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Delayed recovery of giant kelp near its southern range limit in the North Pacific following El Niño

Received: 14 June 2004 / Accepted: 29 November 2004 / Published online: 19 January 2005
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Abstract The northern distribution limit of giant kelp, *Macrocystis pyrifera* (Agardh), along the Pacific coast of North America is relatively stable near Point Año Nuevo, California, but its southern limit has varied over hundreds of kilometers along the Baja California peninsula during the past 20 years. The factors that drive this variability in the southern limit were examined by: (1) quantifying the abundances of *M. pyrifera* and the subsurface stipitate kelp, *Eisenia arborea* (Areschoug), near *M. pyrifera*'s then southern limit at Punta San Roque (27°15'N; 114°42'W) on ten occasions between August 1997 and June 2002 (prior to and following the 1997/1998 El Niño Southern Oscillation); (2) initiating a field manipulation at Punta San Roque in June 2000 to examine competition between these two kelp species; and (3) surveying 20 additional sites near Punta San Hipólito (27°01'N; 114°00'W) in June 2002 to determine whether *M. pyrifera* populations had recovered to their pre-1982/1983 El Niño southern range limit after ~20 years of absence. These observations and the experimental results suggest that *M. pyrifera* is removed from its southern limit by the high temperatures and large waves associated with El Niños, while *E. arborea* is able to survive and recruit in high densities and thereby delay or even prevent *M. pyrifera*'s recovery. An inverse relationship was observed between these two species over the 5-year study. The field experiment showed that at both 4 months and 1 year after areas occupied by *E. arborea* were cleared, substantial recruitment of *M. pyrifera* occurred, while recruitment was negligible in

uncleared areas. This study suggests that the southern range limit of *M. pyrifera* is determined by increased mortality and recruitment failure following the warm temperatures and low nutrient conditions associated with El Niños, limited substrate availability, and by competition with the more persistent populations of *E. arborea*.

Introduction

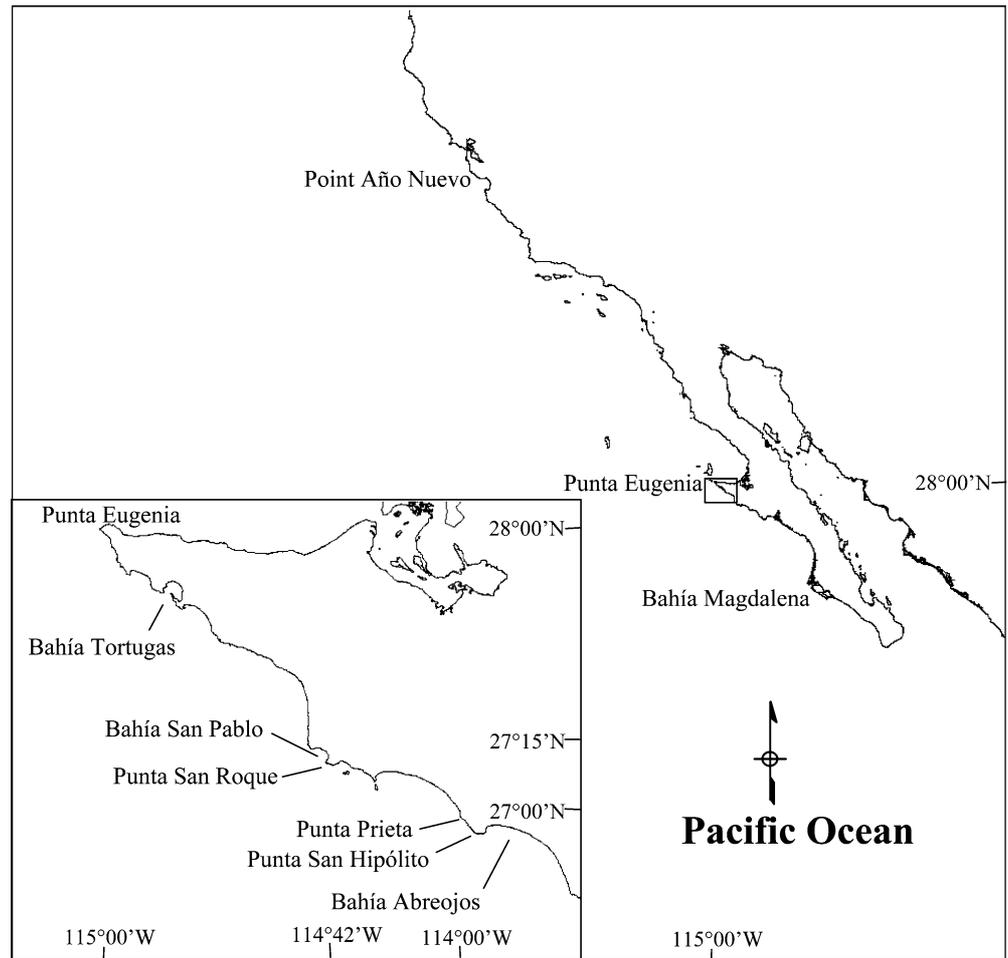
The giant kelp, *Macrocystis pyrifera*, forms dense forests on shallow rocky reefs along the west coast of North America, from central Baja California, Mexico, to central California, USA (Fig. 1). Its northern range limit is relatively stable and primarily set by hydrodynamic forces and competition with the more wave-tolerant bull kelp, *Nereocystis leutkeana*, near Point Año Nuevo, California. In contrast, the species' southern range limit is dynamic, varying over hundreds of kilometers along the Baja California peninsula and largely set by high temperature and low nutrient conditions and a low availability of rocky reef (Dayton 1985; Foster and Schiel 1985; Edwards 2004). *M. pyrifera* has been reported as far south as Bahía Magdalena, Baja California Sur (Setchell and Gardner 1925), although more recent reports suggest Punta San Hipólito as the species' true southern limit in the Northern Hemisphere (Druehl 1970; Guzmán-del-Prío et al. 1971; Hernández-Carmona et al. 2001). Throughout its range, factors such as wave activity, grazing, substrate stability, benthic irradiance, ocean temperature, and nutrient availability are considered to be the primary agents regulating *M. pyrifera* distribution and abundance (reviewed by Dayton 1985; Foster and Schiel 1985; North et al. 1986). However, the periodic occurrence of anomalously warm, nutrient-poor ocean water and unusually large storm-driven waves, the changes in ocean current patterns, and the reduced coastal upwelling associated with El Niño

Communicated by J.P. Grassle, New Brunswick

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Fig. 1 Map showing geographic range (Point Año Nuevo to Punta San Hipólito) of *Macrocystis pyrifera* along the west coast of North America. *Inset* shows region from Punta Eugenia to Punta San Hipólito, including Punta San Roque where manipulative experiments were done. Other sites mentioned in the text are also shown



Southern Oscillations (hereafter El Niño) can be very important to large-scale patterns in *M. pyrifera* distribution and abundance, especially throughout the southern half of the species' range along the Baja California peninsula (Hernández-Carmona 1987; Dayton and Tegner 1990; Ladah et al. 1999; Hernández-Carmona et al. 2001; Edwards 2004). While it is clear that El Niños are important to short-term (i.e. months to years) variability in the location of *M. pyrifera*'s southern range limit via increased mortality, their influence over longer term (i.e. years to decades) variability in the species' southern limit is less well understood and the focus of the present study.

Over the past two decades, several El Niños of varying strength have impacted the eastern Pacific Ocean (Wolter and Timlin 1998) and resulted in widespread mortality in many finfish, seabird, and marine mammal populations (reviewed by Wooster and Fluharty 1985). These events have also resulted in widespread mortality of *M. pyrifera* along the west coast of North America and increased variability in the location of the species' southern range limit along the Baja California peninsula (Hernández-Carmona 1987; Dayton and Tegner 1990; Ladah et al. 1999; Hernández-Carmona et al. 2001; Edwards 2004). Although these pop-

ulations have generally recovered within 1–2 years after the El Niños ended, longer term changes (i.e. delayed recovery over the span of several years to decades) near the species' southern range limit may also have resulted from competitive interactions with subsurface kelps and turf algae that were able to survive the El Niños (Hernández-Carmona 1987; Hernández-Carmona et al. 2001). Along much of the Baja California peninsula, the stipitate kelp *Eisenia arborea*, which occurs from Bahía Magdalena, to Vancouver Island, British Columbia (Abbott and Hollenberg 1976), forms extensive subsurface canopies, 1–2 m above the bottom, and can become the dominant alga in the absence of *M. pyrifera*. It has been suggested that *E. arborea* may store sufficient nitrogen in its tissues to survive extended periods of nutrient limitation such as those observed during El Niños (Dayton et al. 1984; Hernández-Carmona et al. 2000). In contrast, tissue nitrogen reserves of *M. pyrifera* appear to last for only about 2–4 weeks when its populations begin to senesce due to nitrogen limitation (Gerard 1982; Zimmerman and Kremer 1986). As a result, Hernández-Carmona et al. (2001) observed that during the 1997/1998 El Niño, *E. arborea*'s tissue nitrogen reserves declined more slowly than those of *M. pyrifera* near Punta San Roque. It has also been sug-

gested that *E. arborea*'s microscopic propagules may be more tolerant of El Niño conditions than those of *M. pyrifera* and that this may allow *E. arborea* to recover more rapidly following El Niño-induced mortality to the adults (Hernández-Carmona et al. 2001). As a consequence, if *E. arborea* exhibits greater survival and recruitment during and following an El Niño, it may gain a competitive advantage over and temporarily exclude *M. pyrifera* (e.g. Hernández-Carmona et al. 2001). This should be most pronounced near *M. pyrifera*'s southern range limit, where poor temperature and nutrient conditions are most extreme. Here, we examined patterns of mortality and recovery for *M. pyrifera* and *E. arborea* near the southern range limit of *M. pyrifera* at Punta San Roque during and after the 1997/1998 El Niño. We then examined the effects of competition from *E. arborea* on *M. pyrifera* recovery to its pre-El Niño southern limit through a manipulative field experiment and community monitoring over a 5-year period (1997–2002). Finally, we chronicled the recovery of *M. pyrifera* to its pre-1982/1983 El Niño southern limit at Punta San Hipólito following 20 years of absence and discuss the factors likely to be most important in driving temporal variability in the species' southern limit.

Materials and methods

To assess the abundances of *Eisenia arborea* (Areschoug) and *Macrocystis pyrifera* (Agardh) near *M. pyrifera*'s southern limit, we estimated the densities of both species at six randomly selected sites (8–12 m depth) along the northern and western sides of Punta San Roque (Fig. 1) over a 5-year period (1997–2002). Within each site, we estimated the density of all adult *M. pyrifera* (individuals > 1 m tall) along three randomly directed 20 m × 2 m transects and all *E. arborea* and juvenile *M. pyrifera* (individuals < 1 m tall) within five 1-m² randomly placed quadrats along each transect. On each sample date (usually June and October), mean *E. arborea* and juvenile *M. pyrifera* densities were estimated for each transect from its five quadrats, mean *E. arborea*, juvenile, and adult *M. pyrifera* densities were estimated for each site from its three transects, and the densities of all three were then estimated for Punta San Roque from the average of the six sites. Due to logistical constraints, we were occasionally unable to sample all three transects per site or all five quadrats per transect. We graphically assessed the relationship between *E. arborea* and adult *M. pyrifera* densities observed along 67 of these transects (excluding all dates for which *M. pyrifera* adults had not yet recovered to Punta San Roque's western face) and between *E. arborea* and juvenile *M. pyrifera* densities in 745 quadrats (all quadrats sampled during the study). For each of the 22 different observed densities of *E. arborea* on the transects, we determined the corresponding maximum adult *M. pyrifera* density and assessed if they were correlated with one another using

Pearson's correlation analysis (Zar 1986). For each of the 17 different levels of *E. arborea* density observed within quadrats, we determined the maximum corresponding density of juvenile *M. pyrifera* and assessed if they were correlated with one another using Pearson's correlation analysis.

Following the recovery of *M. pyrifera* on the northern side of Punta San Roque (see "Results") in June 2000, we examined the effects of competition from *E. arborea* canopies on *M. pyrifera* recovery to its pre-El Niño southern limit along the western face of Punta San Roque with a manipulative experiment. Three replicate 100-m² sites (10–12 m depth) were haphazardly chosen along the western face of Punta San Roque and cleared of all *E. arborea* in June 2001, by cutting their stipes a few centimeters above the substrate and transporting the thalli away in mesh bags. These sites were separated from one another by ~500 m and were located 1–3 km south of the then southern limit of *M. pyrifera* on the northern side of Punta San Roque in Bahía San Pablo (Fig. 1). In addition, an unmanipulated control area of equal size was established adjacent to each clearing by marking its corners with plastic tape. All clearings and controls were surveyed for *M. pyrifera* recruitment after 4 months (October 2001), at which time all *E. arborea* were again removed from clearings, and after 1 year (June 2002), at which time the experiment was terminated. Data between the clearings and controls were heteroscedastic and therefore square-root transformed [$\sqrt{(x+1)}$]. Following this, differences in giant kelp density between the clearings and control areas on the two sample dates were assessed with a two-way fixed-factor ANOVA. Finally, we chronicled *M. pyrifera*'s recovery to its pre-1982/1983 El Niño southern limit at Punta San Hipólito after almost 20 years of absence by surveying 20 sites between Punta Prieta and Punta San Hipólito (Fig. 1) in June 2002. To examine how extensive this recovery was, we assessed differences in *M. pyrifera* abundance between Punta San Hipólito and Punta San Roque and between Punta San Hipólito and Punta Prieta with a one-factor ANOVA followed by Bonferroni-adjusted planned comparisons.

Results

In August 1997, *Macrocystis pyrifera* and *Eisenia arborea* were both abundant at Punta San Roque (Fig. 2), which marked the southern range limit of *M. pyrifera* along the Baja California peninsula. The El Niño conditions from September 1997/1998 resulted in total mortality of *M. pyrifera* at Punta San Roque, while *E. arborea* densities increased dramatically during the 6 months immediately following the El Niño. These densities reached levels nearly twice those observed immediately prior to the El Niño (Fig. 2) and persisted over the following year (1998/1999), effectively shading almost 100% of the substrate. In June 2000, a dense recruitment of *M. pyrifera* was observed on the north

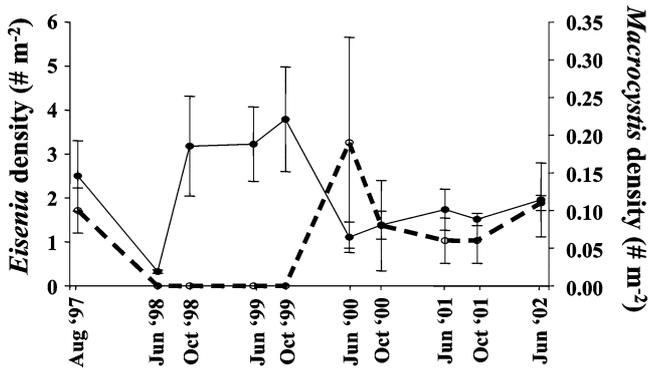


Fig. 2 *Macrocyctis pyrifera* (open circles, dashed line) and *Eisenia arborea* (closed circles, solid line). Densities (mean \pm SE) at Punta San Roque in August 1997–June 2002

side of Punta San Roque in Bahía San Pablo, but *M. pyrifera* had still not recovered along the western face of Punta San Roque. However, because densities along the point's northern face were extremely high (made up of numerous small plants), the overall density for Punta San Roque appeared greater than that observed immediately prior to the El Niño (Fig. 2). At this time, *E. arborea* densities at Punta San Roque had declined to levels observed before the El Niño. By October 2000, *M. pyrifera* had formed extensive canopies in Bahía San Pablo, and, although *M. pyrifera* had still not recovered along Punta San Roque's western face, overall densities of both species had returned to levels similar to those observed before the El Niño (Fig. 2). In areas where these two species co-occurred, their densities were negatively correlated; the maximum density observed for juvenile ($r = -0.853$, $n = 17$, $P < 0.001$) and adult ($r = -0.466$, $n = 22$, $P = 0.03$) *M. pyrifera* were both negatively correlated with the corresponding maximum density observed for *E. arborea* over the 5 years of this study (Fig. 3). In June 2001, *M. pyrifera* was finally observed on Punta San Roque's western face, but was limited to within ~ 200 m of its northern end, where large breaking waves made boating and diving hazardous (Edwards, personal observation).

Three *E. arborea* clearings were established at approximately the northern, central, and southern portions of Punta San Roque's western face in June 2001. Four months later (October 2001), *M. pyrifera* had still not recovered along the western face, although numerous individuals were observed in all three of the experimental clearings (average *M. pyrifera* density in the clearings was 0.23 ± 0.13 individuals m^{-2} ; mean \pm SE). In contrast, only a single *M. pyrifera* was observed in a canopy gap in one of the control areas (average giant kelp density in the control areas was 0.03 ± 0.03 individuals m^{-2} ; mean \pm SE). Eight months later (June 2002), *M. pyrifera* had finally recovered to unmanipulated areas along Punta San Roque's western face, and densities for the location as a whole were similar to those observed before the El Niño (Fig. 2). *M. pyrifera* was significantly more abundant in the clearings than in the

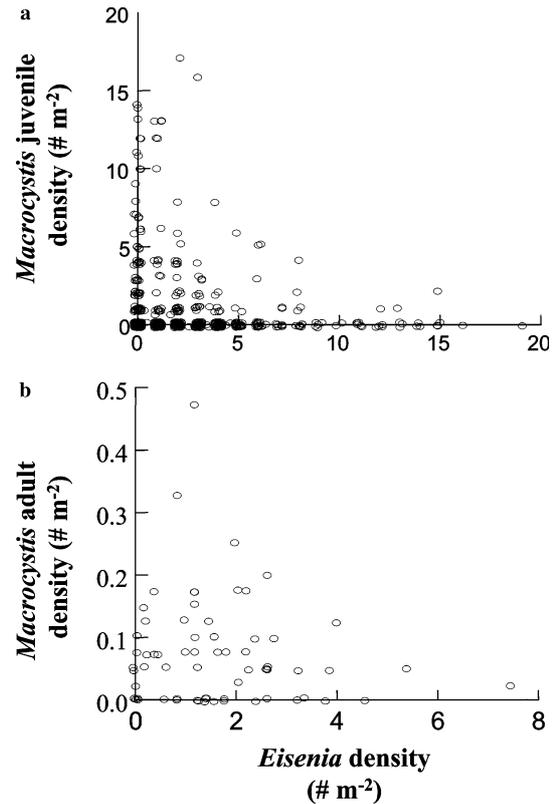


Fig. 3a, b *Macrocyctis pyrifera*, *Eisenia arborea*. Scatter plots showing relationships between densities of the two species at Punta San Roque over a 5-year period (1997–2002). a *E. arborea* density versus juvenile *M. pyrifera* density, observed within 745 quadrats of $1 m^2$. b *E. arborea* density versus adult *M. pyrifera* density, observed along 67 transects of $20 m \times 2 m$. Overlapping data points randomly displaced for discrimination

areas where *E. arborea* had not been cleared (ANOVA: $F_{1,8} = 6.85$, $P = 0.03$; Fig. 4). We concluded that recovery was delayed and largely reduced by competition with *E.*

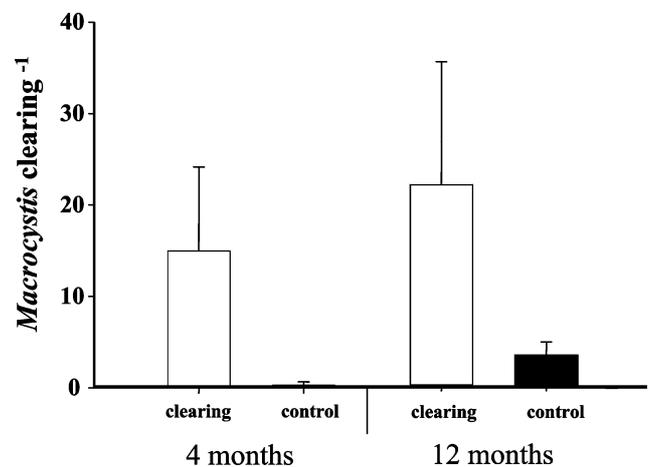


Fig. 4 *Macrocyctis pyrifera*. Mean number of juvenile and adult giant kelp ($+1$ SE) observed in *Eisenia arborea* clearings ($n = 3$) and control areas ($n = 3$) at Punta San Roque, 4 months and 1 year after initial clearings were established

arborea. This pattern did not differ between sample dates (Date×Treatment interaction: $F_{1,8}=0.075$, $P=0.6$).

In June 2002, we observed *M. pyrifera* growing south of Punta San Roque at Punta Prieta and at the species' pre-1982/1983 El Niño southern limit near Punta San Hipólito. Interviews with local fishermen (J. Murillo-Cruz and A. Redona, personal communication) and Punta San Hipólito's fishing cooperative technician (F. Lopez, personal communication) verified that giant kelp had only recently (a few months prior) recovered in these areas, after an absence of almost 20 years. Although this marked *M. pyrifera*'s return to its true southern range limit in the North Pacific, *M. pyrifera* density was lower at Punta San Hipólito (0.006 ± 0.006 plants m^{-2} ; mean \pm SE) than at either Punta Prieta (0.04 ± 0.013 plants m^{-2} ; mean \pm SE; Bonferroni-adjusted $P=0.06$) or Punta San Roque (0.08 ± 0.06 plants m^{-2} ; mean \pm SE; Bonferroni-adjusted $P=0.001$). We believe this to be at least partially because Punta Prieta and Punta San Roque are both dominated by rocky reefs (all six monitoring sites were $>80\%$ rocky reef), while Punta San Hipólito is dominated by sandy bottom (9 out of the 14 monitoring sites were 100% sandy bottom and the remaining 5 were a mixture of sandy bottom and rocky reef). Further, *E. arborea* dominated the rocky reefs at Punta San Hipólito, likely excluding *M. pyrifera* from the small amount of available habitat. As a result, *M. pyrifera* surface canopies were extensive at Punta San Roque and Punta Prieta, while surface canopies were rare and small at Punta San Hipólito. At this time, the southernmost *M. pyrifera* was found on a small rocky reef approximately 100 m offshore of the Punta San Hipólito lighthouse, a position marking the northern end of the sandy bottom at Bahía San Hipólito.

Discussion

The 1982/1983 and 1997/1998 El Niños were two of the strongest on record (Wolter and Timlin 1998), with each resulting in almost complete mortality of *Macrocystis pyrifera* along the Baja California peninsula (Hernández-Carmona 1987; Ladah et al. 1999; Edwards 2004). Although these populations quickly recovered throughout much of their range following the 1982/1983 El Niño, they did not recover at their pre-El Niño southern limit near Punta San Hipólito (Hernández-Carmona et al. 2000, 2001), and *M. pyrifera*'s southern limit shifted northward ~ 50 km to Punta San Roque (Hernández-Carmona et al. 1991), where it remained for almost 20 years. Similarly, *M. pyrifera* populations recovered throughout most of their range following the 1997/1998 El Niño, but they did not recover to their pre-El Niño limit near Punta San Roque, and the species' southern limit again shifted northward ~ 70 km to Bahía Tortugas (Hernández-Carmona et al. 2001). However, unlike following the 1982/1983 El Niño, this northward shift lasted only ~ 2 years, and *M. pyrifera* recovered at Punta San Roque in 2000. Then, in 2002, *M. pyrifera* recovered at Punta San Hipólito after almost 20 years of

absence, marking a return to its true range limit in the North Pacific.

Similar to *M. pyrifera*, there was also unusually high mortality of *E. arborea* at Punta San Roque during both El Niños, although upon the return of cool nutrient-rich conditions, the species rapidly recovered and dominated the benthos (see also Hernández-Carmona 1987; Hernández-Carmona et al. 2001). While the mechanisms by which this occurred are still not entirely clear, we believe likely reasons include: (1) some kelps build internal nitrogen reserves in their tissues that are used during periods of extremely low nutrient supply (Gerard 1982), and *E. arborea* appears to maintain greater reserves than *M. pyrifera* (Hernández-Carmona et al. 2001); (2) due to its stipitate morphology, *E. arborea* may be more tolerant of physical disturbance from wave stress than *M. pyrifera* (Dayton et al. 1984, 1992) and therefore more resistant to El Niño's increased wave actions; and (3) *E. arborea*'s microscopic propagules appear more tolerant of low nutrient-high temperature conditions and thus better able to survive to produce new recruits immediately following El Niños (Hernández-Carmona et al. 2001). Regardless of the mechanism(s), it is clear that the ability of *E. arborea* to better survive during (see also Dayton et al. 1992) and recover more rapidly following (see also Hernández-Carmona 1987) El Niños allow it to gain a competitive advantage over *M. pyrifera* and thereby delay or even prevent *M. pyrifera*'s recovery near its southern range limit.

As ocean temperatures cooled and nutrients increased during 1998 and 1999, *M. pyrifera* recovered rapidly at many locations along the Baja California peninsula, where its propagules presumably survived (e.g. Bahía Tortugas; Ladah et al. 1999). In contrast, *M. pyrifera* did not recover in areas where these microscopic stages presumably did not survive (e.g. Punta San Roque; Hernández-Carmona et al. 2001). *E. arborea* instead recovered to these areas in densities high enough to prevent *M. pyrifera*'s recruitment for as long as 2 years and perhaps longer in other areas (e.g. Punta San Hipólito). It is believed that this same process occurred following the 1982/1983 El Niño (Hernández-Carmona 1987; Dayton and Tegner 1990). Following the removal of all *E. arborea* from the experimental plots, then, *M. pyrifera* recruited and formed surface canopies within just a few months. Together, this indicated a strong negative relationship between these two species, which was further demonstrated by the negative correlation between their maximum densities. Similarly, Dayton et al. (1984) observed that in southern California, *M. pyrifera* rarely invades areas of dense understory kelp canopies, although following removal or thinning of these canopies *M. pyrifera* can recruit and become the competitive dominant. As *M. pyrifera* eventually recovered at Punta San Roque 2 years after the El Niño ended, *E. arborea* abundance declined and both species ultimately returned to densities similar to those observed prior to the El Niño.

The ultimate recovery of *M. pyrifera* to Punta San Hipólito after almost 20 years of absence marked its

return to its true southern limit in the Northern Hemisphere (Druehl 1970; Guzmán-del-Próo et al. 1971) and provided us the opportunity to examine the factors likely responsible for setting this limit. In June 2002, *M. pyrifera* had established extensive beds a few kilometers to the north of Punta San Hipólito, at Punta Prieta, but only small isolated beds at Punta San Hipólito. While these locations were only a few kilometers from one another, they differed greatly in the availability of rocky reef; Punta Prieta is dominated by rocky reefs, while Punta San Hipólito is largely a sandy bottom with patchily distributed rocky reefs. Further, the rocky reefs that were observed at Punta San Hipólito supported dense stands of *E. arborea*, likely reducing *M. pyrifera* recruitment further. The southernmost of these reefs occurred approximately 100 m offshore of the Punta San Hipólito lighthouse, where just a few meters to the south the substrate changes to a sandy bottom that extends beyond *M. pyrifera*'s geographic range into Bahía Abreojos. This reef supported a moderate stand of *E. arborea* and a few *M. pyrifera*, while several nearby (within 50 m) reefs supported dense stands of *E. arborea* but no *M. pyrifera*. We therefore believe that *M. pyrifera*'s true southern limit is set in part by the availability of rocky reefs as previously reported (see reviews by Dayton 1985; Foster and Schiel 1985; North et al. 1986), but also by an absence of dense *E. arborea* canopies. Following the removal or thinning of *E. arborea* from these reefs, *M. pyrifera* recruitment is likely dependent on periods of suitable light, temperature, and nutrient conditions (i.e. "recruitment windows"; sensu Deysher and Dean 1986).

While *M. pyrifera*'s northern range limit is relatively stable (near Point Año Nuevo, California), its southern range limit along the Baja California peninsula is highly dynamic, apparently driven by a number of factors operating at different temporal scales. First, with the exception of rare reports near Bahía Magdalena (Setchell and Gardner 1925), *M. pyrifera*'s long-term true southern limit occurs at Punta San Hipólito (Druehl 1970; Guzmán-del-Próo et al. 1971; Hernández-Carmona et al. 2001) and is set by unfavorable temperature and nutrient conditions and the availability of rocky reef. Longer term (years to decades) variability within this limit occurs from interspecific differences in the mortality of adult populations and their microscopic propagules and from competitive interactions with *E. arborea*. Given that *M. pyrifera* is the primary habitat-forming structure throughout most of its range (reviewed by Foster and Schiel 1985), this can have substantial impacts on both local and regional patterns of biodiversity and ecosystem function. The impacts of El Niños on eastern Pacific kelp forests, consequently, may be complex and long lasting, and should be considered at appropriate temporal and spatial scales. Considerations of how populations recover following widespread mortality should incorporate biological interactions among the impacted species.

Acknowledgements We thank our many assistants without whose help the fieldwork would not have been possible. We are grateful to M. Kenner and J. Estes for their logistical support during the early stages of this project and to D. Canestro, P. Dal Ferro, and S. Claibusch for their assistance with diving activities. We thank M. Kailey for moral support in the field and Tony and Edith for their excellent fish tacos. We are also grateful to the fishing cooperatives at Punta San Roque, Punta Eugenia, and Punta San Hipólito for their generous assistance with logistical matters and E. Danner and M. Tinker for help with imagery. This work was supported in part by grants from UC Mexus and the PADI Foundation to M. Edwards and CONACYT (4113000-5-029PN-1297) to G. Hernández. G. Hernández is Becario of the programs COFAA-IPN and EDI-IPN.

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