

# Catastrophe, recovery and range limitation in NE Pacific kelp forests: a large-scale perspective

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**ABSTRACT:** The 1997–98 El Niño was one of the strongest on record and resulted in widespread losses of the giant kelp *Macrocystis pyrifera* (Agardh) along the west coast of North America. Drawing on a rich history of studies that have shown abnormally large waves and warm nutrient-poor water associated with El Niños to negatively impact giant kelp populations at some locations in southern and Baja California, we examined (1) how these impacts scale up when considered across the species' geographic range in the NE Pacific Ocean and (2) if these impacts are generalizable over broad spatial scales. Working at 56 sites in 14 study locations over a 3 yr period (1997 to 2000), we examined how giant kelp populations were impacted by and recovered following the 1997–98 El Niño over a ~1500 km span along the west coast of North America. Our results indicate that while nearly all giant kelp disappeared from the southern one-third of the species' range along the coast of Baja California, Mexico, and heavy losses occurred throughout the central one-third of the species' range in southern California, USA, only minor impacts were observed throughout the northern one-third of the species' range in central California. Further, although highly variable among regions, these impacts were similar and generalizable among locations within each region. Our results also suggest that, as has been observed in local-scale studies, this large-scale variability in giant kelp mortality was driven by large-scale patterns in ocean temperature (nutrient concentration) and wave intensity. Recovery following El Niño, in contrast, was variable at multiple spatial scales and although not directly tested here, presumably influenced by numerous factors such as proximity to upwelling areas, competition with other algae, grazing, and propagule availability. Further, variability in the rates of recovery among locations resulted in a generally slow recovery of giant kelp throughout most of Baja California, and residual large-scale impacts of the El Niño were still evident 2 yr after the El Niño ended. As global climate change may lead to increases in the frequency and intensity of El Niños, our findings have broad implications for the ways in which ecosystems might be expected to respond to them and provide a measure by which their impacts to giant kelp ecosystems may be compared among events.

**KEY WORDS:** Biogeography · El Niño · Generality · Giant kelp · La Niña · Scale

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## INTRODUCTION

A fundamental goal of ecology is to understand patterns of species distribution and abundance over broad geographic areas and long time periods. Because such patterns tend to vary among multiple spatial and temporal scales, choosing the appropriate scale(s) at which to work can be an essential step in designing ecological studies (Dayton & Tegner 1984a, Levin 1992, 2000,

Lawton 1996, Gaston & Blackburn 1999, Underwood et al. 2000), especially those that examine how environmental processes influence species over large portions of their geographic ranges (e.g. Dayton & Tegner 1990, Zholdasova 1997, Connolly & Roughgarden 1998, Fowler-Walker & Connell 2002, Edwards 2004). However, while our understanding of small-scale processes has increased greatly over the past decades, difficulties in predicting catastrophic events and logistical

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challenges associated with conducting simultaneous field studies at a large number of widely separated sites have made the chronicling of range-wide responses by species to environmental catastrophes exceedingly difficult. One solution to this problem is to design studies that both span the geographic ranges of disturbances and target the spatial scales at which their impacts most strongly occur (Dayton & Tegner 1984a, Levin 1992, 2000, Carpenter 1998, Gaston & Blackburn 1999, Underwood et al. 2000, Edwards 2004). Such studies may also offer greater insight into the processes that create repeatable, generalizable biogeographic patterns that are not evident at smaller spatial scales, and thus help place small-scale experiments into a larger geographical context (Foster 1990, Underwood & Petraitis 1993, Lawton 1996, Gaston & Blackburn 1999, Fowler-Walker & Connell 2002).

One of the most important large-scale environmental disturbances to affect coastal marine ecosystems is the El Niño–Southern Oscillation (hereafter El Niño). Once used to describe the seasonal replacement of the cold north-flowing Peruvian Current with the southerly flow of warm water along the coasts of Ecuador and northern Peru, El Niño has come to represent interannual episodes of anomalously warm water, elevated sea level, and increased rainfall in the eastern tropical Pacific (Barber & Chavez 1983, Wooster & Fluharty 1985, Glynn 1988, Chavez et al. 1999). Although El Niños are generally thought of as low latitude events, they can transfer energy to mid and high latitudes, thereby affecting oceanographic and atmospheric conditions globally (Chelton et al. 1982, Wooster & Fluharty 1985, Glynn 1988, Chavez 1996). Historically, the extension of El Niño-related conditions into higher latitudes has resulted in range extensions, habitat redistributions, and massive mortalities in many seaweed, invertebrate, finfish, marine mammal, and seabird populations throughout much of the eastern Pacific Ocean (Chelton et al. 1982, Dayton & Tegner 1984b, 1990, Wooster & Fluharty 1985, Edwards 2004). Ecosystem recovery following El Niños, in turn, has been enhanced by anomalously cold, nutrient-rich water that arises during El Niño's counterpart, La Niña, which follows some (but not all) El Niños (Fielder 1984, Dayton et al. 1992, Tegner et al. 1997, Hayward et al. 1999).

Along the west coast of North America, ocean temperature is negatively correlated with ocean nutrient concentration such that coastal waters are largely nutrient depleted ( $<0.5 \mu\text{g-at NO}_3 \text{ l}^{-1}$ ) at temperatures above  $\sim 16^\circ\text{C}$  in southern and central California (Gerard 1982, Zimmerman & Kremer 1984), and above  $\sim 18^\circ\text{C}$  in Baja California (Hernández-Carmona et al. 2001). These conditions can be especially harmful to populations of the giant kelp *Macrocystis pyrifera*

(Agardh), which require concentrations of at least  $1 \mu\text{g-at NO}_3 \text{ l}^{-1}$  for growth and survival (Gerard 1982). While the coastal surface waters off southern and Baja California routinely exceed these temperatures during the summer, the effects are often ameliorated by horizontal advection of nutrient-rich water from adjacent areas, periodic wind-induced upwelling events, and vertical oscillations of the thermocline (internal waves) that pulse nutrient-rich water along the benthos into shallow subtidal habitats (Zimmerman & Kremer 1984). During El Niños, the thermocline deepens, thereby thickening the nutrient-poor surface layer and reducing the frequency and effectiveness of the nutrient pulses (Zimmerman & Robertson 1985). If these conditions persist for longer than  $\sim 2$  wk (as is the case during El Niños), giant kelp can become nutrient-stressed, begin to senesce (e.g. Gerard 1982, Zimmerman & Robertson 1985, Dean & Jacobsen 1986, Hernández-Carmona et al. 2001), and thus may become more vulnerable to removal by large waves. For example, the unusually large waves and nutrient-poor water associated with both the 1982–83 and 1997–98 El Niños resulted in severe mortality of giant kelp populations at numerous locations along southern California, USA, and Baja California, Mexico, although these impacts were highly variable within and among even closely situated populations (Dayton & Tegner 1984b, 1990, Foster & Schiel 1985, 1993, Zimmerman & Robertson 1985, Dayton et al. 1999, Lada et al. 1999, Hernández et al. 2000, 2001). How these local patterns of disturbance impacts scale up to drive regional patterns and whether they are generalizable across broad spatial scales is unclear, and is the focus of this study.

In early 1997, the trade winds in the western equatorial Pacific began to weaken, identifying the start of one of the strongest El Niños ever recorded (Wolter & Timlin 1998, Chavez et al. 1999). By April 1997, the thermocline in the eastern tropical Pacific had deepened by more than 90 m, reducing the efficiency of coastal upwelling and causing waters off the coast of Peru to become anomalously warm and nutrient-depleted. As the El Niño developed, these oceanographic conditions propagated toward higher latitudes, appearing off the west coast of California, USA, in August 1997 and persisting until April 1998. During this time, the region was also affected by unusually large ocean waves, some of which were caused by a series of strong El Niño-driven storms. Here, we report patterns of disturbance during and recovery following the 1997–98 El Niño in giant kelp forests throughout a  $\sim 1500$  km span of coastline along the west coast of North America (see Fig. 1). Our study effectively spans the continuous geographic range of giant kelp in the northeast Pacific Ocean, from Point Año Nuevo (Santa Cruz county, USA:  $37^\circ 06' \text{ N}$ ,  $122^\circ 20' \text{ W}$ ) to Punta Hipó-

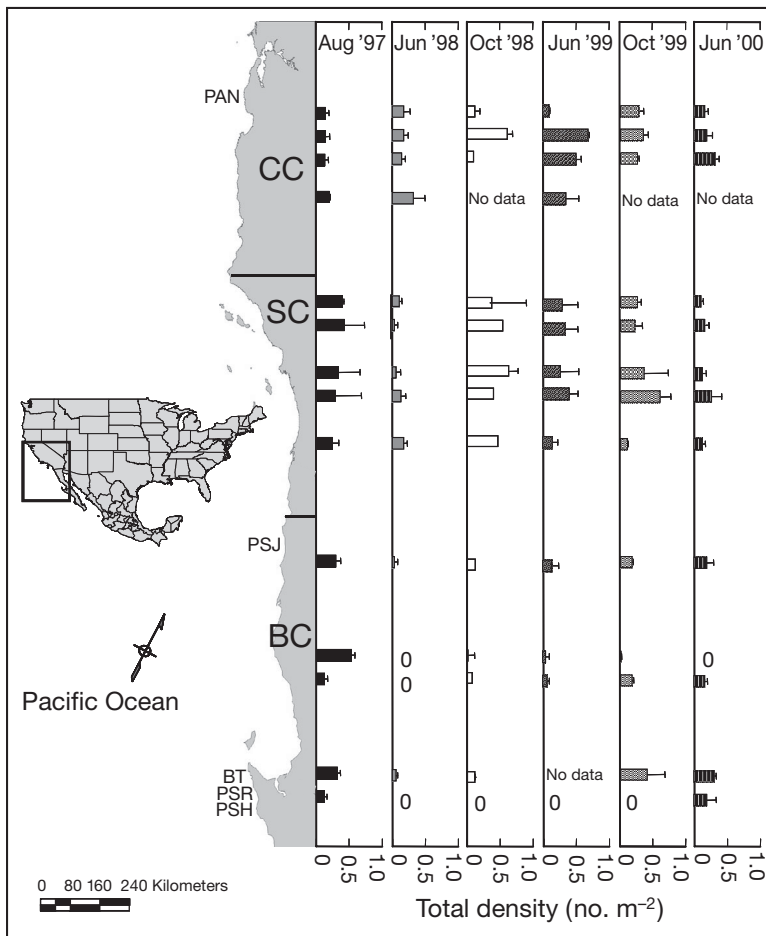


Fig. 1. *Macrocyctis pyrifera*. Mean (+1 SE) density at each of the 14 locations studied. Data include all individuals >1 m tall. Specific locations referred to in text but not sampled are also shown. PAN: Point Año Nuevo; PSJ: Punta San José; BT: Bahía Tortugas; PSR: Punta San Roque; PSH: Punta San Hipólito. The 6 survey periods are presented sequentially from left to right, the graphs are vertically oriented, and the 14 survey locations lie opposite to their placement on the coast. CC, SC, BC are central, southern and Baja California, respectively

lito (Baja California Sur, Mexico: 27° 11' N, 114° 23' W; Druehl 1970, Dayton 1985, Foster & Schiel 1985), with the possible exception of a few 'scattered pockets' of giant kelp that have been reported along the coast of SE Alaska (Gabrielson et al. 2000). The early forecast of this El Niño allowed us to establish a pre-disturbance record of giant kelp abundance at 56 sites from 14 locations across this range while El Niño's brief and punctuated nature, the giant kelp's relatively short generation time (<6 mo), and the occurrence of the strong 1998–99 La Niña (Hayward et al. 1999) facilitated our ability to chronicle both the impacts of this disturbance and the patterns of recovery following it. While the impacts of El Niño on giant kelp populations have been well described at local scales, especially in southern and Baja California (e.g. Dayton & Tegner

1984b, 1990, Zimmerman & Robertson 1985, Tegner et al. 1997, Ladah et al. 1999, Hernández-Carmona et al. 2001), we tested the hypothesis that these impacts were widespread and generalizable across broad spatial scales by examining them at 56 sites spanning the giant kelp's geographic range in the North Pacific Ocean over a 3 yr period. We then compared these impacts with large-scale changes in ocean temperature and wave intensity, factors known to have strong influences on kelp survival and recovery at local scales, to evaluate their potential for causing regional patterns of kelp mortality and recovery.

## MATERIALS AND METHODS

To examine large-scale impacts of El Niño on giant kelp populations in the NE Pacific, we divided the geographic range of the giant kelp *Macrocyctis pyrifera* into 3 regions, each encompassing 400 to 600 km of coastline and defined by unique oceanographic conditions (see Edwards 2004). These were identified as 'Baja California' (Punta San Hipólito to Punta Banda), 'southern California' (Punta Banda to Point Conception) and 'central California' (Point Conception to Point Año Nuevo) (Fig. 1). Within each region, we identified 5 locations, and within each location we identified four 8 to 12 m deep sites. Locations were haphazardly selected based on their accessibility and to approximate even geographic coverage within each region, and sites within each

location were selected based on the presence of rocky substrate. However, 1 location in central California had to be dropped from the study due to lost accessibility, thus reducing the number of locations in that region to 4. We then estimated giant kelp density at each site in August 1997, June 1998, October 1998, June 1999, October 1999, and June 2000 (summer and autumn) by counting all individuals >1 m tall along three randomly directed 20 m × 2 m transects. Due to difficulties of relocating exact transect lines on subsequent surveys, transect positions were randomly re-selected on each sample date. Density estimates for each site were then determined from the average of its 3 transects, estimates for each location were determined from the average of its 4 sites, and estimates for each region were determined from the average of its

4 (central California) or 5 (southern and Baja California) locations. However, due to problems associated with unsafe or prohibitory diving conditions, we were unable to sample all sites on every sampling date. This introduced a small amount of imbalance into our sampling design when considered across all sample dates. To resolve this, we imposed balance by setting our level of replication for sites within each location at 4 on all sample dates. In the few cases where only 3 sites were sampled, we estimated the value for the remaining site from the average of the other 3 sites (Shaw & Mitchell-Olds 1993, Underwood 1997). In contrast, when all data for a given location were missing from the model we believed removing that location from the model would result in too great a loss of information and therefore kept the statistical model consistent with the sample design, and simply alert the reader to the difference in sample sizes (Underwood 1997) and advise caution regarding strict interpretation of the reported *p*-values, especially those near the 5% critical level.

Our sample design included 56 sites dispersed among 14 study locations that spanned almost 1500 km of coastline. Consequently, logistical constraints associated with working over such a large area resulted in a loss of local spatial and temporal detail in lieu of enhanced understanding of broad scale and long-term patterns. As a result, and because our sampling design resulted in a period of ~7 mo between the October and June surveys, differences in total (all individuals >1 m tall) giant kelp abundance between sample dates resulted not only from changes (i.e. mortality) in the existing plants, but also included recruitment of new individuals (see Edwards 2004). Consequently, strict interpretation of changes in total kelp abundance may be misleading because they are likely to be confounded by both loss of existing plants and the recruitment of new individuals. To resolve this, we examined changes in (older) adult (individuals with  $\geq 4$  stipes per plant: Dayton et al. 1984, 1992) giant kelp density among geographic regions, locations within each region, and sample dates with a 3-factor, mixed-model, nested ANOVA (with region as a fixed factor and location nested within region and sample date as random factors). Pairwise differences in adult giant kelp density between successive sample dates were subsequently assessed for each region separately using Bonferroni-adjusted post hoc comparisons. Because of the large number of possible comparisons of interest ( $n = 15$ ) and the corresponding reduction in statistical power for each comparison (*p* would need to be <0.0035 to detect a significant difference between 2 sample dates within any region if the overall Type I error rate were held at 0.05), we believe adjusting our Type I error for all 15 comparisons would too greatly

increase the probability of Type II errors. Thus, we controlled for Type I error inflation only for comparisons between sequential dates for the 3 regional contrasts (i.e. Baja vs. southern California, Baja vs. central California, and southern vs. central California) (i.e.  $n = 3$  comparisons) and we advise the reader to weigh the importance of Type I vs. Type II errors when interpreting the results of these post hoc tests.

Ocean temperatures (SSTs) were recorded at 3 locations (roughly at the southern, middle and northern portions) within each region. Mexico's Centro de Investigaciones Biológicas del Noroeste (CIBNOR) in La Paz kindly provided SST data for Baja and southern California, while data for central California were provided by Granite Canyon Marine Laboratories (California Department of Fish and Game), the National Oceanic and Atmospheric Administration's (NOAA) California Buoy Data web page and Hopkins Marine Station (Stanford University). Ocean wave data (significant wave height and dominant wave period) for central and southern California were obtained for a single offshore location near the center of each region from NOAA's California Buoy Data web page, and the corresponding estimates of wave intensity, horizontal orbital displacement ( $D_H$ ) at the surface, were calculated at the surface over 12 m depth using:

$$D_H = -\left(\frac{ht}{2}\right) \times \left(\frac{\frac{\cosh(2\pi)^2 d}{gp}}{\frac{\sinh(2\pi)^2 d}{gp}}\right)$$

where  $ht$  = significant wave height,  $d$  = depth of water (12 m),  $g$  = gravitational acceleration; and  $p$  = dominant wave period (Denny 1988).

## RESULTS

Sea surface temperatures in the coastal waters off some locations in central California exceeded 16°C for a brief (<2 wk) period in August and September 1997, whereas temperatures exceeded 16°C for nearly a full year (April 1997 to March 1998) in the coastal waters throughout southern and Baja California (Fig. 2A). Consequently, these waters were largely limiting in nutrient availability (<0.5  $\mu\text{g-at NO}_3\text{I}^{-1}$ ; Fig. 3). During this period, unusually large ocean waves associated with intensified winter storms also impacted the west coast of North America, although these waves were much larger in central than in southern California (Fig. 2B). While wave-height data are not available for Baja California, particularly large wave events were observed during Hurricane Linda in September 1997 (G. Hernández-Carmona pers. comm.). While these anomalous conditions, either separately or in combina-

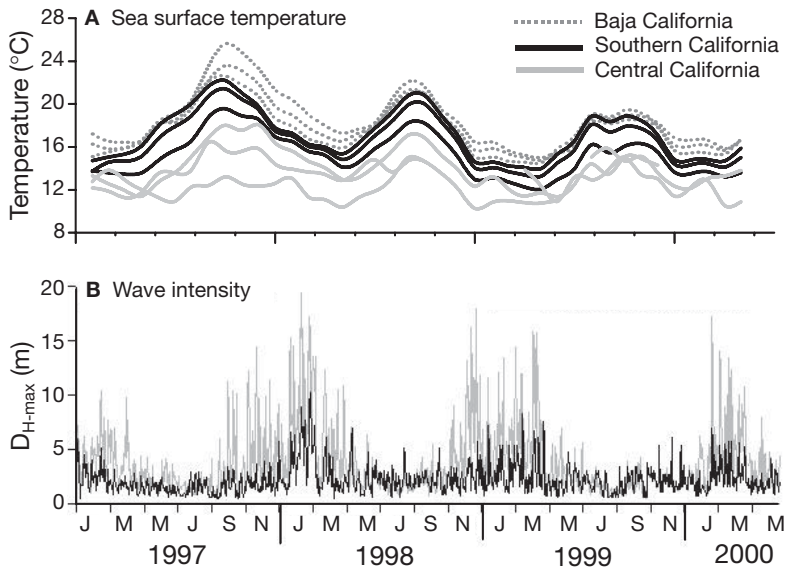


Fig. 2. (A) Average monthly sea surface temperature and (B) daily wave intensity for central, southern and Baja California (1997 to 2000). Sea surface temperature data were obtained for 3 locations (approximately from southern, middle and northern end of each region) within each region; wave intensity was determined by calculating maximum horizontal orbital displacement ( $D_H$ ) at the surface using significant wave height and period data

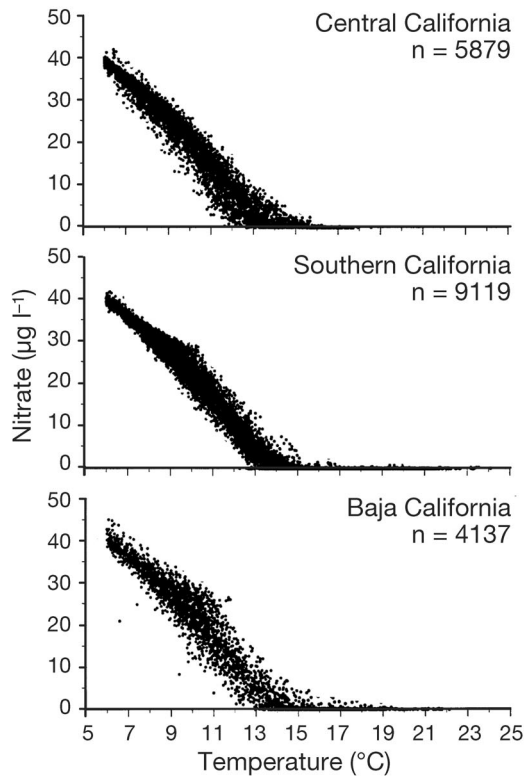


Fig. 3. Relationship between ocean temperature and nutrient concentration for central, southern and Baja California. Data obtained from the California Cooperative Oceanic Fisheries Investigation (CalCOFI) database for the upper 40 m of water from inshore stations. Data were compiled using Ocean Data View (Version 4.0.012)

tion, are widely known to negatively impact giant kelp populations when considered at local scales (Dayton & Tegner 1984b, 1990, Zimmerman & Robertson 1985, Hernández-Carmona et al. 2001), our results indicate that they can be scaled up and thus result in large-scale mortality to giant kelp populations when considered over the species' geographic range along the west coast of North America (see also Edwards 2004).

Although changes in adult, giant kelp density among the geographic regions were not statistically significant when considered over the entire 3 yr study (Date  $\times$  Region interaction;  $p \leq 0.199$ ; Table 1), changes between successive sample dates for both Baja and southern California, when analyzed separately following ANOVA, were significant. Specifically, during the El Niño (August 1997 vs. June 1998), adult giant kelp mortality was relatively low ( $\sim 27\%$ ) and statistically insignificant (Bonferroni  $p \leq 0.999$ ) in central California, but was much greater ( $\sim 88\%$ ) and highly significant in southern (Bonferroni  $p \leq 0.008$ ) and Baja ( $>99\%$ ; Bonferroni  $p \leq 0.002$ ; California) (Table 2, Fig. 4). In fact, except for a few individuals reported to have survived near Punta San José (Ladah et al. 1999), adult giant kelp disappeared entirely from the Baja California peninsula and a large portion of southern California. Thus, prior to the El Niño, adult giant kelp density appeared similar among the 3 regions whereas immediately following the El Niño, large differences were observed (Fig. 4).

Immediately following the El Niño, the west coast of North America experienced a period of cold, nutrient-rich, water during the 1998–99 La Niña (Fig. 2A). Although highly variable among locations within each region (Fig. 1), a rapid recovery of giant kelp populations during this period throughout southern California allowed the species to re-establish itself across much of the central third of its range within 6 mo after the El Niño ended. While we recognize that giant kelp density has been inherently dynamic over the past several decades, our August 1997 densities were similar to those obtained from long-term monitoring programs at 3 locations: Point Loma (Dayton et al. 1992), San Nicolas Island (J. A. Estes unpubl. data), and Stillwater Cove (M. S. Foster unpubl. data). Therefore, while we define 'recovery' as a return to pre-El Niño densities, we believe that the August 1997 survey date provides an appropriate benchmark against which to assess recovery in general following the El Niño. This occurred primarily through recruitment of new indi-

Table 1. *Macrocystis pyrifera*. Results of a 3-factor, mixed-model, nested ANOVA testing effects of survey date (random), region (fixed), and location within region (random) on density of all adult ( $\geq 4$  stipes) giant kelp

Source	SS	df	MS	F	p
Date	0.042	4	0.011	0.269	0.896
Region	0.170	1	0.170	3.541	0.084
Location (Region)	0.662	10	0.066	1.698	0.109
Date $\times$ Region	0.576	12	0.048	1.451	0.145
Date $\times$ Location (Region)	1.794	46	0.039	1.178	0.218
Error	7.217	218	0.033		

Table 2. *Macrocystis pyrifera*. Results (p-values) of Bonferroni-adjusted (for 3 comparisons), post hoc, planned comparisons assessing differences in adult density between successive sample dates within each region. Boldface indicates significant differences ( $p \leq 0.05$ ) between sample dates

Region	Aug '97	Jun '98	Oct '98	Jun '99	Oct '99
	vs. Jun '98	vs. Oct '98	vs. Jun '99	vs. Oct '99	vs. Jun '00
Baja California	<b>0.002</b>	0.999	0.999	0.999	0.570
Southern California	<b>0.008</b>	<b>0.002</b>	0.999	0.999	0.999
Central California	0.999	0.999	0.999	0.870	0.999

individuals; regrowth from surviving holdfasts was rarely observed. In contrast, giant kelp recovery throughout the southern third of its range in Baja California was generally poor immediately following the El Niño, occurring in some locations but requiring considerably more time in others (Fig. 1). In fact, a complete absence of both juvenile and adult giant kelp persisted at many locations in Baja California until nearly 2 yr after El Niño ended. Exceptions occurred at locations with strong coastal upwelling (e.g. Bahía Tortugas and Isla San Martín; Dawson 1951) and where propagule availability may have been greater because of the enhanced survival of microscopic life stages of the giant kelp (e.g. Ladah et al. 1999, Hernández-Carmona et al. 2001).

During the following 18 mo, giant kelp recovered throughout most of Baja California, although residual impacts of the 1997–98 El Niño on giant kelp abundance remained evident at a regional scale (Figs. 1

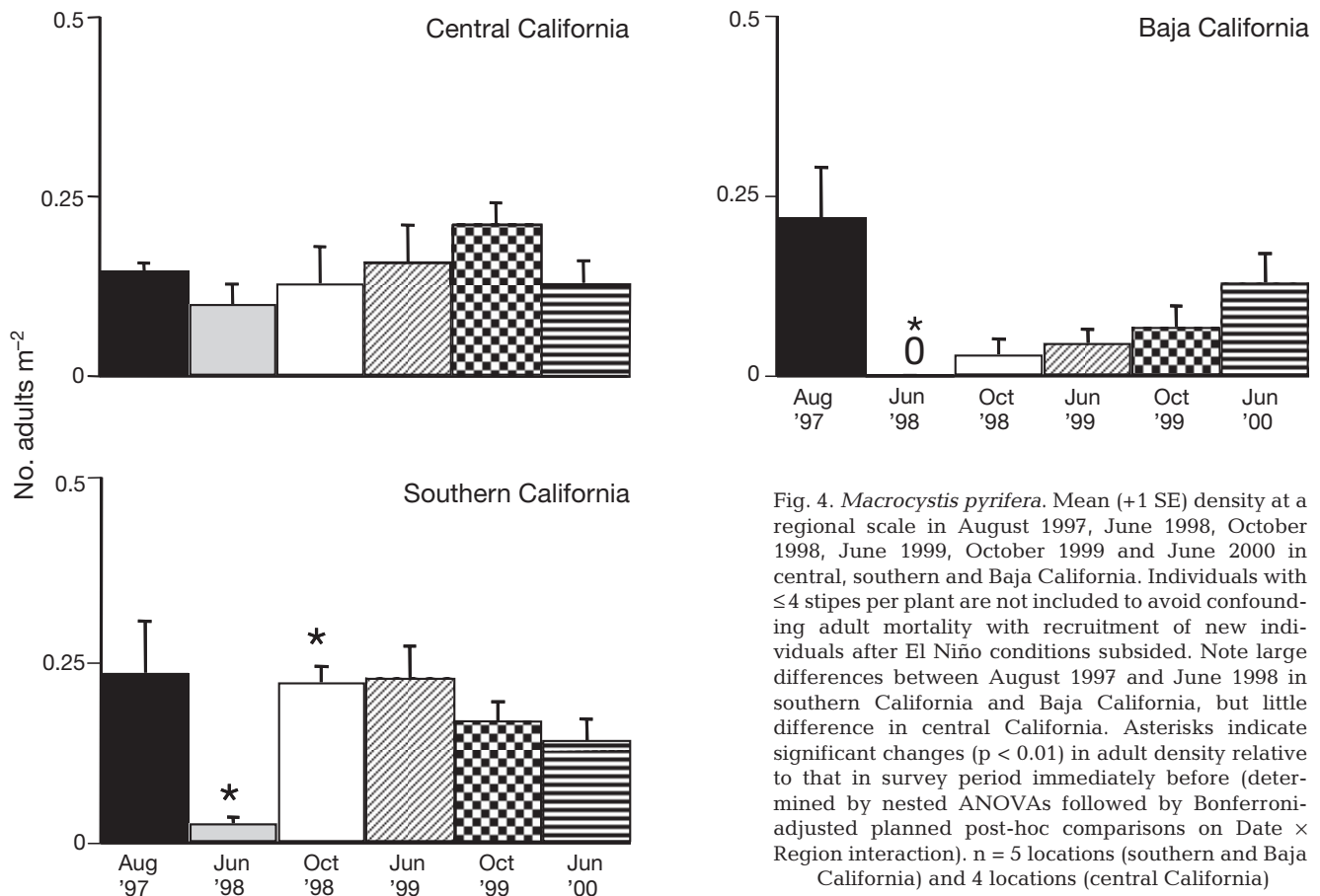


Fig. 4. *Macrocystis pyrifera*. Mean (+1 SE) density at a regional scale in August 1997, June 1998, October 1998, June 1999, October 1999 and June 2000 in central, southern and Baja California. Individuals with  $\leq 4$  stipes per plant are not included to avoid confounding adult mortality with recruitment of new individuals after El Niño conditions subsided. Note large differences between August 1997 and June 1998 in southern California and Baja California, but little difference in central California. Asterisks indicate significant changes ( $p < 0.01$ ) in adult density relative to that in survey period immediately before (determined by nested ANOVAs followed by Bonferroni-adjusted planned post-hoc comparisons on Date  $\times$  Region interaction).  $n = 5$  locations (southern and Baja California) and 4 locations (central California)

& 4). However, variability in recovery rates among locations in Baja California resulted in a ~70 km temporary northward shift in the giant kelp's southern limit, from Punta San Roque to Bahía Tortugas, that persisted for almost 2 yr following the El Niño. A similar pattern occurred following the 1982–83 El Niño, when the giant kelp's southern range limit shifted northward ~50 km from Punta San Hipólito to Punta San Roque (Hernández-Carmona et al. 2001). This shift persisted for almost 20 yr, with giant kelp finally returning to Punta San Hipólito in late 2001 (Edwards & Hernández-Carmona 2005). Such demographic and distributional impacts on giant kelp were not observed at the species' northern range limit, although observations made during the 1982–83 El Niño indicate that significant giant kelp loss occurred in central California (Dayton & Tegner 1990). Taken together, our results indicate that while the impacts of El Niño were strongest and most easily identified at very large spatial scales (see also Edwards 2004), recovery was spatially complex and variable among locations within each region. Furthermore, these results indicate that strong El Niños can cause substantial temporary reductions in abundance rather than simple latitudinal shifts in the distribution of giant kelp, thus suggesting that increases in the frequency and/or intensity of these events resulting from global warming (e.g. Rodbell et al. 1999) may result in a reduction or increased variability in the geographic range of this ecologically dominant species in the northeast Pacific Ocean.

## DISCUSSION

Our conclusions that the 1997–98 El Niño resulted in widespread mortality to populations of giant kelp along the west coast of North America and that these impacts were driven, at least in part, by anomalously warm ocean temperatures (low nutrient availability) and increased wave activity are certainly not novel (e.g. Dayton & Tegner 1984b, 1990, Dayton et al. 1984, 1992, Foster & Schiel 1985, 1993, Zimmerman & Robertson 1985, Tegner et al. 1997, Ladah et al. 1999, Hernández-Carmona et al. 2000, 2001, Edwards 2004). However, while similar conclusions about El Niño impacts on giant kelp can be discerned from a review of other studies, each of these studies found considerable variation in these disturbance impacts both within and among even closely situated populations. This smaller-scale variation has largely been attributed to spatial heterogeneity in factors such as species-specific interactions with subsurface kelps and understory algae, urchin grazing, relative positioning along long-shore current and wave-exposure gradients, substrate stability and depth, and spatial heterogeneity in the

vertical stratification of temperature, nutrients and salinity. Our study also found small-scale variability in disturbance impacts, but when placed in a larger geographical context, this local scale variability was largely insignificant compared with regional patterns of variability in these impacts (see also Edwards 2004). We believe this to be a novel perspective that provides us with a metric by which these disturbance impacts can be more clearly described and perhaps compared among different El Niños. Furthermore, although our analyses are primarily correlative in nature, understanding the spatial scale at which these impacts most strongly occurred allowed us to link them to the appropriate environmental variables believed responsible for causing them. For example, we believe the regional differences in giant kelp mortality resulted from regional variability in the synergistic effects of temperature and wave stress, which dominated factors operating at smaller scales and thus swamped smaller-scale variability (e.g. Tegner et al. 1997). We again are careful to point out that these factors, both alone and in combination, are well-known to have dramatic negative impacts on giant kelp when examined at local scales. However, our study again suggests that the impacts of these factors can override local scale processes and be scaled up to result in widespread losses of giant kelp populations over a large portion of their geographic range. This, however, was not true for the recovery of giant kelp populations following El Niño, which was variable at both regional and local scales and not as easily linked to specific generalizable environmental factors. One striking observation to emerge from this study was that the absence of giant kelp recruitment at some locations in Baja California during the 2 yr following the El Niño resulted in overall poor giant kelp recovery throughout the southern third of the species' range. This, in turn, resulted in regional-scale impacts that were still evident long after the El Niño ended, and a corresponding shift in the species' southern range limit (see also Edwards & Hernández-Carmona 2005).

In view of the extremely large-scale nature of some human-induced impacts on global ecosystems (Vitousek et al. 1997) and the inevitability of future environmental catastrophes, our findings raise several points of wider concern over the manner in which ecosystems are likely to respond to extreme events. First, catastrophes can negatively impact species across most or all of their ranges (e.g. Zholdasova 1997), raising the need for large-scale studies to examine them (Carpenter 1998). In this study, we found that the 1997–98 El Niño resulted in very large-scale impacts to giant kelp populations along the west coast of North America, as demonstrated by the near-complete loss of all giant kelp throughout the southern one-third to one-half of

the species' range, but only small impacts throughout the northern one-third of this range. This widespread loss represented an overall reduction in total abundance rather than a northward shift in the species' geographic range. Second, the scale of ecosystem recovery following environmental catastrophes may be quite different from the scale of the original impact (Turner & Dale 1998). For example, while the impacts of the 1997–98 El Niño were most easily described at regional scales, recovery following the El Niño was spatially complex and variable at multiple spatial scales, especially among locations within each region (see also Edwards 2004). Third, the factors responsible for these impacts and recovery from them can be the interactive effects of different forcing factors. Numerous studies in southern and Baja California have shown very clearly that elevated sea temperatures (reduced nutrients) and increased wave stress associated with El Niños can result in severe mortality to giant kelp populations (Dayton & Tegner 1984b, 1990, Dayton et al. 1984, 1992, Foster & Schiel 1985, 1993, Zimmerman & Robertson 1985, Tegner et al. 1997, Ladah et al. 1999, Hernández-Carmona et al. 2000, 2001, Edwards 2004). While this has largely been discerned from studies at a few locations in southern and Baja California, our study shows that changes in these environmental conditions can be applied across very large scales (hundreds to thousands of kilometers) and thereby be responsible for regional patterns of giant kelp mortality. However, considered across the giant kelp's geographic range, these factors appeared insufficient to individually account for the smaller-scale differences in recovery following El Niño. Rather, other factors such as proximity to upwelling areas, competition, grazing, and propagule availability are probably important to recovery (Dayton & Tegner 1990, Dayton et al. 1992, 1999, Ladah et al. 1999, Hernández-Carmona et al. 2001, Edwards & Hernández-Carmona 2005).

Obvious tradeoffs exist when allocating sampling effort to one or a few locations versus spreading this effort over a larger number of locations. Large-scale sampling necessarily means that less effort can be allocated to each location, resulting in a reduction in local scientific detail. This can be especially important if factors operating at small scales are the most important factors in structuring biological communities. Nonetheless, we support a growing body of literature (e.g. Dayton & Tegner 1984a, Weins 1989, Levin 1992, 2000, Lawton 1996, Carpenter 1998, Underwood et al. 2000, Edwards 2004) that recommends that future studies on the ecological impacts of large-scale disturbances carefully consider the spatial extent over which they are likely to occur, focus their findings on those scales that best describe the impacts of interest, and correlate

these impacts with the appropriate factors operating at these scales (see also Chapman et al. 1995, Connell et al. 1997, Karlson & Cornell 1998, Hughes 1999). Doing so will greatly enhance our ability not only to fully describe the larger-scale nature and magnitude of catastrophic events, but also to provide a better metric by which these events can be compared to each other.

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#### LITERATURE CITED

- Barber RT, Chavez FP (1983) Biological consequences of El Niño. *Science* 222:1203–1210
- Carpenter SR (1998) The need for large-scale experiments to assess and predict the response of ecosystems to perturbation. In: Pace ML, Groffman PM (eds) *Successes, limitations, and frontiers in ecosystem*. Science. Springer-Verlag, Berlin, p 287–312
- Chapman MG, Underwood AJ, Skilleter GA (1995) Variability at different spatial scales between a subtidal assemblage exposed to the discharge of sewage and two control assemblages. *J Mar Biol Ecol* 189:103–122
- Chavez FP (1996) Forcing and biological impact of onset of the 1982–83 El Niño in central California. *Geophys Res Lett* 23:265–268
- Chavez FP, Strutton PG, Friederich GE, Feely RA, Feldman GC, Foley DG, McPhaden MJ (1999) Biological and chemical response of the Equatorial Pacific Ocean to the 1997–98 El Niño. *Science* 286:2126–2131
- Chelton DB, Bernal PA, McGowan JA (1982) Large-scale interannual physical and biological interaction in the California Current. *J Mar Res* 40:1095–1125
- Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol Monogr* 67:461–488
- Connolly SR, Roughgarden J (1998) A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. *Am Nat* 151:311–326
- Dawson EY (1951) A further study of upwelling and associated vegetation along Pacific Baja California, Mexico. *J Mar Res* 10:39–58
- Dayton PK (1985) Ecology of kelp communities. *Annu Rev Syst Ecol* 16:215–245
- Dayton PK, Tegner MJ (1984a) The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In: Price PW, Slobodchikoff CN, Gaud WS (eds) *A new ecology: novel approaches to interactive systems*. John Wiley & Sons, New York, p 458–481
- Dayton PK, Tegner MJ (1984b) Catastrophic storms, El Niño, and patch stability in a southern California kelp community. *Science* 224:283–285



- Dayton PK, Tegner MJ (1990) Bottoms beneath troubled waters: benthic impacts of the 1982–1984 El Niño in the temperate zone. In: Glynn PW (ed) *Global ecological consequences of the 1982–83 El Niño–Southern Oscillation*. Elsevier, Miami, FL, p 433–472
- Dayton PK, Currie V, Gerrodette T, Keller BD (1984) Patch dynamics and stability of some California kelp communities. *Ecol Monogr* 54:253–289
- Dayton PK, Tegner MJ, Parnell PE, Edwards PB (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol Monogr* 62:421–445
- Dayton PK, Tegner MJ, Edwards PB, Riser KL (1999) Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecol Monogr* 69:219–250
- Dean TA, Jacobsen FR (1986) Nutrient-limited growth of juvenile kelp, *Macrocystis pyrifera*, during the 1982–1984 'El Niño' in southern California. *Mar Biol* 90:597–601
- Denny MW (1988) *Biology and the mechanics of the wave-swept environment*. Princeton University Press, Princeton, NJ
- Druehl L (1970) The pattern of Laminariales distribution in the northeast Pacific. *Phycologia* 9:237–247
- Edwards MS (2004) Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the Northeast Pacific. *Oecologia* 138:436–447
- Edwards MS, Hernández-Carmona (2005) Delayed recovery of giant kelp near its southern range limit in the North Pacific Ocean following El Niño. *Mar Biol* 147:273–279
- Fielder PC (1984) Satellite observations of the 1982–1983 El Niño along the US Pacific coast. *Science* 224:1251–1254
- Foster MS (1990) Organization of macroalgal communities in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia* 192:21–34
- Foster MS, Schiel DR (1985) The ecology of giant kelp forests in California: a community profile. *US Fish Wildl Serv Biol Rep* 85(7.2)
- Foster MS, Schiel DR (1993) Zonation, El Niño disturbance, and the dynamics of subtidal vegetation along a 30 m depth gradient in two giant kelp forests. In: Battershill CN, Schiel DR, Jones GP, Creese RG, MacDiarmid AB (eds) *Proc 2nd Int Temp Reef Symp*. NIWA Marine, Wellington, p 151–162
- Fowler-Walker MJ, Connell SD (2002) Opposing states of a subtidal habitat across temperate Australia: consistency and predictability in kelp canopy–benthic associations. *Mar Ecol Prog Ser* 240:49–56
- Gabrielson PW, Widdowson TB, Lindstrom SC, Hawkes MW, Scagel RF (2000) Keys to the benthic marine algae and seagrasses of British Columbia, Southeast Asia, Washington, and Oregon. University of British Columbia, Vancouver
- Gaston KJ, Blackburn TM (1999) A critique for macroecology. *Oikos* 84:353–368
- Gerard VA (1982) Growth and utilization of internal nitrogen reserves by the giant kelp *Macrocystis pyrifera* in a low nitrogen environment. *Mar Biol* 66:27–35
- Glynn PW (1988) El Niño–Southern Oscillation 1982–1983: nearshore population, community, and ecosystem responses. *Annu Rev Ecol Syst* 19:309–345
- Hayward TL, Durazo R, Murphree T, Baumgartner TR and 8 others (1999) The state of the California Current in 1998–1999: transition to cool-water conditions. *Calif Coop Ocean Fish Investig* 40:29–62
- Hernández-Carmona G, García O, Robledo D, Foster MS (2000) Restoration techniques for *Macrocystis pyrifera* (Phaeophyceae) populations at the southern limit of their distribution in México. *Bot Mar* 43:273–284
- Hernández-Carmona G, Robledo D, Serviere-Zaragoza E (2001) Effect of nutrient availability on *Macrocystis pyrifera* recruitment survival near its southern limit of Baja California. *Bot Mar* 44:221–229
- Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397:59–63
- Karlson RH, Cornell HV (1998) Scale-dependent variation in local vs. regional effects on coral species richness. *Ecol Monogr* 68:259–274
- Ladah LB, Zertuche-González JA, Hernández-Carmona G (1999) Giant kelp (*Macrocystis pyrifera*, Phaeophyceae) recruitment near its southern limit in Baja California after mass disappearance during ENSO 1997–1998. *J Phycol* 35:1106–1112
- Lawton JH (1996) Patterns in ecology. *Oikos* 75:145–147
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Levin SA (2000) Multiple scales and the maintenance of biodiversity. *Ecosystems* 3:498–506
- Rodbell TD, Seltzer GO, Anderson DM, Abbott MB, Enfeld DB, Newman IJH (1999) A ~15,000-year record of El Niño alluviation in southwestern Ecuador. *Science* 283:516–520
- Shaw RG, Mitchell-Olds T (1993) ANOVA for unbalanced data: an overview. *Ecology* 74:1638–1645
- Tegner MJ, Dayton PK, Edwards PB, Riser KL (1997) Large-scale, low-frequency oceanographic effects on kelp forest successions: a tale of two cohorts. *Mar Ecol Prog Ser* 146: 117–134
- Turner MG, Dale VH (1998) Comparing large, infrequent disturbances: what have we learned? *Ecosystems* 1:493–496
- Underwood AJ (1997) *Experiments in ecology*. Cambridge University Press, Cambridge
- Underwood AJ, Petraitis PS (1993) Structure of intertidal assemblages in different locations: how can local processes be compared? In: Ricklefs R, Schluter D (eds) *Species diversity in ecological communities*. University of Chicago Press, Chicago, IL, p 38–51
- Underwood AJ, Chapman MG, Connell SD (2000) Observations in ecology: you can't make progress on process without understanding the patterns. *J Exp Mar Biol Ecol* 250:97–115
- Vitousek PM, Mooney HA, Lobchenco J, Melillo JM (1997) Human domination of earth's ecosystems. *Science* 277: 494–499
- Weins JA (1989) Spatial scaling in ecology. *Funct Ecol* 3: 385–397
- Wolter K, Timlin MS (1998) Measuring the strength of ENSO events: how does the 1997/98 rank? *Weather* 53:315–324
- Wooster WS, Fluharty DL (1985) El Niño North. Washington Sea Grant Program, Seattle, WA
- Zholdasova I (1997) Sturgeons and the Aral Sea ecological catastrophe. *Environ Biol Fish* 48:373–380
- Zimmerman RC, Kremer JN (1984) Episodic nutrient supply to a kelp forest ecosystem in Southern California. *J Mar Res* 32:591–604
- Zimmerman RC, Robertson DL (1985) Effects of El Niño on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California. *Limnol Oceanogr* 30:1298–1302