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Recruitment of intertidal invertebrates in the southeast Pacific: Interannual variability and the 1997–1998 El Niño

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Abstract

We evaluated interannual variability and the effect of the 1997–1998 El Niño event on recruitment of intertidal mussels and barnacles along the coast of central Chile in the southeast Pacific. Monthly monitoring of recruitment at 11 sites spread over 900 km (29–34°S) during the 1997–1998 El Niño and over the same months in 1998–1999 and 1999–2000 allowed us to assess geographic patterns in interannual recruitment variation. The geographically most consistent interannual trend was observed for the mussel *Perumytilus purpuratus,* which showed overall lower recruitment rates during the 1997–1998 El Niño year. However, the magnitude of the effect at any given site was small. Interannual variation in recruitment rates of the other two intertidal mussel species, as well as two chthamaloid barnacles, were not consistent across the region, and overall, few sites exhibited significant differences among years. Differences between two and three orders of magnitude in mean annual recruitment of mussels and barnacles were observed among sites, yet the relative ranking of sites was fairly similar among years for most species. Contrary to the large positive effect that the 1997–1998 El Niño had on barnacle recruitment along the coast of central and northern California, our results show that recruitment of dominant intertidal barnacles along central Chile were not significantly altered by this strong oceanographic event. Lack of consistent trends among sites emphasizes the need to study several sites when looking at large-scale oceanographic anomalies and shows that El Niño effects on interannual recruitment variation are not predictable.

Over the past few decades, benthic marine ecology has made great advances in understanding the dynamics of species interactions and their consequences for the rest of the community. There is now general consensus, however, that further development will only be achieved by improving our understanding of the factors that produce variability in the settlement and recruitment of benthic species (Gaines and Roughgarden 1985). The specific processes and mechanisms by which larvae of benthic species return to the adult habitat after their pelagic life are still scarcely understood and, for the most part, unexplored in all but a few places in the world. Because larvae of invertebrates are small and cannot swim long distances, it is generally accepted that physical processes are largely responsible for larval transport and settlement events on the shore (e.g., Roughgarden et al. 1988; Shanks 1995). Large variability in recruitment is therefore expected to occur over broad temporal and spatial scales, and association between recruitment variability and physical processes has become a central focus of research (e.g., Shanks 1995; Wing et al. 1995). One aspect of this research centers on identifying the specific mechanisms responsible for larval transport and subsequent settlement events on the shore (e.g., Wing et al. 1995). A complementary research program focuses on evaluating the effects of variability in oceanographic processes on recruitment to benthic populations over longer periods of time, which can have direct consequences on population and community dynamics (e.g., Cury and Roy 1989; Connolly and Roughgarden 1999).

One of the main factors causing large interannual variation in oceanographic conditions is the El Niño–Southern Oscillation (ENSO), which is considered to be the major oceanographic and climate anomaly in the Pacific Ocean (Philander 1989). During ENSO events, important climatic and hydrographic changes occur in the Pacific ocean, such as changes in sea level, surface temperature, the strength and general pattern of circulation, the intensity of equatorward winds, and the availability of nutrients and phytoplankton productivity (Philander 1989). Therefore, it is expected that El Niño would cause major and clearly detectable changes in patterns of recruitment of benthic and pelagic invertebrates and fish. Indeed, several studies have attributed increased or decreased recruitment of different species to El Niño (Paine 1986; Ebert et al. 1994; Moreno et al. 1998; Davis 2000). However, the strength of the evidence for El Niño effects on recruitment is limited by the temporal and spatial scope of the studies; most studies are short in duration and limited to one or a few sites. Because the environmental change produced by El Niño is expected to have geographically broad effects, sites spread over tens to hun-

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dreds of kilometers must show similar responses, and the magnitude of the effect must be larger than the background year-to-year recruitment variation (Connolly and Roughgarden 1999). Regardless of the specific mechanisms by which El Niño could increase, decrease, or prevent specific settlement events of some species (Lundquist et al. 2000), demonstration of overall enhancement or reduction of recruitment during El Niño is important, for it suggests that the effects of this large-scale anomaly are essentially predictable.

In a recent study, Connolly and Roughgarden (1999) showed that the strong 1997–1998 El Niño had positive effects on barnacle recruitment across nine sites spread over 750 km along the coast of California. The similarity of the interannual change across sites, as well as the magnitude of the change, strongly suggested that observed recruitment variation was due to El Niño. Connolly and Roughgarden (1999) attributed the increased barnacle recruitment to the general depression of upwelling intensity during El Niño (Ramp et al. 1997). Indeed, an important cross-shelf transport process on the coast of California is the shoreward movement of larvae in upwelling fronts during relaxation of equatorward winds (e.g., Wing et al. 1995; Morgan et al. 2000). Increased frequency of relaxation events during El Niño should then lead to increased recruitment, rendering the effects of El Niño on barnacle recruitment predictable at the regional level.

Here, we evaluated the magnitude of interannual variability and the generality of El Niño effects on recruitment of mussels and barnacles on the much less studied Pacific coast of South America. As in the northern hemisphere, the region is characterized by an offshore equatorward current (Humboldt Current) and the presence of coastal upwelling, where the more saline sub-superficial water, rich in nutrients, is upwelled to the surface, particularly in spring and summer months when equatorward winds are stronger (Kelly and Blanco 1984; Strub et al. 1998). Similar to California, onshore movement of upwelling fronts following wind relaxation has been documented in central southern Chile (Peterson et al. 1988). The negative effects of El Niño on primary and secondary productivity have been well documented in the past (Avaría and Muñoz 1987), but information about its effects on nearshore currents are scarce. Observations in northern Chile (ca. 20°S) show that the 1997–1998 El Niño was first detected as a pulse of warm water in March 1997, with peaks in surface temperature and sea level in May and September of the same year (Thomas et al. 2001; Ulloa et al. 2001). The thermocline was depressed down from the normal 40–60 m to 150–200 m deep, and strong poleward flow was measured in the first 100 m (Blanco et al. 2001; Thomas et al. 2001). A sharp decrease in nearshore chlorophyll *a* concentration was evident during El Niño warming (González et al. 1998; Thomas et al. 2001). As with previous El Niño events, a period of colder than normal conditions, or La Niña, followed the strong 1997–1998 El Niño event, but the intensity of La Niña was weak to moderate (Wolter 2001).

The only connection between El Niño and invertebrate recruitment in temperate latitudes along the coast of Chile has been made at one site near 40°S. There, strong El Niño events and the associated predominance of poleward winds were linked to failure in intertidal recruitment of the muricid gastropod *Concholepas concholepas* (Moreno et al. 1993, 1998). General patterns of intertidal mussel and barnacle recruitment have been documented at a few sites in central and northern Chile (Navarrete and Castilla 1990; Camus and Lagos 1994), but we have no information about the effects of upwelling–relaxation or other transport processes on recruitment events. Because larvae of mussels and barnacles are planktotrophic, spend considerable time in the water column, and settle predominantly during spring and summer, they can all be affected by the general decrease in phytoplankton biomass, increased surface temperature, and changes in nearshore currents that presumably occur during El Niño events.

Materials and methods

In April 1997, we initiated monthly monitoring of recruitment of intertidal mussels and barnacles at 11 sites along the coast of central Chile covering 900 km of coastline (Fig. 1). Three sites were spread over ~1 km of coast toward the center of the region (ECIM-Norte, ECIM-Sur, Las Cruces; Fig. 1). Recruitment of barnacles was quantified on 10×10 cm Plexiglas® plates covered with Safety-Walk (3M®), a nonslip surface that provides substratum heterogeneity and ensures homogeneity of conditions across plates and sites (Menge et al. 1994). Five barnacle recruitment plates were deployed over a 20–50 m transect at the upper intertidal zone of wave-exposed benches at each study site. In 1997 we missed several months of barnacle recruitment at Quintay because of lost plates. Therefore, this site was not included in analysis of barnacle recruitment. Recruitment of mussels was quantified on 7-cm-diameter scrub pads (Tuffy®), which emulate the complex microhabitat preferred by mussel larvae (Navarrete and Castilla 1990; Menge et al. 1994). Five Tuffy pads were deployed in the mid intertidal zone of the same benches with barnacle plates. Plates and pads were replaced every 25 to 70 d, depending mostly on weather conditions and accessibility to the sites, then brought to the laboratory and examined under dissecting scopes. In other studies (S. Navarrete unpubl. data), we have determined that five collectors per site do not capture the full within-site variability, but they represent well the geographic trends and ranking of sites across the region.

Two common species of chthamaloid barnacles are found in the upper intertidal zone at roughly similar abundances: *Jehlius cirratus* and *Notochthamalus scabrosus.* They both recruit and survive on the monitoring plates, but they cannot safely be separated into species at small postmetamorphic size (set). Thus, we pooled both species of barnacles in analyses. Other barnacle species rarely settle in the upper intertidal zone and they can be identified easily. All three mussel species typically found in the intertidal zone of central Chile—*Perumytilus purpuratus, Semimytilus algosus,* and *Brachidontes granulata*—were observed in Tuffy pads and identified to species level. On several occasions, all mussels in the Tuffy pads were measured under the scope to evaluate the potential for secondary settlement (Hunt and Scheibling

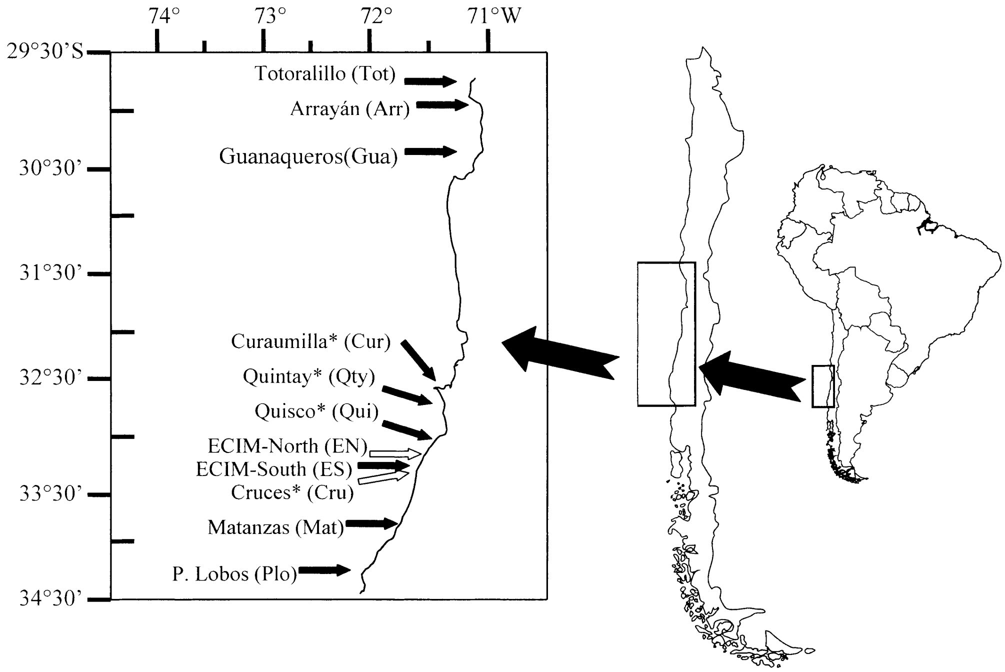

Fig. 1. Map of central Chile showing geographic position of study sites. Solid arrows indicate sites where temperature loggers were placed, and a star next to the site name indicates the temperature records used in calculation of SST for 33°S. Abbreviations of site names in parenthesis as used in tables.

1998). In all cases, judging by spat size and shape, we estimated that most settlers (>90%) corresponded to individuals settling directly from the plankton over the past few days to weeks (Ramorino and Campos 1979).

Larval duration and timing in the water column are important to determine susceptibility to El Niño. The larval phase of the mussel species varies from 17 to 20 d in the case of *P. purpuratus* to >40 d in the case of *B. granulata* (Campos and Ramorino 1979; Ramorino and Campos 1979). Settlement occurs throughout the year in all species, with major peaks in summer (December–February) and fall (March–May) months in the case of *P. purpuratus* and *B. granulata* and summer and, secondarily, winter months (June–August) in the case of *S. algosus* (this study). Larvae of the two chthamaloid barnacles reach competent cyprid stage between 20 and 31 d from release (Venegas et al. 2000). Settlement of barnacles is more discrete than that of mussels, occurring as one or a few pulses between spring and summer months.

At all sites, recruitment time series encompassed the period during the 1997–1998 El Niño and the following 2 yr, when the warming event was no longer detectable along the central coast of Chile and nearly neutral conditions prevailed (see below). To evaluate the hypothesis of El Niño effects versus "normal" interannual variability, we compared recruitment rates between July 1997 and May 1998 (1997–1998) versus those between July 1998 and May 1999 (1998–1999) and between July 1999 and May 2000 (1999–2000). The period was determined according to data from González et al. (1998) and Blanco et al. (2001) for northern Chile and by in situ temperature loggers in central Chile (*see also* the National Oceanic and Atmospheric Administration (NOAA) altimeter and global coverage satellite observations, http://www.cdc.noaa.gov/~kew/MEI/mei.html). Surface conditions in the central eastern Pacific between 1998 and 2000 have been characterized as slightly cooler than normal (La Niña; Davis 2000; Wolter 2001), but the effect was weak in central Chile (Fig. 2). Therefore, the 2 yr following El Niño can be considered as nearly neutral or as weak La Niña conditions (Blanco et al. 2001, Thomas et al. 2001).

In situ temperature loggers ("tidbits," StowAway®) were deployed 1–2 m deep at nine sites along the region (Fig. 1). Here, we present means of surface temperature from four sites centered 1° around 33°S for which we have data for the 1997–2000 period. Monthly upwelling indices (offshore Ekman transport, OET) spanning the latitudes of the present study (30°S, 73°W; 33°S, 74°W; and 36°S, 74°W) from 1997 to 2000 were provided by Pacific Fisheries Environmental Laboratories, a division of the NOAA National Marine Fisheries Service, and are publicly available (http://www.pfeg.noaa.gov). These indices are calculated on quadrants of 3° × 3° of latitude by longitude based on average wind fields and the Coriolis parameter for that latitude. Therefore, they did not provide site-specific information about upwelling intensity but were used to determine temporal trends. The OET index varies latitudinally, but temporal trends were closely similar within the study region between 33 and 36°S (*see Results*). As estimates of the strength of El Niño (and La Niña), monthly values of the Southern Oscillation index (SOI) and the multivariate ENSO index (MEI) were obtained from the Bureau of Meteorology, Australia (http://www.bom.gov.au/climate/current/soi2.shtml) and the Climate Diagnostic Center of NOAA (http://www.cdc.noaa.

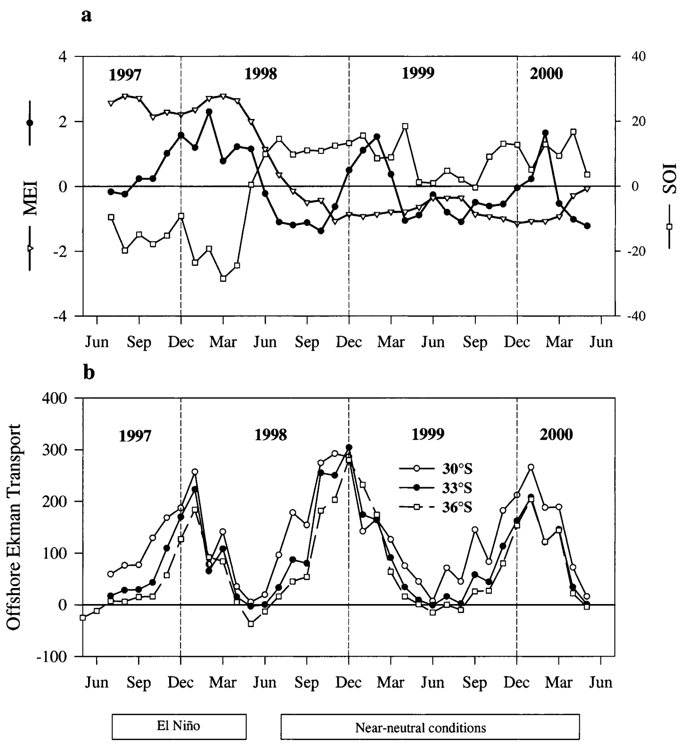

Fig. 2. (a) Surface temperature anomaly at 33°S, Southern Oscillation index (SOI) and multivariate ENSO index (MEI) for the period of the study. (b) Upwelling indices (offshore Ekman transport, OET) at 74°W and 30, 33, and 36°S for the period of the study.

gov/∼kew/MEI/mei.html), respectively. The SOI index is calculated as the sea level pressure differential between Tahiti (150°W) and Darwin, east Australia (150°E). It represents the general state of the tropical Pacific and does not vary latitudinally. A negative SOI value, which occurs during El Niño events, reflects lower pressure over Tahiti and the movement of warm west Pacific waters to the eastern Pacific. The MEI index corresponds to the rotated first axis of a principal components analysis (PCA) ordination of six main state variables over the tropical Pacific: sea level pressure, zonal and meridional components of surface winds, SST, surface air temperature, and cloudiness (Wolter 2001). The MEI index does not vary with latitude.

Two different statistical analyses were conducted to evaluate the hypothesis of El Niño effects on recruitment. First, monthly recruitment means for each period were compared using a two-way analysis of variance with Year and Site as fixed and random factors, respectively. The means of five plates or Tuffy pads for each month were used as replicates (Connolly and Roughgarden 1999; Lundquist et al. 2000). When a significant Site × Year interaction was found, Tukey's multiple comparison tests were used to determine the direction of among-year differences in each site. These analyses included only sites where nonzero recruitment was observed in all years, which allowed us to compare results with data presented by Connolly and Roughgarden (1999) for intertidal barnacles in California. Second, we calculated Pearson correlations between monthly recruitment of each species and the values of OET, MEI, and SOI for each study site. Correlation analyses used the entire time series of recruitment from July 1997 through April 2000.

Table 1. (A) Yearly mean (±SE) upwelling indices (offshore Ekman transport, $m^3\ s^{-1}$ per 100 m coastline) for quadrants of 3° × 3° of latitude by longitude along central Chile. (B) Results of two-way ANOVA comparing upwelling indices among latitudes and years. Boldface indicates significant differences at $\alpha = 0.05$. df, degrees of freedom; MS, mean square.

(A) Latitude (°S)	Year 1997	1998	1999
30	100.6(±18.2)	151.2(±30.9)	108.2(±18.2)
33	71.2(±18.7)	118.1(±31.8)	72.2(±19.2)
36	49.1(±18.4)	91.2(±28.7)	62.3(±23.5)

(B) Source of variation	df	MS	*F*	*P*
Year	2	22,578.8	3.34	**0.0395**
Latitude	2	25,287.1	3.74	**0.0271**
Year × Latitude	4	276.55	0.04	0.9968
Residual	99	6,759.4		

Results

Hydrography—The sea surface temperature anomaly at 33°S, calculated as the average temperature at four sites around 33°S minus the overall mean for the period 1997–2000, showed clear warming between July 1997 and April–May 1998, corresponding well with the period of negative SOI and high (>1.6) MEI values (Fig. 2a). Indeed, SST at 33°S was negatively correlated to SOI ($r = -0.48$, $P = 0.0034$) and positively correlated to MEI ($r = 0.45$, $P = 0.0063$). Maximum El Niño warming was observed between November and December 1997 and then again between April and May 1998 when water temperature was between 1.0 and 1.6°C above that observed on the same months the following 2 yr (Fig. 2a). After May 1998, monthly water temperature was similar to the following 2 yr (within 1°C), with slightly colder values in 1999–2000 than the previous year, suggesting only a mild effect of La Niña conditions on surface water temperature at this latitude. Upwelling indices at 33°S (estimated OET toward the center of the study region) showed maximum values in austral spring and summer months, reaching nearly neutral or slightly downwelling conditions in winter months (Fig. 2b). Significant differences in upwelling indices were observed among years (Table 1). Upwelling indices in 1998–1999 were significantly higher than those in 1997–1998, whereas values in 1997–1998 were similar to those in 1999–2000 (a posteriori Tukey tests, Fig. 2b). The same temporal trend in OET was observed at 30, 33, and 36°S (Fig. 2b), with a weak but significant latitudinal trend to increasing mean upwelling indices to lower latitudes, a geographic trend that was consistent among years (Table 1). Mean upwelling indices were roughly comparable in magnitude to those reported for the coast of California (Connolly and Roughgarden 1999). Thus, it appears that upwelling of water did occur during El Niño in the austral

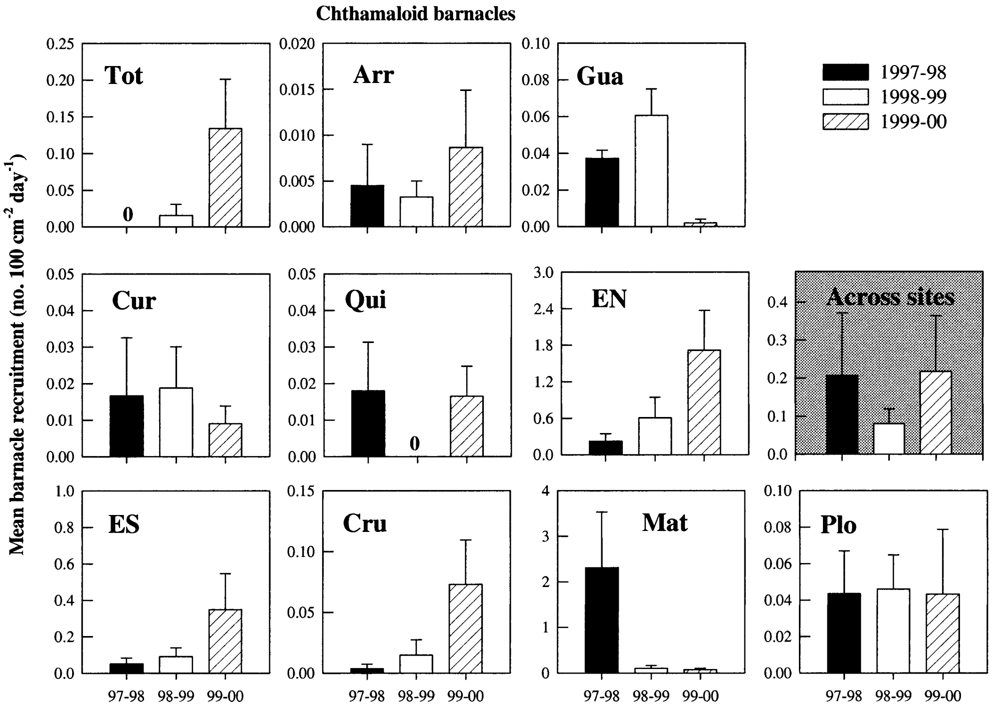

Fig. 3. Mean (±SE) yearly barnacle recruitment rates at study sites for 1997–1998, 1998–1999, and 1999–2000. Sites are ordered north to south going from left to right and top to bottom panels. Note the different *y*-axis scales among panels used to highlight among-year differences within each site. The shaded panel on the right corresponds to yearly averages (±SE) across all sites, including those with zero recruitment. Site abbreviations as in Fig. 1.

spring–summer 1997–1998, but the temperature of upwelled water was warmer than in normal years (González et al. 1998; Blanco et al. 2001).

Recruitment—Across the study region and in all years, mean barnacle recruitment rates varied by almost two orders of magnitude among sites (Fig. 3). The magnitude and the direction of among-year differences varied across sites, however, and a two-way analysis of variance showed a significant Site × Year interaction (Table 2). Multiple contrasts for each site showed significant among-year differences at only 3 of the 11 sites, and only one site, Matanzas, showed significantly higher recruitment during El Niño than the 2 yr after (Table 2). Moreover, there was no detectable latitudinal trend in the direction nor in the magnitude of the interannual differences. Despite the significant differences in the pattern of interannual variability across sites, the ranking of sites was generally maintained between successive years; that is, sites with high barnacle recruitment one year had high recruitment the following year (Table 3). This order broke, however, when comparing recruitment rates between 1997–1998 and those in 1999–2000, the two seasons with similar upwelling indices (Fig. 2b).

Recruitment rates of the mussels *P. purpuratus* and *S. algosus* varied by more than three orders of magnitude across sites, with generally higher rates toward southern sites within the region (except Totoralillo for *S. algosus*) (Figs. 4, 5). Both the magnitude and direction of interannual variation changed between species and sites. The most geographically consistent pattern was observed in *P. purpuratus,* for which recruitment rates were generally higher in 1998–1999 or 1999–2000 than during the 1997–1998 El Niño year at 9 of the 11 sites (Fig. 4), rendering a significant year effect and a nonsignificant Year × Site interaction (Table 4). A Tukey's multiple comparison test showed that, on average across all sites, recruitment rates were significantly lower during 1997–1998 than the 2 yr after. However, multiple comparisons showed that only three sites presented significant among-year differences in recruitment (experimentwise $\alpha = 0.05$). In contrast to *P. purpuratus,* the pattern of interannual variation in recruitment rates of *S. algosus* varied significantly across sites (Fig. 5), rendering a significant Site × Year interaction and highly significant main effects of Site (Table 4). Multiple contrasts for each site showed significantly higher recruitment rates during 1997–1998 and 1999–2000 than 1998–1999 at one site, Guanaqueros, but significantly lower rates in 1997–1998 and 1999–2000 than 1998–1999 at El Quisco. Recruitment rates at ECIM-Sur and Punta Lobos were greatest during 1999–2000 (Table 4).

In agreement with the relative abundances of adults in the field (Broitman et al. 2001), recruitment rates of *B. granulata* were 10 to 100 times lower than those of *P. purpuratus* and *S. algosus* across the region. Interannual variation in recruitment rates of *B. granulata* also changed across sites (Fig. 6; Table 4), producing a significant Site × Year interaction term and highly significant main effects of Site. Multiple comparisons showed that interannual differences were statisti-

Table 2. (A) Two-way ANOVA comparing barnacle recruitment rates across sites and among years (1997–1998, 1998–1999, 1999–2000). Year was considered as fixed and Site as a random factor. Only the eight sites where recruitment was observed on each year were considered in this analysis. Boldface indicates significant effect at $\alpha = 0.05$. (B) Direction of statistically significant interannual change in mean barnacle recruitment according to Tukey's multiple comparison tests. 97, period 1997–1998; 98, 1998–1999; and 99, 1999–2000 (experimentwise error rate $\alpha = 0.05$). Abbreviations for sites as used in figures and tables. ns, non significant differences among years; nd, no data available; ni, not included in statistical analyses because there was no recruitment for an entire period; df, degrees of freedom.

(A)

Source of variation	df	MS	F	P
Site	7	0.085	7.53	**0.0001**
Year	2	0.014	0.37	0.6963
Site × Year	14	0.041	3.68	**0.0001**
Residual	263	0.011		

(B)

Site	Direction
Totoralillo (Tot)	ni
Arrayán (Arr)	ns
Guanaqueros (Gua)	99<97=98
Curaumilla (Cur)	ns
Quintay (Qty)	nd
El Quisco (Qui)	ni
ECIM Norte (EN)	99>97
ECIM Sur (ES)	ns
Las Cruces (Cru)	ns
Matanzas (Mat)	97>98=99
Punta Lobos (Plo)	ns

cally significant at only three sites, with no consistent interannual variability among these sites (Table 4).

Despite differences in the direction of interannual changes in mussel recruitment rates across the region, the pattern of among-site differences tended to be preserved from one year to the next, including the 1997–1998 El Niño year. The temporally most robust among-site differences were observed in *P. purpuratus*, for which the ranking of sites (and overall rates) was tightly maintained ($r > 0.86$) from year to year (Table 3). The most variable pattern of among-site differences was that of *B. granulata*, in which a similar pattern of recruitment across sites was observed between 1997–1998 and 1999–2000 but was different when comparing other years (Table 3). Moreover, there was no detectable latitudinal trend in the direction nor the magnitude of interannual differences for any of the mussel species.

Among-site variability in recruitment of mussel and barnacle species was larger than among-year variation, as revealed by coefficients of variation calculated across the 3 yr and among all study sites (Table 5). The same trend was observed in all species, but it was particularly striking for barnacles and *P. purpuratus*, for which recruitment rates were on average between 2 and 2.5 times more variable among sites than among years. A complete analysis of spatial and temporal variation in recruitment time series will be presented elsewhere.

Table 3. Pearson correlation coefficients and significance (in parentheses) comparing mean recruitment rates per site from year to year. Significantly positive correlation indicates maintenance of among-sites pattern. Boldface figures indicate significant correlations at $\alpha = 0.05$.

	1997–1998 vs. 1998–1999	1998–1999 vs. 1999–2000	1997–1998 vs. 1999–2000
Chthamaloid barnacles	0.71	0.77	0.46
	(**0.0067**)	(**0.0019**)	(0.1366)
Perumytilus purpuratus	0.87	0.93	0.96
	(**0.0011**)	(**0.0001**)	(**0.0001**)
Semimytilus algosus	0.75	0.86	0.60
	(**0.0131**)	(**0.0014**)	(0.0691)
Brachidontes granulata	0.17	−0.24	0.71
	(0.6401)	(0.5054)	(**0.0221**)

The patterns of interannual variability described above for mussels and barnacles were not affected by the specific months included in the analyses. That is, similar trends (or lack thereof) were observed when using our functional classification of years following the months of El Niño anomaly in central Chile or whether the calendar year was used. Also, selecting only the 4 months of maximum El Niño effect, October–January, did not alter the conclusions.

Recruitment and ENSO indices—To look at the potential association between El Niño and OET indices versus recruitment of barnacles and mussels across the entire region, we rescaled recruitment at each site as the percentage of the maximum recruitment observed throughout the time series at that site. When expressing recruitment in this manner and pooling all sites together, we found no pattern of association between El Niño or upwelling indices and barnacle recruitment (Fig. 7a). For instance, the maximum barnacle recruitment ever registered at some sites was observed during months of intense El Niño (e.g., negative SOI values), but at many other sites, maximum recruitment was observed in periods of nearly normal or La Niña conditions (Fig. 7a). Examining the association between recruitment and El Niño indices for each site using the entire time series of barnacle recruitment (April 1997–May 2000), recruitment rates appeared weakly but significantly correlated to the intensity of El Niño/La Niña expressed by the MEI index only at two close sites (ECIM-Norte: $r = -0.36$, $P = 0.0293$; ECIM-Sur: $r = -0.35$, $P = 0.0343$), but a Bonferroni correction for multiple comparisons (corrected $\alpha = 0.005$) rendered these correlations nonsignificant. No other correlation with MEI, SOI, or OET was observed.

No associations with El Niño or OET indices were observed in recruitment of *S. algosus* or *B. granulata* when pooling all sites across the region (Fig. 7c,d). Separate correlations between recruitment of these mussel species and SOI and MEI indices for each site evidenced significant association at six sites, but the direction of change (positive or negative with respect to El Niño intensity) was not consistent among them. Only one, a negative correlation with MEI values at ECIM Sur (ES) remained significant after Bonferroni correction.

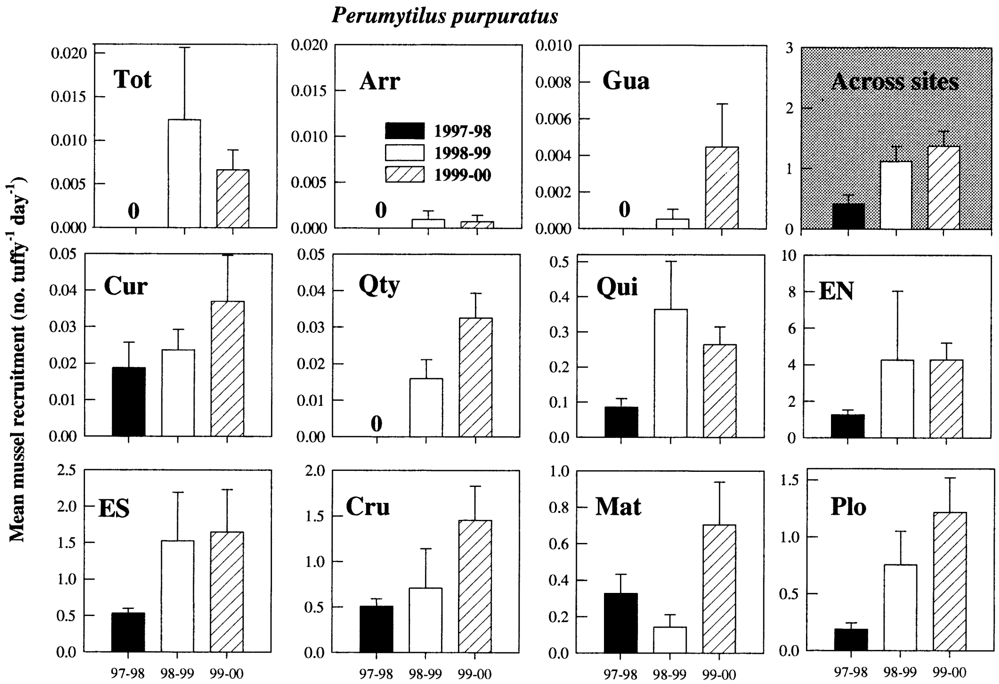

Fig. 4. Mean (±1 SE) yearly recruitment rates of the mussel *Perumytilus purpuratus* at study sites for 1997–1998, 1998–1999, and 1999–2000. Sites are ordered north to south going from left to right and top to bottom panels. Note the different *y*-axis scales among panels used to highlight among-year differences within each site. The shaded panel on the top right corresponds to yearly averages (±SE) across all sites, including those with zero recruitment. Site abbreviations as in Fig. 1.

In contrast to barnacle and other mussel species, the depression caused by El Niño on *P. purpuratus* recruitment across all sites in the study region was apparent both with SOI and MEI indices (Fig. 7b). During months of intense El Niño, no site exhibited more than 60% of the maximum recruitment observed under either normal or La Niña conditions. Correlations between monthly mussel recruitment and monthly values of SOI, MEI, and OET for each site

Table 4. (A) Two-way ANOVA comparing mussel recruitment rates across sites and among years (log-transformed data). A separate analysis was conducted for each species. (B) Direction of interannual change at each study site from Tukey's multiple comparison tests (experimentwise error rate $\alpha = 0.05$). Only sites with nonzero recruitment were considered. Abbreviations as in Table 2.

(A)	*Perumytilus*				*Semimytilus*				*Brachidontes*			
Source	df	MS	*F*	*P*	df	MS	*F*	*P*	df	MS	*F*	*P*
Site	6	0.446	13.2	**0.0001**	9	0.377	25.8	**0.0001**	8	0.0009	4.6	**0.0001**
Year	2	0.374	9.4	**0.0035**	2	0.094	1.9	0.1687	62	0.0009	1.8	0.1907
Site × Year	14	0.040	1.2	0.2970	18	0.054	3.7	**0.0001**	16	0.0005	2.3	**0.0031**
Residual	178	0.034			240	0.014			208	0.0002		

(B) Site	Direction	Direction	Direction
Tot	ni	ns	ns
Arr	ni	ni	ni
Guan	ni	97=99>98	99>98=97
Cur	ns	ns	ns
Qty	ni	ns	ni
Qui	98=99>97	98>97=99	ns
EN	98=99>97	ns	ns
ES	ns	99>97=98	97=99>98
Cru	ns	ns	97=99>98
Mat	ns	ns	ns
Plo	98=99>97	99>97=98	ns

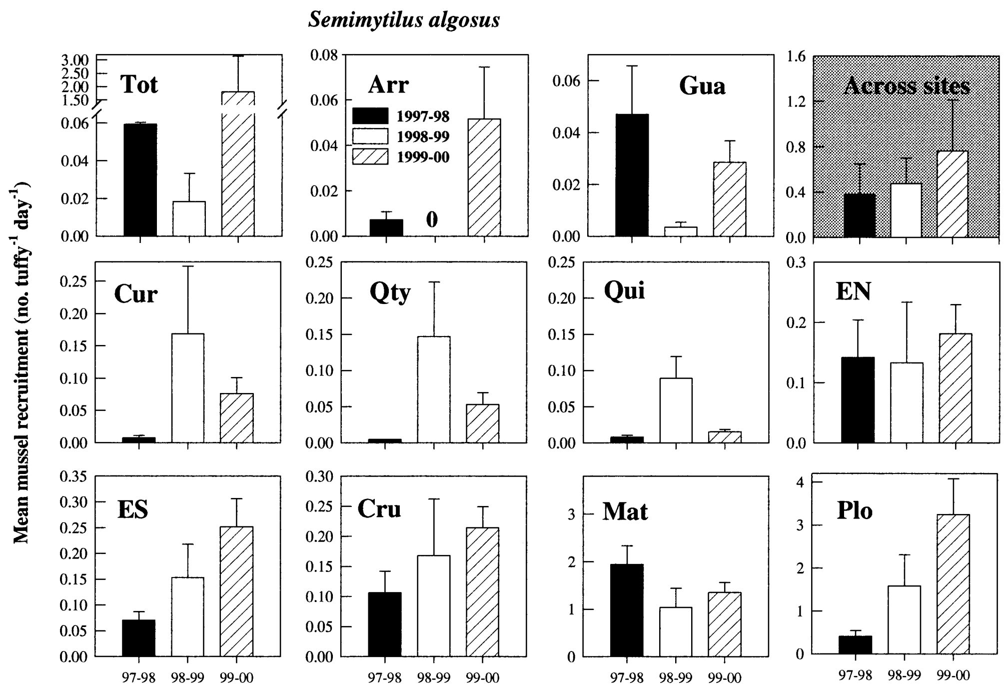

Fig. 5. Mean (±1 SE) yearly recruitment rates of the mussel *Semimytilus algosus* at study sites for 1997–1998, 1998–1999, and 1999–2000. Sites are ordered north to south going from left to right and top to bottom panels. Note the different *y*-axis scales among panels used to highlight among-year differences within each site. The shaded panel on the top right corresponds to yearly averages (±SE) across all sites, including those with zero recruitment. Site abbreviations as in Fig. 1.

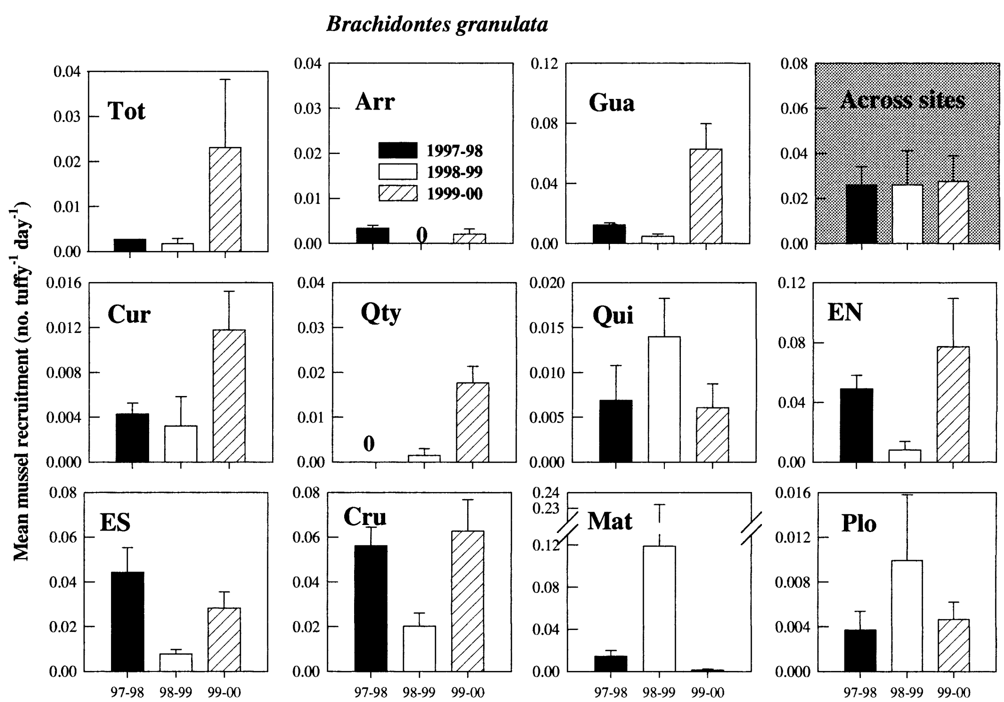

Fig. 6. Mean (±1 SE) yearly recruitment rates of the mussel *Brachidontes granulata* at study sites for 1997–1998, 1998–1999, and 1999–2000. Sites are ordered north to south going from left to right and top to bottom panels. Note the different *y*-axis scales among panels used to highlight among-year differences within each site. The shaded panel on the top right corresponds to yearly averages (±SE) across all sites, including those with zero recruitment. Site abbreviations as in Fig. 1.

Table 5. Average among-site and among-year coefficients of variation (mean C.V.) and 95% confidence intervals (95% C.I.) for barnacle and mussel recruitment.

Species	Among-site Mean C.V.	Among-site 95% C.I.	Among-year Mean C.V.	Among-year 95% C.I.
Chthamaloid barnacles	223.19	196.72	87.08	63.18
Perumytilus purpuratus	157.50	91.97	75.71	41.98
Semimytilus algosus	180.92	180.62	84.67	63.02
Brachidontes granulata	139.35	250.08	92.08	51.87

were also more consistent for *P. purpuratus* than for any other species. At two sites, recruitment of *P. purpuratus* appeared significantly and positively associated to SOI values (Punta Lobos: $r = 0.43$, $P = 0.0093$; Quisco: $r = 0.48$, $P = 0.0023$) and at four sites negatively associated to MEI (Las Cruces: $r = -0.33$, $P = 0.0441$; ES: $r = -0.38$, $P = 0.0187$; Punta Lobos: $r = -0.55$, $P = 0.0006$; Quisco: $r = -0.48$, $P = 0.0025$), suggesting lower recruitment when El Niño conditions intensify. Three of these correlations were significant after Bonferroni correction (corrected $\alpha = 0.005$).

Discussion

Along the coast of central and northern California, Connolly and Roughgarden (1999) and others (Roughgarden et al. 1988; Ebert et al. 1994) have shown consistent patterns of interannual variation in barnacle and sea urchin recruitment produced, apparently, by El Niño events (Ebert et al. 1994; Connolly and Roughgarden 1999; *see also* Roughgarden et al. 1988). Our results along the coast of central Chile show that recruitment rates of two barnacles and two intertidal mussel species were not significantly altered by the strong 1997–1998 El Niño or by the weak La Niña conditions that ensued. Recruitment of the competitively dominant intertidal mussel, *P. purpuratus,* exhibited significantly lower recruitment across the region in the 1997–1998 El Niño than during the same months the following 2 yr. We interpret this result as a weak, but significantly negative, effect of El Niño on recruitment of this species. However, when examining individual sites, significant interannual changes were observed at only three of seven sites, and although no recruitment of *P. purpuratus* was observed in the three northernmost sites in 1997–1998, recruitment rates at these sites in subsequent years were among the lowest recorded for the study region. Therefore, it appears that El Niño did reduce average recruitment rates of *P. purpuratus* across the entire study region (Fig. 7b).

The main goal of this study was to evaluate whether an El Niño event produced a clear, and therefore geographically and temporally predictable, signal in recruitment to benthic populations. From this point of view, mean or total recruitment measured over the entire recruitment season of the species, as in this study, will be the most sensitive variable determining dynamics of adult populations and communities (Sutherland 1990). As indicated earlier, our calculations of mean recruitment encompassed the recruitment season of the species, thus representing well the total recruitment for that year. The relatively low frequency (ca. monthly) of our recruitment time series compromises our ability to resolve potential El Niño effects on individual settlement events. However, if such effects occurred, our results showed that depression or enhancement of settlement events did not produce differences in recruitment at the end of the month in all species studied, except *P. purpuratus* (Fig. 7). It must be noted that monthly recruitment rates might not represent well the addition of all settlement events occurring in the time elapsed between successive samplings (replacement of collectors), which probably also varies from species to species because of differences in rates of mortality and gregarious settlement. However, given the roughly similar sampling times throughout the study period (1997–2000) and the consistency of the settlement substrata across sites and years, it seems unlikely that these effects could substantially alter the results presented here.

Because one of the strongest and more general effects of El Niño in the southeastern Pacific is the reduction of phytoplankton biomass (Avaría and Muñoz 1987; Thomas et al. 2001), a distinct possibility is that low food availability produced unusually high larval mortality of *P. purpuratus,* which in turn led to overall lower recruitment rates across the region. Indeed, experiments conducted at five sites within the same study region showed that the 1997–1998 El Niño had significantly negative effects on growth rates of intertidal adults of this mussel species (Finke, Navarrete, and Venegas unpubl. data). Available data are insufficient to determine whether cross-shelf larval transport of *P. purpuratus* was altered by El Niño. However, lack of correlation between monthly recruitment rates and either SST or upwelling indices (OET) at any of the 11 sites studied suggests that the upwelling–relaxation model (e.g., Wing et al. 1995; Connolly and Roughgarden 1999) does not strongly determine recruitment of this species in central Chile. Higher frequency data and in situ measures of wind stress are needed to evaluate this proposition.

Less coherent patterns of interannual variation were observed in the other two intertidal mussel species, for which the direction of the few significant interannual changes varied across sites. This suggests that the processes determining year-to-year variation in recruitment of these species are site-specific and not geographically coupled by the temporal changes in larger scale oceanographic processes, such as El Niño.

Clearly, different patterns were found in the effects of El Niño on intertidal barnacle recruitment in central Chile and in those observed in central and northern California (Roughgarden et al. 1988; Connolly and Roughgarden 1998). Using basically the same methodology to that used here, and with a geographically similar scope and intensity, Connolly and Roughgarden (1999) showed that the 1997–1998 El Niño produced increased barnacle recruitment across northern and central California. The mechanism producing such changes seems to be related to the weakening of upwelling-favorable winds during El Niño, which have been shown to increase the frequency of recruitment pulses of barnacle and other invertebrates (e.g., Wing et al. 1995; Morgan et al. 2000). No such barnacle recruitment pattern was observed in central Chile. Upwelling indices for the study region were lower in

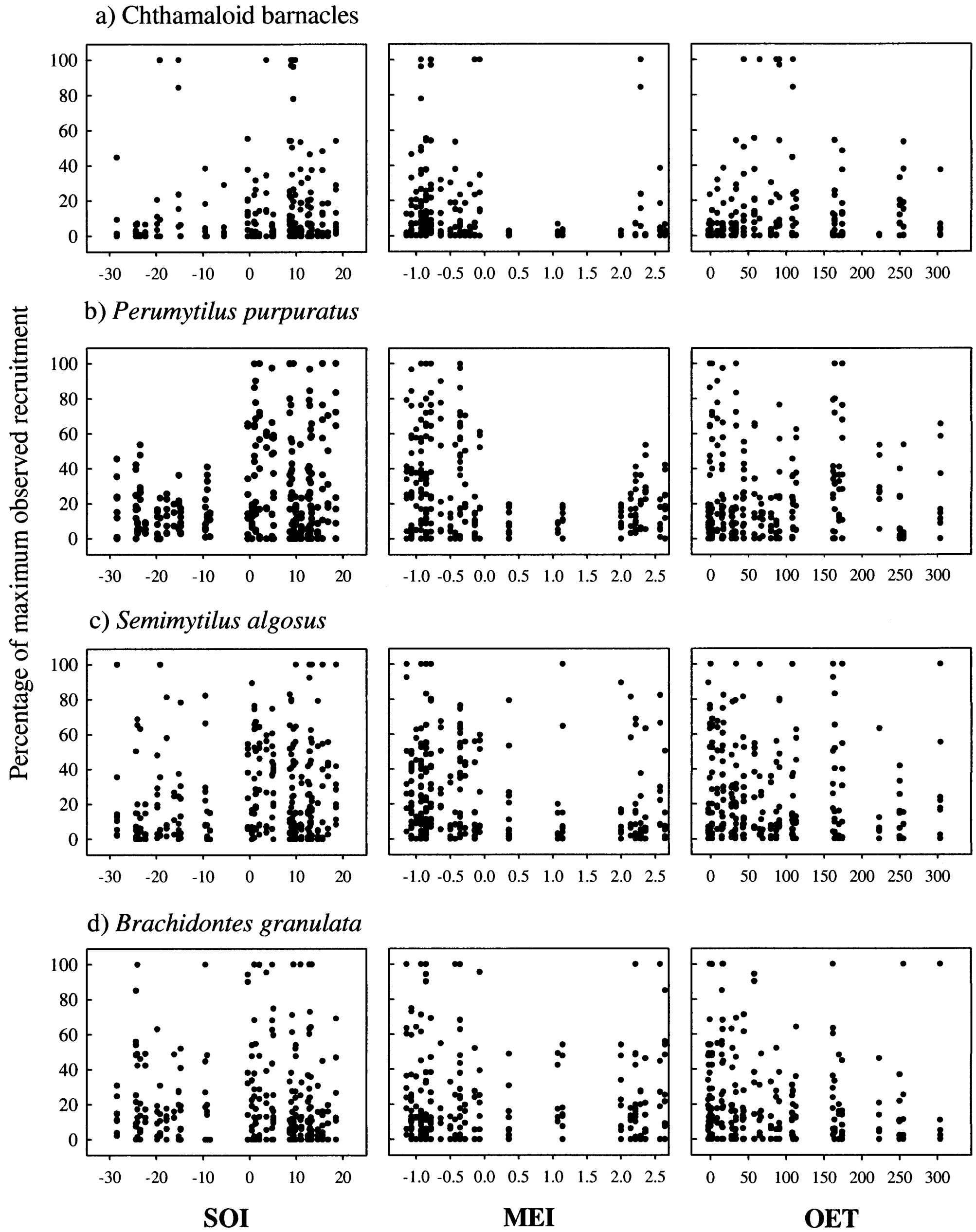

Fig. 7. Scatter plots of monthly recruitment, expressed as the percentage (%) of the maximum recruitment observed at a given site over the course of the study, versus Southern Oscillation index (SOI), multivariate ENSO index (MEI), and offshore Ekman transport (OET) at 33°S. (a) Chthamaloid barnacles, (b) *Perumytilus purpuratus,* (c) *Semimytilus algosus,* and (d) *Brachidontes granulata.* All sites were pooled to evaluate trends across the region.

1997 than 1998, but similar to those in 1999 and wind stress in northern Chile (ca. 20°S) was not strongly reduced during the 1997–1998 El Niño (Blanco et al. 2001). Thus, it is not clear that El Niño significantly reduces wind forcing and therefore increases the frequency of upwelling–relaxation events along the coast of Chile. Significant among-year differences in upwelling indices did occur (higher OET values in 1998), but unlike the pattern shown by Lundquist et al. (2000) for cancrid crab settlement, these differences were not clearly associated with El Niño and did not lead to among-year differences in barnacle recruitment. Moreover, lack of consistent trends between recruitment and OET or SST suggests that barnacle settlement does not follow the upwelling–relaxation model in a simple manner. Daily settlement data at one site in central Chile (Las Cruces) also failed to show correlations between settlement and locally measured wind stress/relaxation and temperature (R. Venegas and S. Navarrete unpubl. data). As suggested by Ebert et al. (1994) for southern California, differences in mesoscale alongshore circulation patterns among sites could swamp the regional signal of El Niño. Recent studies by Lundquist et al. (2000) conducted at one site in central California, but at higher sampling frequency, also suggest that the upwelling–relaxation model and its interaction with El Niño can be much more complex and less predictable than originally envisioned on the coast of California. Another interesting difference between our study and that of Connolly and Roughgarden (1999) is the generally lower interannual variability observed in Chile in comparison to among-site variation (Table 5). This pattern suggests marked spatial differences in transport or retention processes along what appears to be a fairly homogeneous coastline in central Chile. These spatial differences are persistent over time, highlighting the importance of coastal geomorphology. Much more research is needed to determine the processes responsible for regional and interhemispheric differences.

Our results suggest the existence of regional differences in the way large-scale oceanographic anomalies interact with local processes to determine patterns of recruitment of benthic species. In general, the effects of El Niño on recruitment of intertidal species, if any, were not consistent across sites and therefore are unpredictable. The broad similarities of the physical environment along the Pacific coast of both hemispheres (Longhurst 1998) makes such differences particularly intriguing and they deserve further investigation. As more biological and physical data become available, particularly in the southern hemisphere, we will be able to understand the mechanisms behind such differences and regularities.

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