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Long term variability in the structure of kelp communities in northern Chile and the 1997–98 ENSO

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Abstract

This is the first study on the south eastern Pacific coast of South America which details long term, interannual variability in the structure of subtidal rocky-bottom kelp-dominated communities before, during, and after the El Niño Southern Oscillation (ENSO) event of 1997–1998 in northern Chile (23°S). The temporal patterns of the main components of these ecosystems, which included *Macrocystis integrifolia*, *Lessonia trabeculata*, echinoids and asteroids, were evaluated seasonally between 1996 and 2004. *M. integrifolia* demonstrated high interannual variability in temporal patterns of abundance. The 1997–1998 ENSO did not significantly modify the temporal patterns of *Macrocystis*, although local extinction of *M. integrifolia* beds occurred during negative thermal anomalies in 1999–2000 (La Niña event), facilitating the establishment of urchin dominated "barren grounds". The abundance of *Lessonia trabeculata* showed little temporal variability, and this species dominated the deeper regions of the kelp assemblage (8–13 m depth).

The structure of the kelp communities in the study area is regulated by a trophic cascade which modulates alternation between kelp dominated areas and sea urchin barrens. In this context, frequent and intense upwelling of cold water high in nutrients favors the establishment and persistence of kelp assemblages. During ENSO, coastal upwellings can mitigate superficial warming of coastal water and increase the nutrient concentration in the water column. Superficial warming during the 1997–1998 ENSO induced spawning by different species of echinoderms, which resulted in major recruitment of these species during 1999. Top-down events, such as the decrease in densities of the asteroids after the 1997–1998 ENSO event, favored increases in densities of benthic grazers, which caused significant decreases in abundance of *M. integrifolia*. The re-establishment of the adult fraction of the carnivore (starfish) guild coincided with a decrease in the density of sea urchins and thus re-establishment of the kelp. In the temperate south eastern Pacific, oceanographic events, which act on different spatial-temporal scales, trigger trophic cascades that act at local levels, producing interannual variability in the structure of kelp communities. On the other hand, considering the high macroinvertebrate diversity associated with kelp assemblages, the transitions between kelp-dominated areas and sea urchin barrens do not appear to significantly affect the biodiversity of these assemblages of benthic invertebrates.

Introduction

El Niño Southern Oscillation (ENSO) is an irregular fluctuation involving the entire tropical Pacific Ocean and global atmosphere (Fiedler, 2002). ENSO itself consists of an unstable interaction between sea surface temperature (SST) and atmospheric pressure. ENSO produces interannual variability in the oceanographic climate (Dayton et al., 1999), with alternating warm and cold periods resulting from positive (El Niño), and negative (La Niña) thermal anomalies of the SST, in 2 to 7 year feedback cycles (Fiedler,

2002). Differences in frequency, intensity, and magnitude of ENSO events have been associated with ocean regime-shifts caused by the Pacific Decadal Oscillation (PDO) and global warming (Steneck et al., 2002). During high-intensity, high-magnitude ENSO events (eg. 1982–1983 El Niño, 1997–1998 El Niño), Kelvin waves are propagated from the tropics both northward (North America) and southward (South America) along the eastern Pacific coastline. Although their manifestation decreases with increase in latitude, they may be detected beyond 35° (Halpin et al., 2004). The advance of these waves impinging on the coastline lowers the thermocline, increases sea level, modifies the direction and velocities of currents, and decreases or prevents coastal upwelling (Takesue et al., 2004). Changes in the oceanographic climate caused by high-intensity ENSO events have an important role as a disturbing process at temperate latitudes along the eastern Pacific coastline, producing bathymetric migrations of organisms, invasions of exotic species, behavioral alterations, and positive or negative changes in abundance, the latter of which may reduce population densities to local extinction (see Tegner & Dayton, 1987; Glynn, 1988; Dayton et al., 1999). Modifications of the coastal biota may be observed on both local and regional geographic scales (Camus, 2001; Edwards, 2004). Reductions in populations or local extinction processes generated by ENSO events are very important for "engineer species" in ecosystems (*sensu* Jones et al., 1994) such as kelp. The presence of these species determines the diversity, complexity, structure, and functioning of their associated communities (Graham, 2004).

Long-term studies on the North America west coast have shown that ENSO events alter the structure and organization of subtidal kelp communities in temperate latitudes, modifying patterns of persistence, stability, succession, species diversity, and abundance (Dayton et al., 1992, 1999; Tegner et al., 1997). Moreover, ENSO events have been considered as large-scale disturbances, which produce phase shifts between, kelp-dominated to sea urchin-dominated states (Tegner & Dayton, 1991; Steneck et al., 2002). In kelp forests, population changes in top predators commonly drive these shifts through top-down forcing processes (Estes et al., 2004). However, in California kelp forests, factors connected with anthropogenic impacts (see Tegner & Dayton, 1991; Dayton et al., 1998), may have buffered the phase shift to sea urchin-dominated states and facilitated recovery from ENSO disturbances (Steneck et al., 2002). In contrast, most studies of subtidal kelp communities in the Southern Hemisphere are short-term (one–two years), or are limited to high latitudes (≥40°S) where the influence of ENSO is minimal (Halpin et al., 2004). As such, there are no long-term data concerning the effects of large-scale, low frequency ENSO events on the structure of South American kelp communities.

In northern Chile and southern Peru (10°–30°S), protected and semi-exposed shallow subtidal hard-bottom environments (*ca.* 20 m depth) are dominated by two kelp species from the Order Laminariales, including *Lessonia trabeculata* Villouta & Santelices and *Macrocystis integrifolia* Bory. Although there are some reports in the literature on the ecology of *Lessonia trabeculata* (see Vásquez, 1992; Tala et al., 2004), data are scarce on the population biology of *M. integrifolia* and the *Macrocystis-Lessonia* assemblage in northern Chile. Available information is restricted only to standing stock evaluations and observations on reproductive activity in controlled environments and in the field (Buschmann et al., 2004; Vega et al., 2004).

The subtidal kelp ecosystems on the South American west coast are highly productive, hosting diverse and abundant macroinvertebrates and fishes (Vasquez et al., 2001a). *M. integrifolia* and *L. trabeculata*, are highly sensitive to positive SST anomalies and low nutrient concentrations on the coast caused by ENSO events, and experienced high mortalities during the 1982–83 (Tomicic, 1985; Soto, 1985; Glynn, 1988) and 1997–98 (Godoy, 2000; Llellish et al., 2001) ENSO events. Without kelp assemblages, subtidal rocky reefs form alternative states, the most common of which is the "barren-ground" associated with sea urchins (Vásquez, 1992). The most important grazers in such systems are the sea urchins *Tetrapygus niger* (Molina) and the sympatric but less common species *Loxechinus albus* (Molina) (Rodriguez & Ojeda, 1993). *T. niger* is an omnivore, while *L. albus* is an herbivore and feeds on foliose algae and drifting algal rafts (Contreras & Castilla, 1987). Although both species can completely destroy kelp beds on a local scale (see Dayton, 1985; Buschmann et al., 2003), *T. niger* is primarily responsible for generation and maintenance of the barren grounds typically observed in northern Chile (Vásquez & Buschmann, 1997).

A guild of carnivores (starfish), regulates spatial and temporal patterns of abundance and diversity of the benthic grazers (Viviani, 1978; Vásquez & Buschmann, 1997). The fishes associated with the kelp