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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 communities have a broad trophic spectrum and eat few sea urchins (Medina et al., 2004). In northern Chile ENSO produces trophic cascades by top-down processes (starfish↔sea urchins↔kelp), which modify the patterns of biodiversity, stability and persistence of subtidal kelp communities (Vásquez & Vega, 2004). In this context long-term monitoring has permitted postulation that the 1997–1998 ENSO event generated: (1) interannual variability in the abundance of the main functional groups associated with the kelp, (2) differential responses of the species or functional groups, and (3) changes in the structure and organization of the kelp communities.

The present study evaluates long term patterns of abundance in key species which regulate subtidal communities on rocky bottoms dominated by kelp in northern Chile, and incorporates the effects of the 1997–1998 ENSO event. Data were obtained from before, during, and after this ENSO event. Data are presented on the effects of different groups of key benthic species on the structure and organization of these subtidal kelp communities, including the kelp species, grazers (sea urchins), predators (sea stars), and macroinvertebrate species forming the more common assemblages in this region.

Materials and methods

Study area

Shallow, subtidal, rocky-bottom communities dominated by kelp were evaluated seasonally between July 1996 and August 2004 at Caleta Constitución (23°26′S, 70°36′W). This bay, on the southern end of the Mejillones Peninsula in northern Chile (Figure 1) is in a region of permanent upwelling (Takesue et al., 2004), semi-protected from prevailing winds by Santa Maria Island. The bottom substrate consists of rocky platforms, which drop to depth, plus scattered boulders separated by channels floored with coarse sand. Kelp beds are widely distributed throughout the bay; the sub-canopy undergrowth comprises various foliose, turf, and crustose macroalgae. These include crustose Corallinales, turfs of Gelidiales and/or Ceramiales, and often patches of *Halopteris spp*., *Glossophora kunthii* (C. Ag.) J. Ag., *Asparagopsis armata* Harley and *Rhodymenia spp*. and *Chondrus canaliculatus* (C. Ag.) Grev. (Vásquez et al., 2001b). Descriptions of the study site and marine ecosystem are given by Vásquez et al. (1998).

Oceanographic conditions

Mean daily *in situ* water temperatures were measured on continuous-register thermographs (Onset Computer Corp., MA, USA) placed at 3 m depths along the shallow limits of the kelp. When *in situ* records of oceanographic variables were discontinued, large-scale climatic indexes were used, which permitted description of oceanographic conditions, and for making approximations of ecological processes that acted on smaller scales (Stenseth et al., 2003). Warm and cool phases of the ENSO were determined using monthly averages of the Southern Oscillation Index (SOI) and the Multivariate El Niño Index (MEI) for the period (1996–2004), from the Bureau of Metereology, Australia (www.bom.gov.au/climate/current/) and Climate Diagnostic Center of NOAA (www.cdc.noaa.gov/~kew/MEI/mei.html), respectively. Information on the temporal variability of upwelling events in the region (23–25°S) was obtained from the monthly average index of upwelling (Offshore Eckman Transport, OET) between 1996 and 2001, from the Pacific Environmental Laboratory (PFEL, (www.pefg.noaa.gov/products/PFELindices.html). A detailed description of this calculation, and characteristics of the area of influence of the SOI, MEI and OET indexes is presented by Navarrete et al. (2002).

Temporal patterns of kelp abundance

Temporal patterns of abundance of *M. integrifolia* and *L. trabeculata* were evaluated seasonally on four haphazardly chosen transects which were established perpendicular to the coastline from the intertidal to 15 m depth. Each transect was 160 m long and 1 m wide. Two SCUBA divers swam each transect, counting juvenile and adult sporophytes within 0.5 m on each side of it's axis. Kelp juveniles were sporophytes with up to two lanceolate and laminar fronds, without reproductive structures, and with maximum holdfast diameters of $\leq$1 cm. Densities of juveniles and adults were expressed as the number of plants per m^2 ($N = 4$).

Temporal patterns of grazer (sea urchins) abundance

Temporal changes in the density of grazers were determined by seasonal evaluation of 34 steel-frame quadrats of $0.25\,m^2$ each, haphazardly tossed from a boat between the perpendicular transects described above. Densities of the sea urchins were expressed as the number of individuals per $0.25\,m^2$.

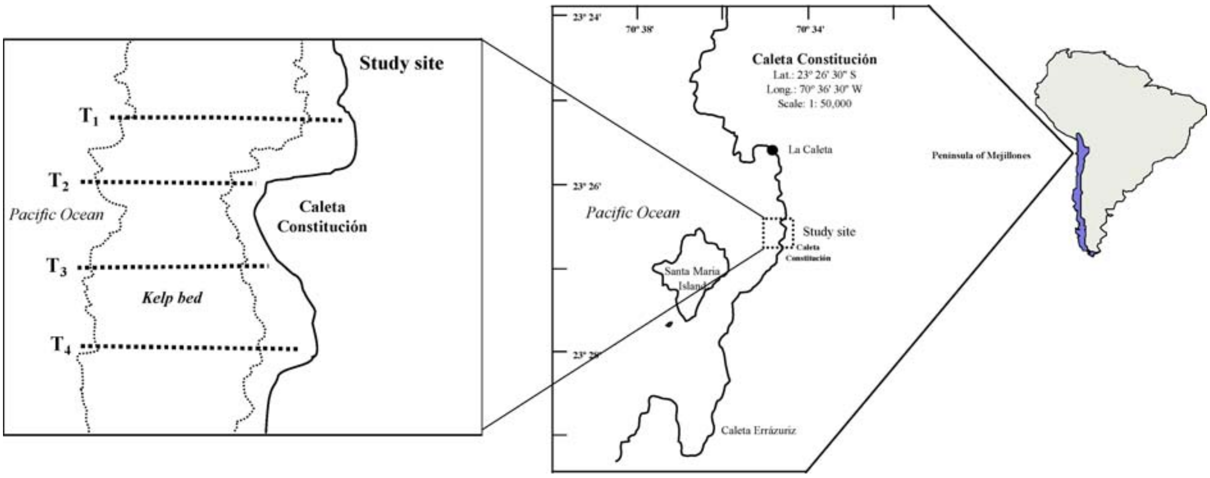

Figure 1. Geographic location of the study area, showing sampling sites and positions of transects.

Temporal patterns of carnivore (sea stars) abundance

To evaluate the temporal distribution of the sea star carnivorous guild, we used the same methods and sampling units as for the kelp assemblage. The number of asteroids per species was counted for each sampling unit ($N = 4$, transect of 160 m^2), with individual densities expressed per m^2.

Temporal patterns of macroinvertebrate assemblages in subtidal kelp beds

Changes in hard-bottom community structure before (1996), during (1997–98), and after (1999–2000) the 1997–1998 ENSO were evaluated seasonally by means of analysis of benthic macroinvertebrate assemblages associated with subtidal kelp beds. The composition and abundance of the benthic macroinvertebrates species was evaluated using destructive sampling with 0.25 m^2 quadrats. Twenty steel-frame quadrats were thrown haphazardly from a boat over depths of between two and 15 m, covering the entire range of the kelp beds (2–15 m depth). Divers, using numbered, 1-mm mesh collecting bags, recovered all the fauna occurring within the quadrats. Collected material was transferred to numbered plastic bags onshore, fixed in 8% formalin dissolved in seawater and later preserved in 70% alcohol. In the laboratory, the invertebrates were sorted and identified to the lowest taxonomic level possible using literature listed by Lancelloti and Vásquez (1999, 2000). The number of individuals of each macroinvertebrate species was counted in each sample unit. Temporal patterns of invertebrate assemblages associated with subtidal kelp beds was analyzed using univariate biodiversity indexes (species richness (S')) and biodiversity index of Shannon Weiner [H', J']).

Statistical analyses

A multifactorial analysis of variance (ANOVA) using the species, years and seasons as the main variables was used to evaluate the hypothesis that ENSO events generated long-term variability in patterns of abundance of key species (kelp, sea urchins and starfish), which structured subtidal kelp communities at the study site. The multifactorial analysis of variance (ANOVA) was done after visual determination of normality of the data and homoscedasticity of variances by means of a Bartlett test (Sokal & Rohlf, 1981), using SYSTAT 8.0® computational software for Windows; transformations (root abundance + 1) were applied when necessary to improve homoscedasticity (Sokal & Rohlf, 1981). An *a posteriori* Tukey test was used in order to determine which groups differed from others (Sokal & Rohlf, 1981). The relationship between mean abundance of kelp, sea urchins and starfish was determined using a Pearson Correlation Analysis (Sokal & Rohlf, 1981).

Results

Oceanographic conditions

In situ sea temperature showed a seasonal pattern, with warm water between December and March (summer)

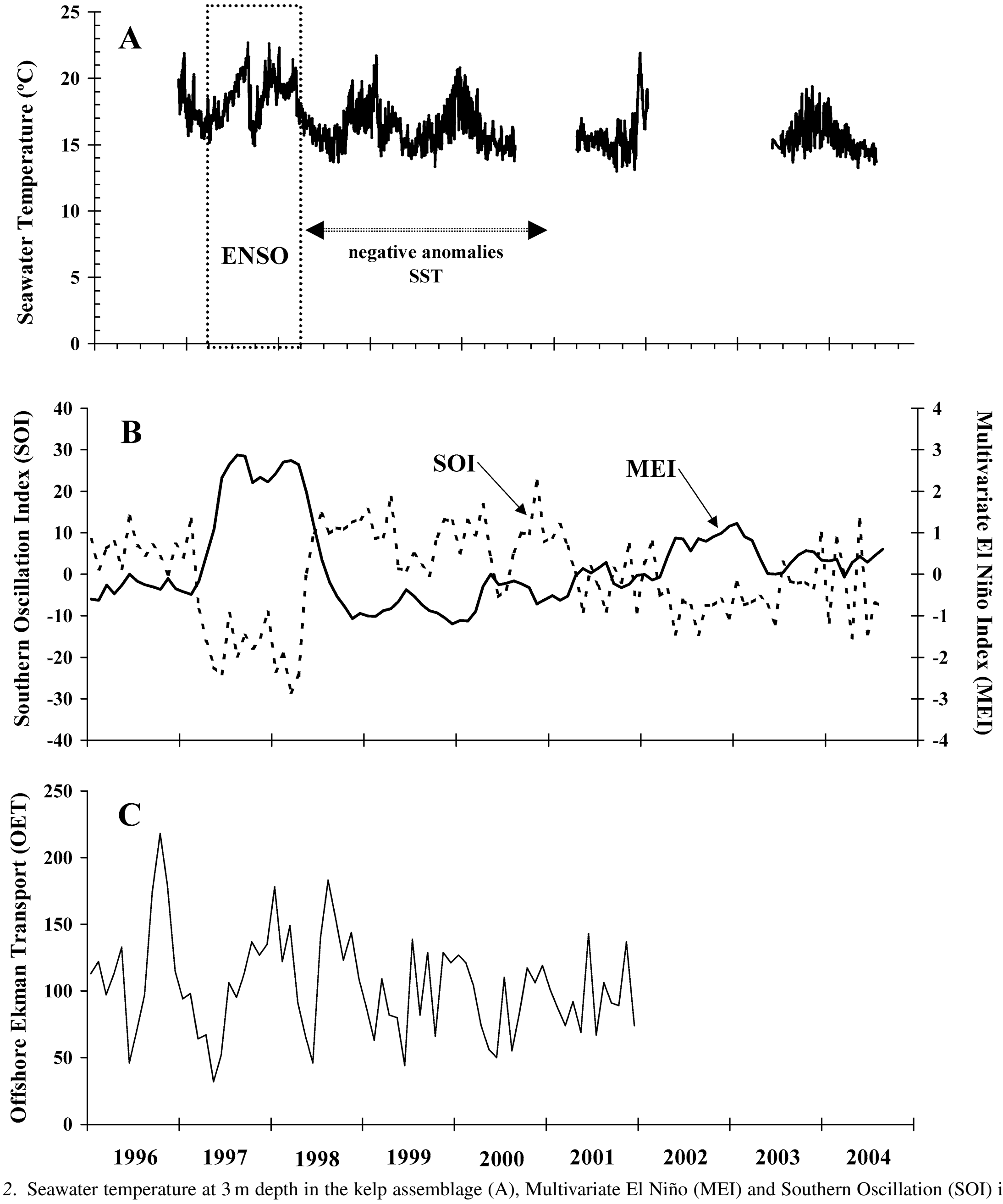

Figure 2. Seawater temperature at 3 m depth in the kelp assemblage (A), Multivariate El Niño (MEI) and Southern Oscillation (SOI) indexes (B), and upwelling index (Eckman transport, OET) (C) during the study period.

and cool water between June and September (winter) (Figure 2A). Between April 1997 and March 1998 the water was unusually warm, with maximum positive thermal anomalies fluctuating between +2° and +2.5°C; an exception occurred between August and November 1997 when upwelling lowered the seawater temperatures, interrupting the continuity of the anomalous warm period. Beginning in April 1998, cooling of the water began with weak, moderate, and strong levels when the anomaly ranged between −0.5° and −1.5 °C until the end of 2000 (La Niña event; Figure 2A). The Southern Oscillation Index (SOI, Figure 2B) and the Multivariate El Niño Index (MEI, Figure 2B) detected normal conditions in 1996 lasting until summer 1997. An ENSO event was recorded between May 1997 and March 1998, which was of high intensity and magnitude, coinciding with the thermal anomaly detected by the *in situ* temperature records (Figure 2A). Following the normal-cold period of 1998–2001, a new ENSO manifestation was detected which was of low to moderate intensity between April 2002 and April 2003 (Figure 2B), with a positive thermal anomaly of +1 °C. The mean values for the upwelling index (OET) were always positive during the study period, and represented continuity over time of the Ekman transport in the region (Figure 2C). The upwelling index showed a greater offshore transport between September and December (spring), and lower intensities of upwelling between April and July of each year (Figure 2C). The highest upwelling activity occurred during the spring of 1996, decreasing significantly in May 1997 at the beginning of the 1997–1998 ENSO event. Nevertheless, the Ekman transport remained active, constant, and intense between July 1997 and February 1998 (Figure 2C) during the maximum positive thermal anomalies of the 1997–1998 ENSO.

Temporal patterns of kelp abundance

The temporal patterns of abundance of *M. integrifolia* differed significantly from those of *L. trabeculata* (Table 1A). *M. integrifolia* showed marked annual changes, with maximum abundances of adult sporophytes during 1997–1998 (1997–1998 ENSO period) and minima during 2000–2002 (period of negative SST anomalies), reaching critical levels of abundance (0.1 to 0.6 sporophytes/m^2) in 2000 (Figures 3A–B). In the fall of 2001, the population of *M. integrifolia* started to become re-established, reaching its maximum density during 2003 (Figure 3A). In contrast, the average abundance of *L. trabeculata* during the study period was 0.5 ± 0.9 sporophytes/m^2, with stochastic changes (Figures 3 C–D). The temporal patterns of juveniles of *M. integrifolia* were significantly different from those of *L. trabeculata* (Table 1B, Figures 3 B–D). The abundances of juveniles of *M. integrifolia* increased during the 1997–1998 ENSO, and during the re-establishment of kelp bed from 2001 to 2003 (Figure 3C). There was, however, a decrease due to a failure in recruitment in 1999–2000, which helped cause the disappearance of the *M. integrifolia* bed during the negative SST anomalies (La Niña event). In contrast, the abundance of *L. trabeculata* juveniles increased mainly in the spring (Figure 3D), even though juveniles of this species can be present throughout the entire year (i.e. 2003; Figure 3D).

Table 1. Multifactorial Analysis of Variance (ANOVA) using species, year and season as main variables to evaluate the hypothesis that ENSO event generate long-term variability in abundance of key species (kelp, sea urchins and starfish).

Factor	df	MS	F	*p*-level
(A) Kelp adults				
Species	1	0.181	4.797	0.116
Year	6	1.408	8.821	0.001
Season	3	0.014	5.542	0.001
Species vs Year	6	1.185	10.685	0.001
Species vs Season	3	0.038	14.486	0.001
Year vs Season	18	0.160	61.231	0.001
Species vs Year vs Season	18	0.111	42.539	0.001
Residuals	168	0.003		
(B) Kelp juveniles				
Species	1	4.432	4.777	0.117
Year	6	3.554	2.196	0.092
Season	3	0.562	17.701	0.001
Species vs Year	6	3.932	2.144	0.098
Species vs Season	3	0.927	29.231	0.001
Year vs Season	18	1.618	50.970	0.001
Species vs Year vs Season	18	1.833	57.730	0.001
Residuals	168	0.032		
(C) Sea Urchins				
Species	1	363.45	274.92	0.001
Year	6	36.66	23.39	0.001
Season	3	3.61	3.49	0.015
Species vs Year	6	29.18	12.63	0.001
Species vs Season	3	1.32	1.28	0.280
Year vs Season	18	1.57	1.52	0.075
Species vs Year vs Season	18	2.31	2.23	0.002
Residuals	1848	1.03		
(D) Sea Star				
Species	3	0.1577	16.792	0.001
Year	6	0.0746	3.535	0.017
Season	3	0.0267	137.647	0.001
Species vs Year	18	0.0222	3.075	0.001
Species vs Season	9	0.0094	48.510	0.001
Year vs Season	18	0.0211	109.032	0.001
Species vs Year vs Season	54	0.0072	37.273	0.001
Residuals	336	0.0002		

Significant differences $p < 0.05$.

Temporal patterns of grazer (sea urchin) abundance

The black sea urchin (*T. niger*) was the most conspicuous herbivore at Caleta Constitución, coexisting with the significantly less abundant sea urchin *L. albus* (Figure 4). The benthic grazer abundances varied significantly between years (Table 1C), showing

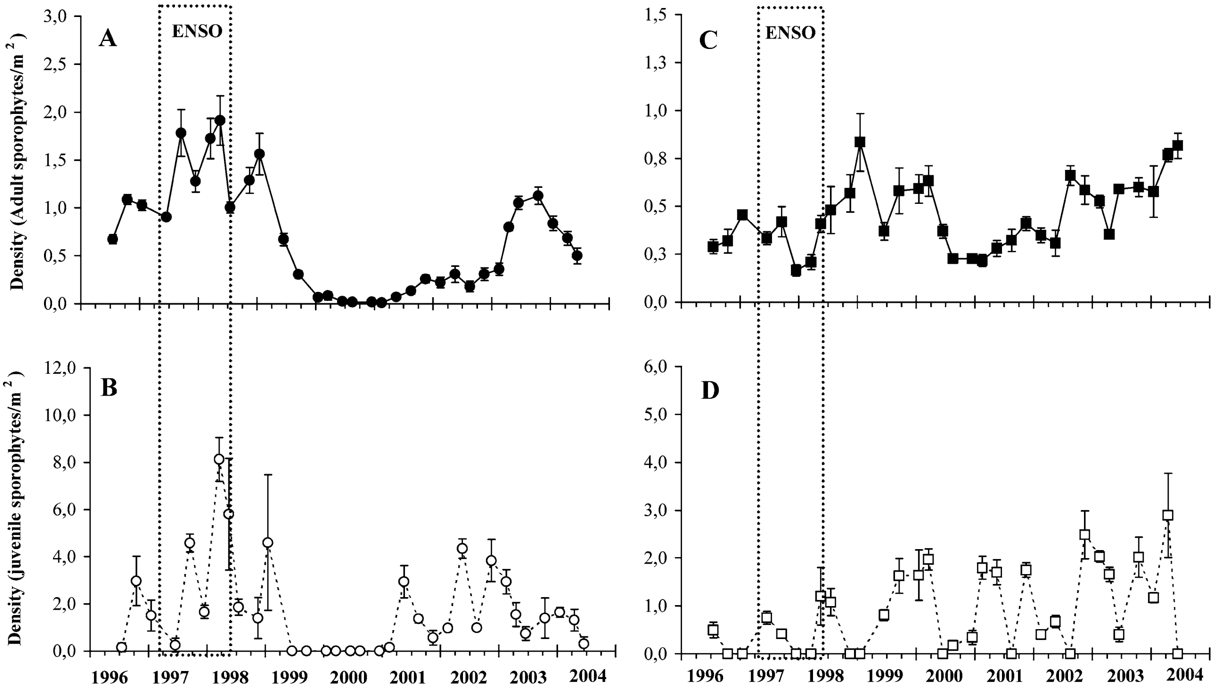

Figure 3. Long-term variability of kelp densities (1996–2004): Density of adult (A) and juvenile (B) sporophytes of *Macrocystis integrifolia*, and adults (C) and juveniles (D) of *Lessonia trabeculata* in subtidal habitats at Caleta Constitución, Antofagasta, Chile.

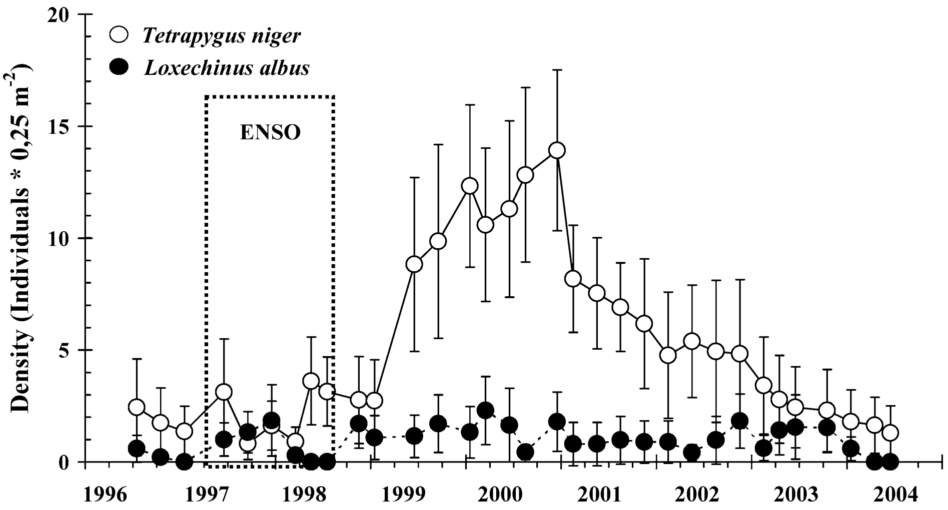

Figure 4. Long-term variability of grazer densities (1996–2004): *Tetrapygus niger* and *Loxechinus albus* in rocky subtidal habitats at Caleta Constitución, Antofagasta, Chile.

three different population levels throughout the study period. Sea urchins were less abundant between 1996 and 1998, including the 1997–1998 ENSO (Figure 4). During periods of negative SST anomalies (1999–2000), the mean density of grazers increased, tripling its mean density between 1996–1998 (Figure 4). This change in temporal patterns of abundance of *T. niger* coincided with the local extinction of the *M. integrifolia* population. An inverse and significant correlation suggested that the density of juvenile and adult *M. integrifolia* sporophytes decreased with increasing numbers of *T. niger* (Table 2). In contrast, there were no significant correlations between *T.*

Table 2. Pearson correlation coefficient (probability in parentesis) between sea urchins and kelp abundance.

	Tetrapygus niger	*Loxechinus albus*
Macrocystis integrifolia		
Adults	−0,67	−0,17
	(0,0001)	(0,3631)
Juveniles	−0,51	0.06
	(0,0036)	(0,7374)
Lessonia trabeculata		
Adults	−0,22	0,30
	(0,2343)	(0,1075)
Juveniles	−0,36	0,25
	(0,0507)	(0,1868)

Boldface indicates significant association, alpha = 0.05.

niger and *L. trabeculata* or between *L. albus* and both kelp species (Table 2). Beginning in 2001, the abundance of *T. niger* began to decrease significantly until the end of 2003, giving values similar to those encountered between 1996–1998 (Figure 4).

Temporal patterns of carnivore (sea star) abundance

The asteroid species of this benthic system differed significantly in annual and seasonal patterns of abundance (Table 1D). *Heliaster helianthus* increased significantly in 1998–2000 with a maximum in 1999, including the 1997–1998 ENSO period (Figure 5A). From 2001 to the end of the study period, densities of *Heliaster helianthus* remained comparatively low, with averages similar to those found in 1996 (Figure 5A). In contrast, the temporal patterns of abundance of *Stichaster striatus* underwent significant increases during the spring: these were particularly notable in 1999, 2002, and 2003 (Figure 5B). The seasonal increases in *S. striatus* were caused by reproductive aggregations in shallow water. *Meyenaster gelatinosus* and *Luidia magellanica* showed similar tendencies in their temporal patterns (Figures 5C y D): both decreased significantly in 1998, immediately after the 1997–1998 ENSO, and re-established their densities during the cool period of 1999–2000. There were positive and significant correlations among the different species of asteroids as well as among the asteroids and echinoids (Table 3), suggesting common populational responses to interannual variations in the oceanographic climate within this subtidal ecosystem.

Temporal patterns of benthic macroinvertebrate assemblages

The temporal variation in species richness of the macroinvertebrate assemblage associated with the kelp assemblages fluctuated between 50 and 80 species during the study period, without detection of relevant breaks during the 1997–1998 ENSO (Figure 6A). The biodiversity (H') and uniformity (J') indexes only detected a break in the temporal patterns in fall 1998 (Figure 6B), during the decline of the 1997–1998 ENSO event. There was a decrease in the diversity indices as a consequence of the numerical dominance of filter-feeding species (i.e. tunicates, mussels) that cover rocky bottom. The total macroinvertebrate density, in contrast to the other community variables, showed high temporal variability before (1996), and after the 1997–1998 ENSO, in contrast with the low densities during ENSO (Figure 6C).

Discussion

The present study demonstrates some of the effects of the El Niño Southern Oscillation (ENSO) event on the structure and organization of subtidal rocky communities dominated by kelp in South America. These are the first observations of this type on a such a large-scale, low frequency oceanographic. Of the two common kelp species, *Macrocystis integrifolia* and *Lessonia trabeculata*, only the former varies significantly in abundance seasonally and annually. In this context, the temporal variation in abundance of the giant kelp M*acrocystis pyrifera* in the northern hemisphere is correlated with thermal anomalies coupled to annual temperature (Steneck et al., 2002). These thermal oscillations co-vary inversely with the availability of nutrients, producing different seasonal patterns of abundance (Tegner et al., 1997; Dayton et al., 1992, 1998, 1999). The populations of *M. integrifolia* in northern Chile are made up of perennial sporophytes, which maintain average abundances throughout the year, with seasonal variability only in growth and reproduction (Buschmann et al., 2004). As in populations of *M. pyrifera* in California and Mexico (Ladah et al., 1999; Edwards, 2004), it may be predicted that the temporal stability of South American populations of *M. integrifolia* could be interrupted by (1) positive thermal anomalies generated by ENSO events which produce local mortalities with highest intensity at the lower latitudes, and (2) the rate of post-ENSO

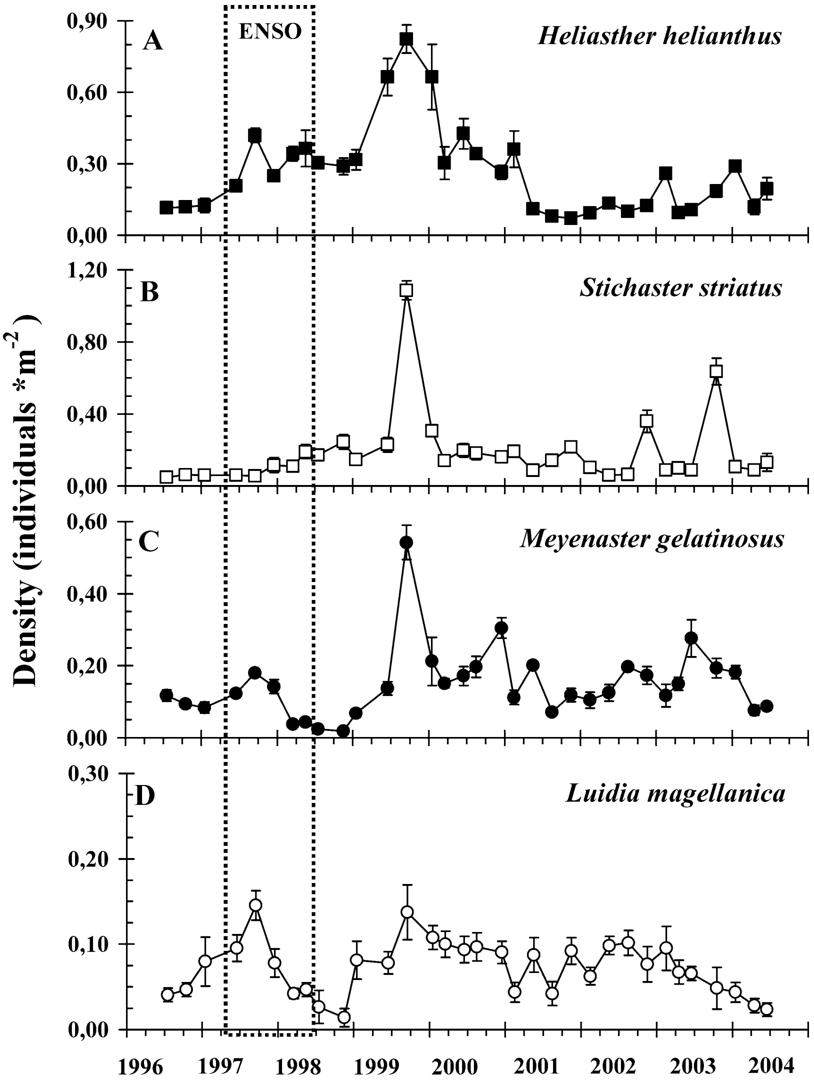

Figure 5. Long term variability of sea star densities (1996–2004): (A*) Heliasther helianthus*, (B) *Stichaster striatus*, (C) *Meyenaster gelatinosus* and (D) *Luidia magellanica* at Caleta Constitución, Antofagasta, Chile.

recovery, that may depend on the intensity of negative thermal anomalies (La Niña). Both factors would be expected to generate interannual variability that have not always been taken into account in understanding the functioning of these communities. Our observations of the structure and organization of the kelp assemblages in northern Chile, made during the study period which included the 1997–1998 ENSO event, nevertheless were an exception to the above two possibilities, since the abundance of *M. integrifolia;* (1) increased significantly during the 1997–1998 ENSO event, (2) decreased during the 1999–2001 La Niña event to levels near zero in 2000, and (3) became re-established during a period with a positive thermal anomaly in 2002–2003. In this context, a few fertile sporophytes survived the local disappearance of *M. integrifolia*, generating reproductive propagules for the re-establishment of the population (Vega et al., 2004). Also, drifting rafts and seed banks of microscopic dormant stages (gametophytes) may be included in possible complementary strategies for repopulation of this kelp species (Ladah et al., 1999; Buschmann et al., 2004; Vega et al., 2004).

Populations of *L. trabeculata* in northern Chile are made up of perennial and long-lived sporophytes (Vásquez, 1992; Tala et al., 2004), partially

Table 3. Pearson correlation coefficient (probability in parentesis) between Echinoids and Aesteroids abundance.

	Echinoids		Asteroids		
Asteroideos	*T. niger*	*L. albus*	*H. helianthus*	*S. striatus*	*M. gelatinosus*
Heliasther helianthus	0,45 **(0,0096)**	0,23 (0,2040)	–	–	–
Stichaster striatus	0,30 **(0,0992)**	0,37 **(0,0387)**	0,57 **(0,0006)**	–	–
Megenasster gelatinosus	0,47 **(0,0063)**	0,49 **(0,0043)**	0,43 **(0,0148)**	0,65 **(0,0001)**	–
Luidia magellanica	0,42 **(0,0163)**	0,38 **(0,0317)**	0,38 **(0,0320)**	0,23 (0,2124)	0,62 **(0,0002)**

Boldface indicates significant association, alpha = 0.05.

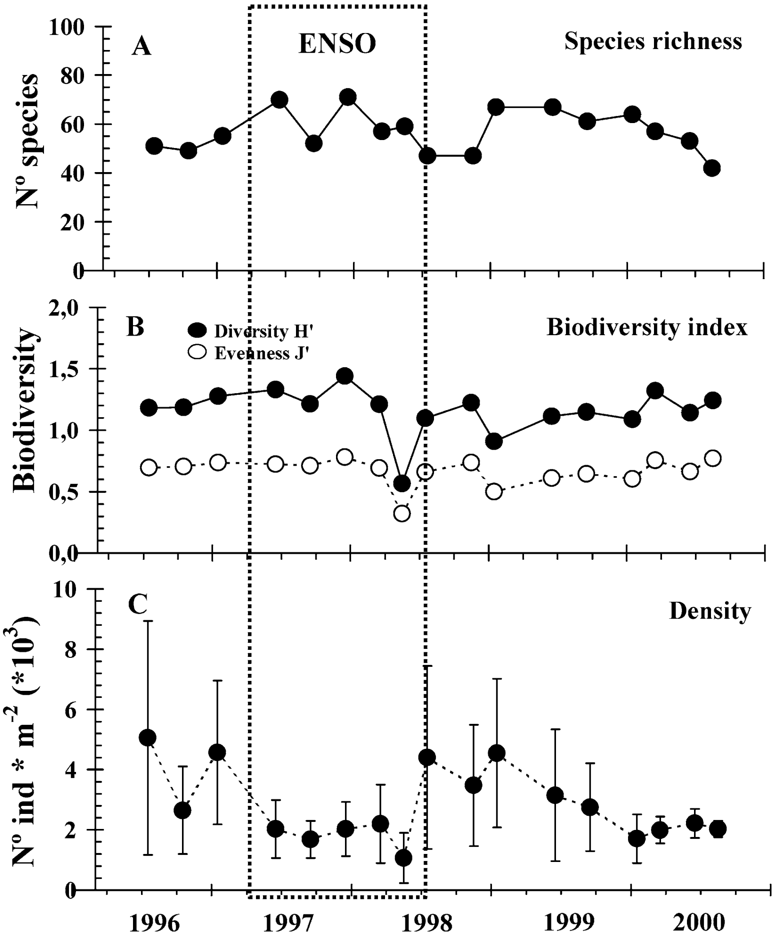

Figure 6. Long term variability of biodiversity indexes (1996–2000) in subtidal kelp communities at Caleta Constitución, Antofagasta, Chile: (A) Species richness, (B) Diversity (H'), Evenness (J'), and (C) Total density of macroinvertebrates.

explaining the temporal patterns of bathymetric distribution of *L. trabeculata* between 1996 and 2004. On the Peruvian coast, the mortality rates of *L. trabeculata* sporophytes during the 1997–1998 ENSO were inversely correlated with depth, with highest survival between 12 and 15 depths (Fernández et al., 1999). *M. integrifolia* dominated rocky bottoms at 5–8 m in the area of the present study, while *L. trabeculata* was dominant at greater depths (8–13 m; Vega et al., 2004).

The temporal pattern of abundances of juveniles differed between the two kelp species over long-term periods. Whereas *M. integrifolia* recruits throughout the year (as in other wave-protected environments; see Graham et al., 1997), *L. trabeculata* recruits during the winter months, thus producing a greater abundance of juveniles during the spring. These differences in recruitment patterns (annual *vs* seasonal) suppose different reproductive strategies that may in part explain the temporal dynamics and longevity of the assemblage. These hypotheses need to be studied, experimentally, in the future.

Although the 1997–1998 ENSO event was a catastrophic occurrence which produced local kelp extinctions at low latitudes on the coasts of both Chile and Peru in the Southern Hemisphere (Fernández, et al., 1999; Godoy, 2000; Llellish et al., 2001; Martínez et al., 2003), and in California and Mexico in the Northern Hemisphere (Ladah et al., 1999; Edwards, 2004), local conditions permitted persistence of the kelp assemblages (Martínez et al., 2003; Vega et al., 2004). Here, the maintenance of temporal patterns of *M. integrifolia* and *L. trabeculata* during the 1997–1998 ENSO event in northern Chile, may be explained by the frequency and intensity of coastal upwelling (Lagos et al., 2002), which minimized the warming effects at the SST, maintaining high concentrations of nutrients within coastal environments (Takesue et al., 2004).

On the California coast, the recovery of *Macrocystis* post 1997–1998 ENSO was favored by the rapid establishment of a cold period (1998–2000 La Niña; Edwards, 2004) and the survival of sporophytes in deep environments (Ladah et al., 1999). In the Southern Hemisphere the re-colonization rate of the kelp assemblages occurred comparatively slowly (Martínez et al., 2003), although cool conditions of 1998–2000 added to the effects of upwelling. The abundance of *M. integrifolia* in the study area was modified by a significant reduction in the adult population and lack of recruitment of juvenile sporophytes. Thus, the disappearance of the *M. integrifolia* population occurred two years after the 1997–1998 ENSO event, and was significantly, inversely correlated with the increase in the population of the black sea urchin *Tetrapygus niger*. This contrasts with information from other areas of the south eastern Pacific during the 1997–1998 ENSO event, where superficial warming decreased the abundance of kelp on shallow bottoms, inducing migrations of grazers to deeper zones in search of food (Vásquez & Buschmann, 1997; Fernández et al., 1999; Godoy, 2000; Llellish et al., 2001). This type of migratory behavior of benthic grazers such as sea urchins and gastropods on hard bottoms produces communities dominated by crustose calcareous algae ("barren ground", *sensu* Lawrence, 1975). In the Northern Hemisphere, events that impact the abundances of high-level predators, and low levels of availability of drift algae promote the formation of barren ground; this occurrence is not necessarily linked to ENSO (Tegner & Dayton, 1991; Steneck et al., 2002; Estes et al., 2004). The urchin-crustose algae association persists until the sea urchin population is decimated by disease, migration, or predator pressure, which act together to promote reestablishment of the kelp (Dayton et al., 1992; Estes et al., 2004; Graham, 2004).

It has been noted that areas with intense and permanent offshore transport, such as the study area on the Mejillones Peninsula, are typified by high survival, retention, and transport of echinoderm larvae toward the coast (Ebert & Russell, 1988). During the ENSO cycle (1997–1998 El Niño and 1998–2000 La Niña), different events favored an increase in the urchin population during the cool phase, including (1) induction of spawning due to increases in SST and persistence of upwelling events, (2) significant reductions in densities of adult individuals of *M. gelatinosus* and *L. magellanica* (Vásquez et al., 1998; Vásquez & Vega, 2004) and (3) changes in the feeding behavior of *H. helianthus* (Tokeshi & Romero, 1995; Vásquez et al., 1998).

In the absence of other large predators on the south eastern Pacific coast, the sea stars form a predatory guild, which significantly lower the abundance of benthic herbivores such as the sea urchins and gastropods (Vasquez & Buschmann, 1997). Although fishes such as *Graus nigra* and *Semicosyphus maculatus* may prey upon juvenile urchins, the sea urchins do not exceed 17% of their diets (Medina et al., 2004). The re-establishment of adult densities of *Meyenaster gelatinosus*, *Stichaster striatus*, *Heliater helianthus* and *Luidia magellanica* was associated with the temporal recovery of kelp assemblages in the study area. *Meyenaster* and *Luidia* also prey upon *H. helianthus and S.* striatus (Dayton et al., 1977; Viviani, 1978; Tokeshi & Romero, 1995). There is spatial segregation on a bathymetric gradient between the different species of sea stars (Vásquez & Vega, 2004). Encounters between these high level predators often result in autotomy of one or more of their rays (Lawrence & Vásquez, 1996). Here, sublethal predation between

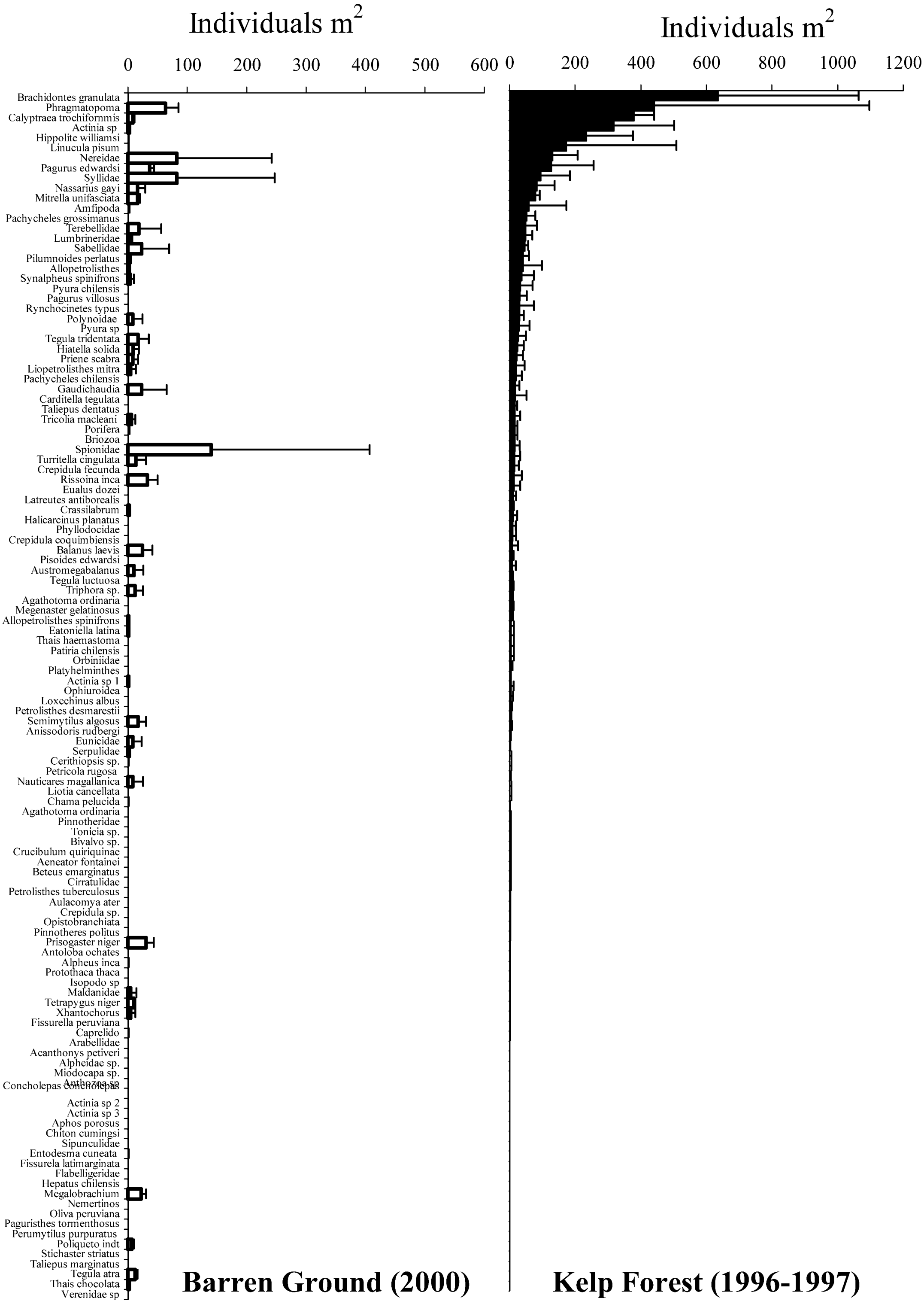

Figure 7. Abundance and species richness in kelp and sea urchin dominated areas (barren ground).

components of the asteroid guild has been suggested as evidence to explain the segregated patterns of distribution on the benthic gradient (Lawrence & Vásquez, 1996).

Different bottom-up and top-down events may regulate long-term ecosystem changes in northern Chile including: (**1**) The intensity and frequency of upwelling buffer the positive thermal anomalies in SST, maintaining high nutrient levels which favor the kelp during ENSO events. (**2**) Site-dependent oceanographic conditions may generate optimal conditions for spawning, larval development, and recruitment of echinoderms during and/or after ENSO event. (**3**) The population dynamics of adult starfish and sea urchins during ENSO events are essentially species-specific. (**4**) Species-specific population dynamics (i.e. *L. magellanica*) and changes in dietary composition (i.e. *H. helianthus*) during ENSO events, may promote population increases in *T. niger*. This seems to be a key factor in alternation of environments dominated by kelp beds and barren grounds. (**5**) The increase in population density of the adult fraction of the carnivore guild is correlated with the decline in densities and/or displacement to shallow bottoms of the more conspicuous herbivorous grazers.

Discrete and local oceanographic events (upwelling) as well as large-scale, low-frequency events (ENSO) generate interannual variability in species or groups of key species, which structure and organize subtidal, rocky reef communities in northern Chile. This translates to trophic cascades that modulate the temporal alternation of states dominated by kelp, and sea urchin barrens. These changes in submarine seascapes have been treated as "catastrophic" in the literature (Tomicic, 1985; Soto, 1985), although simple species diversity indexes revealed no significant changes with (1996–1998), or without (1999–2000) the presence of kelp assemblages (Figure 7). Here, the composition and species richness seem to indicate different organizational states of these communities. On a regional scale, this characteristic suggests the presence of a mosaic of subtidal seascapes in different seral stages of ecological succession (Tomicic, 1985; Vasquez et al., 1998; Camus, 2001, Dayton et al., 1998, 1999, Edwards 2004). Graham (2004), recently contrasting biodiversity and trophic complexity in sea urchin barrens and kelp-dominated habitats (*Macrocystis pyrifera*), did not find significant differences between alternate states. This also suggests a temporal resilience in the trophic web of the kelp forest over the long term, with few species exclusively associated with a determinate state.

Finally, the interannual variability in the structure and organization of subtidal kelp communities suggests the need for long term (8^+ yrs) monitoring programs. These would detect changes over time, which would not be evident in short or medium-term studies. This type of data would be useful in evaluating conservation and management of resources, and would broaden knowledge of the sustainability of the biological diversity of Chile's continental coastal marine ecosystem (Vasquez et al., 2001a). In this context, Chile's extensive coastline (18°–56°S) offers an ecological scenario that is unique in the world for evaluation of the effects of events that operate on different geographic scales.

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