JP1.25 RESPONSE OF EASTERN PACIFIC GIANT KELP COMMUNITIES TO ENSO-DRIVEN OCEAN CHANGES

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1. INTRODUCTION

Large-scale climatic events such as the El Niño-Southern Oscillation (ENSO) have been associated with numerous impacts to both terrestrial and aquatic ecosystems. For example, ENSO fluctuations in storm patterns and thermal/precipitation regimes have been associated with modification of population dynamics of opportunistic pests, disease vectors, and various keystone species in particular ecosystems. Giant kelp (*Macrosystis spp*.) communities of the eastern Pacific Ocean have been affected to various degrees by storm-produced wave action and rises in ocean temperature often found during ENSO conditions. This paper reviews the recent literature concerning the temporal and spatial dynamics of kelp forest damage, recruitment, and community structure both during and after ENSO events in the eastern Pacific Ocean.

Giant kelps are the most recognized species of marine algae belonging to the taxononomic order Laminariales (Phylum: Heterokontophyta). Although limited in distribution in tropical oceans (Joly and Oliveira 1967; Petrov Suchovejeva and Avdejev 1973; Graham et al. 2007), kelps are widespread along coldwater rocky marine coasts in temperate and arctic waters, reaching their greatest diversity within the northeastern Pacific Ocean. Kelps commonly exist in forest communities in which a layering of component species is well evident. Floating *canopy* kelps with fronds (leaf-like attachments) at or near surface dominate the upper layer, while *stipitate* kelps dominate a few meters above the geological substrate. *Prostate* kelps extend over the sea floor and are associated with the *benthic assemblage*, which consists of other algal and sessile species. *Encrusting coralline algae*, found often with sea urchins, widely cover the rock substrate. Within each ecological guild are assemblages of associated herbivorous and carnivorous species, which vary according to the particular location (Dayton 1985).

Requirements for kelp survival include adequate light, hard (rocky) substrate, and high nutrient (e.g., nitrogen, phosphorus) levels. Giant kelp communities are particularly productive where oceanographic upwelling occurs, due to regular delivery of cool, nutrient-rich waters from the deeper ocean. Water movement and turbulence enhance mixing of nutrients throughout the water column, promoting nutrient absorption across the frond-sea interface (Dayton 1985).

The development of ENSO conditions may bring substantive changes to the near-shore marine environment. High-intensity storms produce strong wave action which may result in breakage of the giant kelp canopy and tearing of holdfasts from the rock substrate (Dayton et al. 1992). Martinez et al. (2003) found massive mortality within kelp beds of the western coast of North and South America after the ENSO event of 1982-3. Edwards and Hernández-Carmona (2005) reported the 1997-98 ENSO resulted in near-to-complete loss of giant kelp species across two-thirds their range on the west coast of North America. The resulting clearings provide increased penetration of light to greater depth, providing increased opportunities for light-limited species in the understory. Vásquez et al. (2006) did not find immediate major giant kelp die-offs in the Chilean subtidal coastal zone during ENSO 1997-98, but rather one year later due to decreases in predator populations with subsequent rises in giant kelp grazers. Outside of wave action, the lowering of the oceanographic thermocline and suppression of oceanographic upwelling bring superficial warming of coastal water that limits nutrients available for kelp forest repair, growth, and recruitment.

2. PATCH DYNAMICS

A considerable amount of research related to ENSO impacts on giant kelp communities has explored temporal-spatial patterns of kelp patch survivorship and recovery.

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2.1 *Patterns of Growth and Survivorship*

Zimmerman and Robertson (1985) found severe nutrient depletion associated with the 1983 El Niño at Santa Catalina Island, CA resulted in very low giant kelp productivity during the second half of 1983. Because frond growth rates were so slow, terminal blades developed before extending to the surface, reducing density of canopy vegetation. Average plant size was reduced, especially those extending above 10m, and there was greater survivorship for those at 20 m. Ladah and Zertuche-González (2004) found a similar situation following the ENSO event of 1997-98, in which most of the giant kelp populations off the coast of Baja California disappeared. Large adults remained in deeper waters, though the surface canopy growth died down to 15m depth. Survival of the deep-water kelps was seen likely a result of internal wave action which produced nutrient pulses from below the thermocline. Giant kelp survival at depth enabled ensuing rapid recruitment and post-disturbance recovery. Ladah (2003) suggested that survival of giant kelp near their southern range boundary in central Baja California during past El Niños can be attributed to periodic nutrient enrichment of near-shore waters by shoaling of subsurface water of the California Undercurrent.

Direct storm wave impacts also influence the spatial distribution of giant kelp survival. Seymour et al. (1989) found the pattern of storm mortality at Point Loma, CA is depth dependent, with the off-shore distance of the shallower, shore-facing end of the patch determined by the height of breaking waves. In addition to cross-shore trends, significant long-shore variation may exist. Dayton et al. (1992) found longshore ends of patches had significantly higher mortality after ordinary strong storm events than did interior sectors at Point Loma. However, this longshore pattern was reversed after the summer of the 1983 ENSO. The end locations had greater exposure to nutrients within the longshore currents than did interior sectors which received less nutrient–rich water. Prior nutrient removal by plants further up current resulted in rises in kelp mortality in interior sectors. The authors noted the role of spatial differences in longshore currents, light, temperature, wave energy, understory algae populations, intraspecific competition, competitive dominance of *Mycrocsistis pyrfera*, and grazing patterns in intersite variations in survival and recovery.

While the preceding studies assume that site-specific factors play a dominant role in giant kelp survivorship patterns, Edwards and Hernández-Carmona (2000) determined that among-region differences in survival off the Baja coast after the 1997-98 ENSO were attributed at least in part to ENSO-caused differences in ocean climate. Edwards (2004), investigating giant kelp populations across 90 northeastern Pacific sites at 5 spatial scales using variance components analysis, found that during the 1997-98 ENSO, environmental factors exerting regional control of kelp populations took predominance over those exerting local control. Local control returned with kelp recovery, about 6 months in southern California.

2.2 *Patterns of Recovery*

Numerous studies have found recovery of giant kelp beds after ENSO occurrences complex and impacted by numerous factors across multiple spatial scales. For example, the southern limit of giant kelp *M. pyrifera* off the Baja coast has varied over hundreds of kilometers since the 1983 ENSO event. Studies show ENSO-generated high temperatures and waves removed *M. pyrifera* from its southern range, but understory *E. arborea* was able to survive the ENSO-modified environment and subsequently recruit in high densities, hindering reestablishment by *M. pyrifera* (Dayton and Tegner 1984; Edwards and Hernández-Carmona 2005).

After the ENSO of 1982-3 and widespread destruction of kelps off the west coasts of North and South America, kelp abundance and community biodiversity returned, but recolonization rates were comparatively slow off the coast of Chile while rapid in the northern hemisphere (Martinez et al. 2003). Genetic diversity of *L. nigrescens* at the two most impacted sites was considerably less than at the least impacted sites. Recovery at Baja after the ENSO of 1982-3 was scale dependent and promoted by different variables that those associated with the damage (Edwards and Hernández-Carmona 2000)

Ladah et al. (1999) evaluated density and population structure for giant kelp at Bahia Tortugas, Baja after the ENSO of 1997-98 and found return of giant kelp in less than one year after complete loss of macroscopic plant life. Because the nearest spore sources were over 100km away, it was believed that a microscopic stage of giant kelp not visible during the dive surveys had survived, producing the recruitment activity.

Dayton et al. (1992) note that regional-scale periodic events such as ENSO may exert substantial impact on canopy kelps, but local-scale processes such as recruitment often permit rapid return to pre-ENSO patterns.

3. TROPHIC ECOLOGY

While research related to ENSO impacts on kelp patch dynamics has focused primarily on canopy kelp abundance, other studies have explored trophic interactions among numerous kelp community species. Bottom-up processes shaping trophic structure include the influences of abiotic factors such and light and nutrients levels on the proliferation of primary producers, which in turn supports herbivorous sea urchin populations, and ultimately predatory populations of sea otters, large fish, and/or lobsters. Top-down processes involve impacts of predator abundance on populations of herbivorous grazers, often with subsequent impacts for kelp abundance.

Ebeling et al. (1985) found that winter storms could have profound and different effects on community structure depending on the state of the community before the storm. One storm removed the canopy kelps along with the drift kelp normally derived from broken pieces of canopy kelp. Without their usual drift kelp diet, herbivorous sea urchins consumed much of the remaining vegetation, including the understory kelps. A few years later another catastrophic storm swept away the unprotected urchins, enabling return of canopy and understory kelps.

Vásquez et al. (2006), studying kelp community structure in northern Chile during the 1997-98 El Niño found the structure of kelp communities is characterized by transitions between kelp forest and sea urchin barrens. Declines in densities of carnivorous starfishes after the 1997-98 ENSO prompted rises in benthic herbivores, in turn resulting in a drop in *M. integrifolia* abundance. With the later return of starfish populations, sea urchin density decreased, promoting kelp recovery.

While most studies of giant kelp community structure have emphasized relationships between giant kelp, sea urchins, and sea urchin predators for specific environments over limited time spans, Halpern and Cottonie (2007) examined abundances of 49 subtidal species over 16 sites for 18 years within the Channel Islands National Marine Sanctuary, covering about 4300km^2. Local, regional, and global scale climatic variable were related to the community abundance data to examine the scale at which community-wide effects of ENSO events can be detected. Although this study confirmed the sometimes dramatic effect ENSO environmental changes can have for giant kelp populations, climate variation at any scale had little relationship with kelp forest community structure. Rather, local physical and/or biological variables explained the largest portion of the variation in community structure.

4. CONCLUSIONS

El Nino-Southern Oscillation events can produce significant changes in ocean climate of giant kelp forests. Strong wave action and influx of warm, nutrient-depleted surface waters can sharply reduce giant kelp survivorship and recruitment with subsequent ramifications for obligatory dependents. These conditions also shape the spatio-temporal dimensions of giant kelp abundance. However, it is not clear that other kelp community members are strongly affected, and in many cases, kelp recovery after damage has been achieved relatively quickly.

5. REFERENCES

Dayton, P.K., 1985: Ecology of kelp communities. *Annu. Rev. Ecol. Syst*, 16, 215-245.

Dayton, P.K., and M.J. Tegner, 1984: Catastropic storms, El Niño, and patch stability in a southern California kelp community. *Science*. 224(4646), 283-285.

Dayton, P.K., M.J. Tegner, P.E. Parnell and P.B. Edwards, 1992: Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecolog. Monographs* 62, 421-445.

Ebeling, A.W., D.R. Laur, and R.J. Rowley, 1985: Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Marine Biol*. 84, 287-294.

Edwards, M.S., 2004: Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the northeast Pacific. *Oecologia*. 138, 436-447.

Edwards, M.S. and G. Hernández-Carmona, 2000: Scale-dependent patterns of disturbance and recovery in giant kelp forests. *J. Phycol.* 36, 20.

Edwards, M.S. and G. Hernández-Carmona, 2005: Delayed recovery of giant kelp near its southern range limit in the North Pacific following El Niño. *Marine Biol*. 147, 273-279.

Graham, M.H., P.P. Kinlan, L.D. Druehl L.E. Garske, and S. Banks, 2007: Deep-water kelp refugia as potential hotspots of tropical marine diversity and productivity. *Proc. Nat. Academ. Sci*. 104, 16576-16580.

Halpern, B.S. and K. Cottonie, 2007: Little evidence for climate effects on local-scale structure and dynamics of California kelp forest communities. *Glob. Change Biol* 13, 236-251*.*

Joly, A.B. and E.C. Oliveira, 1967: Two Brazilian *Laminarias*. *Instituto de Pesquisas da Marinha*, 4, 1-7.

Ladah, L.B., 2003: The shoaling of nutrient-rich subsurface waters as a mechanism to sustain primary productivity off Central Baja California during El Niño winters. *J Marine Syst.* 42, 145-152.

Ladah, L.B. and J.A. Zertuche-González, 2004: Giant kelp (*Macrocystis pyrifera*) survival in deep water (25-40m) during El Niño of 1997-1998 in Baja California, Mexico. Botan. Marina. 47, 367-372.

Ladah, L.B., J.A. Zertuche-González, and G. Hernandez-Carmona, 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.

Martinez, E.A.,L. Cárdenas, and R. Pinto, 2003: Recovery and genetic diversity of the intertidal kelp *Lessonia Nigrescens* (Phaeophyceae) 20 years after El Niño 1982/83. *J. Phycol*. 39, 504-508.

Petrov, J.E, M.V. Suchovejeva, and G.V. Avdejev, 1973: New species of the genus Laminaria from the Philippines Sea. *Nov. Sistem. Nizch. Rast*., 10, 59-61.

Seymour, R.J., J.J. Tegner, P.K. Dayton, and P.E. Parnell, 1989: Storm wave induced mortality of giant kelp, Macrocystis pyrifera, in Southern California. Estuar., Coast. Shelf Sci. 28: 277-292.

Vásquez, J.A., J.M. Alonso Vega, and A.H. Buschmann, 2006: Long term variability in the structure of kelp communities in southern Chile and the 1997-98 ENSO. *J Appl. Phycol*. 18, 505-519.

Zimmerman, R.C. and D.L. Robertson, 1985: Effects of El Niño on local hydrography and growth of the giant kelp, *Macrocystis pyifera*, at Santa Catalina Island, California. *Limnol. Oceanogr*. 30, 1298-1302.