Exercícios 03

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Dados para o exercício

Neste exercício, usaremos dados publicados sobre efeitos de kelp gigante na estrutura de comunidades bentônicas. O artigo está no final dos exercícios. Replicaremos as análises da figura 5. Os dados estão no pacote `semeco`:

```
library(semeco)
data(arkema)
arkema <- arkema[, -c(1:3)]
```

1. Qual o número máximo de parâmetros que poderiam ser estimados com os dados disponibilizados?
2. Os dados não seguem uma distribuição normal multivariada, como os próprios autores disseram em um dos materiais suplementares do artigo. Utilize a função `mardiaTest` do pacote `MVN` para confirmar que os dados realmente não seguem uma distribuição normal multivariada.
3. Há possíveis outliers nos dados? Para fazer isso, padronize os dados e veja se todos os valores das variáveis estão dentro do esperado (Z >= 3 e Z <= -3). A função que padroniza os dados é a `scale`.
4. Há indicação de multicolinearidade? Utilize a matriz de correlação e, se preciso, a função `vif` do pacote `car`.
5. Todas as covariâncias estão dentro do esperado?

```
sds <- sqrt(diag(cov(arkema)))
max.cov <- outer(sds, sds)
max.cov < cov(arkema)
```

```
##                          giant.kelp.frond.density giant.kelp.percent.cover
## giant.kelp.frond.density                     TRUE                    FALSE
## giant.kelp.percent.cover                    FALSE                    FALSE
## midcanopy.kelps                             FALSE                    FALSE
## understory.algae                            FALSE                    FALSE
## sessile.invertebrates                       FALSE                    FALSE
##                          midcanopy.kelps understory.algae
## giant.kelp.frond.density           FALSE            FALSE
## giant.kelp.percent.cover           FALSE            FALSE
## midcanopy.kelps                    FALSE            FALSE
## understory.algae                   FALSE            FALSE
## sessile.invertebrates              FALSE            FALSE
##                          sessile.invertebrates
## giant.kelp.frond.density                 FALSE
```

```
## giant.kelp.percent.cover                FALSE
## midcanopy.kelps                          FALSE
## understory.algae                         FALSE
## sessile.invertebrates                     TRUE
```

6. Construa o modelo usando a sintaxe do lavaan. Caso tenha dificuldade, veja o modelo construído com o comando:

```
cat(arkema.model)
```

7. Encontre os parâmetros e determine o ajuste do modelo com a função `sem` do pacote `lavaan`. Utilize o argumento `estimator = "MLM"` para usar um estimador robusto e levar em consideração que os dados não seguem uma normal multivariada.
8. O modelo foi capaz de explicar os dados? Por quê?
9. Os coeficientes padronizados e não padronizados são iguais aos publicados?
10. Utilize a função `inspect` para determinar os R^2 das variáveis endógenas.

Direct and indirect effects of giant kelp determine benthic community structure and dynamics

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Abstract. Indirect facilitation can occur when a species positively affects another via the suppression of a shared competitor. In giant kelp forests, shade from the canopy of the giant kelp, *Macrocystis pyrifera,* negatively affects understory algae, which compete with sessile invertebrates for space. This raises the possibility that giant kelp indirectly facilitates sessile invertebrates, via suppression of understory algae. We evaluated the effect of giant kelp on the relative abundance of algae and invertebrates by experimentally manipulating kelp abundance on large artificial reefs located off San Clemente, California, USA. The experiments revealed a negative effect of giant kelp on both light availability and understory algal abundance and a positive effect on the abundance of sessile invertebrates, which was consistent with an indirect effect mediated by shade from the kelp canopy. The importance of these processes to temporal variability in benthic community structure was evaluated at 16 locations on natural reefs off Santa Barbara, California, over an eight-year period. Interannual variability in the abundance of understory algae and in the abundance of sessile invertebrates was significantly and positively related to interannual variability in the abundance of giant kelp. Analysis of these observational data using Structural Equation Modeling (SEM) indicated that the magnitude of the indirect effect of giant kelp on invertebrates was six times larger than the direct effect on invertebrates. Results suggest that the dynamics of this system are driven by variability in the abundance of a single structure-forming species that has indirect positive, as well as direct negative, effects on associated species.

Key words: benthic community structure; giant kelp; indirect facilitation; interannual variability; macroalgae; Macrocystis pyrifera; *sea urchin; sessile invertebrate; temporal variability.*

Introduction

Numerous studies have shown that both facilitation and competition play important roles in structuring ecological communities (Bertness and Callaway 1994, Bruno et al. 2003). A common facilitative interaction occurs indirectly when a third species reduces the abundance or competitive effect of one of two competitors, thereby leading to an increase in the abundance of the other competitor (Wootton 1994, Hay et al. 2004). Some of the earliest experimental evidence for this type of interaction has shown that a mobile consumer can have a positive, indirect effect on a sessile species by consuming the species that competes for space (Paine 1966, Foster 1975, Lubchenco and Menge 1978). More recent experiments involving terrestrial plants have explored how positive, indirect interactions operate in communities consisting of only sessile organisms. In these studies, the indirect positive effect of one species on another, via suppression of a common competitor

(termed indirect facilitation), was often stronger than the direct effects of competition (Miller 1994, Levine 1999, Callaway and Pennings 2000, Pages et al. 2003). Not surprisingly, spatial variation in the abundance of species that are indirect facilitators can influence the distribution and abundance of associated species engaged in competition (Miller 1994, Levine 1999, Callaway and Pennings 2000). Dynamical consequences of fluctuations in the abundance of an indirect facilitator have been explored less well.

Interactions involving indirect facilitation are thought to be most widespread in assemblages where pairs of competing species have few resources in common (Levine 1999). Such is the case for shallow hard-bottom marine communities where the primary space holders (i.e., macroalgae and sessile suspension-feeding invertebrates) occupy different trophic levels. Macroalgae are primary producers that derive their nutrition from sunlight and dissolved nutrients, whereas sessile invertebrates are consumers that are nourished by filtering plankton and other organic matter from the water column. Variation in unshared resources such as light or plankton may determine the outcome of space competition between macroalgae and sessile invertebrates. Evidence for this comes from studies that have experimentally showed that light affects the relative

abundance of macroalgae and sessile invertebrates, and that a variety of abiotic and biotic factors may influence light availability (Kennelly 1989, Glasby 1999, Irving and Connell 2002, Miller and Etter 2008). Whereas many abiotic factors that affect light remain constant over time (e.g., depth and substrate orientation), biotic factors such as canopy-forming vegetation tend to vary in time as well as in space (Dayton et al. 1992, Graham et al. 1997, Wernberg and Goldberg 2008). Such temporal variation could have important consequences for the dynamics of underlying algae and invertebrates, mirroring results from terrestrial systems that show that spatial patterns can arise from variation in the distribution and abundance of plants that act as indirect facilitators (Miller 1994, Levine 1999, Callaway and Pennings 2000).

Giant kelp forests are an ideal system for exploring how the population dynamics of a foundation species (sensu, Dayton 1975) and/or ecosystem engineer (sensu, Jones et al. 1994) affect temporal variation in the abundance and species composition of the associated community. The giant kelp, *Macrocystis pyrifera*, is a canopy-forming brown alga that occurs in dense stands (commonly referred to as kelp forests) on shallow temperate reefs worldwide (Graham et al. 2007). Surface canopies of giant kelp off the California coast can reduce the amount of light reaching the bottom by more than 95% (Pearse and Hines 1979, Reed and Foster 1984). Shading by giant kelp, however, is not constant, as the local density and biomass of *M. pyrifera* can vary dramatically over time in response to intra- and interannual disturbance and the potential for rapid recolonization (Dayton et al. 1999, Edwards and Estes 2006, Reed et al. 2008). The negative effects of giant kelp on bottom light and the abundance of understory macroalgae have been well-documented via field experiments and correlative studies (reviewed in Dayton 1985, Foster and Schiel 1985). Much less is known about the direct effects of giant kelp on assemblages of sessile invertebrates or about the extent to which *M. pyrifera* may indirectly facilitate invertebrates by shading out their major space competitor, understory algae.

We examined the direct and indirect effects of giant kelp on understory algae and sessile invertebrates using both experimental and observational approaches. Specifically, we conducted a field experiment on a large-scale artificial reef complex to test the effect of *M. pyrifera* on the abundance of understory algae, sessile invertebrates, and light. We expected that kelp would negatively affect understory algae, positively affect sessile invertebrates, and decrease light availability, findings that would be consistent with the hypothesis that kelp indirectly facilitates sessile invertebrates. Observational data collected at natural reefs over an eight-year period were analyzed using Structural Equation Modeling (SEM; Grace 2006) to estimate and compare the strength of the direct vs. indirect effect of giant kelp on sessile invertebrates. We also investigated

whether interannual variability in the abundances of understory algae and sessile invertebrates was related to interannual variability in the abundance of giant kelp. Our combined approach allowed us to determine whether the interactions among kelp, understory algae, and sessile invertebrates observed experimentally in space led to predictable patterns over time on natural reefs.

METHODS

Experiment to test the effect of giant kelp on the benthic community

We tested the effects of *M. pyrifera* on the abundances of understory algae and sessile invertebrates using a field experiment in which we removed the giant kelp canopy and manipulated the amount of unoccupied space on the bottom. The experiment was conducted on a large artificial reef complex located 13–16 m deep off the coast of San Clemente, California, USA (117°37′ N, 33°25′ W; see Reed et al. [2006] for a detailed description of the reef). Established in late 1999, the reef complex comprises seven sets (hereafter "blocks") of eight reef modules spread relatively evenly along 3.5 km of coastline. Each module consists of quarried boulders distributed uniformly in a single layer across a 40 m × 40 m area of sand bottom. The present study involved 12 modules, two modules from each of six blocks, which were first colonized by kelp in 2001. The use of appropriately large and similarly constructed reef modules replicated across a relatively uniform area of coast allowed for a test of the effects of *M. pyrifera* and unoccupied space on the benthic community without potential confounding effects caused by differences in reef topography and structural complexity.

As the density of the surface canopy of giant kelp matured during the early development of the artificial reef community, the percent cover of understory algae dramatically decreased, and the percent cover of sessile invertebrates increased (Reed et al. 2006). These findings were consistent with the hypothesis that giant kelp facilitates sessile invertebrates by inhibiting understory algae, their primary competitor for space. We set up an experiment aimed at determining whether the removal of giant kelp caused the benthic community to revert back to a prevalence of understory algae. In March 2004 *M. pyrifera* canopy was removed from one of the two focal modules in each of the six blocks ($N = 6$ *M. pyrifera* removal modules) by trimming all giant kelp to within 1 m of the bottom. *M. pyrifera* was left intact on the other six modules used in the study ($N = 6$ *M. pyrifera* control modules). The amount of unoccupied space available to algae and invertebrates was manipulated by removing all benthic organisms in six 1-m^2 quadrats arranged uniformly in each of the kelp removal and control modules. The benthos in six additional 1-m^2 quadrats on each module was left undisturbed and served as a control for the benthos removed treatment. These manipulations were designed to represent a range of

disturbance levels common on natural reefs (e.g., small waves that might remove the surface canopy of giant kelp, but leave the bottom communities intact vs. large waves that can remove entire plants of giant kelp and scour the bottom, thereby removing understory algae and sessile invertebrates). The undisturbed quadrats in the *M. pyrifera* control modules can be thought of as sites and/or years with little disturbance (natural disturbance was low during the experiment). The undisturbed quadrats in *M. pyrifera* removal modules and the scraped quadrats in *M. pyrifera* control modules simulated intermediate levels of disturbance, while the scraped quadrats in *M. pyrifera* removal modules represented high levels of disturbance.

In November 2004 we assessed the effect of the experimental manipulations on the percent cover of understory algae, sessile invertebrates, and unoccupied hard substrate within each of the benthos removal and benthos control quadrats. We identified the primary space holder (to species, where possible) at 20 points arranged in a uniform grid overlying each quadrat, categorized each space holder as an understory alga, sessile invertebrate, or giant kelp holdfast, and recorded the substrate type of each point as either hard (e.g., bedrock, boulder) or soft (e.g., sand, shell debris). Because reef algae and invertebrates occur on hard substrate, their percent cover within a quadrat was estimated as the fraction of points on hard substrate that they occupied multiplied by 100. All species of reef-associated sessile invertebrates and macroalgae were included in the analyses, with the exception of crustose coralline algae, which was treated as bare space because many sessile invertebrates and erect forms of macroalgae commonly settle and grow on it (Sebens 1986*a*).

A split plot experimental design tested the main and interactive effects of the removal of *M. pyrifera* and the benthos on the percent cover of understory algae, sessile invertebrates, and unoccupied space. The benthos removal and control quadrats (i.e., split plot units) were treated as subplots within the kelp removal and control reef modules (i.e., whole plot units), which were replicated as blocks. Separate analyses were done for each of the three response variables: percent cover of understory algae, sessile invertebrates, and unoccupied space. We used a priori pair-wise contrasts involving data from the different experimental treatments to test our hypotheses regarding the effects of giant kelp canopy on the benthic community. We used *t* tests with the data paired by block in order to evaluate whether the differences in percent cover between kelp removal and control treatments were >0 for algae (one-tailed *t* test), <0 for invertebrates (one-tailed *t* test), and =0 for open space (two-tailed *t* test; see Appendix A: Table A1 for a more detailed list of hypotheses and planned contrasts). We used the sequential Bonferroni adjustment to account for multiple tests.

We measured light availability in the *M. pyrifera* removal and control modules on 7 December 2004 using a Li-Cor quantum meter (Model Li-250A; Li-Cor Biosciences, Lincoln, Nebraska, USA) and underwater quantum sensor (Model Li-192) to determine the extent to which giant kelp reduced bottom irradiance. The percentage of light reaching the benthos on each module was calculated from measurements of photosynthetically active radiation (PAR) taken at the water surface and near the sea floor.

Temporal variability in the community structure of natural reefs

We examined the relationship between interannual variability in kelp abundance and interannual variability in the percent cover of algae and invertebrates on three natural reefs off the coast of Santa Barbara, California, over an eight-year period to determine whether the patterns observed in the artificial reef experiment were consistent with those on natural reefs. Data used for these analyses were collected by the Santa Barbara Coastal Long Term Ecological Research project in the summers of 2000 through 2007 at Naples Reef (34°25′20″ N, 119°57′10″ W) and Carpinteria Reef (34°23′30″ N, 119°32′29″ W), and in the summers of 2001 through 2007 at Mohawk Reef (34°23′39″ N, 119°43′47″ W). These data are *available online*.[4]

Data were collected in fixed 40 m × 2 m transects at depths ranging from 4 m to 14 m (*N* = 7, 2, and 7 transects for Naples, Mohawk, and Carpinteria, respectively). Two types of data on the abundance of giant kelp were collected on each transect: the density of fronds >1 m tall and the percentage of the bottom occupied by holdfasts. The percent cover of giant kelp holdfasts, understory algae, and sessile invertebrates in the transects was estimated using a point contact method similar to that employed in the artificial reef experiment, with the exception that points (*N* = 80 per transect) were distributed uniformly along the length of the transect rather than within quadrats.

Interactions among kelp, understory algae, and sessile invertebrates might be different in sparsely populated areas intensively grazed by sea urchins (commonly referred to as sea urchin barrens). Data on the density of sea urchins collected in fixed 1-m^2 quadrats distributed uniformly along each transect (*N* = 6 quadrats per transect) were used in combination with data on kelp frond density to identify sea urchin barrens in the data set. Analyses of these data showed that giant kelp was absent when the density of sea urchins was ≥28/m^2 (Fig. 1). Hence a threshold value of 28 sea urchins/m^2 was used to classify whether a transect in a given year was or was not in an urchin barren state. Hereafter we refer to the state with <28 urchins/m^2 as "non-urchin barrens," rather than another term such as "forested" states, because fronds of *M. pyrifera* (or "forests") are not a requirement for non-urchin barrens (Fig. 1). Eleven of
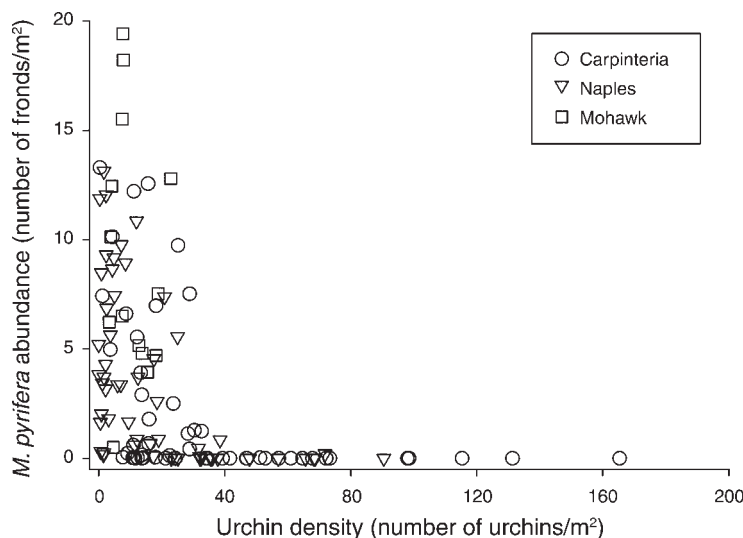
FIG. 1. The relationship between kelp (*Macrocystis pyrifera*) frond density and sea urchin density on three natural reefs in the Santa Barbara Channel, California, USA. Data represent mean densities observed on a given transect ($N = 16$) during a given year ($N = 8$ years for Carpinteria Reef and Naples Reef, and $N = 7$ years for Mohawk Reef).

the 16 transects were either never in an urchin barren state or were occupied by ≥ 28 urchins/m^2 only during the first one to two years of the study period. The years that these transects had <28 urchins/m^2 were classified as "non-urchin barren" states ($N = 69$, which includes 4 transects $\times$ 7 yr + 6 transects $\times$ 6 yr + 1 transect $\times$ 5 yr); the remaining years and the other five transect $\times$ year combinations were classified as "urchin barren" states ($N = 57$, which includes 5 transects $\times$ 8 yr + 1 transect $\times$ 3 yr + 6 transects $\times$ 2 yr + 2 transects $\times$ 1 yr). Because we were interested in competition between understory algae and sessile invertebrates, we wanted to determine whether their abundances were negatively correlated in all years and on all transects, and whether the direction of the relationship differed between urchin and non-urchin barren states. We evaluated the relationship between algae and invertebrates separately for urchin barren and non-urchin barren states because sea urchin grazing affects understory algae and sessile invertebrates, as well as giant kelp, and thus eliminates the potential for direct or indirect interactions between kelp and the sessile benthic community. Thus we expected, a priori, that the relationships among giant kelp, understory algae, and sessile invertebrates would differ between urchin barren and non-urchin barren states.

In additional analyses, we focused on the consecutive years that the 11 transects were in a "non-urchin barren" state ($N = 69$). In this case we assessed whether the correlation between the abundances of kelp and algae, and the correlation between the abundances of kelp and sessile invertebrates through time on natural reefs were consistent with the effects of kelp observed spatially in our short-term experiment on the artificial reef. The correlation coefficient was used as a metric to summarize temporal relationships on each transect between (a)

density of kelp fronds and percent cover of understory algae and (b) density of kelp fronds and percent cover of sessile invertebrates. Correlation coefficients with negative values were indicative of abundances of kelp and understory algae (or kelp and sessile invertebrates) changing in opposite directions over time, whereas a positive correlation coefficient indicated that abundances of kelp and algae (or kelp and sessile invertebrates) changed in the same direction over time. A one-tailed t test was used to determine whether the mean of the distribution of correlation coefficients ($N = 11$ transects) was significantly less than zero for kelp and understory algae (consistent with the hypothesis that kelp has a negative effect on understory algae) and significantly greater than zero for kelp and sessile invertebrates (consistent with the hypothesis that kelp indirectly facilitates sessile invertebrates). Because the response of the benthic community to changes in the abundance of giant kelp may not be immediate (due to variation in biotic and abiotic factors favorable to colonization), one-tailed t tests of the means against zero were performed on data with no time lag (i.e., algae or invertebrate abundance correlated to kelp abundance in the same year) and with a 1-yr lag time (algae or invertebrate abundance correlated to kelp abundance in the previous year). We also calculated correlation coefficients for the relationships between the abundance of algae and time (i.e., from 2000 to 2007) and sessile invertebrates and time (i.e., from 2000 to 2007) to examine the possibility that relationships between algae and invertebrates could be due to temporal autocorrelations rather than the influence of giant kelp. The same analyses described previously were performed on this second set of data to inform us about whether the patterns were due to a kelp effect or if they were being

driven by autocorrelation that may have existed in the time series.

We examined the influence of two possible mechanisms by which kelp affects the benthic community: (1) direct and indirect interactions mediated by shading from kelp fronds, and (2) direct competition for primary space on the bottom. To do this, we used two types of data on kelp abundance: frond density and percent of the bottom occupied by kelp holdfasts. The density of fronds >1 m tall is strongly correlated to the density of the surface canopy (K. Cavenaugh, *personal communication*) and thus the amount of light reduction imposed by the canopy, whereas the percent of the bottom covered by kelp holdfasts is a measure of the ability of *M. pyrifera* to occupy primary space.

We explored possible dynamical consequences of the suite of direct and indirect interactions in this community by examining whether interannual variability in the abundance of understory algae and sessile invertebrates was related to interannual variability in the abundance of giant kelp. Standard deviations of yearly values of the density of kelp fronds and the percent cover of kelp holdfasts, algae, and invertebrates for each transect over the eight-year period were used as measures of interannual variability. The standard deviation was chosen in order to estimate the magnitude of temporal variability in absolute abundances, rather than the variability relative to the mean (e.g., coefficient of variation). This choice reflects the fact that the mechanisms by which giant kelp affects the benthic community (e.g., shading) depend on changes in the absolute abundance, rather than the relative abundance, of giant kelp. We used regression analyses to determine whether the pattern of temporal variation of the benthos (understory algae and sessile invertebrates) over the eight years was predicted by fluctuations in the density of kelp fronds and/or the percent cover of kelp holdfasts. We compared the r^2 and significance of the relationships to evaluate whether the influence of giant kelp on benthic variability was better explained by its ability to reduce light or its ability to monopolize space on the bottom. This analysis was predicated on the previous analysis of correlation coefficients, which allowed us to determine the direction of the effect of frond density on algae and invertebrates through time. Our purpose in performing regression analysis on the standard deviations was to determine whether transects characterized by high temporal variability in kelp abundance were also areas where algae and invertebrates were highly variable. This analysis provided information on the degree to which the among-transect variation in the interannual variability of algae or invertebrates could be explained by interannual variability in kelp frond density or holdfast percent cover.

Strength and significance of direct and indirect effects

Using the analytical results of our experimental and observational data and an extensive literature on space competition among algae and invertebrates (Witman 1987, Coyer et al. 1993, Baynes 1999, Glasby 1999, Irving and Connell 2002, Miller and Etter 2008) and canopy shading by giant kelp (Pearse and Hines 1979, Reed and Foster 1984, Dayton 1985, Foster and Schiel 1985, Clark et al. 2004), we developed a model of the direct and indirect relationships among these groups. The model consisted of direct and indirect paths from giant kelp and midcanopy kelps to understory algae and sessile invertebrates and a direct path from understory algae to sessile invertebrates to represent its competitive dominance (see Appendix C for a full description of the model). Recognizing the limitation of our experimental and observational results in teasing apart the significance and strength of potential direct and indirect effects, we used Structural Equation Modeling (SEM; Grace 2006) to parameterize the model and evaluate its fit to the data from the natural reefs ("non-urchin barren" case, $N = 69$). This approach does not prove causality, but it can be useful for parameterizing direct and indirect interactions based on observational data (Grace 2006).

Parameter estimation and testing of model fit were performed using R (R Core Development Team 2008) with the sem (Fox 2006) and sem.additions (Byrnes 2008) libraries. As the data for the model were non-normal (Shapiro-Wilks test for multivariate normality, $W = 0.95$, $P < 0.006$), we used the Satorra-Bentler chi-square (Satorra and Bentler 1988) for this test of model fit. We examined whether the coefficient for each path was different from zero using robust estimates of error (Bentler and Dudgeon 1996). Because the data comprised two different units, density and percent cover, we also calculated standardized coefficients and used them to compare the magnitude of the paths. Lastly, we looked at the proportion of variance of each variable explained by the model (i.e., an R^2 value) using the formula $R^2 = 1 - V_e/V_o$ where V_e is the estimated variance and V_o is the observed variance.

RESULTS

Effects of giant kelp manipulations on benthic community composition

Removal of *M. pyrifera* generally resulted in an increase in understory algae (Fig. 2a) and a decrease in sessile invertebrates (Fig. 2b); however, the magnitude of these changes depended on whether the benthos was scraped or left intact ($F_{1,10} = 12.44$, $P < 0.005$ and $F_{1,10} = 22.79$, $P < 0.001$ for *M. pyrifera* × benthos interaction for understory algae and sessile invertebrates, respectively; Appendix A). For instance, the removal of giant kelp resulted in an increase in the percent cover of understory algae of 43% in scraped quadrats compared to 7% in unscraped quadrats (Fig. 2a; Appendix A), and a decrease in the percent cover of invertebrates of 39% in scraped quadrats compared to 12% in unscraped quadrats (Fig. 2b; Appendix A). Removing giant kelp and scraping the benthos had no effect on the amount of

unoccupied space (Fig. 2c; $F < 0.99$ and $P > 0.3$; Appendix A), such that the abundances of algae and invertebrates were negatively correlated in the experiment ($r = -0.86$, $P < 0.0001$). Removal of *M. pyrifera* also increased the amount of light available to the benthic community, as the percentage of surface PAR reaching the bottom in *M. pyrifera* removal treatments ($1.70\% \pm 0.94\%$ [mean $\pm$ SE]) was more than twice as high as that in *M. pyrifera* control treatments ($0.68\% \pm 0.41\%$).

Treatment effects occurred after only eight months, suggesting that a natural change in the abundance of *M. pyrifera* can lead to significant changes in understory algal and sessile invertebrate abundance within the same year. Importantly, the understory species composition was generally similar in the experimental treatments and controls (Appendix B), suggesting that treatment effects were not driven by species-specific responses. Filamentous red algae, ovate fleshy red algae in the genera *Kallymenia* and *Schizymenia*, and foliose red algae in the genus *Rhodymenia* formed the dominant algal cover in both *M. pyrifera* control and removal treatments. Abundant sessile invertebrates common to both *M. pyrifera* control and removal treatments included the compound tunicate *Chelyosoma productum*, the arborescent bryozoans *Bugula californica*, *Crisia* spp., *Cellaria* spp., and *Diaperoecia californica*, the hydroid *Plumularia* spp., and species of encrusting bryozoans and sponges (Appendix B).

Temporal variability in the community structure of natural reefs

The direction and strength of the relationship between understory algae and sessile invertebrates varied among the natural reefs, and as expected, between urchin barren and non-urchin barren states. The percent cover of understory algae and invertebrates was negatively correlated in non-urchin barrens (Fig. 3a; Carpinteria, $N = 17$, $r = -0.75$, $P < 0.001$; Naples, $N = 38$, $r = -0.76$, $P < 0.0001$; Mohawk, $N = 14$, $r = -0.90$, $P < 0.0001$), and uncorrelated in urchin barrens (Fig. 3b; Carpinteria, $N = 39$, $r = 0.19$, $P > 0.2$; Naples, $N = 18$, $r = -0.15$, $P > 0.5$). These results suggest that competition between algae and sessile invertebrates for space may only occur when sea urchin densities are relatively low (i.e., $<28/m^2$), possibly because high densities of urchins maintain open space by foraging on the bottom. Evidence for this comes from our observation that the percent cover of unoccupied hard substrate was over three times higher in urchin barren areas compared to non-urchin barren areas (54% vs. 15%; $F_{1, 125} = 109.5$, $P < 0.0001$).

Consistent with our experimental results on the artificial reef was our finding that natural fluctuations in abundance of *M. pyrifera* led to rapid responses in the abundances of understory algae and sessile invertebrates on natural reefs. The mean of the distribution of transect correlation coefficients describing the relationship between the density of kelp fronds and percent cover of
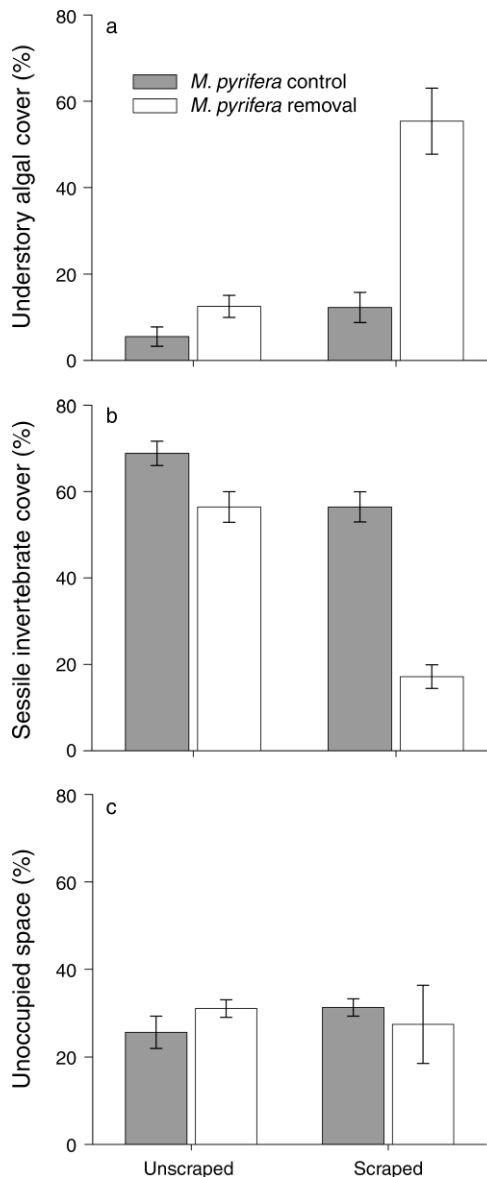

FIG. 2. Eight months after the removal of giant kelp, *Macrocystis pyrifera*, the effects on the percent cover of hard substrate occupied by (a) understory algae, (b) sessile invertebrates, and (c) open space in quadrats in which the benthos was removed (scraped) or left intact (unscraped). Data are means $\pm$ SE ($N = 6$ modules). See *Methods: Experiment to test the effect of giant kelp on the benthic community*.

algae on natural reefs was significantly negative when the frond density and algal data were examined contemporaneously (mean $= -0.41 \pm 0.13$ [$\pm$SE], $N = 11$, $t = -3.3$, df $= 10$, $P < 0.01$), but was not significantly negative when frond density was related to algal cover in the following year (mean $= -0.02 \pm 0.15$, $N = 11$, $t = -0.2$, df $= 10$, $P > 0.4$). The mean of the distribution of transect correlation coefficients describing the relationship between the density of kelp fronds and the percent cover of sessile invertebrates was significantly positive
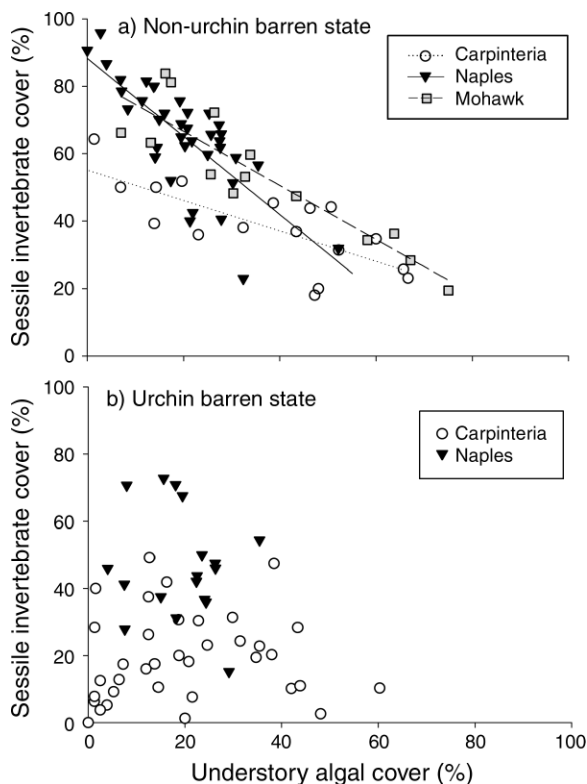
FIG. 3. The relationship between the percent cover of sessile invertebrates and the percent cover of understory algae in (a) non-urchin barren states, and (b) urchin barren states on three natural reefs. Each data point represents a transect in a given year. (Note that $N = 4$ overlaid points at 0% algae and 0% invertebrates.) See *Methods: Temporal variability in the community structure of natural reefs.*

when the frond density and invertebrate data were examined contemporaneously (mean $= 0.48 \pm 0.09$, $N = 11$, $t = 5.5$, df $= 10$, $P < 0.0001$), but not significantly positive when frond density was related to invertebrate cover in the following year (mean $= -0.04 \pm 0.94$, $N = 11$, $t = -0.29$, df $= 10$, $P > 0.6$). The nonsignificant results for a lag time of one year suggest that autocorrelation among years was not driving the observed temporal relationships between the benthic community and giant kelp. Furthermore, the mean of the correlation coefficients for the percent cover of understory algae and time was not significantly negative (algae lag 0, $t = -1.5$, $P > 0.09$; algae lag 1, $t = 0.4$, $P > 0.6$). Nor was the mean significantly positive for the percent cover of sessile invertebrates and time (invertebrates lag 0, $t = -0.5$, $P > 0.6$; invertebrates lag 1, $t = -2.5$, $P > 0.9$). These findings imply a lack of strong autocorrelation in the data.

The magnitude of interannual variability in *M. pyrifera* frond density differed by more than three-fold among transects (Fig. 4). Variation in the percent cover of understory algae and sessile invertebrates was associated with spatial and temporal variability in the

abundance of giant kelp. Interannual variability in the percent cover of the two understory groups was significantly and positively related to interannual variability in kelp frond density (Fig. 4a, c; algae, $F_{1,10} = 25.6$, $P < 0.001$; invertebrates, $F_{1,10} = 7.6$, $P < 0.03$), which explained 74% and 46% of the among-transect variation in the standard deviation of the abundance of algae and invertebrates, respectively. In contrast to frond density, interannual variability in the percent cover of the bottom occupied by giant kelp holdfasts explained only 12% and 8% of interannual variability in algal and invertebrate percent cover, respectively, and the relationship was not significant (Fig. 4b, d; algae, $F_{1,10} = 1.2$, $P > 0.3$; invertebrates, $F_{1,10} = 0.77$, $P > 0.4$).

The species composition of algae on the natural reefs was largely similar to that of the artificial reefs. Filamentous red algae and the foliose red alga, *Rhodymenia* spp., were two of the three most dominant taxa, accounting for 37% of all algae observed. The natural reefs also shared many of the dominant invertebrate species with the artificial reefs, including the arborescent bryozoans *Bugula* spp., *Crisia* spp., and *Diaperoecia californica,* and encrusting bryozoans and sponges (Appendix B).

Strength and significance of direct vs. indirect effects

The fitted model and estimates of path coefficients (Fig. 5; Appendix C) were consistent with the interpretation that giant kelp negatively affects understory algae via canopy shading (-1.26 ± 0.59 [coefficient estimate $\pm$ SE], $Z = -10.0$, $P = <0.0001$, standardized coefficient estimate $= -0.39$), algae negatively affects sessile invertebrates through space competition (-0.72 ± 0.07, $Z = -10.0$, $P = <0.0001$, standardized coefficient estimate $= -0.74$), and giant kelp indirectly facilitates sessile invertebrates. In fact, the magnitude of the indirect effect of giant kelp frond density on sessile invertebrates ($0.29 = -0.39 \times -0.74$) was nearly six times greater than the magnitude of the direct effect (standardized coefficient estimate $= -0.05$; Fig. 5; Appendix C). The coefficient for the path representing the direct effect of giant kelp frond density on sessile invertebrates was not significantly different from zero ($P = 0.6$), nor were the paths between the percent cover of giant kelp holdfasts and the percent cover of understory algae and sessile invertebrates ($P = 0.7$ and $P = 0.1$, respectively; Fig. 5; Appendix C). Of note was the significance and strength of the path representing the direct negative effect of midcanopy kelps on sessile invertebrate abundance (-1.19 ± 0.47 [coefficient estimate $\pm$ SE], $Z = -2.54$, $P = 0.01$, standardized coefficient $= -0.19$). The fitted model explained 62% of the variation in sessile invertebrate abundance, 11% of the variation in understory algae, and 0.8% of the variation in midcanopy kelps (Appendix C). Overall, the model fit the observed data (Satorra-Bentler $\chi^2 = 0.13$, df $= 1$, $P = 0.74$). The nonsignificant P value indicated that the pattern of covariance predicted by the model was not
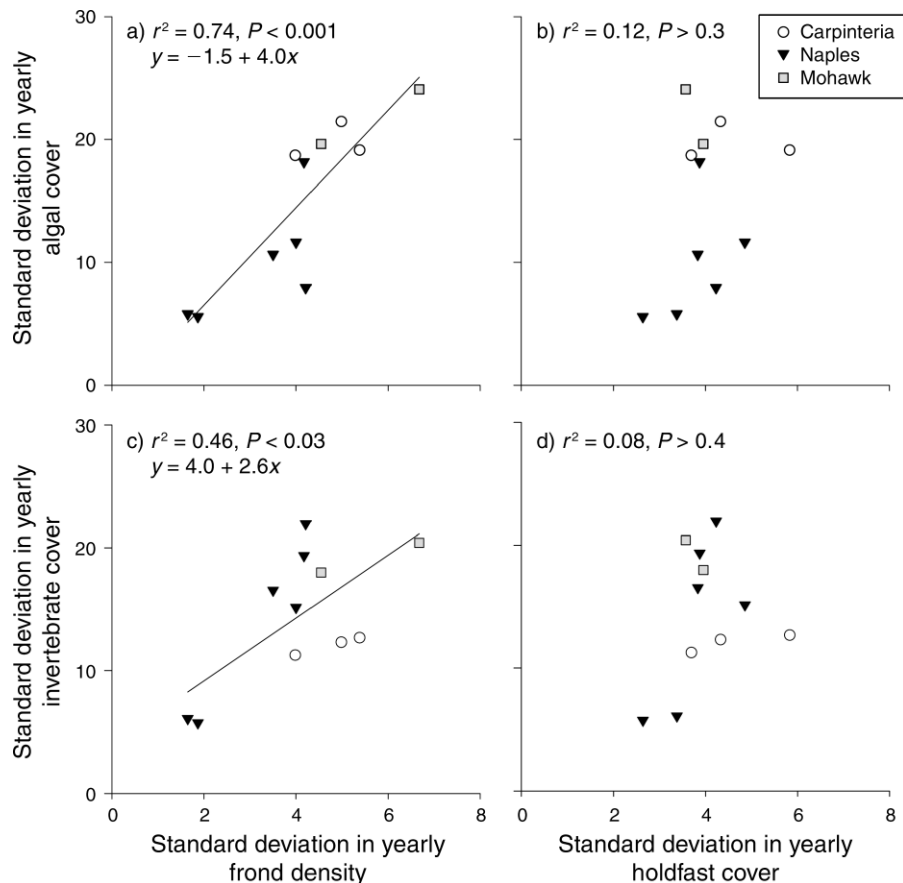
FIG. 4. Relationship between interannual variability in the structure of the benthic community (percent cover of understory algae and sessile invertebrates) and interannual variability in the abundance of giant kelp (frond density and holdfast percent cover) on three natural reefs. Interannual variability was measured as the standard deviation of abundance (density or percent cover) calculated among years for each transect ($N = 11$ transects). (a) Understory algae vs. kelp fronds, (b) understory algae vs. kelp holdfasts, (c) sessile invertebrates vs. kelp fronds, and (d) sessile invertebrates vs. kelp holdfasts.

distinguishable from the observed covariance, and thus that the model reflected the patterns in the data. The alternative, a significant P value, would have falsified our hypothesis that kelp indirectly affects invertebrates via its effect on algae.

DISCUSSION

A growing body of empirical work indicates that sessile organisms can reduce competitive stress by living with or near a competitor of the species with which they compete (reviewed by Stachowicz 2001). Evidence for the role of this type of indirect facilitation in determining the distribution and abundance of sessile organisms comes mainly from terrestrial plant communities (Miller 1994, Levine 1999, Callaway and Pennings 2000, Pages et al. 2003). Not to be overlooked is one of the earliest examples of indirect facilitation that comes from a kelp forest off southern California. The midcanopy kelp *Eisenia arborea* excluded the understory brown alga *Halidrys dioica* and facilitated its competitor, the red alga *Pterocladia capillacea* (Kastendiek 1982). Our study is novel in providing observational and experimental

field evidence of indirect facilitation involving marine primary producers and consumers, and it shows that temporal, as well as spatial, variation in the abundance of the facilitator can influence the distribution and abundance of two competing species.

Our field experiment revealed a positive effect of giant kelp on sessile invertebrates and a negative effect on understory algae. The reduction in light caused by the kelp canopy, the opposite and balanced differences in the abundance of understory algae and sessile invertebrates between *M. pyrifera* treatments, and the constant amount of open space, suggests that understory algae are competitively superior to sessile invertebrates, and that *M. pyrifera* positively and indirectly affected invertebrates by releasing them from competition for space with algae through shading. Results of the observational data showed that the interaction web between giant kelp, understory algae, and sessile invertebrates was context dependent, with little evidence for competition between algae and invertebrates in sea urchin barrens where kelp was absent (due to heavy grazing by sea urchins) and open space was abundant. In
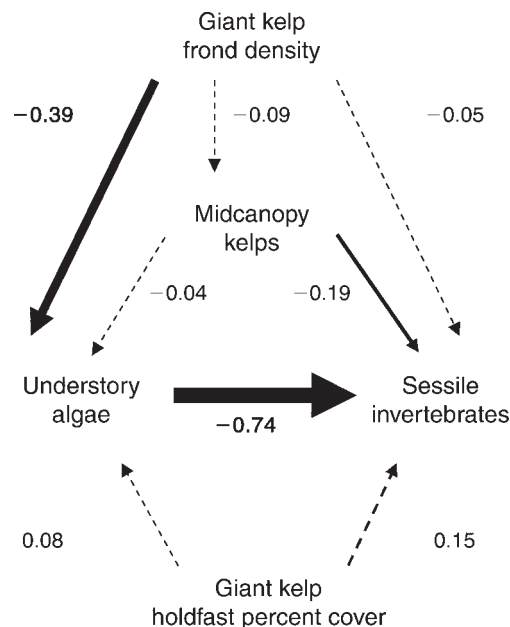
FIG. 5. The fitted competition and facilitation model used to estimate the strength of direct and indirect effects. Values are standardized coefficient estimates. Solid lines indicate significant paths ($P < 0.05$). Dashed lines are nonsignificant. For additional details on coefficients (i.e., corrected standard errors, z values, and significance levels) see Appendix C.

non-urchin barrens a strong negative correlation between algae and invertebrates was indicative of competition for space, and results suggest that the outcome varied across a gradient of kelp abundance and light availability. Importantly, the effects of kelp on algae and invertebrates appeared to accrue rapidly (<1 year), causing interannual variability in the structure of the benthic community to correlate positively with interannual variability in the abundance of giant kelp. A similar rapid response of the benthic assemblage to the removal of kelp is common and has been reported elsewhere (e.g., Kastendiek 1982, Reed and Foster 1984, Wernberg and Connell 2008; but see Clark et al. 2004). Results from the Structural Equation Modeling (SEM) indicated that the positive indirect effect of kelp on invertebrates, based on the negative effects of frond density on algae, and algae on invertebrates, was larger than the direct effect, providing further evidence that indirect facilitation plays an important structuring role in this system. That the species composition between the natural and artificial reefs was similar, suggests that the relative importance of direct and indirect interactions was comparable in the two studies.

Variation in the abundance of canopy-forming species on land and in the ocean can influence a variety of environmental conditions experienced by understory species, including light availability, temperature, humidity, and water flow. Giant kelp in particular has been shown to dampen current speeds (Jackson 1997, Gaylord et al. 2007), which could increase rates of

sedimentation, decrease light (Pearse and Hines 1979, Reed and Foster 1984), and alter the abundance of grazers and predators (Foster and Schiel 1985). We suspect that the large influence of giant kelp on the structure of the benthic communities on the artificial and natural reefs in our study was most likely caused by its effect of reducing light. Evidence from previous work is consistent with this hypothesis. Others have tested the combined effects of light and sedimentation (Irving and Connell 2002) or light and predation (Miller and Etter 2008), on the relative abundance of algae and sessile invertebrates and found that light often plays the primary role (but see Sebens 1986b). The reduction of light by kelp could affect sessile invertebrate abundance directly, by facilitating settlement of larvae that exhibit negative phototaxis (e.g., Linares et al. 2008); however, this hypothesis was not supported by the insignificant and weakly negative path between frond density and sessile invertebrates in our fitted model. Our finding that algal and invertebrate abundance changed in opposite directions and in similar abundances, and the significant negative correlations between frond density and algae, and between algae and invertebrates, suggest that M. pyrifera indirectly facilitated sessile invertebrates by reducing the abundance of macroalgae. Macroalgae can inhibit invertebrate recruitment (Baynes 1999), cause overgrowth-induced mortality (Witman 1987, Coyer et al. 1993), and outcompete invertebrates for space (Baynes 1999). The proportionally higher abundance of sessile invertebrates on the artificial reef at the beginning of the experiment reflected the low light environment caused by a dense kelp canopy at the surface and high turbidity throughout the 15-m water column. Under these conditions, invertebrates were able to prevent algae from increasing in coverage by more then 7% (although this was a two-fold increase from the initial abundance), even when kelp was removed. Once space as well as light became available, as it does naturally when a kelp holdfast is pulled from the substratum or boulders are overturned by storm disturbance, algae became the dominant group.

Kelp may also affect understory algae and sessile invertebrates through its role as a space competitor. However, our study suggests that the canopy had a greater influence on benthic community structure and dynamics than did the ability of kelp to monopolize primary space. Interannual variability in the understory community was significantly related to interannual variability in frond density, but not holdfast percent cover, and the paths from holdfast percent cover to algae and invertebrates in the fitted model were not significant. Not surprisingly, frond density and holdfast percent cover were not interchangeable metrics. Kelp forests are similar to terrestrial forests, where a few large trees with extensive canopies can have a sizable impact on light, while many smaller individuals may occupy more space, but block less light.

The results of this study imply that indirect facilitation by giant kelp may in part engender the dramatic shifts in community structure observed in some kelp forests, in which the benthic assemblage alternates between dominance by macroalgae and dominance by suspension-feeding invertebrates (Behrens and Lafferty 2004, Rassweiler 2008). Such shifts have important consequences for the reef food web, as the identity of the primary space holders determines whether energy is derived from local, benthic primary production or from allochthonous inputs of pelagic primary production. In the case of the former, understory macroalgae dominate the benthos and support mobile herbivores and detritivores, which are in turn fed upon by a suite of predatory invertebrates, fishes, and mammals, while in the case of the latter, sessile suspension feeders (supported primarily by plankton produced outside the forest) dominate the benthos and serve as prey for a different suite of predators. Not only does the presence of giant kelp alter the food web structure of the benthos (via indirect facilitation), but it also supports an assemblage of invertebrates and fish that live higher up in the water column (Feder et al. 1974, Coyer 1987, Holbrook et al. 1990), thus magnifying its effect on the energy flow of shallow reef ecosystems.

Kelps have long been considered "foundation species" (Dayton 1975) in that their structure provides food and habitat for a wide diversity of other species (Darwin 1839). However, kelps differ from many other foundation species (e.g., trees and corals) because their abundance fluctuates greatly over short time scales (from months to a few years; Dayton et al. 1992, 1999, Wernberg and Goldberg 2008). This is consonant with one of the most striking results of our study: the rapid response of understory algae and sessile invertebrates to natural changes (increases and decreases) in giant kelp abundance, as well as experimental removals. The dramatic variation in the abundance of *Macrocystis* in the non-urchin barren transects during the eight-year survey period reflects disturbance from storm-generated swells whose intensity varies greatly in time and space. In years when storm disturbance is minimal, little change occurred in the benthic community. In contrast, large waves remove entire populations of giant kelp, scour and/or break up the reef, and create substantial amounts of unoccupied space during years of high storm activity (reviewed in Tegner and Dayton 1987). The extent of wave disturbance during any given storm can vary greatly among sites depending on site exposure, swell direction, and depth (Seymour et al. 1989). The structure of the postdisturbance community depends on a suite of factors that vary greatly in time and space including abiotic conditions, the available pool of propagules, and interactions among the colonizing species (e.g., kelp, understory algae, and sessile invertebrates). Collectively, these processes influenced the pattern of spatial variability in the temporal dynamics of reef communities observed in this study (Fig. 5).

Similar phenomena have been reported in other kelp systems (Wernberg and Connell 2008).

While disturbance from storms plays a role in reducing densities and thus competitive stress, harsh conditions alone cannot lead to coexistence (Chesson and Huntly 1997). Rather, coexistence is favored when harshness is combined with some other mechanism that reduces the abundance of the superior competitor for a limiting resource, either locally or globally. Such is the case in giant kelp forest ecosystems. Storm disturbance decreases giant kelp abundance, causing conditions to change from a low light environment in the presence of giant kelp to a high light environment in its absence. Because understory algae and sessile invertebrates have different light requirements, giant kelp facilitates temporal and spatial coexistence of these competitors by creating alternative niches for them to occupy. Such mechanisms of coexistence likely operate on a species-specific scale. For instance, the loss of giant kelp may favor "light adapted" understory algal species, such as *Rhodymenia* spp., *Callophyllis flabellulata*, and *Chondracanthus corymbiferus* (Clark et al. 2004), which occurred on both the artificial and natural reefs in our study.

Many studies have shown that spatial variation in the abundance of foundation species and ecosystem engineers, such as giant kelp, can contribute to the spatial coexistence of other species or groups of species (Bruno et al. 2003, Wright and Jones 2006, Hastings et al. 2007). Our study makes the additional point that interactions involving a foundation species, combined with the abiotic effects of disturbance, can maintain temporal coexistence of associated taxa. Our results also show that competitive and facilitative interactions in giant kelp forests can lead to rapid variation in community structure, suggesting that indirect facilitation can contribute to high frequency changes, as well as long-term trajectories in the dynamics of communities. The largely correlational nature of our results motivate future research to disentangle the mechanisms underpinning potential direct and indirect effects among kelp, algae, and invertebrates, and to verify causal relationships. By revealing the relative interaction strengths across broad spatial and temporal scales, our findings provide a broader context for more restrictive experimentation (Graham et al. 2008). The power of our study resides in its three-pronged approach. Through manipulative field experiments, independent observations of a natural system, and model fitting, we elucidate the role of indirect facilitation in determining the structure and dynamics of rocky reef communities.

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APPENDIX A

Results of planned pair-wise contrasts and summary of ANOVAs testing for the effects of *M. pyrifera* removal and benthic scraping on the percent cover of understory algae, sessile invertebrates, and open space (*Ecological Archives* E090-224-A1).

APPENDIX B

Relative abundance of understory algal and sessile invertebrate taxa in giant kelp control and removal treatments and on natural reefs (*Ecological Archives* E090-224-A2).

APPENDIX C

Model construction and SEM evaluation (*Ecological Archives* E090-224-A3).

Katie K. Arkema, Daniel C. Reed, and Stephen C. Schroeter. 2009. Direct and indirect effects of giant kelp determine benthic community structure and dynamics. *Ecology* **90:3126–3137.**

Appendix C. Model construction and SEM evaluation.

We developed a model describing the direct and indirect relationships among giant kelp, understory algae, and sessile invertebrates. Model construction was based on the results from the experimental and observational studies, and the extensive literature on space competition among algae and invertebrates (Witman 1987, Coyer et al. 1993, Baynes 1999, Glasby 1999, Irving and Connell 2002, Miller and Etter 2008) and canopy shading by giant kelp (Pearse and Hines 1979, Reed and Forester 1984, Dayton 1985, Foster and Schiel 1985, Clark et al. 2004). Recognizing the limitation of our experimental and observational data in teasing apart the significance and strength of potential direct and indirect effects, we used Structural Equation Modeling (SEM; Grace 2006) to parameterize the model and evaluate its fit to the observed data.

The model consisted of direct and indirect paths from giant kelp and mid-canopy kelps to understory algae and sessile invertebrates, and a path from understory algae to sessile invertebrates to represent its competitive dominance. Paths from frond density to algae and invertebrates represented potential direct effects of the canopy, such as light reduction, on algal abundance (Reed and Foster 1984) and invertebrate larval recruitment (Lineras et al. 2008). The path from frond density to invertebrates also encompassed the dampening effect of giant kelp on current speed (Jackson 1997, Gaylord et al. 2007), which may diminish the delivery of food to suspension feeders and increase sedimentation rates. Paths from holdfast percent cover to understory algae and sessile invertebrates were used to represent the effect of kelp as a competitor for primary space. Kelp indirectly affected sessile invertebrates via its effect on algae. We also included the density of mid-canopy kelps in the model. Like giant kelp, mid-canopy kelps, such as *Pterygophora californica,Cystoseira osmundaceae*, *Laminaria farlowii* and *Egregia menziesii*, may affect the understory by diminishing light, dampening water flow (Eckman and Duggins 1991) and abrasion (Connell 2003).

Parameter estimation and testing of model fit were performed using R (R Core Development Team 2008) with the sem (Fox 2006) and sem.additions (Byrnes 2008) libraries. We assessed the fit of the model to the data collected from the natural reefs during the consecutive years that the 11 transects were "non-urchin barrens" ($N = 69$, see *Methods* for further explanation). To account for site-specific variation in the abundance of understory algae, sessile invertebrates and mid-canopy kelps, we first fit three linear models with site as the predictor variable and used the calculated residuals in the SEM evaluation. To fit the model employing SEM, we calculated the covariance matrix of the data, specified the fixed exogenous variables (i.e., giant kelp frond density and holdfast percent cover) and used maximum likelihood to estimate path coefficients. We assessed the fit of the model to the data using a Chi-Squared goodness-of-fit test, in which the covariance in the observed data was compared with the expected covariance if the model were true. A non-significant value indicates that the pattern of covariance predicted by the model was not distinguishable from that observed, and thus that the model reflects the pattern in the data. A significant value falsifies the model. As the data were non-normal (Shapiro-Wilks Test for Multivariate Normality, $W = 0.95$, $P < 0.006$), we used the Satorra-Bentler Chi Square (Satorra and Bentler 1988) for this test of model fit. The Satorra-Bentler Chi Square uses information on the multivariate normality of the data, as well as the sensitivity of the model to changes in parameter values, to calculate a factor by which the original Chi Square value is scaled. We also examined whether the coefficient for each path was different than 0 using robust estimates of error (Bentler and Dudgeon 1996). Because the data comprised two different units, density and percent cover, we calculated standardized coefficients and used these to compare the strengths of the direct and indirect effects. Lastly, we looked at the proportion of variance of

each variable explained by the model (i.e., an R^2 value) using the formula $R^2 = 1 - V_e/V_o$ where V_e is the estimated variance and V_o is the observed variance. Coefficient estimates, corrected standard errors and tests of significance of the paths are presented below in Table C1. The results from the model fit, the R^2 values, and the strength of the indirect path from kelp to invertebrates are reported in the *Results*, Fig. 5 and below in Table C2.

TABLE C1. Coefficient estimates, corrected (for non-normality) standard errors and tests of significance for the paths representing interactions between giant kelp, understory algae, sessile invertebrates and mid-canopy kelps in the fitted model.

Path	Coefficient estimates	SE	Z	P	Standardized coefficient estimates
Understory algae --> sessile invertebrates	-0.72	0.07	-10.0	**<0.0001**	-0.74
Giant kelp fronds --> understory algae	-1.26	0.59	-2.14	**0.03**	-0.39
Giant kelp fronds --> sessile invertebrates	-0.16	0.34	-0.46	0.6	-0.05
Giant kelp fronds --> mid-canopy kelps	-0.05	0.05	-0.84	0.4	-0.09
Mid-canopy kelps --> understory algae	-0.26	0.61	-0.42	0.7	-0.04
Mid-canopy kelps --> sessile invertebrates	-1.19	0.47	-2.54	**0.01**	-0.19
Giant kelp holdfasts --> understory algae	0.27	0.73	0.37	0.7	0.08
Giant kelp holdfasts --> sessile invertebrates	0.53	0.36	1.50	0.1	0.15

TABLE C2. The proportion of variance in each endogenous variable explained by the fitted model.

Variable	R^2
Understory algae	0.11
Sessile invertebrates	0.62
Mid-canopy kelps	0.008

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