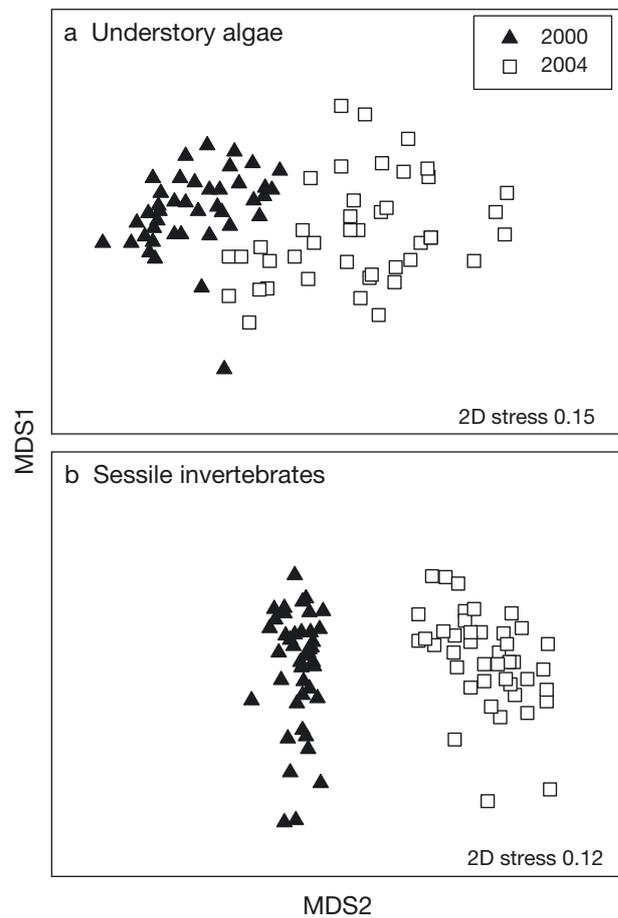

Fig. 5. Multidimensional scaling (MDS) plots comparing benthic assemblages between 2000 and 2004 for (a) understory algae and (b) sessile invertebrates

was observed when frond density was used as a covariate (Fig. 6d; $F_{1,6}$ = 12.3, p < 0.013 for taxon × kelp interaction).

Table 3. Differences in total abundance (% cover), and individual and cumulative Bray-Curtis dissimilarity in understory algal assemblages between 2000 and 2004. Average Bray-Curtis dissimilarity between years was 74.68%. Total richness was 31 in 2000 and 22 in 2004

Taxon	Major group	Avg. % cover		—— Bray-Curtis dissimilarity ——	
		2000	2004	% Contribution	Cumulative %
Polysiphonia sp.	Filamentous red	3.23	0.75	24.15	24.15
Filamentous brown	Filamentous brown	1.50	0.05	14.44	38.59
Sarcodiotheca furcata	Fleshy red	1.36	0.10	10.55	49.14
Unknown fleshy red	Fleshy red	1.68	0.95	9.98	59.12
Polyneura latissima	Bladed red	1.23	0.06	9.57	68.70
Rhodymenia sp.	Bladed red	0.83	0.37	6.63	75.33
Callophyllis flabulata	Bladed red	0.67	0.06	5.04	80.37
Ovate fleshy red	Fleshy red	0.25	0.34	3.90	84.27
Filamentous red	Filamentous red	0.18	0.22	2.86	87.13
Rhodoptilum plumosum	Bladed red	0.32	0.02	2.52	89.65
Sarcodiotheca gaudichaudii	Fleshy red	0.17	0.20	2.51	92.17

Table 4. Differences in total abundance (% cover), and individual and cumulative Bray-Curtis dissimilarity in sessile inverte-brate assemblages between 2000 and 2004. Average Bray-Curtis dissimilarity between years was 88.45%. Total richness was 32 in 2000 and 76 in 2004

Taxon	Major group	Avg. % cover		—— Bray-Curtis dissimilarity ——	
		2000	2004	% Contribution	Cumulative %
Chelyosoma productum	Solitary ascidian	23.25	14.06	16.54	16.54
Diopatra ornata	Polychaete	0.15	8.25	11.33	27.86
Encrusting sponge A	Sponge	0.56	6.24	7.69	35.56
Plumularia sp.	Hydroid	0.00	5.03	6.69	42.24
Filicrisia sp.	Bryozoan	0.00	4.38	6.06	48.30
Bugula californica	Bryozoan	3.69	4.16	4.80	53.11
Unknown fine hydroid A	Hydroid	3.49	0.00	4.56	57.66
Cellaria sp.	Encrusting bryozoan	0.07	3.33	4.45	62.11
Unknown encrusting sponge B	Sponge	0.00	2.60	3.62	65.73
Thalamoporella californica	Bryozoan	0.22	2.30	2.92	68.64
Crisia sp.	Bryozoan	0.00	2.12	2.80	71.44
Encrusting bryozoan A	Bryozoan	1.54	2.62	2.65	74.09
Cryptoarachnidium sp.	Encrusting bryozoan	0.00	1.82	2.31	76.40
Didemnum sp.	Colonial ascidian	0.06	1.65	2.09	78.49
Bugula neritina	Bryozoan	1.58	0.43	1.95	80.44
Pholad clam	Bivalve	1.37	0.00	1.84	82.28
Diaperoecia californica	Encrusting bryozoan	0.18	1.38	1.73	84.01
Leucilla nuttingi	Sponge	1.44	0.58	1.73	85.74
Aglaophenia struthionides	Hydroid	0.41	0.82	1.51	87.25
Barentsia sp.	Entoproct	0.00	1.06	1.40	88.65
Pycnoclavella stanleyi	Solitary ascidian	0.38	1.13	1.36	90.02

DISCUSSION

The primary aim of this study was to assess the degree to which the physical structure of rocky reefs affects assemblages of reef-associated algae and sessile invertebrates. A number of experimental and observational studies have demonstrated the direct and indirect effects of physical characteristics of rocky reefs on benthic community structure (e.g. Hutchings et al. 1992, Anderson & Underwood 1994, Svane & Peterson 2001, Chapman & Bulleri 2003, Toohey 2007, Miller & Etter 2008). The present study adds to this work by experimentally testing the relative magnitude of the correlations with different physical attributes of reef structure at a realistic reef scale and determining the degree to which these effects are likely to change over the course of succession. We found that the variability explained by the physical features of the reef (i.e. percent cover and slope of hard substrate) declined over time, suggesting that reef physical structure is most important during early stages of succession. This result is consistent with Foster's (1975b) finding that small-scale (i.e. cm) physical characteristics (i.e. the presence of sharp edges on experimental concrete blocks) affected patterns of initial colonization that were subsequently altered by biological interactions as time pro-

gressed. Our study adds further insight into how such colonization might vary with distance from a propagule source, which Foster (1975b) was unable to assess because his experimental units were embedded within a mature kelp forest.

Our finding of a positive relationship between substrate slope and percent coverage of understory algae differs from findings of other studies that found greater abundance of algae on horizontal versus vertical surfaces (e.g. Baynes 1999, Murdock & Dodds 2007, Toohey 2007, Miller & Etter 2008). One possible source of this difference is that the reef in our study was low relief, with differences in average slope among modules that were not as extreme (mean: 26°, range: 15°–38°) as in the aforementioned studies that compared communities on horizontal versus vertical surfaces. The lower average slope in our study likely had less of an effect on shading than the steep vertical slopes studied by others.

Although statistically significant, the amount of variability in the abundance and diversity of understory algae explained by purely physical reef characteristics (substrate type, slope, and percent cover) was relatively small (i.e. 10–28%). It is worth noting that not all physical attributes known to influence reef biota were evaluated in this study. For example, the vertical relief and depth of a reef can have pro-
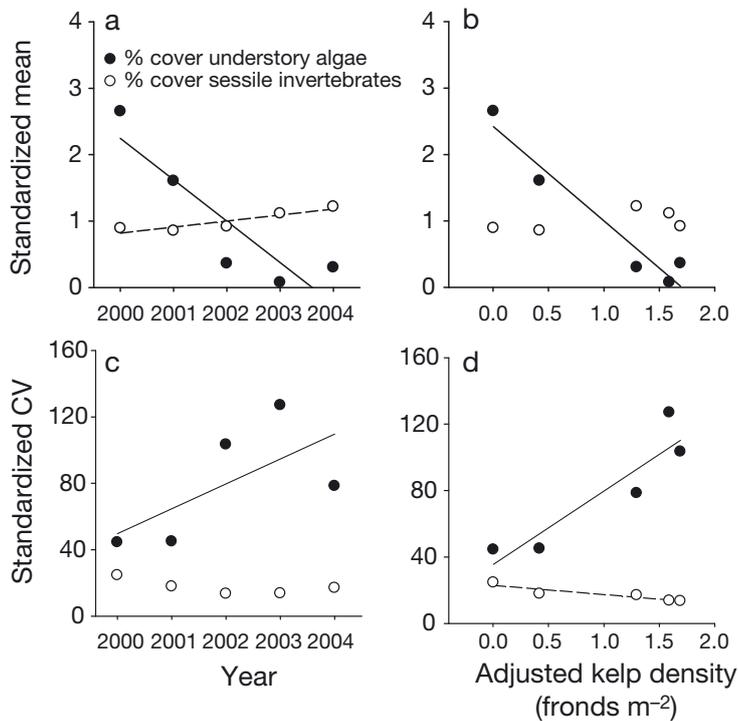
Fig. 6. Standardized mean % cover of understory algae and sessile invertebrates as a function of (a) time and (b) giant kelp *Macrocystis pyrifera* frond density; and spatial variability (coefficient of variation [CV]) of standardized mean percent cover as a function of (c) time and (d) giant kelp frond density. Data were standardized to the mean percent cover averaged over the 5 yr study period (see 'Materials and methods'). Means in (a,b) represent values of standardized percent cover averaged over all locations, which varied in their distance from the nearest natural reef. CVs in (c,d) represent spatial variation in standardized percent cover calculated among locations
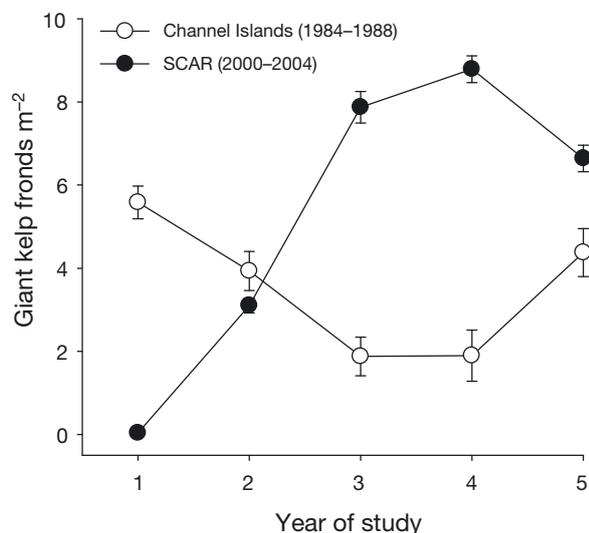

Fig. 7. Temporal trends in density of giant kelp *Macrocystis pyrifera* fronds (±1 SE) at the Channel Islands of California for 1984–1988 (Kushner et al. 2013) and San Clemente Artificial Reef (SCAR) for 2000–2004

found effects on community structure and dynamics (Sebens 1985, Dayton et al. 1992, Leichter & Witman 1997, Wernberg et al. 2003, Connell & Irving 2008). These characteristics, however, were intentionally held constant in the design of SCAR in order to mimic natural low-relief reefs in the region. Consequently, it was not possible to isolate the effects of these factors on the abundance and diversity of sessile reef organisms in this study.

Another possibility for the relatively small explanatory power of the physical characteristics of SCAR, particularly after 5 yr of reef community development, is that ecological interactions not targeted in our experimental design played a significant role in determining the composition and abundance of the sessile reef biota. One such mechanism involves the direct and indirect effects of the giant kelp *Macrocystis pyrifera* on understory algae and sessile invertebrates. Macroalgae and sessile invertebrates compete for space on the reef. Shading by the surface canopy of giant kelp has a direct negative effect on understory algae beneath it and an indirect positive effect on sessile reef invertebrates due to reduced competition with understory algae (Arkema et al. 2009). The spatial and temporal patterns of abundance of understory algae and sessile invertebrates that we observed at SCAR can be explained in part by the presence of giant kelp. Much like understory algae, the initial colonization of giant kelp at SCAR declined with distance from the nearest kelp bed, which produced a south-to-north gradient in kelp density (Reed et al. 2004, 2006a); however, because most of the giant kelp observed in 2000 were small newly recruited individuals, the overall density of kelp fronds was low (Fig. 7) and had little effect on shading the understory. By 2004, these recruits had become adults and kelp frond density increased by over 2 orders of magnitude, producing a dense and relatively uniform surface canopy that shaded the understory throughout SCAR (Reed et al. 2006a). During this time, the percent cover of understory algae became uniformly low across the reef, while that of sessile invertebrates became uniformly high (Reed et al. 2006a)

The indirect facilitation of sessile invertebrates via shading of macroalgae that we observed in this study appears to be a common phenomenon in marine systems. Examples from marine fouling communities include Glasby (1999), who found that shading on pier pilings reduced the abundance of algae and led

to an increase in the abundance of sessile invertebrates, while Baynes (1999) and Miller & Etter (2008) found that shading on vertical surfaces led to higher abundances of sessile invertebrates and lower abundances of macroalgae compared to horizontal surfaces where light levels were high. Indirect facilitation via shading need not only be between algae and sessile invertebrates. Kastendiek (1982) provides an interesting example of indirect facilitation among algal species. He found that shading by one brown alga, *Eisenia arborea*, reduced the abundance of *Halidrys dioica*, another brown alga, which permitted the red alga, *Pterocladia capillacea*, to persist. In the absence of *Eisenia*, *Halidrys* became abundant and competitively eliminated *Pterocladia*.

Fish predation also has been shown to influence the structure of benthic reef communities in other temperate reef systems (Russ 1980, Ojeda & Dearborn 1991, Hixon & Brostoff 1996, Guidetti 2006, Clemente et al. 2009, Santos et al. 2010). Although this factor was not explicitly addressed in our study design, it could have accounted for some of the unexplained variability that we observed. We previously reported that reef fish rapidly colonized SCAR, and their abundance tended to be positively related to the cover of reef substrate, particularly during the initial stages of colonization (Reed et al. 2006b).

The provision of free space created by the construction of a large artificial reef such as SCAR is in many ways similar to that resulting from a severe disturbance on natural reefs (Bartone 2006); in both cases, large amounts of free space are created in areas removed from local source populations. Thus, it is not surprising that the patterns of colonization that we observed on SCAR resembled those documented for nearby natural reefs in the Channel Islands of California National Park following large disturbances associated with the 1982−83 El Ninõ (Reed et al. 2000). Like the initial colonization of SCAR, recovery of reefs at the Channel Islands following the El Niño was related to dispersal potential, as spatial variation in the colonization of short-range dispersers (mainly algae) was higher than that of long-range dispersers (mainly invertebrates). However, the progression of community development at SCAR differed from the patterns of post-disturbance succession observed at the Channel Islands. Although the abundances of short- and long-range dispersers (i.e. algae and sessile invertebrates) were inversely related through time, they showed a pattern opposite to that seen at the Channel Islands, with the abundance of algae decreasing and that of sessile invertebrates increasing. Patterns of spatial variability also differed

between SCAR and the Channel Islands. Variability of understory algae increased whereas that of sessile invertebrates decreased during the 5 yr post colonization. We attribute this difference to the much higher densities of giant kelp at SCAR compared to the Channel Islands following the 1983 El Niño disturbances, particularly during years 3 and 4 of both studies, when densities of giant kelp fronds at SCAR were more than 4 times greater than those at the Channel Islands (Fig. 7). Experiments involving the removal of giant kelp at SCAR showed that shading by dense giant kelp led to direct suppression of understory algae, which resulted in indirect positive effects (i.e. facilitation) on the longer-dispersing sessile invertebrates (Arkema et al. 2009). We speculate that the lower density of giant kelp at the Channel Islands following the 1983 El Ninõ was not sufficient to alter the dynamics between algae and sessile invertebrates in a manner similar to that observed at SCAR.

In conclusion, our predictions concerning dispersal potential and patterns of spatial heterogeneity following disturbance were borne out by our observations of colonization and community development at SCAR. Patterns of colonization by macroalgae were potentially influenced by proximity to source populations, while those of sessile invertebrates were not. It is interesting that our findings for invertebrate colonization are in accord with the earlier studies of Osman & Dean (1987), whose findings suggest that invertebrate colonization was not influenced by source populations in the San Mateo kelp forest at distances greater than about 500 m (SCAR lies beyond this distance). Collectively, our findings suggest that physical attributes of reef structure may play a significant part in the establishment of subtidal reef communities following large disturbances, but that their role diminishes with time as ecological interactions involving established reef organisms become increasingly important, a finding that accords with several past small-scale manipulative experiments. In the case of our study, shading by very high densities of giant kelp strongly affected the abundance and spatial variability of both taxonomic groups over time and produced a pattern very different from those seen following large natural disturbances. Such insight into the role of distant source populations to colonization and subsequent development of reef communities post disturbance is not easily obtained from small-scale experiments embedded within natural reefs or with small artificial structures placed away from natural reefs that are unable to develop communities of sufficient size to constitute local source populations.

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