Journal of Applied Phycology (2006) DOI: 10.1007/s10811-006-9056-4

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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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- Q1 8 Received xxx; accepted xxx
 - 9 Key words: Lessonia, Macrocystis, southern hemisphere, subtidal rocky shore

10 Abstract

This is the first study on the south eastern Pacific coast of South America which details long term, interannual 11 variability in the structure of subtidal rocky-bottom kelp-dominated communities before, during, and after the El 12 Niño Southern Oscillation (ENSO) event of 1997-1998 in northern Chile (23°S). The temporal patterns of the 13 14 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 15 variability in temporal patterns of abundance. The 1997-1998 ENSO did not significantly modify the temporal 16 patterns of Macrocystis, although local extinction of M. integrifolia beds occurred during negative thermal anomalies 17 in 1999–2000 (La Niña event), facilitating the establishment of urchin dominated "barren grounds". The abundance 18 of Lessonia trabeculata showed little temporal variability, and this species dominated the deeper regions of the kelp 19 20 assemblage (8–13 m depth). The structure of the kelp communities in the study area is regulated by a trophic cascade which modulates 21 22 alternation between kelp dominated areas and sea urchin barrens. In this context, frequent and intense upwelling of 23 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 24 column. Superficial warming during the 1997–1998 ENSO induced spawning by different species of echinoderms, 25 which resulted in major recruitment of these species during 1999. Top-down events, such as the decrease in densities 26 of the asteroids after the 1997-1998 ENSO event, favored increases in densities of benthic grazers, which caused 27 28 significant decreases in abundance of *M. integrifolia*. The re-establishment of the adult fraction of the carnivore 29 (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 30 31 trophic cascades that act at local levels, producing interannual variability in the structure of kelp communities. On

32 the other hand, considering the high macroinvertebrate diversity associated with kelp assemblages, the transitions 33 between kelp-dominated areas and sea urchin barrens do not appear to significantly affect the biodiversity of these

34 assemblages of benthic invertebrates.

35 Introduction

- 36 El Niño Southern Oscillation (ENSO) is an irreg-
- 37 ular fluctuation involving the entire tropical Pacific
- 38 Ocean and global atmosphere (Fiedler, 2002). ENSO
- 39 itself consists of an unstable interaction between sea

surface temperature (SST) and atmospheric pressure. 40 ENSO produces interannual variability in the oceanographic climate (Dayton et al., 1999), with alternating warm and cold periods resulting from positive 43 (El Niño), and negative (La Niña) thermal anomalies 44 of the SST, in 2 to 7 year feedback cycles (Fiedler, 45 46 2002). Differences in frequency, intensity, and magnitude of ENSO events have been associated with ocean 47 48 regime-shifts caused by the Pacific Decadal Oscilla-49 tion (PDO) and global warming (Steneck et al., 2002). 50 During high-intensity, high-magnitude ENSO events (eg. 1982-1983 El Niño, 1997-1998 El Niño), Kelvin 51 waves are propagated from the tropics both northward 52 53 (North America) and southward (South America) along 54 the eastern Pacific coastline. Although their manifes-55 tation decreases with increase in latitude, they may be detected beyond 35° (Halpin et al., 2004). The 56 advance of these waves impinging on the coastline 57 lowers the thermocline, increases sea level, modifies 58 59 the direction and velocities of currents, and decreases or prevents coastal upwelling (Takesue et al., 2004). 60 Changes in the oceanographic climate caused by high-61 intensity ENSO events have an important role as a 62 63 disturbing process at temperate latitudes along the east-64 ern Pacific coastline, producing bathymetric migrations 65 of organisms, invasions of exotic species, behavioral alterations, and positive or negative changes in abun-66 67 dance, the latter of which may reduce population densities to local extinction (see Tegner & Dayton, 1987; 68 Glynn, 1988; Dayton et al., 1999). Modifications of 69 70 the coastal biota may be observed on both local and 71 regional geographic scales (Camus, 2001; Edwards, 2004). Reductions in populations or local extinction 72 processes generated by ENSO events are very impor-73 74 tant for "engineer species" in ecosystems (sensu Jones 75 et al., 1994) such as kelp. The presence of these species 76 determines the diversity, complexity, structure, and 77 functioning of their associated communities (Graham, 2004). 78

79 Long-term studies on the North America west coast 80 have shown that ENSO events alter the structure and organization of subtidal kelp communities in temper-81 ate latitudes, modifying patterns of persistence, sta-82 bility, succession, species diversity, and abundance 83 (Dayton et al., 1992, 1999; Tegner et al., 1997). 84 Moreover, ENSO events have been considered as large-85 86 scale disturbances, which produce phase shifts between, kelp-dominated to sea urchin-dominated states 87 (Tegner & Dayton, 1991; Steneck et al., 2002). In 88 kelp forests, population changes in top predators 89 90 commonly drive these shifts through top-down forcing processes (Estes et al., 2004). However, in Cal-91 ifornia kelp forests, factors connected with anthro-92 93 pogenic impacts (see Tegner & Dayton, 1991; Day-94 ton et al., 1998), may have buffered the phase shift 95 to sea urchin-dominated states and facilitated recov-96 ery 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 ($\geq 40^{\circ}$ S) 99 where the influence of ENSO is minimal (Halpin 100 et al., 2004). As such, there are no long-term data 101 concerning the effects of large-scale, low frequency 102 ENSO events on the structure of South American kelp 103 communities. 104

In northern Chile and southern Peru $(10^{\circ}-30^{\circ}S)$, 105 protected and semi-exposed shallow subtidal hard- 106 bottom environments (ca. 20 m depth) are dominated 107 by two kelp species in the Order Laminariales, includ- 108 ing Lessonia trabeculata Villouta & Santelices and 109 Macrocystis integrifolia Bory. Although there are some 110 reports in the literature on the ecology of Lessonia 111 trabeculata (see Vásquez, 1992; Tala et al., 2004), data 112 are scarce on the population biology of *M. integrifolia* 113 and the Macrocystis-Lessonia assemblage in north- 114 ern Chile. Available information is restricted only to 115 standing stock evaluations and observations on re- 116 productive activity in controlled environments and 117 in the field (Buschmann et al., 2004; Vega et al., 118 2004). 119

The subtidal kelp ecosystems on the South Ameri- 120 can west coast are highly productive, hosting diverse 121 and abundant macroinvertebrates and fishes (Vasquez 122 et al., 2001a). M. integrifolia and L. trabeculata, are 123 highly sensitive to positive SST anomalies and low nu- 124 trient concentrations on the coast caused by ENSO 125 events, and experienced high mortalities during the 126 1982-83 (Tomicic, 1985; Soto, 1985; Glynn, 1988) and 127 1997-98 (Godoy, 2000; Llellish et al., 2001) ENSO 128 events. Without kelp assemblages, subtidal rocky reefs 129 form alternative states, the most common of which 130 is the "barren-ground" associated with sea urchins 131 (Vásquez, 1992). The most important grazers in such 132 systems are the sea urchins Tetrapygus niger (Molina) 133 and the sympatric but less common species Loxechinus 134 albus (Molina) (Rodriguez & Ojeda, 1993). T. niger is 135 an omnivore, while L. albus is an herbivore and feeds 136 on foliose algae and drifting algal rafts (Contreras & 137 Castilla, 1987). Although both species can completely 138 destroy kelp beds on a local scale (see Dayton, 1985; 139 Buschmann et al., 2003), T. niger is primarily respon- 140 sible for generation and maintenance of the barren 141 grounds typically observed in northern Chile (Vásquez 142 & Buschmann, 1997). 143

A guild of carnivores (starfish), regulates spatial 144 and temporal patterns of abundance and diversity 145 of the benthic grazers (Viviani, 1978; Vásquez & 146 Buschmann, 1997). The fishes associated with the kelp 147 148 communities have a broad trophic spectrum and eat 149 few sea urchins (Medina et al., 2004). In northern 150 Chile ENSO produces trophic cascades by top-down 151 processes (starfish⇔sea urchins⇔kelp), which modify the patterns of biodiversity, stability and persistence of 152 subtidal kelp communities (Vásquez & Vega, 2004). In 153 this context long-term monitoring has permitted postu-154 155 lation that the 1997–1998 ENSO event generated: (1) 156 interannual variability in the abundance of the main 157 functional groups associated with the kelp, (2) differential responses of the species or functional groups, 158 and (3) changes in the structure and organization of the 159 kelp communities. 160

161 The present study evaluates long term patterns of abundance in key species which regulate subtidal 162 communities on rocky bottoms dominated by kelp 163 in northern Chile, and incorporates the effects of the 164 1997-1998 ENSO event. Data were obtained from 165 before, during, and after this ENSO event. Data are 166 167 presented on the effects of different groups of key benthic species on the structure and organization of 168 169 these subtidal kelp communities, including the kelp 170 species, grazers (sea urchins), predators (sea stars), and macroinvertebrate species forming the more common 171 172 assemblages in this region.

173 Materials and methods

174 Study area

Shallow, subtidal, rocky-bottom communities dom-175 inated by kelp were evaluated seasonally between 176 July 1996 and August 2004 at Caleta Constitución 177 $(23^{\circ}26'S, 70^{\circ}36'W)$. This bay, on the southern end of 178 179 the Mejillones Peninsula in northern Chile (Figure 1) is in a region of permanent upwelling (Takesue et al., 180 2004), semi-protected from prevailing winds by Santa 181 Maria Island. The bottom substrate consists of rocky 182 183 platforms, which drop to depth, plus scattered boulders separated by channels floored with coarse sand. 184 185 Kelp beds are widely distributed throughout the bay; the sub-canopy undergrowth comprises various foliose, 186 187 turf, and crustose macroalgae. These include crustose 188 Corallinales, turfs of Gelidiales and/or Ceramiales, and often patches of Halopteris spp., Glossophora 189 kunthii (C. Ag.) J. Ag., Asparagopsis armata Harley 190 and Rhodymenia spp. and Chondrus canaliculatus (C. 191 192 Ag.) Grev. (Vásquez et al., 2001b). Descriptions of the 193 study site and marine ecosystem are given by Vásquez et al. (1998). 194

Oceanographic conditions

Mean daily in situ water temperatures were measured 196 on continuous-register thermographs (Onset Computer 197 Corp., MA, USA) placed at 3 m depths along the 198 shallow limits of the kelp. When in situ records of 199 oceanographic variables were discontinued, large-scale 200 climatic indexes were used, which permitted descrip- 201 tion of oceanographic conditions, and for making ap-202 proximations of ecological processes that acted on 203 smaller scales (Stenseth et al., 2003). Warm and cool 204 phases of the ENSO were determined using monthly 205 averages of the Southern Oscillation Index (SOI) and 206 the Multivariate El Niño Index (MEI) for the pe- 207 riod (1996–2004), from the Bureau of Metereology, 208 Australia (www.bom.gov.au/climate/current/) and Cli- 209 mate Diagnostic Center of NOAA (www.cdc.noaa.gov/ 210 ~kew/MEI/mei.html), respectively. Information on the 211 temporal variability of upwelling events in the re- 212 gion (23-25°S) was obtained from the monthly aver- 213 age index of upwelling (Offshore Eckman Transport, 214 OET) between 1996 and 2001, from the Pacific En- 215 vironmental Laboratory (PFEL, (www.pefg.noaa.gov/ 216 products/PFELindices.html). A detailed description of 217 this calculation, and characteristics of the area of influ- 218 ence of the SOI, MEI and OET indexes is presented by 219 Navarrete et al. (2002). 220

Temporal patterns of kelp abundance

Temporal patterns of abundance of *M. integrifolia* and 222 L. trabeculata were evaluated seasonally on four hap-223 hazardly chosen transects which were established per- 224 pendicular to the coastline from the intertidal to 15 m 225 depth. Each transect was 160 m long and 1 m wide. 226 Two SCUBA divers swam each transect, counting ju-227 venile and adult sporophytes within 0.5 m on each side 228 of it's axis. Kelp juveniles were sporophytes with up to 229 two lanceolate and laminar fronds, without reproduc-230 tive structures, and with maximum holdfast diameters 231 of ≤ 1 cm. Densities of juveniles and adults were ex-232 pressed as the number of plants per m^2 (N = 4). 233

Temporal patterns of grazer (sea urchins) abundance 234

Temporal changes in the density of grazers were de-235 termined by seasonal evaluation of 34 steel-frame 236 quadrats of 0.25 m^2 each, haphazardly tossed from 237 a boat between the perpendicular transects described 238 above. Densities of the sea urchins were expressed as 239 the number of individuals per 0.25 m^2 . 240

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

241 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

245 asteroids per species was counted for each sampling

246 unit (N = 4, transect of 160 m²), with individual den-

247 sities expressed per m^2 .

248 Temporal patterns of macroinvertebrate assemblages249 in subtidal kelp beds

250 Changes in hard-bottom community structure before 251 (1996), during (1997–98), and after (1999–2000) the 1997–1998 ENSO were evaluated seasonally by means 252 of analysis of benthic macroinvertebrate assemblages 253 254 associated with subtidal kelp beds. The composi-255 tion and abundance of the benthic macroinvertebrates species was evaluated using destructive sampling with 256 $0.25 \,\mathrm{m}^2$ quadrats. Twenty steel-frame quadrats were 257 258 thrown haphazardly from a boat over depths of between 259 two and 15 m, covering the entire range of the kelp beds (2-15 m depth). Divers, using numbered, 1-mm 260 mesh collecting bags, recovered all the fauna occurring 261 within the quadrats. Collected material was transferred 262 to numbered plastic bags onshore, fixed in 8% formalin 263 264 dissolved in seawater and later preserved in 70% alco-265 hol. In the laboratory, the invertebrates were sorted and identified to the lowest taxonomic level possible us-266 ing literature listed by Lancelloti and Vásquez (1999, 267 268 2000). The number of individuals of each macroinver-269 tebrate species was counted in each sample unit. Tem-270 poral patterns of invertebrate assemblages associated

with subtidal kelp beds was analyzed using univariate 271 biodiversity indexes (species richness (S') and biodiversity index of Shannon Weiner [H', J']). 273

Statistical analyses 274

A multifactorial analysis of variance (ANOVA) using 275 the species, years and seasons as the main variables was 276 used to evaluate the hypothesis that ENSO events gen- 277 erated long-term variability in patterns of abundance 278 of key species (kelp, sea urchins and starfish), which 279 structured subtidal kelp communities at the study site. 280 The multifactorial analysis of variance (ANOVA) was 281 done after visual determination of normality of the 282 data and homoscedasticity of variances by means of 283 a Bartlett test (Sokal & Rohlf, 1981), using SYSTAT 284 8.0^K computational software for Windows; transfor- 285 mations (root abundance + 1) were applied when nec-286 essary to improve homoscedasticity (Sokal & Rohlf, 287 1981). An a posteriori Tukey test was used order to 288 determine which groups differed from others (Sokal 289 & Rohlf, 1981). The relationship between mean abun-290 dance of kelp, sea urchins and starfish was determined 291 using a Pearson Correlation Analysis (Sokal & Rohlf, 292 1981). 293

Results

Oceanographic conditions 295

294

In situ sea temperature showed a seasonal pattern, with 296 warm water between December and March (summer) 297



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.

298 and cool water between June and September (winter) 299 (Figure 2A). Between April 1997 and March 1998 300 the water was unusually warm, with maximum positive thermal anomalies fluctuating between $+2^{\circ}$ and 301 302 +2.5°C; an exception occurred between August and 303 November 1997 when upwelling lowered the seawa-304 ter temperatures, interrupting the continuity of the anomalous warm period. Beginning in April 1998, 305

cooling of the water began with weak, moderate, 306 and strong levels when the anomaly ranged between 307 -0.5° and -1.5° C until the end of 2000 (La Niña 308 event; Figure 2A). The Southern Oscillation Index 309 (SOI, Figure 2B) and the Multivariate El Niño Index (MEI, Figure 2B) detected normal conditions in 311 1996 lasting until summer 1997. An ENSO event was 312 recorded between May 1997 and March 1998, which 313 314 was of high intensity and magnitude, coinciding with 315 the thermal anomaly detected by the in situ temperature 316 records (Figure 2A). Following the normal-cold period 317 of 1998-2001, a new ENSO manifestation was detected 318 which was of low to moderate intensity between April 2002 and April 2003 (Figure 2B), with a positive ther-319 320 mal anomaly of +1 °C. The mean values for the up-321 welling index (OET) were always positive during the 322 study period, and represented continuity over time of 323 the Ekman transport in the region (Figure 2C). The 324 upwelling index showed a greater offshore transport 325 between September and December (spring), and lower 326 intensities of upwelling between April and July of each 327 year (Figure 2C). The highest upwelling activity oc-328 curred during the spring of 1996, decreasing signifi-329 cantly in May 1997 at the beginning of the 1997–1998 330 ENSO event. Nevertheless, the Ekman transport re-331 mained active, constant, and intense between July 1997 332 and February 1998 (Figure 2C) during the maximum 333 positive thermal anomalies of the 1997–1998 ENSO.

334 Temporal patterns of kelp abundance

335 The temporal patterns of abundance of *M. integrifolia* 336 differed significantly from those of L. trabeculata (Table 1A). M. integrifolia showed marked annual 337 338 changes, with maximum abundances of adult sporo-339 phytes during 1997-1998 (1997-1998 ENSO period) and minima during 2000-2002 (period of negative SST 340 341 anomalies), reaching critical levels of abundance (0.1 to 0.6 sporophytes/m²) in 2000 (Figures 3A–B). In the 342 343 fall of 2001, the population of M. integrifolia started 344 to become re-established, reaching its maximum den-345 sity during 2003 (Figure 3A). In contrast, the average abundance of L. trabeculata during the study period 346 347 was 0.5 ± 0.9 sporophytes/m², with stochastic changes 348 (Figures 3 C–D). The temporal patterns of juveniles of 349 *M. integrifolia* were significantly different from those 350 of L. trabeculata (Table 1B, Figures 3 B-D). The abundances of juveniles of *M. integrifolia* increased during 351 the 1997-1998 ENSO, and during the re-establishment 352 353 of kelp bed from 2001 to 2003 (Figure 3C). There was, 354 however, a decrease due to a failure in recruitment in 1999–2000, which helped cause the disappearance of 355 the *M. integrifolia* bed during the negative SST anoma-356 lies (La Niña event). In contrast, the abundance of L. 357 358 trabeculata juveniles increased mainly in the spring 359 (Figure 3D), even though juveniles of this species 360 can be present throughout the entire year (i.e. 2003; 361 Figure 3D).

Table	1.	Multifa	ctorial	Analysis	of	Variance	(ANOVA)	using
specie	s, y	ear and s	eason a	s main vai	iabl	es to evalu	ate the hypo	thesis
that El	NSO) event g	generate	long-tern	n va	riability in	abundance	of key
specie	s (k	elp, sea	urchins	and starfi	sh).			

Factor	df	MS	F	p-level
(1	A) Kelp a	dults		
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 juv	veniles		
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		
(0	C) Sea Ur	chins		
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 S	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 362

The black sea urchin (*T. niger*) was the most conspicuous herbivore at Caleta Constitución, coexisting with the significantly less abundant sea urchin *L.* 365 *albus* (Figure 4). The benthic grazer abundances varied significantly between years (Table 1C), showing 367



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 375 local extinction of the *M. integrifolia* popula-376 tion. An inverse and significant correlation sug-377 gested that the density of juvenile and adult 378 *M. integrifolia* sporophytes decreased with increas-379 ing numbers of *T. niger* (Table 2). In contrast, 380 there were no significant correlations between *T.* 381

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).

388 Temporal patterns of carnivore (sea star) abundance

389 The asteroid species of this benthic system differed 390 significantly in annual and seasonal patterns of abundance (Table 1D). Heliaster helianthus increased sig-391 nificantly in 1998-2000 with a maximum in 1999, 392 393 including the 1997–1998 ENSO period (Figure 5A). From 2001 to the end of the study period, densi-394 ties of Heliaster helianthus remained comparatively 395 396 low, with averages similar to those found in 1996 397 (Figure 5A). In contrast, the temporal patterns of abundance of Stichaster striatus underwent significant in-398 creases during the spring: these were particularly 399 notable in 1999, 2002, and 2003 (Figure 5B). The 400 401 seasonal increases in S. striatus were caused by reproductive aggregations in shallow water. Meyenaster 402 gelatinosus and Luidia magellanica showed similar 403 404 tendencies in their temporal patterns (Figures 5C y 405 D): both decreased significantly in 1998, immediately after the 1997-1998 ENSO, and re-established their 406 densities during the cool period of 1999-2000. There 407 were positive and significant correlations among the 408 different species of asteroids as well as among the 409 asteroids and echinoids (Table 3), suggesting com-410 411 mon populational responses to interannual variations in the oceanographic climate within this subtidal 412 413 ecosystem.

The temporal variation in species richness of the 416 macroinvertebrate assemblage associated with the kelp 417 assemblages fluctuated between 50 and 80 species 418 during the study period, without detection of relevant 419 breaks during the 1997–1998 ENSO (Figure 6A). The 420 biodiversity (H') and uniformity (J') indexes only de- 421 tected a break in the temporal patterns in fall 1998 422 (Figure 6B), during the decline of the 1997-1998 423 ENSO event. There was a decrease in the diversity in- 424 dices as a consequence of the numerical dominance of 425 filter-feeding species (i.e. tunicates, mussels) that cover 426 rocky bottom. The total macroinvertebrate density, in 427 contrast to the other community variables, showed 428 high temporal variability before (1996), and after the 429 1997–1998 ENSO, in contrast with the low densities 430 during ENSO (Figure 6C). 431

432

Discussion

The present study demonstrates some of the effects 433 of the El Niño Southern Oscillation (ENSO) event 434 on the structure and organization of subtidal rocky 435 communities dominated by kelp in South America. 436 These are the first observations of this type on a 437 such a large-scale, low frequency oceanographic. Of 438 the two common kelp species, Macrocystis integrifo- 439 lia and Lessonia trabeculata, only the former varies 440 significantly in abundance seasonally and annually. In 441 this context, the temporal variation in abundance of 442 the giant kelp Macrocystis pyrifera in the northern 443 hemisphere is correlated with thermal anomalies cou- 444 pled to annual temperature (Steneck et al., 2002). These 445 thermal oscillations co-vary inversely with the avail- 446 ability of nutrients, producing different seasonal pat- 447 terns of abundance (Tegner et al., 1997; Dayton et al., 448 1992, 1998, 1999). The populations of M. integrifolia 449 in northern Chile are made up of perennial sporophytes, 450 which maintain average abundances throughout the 451 year, with seasonal variability only in growth and re- 452 production (Buschmann et al., 2004). As in popula- 453 tions of M. pyrifera in California and Mexico (Ladah 454 et al., 1999; Edwards, 2004), it may be predicted that 455 the temporal stability of South American populations 456 of *M. integrifolia* could be interrupted by (1) pos- 457 itive thermal anomalies generated by ENSO events 458 which produce local mortalities with highest intensity 459 at the lower latitudes, and (2) the rate of post-ENSO 460



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 461 462 thermal anomalies (La Niña). Both factors would be ex-463 pected to generate interannual variability that have not always been taken into account in understanding the 464 465 functioning of these communities. Our observations of the structure and organization of the kelp assem-466 467 blages in northern Chile, made during the study period which included the 1997-1998 ENSO event, neverthe-468 469 less were an exception to the above two possibilities, since the abundance of *M. integrifolia;* (1) increased 470 471 significantly during the 1997–1998 ENSO event, (2) decreased during the 1999-2001 La Niña event to lev-472 473 els near zero in 2000, and (3) became re-established

during a period with a positive thermal anomaly in 474 2002–2003. In this context, a few fertile sporo-475 phytes survived the local disappearance of M. 476 *integrifolia*, generating reproductive propagules for the 477 re-establishment of the population (Vega et al., 2004). 478 Also, drifting rafts and seed banks of microscopic dor-479 mant stages (gametophytes) may be included in possible complementary strategies for repopulation of this 481 kelp species (Ladah et al., 1999; Buschmann et al., 482 2004; Vega et al., 2004). 483

Populations of *L. trabeculata* in northern Chile 484 are made up of perennial and long-lived sporo- 485 phytes (Vásquez, 1992; Tala et al., 2004), partially 486

	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)

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

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.

487 explaining the temporal patterns of bathymetric dis488 tribution of *L. trabeculata* between 1996 and 2004.
489 On the Peruvian coast, the mortality rates of *L.*490 *trabeculata* sporophytes during the 1997–1998 ENSO

were inversely correlated with depth, with highest survival between 12 and 15 depths (Fernández et al., 492 1999). *M. integrifolia* dominated rocky bottoms at 5– 8 m in the area of the present study, while *L. trabeculata* 494 495 was dominant at greater depths (8–13 m; Vega et al.,496 2004).

497 The temporal pattern of abundances of juveniles differed between the two kelp species over long-term 498 periods. Whereas *M. integrifolia* recruits throughout 499 the year (as in other wave-protected environments; see 500 Graham et al., 1997), L. trabeculata recruits during the 501 502 winter months, thus producing a greater abundance of 503 juveniles during the spring. These differences in re-504 cruitment patterns (annual vs seasonal) suppose different reproductive strategies that may in part explain the 505 temporal dynamics and longevity of the assemblage. 506 These hypotheses need to be studied, experimentally, 507 508 in the future.

509 Although the 1997-1998 ENSO event was a catastrophic occurrence which produced local kelp extinc-510 tions at low latitudes on the coasts of both Chile and 511 512 Peru in the Southern Hemisphere (Fernández, et al., 1999; Godoy, 2000; Llellish et al., 2001; Martínez et al., 513 514 2003), and in California and Mexico in the Northern Hemisphere (Ladah et al., 1999; Edwards, 2004), lo-515 516 cal conditions permitted persistence of the kelp assem-517 blages (Martínez et al., 2003; Vega et al., 2004). Here, 518 the maintenance of temporal patterns of *M. integrifolia* 519 and L. trabeculata during the 1997-1998 ENSO event 520 in northern Chile, may be explained by the frequency and intensity of coastal upwelling (Lagos et al., 2002), 521 522 which minimized the warming effects at the SST, main-523 taining high concentrations of nutrients within coastal environments (Takesue et al., 2004). 524

525 On the California coast, the recovery of Macrocystis 526 post 1997-1998 ENSO was favored by the rapid establishment of a cold period (1998-2000 La Niña; 527 Edwards, 2004) and the survival of sporophytes in 528 529 deep environments (Ladah et al., 1999). In the South-530 ern Hemisphere the re-colonization rate of the kelp 531 assemblages occurred comparatively slowly (Martínez et al., 2003), although cool conditions of 1998-2000 532 533 added to the effects of upwelling. The abundance of M. integrifolia in the study area was modified by a sig-534 535 nificant reduction in the adult population and lack of recruitment of juvenile sporophytes. Thus, the disap-536 pearance of the *M. integrifolia* population occurred two 537 years after the 1997-1998 ENSO event, and was sig-538 539 nificantly, inversely correlated with the increase in the 540 population of the black sea urchin Tetrapygus niger. 541 This contrasts with information from other areas of the south eastern Pacific during the 1997-1998 ENSO 542 543 event, where superficial warming decreased the abun-544 dance of kelp on shallow bottoms, inducing migrations 545 of grazers to deeper zones in search of food (Vásquez

& Buschmann, 1997; Fernández et al., 1999; Godoy, 546 2000; Llellish et al., 2001). This type of migratory be-547 havior of benthic grazers such as sea urchins and gas- 548 tropods on hard bottoms produces communities dom- 549 inated by crustose calcareous algae ("barren ground", 550 sensu Lawrence, 1975). In the Northern Hemisphere, 551 events that impact the abundances of high-level preda-552 tors, and low levels of availability of drift algae pro-553 mote the formation of barren ground; this occurrence 554 is not necessarily linked to ENSO (Tegner & Dayton, 555 1991; Steneck et al., 2002; Estes et al., 2004). The 556 urchin-crustose algae association persists until the sea 557 urchin population is decimated by disease, migration, 558 or predator pressure, which act together to promote re- 559 establishment of the kelp (Dayton et al., 1992; Estes 560 et al., 2004; Graham, 2004). 561

It has been noted that areas with intense and per-562 manent offshore transport, such as the study area on 563 the Mejillones Peninsula, are typified by high survival, 564 retention, and transport of echinoderm larvae toward 565 the coast (Ebert & Russell, 1988). During the ENSO 566 cvcle (1997–1998 El Niño and 1998–2000 La Niña). 567 different events favored an increase in the urchin pop-568 ulation during the cool phase, including (1) induction 569 of spawning due to increases in SST and persistence 570 of upwelling events, (2) significant reductions in den- 571 sities of adult individuals of M. gelatinosus and L. 572 magellanica (Vásquez et al., 1998; Vásquez & Vega, 573 2004) and (3) changes in the feeding behavior of H. 574 helianthus (Tokeshi & Romero, 1995; Vásquez et al., 575 1998). 576

In the absence of other large predators on the south 577 eastern Pacific coast, the sea stars form a predatory 578 guild, which significantly lower the abundance of ben- 579 thic herbivores such as the sea urchins and gastropods 580 (Vasquez & Buschmann, 1997). Although fishes such 581 as Graus nigra and Semicosyphus maculatus may 582 prey upon juvenile urchins, the sea urchins do not 583 exceed 17% of their diets (Medina et al., 2004). The 584 re-establishment of adult densities of Meyenaster 585 gelatinosus, Stichaster striatus, Heliater helianthus 586 and Luidia magellanica was associated with the tem- 587 poral recovery of kelp assemblages in the study area. 588 Meyenaster and Luidia also prey upon H. helianthus 589 and S. striatus (Dayton et al., 1977; Viviani, 1978; 590 Tokeshi & Romero, 1995). There is spatial segregation 591 on a bathymetric gradient between the different species 592 of sea stars (Vásquez & Vega, 2004). Encounters 593 between these high level predators often result in 594 autotomy of one or more of their rays (Lawrence & 595 Vásquez, 1996). Here, sublethal predation between 596



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

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

601 Different bottom-up and top-down events may regulate long-term ecosystem changes in northern Chile 602 including: (1) The intensity and frequency of upwelling 603 buffer the positive thermal anomalies in SST, main-604 605 taining high nutrient levels which favor the kelp during 606 ENSO events. (2) Site-dependent oceanographic con-607 ditions may generate optimal conditions for spawning, larval development, and recruitment of echinoderms 608 during and/or after ENSO event. (3) The population dy-609 610 namics of adult starfish and sea urchins during ENSO events are essentially species-specific. (4) Species-611 specific population dynamics (i.e. L. magellanica) and 612 changes in dietary composition (i.e. H. helianthus) dur-613 614 ing ENSO events, may promote population increases in T. niger. This seems to be a key factor in alternation 615 616 of environments dominated by kelp beds and barren grounds. (5) The increase in population density of the 617 618 adult fraction of the carnivore guild is correlated with the decline in densities and/or displacement to shallow 619 620 bottoms of the more conspicuous herbivorous grazers.

621 Discrete and local oceanographic events (up-622 welling) as well as large-scale, low-frequency events (ENSO) generate interannual variability in species 623 624 or groups of key species, which structure and or-625 ganize subtidal, rocky reef communities in northern Chile. This translates to trophic cascades that modu-626 late the temporal alternation of states dominated by 627 628 kelp, and sea urchin barrens. These changes in submarine seascapes have been treated as "catastrophic" 629 in the literature (Tomicic, 1985; Soto, 1985), although 630 631 simple species diversity indexes revealed no significant 632 changes with (1996–1998), or without (1999–2000) 633 the presence of kelp assemblages (Figure 7). Here, 634 the composition and species richness seem to indi-635 cate different organizational states of these communities. On a regional scale, this characteristic suggests 636 637 the presence of a mosaic of subtidal seascapes in different seral stages of ecological succession (Tomi-638 cic, 1985; Vasquez et al., 1998; Camus, 2001, Dayton 639 et al., 1998, 1999, Edwards 2004). Graham (2004), re-640 641 cently contrasting biodiversity and trophic complex-642 ity in sea urchin barrens and kelp-dominated habitats 643 (Macrocystis pyrifera), did not find significant differences between alternate states. This also suggests a 644 645 temporal resilience in the trophic web of the kelp for-646 est over the long term, with few species exclusively 647 associated with a determinate state.

Finally, the interannual variability in the structure 648 and organization of subtidal kelp communities suggests 649 the need for long term (8^+ yrs) monitoring programs. 650 These would detect changes over time, which would 651 not be evident in short or medium-term studies. This 652 type of data would be useful in evaluating conserva-653 tion and management of resources, and would broaden 654 knowledge of the sustainability of the biological di-655 versity of Chile's continental coastal marine ecosys-656 tem (Vasquez et al., 2001a). In this context, Chile's 657 extensive coastline (18°-56°S) offers an ecological 658 scenario that is unique in the world for evaluation of the 659 effects of events that operate on different geographic 660 scales. 661

Acknowledgements

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666

 This study was funded by grants from FONDE 663

 CYT 5960001, 1000044, 1010706 and 1040425 to
 664

 JAV.
 665

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