

# TEMPORAL VARIATION IN THE STATE OF ROCKY REEFS: DOES FISHING INCREASE THE VULNERABILITY OF KELP FORESTS TO DISTURBANCE?

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**Abstract**—Shallow rocky reefs in temperate regions often exist in one of two states: kelp forests or urchin barrens. Because barrens and forests provide different socioeconomic values and ecological functions, a better understanding of what determines the underlying mechanisms behind the maintenance of, or transition between, states is of interest. We used two decades of data collected and provided by the Channel Islands National Park (CINP) long-term kelp-forest monitoring program (KFM). With these data, we conducted a Fisher's linear discriminant analysis to describe a gradient in rocky reef community states from kelp forests to barrens. We investigated how these states changed over time in different regions within the Channel Islands. With the exception of a no-take reserve, northern sites were more likely to remain kelp forests than southern sites. There was a trend for barrens in the warm region. ENSO events typically (but not always) shifted reefs to barrens, but the subsequent recovery of kelp forests was inconsistent among sites. Barrens formation was associated primarily with wave intensity (higher wave intensity resulted in a decrease in the kelp index the following year). In the warm biogeographic region, there was an interaction between wave intensity and water temperature, such that barrens formed most when years with intense waves were associated with warm, nutrient poor water. A striking exception to these patterns was that within the reserve there was less temporal variation and what variation existed was not associated with physical factors.

*Keywords:* climate, El Niño, fishing, kelp, marine reserves, sea urchins

## INTRODUCTION

Episodic recruitment and physical disturbances can create dynamic nearshore communities. This is particularly true of shallow rocky reefs in temperate regions which can support communities that range from kelp forests to urchin barrens (Harrold and Reed 1985, Scheibling and Hennigar 1997, Sala et al. 1998, Babcock et al. 1999). Barrens and forests provide different socioeconomic values and ecological functions and, consequently, a better understanding of the underlying mechanisms behind the maintenance of, or transition between, barrens and forested states is of interest. Here, we investigate whether climatic factors and anthropogenic disturbance alter the state of kelp forests over time.

Large-scale climatic effects can drive temporal variation in the states of rocky reefs (Dayton 1984,

Ebeling et al. 1985, Dayton and Tegner 1989, Seymour et al. 1989, Tegner and Dayton 1991, Dayton et al. 1992, Tegner et al. 1996, Tegner et al. 1997, Tegner and Dayton 2000, Edwards 2004, Edwards and Estes in press). Physical factors that seem likely to affect patterns on a large scale are nutrient availability and storm intensity. El Niño events, for example, have altered current flows that can result in water temperatures 4°C to 10°C degrees warmer than normal (Tegner et al. 1996). This results in a deep thermocline that prevents the upwelling of cool water; the subsequent lack of nutrients leads to high mortality of the giant kelp, *Macrocystis pyrifera* (Dayton 1984). For example, stipes per plant (age) and stipe density (an indication of kelp biomass) were low following the warm years of 1992 to 1994 (Tegner et al. 1996). In addition, some El Niño years have large winter storms that remove adult plants. Reductions in kelp

canopy following storms (Seymour et al. 1989) or warming (Tegner et al. 2001) can be rapid and extensive. For example, there was a five year loss of kelp forests in Southern California following the 1957 to 1959 El Niño (Tegner and Dayton 1991). Similarly, following the storms of the 1982 to 1983 El Niño, the 600-hectare kelp forest canopy off Point Loma, California was reduced to 40 hectares (Dayton 1984). Long-term reductions in kelp forest canopy have been found to be associated with El Niño warm water periods (Tegner et al. 2001). Sometimes, the dramatic changes are temporary because kelp recruitment can be rapid following catastrophic kelp loss (Tegner and Dayton 1991, Graham et al. 1997). Even if a kelp bed is eliminated by a storm, kelp spores can arrive from distant sources (Reed et al. 1988, Reed et al. 2004) or recruitment may result from persistent microscopic stages (Ladah et al. 1999). Such recruitment could dampen the effect that episodic events have on the year to year variation in the state of a reef. This is particularly true if storms that remove kelp are followed by conditions of cool, nutrient-rich water (Dayton et al. 1992, Tegner et al. 1997). These observations lead to the prediction that the warm water and large storm events associated with El Niños should reduce kelp forests. Cooler than normal periods, termed La Niña events, could have opposite effects on kelp forests.

Biogeographic regions could also affect the state of rocky reefs and the effects of fishing and climate on these states (Behrens and Lafferty 2004). The Channel Islands can be roughly grouped into at least two biogeographic regions based on water temperature (Reed et al. 2000). The northwest is colder and has a somewhat different faunal composition than the southeast. For our study, the warm biogeographic region included all sites at Santa Barbara and Anacapa Islands and all sites at Santa Cruz Island except Gull Island. The cold biogeographic region included San Miguel Island and Santa Rosa Island and the Santa Cruz Island site, Gull Island. We suspected that the two biogeographic regions might differ in their response to physical and biological factors based on recent evidence that the effects of El Niño can be region dependent (Edwards and Estes in press). Specifically, the cold biogeographic region should be more buffered from the effects of El Niños.

Overgrazing by sea urchins can prevent the reestablishment of fleshy algae and promotes the establishment of crustose coralline algae that are more resistant to grazing (Harrold and Reed 1985, Watanabe and Harrold 1991, Sala et al. 1998, Tegner and Dayton 2000). Historically, on rocky reefs at the California Channel Islands, a community-level trophic cascade existed where lobsters, and perhaps other predators, kept urchin populations at low levels and maintained kelp forests as the dominant community type. In geographic areas where the main predators on urchins are fished, the cascade is altered such that urchin populations increase to the extent that they overgraze algae, converting forests to barrens, and starvation and disease eventually limit urchin population growth (Lafferty 2004). Fishing may affect kelp forest states by favoring grazers (Babcock et al. 1999, Tegner and Dayton 2000, Behrens and Lafferty 2004, 2004) and fished areas may not recover as rapidly from reductions in kelp following El Niño events.

Another factor that could affect the state of rocky reefs is other (non-fishing) forms of human disturbance. The most publicized disturbance in the area occurred when the 162-m Panamanian commercial bulk carrier, *Pac Baroness*, sank on 27 September 1987 near San Miguel Island after a collision with the *Atlantic Wing*. The *Pac Baroness* was carrying 21,000 metric tons of finely powdered copper concentrate and 340,000 gallons of fuel and oil. Some have speculated that toxicity from this spill could have caused a decline in kelp forests throughout the region. If the *Pac Baroness* impacted kelp forests, we would expect declines in kelp forests to be greatest near San Miguel Island following the accident.

In this paper, we investigate temporal patterns in kelp forests around the Channel Islands. During the study period, major El Niños occurred in 1982 to 1983 and 1997 to 1998 and minor El Niños occurred in 1986 to 1987 and 1992 to 1993. We looked at changes in kelp forest structure following these events, predicting that forests would decline in association with the warm water and high storm intensity that characterize El Niños. We also correlated temporal variation in water temperature, wave intensity and Southern Oscillation index with changes in kelp forest communities at fished and unfished sites.

## STUDY AREA, MATERIALS AND METHODS

### Biological Data

We used data collected and provided by the Channel Islands National Park (CINP) long-term kelp-forest monitoring program (KFM). The CINP established the KFM in 1982 (Davis et al. 1997). The KFM annually samples 16 rocky reef sites from the north and south sides of Santa Barbara, Anacapa, Santa Cruz, Santa Rosa and San Miguel Islands (1 to 3 visits per summer; Fig. 1). Each site consists of a 100-m permanent transect. The KFM uses a variety of methods to quantify taxonomic groups such as kelps, urchins, sea stars, lobsters and fishes. Annual reports from 1990 to 1999 (e.g., Richards and Kushner 1994) describe each year's monitoring efforts and results. For example, divers count urchin densities using 12 to 40, 1 to 2-m<sup>2</sup> quadrats spaced along each transect, reporting densities as individuals per m<sup>2</sup> (differences in quadrat number and size do not have a detectable effect on density estimates). Because the sites are fixed and repeatedly measured each year, year-to-year data are not random representations of a site. This approach is more powerful for detecting changes but less suitable for inferring changes at a site beyond the scale of the transect. The use of sites as replicates within each region increases the extent that data gathered over time can be generalized to changes in the region.

KFM reports did not always clearly classify the sites that were monitored as kelp forests or barrens. Unfortunately, simple indices such as density of kelp or urchins were not sufficient to classify these sites (the density of kelp plants declines as forests mature and some kelp forests can support high urchin densities). To help determine the community state, Behrens and Lafferty (2004) conducted a Fisher's linear discriminant analysis that described and distinguished between sites that were clearly categorized as forests ( $n = 88$ ) or barrens ( $n = 86$ ). They constructed a simple linear discriminant function of two groups using a linear combination of variables ( $X_1 =$  measurement 1) with weights ( $a_i$ ) for each variable  $X$  chosen to maximize the separation between two groups (A and B). A canonical score,  $d$ , is produced by the function  $a_0 + a_1X_1 + a_2X_2 + \dots + a_nX_n$ , for a given set of  $X$

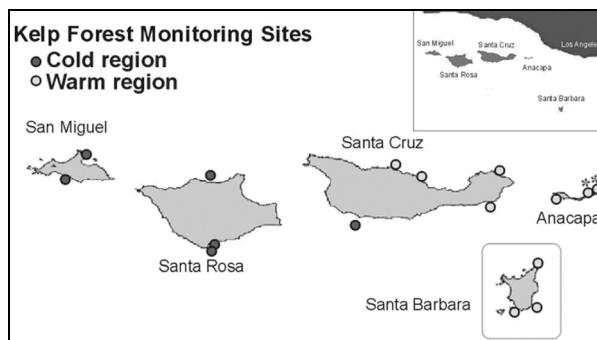


Figure 1. Map of the study area showing the California Channel Islands in the Southern California Bight. Dark circles represent the cold biogeographic region. Light circles represent the warm biogeographic region. Each asterisk indicates a no-take reserve.

values (Klecka 1980, McGarigal et al. 2000). The species most important in separating the two groups, *Macrocystis pyrifera* and *Diaperocia californica*, were positively associated with kelp forests and were assigned positive weights, while *Strongylocentrotus purpuratus*, *Corynactis californica*, *Astrangia lajollaensis*, crustose coralline algae, and bare substrate were associated with barrens (Behrens and Lafferty 2004). The gradient between forests and barrens is clear, with forests as positive values (up to 5.8) and barrens as negative values (down to -3.5; Behrens and Lafferty 2004). We calculated the change in canonical score from one year to the next and used this for our dependent variable (Fig. 2).

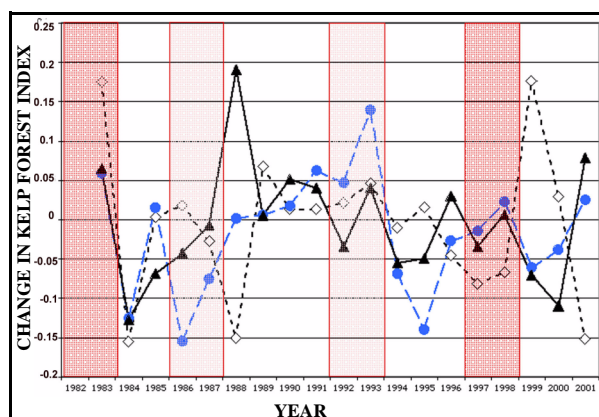


Figure 2. Change in the kelp forest index over time for three groups of rocky reefs. Annual change calculated as Year (N) – Year (N-1). Dark triangles represent the cold biogeographic region, open diamonds represent a no-take reserve in the warm biogeographic region and filled circles represent fished sites in the warm biogeographic region.

### Physical Data

The monitoring program collects in-situ temperature using data loggers that record temperature several times per day. We used the maximum summer temperature (June to July, as these were the two months of complete data for all years) for each year at each site. From this, we calculated the mean annual maximum water temperature at 10 warm and six cold sites (Fig. 3).

The Southern Oscillation Index (SOI) is a measure of the difference between the surface barometric pressure in Tahiti, French Polynesia minus that in Darwin, Australia (Troup 1965). El Niños have negative SOI values. Historical values (by month) are widely available over the internet (see Australian Government Bureau of Meteorology, <http://www.bom.gov.au/>). We were most interested in the SOI index for the year preceding summer sampling. For this reason, we calculated annual mean SOI values from the monthly SOI values between July of the previous year and June of the present year (Fig. 4).

Ocean swell data were obtained from the National Data Buoy Center. This program archives swell heights recorded from a variety of buoys. Station 46025 (Santa Monica Basin at 33°44'42"N 119°05'02"W) was the regional buoy with the most comprehensive time series: 1982 to 2001. This buoy is located approximately 30 km southeast of Anacapa Island and is more protected from winter swells than the exposed coasts of the northern Channel Islands. To create a continuous variable of wave intensity for each sample year, we

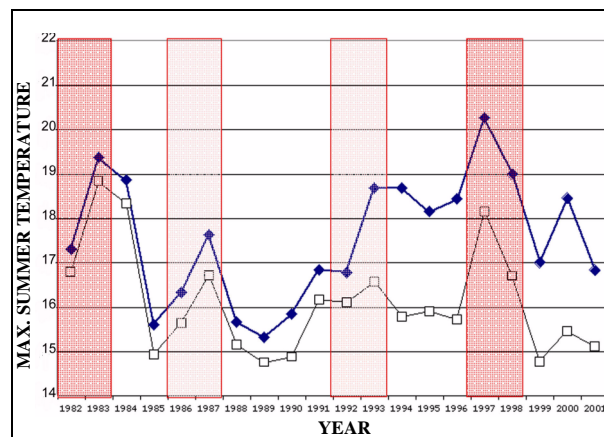


Figure 3. Grand means, over time, of the maximum summer temperature of the cold biogeographic region (open squares) and the warm biogeographic region (filled diamonds).

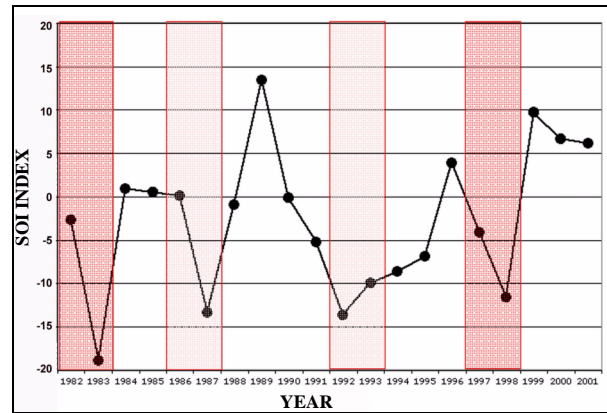


Figure 4. Grand annual means of the average monthly Southern Oscillation Index (an inverse measure of El Niño) over time.

averaged the significant wave heights for values between July of the previous year and June of the present year (Fig. 5).

### Analyses

We used Pearson's correlation to see if two sites had similar year-to-year variation in kelp forest index. Applying this to all possible combinations of sites led to a correlation matrix (with 120 cells). We then used a linear model to determine if island, depth (<11 m, >11 m), exposure (north or south) or biogeographic region (cold or warm, based on mean temperatures) helped explain variation in the correlation matrix (i.e., did sites from the same biogeographic tend to vary together more than sites from opposing biogeographic regions). We then selected the factors (predictors) that helped best group sites that were correlated with each other in time. We designated two sites in the no-fish Anacapa reserve (0.04 square nautical miles, established 1978) as a separate unfished group within the warm biogeographic region (a fully factorial model was not possible since all sites in the cold region were fished). Within each of the three groups, mean kelp forest indices were calculated for each year (with the expectation that these means would reflect broad scale variation in kelp forest index). We compared the mean, trends over time and variance in the kelp forest index among the different groups of reefs.

To see if kelp forests reacted differently to El Niño events than La Niña events, we took the change in kelp forest index at a site for the year

following El Niños (1984, 1988, 1994 and 1999) and, with a paired *t*-test, compared this with the change in kelp forest index at a site for the year following the strong La Niña (1990). We also inspected these trends for consistency across El Niños.

We checked to see whether the physical factors (temp, waves, SOI) were correlated with each other to assess multicollinearity. Then, for the time series analysis, we calculated simple correlations between the average change in the kelp forest index for each group and the physical factors. We estimated the correlation coefficient at time lags ranging from zero to one year. For the lag that had the most promising associations, we conducted a multiple regression in an effort to determine which physical factors (independent variables) explained the most variance in the change in kelp forest index (dependent variable) for each of the three types of rocky reef (fished cold biogeographic region, fished warm biogeographic region, and unfished warm biogeographic region). We ran complete models with all interaction terms and subset models with non-significant interaction terms and main effects deleted.

We looked at trends in the change in kelp forest index after the sinking of the *Pac Baroness* with the prediction that the kelp index would decline in the years following 1987, particularly at the cold sites nearest the site of the putative chemical release.

### RESULTS

The average correlation coefficient, *R*, in the matrix was 0.3. Only biogeographic region was significant in explaining the extent of between site correlation (df model = 1, df error = 119, Model MS = 1.324, Error MS = 0.708, *P* < 0.0001). Sites within each biogeographic region had an average correlation coefficient of 0.4 (0.42 in the warm region and 0.39 in the cold region) compared with an average correlation coefficient of 0.2 for sites in different biogeographic regions (e.g., warm vs. cold).

For the sites in the warm biogeographic region, we separated out the two reserve sites from the fished sites. We then calculated average kelp forest index for each year for the three groups. Reserve sites had significantly higher kelp forest scores

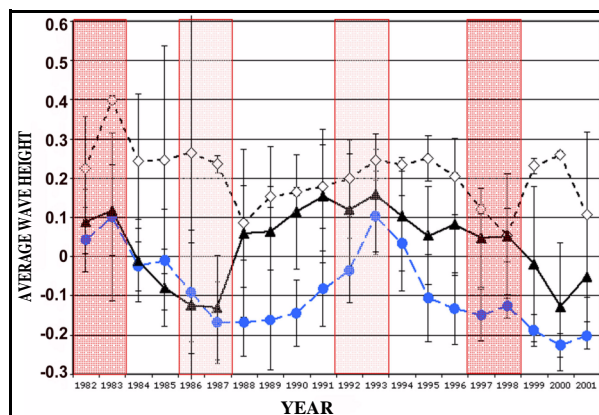


Figure 5. Wave intensity measured as the average significant wave height (heights measured hourly), by year, from the Santa Monica Basin buoy.

(0.204) than fished sites in the warm biogeographic region (-0.086, paired (by year) *t*-test, *P* < 0.001). Fished sites in the cold biogeographic region had an intermediate kelp forest score (0.033) that was lower than the warm reserve sites (paired *t*-test, *P* < 0.0001) but higher than fished sites in the warm biogeographic region (paired *t*-test, *P* < 0.0001). On average, the warm biogeographic region had a significant decline in kelp forest index over time (Fig. 6; *R* = -0.42, *P* = 0.07, for reserve sites and *R* = -0.55, *P* = 0.01, for fished sites). In contrast, rocky reefs in the cold water biogeographic region

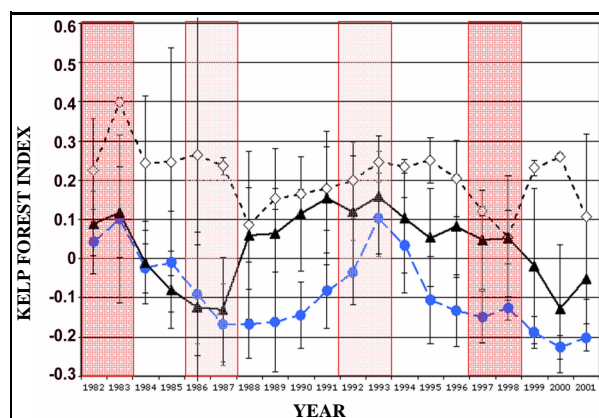


Figure 6. Average kelp forest index over time for three groups of rocky reefs ( $\pm$  95% confidence limits). Positive values represent kelp forest states and negative values represent barren states. Dark triangles represent fished sites in the cold biogeographic region; open diamonds represent a no-take reserve in the warm biogeographic region; and filled circles represent fished sites in the warm biogeographic region. Dark filled bars represent strong El Niños and light filled bars represent mild El Niños.

did not show any trends over time in the kelp forest index ( $R = -0.06$ ,  $P = 0.80$ ). There was no difference in the average temporal variance in kelp forest index between fished sites in the cold and warm biogeographic regions. The temporal variance in kelp forest index was significantly lower in reserve sites (0.11) than fished sites in the warm biogeographic region (0.19) (two tailed unpaired [unequal variance]  $t$ -test of the means of the variances,  $P = 0.026$ ).

A large and consistent decline in kelp forest index among sites followed the 1982 to 1983 El Niño. The response to the other El Niños and the La Niña was less consistent among sites. In particular, the kelp forest index actually increased at 10 of the 16 sites after the unusually calm 1986 to 1987 El Niño. After the three “stormy” El Niños, the kelp forest index declined at all the sites in the cold biogeographic region and at 72% of the fished sites in the warm biogeographic region, but did not decline in the reserve (in the reserve, a decline following 1982 to 1983 El Niño was offset by an increase following the 1997 to 1998 El Niño). After the La Niña, the kelp forest index increased at four of six sites in the cold biogeographic region, five of six of the fished sites in the warm biogeographic region and one of the two sites in the reserve. A paired  $t$ -test revealed that the kelp forest index responded differently to El Niños (all four El Niños, average change of  $-0.04$ ) than the La Niña (average change of  $+0.03$ ) (paired  $t$ -test,  $P = 0.027$ ). This effect was substantially stronger if only the stormy El Niños were compared (stormy El Niños, average change of  $-0.07$ , paired  $t$ -test,  $P = 0.0015$ ).

Not surprisingly, some of the physical factors correlated with each other. Maximum water

Table 1. Correlation coefficients (one year time lags) between kelp forest index and physical factors in three types of sites.

	SOI	Wave	Temp
Cold region	0.04	-0.6	-0.21
Reserve	0.07	0.06	-0.31
Warm region	0.14	-0.34	-0.19

temperatures in both biogeographic regions were highly correlated ( $R = 0.77$ ,  $P < 0.0001$ ). SOI (which is negatively correlated with El Niño) was negatively correlated with the maximum temperature in the cold region ( $R = -0.61$ ,  $P = 0.004$ ) and warm region ( $R = -0.45$ ,  $P = 0.046$ ). Wave intensity was positively correlated with the maximum temperature in the cold region ( $R = 0.45$ ,  $P = 0.046$ ) and warm region ( $R = 0.45$ ,  $P = 0.046$ ) but not significantly correlated with SOI ( $R = -0.21$ ,  $P = 0.37$ ).

Physical measures had stronger univariate associations with a one-year time lag than without a time lag, and we used this one-year time lag for the subsequent analyses. The univariate correlation matrix showed weak correlations between kelp forest index and physical factors (and these differed among reef groups) but, usually, the direction of the correlations were consistent with our predictions (Table 1). Results from the multiple regression analyses also differed among the three rocky reef groups. Changes in kelp forest index were not affected by physical factors in the reserve (Table 2; true for either the fully factorial model or with non-significant interactions removed). This may help explain why the variation in kelp forest index at unfished rocky reefs was lower than at similar fished rocky reefs. Changes in kelp forest index in the cold biogeographic region

Table 2. General linear model of the effects of physical factors on kelp forest index for sites in the no-take reserve (warm bioregion).

Term	Estimate	Std Error	$t$ Ratio	Prob > $ t $
Intercept	0.2676312	0.440295	0.61	0.5556
SOI	-0.004714	0.006167	-0.76	0.4607
Wave	0.3758442	0.431188	0.87	0.4020
Temp	-0.040489	0.024998	-1.62	0.1336
Temp $\times$ Wave	-0.15373	0.328414	-0.47	0.6489
Wave $\times$ SOI	-0.043525	0.04505	-0.97	0.3547
Temp $\times$ SOI	0.0046894	0.004431	1.06	0.3126
Temp $\times$ Wave $\times$ SOI	0.0205335	0.026132	0.79	0.4486

Table 3. (A) General linear model of the effects of physical factors on kelp forest index for fished sites in the cold bioregion; (B) with nonsignificant terms removed.

A

Term	Estimate	Std Error	<i>t</i> Ratio	Prob >   <i>t</i>
Intercept	-0.066589	0.347368	-0.19	0.8515
Temp	0.009366	0.019287	0.49	0.6368
Wave	-0.086709	0.159512	-0.54	0.5976
SOI	-0.003963	0.003033	-1.31	0.2180
Temp × Wave	-0.131163	0.136051	-0.96	0.3557
Wave × SOI	0.0106423	0.016984	0.63	0.5437
Temp × SOI	-0.003694	0.002847	-1.30	0.2210
Temp × Wave × SOI	0.0223191	0.0128	1.74	0.1091

B

Term	Estimate	Std Error	<i>t</i> Ratio	Prob >   <i>t</i>
Intercept	0.3270017	0.206116	1.59	0.1322
Temp	0.0027319	0.013639	0.20	0.8438
Wave	-0.312535	0.1117	-2.80	0.0129

were correlated only with wave intensity and this effect emerged only once non-significant interactions were removed (Table 3b). The greater the wave intensity, the more kelp forests declined the following year. Changes in the kelp forest index at fished rocky reefs in the warm biogeographic region were also significantly correlated with wave intensity (Table 4). Again, the greater the wave intensity, the more kelp forests declined the following year. However, the effect of wave intensity depended on water temperature (Table 4b). Here, declines in the kelp forest index with wave intensity were much stronger when the summer temperature was above 17.6 degrees. If the non-significant three-way interaction was removed, there was also a significant interaction between SOI and wave action (one that appeared to parallel the effect of temperature, in that declines in kelp forest index were stronger during El Niño events; under these conditions, wave intensity tended to aggregate into large storms). No sites had significant associations with physical factors when the sites were analyzed separately.

The sinking of the *Pac Baroness* did not result in corresponding change in kelp forests. Kelp forest index increased at both San Miguel sites in the year following the accident. On a broader scale, the average change in the kelp forest index in the cold biogeographic region was positive in the four

years following the accident. A similar change occurred in the warm biogeographic region, though not as strong. If the *Pac Baroness* had had an effect we would have expected a subsequent decrease in kelp forests in the cold biogeographic region compared to the warm biogeographic region in the years following the accident.

## DISCUSSION

As predicted, kelp forests at most sites declined immediately following El Niños and increased immediately following a La Niña. Strong El Niños had the most consistent effects. However, the changes were, on average, moderate, and the effects of El Niños were more inconsistent in the warm biogeographic region, particularly in the reserve. Because some temperate rocky reefs can recover within six months from even the most dramatic El Niño (Edwards 2004), our analyses would not detect changes occurring at less than annual temporal scales. In addition, some of the inconsistency may derive from the fact that the effects of physical factors can be patchy. For example, understory algae may be much less susceptible to physical disturbance from storms (Dayton 1984) and these algae contribute positively to our kelp forest index (although the correlation between kelp canopy and our kelp

Table 4. (A) General linear model of the effects of physical factors on kelp forest index for fished sites in the warm biogeographic region, (B) with nonsignificant terms removed.

A

Term	Estimate	Std Error	<i>t</i> Ratio	Prob >   <i>t</i>
Intercept	0.5098137	0.24201	2.11	0.0589
Temp	0.0098078	0.01374	0.71	0.4902
Wave	-0.586708	0.237004	-2.48	0.0308
SOI	0.0044648	0.00339	1.32	0.2146
Temp × Wave	0.5255835	0.180514	2.91	0.0141
Wave × SOI	0.022668	0.024762	0.92	0.3796
Temp × SOI	0.0043419	0.002435	1.78	0.1022
Temp × Wave × SOI	-0.015321	0.014364	-1.07	0.3090

B

Term	Estimate	Std Error	<i>t</i> Ratio	Prob >   <i>t</i>
Intercept	0.3995358	0.186753	2.14	0.0520
Temp	0.0021865	0.011594	0.19	0.8533
Wave	-0.376405	0.12609	-2.99	0.0105
SOI	0.0014145	0.001735	0.82	0.4297
Temp × Wave	0.3688388	0.109915	3.36	0.0052
Temp × SOI	0.0059408	0.001533	3.88	0.0019

index was significantly positive,  $R = 0.67$ ,  $P < 0.0001$ , other algae were able to contribute to the forested index). In addition, spatial variation in currents, temperature, light (Dayton et al. 1992), exposure (Graham et al. 1997), and substrate type (Dayton and Tegner 1989) can alter how the physical factors we measured affect kelp forests, resulting in patchiness in the changes on rocky reefs. This patchiness may weaken signals of physical effects at large spatial scales (Edwards 2004). Sometimes, large storms can negatively affect barrens by damaging urchins which are exposed to swell (Ebeling et al. 1985). This sets up the possibility for rocky reef communities to shift in opposite directions following a storm, depending on their starting point.

We were surprised by the overall weak correspondence between kelp forest indices and physical factors when we looked at all years, not just those following an event. Changes in kelp forest index from year to year were positively correlated among sites within a biogeographic region, but not strikingly so, suggesting that region wide physical factors had only minor effects on kelp forests potentially explaining, on average, 16% of the variation in kelp forest index. This could be due, in part, to variable recovery times

following an event. Longer recovery occurred in more southern locations (Edwards 2004), further emphasizing the interaction between vulnerability and biogeographic region. In a broad-scale study of the effects of the 1997 to 1998 El Niño, immediate impacts of large storms followed by poor nutrients were consistently dramatic among sites within a biogeographic region but recovery times varied appreciably within a biogeographic region (Edwards and Estes in press). In conclusion, short, patchy responses to El Niño followed by variable recovery times are likely to greatly reduce the synchronous, broad scale effects of physical factors on kelp forest communities.

The large-scale effects of physical factors that were significant are consistent with previous studies of the effects of El Niño on southern California kelp forests. Region-wide effects of wave intensity were negatively correlated with kelp forest index, particularly in the cold biogeographic region. This was likely due to large waves removing kelp from rocky reefs, resulting in a decrease in kelp forest index the following year. The effect of wave action in the warm biogeographic region only occurred during warm water periods. This may have been because high recruitment of kelp can often follow storms



(Dayton et al. 1992), but high recruitment followed by nutrient poor warm-water conditions can result in no survival of adult kelp plants (Dayton 1984). The reason this interaction did not occur in the cold biogeographic region may have been because temperatures in this region were rarely extreme enough to cause substantial mortality in kelp.

Rocky reefs in the reserve were always forested and had low variation in kelp forest index. Although this is consistent with expectations from the effects of fishing on kelp forests (Tegner and Dayton 2000), the small number of replicates in the reserve and lack of data before reserve establishment makes it difficult to separate innate characteristics of the site from the effects of fishing. Still, the reserves appeared more resilient to physical factors, perhaps because urchin populations are sufficiently low in reserves (Lafferty 2004) that kelp is able to successfully recolonize after storms and periods of low nutrients. Outside of reserves, the potential lack of drift following a punctuated loss of the kelp forest canopy can be followed by more intense grazing pressure by sea urchins which need to come out of hiding for food (Tegner and Dayton 1991). Fishing lobsters may be one reason why fished southern sites declined as kelp forests. Spiny lobsters, a subtropical group, are not as abundant at northern sites and are protected within the reserve (Lafferty 2004). Where lobsters are common, purple urchins are controlled and kelp forests persist (Lafferty 2004). It is interesting to note that most of what we know about the effects of El Niño are from fished kelp forests and, for this reason, our current understanding of climatic effects in southern California might not reflect historical conditions. Our results suggest that rocky reefs were less variable before intensive fishing than they are today. Fishing, by releasing purple urchins from predation, may have increased the vulnerability of kelp forests to El Niño. The recent addition of new reserves to the region will allow a replicated assessment of this hypothesis.

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