

Analysis of Four Macroalgal Assemblages along the Pacific Mexican Coast during and after the 1997–98 El Niño

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ABSTRACT

We examined the changes in four intertidal macroalgal assemblages sampled at 3-month intervals during and after the 1997–98 El Niño. The assemblages were analyzed using several numerical analyses (specific richness, H' diversity) and multivariate techniques (ANOSIM, cluster, and MDS analyses). During El Niño 1997–98, the water temperature in the sampled zone was almost 5°C above the long-term mean. The apparent impact of this factor was greatest in winter–spring 1998. Our results suggest that El Niño influenced the structure of these assemblages in four different ways: (a) El Niño was associated with number of species (lowest in 1998) and H' diversity, which increased in the winter of 1999, when the El Niño–Southern Oscillation (ENSO) was inactive, from 1.2 to 2.3. (b) The average biomass of the macroalgae was significantly greater in the ENSO year (139 g dry weight/m²) than in the non-ENSO year (42 g dry weight/m²) (c) El Niño conditions were associated with a high

population abundance of species of tropical affinity, such as *Agardhiella tenera* (22.05 g dry weight/m² in 1998 versus 0.7 g dry weight/m² in 1999), *Amphiroa misakiensis* (32 versus 1.1), *Caulerpa sertularoides* (15.35 versus 0), *Padina durvillaei* (9.2 versus 0.2), *Jania capillacea* (4.1 versus 0), and *Jania mexicana* (1.5 versus 0). In 1999, other species with a more temperate affinity appeared, such as *Laurencia pacifica* (0.12 versus 8.76 g/m²) and *Colpomenia sinuosa* (0 versus 4.8). (d) The multivariate techniques showed that differences among the structure of the four assemblages were more evident in 1999. The greatest homogeneity was detected during ENSO winter–spring, which suggests a communitywide change consistent with the El Niño event.

Key words: seaweed; intertidal assemblages; rocky shores; tropical shores; structural changes; El Niño; La Niña; temperature; winter thermal stress.

INTRODUCTION

Rocky shores are naturally heterogeneous environments where a diversity of benthic organisms such as macroalgae live in large assemblages that are

highly variable in structure and composition (Kaehler and Williams 1998). These assemblages vary in abundance through time and place, and there is growing evidence that the processes that generate natural variability operate over different scales of space and time (Menge 1976; Dayton and Tegner 1984; Underwood and Chapman 1998).

Biotic traits such as grazing by herbivores (Wil-

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liams 1993) have been reported as key factors in structuring seaweed assemblages on rocky shores. Moreover, some authors (Underwood and others 1983; Chapman and Underwood 1998) have commented on the importance of local physical factors—such as intense heat, desiccation (Buschmann 1990), sedimentation (Littler and others 1983; Airoldi and Virgilio 1998), substratum slope, wave height (Whorff and others 1995), and pollution (Littler and Murray 1975)—in the development of seaweed assemblages.

However, despite recent studies suggesting that most of the annual variability in macrobenthos can be explained by changes in climate (Kröncke and others 1998), there have been few surveys of changes in macrobenthic assemblages in relation to climatic effects such as El Niño (Barry and others 1995).

El Niño, including the strong events that disturb temperate ecosystems in the Northern Hemisphere, is a regular feature of the eastern Pacific Ocean, where it causes unusually high temperatures especially during the winter (Quinn and others 1978). High water temperature is only one element related to the El Niño–Southern Oscillation (ENSO). Other related events occur, such as strong storms, changes in nutrient concentrations, low or high levels of light, a rise in sea level, abundant rainfall, and so on (Suple 1999). In this sense, El Niño is an important stress factor (Paine 1986) that has been associated with a variety of phenomena, including changes in the distribution of seabirds (Ribic and others 1997), the settlement of mollusk larvae (Moreno and others 1998), sea urchin recruitment rates (Tegner and Dayton 1991), and the death of coral reefs (Warwick and others 1990).

In the tropical west Pacific, other climatic events, such as monsoons, have been shown to affect intertidal seaweed assemblages (Kaehler and Williams 1996, 1998); with the advent of hot weather, large areas of bare substratum are liberated in intertidal habitats (Kaehler and Williams 1996). Algal dieback has also been recorded along the Arabian coast following the monsoon; and for much of the year, the intertidal zone is devoid of significant algal growth (Williams 1993; Ormond and Banaimoon 1994).

To date, much of the research published on the effects of El Niño has been done in the temperate waters of the western Pacific and has focused on populations of brown algae, such as kelp forests (Gerard 1984; Dean and Jacobsen 1986; Tegner and Dayton 1987) and particular species of green macroalgae (Gunnill 1985; but see Murray and Horn 1989). Extensive reductions in standing stock and

the death of macroalgae, such as *Macrocystis pyrifera* (Dayton and Tegner 1984), have been attributed to El Niño events along the California coast. El Niño events are also known to dramatically affect the population dynamics of seaweeds from Baja California (Mexico), including *Macrocystis pyrifera* and *Gelidium robustum* (Hernández-Guerrero and others 2000).

The goal of the present study was to determine the effects of the 1997–98 El Niño on the structure of seaweed assemblages in the tropical Pacific coast of Mexico. Despite its obvious importance, the effect of climatic events produced by El Niño on the structure of tropical seaweed assemblages is not yet clear. Murray and Horn (1989) observed variations in total macrophyte abundance and diversity between the 1982–83 El Niño winter and the pre-ENSO winter in areas along the California coast. So far, our study appears to be the only survey that has attempted to relate the effects of a large-scale climatic phenomenon to patterns in the structure of macroalgae assemblages in the tropical eastern Pacific.

MATERIALS AND METHODS

Onset, Duration, and Climatic Effects Related to the 1997–98 ENSO

The El Niño Southern Oscillation (ENSO) is a systematic global climate fluctuation (Philander 1990). Since the 1982–83 El Niño, two similar events have occurred—the moderate 1986–87 El Niño and the prolonged and erratic 1991–94 event (McPhaden 1993). A major El Niño developed rapidly over August–September 1997 and remained very strong until the end of the autumn. The 1997–98 El Niño has been described as comparable to the one in 1982–83 and has been cited as the cause of many climatic disasters around the world (Harrison and Vecchi 2001). Between El Niño events, an opposite extreme event, known as “La Niña,” often occurs (Monastersky 1998). Cold La Niña events followed all three El Niños of 1982–83, 1986–87, and 1994–95. The last La Niña was in 1996; but after summer 1998, a new episode of La Niña appeared to start. La Niña events have a weaker impact on the climate than seasonal changes, while El Niño has powerful effects on global weather (Suple 1999).

Water temperature and levels of light can be easily measured and are thought to be good indicators of the magnitude and duration of an El Niño event. For that reason, water temperature (°C) was measured daily in two zones close to our sampling stations at depths of 5 and 10 m, respectively. Tem-

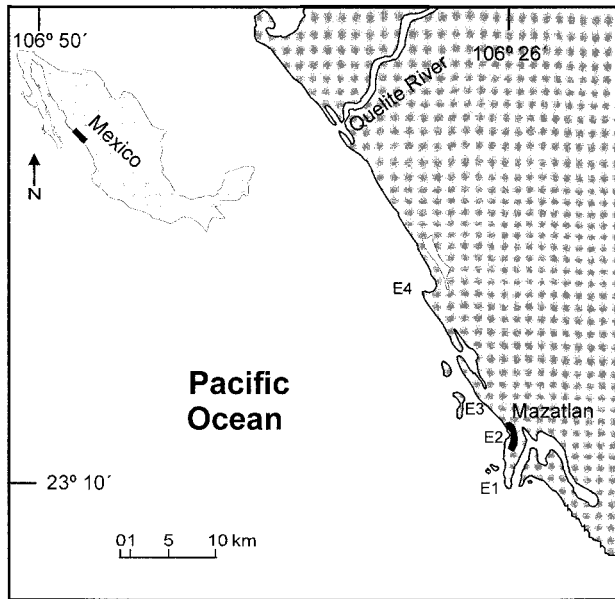


Figure 1. Location of study area showing the sampling stations: E1 (Cerro del Crestón), E2 (Punta Chile), E3 (Isla Lobos), and E4 (Cerritos).

perature was recorded in situ from freshly collected seawater with a Van Dorn bottle using a calibrated mercury thermometer. Later, the monthly average for water temperature was calculated. The insolation was measured with a heliograph as daylight hours, and the data were averaged for each month. Data on rainfall and insolation were provided by the Comisión Nacional del Agua in Mazatlán (National Water Commission).

Study Sites

This study was carried out at four rocky sites located along the Bahía of Mazatlán (Mexico, Pacific Ocean). The sites designated as E1 and E2 were separated from E4 by a sandy coast of about 15 km; E3 was situated on an island located approximately halfway between the E1 and E4 sites (Figure 1). The criterion for choosing a sampling station at each site were that it had a dense cover of algae (at least at the first sampling) and it had to be representative of broad areas (Chapman and Underwood 1998). The general characteristics of the sampling stations at each site were as follows: E1 was on a gently sloping, exposed coast oriented toward the west; E2 was an exposed coast, with a very steep slope, also facing west; E3 was on a gentle slope close to a sand platform, oriented toward the east; E4 was on a gently sloping sandstone platform facing northwest.

Sampling

Quantitative samples of macroalgae were collected according to previous minimum-area calculations done on data collected as part of a pilot study. Before the sampling program commenced, H' diversity versus sampling area was plotted for each site. The area at which the diversity curve was stabilized was considered to be the minimum area required. Data were collected from four, nonoverlapping, randomly placed quadrants (0.25 m^2) sampled in the upper to lower intertidal zone (Ormond and Banaimoon 1994). Three independent replicates were taken at each sampling station; in this way, a total surface of 3 m^2 was sampled at each station per sampling time. Quantitative samples were collected by clearing all macroalgae in each quadrant with a knife. Later, samples were carefully examined in the laboratory under a stereo microscope for sorting, drying, and weighing. To estimate biomass (g dry weight/m^2), all macroalgae were oven-dried at 60°C until a constant weight was obtained (Downing and Anderson 1985). Temporal patterns of distribution were investigated by repeatedly sampling the four stations every 3 months (winter, spring, summer, and autumn) between winter 1998 and autumn 1999 (Ormond and Banaimoon 1994; Nuñez-López and Casas-Valdez 1998).

Analysis of Patterns of Seaweed Assemblages

The seaweed variables used to examine the effect of the unusual water temperature were changes in number of species, changes in H' diversity, and changes in biomass. Analyses were carried out to obtain values for number of species and for diversity according to the Shannon-Wiener index (using logarithm in two bases) at each station for each time of sampling. Tests of the null hypothesis (no significant difference) among the ENSO and non-ENSO seasons were done for biomass, diversity, and number of species data using a one-way analysis of variance (ANOVA) model, after verifying normality (Kolmogorov-Smirnov test) and variance homogeneity (Barlett test). Where there were significant departures from homogeneity, the data were log-transformed as $\log_{10}(X+1)$, which generally resulted in homoscedasticity. The significance of differences found between the treatments was tested using the Tukey test (Sokal and Rohlf 1981).

Analysis of Heterogeneity of Seaweed Assemblages

The structure of the assemblages was analyzed by means of multivariate techniques following a trans-

formation of data using fourth root. This transformation reduced the effects of abundant species relative to rare species and thus minimized the possibility that significant differences among sites and dates would be due simply to chance abundance of highly variable species (Field and others 1982; Underwood and Chapman 1998). Similarities among the sampling stations were established by means of a classification analysis, using the species present as variables in the established zones. The similarity matrix for the classification was calculated by means of the Bray-Curtis index (Bray and Curtis 1957). This index was chosen because it does not consider double absences, frequently found in our database, in its calculations. The results were then graphically described using dendrograms with the unweighted pair-group method algorithm (UP-GMA) (Sneath and Sokal 1973). Finally, an ordination analysis by means of nonmetric multidimensional scaling program (MDS) was carried out, based on the similarity matrix between stations (Kruskal and Wish 1978). The Kruskal stress coefficient was used to assess the adequacy of the ordination obtained by the MDS (Clarke 1993).

Furthermore, the four assemblages were compared through time using a test built on a simple nonparametric permutation procedure combined with a general randomization approach to the generation of significance levels, termed "analysis of similarities" (ANOSIM) (Clarke and Warwick 1994). This test assesses the significance of differences between predefined groupings of replicates against a series of random simulations. The test is based on the corresponding rank similarities between samples in the underlying triangular matrix on the Bray-Curtis measures of dissimilarity, calculated from fourth root-transformed data. From the ANOSIM test, the R statistic is calculated, which will usually fall between 0 and 1, indicating some degree of discrimination between the sites. $R = 1$ only if all replicates within sites are more similar to each other than any replicates from different sites. R is approximately zero if the similarities between and within sites are the same on average. R values from all pairwise comparisons of sites were obtained from each ANOSIM for each time of sampling. We proposed a heterogeneity index (\bar{R}_i) based on R ANOSIM values, as follows:

$$\bar{R}_i = R_i/N$$

where R_i is the total (sum) of all R obtained in the pairwise comparison for a particular significance level (for example, for $P < 0.1$) in a given time (i), and N is the maximum number of pairwise possi-

bilities for a given number of stations (n); $N = \frac{n(n-1)}{2}$. The index is a useful comparative measure of the degree of separation of sites; in our case, it measures the dispersion among the four sampling stations in each sampling time. The index varies from 0 (low heterogeneity) to 1 (high heterogeneity). It is high when there is a large spatial variability among different assemblages (the maximum spatial heterogeneity would be obtained when the four assemblages were completely different from each other). By means of this index, we can determine when the greatest structural differences among the four assemblages occurred. The index is particularly useful for comparing the spatial heterogeneity within different assemblages (different zones) along a temporal sequence. It is statistically useful for making spatiotemporal comparisons within different assemblages; overall, it has great potential for testing the generality of underlying mechanisms that structure marine ecosystems.

RESULTS

Climatic Effects

Figure 2 shows the average monthly water temperature, insolation, and rainfall for the period of the study. The maximum effect of El Niño coincided with our sampling periods in February, May, and July 1998 (vertical dotted line in Figure 2). El Niño started in the autumn of 1997 and reached its maximum from January to May 1998 (vertical dotted line), causing in our zone of study much higher average temperatures than those in previous years (more than 4–5°C). The end of 1999 was governed by La Niña, which appeared to cause a colder autumn than in the previous year. Insolation (daylight hours) was slightly higher during winter-spring 1998 than during the same period in 1999. The decrease in the number of daylight hours in summer 1998–99 was related to cloud cover, which was responsible for the heavy rains during those months. The rainy season in 1998 lasted from June to November, with a peak in September, which corresponds to the lower insolation in 1998 (Figure 2).

Detecting Changes in the Biomass, Number of Species, and Specific Composition among ENSO and Non-ENSO Years.

During winter 1998, the most abundant species were the red seaweeds *Agardhiella tenera* and *Amphiroa misakiensis* (which appeared mainly at station E3) and the green seaweed *Chaetomorpha antennina*

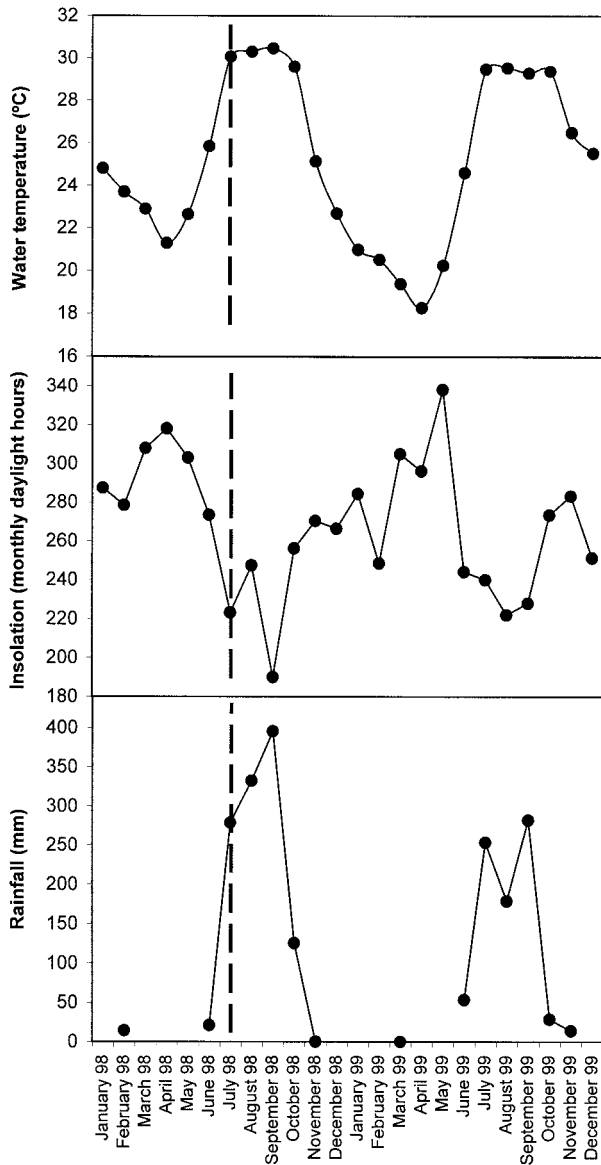


Figure 2. Mean monthly water temperature at Bahía, Mazatlán, daylight hours, and precipitation from 1998 to 1999 (daily measurements). The ENSO and non-ENSO periods are separated by a vertical dotted line.

(which appeared mainly at E1–E2). During spring 1998, the dominant species, in terms of biomass, were again *A. misakiensis*, *C. antennina*, and *Padina durvillaei*. In summer, green seaweeds were barely detected, and biomass was dominated by the red seaweeds *H. pannosa*, *Jania capillacea*, and the brown seaweed *P. durvillaei*. In autumn, the most important species were again *P. durvillaei* and the green seaweeds *Caulerpa racemosa* and *Caulerpa sertularoides*.

The two most abundant species in 1998, *Agardhiella tenera* (winter–spring–summer) and *Amphi-*

roa misakiensis (winter–spring–autumn), were also found in 1999, almost exclusively at E1 and E2, but the biomass was larger in 1998 than in 1999. Other species, such as *Amphiroa rigida*, appeared only in 1998 (in the four stations), although biomass was largest at E1 and E2.

Among the green seaweeds, species including *Ulva lactuca* and *C. antennina* appeared mainly during the winter–spring in both years (almost exclusively at E1 and E2), although the biomass of these species decreased in winter 1999. *Caulerpa racemosa*, the most typical green species in autumn 1998 (especially dominant at E4), and *Caulerpa sertularoides*, one of the most abundant species from May to October 1998, disappeared completely in 1999. It was replaced by *C. mexicana*, the most important species in biomass in summer–autumn 1999 (particularly at E3).

With respect to the brown seaweeds, the most important change in biomass was due to *P. durvillaei*. Although this species was present during all of 1998 and 1999, its biomass was much larger in 1998 for each season. In contrast, *Colpomenia sinuosa* appeared only during the 2nd year.

When we compared the average annual biomass of the main species (Table 1), we found that 25 of 42 species decreased in 1999, including *Agardhiella tenera* (22.05 g/m² in 1998 versus 0.7 g/m² in 1999), *Amphiroa misakiensis* (32 versus 1.1), *Caulerpa sertularoides* (15.35 versus 0), *Hypnea pannosa* (8 versus 0.2), *Jania capillacea* (4.1 versus 0), *Chaetomorpha antennina* (12.1 versus 2.4), and *Padina durvillaei* (9.2 versus 0.2). Twelve species increased in 1999, most notably *Laurencia pacifica* (0.12 versus 8.76 g/m²) and *Colpomenia sinuosa* (0 versus 4); whereas *Bryopsis pennatula* (0.27 versus 0.32 g/m²), *Gracilaria crispata* (0.38 versus 0.59), and *Grateloupia filicina* (0.65 versus 0.83) showed little change.

There were also differences in the number of total and exclusive species for each year (in both cases, higher in 1999) and changes in the proportions of the number of species for divisions were apparent. The number of green algae species were constant in both years, yet the number of brown algae increased during 1999, whereas the red algae did not (Table 2). Moreover, when we analyzed the divisions between each winter, the number of species of brown seaweeds rose considerably in winter 1999.

In summary, seasonal changes in biomass were generally similar in both years, increasing from winter to spring and decreasing in summer (Figure 3). The greatest biomass was recorded in October 1998 (159 g/m²); the smallest was seen in October 1999 (25.3 g/m²). Although we found no signifi-

Table 1. Average Biomass (g/m²) of the Main Species

	1998				1999			
	February	May	July	October	February	May	July	October
<i>Agardhiella tenera</i> (C. Agardh) Kraft & Wyne	27.4 (54.8)	48.6 (57)	12.2 (24.5)		2.6 (2)			
<i>Amphiroa misakiensis</i> Yendo	55.1 (42.5)	67.4 (38)	4 (8)	9.8 (5)	4.4 (8.9)			1.7 (3.1)
<i>Amphiroa rigida</i> Lamouroux	15.3 (13.1)	11.1 (21.7)		0.08 (0.1)				0.08 (0.1)
<i>Ceramium</i> sp.	0.1 (0.1)	1 (1.9)	1.3 (1.7)	3.5 (5.3)		0.4 (0.7)		
<i>Gelidiopsis tenuis</i> Setchell & Gardner	0.01 (0.03)				0.5 (0.8)	0.4 (0.8)	0.7 (0.8)	0.05 (0.09)
<i>Grateloupia</i> sp. C. Agardh	2 (2.4)	2.9 (1.9)	1.5 (3.1)	0.7 (1.2)		0.15 (0.3)	0.1 (0.2)	
<i>Gymnogongrus johnstonii</i> (Setchell et. Gardner) Dawson	0.22 (0.2)	3.5 (7.1)		0.02 (0.04)	3.5 (6.3)	0.3 (0.5)	1.4 (2.7)	
<i>Hypnea panosa</i> J. Agardh	3.1 (5.1)	3.5 (4.2)	18.3 (6.2)	6 (7.2)	0.1 (0.1)		0.8 (1.3)	
<i>Hypnea velentiae</i> (Turner) Montagne	2.8 (2.8)	0.8 (1.2)		0.081 (0.1)	0.5 (0.8)	0.17 (0.2)	0.7 (1.31)	0.1 (0.2)
<i>Hypnea johnstonii</i> Setchell & Gardner	0.21 (0.42)	1.3 (2.4)		0.1 (0.2)	1 (1)	1.6 (2.5)	0.18 (0.2)	0.8 (1)
<i>Jania capillacea</i> Harvey	3.1 (5.1)	2 (4)	9.6 (11.2)	1.8 (3.7)				
<i>Jania mexicana</i> W. R. Taylor	1.0 (2)	1.6 (3)	1.4 (2.8)	1.8 (2.5)				
<i>Jania</i> sp1. Lamouroux					3.2 (3.7)	0.3 (0.6)	1.1 (2.2)	0.2 (0.3)
<i>Jania</i> sp2. Lamouroux					2.2 (3.5)	23.4 (46)	0.5 (0.9)	0.3 (0.4)
<i>Jania tenella</i> (Kütz.) Grunow				1.36 (2.7)		0.07 (0.1)	0.2 (0.4)	
<i>Colpomenia tuberculata</i> Saunders	2.8 (4.3)	0.11 (0.2)	0.6 (1.2)		0.9 (1.8)	0.4 (0.7)		0.2 (0.4)
<i>Ilea fascia</i> O.F. Müller Fries	0.006 (0.01)	0.01 (0.03)			7 (7.7)	0.33 (0.6)	0.6 (0.4)	9.5 (19)
<i>Padina durvillaei</i> Bory	4.4 (6.7)	4 (3.7)	5.9 (8.0)	22.5 (19)	0.5 (0.6)	0.21 (0.4)	0.3 (0.4)	
<i>Ralfsia hesperia</i> Setchell & Gardner	0.05 (0.1)	0.59 (1.1)	3.3 (6.7)		0.6 (0.7)	0.6 (1)	0.18 (0.3)	
<i>Caulerpa mexicana</i> Sonder ex Kützing				1.47 (2.9)	1.2 (2.4)	0.4 (0.8)	0.4 (0.6)	4 (6.8)
<i>Caulerpa racemosa</i> (Forsskal) J. Agardh		0.01 (0.03)	0.057 (0.1)	13.9 (10.8)		0.6 (0.4)	0.2 (0.2)	1 (1.9)
<i>Caulerpa sertularoides</i> (Gmelin) Howe		0.8 (1.6)	35.1 (28.5)	25.5 (19.7)				
<i>Chaetomorpha antenina</i> (Bory de Saint-Vicent) Kützing	18.3 (11.8)	30.1 (20.3)		0.001 (0)	0.5 (0.7)	2.1 (4.2)	4 (7.6)	3.1 (6)
<i>Enteromorpha</i> sp. Link in Nees					0.2 (0.4)	0.1 (0.3)	0.2 (0.4)	
<i>Ulva lactuca</i> Linnaeus	27.5 (31.8)	3 (5.1)		0.06 (1.3)	12.5 (24.6)	16.4 (32.7)	1.9 (3.8)	
<i>Ulva lobata</i> (Kützing) Harvey	18.9 (25.1)	0.05 (0.1)			1.42 (2.84)	0.91 (1.83)		0.05 (0.09)

Only species that appeared at a minimum of four sampling times have been considered. The standard deviation (SD) is shown in parentheses.

Table 2. Total, Exclusive, and Shared Number of Species, and Percentage of Species of Green, Brown, and Red Seaweeds for ENSO (1998) and Non-ENSO Years (1999)

	1998	1999
Total species (each year)	50	74
Exclusive species	8	32
Shared species	42	
% Green algae	20	21.6
% Brown algae	10	12.16
% Red algae	70	66.2

cant differences when we compared ENSO and non-ENSO seasons, the average biomass of the macroalgae sustained by the ecosystem during the ENSO year was significantly larger than it was during the non-ENSO year (139 g/m² in 1998 versus 42 g/m² in 1999) (F-ratio = 40.65; p < 0.0001).

The mean number of species per season (an average of the four assemblages) appeared to fluctuate, with the same pattern each year, reaching maximum values in February. It later decreased to the lowest value in July (1998) and October (1999) (Figure 3). Significant differences were only obtained when we compared the numbers of taxa between ENSO (1998) and non-ENSO winters (1999).

Detecting Changes in H' Diversity in ENSO and Non-ENSO Years

Diversity generally increased from winter to spring-summer and decreased again in autumn. The least diversity occurred in winter 1998, whereas it was at its maximum in winter 1999. H' diversity increased significantly in the non-ENSO winter of 1999 (from 1.2 to 2.3) (F-ratio = 30.38; p < 0.001). In 1998, diversity increased in spring (with values below 1.5 at E1, E3, and E4), decreased in autumn, and later increased again in winter 1999. Generally, changes in diversity resulted from variations in the biomass of the dominant species, rather than from variations in the number of species. For example, station E1 (14 species) had lower H' values than E4 (six species) during winter 1998, due to the highly dominant species *Agardhiella tenera*. The same pattern was seen at E2 and E3 during spring 1998, which had the same number of species (eight) but very different H' values. Moreover, the average values for diversity were more homogeneous at all four stations in 1998 than in 1999.

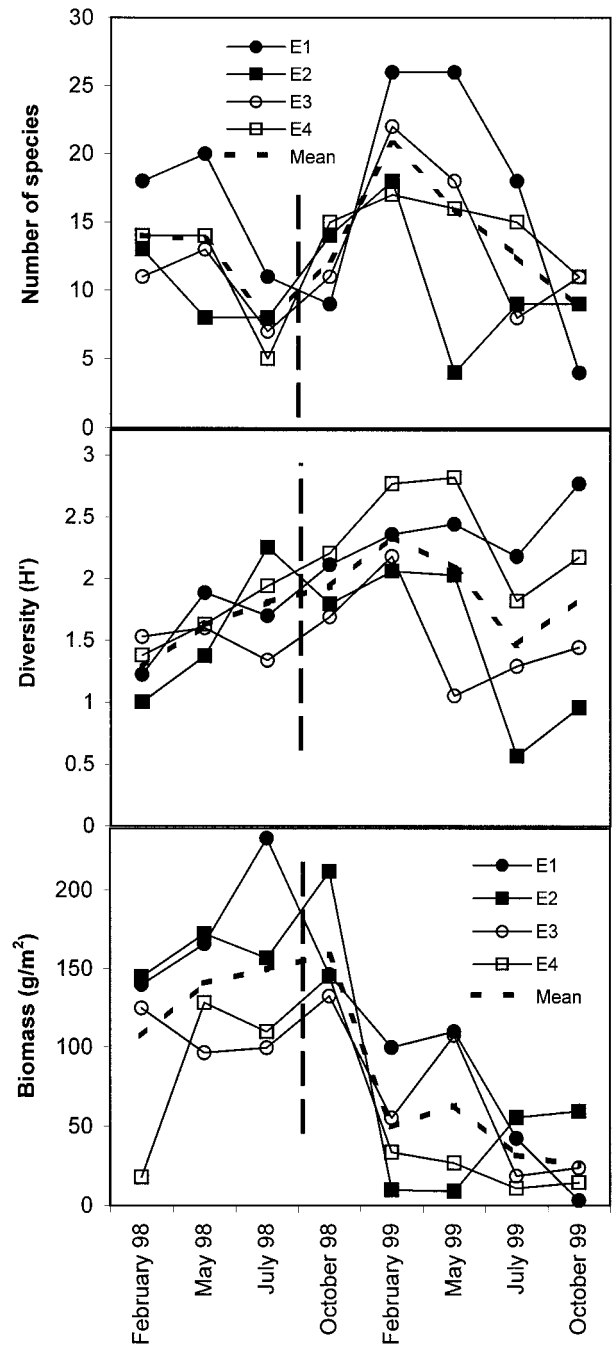


Figure 3. Species number, H' diversity, and biomass at each station per sampling season. The ENSO and non-ENSO periods are separated by a vertical dotted line. The mean values are represented in each plot by a discontinuous line.

Detecting Changes in the Pattern of Structure of the Seaweed Assemblages in ENSO and Non-ENSO Years

The \bar{R}_i index was especially useful for detecting simultaneous changes in the structure of seaweed

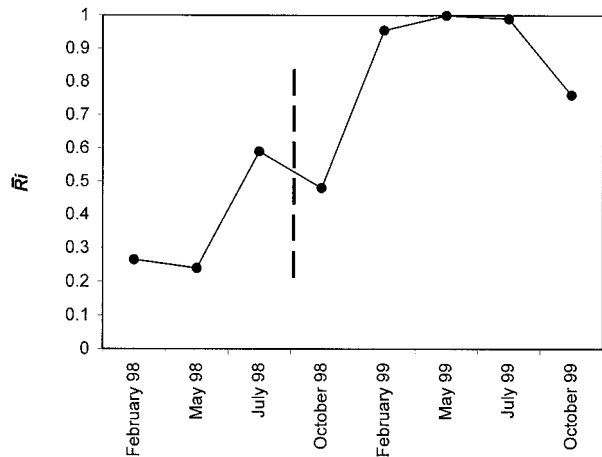


Figure 4. Analysis of heterogeneity of seaweed assemblages (heterogeneity index, R_i) along the sampling time. The ENSO and non-ENSO periods are separated by a vertical dotted line.

communities in a large area such as ours, and it allowed us to detect the moment of greatest spatial variability among assemblages (Figure 4). The lowest values (low spatial heterogeneity) were detected in winter 1998, at the moment when El Niño had its greatest impact. Conversely, the highest values were detected in 1999, when values close to 1 were recorded. The ANOSIM test showed that variability among assemblages was greater in 1999 than in 1998, as indicated by the higher number of comparisons that were significantly different ($P \leq 0.1$; this is the highest significance level achieved by the ANOSIM test for three replicates). In 1998, only two significant pairwise comparisons were obtained, suggesting that seaweed assemblages in the zone were more homogeneous in winter and spring 1998 than at the other sampling times. Moreover, the classification analysis (Figure 5), confirmed by the MDS (stress 0.1), allowed us to (a) differentiate among sampling periods corresponding to ENSO and non-ENSO years and (b) differentiate sampling periods corresponding to stations E1–E2 from stations E3–E4 in 1999. This indicates, in general terms, that spatial differences among the four assemblages, partly stemming from the influence of local factors, were more evident in 1999 than in 1998, the year when the assemblages at the four stations were most similar.

DISCUSSION

Of the several effects related to El Niño (including storms, levels of light, and nutrient concentrations), water temperature is likely to be one of the most

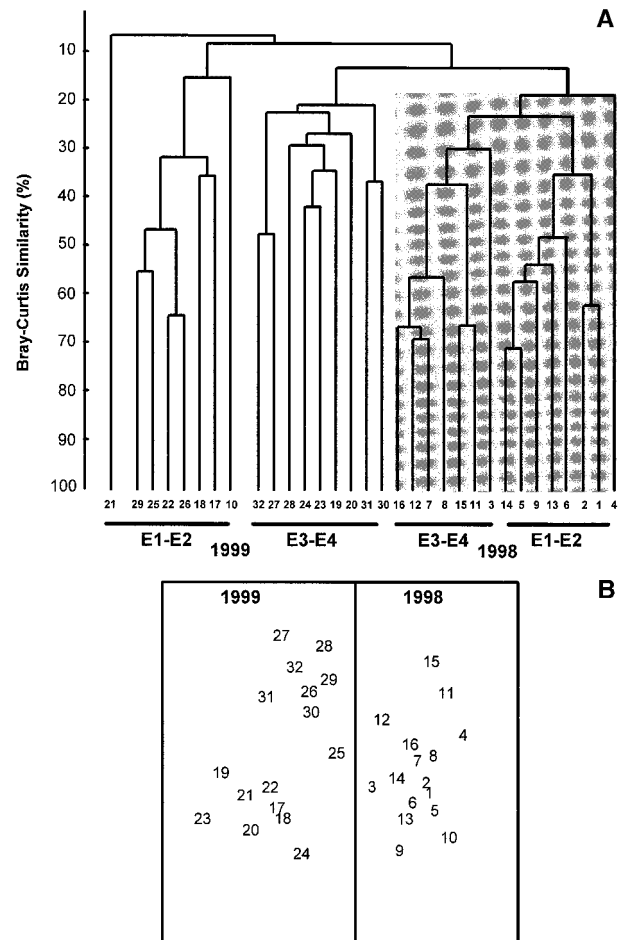


Figure 5. (A) Dendrogram of group-average clustering of Bray-Curtis similarities. (B) MDS configuration of species similarity matrix (stress = 0.17). The numbers in each figure are labeled as follows (month-year-station): 1 = (February 1998–E1), 2 = (February 1998–E2), 3 = (February 1998–E3), 4 = (February 1998–E4), 5 = (May 1998–E1); 6 = (May 1998–E2), 7 = (May 1998–E3), 8 = (May 1998–E4), 9 = (July 1998–E1), 10 = (July 1998–E2), 11 = (July 1998–E3), 12 = (July 1998–E4), 13 = (October 1998–E1), 14 = (October 1998–E2), 15 = (October 1998–E3), 16 = (October 1998–E4), 17 = (February 1999–E1), 18 = (February 1999–E2), 19 = (February 1999–E3), 20 = (February 1999–E4), 21 = (May 1999–E1), 22 = (May 1999–E2), 23 = (May 1999–E3), 24 = (May 1999–E4), 25 = (July 1999–E1), 26 = (July 1999–E2), 27 = (July 1999–E3), 28 = (July 1999–E4), 29 = (October 1999–E1), 30 = (October 1999–E2), 31 = (October 1999–E3), 32 = (October 1999–E4).

important factors affecting macroalgae in our zone of study (water temperature between October 1997 and May 1998 was up to 5°C above the long-term mean).

Our results demonstrated relative changes in species composition and abundance subsequent to the

El Niño event, which are consistent with the effects of water temperature. There were changes in the percentages of red and brown algal species from one year to the next, specifically red algae during 1999, as opposed to brown algae, which probably increased because of its more temperate affinities (Chapman and Chapman 1977; Darley 1982). In fact, some of the dominant species from each of the 2 years sampled can be considered typical of tropical environments or of temperate affinities. Red seaweeds of tropical affinity, such as *Agardhiella tenera*, *Amphiroa rigida*, and *A. misakiensis* (see Setchell 1920); and some green macroalgae, such as *Caulerpa sertularoides*, increased sharply in abundance during El Niño conditions. They were the most important species, in terms of their contribution to assemblage structure, during 1998, but they disappeared dramatically during the cold year of 1999 (see Table 1). This change seems consistent with temperature as the casual factor (Scrosati 2001). In contrast, some of the more abundant or exclusive species in 1999, such as *Colpomenia* spp., *Polysiphonia johnstonii*, *Ilea fascia*, *Laurencia pacifica*, *Ceramium* sp., *Gymnogongrus* sp., *Botryocladia* sp., and so on, are more typical of temperate latitudes (see Mateo and Mendoza 1994; Aguilar Rosas and Aguilar Rosas 1994; McQuaid and Branch 1984; Aguilar Rosas and others 2000). These results contrast with those documented in other tropical Pacific areas, where winter was dominated by brown or green algae, such as *Enteromorpha* species; while red seaweeds typical of tropical environments, such as *Gracilaria pacifica* and *Hypnea valentiae*, dominated in spring, summer, and autumn (Nuñez-López and Casas-Valdez 1998).

Biomass behaved in a manner different from the number of species and H' diversity, with highest values recorded at the time of lowest species richness (1998). But why did the biomass decrease during 1999? It seems that the unusual increase in water temperature in winter–spring reduced the overall number of species but favored the presence and growth of a few particular species, such as *Agardhiella tenera*, *Amphiroa misakiensis*, and some ephemeral green seaweeds with high reproductive output, such as *Chaetomorpha antennina*. This finding is in agreement with Gunnill (1985), who found that the 1981–82 El Niño reduced the abundances of species such as *Egredia menziesii* and *Eisenia arborea* but increased the reproduction recruitment potential of others, such as *Pelvetia fastigata*, and *Sargassum muticum*. Similarly, it supports the findings of Murray and Horn (1989), who detected an increase in cover of crustose coralline algae and a decrease in fleshy red algae.

However, this inverse relationship between species richness and biomass could have alternate explanations involving competitive dominance and annual versus perennial life histories. McQuaid and Branch (1984) showed that while a temperature regime establishes, by exclusion, a framework of species composition on each beach, the biomass of the species present is largely influenced by the degree of exposure. The cluster analyses in their report revealed groupings based primarily on degree of exposure and secondarily on temperature.

With respect to the community structure, the H' values in ENSO winter 1998 were similar to others found in intertidal algae communities with over-dominant species (Metaxas and others 1994), but the higher diversity values in the non-ENSO winter of 1999 were more similar to those recorded in more stable environments (Littler and Littler 1981). The lower temperatures in winter–spring 1999 favored a greater number of species than in winter–spring 1998 (brown seaweeds showed the largest). This finding is consistent with the results reported by Dawson (1996). Our findings also match those of Murray and Horn (1989), who found that variations from pre-ENSO patterns in total macrophyte abundance and diversity were few and mostly limited to the ENSO winter. Similar results were reported by McQuaid and Branch (1984); although they did not find significant differences in richness or evenness in comparisons of cold and warm shores, they found species that favored cold water.

Low heterogeneity, found in the study area at the time when influence by water temperature was greatest, seems to be consistent with El Niño being the main cause. All analyses showed that the four assemblages did not fluctuate in parallel, but that consistent winter ENSO assemblages existed at the moment of greatest influence of El Niño (the lowest spatial heterogeneity). Natural large-scale climatic phenomena can alter the ecosystem both locally and regionally; thus it is reasonable to assume that they can simultaneously affect seaweed assemblages over a large area. We have compared the synchronized monitoring of seaweed assemblages at different locations. If water temperature did have a large influence on seaweed assemblages, as we inferred from our results, then the different assemblages would be structured mainly in relation to this main factor and only secondarily to the different local factors. We should detect low spatial variability among our assemblages, as did indeed occur (all sampling stations were grouped together the lowest \bar{R}_i values were found). In the non-ENSO year, we detected larger spatial variability among these assemblages (stations did not cluster together, and the

highest \bar{R}_i values were detected), indicating that the local assemblages were structured in relation to local influences. In fact, there was a very clear separation between stations E1–E2 and stations E3–E4 during 1998 and 1999, suggesting that other factors such as degree of shelter from or exposure to wave action (higher at E1–E2 than at E3–E4) or proximity of sand platforms (E3–E4), are important structuring factors. Even though it has long been observed that intertidal marine algae tolerate extreme changes in temperature during exposure, it would be reasonable to conclude that the increase in water temperature in winter–spring, due to El Niño, was a very important stress factor and that its influence overshadowed other local factors. Later, a decrease in this stress factor (that is, temperature) may have permitted the seaweeds to structure themselves at each station according to local factors.

Could the higher water temperatures explain all of the changes observed? Temperature is one of the most important abiotic factors that affect seaweed growth rates (Graham and Wilcox 2000). Reductions in effective reproduction have been documented in several marine macroalgal species when temperatures exceeded seasonal averages by more than 5°C (Setchell 1920). The most dramatic changes in seaweed-dominated communities similar to ours were brought about by stress from water temperature and insolation (Bula-Meyer 1989). Other studies have shown that the effects of warm summer temperatures, in association with a reduction in available nutrients, increased the mortality of macroalgal species, such as *Macrocystis pyrifera*, due to canopy deterioration and physiological stress, which reduced their photosynthetic capacity and growth rates (Gerard 1984; Tegner and Dayton 1987). Biological cycles and species occurrence are influenced by the range of annual temperatures and in some cases conditioned by the extreme values of this factor (Dawson 1966). Moreover, water temperature is a significant predictor of the total macroinvertebrate biomass and the best single predictor of grazer biomass on rocky shores (Ricciardi and Bourget 1999). On the other hand, since insolation exerts the greatest control on the photosynthesis and growth of seaweeds (Chapman and Chapman 1977), it is possible that the high insolation values during winter 1999 acted in synergy with the exceptionally warm month of February (Buschmann 1990) to increase the desiccation of seaweeds at low tide and affect the structural parameters of the community.

In conclusion, higher temperatures during winter–spring 1998, brought about by the El Niño event, appeared to cause a decrease in species di-

versity, an increase in biomass, and a change in the structure of macroalgae assemblages. We found significant differences in species richness, H' diversity, and biomass when we compared the ENSO (1998) and non-ENSO (1999) seasons, and our observations are consistent with El Niño as the cause of those differences. During the El Niño period, the assemblages were comprised of species generally associated with tropical waters; whereas during the non-ENSO year, species with more temperate affinities were present. The \bar{R}_i index appears to be a useful means of analyzing macroscopic patterns of organism abundance during long series of temporal data. It allowed us to easily compare the synchronized monitoring of seaweed assemblages and to detect patterns of change in biomass, abundance, and structure when many stations were sampled simultaneously over large geographic scales.

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