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Giant kelp (*Macrocystis pyrifera*) survival in deep water (25–40 m) during El Niño of 1997–1998 in Baja California, Mexico

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Abstract

During the 1997–1998 El Niño, we examined seasonally a giant kelp population in deep water (25–40 m) off the coast of Northern Baja California. Though most populations in the region completely disappeared, large fertile adults survived the entire warming event at depth. At 25 m, there was no significant change in density or number of fronds per individual during the warming period from spring 1997 to spring 1998, though the surface canopy sloughed off (died) down to 15 m depth. By summer 1998, recruitment occurred at all depths at the site. Adult survival at depth was most likely important in post-disturbance recovery in surrounding populations by occupying substratum, providing vegetative growth, and producing spores. Survival in deep water during this extreme El Niño may have been due to local hydrography, such as internal waves bringing cool nitrate-rich water into the deeper regions of the shelf from below the thermocline, providing a refugium against the warm temperatures, low nutrients, and heavy wave action associated with warming events. Deep-water populations may regularly survive El Niño warming in this region due to internal wave activity, and go undetected due to the depth at which they occur and the sloughing of the shallow (<15 m) biomass.

Keywords: deep water macroalgae; El Niño; ENSO; giant kelp; internal waves.

Introduction

El Niño events result in a depressed thermocline and nutricline, a warming of surface waters, and a reduction in primary productivity (Huyer and Smith 1985, Kahru and Mitchell 2000, Durazo and Baumgartner 2002, Ladah 2003). The warm nutrient-poor waters which are typical of El Niños cause significant negative effects in temperate kelp forest ecosystems (North 1994). High ocean temperatures and low inorganic nitrogen availability, which are negatively correlated in temperate waters, result in reduced distribution and abundance of the giant kelp, *Macrocystis pyrifera* C. Agardh (Dayton 1985, Zimmerman and Robertson 1985, Tegner and Dayton 1987, 1991, Tegner et al. 1996, Ladah et al. 1999, Ladah 2003, Edwards 2004).

While the surface waters in a giant kelp population are often nitrate depleted, the deeper parts of giant kelp usually live in a nitrate-replete environment below the thermocline/nutricline (North 1994). During El Niño events, however, the whole water column usually becomes nitrate depleted and inorganic nitrogen deficiency occurs. *Macrocystis pyrifera* can sustain adequate growth above 1–2 μM of nitrate, but tends to be growth limited below 1 μM (Gerard 1982), with only about 3 weeks of nitrogen reserves. The result is often sloughing of the kelp forest canopy and mortality (Gerard 1984, Dayton and Tegner 1984, Tegner et al. 1996), with two possible fates for the population: 1) extirpation of the entire (macroscopic) population or 2) sloughing of the canopy, but with individuals surviving in the deeper regions of the population. If part of the population does survive in deeper water, then, especially if the individuals are of reproductive age, there is a local spore source available for post-disturbance recovery.

Population recovery may be directly related to survival of individuals during disturbance. Survival of sub-surface fertile individuals can prevent invasion of ephemeral or opportunistic species (Kennelly 1987a,b) by occupying space on the substratum. They can provide a base for renewed vegetative growth during recovery, and can provide a local source for spore dispersal to surrounding populations for post-disturbance recruitment, especially to shallow areas which are often more greatly affected both by storm damage and warm water events (Seymour et al. 1989, Dayton et al. 1992). However, if the population is decimated by disturbance, recolonization depends on spore dispersal from nearby surviving stands (Reed et al. 1988, 1992), or survival and regrowth of dormant microscopic stages (Dayton 1985, Hoffman and Santelices 1991, Santelices et al. 1995, Ladah et al. 1999).

Large-scale regional (>100 km) extirpation of macroscopic canopy-forming populations of giant kelp and subsequent recolonization has occurred repeatedly in Baja California, particularly during El Niño events (North 1971, Hernández-Carmona 1991, Ladah et al. 1999, Edwards 2004). If giant kelp survives in deeper waters during these events, the effect of the disturbance on population recovery may be much less than if the entire population were to be destroyed. To date, three populations have been found in Northern Baja California with a depth range extending to 40 m (greater than that of

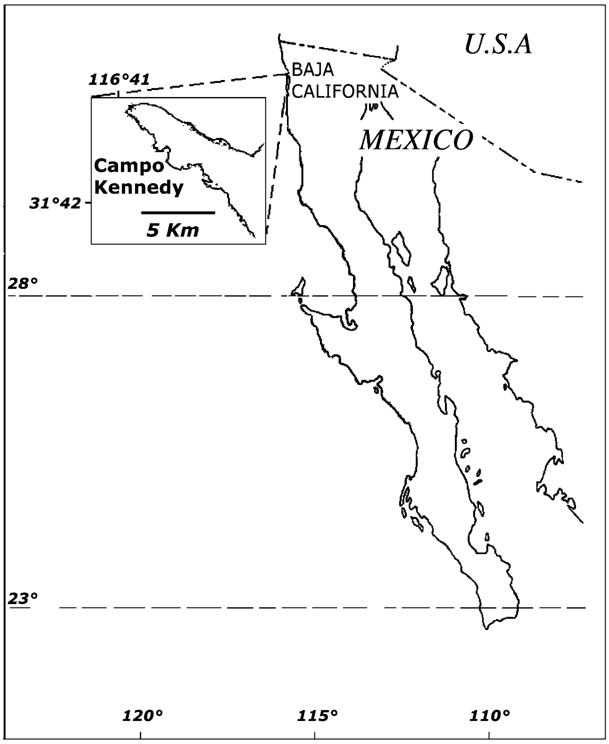

Figure 1 *Macrocystis pyrifera*: map of Baja California, Mexico, showing Campo Kennedy study site.

typical giant kelp forests in the region). The unique and extreme nature of the 1997–98 El Niño event provided a situation in which the *in situ* response of giant kelp to a warming event could be evaluated in a deep water population in Baja California, at a time when mass disappearance of giant kelp occurred (Ladah et al. 1999, Edwards 2004). This study focused on the refuge provided by deep water for adults by evaluating population structure in deep water (25 m) before, during, and after the El Niño event, and related the data to oceanographic factors during the study period. The population study spanned the events of El Niño 1997–98, one of the most extreme ever recorded (Wolter and Timlin 1998), and of La Niña of 1998–99.

Materials and methods

Study site characterization

The population chosen for the study was the Campo Kennedy *Macrocystis pyrifera* forest (31° 41.96 N, 116° 40.90 W) (Figure 1) because of its accessibility and depth range. *M. pyrifera* ranges from 7 to 40 m (MLLW) depth attached to large cobble and bedrock, and is the competitive dominant in the area. The area is generally devoid of much understory and consists only of small patches of red algae. Inshore from the *M. pyrifera* population, occasional patches of the smaller kelps, *Eisenia* and *Egregia*, exist. Depth increases rapidly away from the shoreline and depths greater than 50 m occur within 30 m of shore. The study site, located south of Punta Banda, is highly productive during spring and summer with regionally intense upwelling (Cota-Villavicencio 1972, Bakun 1973, Chavez-Garcia 1975), and lies on a strike-slip fault (the Agua Blanca fault related to the San Andres fault system) (Allen et al. 1960). The area is exposed to wave activity with incident angles ranging from 140 to 285 degrees. Due to isolation from any large human population at this site, effects of anthropogenic discharge are minimal and the water is often very clear.

Kelp dynamics

Density of individuals of giant kelp taller than one meter was determined using 10 m×2 m quadrants placed parallel to shore at 25 m depth, near the offshore edge of the kelp forest. Between three and seven density transects were surveyed seasonally as weather permitted for SCUBA diving. Winter seasons were not evaluated due to storm activity. Frond counts were taken in density transects by counting the number of fronds taller than one meter per individual, as frond counts are a good subsurface indicator of environmental change (Tegner et al. 1996). The frequency of individuals in each frond class (separated every five fronds) was determined using frond count data. Data were further separated into age classes of juveniles and adults, and are presented as a percent of the population counted for each class. For purposes of this study, individuals with fewer than four fronds (>1 m) were considered juveniles (because they often do not produce viable spores) and those with four or more fronds (>1 m) were considered adults (as they are the youngest individuals in which viable spores have been found (Neushul 1963, Dayton et al. 1992).

Oceanographic conditions

Mean sea surface temperatures for each month of the study period (1995–1999) and for the past nine years (1991–1999) were acquired from the National Oceanic and Atmospheric Administration (www.cdc.noaa.gov) for the region. *In situ* mean monthly sea surface temperatures were acquired from a recording thermograph (Onset computer corp., MA, USA) at the site.

Mean monthly upwelling indices for the study period from 1995 to 1999, as well as a nine-year monthly mean from 1991–1999, were provided by the Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov/products/PFELindices.html) for the region.

Statistical analysis

Significant seasonal changes in density and fronds per individual were assessed using a one-way ANOVA (Zar 1984), after homogeneity of variances was confirmed with the Cochran test (Underwood 1997). Multiple comparison tests were performed using the SNK multiple comparison. In all cases, an alpha of 0.05 was chosen. All data in text are reported as means±one standard deviation. Error bars are explained in each graph.

Results

Oceanographic conditions

Sea surface temperature Sea surface temperatures detected by satellite for the study region show a yearly

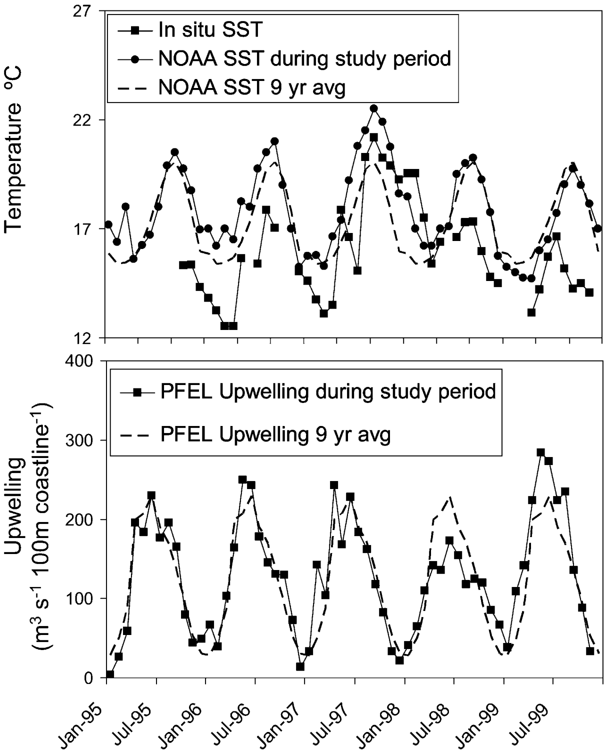

Figure 2 *Macrocystis pyrifera*: sea surface temperature (SST) and upwelling for the Campo Kennedy study site. PFEL=Pacific Fisheries Environmental Laboratory.

pattern with warmest temperatures during September and coolest temperatures from February to April (Figure 2). During the study period, the latter half of 1997 (after March) and the first half of 1998 (until April) were unusually warm. By the end of 1998 and for most of 1999, temperatures returned to normal and then dropped below the mean of previous years. The temperature anomaly was greater than +2.5°C for five consecutive months from September 1997 to February 1998. By summer 1998, temperatures approached normal and by winter 1998–99 had dropped below the average. From February to April 1999, temperatures were below 15°C. Temperatures throughout 1999 were generally below average with cooler than normal temperatures throughout summer 1999 (Figure 2).

In situ temperature behaved much the same way as temperature detected by satellite, with slight discrepancies (Figure 2). The satellite detected sea surface temperatures were usually 1–2°C higher than the *in situ* temperatures, particularly in summer. The *in situ* temperatures showed warming in May 1997, and sustained warming from August 1997 to May 1998, with cooling for the rest of 1998 and through 1999.

Upwelling Mean monthly upwelling indices showed positive numbers representing offshore transport in every month analyzed (Figure 2) for the region. The upwelling index shows greatest offshore transport from April to June (the major upwelling season) and weakest upwelling in December and January. During the study period, upwelling anomalies (compared to the average of 1991–1999) were negative (below average upwelling) from May to December 1997 and from April to September 1998. Low upwelling often coincided with high temperatures. Late 1998 and most of 1999 had increased upwelling and positive upwelling anomalies, with May and June 1999 having the greatest upwelling indices (Figure 2).

Kelp dynamics

The entire surface canopy of this kelp forest disappeared after fall 1997. By February 1998, all giant kelp growing at 15 m depth or shallower died (personal observations). *Macrocystis pyrifera* adults at 25 m survived throughout the El Niño event and individuals had reached the surface again at both depths by fall 1998.

Density at 25 m did not change from spring 1997 to spring 1998, showing little negative effect during the most intense temperature anomaly period of the El Niño event. Density rose after spring 1998 and reached its maximum in fall 1998. Density dropped again in spring 1999, possibly due to population thinning as recruits grew. There was a significant effect of season on density (ANOVA $p<0.001$, $F_{6,\ 18}=8.73$), with density in fall 1998 being significantly greater than the other seasons (SNK multiple comparisons) during a post-El Niño recruitment event (Figure 3a).

The number of fronds per individual (Figure 3b) also showed little difference from spring 1997 to spring 1998, and dropped significantly after spring 1998, remaining low throughout the rest of the study period (Figure 3b). There was a significant effect of season on the number of fronds per individual (ANOVA $p<0.001$, $F_{6,\ 10}=7.4$). Fronds showed a similar pattern to density, with a significant change from large individuals (during El Niño warming) to smaller individuals with fewer fronds (during recruitment events after El Niño and during La Niña) after spring 1998 (SNK multiple comparisons) (Figure 3b,c,d).

The population structure of juveniles *versus* adults showed a mature population in spring and summer 1997. In spring 1998, there were some juveniles present, but not until summer 1998 did juveniles exceed adults, which they then continued to do until the end of the study period (Figure 3c).

The frond class distribution showed concentration of the population in the larger classes through the onset of El Niño in spring and summer 1997. As El Niño effects waned in spring 1998, a dramatic change occurred in the class distribution and the smaller frond classes became more prominent (Figure 3d). Widespread recruitment occurred and recruits outnumbered larger individuals. This condition – many individuals with few fronds and some larger individuals – persisted to the end of the study period showing almost a consistent gap in the medium-sized generation.

Discussion

During the El Niño event of 1997–1998, all *Macrocystis pyrifera* canopies and most macroscopic populations disappeared along the Baja California coast. In this study, however, large fertile adults were documented during the warming event between 25 and 40 m depth, and did not show a great change in density or frond structure during

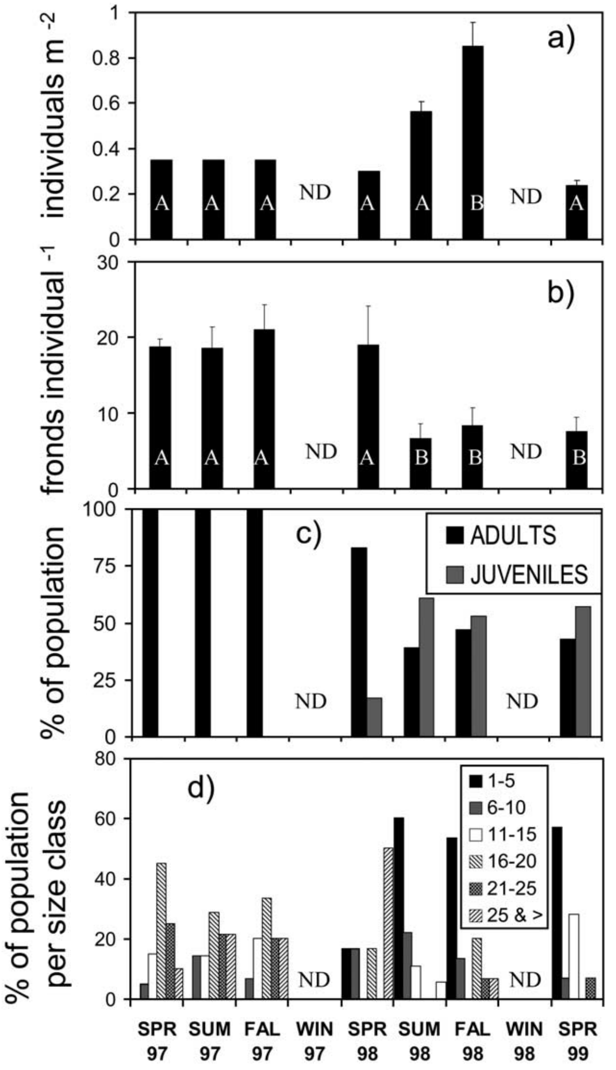

Figure 3 *Macrocystis pyrifera*: population structure in deep water in Northern Baja California.
(a) Density, (b) fronds per individual, (c) juveniles vs. adults, and (d) frond classes in number of fronds per individual separated every five fronds. ND=no data; error bars show standard deviation; letters show SNK mutliple comparison groupings.

the El Niño at 25 m, suggesting that deep water can provide a refugium against warm water, low nutrients, and increased storm activity for giant kelp even during extreme El Niño events and massive regional mortality. Survival of fertile adults in deep water during catastrophic widespread disappearance, such as occurred in Baja California during the 1997–98 El Niño (Ladah et al. 1999, Edwards 2004), may be very important for post disturbance recovery and help *M. pyrifera* to regain its regional competitive dominance after disturbances that have an exaggerated effect at shallow sites. The unique location of this kelp forest, which lies along the Agua Blanca faultline just inshore of a deep-water canyon, brings to light the importance of local hydrographic conditions, such as the frequency and duration of internal waves, on population survival during extreme events.

Macrocystis pyrifera canopy sloughing (bleaching and necrosis of the shallow part of the forest floating near the surface) and mortality during this study was not surprising, considering the well established adverse effects of El Niño on giant kelp (Tegner and Dayton 1987, 1991, Seymour et al. 1989, North 1994, Tegner et al. 1996). The oceanographic conditions along the Baja California coastline were extreme during the 1997–99 El Niño, with a warm water pool in the coastal region off Punta Eugenia (Durazo and Baumgartner 2002). Because many populations in Baja California grow typically at less than 20 m depth, their disappearance is easily explained by increased wave action and temperature, and by reduced nutrients and upwelling during El Niño (Dayton and Tegner 1984, Seymour et al. 1989).

In contrast to many other sites in this region, however, the Campo Kennedy site is one of three in Baja California where giant kelp occurs in waters deeper than 30 m; in all three sites giant kelp survived El Niño (personal observations). Deep water kelp populations have been documented at 30 m depth in Central California and while it is thought that assemblages at this depth form stable persistent populations, the giant kelp, *Macrocystis pyrifera*, is considered rare in that area (Spalding et al. 2003). The extension of giant kelp to deeper waters in Baja California in strong upwelling areas may be due to the greater penetration of light, as little run-off or anthropogenic discharge affects this arid unpopulated region, particularly south of Punta Banda where the human coastal population is minimal. Increased light in deeper water may allow recruitment and survival to occur deeper than 30 m. When spores are available, kelp recruitment is usually limited by either light or nutrients (Deysher and Dean 1986). Unfortunately neither of these factors was measured during this study, but the recruitment documented at this depth suggests sufficient amounts of both at the site.

The survival of individuals between 25 and 40 m depth during the extreme warming of this El Niño, the lack of visible damage to the thalli at this depth, and the fact that density and fronds numbers did not change at 25 m, was unexpected considering the conditions and the mass disappearance throughout Baja California (Ladah et al. 1999, Edwards 2004). During and after the El Niño, the adults at 25 m showed greater density and fronds than has been measured in other Northern Baja California populations, and even other California populations at the same time (Edwards 2004), most probably due to the depth at which the present study took place as deep thalli often respond differently from those in shallower water (Dayton et al. 1992). Survival in deep water during such prolonged oligotrophic episodes leads to speculation on a mechanism of nutrient provision to the population, since the thermocline during El Niño is usually depressed to 50 m depth (Miller 1996, Tegner et al. 1996).

We speculate that internal waves (a particularly important source of nutrients during El Niño events (Zimmerman and Kremer 1984, Zimmerman and Robertson 1985) and tidal bores [implicated in increasing nutrient supply to deeper regions of the euphotic zone (Pineda 1991, Leichter et al. 1996)] could have provided nutrients from below the thermocline (as in Leichter et al. 2003 in coral reefs) to deep water adults. Even short nutrient pulses from internal motions may be sufficient to replenish tissue nitrogen in giant kelp, as this mechanism can increase nutrient concentrations up to 40-fold, particularly in deep regions where the magnitude and duration of nutrient pulses increases (Leichter et al. 2003). Internal tidal motions can have an amplitude of 27 m, thereby having the ability to rapidly uplift a depressed thermocline from 50 m up to 30 m depth, reaching the base of a deep-water kelp forest, even during El Niño. Between Punta Banda and Santo Tomas (where three deep-water kelp forests survived the 1997–98 El Niño), the sea floor becomes very deep within 50 m from shore, producing the type of bank or ledge needed for internal wave formation. Unfortunately no consistent high-frequency bottom temperatures or water nitrogen samples were available from the study period in this site, and this remains a speculation. Even if these data were available as point measurements, they would probably not reveal the high frequency events (on the order of minutes) proposed to have caused the survival of the adults at depth.

In deeper waters, individuals would have also been protected from intensified wave activity during El Niño, as well as from high temperatures and low nutrients, particularly if the canopy was absent and did not cause any drag force during wave events. During El Niño events, the northern storm track is amplified and produces stronger westerly (rather than the typical north-westerly) waves due to a strengthened Aleutian atmospheric low pressure area and a weakened North Pacific atmospheric high pressure area (Emery and Hamilton 1985, Seymour 1998). Wave action and warming are usually more intense in shallow waters (Seymour et al. 1989, Dayton et al. 1992). The large individuals may have survived the storms due to a deep water buffer zone (Seymour et al. 1989), and also because the surviving individuals were shorter with less drag once the canopy and the surface 15 m of biomass sloughed off prior to the storms.

The post-El Niño recruitment, associated with higher densities and lower frond numbers, would have been expected in an area where fertile adults survived. Recruitment often occurs if spores are available and if ambient conditions are adequate (Deysher and Dean 1986). The increased light that often occurs after canopy removal apparently resulted in spore development and the post-El Niño recruitment events during the cool nitrate-rich period after El Niño, whether from dormant microscopic stages (per Ladah et al. 1999 and Kinlan et al. 2003) or from local spore dispersal. Microscopic vital rates of *Macrocystis pyrifera* include transitions between several distinct ecological phases, all of which are difficult to study in the field because of their small size (Deysher and Dean 1986, Schiel and Foster 1986), therefore it is impossible at this time to determine if the recruits resulted from new spores produced by the survivors or from a seed bank of microscopic forms. However, in this study, the recruits most probably resulted from newly produced spores from nearby fertile individuals surviving in deeper waters, as unpublished data suggest that populations in Northern Baja California are less able to survive in a seed bank during warm nutrient-poor periods than those in Southern Baja California (personal observations), again suggesting the importance of deep water survival during the event in this area.

Competition may also play an important role during recolonization since absence of kelp canopy results in greater abundance of understory and turf competitors (Reed and Foster 1984, Kennelly 1987a,b, Dayton et al. 1992). During this El Niño, the area from which individuals completely disappeared was freed from 1) competition for light with the overlying canopy and 2) from competition for space with substratum-occupying holdfasts (i.e., the bottom became available for colonization). In many areas in Baja California, when giant kelp disappeared during the El Niño, a large subtropical species of *Sargassum* colonized the areas. Yet, in this study, giant kelp survived the warming event, thereby dominating the substratum and the subsurface canopy.

The survival of deep water individuals during this study supported the hypothesis that even though the depth of the thermocline is depressed below the deeper regions of even the deepest kelp forests in Baja California during El Niño, deep water can still provide a refugium against the negative effects of warming events on giant kelp. We speculate that this is due to access to cooler nutrient-rich waters from below the thermocline through internal wave motions. Because of the depth at which they grow, deep water individuals are also protected from intense wave events. Baja California is a region where giant kelp extends deeper than in many areas in the region. This is important to consider when monitoring kelp forests, because canopy absence does not mean population disappearance. The only true way to evaluate population conditions is using *in situ* evaluations.

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