

Changes in a tidepool fish assemblage on two scales of environmental variation: Seasonal and El Niño Southern Oscillation

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Abstract

Intertidal organisms are influenced by the tidal, daily, and seasonal environmental variability of their habitat. Interannual variability, although often less severe than shorter-scale variability, may also be important in structuring intertidal systems. This study compares the magnitude of changes in a rocky intertidal fish guild occurring on a seasonal scale with those occurring during an El Niño Southern Oscillation (ENSO). I examined tidepool fish assemblage structure and habitat use in two southern California sites approximately every 3 months from 1996 to 2000, a period including non-ENSO conditions, the 1997–1998 El Niño, and the 1998–1999 La Niña. During each sampling period, I censused fish abundance in 105 tidepools of differing intertidal height, depth, and surface area. Several aspects of habitat use varied seasonally for the four most common species: *Clinocottus analis* (woolly sculpin), *Girella nigricans* (opaleye), *Gobiesox rhessodon* (California clingfish), and *Hypsoblennius gilberti* (notch-brow blenny). All four species migrated vertically within the intertidal zone on a seasonal scale, corresponding to seasonal changes in sea level. The assemblage dominant, *C. analis*, occupied tidepools of different sizes depending on season. Although seasonality in habitat use suggests an influence of environmental variability on seasonal scales, fish habitat was generally not altered by temperature and sea level changes imposed by the El Niño. Species assemblage, however, differed among climate conditions. *C. analis* declined in abundance during the El Niño because of lack of recruitment but increased immediately after its conclusion. *Paraclinus integripinnis* (reef finspot), usually rare, was more abundant during the El Niño. Effect of the El Niño on the other four species was not detected. Assemblage changes suggest that although intertidal fishes regularly experience large tidal, daily, and seasonal environmental fluctuations, interannual changes in environmental factors, even when relatively small in magnitude, can perturb the system. Perturbations in the present system, however, did not persist beyond the end of the El Niño event as they often do in lower-latitude nearshore areas.

Coastal habitats such as the rocky intertidal zone are characterized by dynamic environmental conditions. Properties such as wave action, temperature, and water chemistry have large ranges, cycling on tidal, daily, seasonal, and interannual time scales (Metaxis and Schiebling 1993; Barry et al. 1995). Environmental variation on each scale has potential to affect intertidal populations and assemblage structure. For example, tidal and daily cycles may affect individual feeding and habitat use patterns on the centimeter-to-meter scale (Gibson 1999). Interannual cycles may affect abundance and distribution of populations on the scale of kilometers (Barry et al. 1995).

Seasonal cycles in environmental factors are important on

a range of spatial scales and drive many rocky intertidal population and community processes. For example, seasonal storms may lead to increased mortality of intertidal algae (Gunnill 1985). Seasonal fluctuations in temperature may structure fish, invertebrate, and algal reproductive and recruitment cycles, and therefore cycles of population size and size structure of individuals (Chen and Chen 1992; Schoschina et al. 1996; Pfister 1999). Changes in sea level on a seasonal scale might be expected to impose cycles of vertical migration in mobile intertidal organisms. Seasonal changes in population size and size structure of one species may have community-level implications, affecting predator, prey, and other associated species. For example, seasonal cycles in algal composition of an Asian rocky shore resulted in seasonal diet switching by, and ultimately seasonal growth and reproductive cycles of, an herbivorous crab (Kennish et al. 1996).

Episodic climatic events such as the El Niño Southern Oscillation (ENSO) also have potential to affect communities and to interfere with community fluctuations that occur on seasonal and other temporal cycles. Intertidal communities may be sensitive to ENSO-induced environmental changes in part because the intertidal habitat marks the intersection of terrestrial and marine environments and therefore is exposed to environmental changes in both realms. Many intertidal species occupy a wide range of habitats throughout their lifetimes, sometimes ranging from tens or hundreds of kilometers offshore during a planktonic larval phase to the nearly terrestrial splash zone. A change in environmental conditions in any of those areas could, by influencing individual populations, affect entire intertidal systems

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Acknowledgments

Thanks to Lisa Levin for advice throughout the project and careful readings of various drafts of this manuscript. Thanks also to Paul Dayton, Paul Smith, Trevor Price, Dave Checkley, and Clint Winant for reading the manuscript. I am very grateful to Nicole Dederick, Erin Hubbard, Julie Frost, Edward Vowles, Andrew Juhl, and other volunteers for field assistance. Thanks to Richard Rosenblatt for fish identifications. Data were made available by the University of Hawaii Sea Level Center, the National Oceanic and Atmospheric Association, and the Scripps Institution of Oceanography. Salary and research support was provided by the J. M. Hepps and the Department of Defense National Defense Science and Engineering Graduate Fellowships, the Sigma Xi Foundation, the PADI Foundation, Sigma Delta Epsilon Graduate Women in Science, the Mildred Mathias Foundation, and the Scripps Institution of Oceanography Graduate Department.

(Sanford 1999). Although intertidal organisms are adapted to fluctuating environments, some may exist close to their upper or lower tolerances of environmental factors, and changes in climate could cause an extension of the environmental range beyond tolerable conditions (Tomanek and Somero 1999).

In southern California, signals of El Niño span the gradient from marine to terrestrial, including increases in air temperature, ocean temperature, sea level, storm activity, rainfall, and terrestrial runoff; decreases in coastal upwelling and nearshore productivity; and changes in nearshore currents (McGowan 1984; Norton et al. 1985; Glynn 1990). Fewer generalizations can be made about La Niña events, the phase of the ENSO opposite to El Niño, but they tend to be characterized by decreases in temperature, sea level, and rainfall and increases in upwelling and productivity (Philander 1990). Almost all characteristic ENSO signals have been identified as agents of ecological change to intertidal communities. An increase in water temperature can change the role of keystone predators in structuring communities (Sanford 1999) and can alter community composition by increasing survivorship of warm-tolerant species and decreasing survivorship of cold-water species (Arntz and Tarazona 1990). A decrease in offshore transport of surface waters during El Niño, a result of upwelling relaxation, can cause assemblage changes by enabling onshore advection of typically offshore species (Brodeur et al. 1985; Arntz and Tarazona 1990). Increases in storm activity during El Niño can cause mortality of certain species (Dayton and Tegner 1984; Gunnill 1985), leaving habitat open for colonization by other species.

The purposes of this study were to identify the extent to which assemblage structure of a midlatitude (San Diego, California) intertidal fish guild changed during the 1997–1998 El Niño event, to measure seasonal patterns in fish habitat use, and to determine the extent to which the ENSO event interfered with seasonal habitat use patterns. Because the study included only one El Niño event and did not include climatic replication, results cannot be generalized to all El Niño events. Instead, the study's goals are to determine changes that occurred in the fish assemblage during the 1997–1998 event only and to compare these results with those of other El Niño studies set in similar habitat types. As ENSO prediction improves, facilitating the planning of future ENSO studies, results and broad hypotheses generated by studies of single El Niño events can be compared and tested.

I addressed four questions in the present study: (1) Did assemblage structure change during El Niño? Species that are members of warm-water families were expected to increase in abundance, and cold-water family members were expected to decrease in abundance during El Niño. (2) Did intertidal fishes exhibit seasonal patterns in use of tidepools as a function of intertidal height, depth, and surface area? Seasonal cycles of sea level and temperature were expected to drive seasonal patterns of habitat use. (3) Did intertidal fishes change pool use patterns over vertical tidal scales during the El Niño period? Higher temperatures of middle and upper intertidal tidepools were expected to cause a redistribution of middle and upper intertidal fishes to lower pools.

Higher sea level, which temporarily forced subtidal conditions onto low intertidal habitat, was expected to cause low intertidal fishes to move to higher pools to conserve the amount of time they spent isolated from the subtidal zone. As a result of these two processes, the horizontal band of available intertidal fish habitat was expected to narrow. (4) Was fish use of pool depth and surface area altered during El Niño? Increased air and water temperatures during El Niño were expected to induce fishes to relocate to bigger, deeper tidepools, which do not heat up as much during daytime low tides (Davis unpubl. data).

Methods

I measured fish abundance in one set of 55 tidepools from November 1996 to August 1999 and a second set of 50 tidepools from November 1996 to March 2000. The first set was located in the conglomerate sandstone outcrops of False Point (FP), and the second was located in a flat shale bench in Ocean Beach (OB), San Diego, California. Censuses were taken during all four seasons on a quarterly schedule, with sampling dates during November, February, May, and August. Two deviations from this schedule occurred during the study period. First, several additional sampling periods were added (June 1998, October 1998, and March 1999 at both sites and March 2000 at OB). Second, 1999 spring sampling at OB was conducted in June instead of May.

Tidepool fish abundance, species composition, and fish size were measured by collecting all fish in each pool. Pools were drained by bailing or by siphoning using hoses with mesh-covered openings. Rocks were removed, and crevices were searched for fish. All fish were identified to species and their total lengths (TL) measured to the nearest millimeter. The rocks were then replaced, the pool refilled, and the fish returned. Data were collected only during the day and only during tides lower than 30 cm above mean lower low water (MLLW). Three of the lowest pools at FP were in regions of shifting rocks and boulders; if a pool was no longer present during subsequent seasonal sampling, a substitute pool with similar characteristics was located.

El Niño signals—To characterize the ENSO conditions at the time of fish sampling, sea level and temperature data measured at the Scripps Pier, La Jolla, California, 7 km north of FP and 15 km north of OB, were used. Scripps Pier sea level values were obtained from the University of Hawaii's Sea Level Center data server (<ftp://ilikai.soest.hawaii.edu/rqds/pacific>). Sea level relative to a fixed reference point on shore was measured in millimeters at hourly intervals, from which monthly means were computed. Using data from January 1966 through December 1996, mean values were calculated for each month of the year to determine seasonal sea level fluctuations. Monthly sea level anomaly was calculated as the difference between a monthly sea level mean (1966–1996) and the mean sea level for the entire period of 1966–1996. Sea level anomalies for the months during the study period were calculated as the difference between the value for a particular study period month and the mean value for that month during the 1966–1996 period (Fig. 1).

Scripps Pier water temperatures were obtained from the

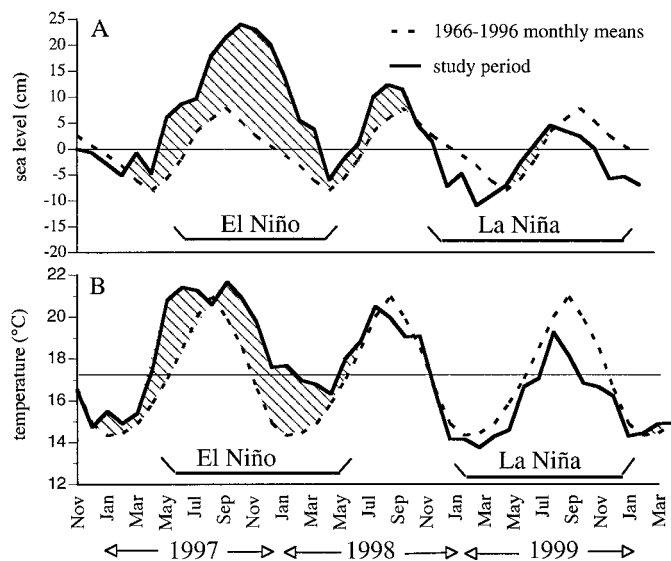


Fig. 1. (A) Sea level and (B) water temperature at the Scripps Pier, San Diego. The solid line in (A) represents monthly sea level over the course of the study (November 1996 to March 2000), calculated as the difference in sea level from the long-term 1966–1996 mean. The solid line in (B) represents mean monthly water temperature over the course of the study. The dashed lines in (A) and (B), representing mean sea level anomalies (relative to a fixed point on shore) and mean water temperature for each calendar month from 1966 to 1996, are included to denote normal seasonality in the two parameters. Mean values for the 1966–1996 period (0 cm in [A] and 17.2°C in [B]) are marked with thin lines.

Scripps Institution of Oceanography data servers (<http://www.opsd.nos.noaa.gov> and <ftp://nemo.ucsd.edu/pub/shore>). Mean monthly water temperatures were calculated by averaging hourly values. Months in which fish were sampled were divided into the categories of El Niño, “normal,” or La Niña, defined by extended positive or negative sea level and temperature anomalies or lack thereof (Fig. 1).

Patterns in species composition—To assess changes in species composition of the San Diego rocky intertidal zone during ENSO conditions, the total number of individuals of each fish species collected during each sampling period was tallied. Data from the two sampling sites were analyzed separately but were combined across all tidepools at a site. A modification of the Simpson’s species diversity index was calculated using the equation described by Rosenzweig (1995):

$$-\ln(SI) = \sum [(n^2 - n)/(N^2 - N)],$$

where n is the number of individuals present of a particular species and N is the total number of individuals present. This index was chosen as a measure of species evenness because it incorporates information on species’ proportional abundances and focuses on dominance patterns rather than richness (Magurran 1988); richness in the present system is not highly variable. Species evenness ($-\ln(SI)$), as well as abundance of the six most common fish species, were compared among El Niño, normal, and La Niña months using analyses of variance (ANOVAs). Normality of the data was deter-

mined using Lilliefors test of residuals. When Lilliefors $P > 0.05$, abundance values were log-transformed to meet the ANOVA assumption of normality.

Habitat use—Surface area, depth, and intertidal height of all study tidepools were measured in fall 1996. Surface area was approximated as the product of length, the maximum distance measured in centimeters across the top of the pool, and width, the distance perpendicular to the length axis at the midpoint of the pool. Tidepool depth was approximated as the average of 10 haphazardly distributed depth measurements to the nearest 0.5 cm. With the exception of the three lowest pools at FP, these parameters were not remeasured over the course of the study. On the basis of calculated rates of tidepool erosion (Emery 1946), changes in depth or surface area during a 3-year period were most likely negligible and within measurement error of the methods used to measure these parameters.

The intertidal height value of each pool relative to MLLW was obtained in November 1996 (Davis 2000). Time to the nearest minute of each tidepool’s isolation point by the ebbing tide was noted, then Harbor MasterTM software was used to determine tidal height to the nearest 3 cm above MLLW at that time. Isolation point was defined as the time at which water ceased to enter (by wave, surge, or splash) or drain from the pool. Two days in November 1996, one calm and one relatively rough, were devoted to this exercise at each site. Intertidal heights determined for these different sea states differed only by as much as 6 cm, so averages were used when discrepancies occurred.

Seasonal and ENSO changes in the types of tidepools occupied by the four most common species, *C. analis*, *G. rhesodon*, *G. nigricans*, and *H. gilberti*, were evaluated separately for the two sites. Within a particular month, the average of each habitat parameter (intertidal height, surface area, and depth) was computed for all pools at a site containing individuals of a particular species. Monthly values were not calculated for sampling periods in which a species was found in fewer than four pools at a site.

To determine whether habitat use had a seasonal component, I regressed average intertidal height of each species against monthly sea level and average tidepool depth and surface area of each species against monthly water temperature. Because habitat use might be expected to lag the environmental signal, sea level and temperature were offset by -2 , -1 , and 0 months to explore the best and most consistent regression fit for all species. To determine climate effect on habitat use, I used ANOVAs to compare values of habitat parameters among El Niño, normal, and La Niña periods. Normality of the data was established using Lilliefors test ($P > 0.05$).

Results

Seasonal, El Niño, and La Niña environmental anomalies—Using sea level and water temperature anomalies measured in La Jolla, I identified seasonal environmental cycles and ENSO conditions. The mean seasonal range in sea level (1966–1996) measured in La Jolla was 16 cm, with values highest in September and lowest in April (Fig. 1). From

about April/May of 1997 to about April 1998, sea levels were higher than normal. The largest anomaly during this El Niño period was measured in November of 1997, when sea level was 18.3 cm higher than the November average from 1966–1996. This El Niño sea level anomaly (18.3 cm) was larger than the normal seasonal range (16 cm).

The mean (1966–1996) seasonal water temperature range measured in La Jolla was 6.6°C, with values highest in August and lowest in January. Water temperature at the Scripps Pier was anomalously high from about May 1997 to May 1998, staying above 20°C for six consecutive months. Monthly temperature usually averages above 20°C for only three summer months. The greatest El Niño temperature anomaly occurred in January of 1998, when water temperature was 3.3°C higher than the long-term January mean. This value is half that of the normal seasonal range during the 1966 to 1996 period (6.6°C).

The El Niño sea level and water temperature signals differed in two major ways. First, the El Niño sea level anomaly was greater than the seasonal sea level range, whereas the El Niño water temperature anomaly was less than the seasonal water temperature range. Second, the El Niño had its greatest influence on sea level during the fall, the season of highest sea level, and as a result intensified seasonal sea level differences. The El Niño had its greatest influence on water temperature during the winter, the season of lowest water temperature, and therefore served to dampen seasonal water temperature differences.

The La Niña period following the 1997–1998 El Niño did not produce signals as strong as those of the El Niño. Sea level was lower than normal from November 1998 to April 1999 and again from August 1999 through January 2000, with a maximum deviation from normal conditions (1966 to 1996) of 10 cm. Water temperature was lower than normal from about August 1998 through January 2000, but by an average of less than 1°C.

In this study, the El Niño period has been defined as June 1997 through May 1998. Fish data collected in August 1997, November 1997, February 1998, and May 1998 were considered to fall within the El Niño period. Data collected from February to November 1999 were considered to fall within the La Niña period. Data collected during the first period of the study (November 1996 to May 1997), during the period between El Niño and La Niña (June 1998 to November 1998), and after La Niña (February and March 2000) were considered data from normal conditions.

Species composition—Fifteen fish species were found in the tidepools of FP and OB during the study period. Six species were common, found at each site in six or more sampling months, including *C. analis*, (woolly sculpin), juvenile *G. nigricans* (opaleye), *G. rhessodon* (California clingfish), *H. gilberti* (notchbrow blenny), *Gibbonsia elegans* (spotted kelpfish), and *Paraclinus integripinnis* (reef finspot). The other nine species were represented by fewer than 25 individuals throughout the study period and were collected in four or fewer sampling months. These included *Atherinops affinis*, (topsmelt), juvenile *Hermosilla azurea* (zebraperch), juvenile *Paralabrax clathratus* (kelp bass), *Hydroblennius jenkinsi* (mussel blenny), *G. metzi* (striped

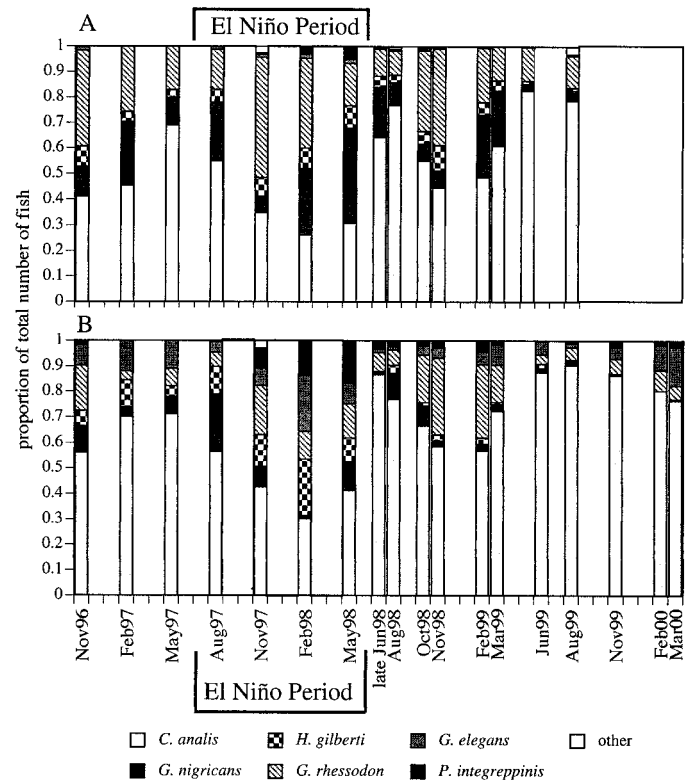


Fig. 2. Proportional species composition of intertidal fishes at (A) FP from November 1996 to August 1999 and (B) OB from November 1996 to March 2000.

kelpfish), juvenile *Hypsypops rubicundus* (garibaldi), juvenile *Micrometris minimus* (dwarf surfperch), *Scorpaenichthys marmoratus* (cabezon), and juvenile *Sebastes rastrelliger* (grass rockfish).

Before the El Niño event, *C. analis* was the assemblage dominant, constituting from about 40–70% of the total number of fishes present at the two sites (Fig. 2). At FP, *G. rhessodon* and *G. nigricans* were the second and third most abundant species, making up about 20–40% and 10–25% of the total assemblage, respectively (Fig. 2A). At OB, that component of the assemblage not attributable to *C. analis* was more evenly divided among *G. rhessodon*, *G. nigricans*, *H. gilberti*, and *G. elegans* (Fig. 2B).

Several changes in the species assemblage occurred during the 1997–1998 El Niño. The number of individuals of the usually dominant *C. analis* was significantly different among El Niño, normal, and La Niña months, lower during the El Niño period than during the other two periods (Table 1, Fig. 3). The decrease in numbers of *C. analis* was mainly attributable to low numbers of larvae recruiting from the plankton to FP (Fig. 4) and OB. Recruitment occurred during the non-El Niño winter and spring periods of 1997 and 1999; however, during the winter and spring of 1998 (El Niño), recruitment was low. In 1998, recruitment began in June, indicated by the recovery of the populations at this time (Fig. 3), after the environmental influence of the El Niño had dissipated but before the La Niña phase began.

P. integripinnis, absent or rare before the El Niño, in-

Table 1. Comparison of species evenness and tidepool fish abundance among climate periods at False Point (FP) and Ocean Beach (OB). Mean values of $-\ln$ (Simpson's index) and mean abundance of each species (mean number individuals per site) are presented for El Niño months (August 1997 to May 1998; $n=4$), normal months (November 1996 to May 1997, June 1998 to November 1998, February 2000 to March 2000; $n=7$ for FP and 9 for OB), and La Niña months (February 1999 to November 1999; $n=4$ for FP and 5 for OB). ANOVAs were used to compare evenness and abundance among El Niño, normal, and La Niña periods ($df=14$ for FP, $df=17$ for OB). When ANOVA model P values were < 0.10 , Fisher's least significant difference test was used to compare pairs of climate periods. Significant post hoc comparison results ($P<0.05$) are listed below (EN = El Niño, norm = normal, LN = La Niña).

Variable	El Niño mean	Normal mean	La Niña mean	F statistic	P value	Post hoc comparisons
Species evenness						
FP	1.17	0.88	0.68	3.97	0.047	EN>LN
OB	1.34	0.62	0.47	15.77	<0.001	EN>norm, EN>LN
<i>C. analis</i>						
FP	106.8	223.7	449.3	3.62	0.059	LN>EN
OB	61.8	142.1	150.0	4.43	0.031	LN>EN
<i>P. integrripinnis</i>						
FP	3.8	1.0	0.0	3.51	0.063	EN>LN
OB	10.0	3.8	3.4	3.90	0.043	EN>norm, EN>LN
<i>H. gilberti</i>						
FP	18.3	18.7	13.0	1.15	0.350	
OB	17.0	5.0	2.2	18.72	<0.001	EN>norm, EN>LN
<i>G. nigricans</i>						
FP	55.3	44.3	55.5	0.18	0.841	
OB	17.5	9.9	3.4	0.88	0.436	
<i>G. rhessodon</i>						
FP	73.5	84.6	87.0	0.13	0.884	
OB	16.5	26.4	21.8	0.10	0.906	
<i>G. elegans</i>						
FP	3.3	1.6	2.0	1.65	0.232	
OB	11.0	11.7	10.0	0.13	0.877	

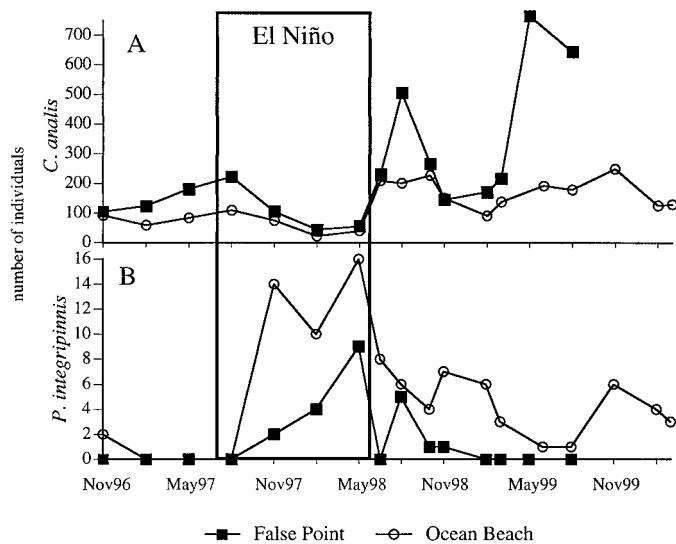


Fig. 3. Abundance of *C. analis* and *P. integrripinnis* from November 1996 to March 2000 in all 55 pools at FP and 50 pools at OB. The boundaries of the El Niño period, estimated from sea level and sea surface temperature anomalies, are marked with vertical lines. At both sites, number of *C. analis* individuals was lower and number of *P. integrripinnis* individuals was higher during the 1997–1998 El Niño (see Table 1).

creased in abundance at both sites during the El Niño period and declined as the El Niño waned in June 1998 (Table 1; Fig. 3). This species did not appear at the onset of the El Niño, but first increased in November 1997. *H. gilberti* was more abundant during El Niño than during La Niña or normal months at OB, but not at FP (Table 1; Fig. 5). Abundance of *G. nigricans*, *G. rhessodon*, and *G. elegans* did not change at either site during El Niño or La Niña (Table 1; Fig. 5).

Mainly as a result of the decrease in abundance of the assemblage dominant, *C. analis*, species evenness increased significantly during the El Niño. Because the other major species did not also decrease in number, *C. analis*'s decrease resulted in the decline of its relative contribution to the assemblage. Contribution by this species dropped to lows of 26% at FP and 30% at OB during February 1998, one of the most anomalously warm months of the El Niño (Fig. 2). This drop, along with the increase in abundance of the rare *P. integrripinnis*, led to higher species evenness during El Niño months than during normal or La Niña months at both sites (Table 1).

Habitat use—The four most common species, *C. analis*, *G. nigricans*, *G. rhessodon*, and *H. gilberti*, displayed seasonal patterns of tidepool use with respect to intertidal

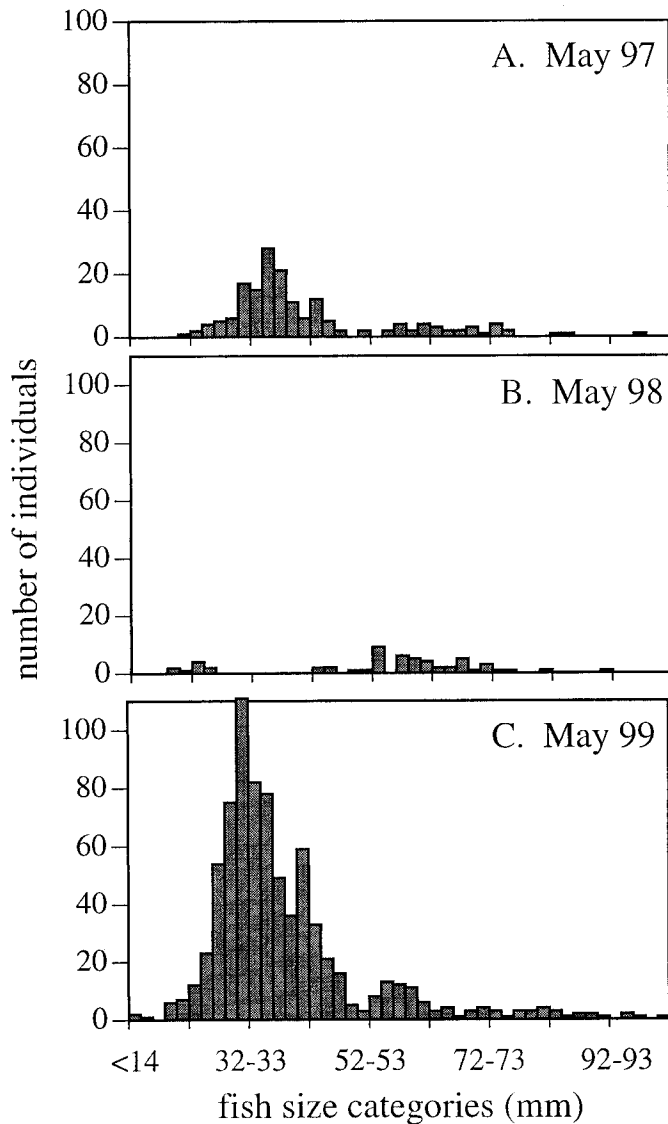


Fig. 4. Size–frequency histograms portraying population structure of *C. analis* at FP in (A) May 1997, before El Niño; (B) May 1998, during El Niño; and (C) May 1999, during La Niña. Histograms are constructed with 2-mm-size bins. In the histograms of May of 1997 and 1999, the smallest-sized cohorts are the result of recruitment from late March to April. The next largest cohorts are the survivors of January–February recruitment events. In 1998, no winter recruitment was measured, and few recruits appeared by May.

height. All four species moved vertically in the intertidal zone within at least one of the study sites. When sea level reached its seasonal maximum in the fall, the average intertidal height (relative to the MLLW mark of November 1996) of pools occupied by members of these species increased (Fig. 6). Of offsets in mean sea level by -2 , -1 , and 0 months, an offset in sea level by -1 month provided the best regression fit for pool height of all species, suggesting that the fishes' tidal height response lagged sea level changes by 1 ± 0.5 months. Relationships were significant for *C. analis* and *G. rhessodon* at FP, *G. nigricans* at both sites,

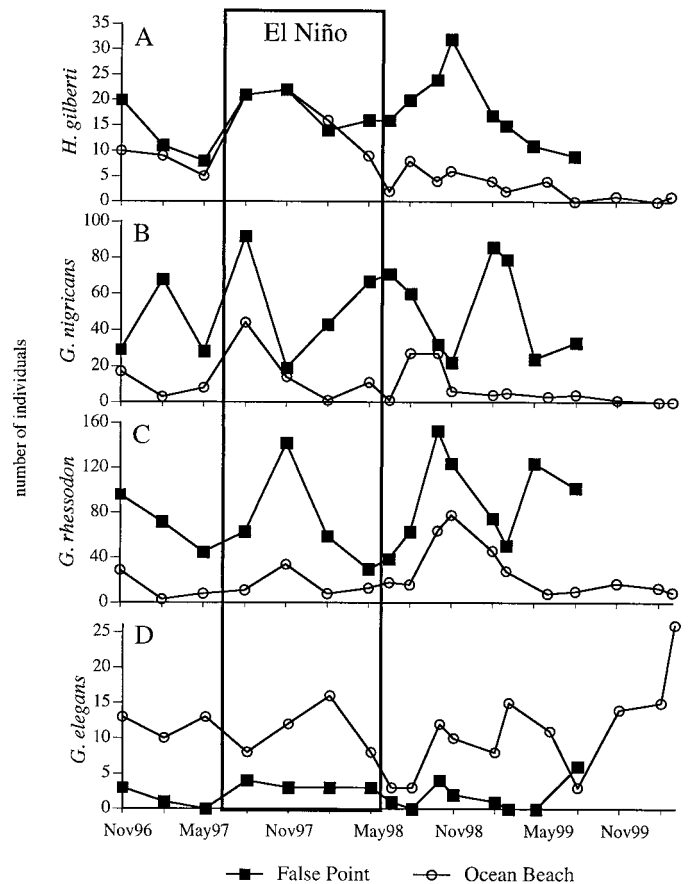


Fig. 5. Abundance of *H. gilberti*, *G. elegans*, *G. nigricans*, and *G. rhessodon* from November 1996 to March 2000 in 55 pools at FP and 50 pools at OB. Number of *H. gilberti* individuals increased at OB during the 1997–1998 El Niño. None of the other species changed significantly in abundance during El Niño (see Table 1).

and *H. gilberti* at OB (Table 2). Low abundance of *G. rhessodon* at OB and *H. gilberti* at both sites may explain the lack of consistency between sites for these species.

The magnitude of seasonal vertical shifts by the fishes generally matched the magnitude of seasonal sea level anomalies during non-El Niño periods, but not sea level anomalies of the 1997–1998 El Niño. For example, fall 1998, a period of normal sea level conditions, brought an increase in sea level of 17 cm from the previous May, an increase matched by intertidal height shifts of all fish populations except *C. analis*. Average intertidal height of *G. nigricans*, *H. gilberti*, *G. rhessodon* at FP, and *C. analis* increased by 15–20, 15–17, 12, and 4–8 cm, respectively, from May to November 1998 (Fig. 6). In contrast, sea level during the El Niño fall of 1997 rose 30 cm from the previous May, almost double the magnitude of normal years (Fig. 1). However, *G. nigricans* at FP, *H. gilberti*, *G. rhessodon* at FP, and *C. analis* rose only 18, 13–18, 16, and 12–15 cm, respectively. Only *G. nigricans* at OB matched the 30-cm magnitude of sea level rise, increasing in mean height by 40 cm. However, the maximum intertidal height occupied by this species during the 1997 El Niño fall was similar to that

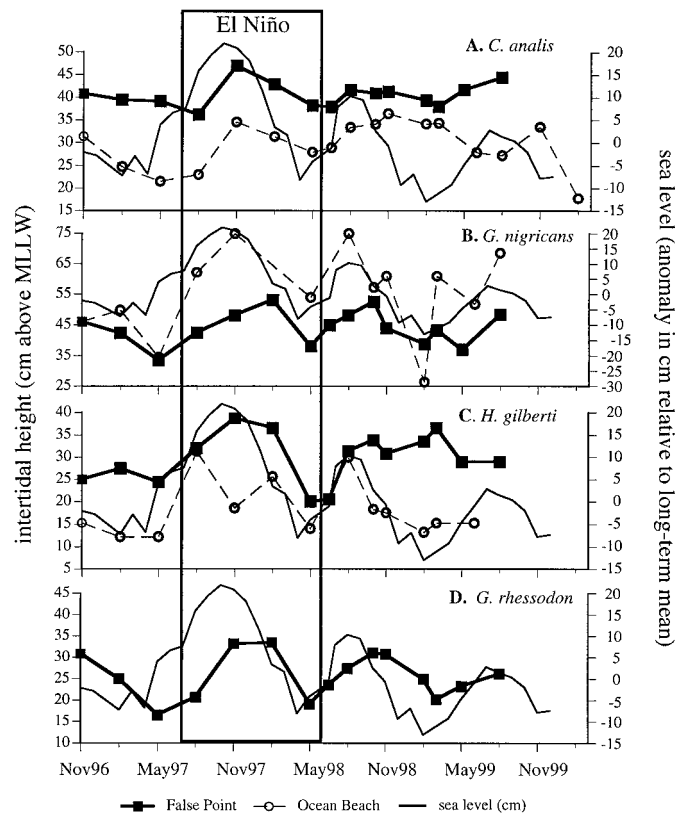


Fig. 6. Mean intertidal height of pools containing fishes (relative to intertidal heights measured in November 1996) and mean monthly sea level anomaly from November 1996 to March 2000. Both sea level and intertidal height of fishes fluctuated seasonally, with fish height values lagging sea level changes by approximately 1 month (see Table 2). These relationships were significant for *C. analis* at FP, *G. nigricans* at FP and OB, *G. rhessodon* at FP, and *H. gilberti* at OB. A monthly intertidal height value for a species was not included in the analyses if individuals of the species were present in fewer than four pools.

Table 2. Linear regressions between intertidal height of fishes and sea level (lagged by 1 month). Sea level values were calculated as deviations from the long-term mean (1996 to 1999). Intertidal height values for each species during each sampling period were calculated by averaging the intertidal height of all pools containing individuals of the species in question. Intertidal height values were not included in the analysis for sampling periods in which a species was found in fewer than three pools at a site.

Species	Site	Slope	<i>n</i>	<i>r</i> ²	<i>P</i>
<i>C. analis</i>	False Point	+0.17	15	0.36	0.018
	Ocean Beach	+0.19	17	0.10	0.207
<i>G. nigricans</i>	False Point	+0.44	15	0.55	0.002
	Ocean Beach	+0.88	12	0.37	0.036
<i>H. gilberti</i>	False Point	+0.26	13	0.19	0.106
	Ocean Beach	+0.38	11	0.35	0.033
<i>G. rhessodon</i>	False Point	+0.42	15	0.57	0.001
	Ocean Beach	-0.09	17	0.05	0.411

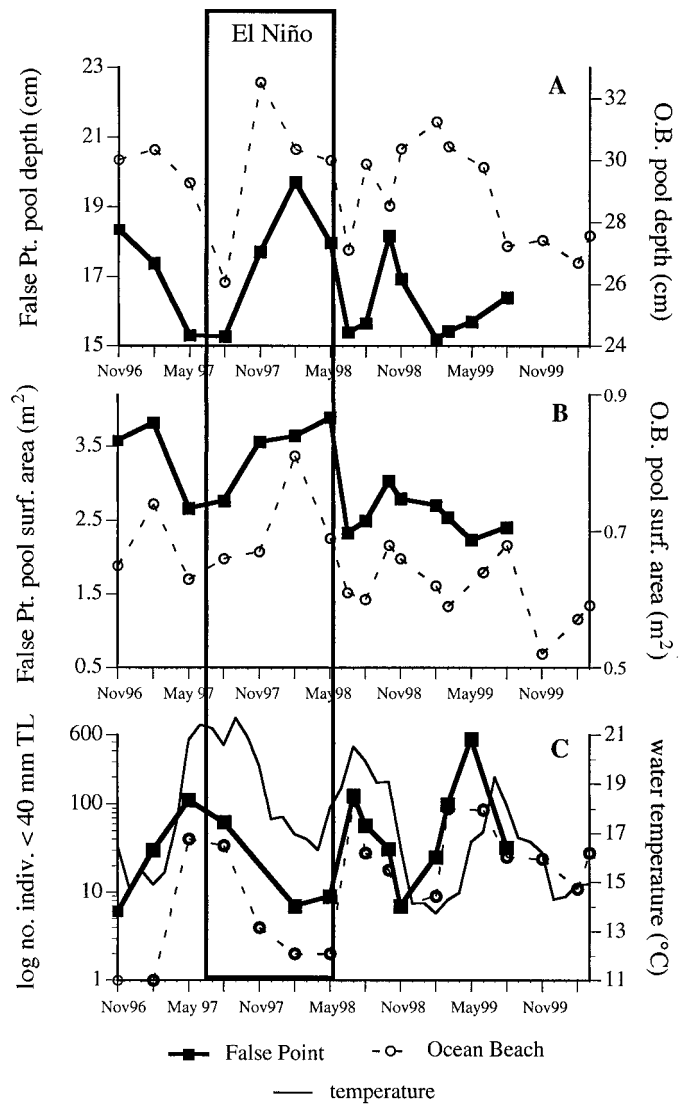


Fig. 7. Seasonal fluctuations of depth and surface area of pools occupied by *C. analis* from November 1996 to March 2000 relative to temperature and the number of small individuals. (A) Mean tide-pool depth and (B) mean pool surface area at FP and OB. (C) Number of individuals <40 mm TL at FP and OB, and water temperature at the Scripps Institution of Oceanography Pier. Tidepool depth and surface area were not correlated with temperature (except depth at OB), but were correlated with the number of small individuals present in the population (see text).

occupied during fall 1998 (Fig. 6). *G. rhessodon* at OB and *G. elegans* were not abundant enough for similar analysis.

Use of pool depth and surface area by one species, *C. analis*, had seasonal components (Fig. 7). Average depth and surface area of pools occupied by this species tended to be lowest during spring and summer. Although pool depth and surface area were not correlated with Scripps Pier water temperature ($P > 0.05$, with the exception of depth at OB: $n = 18$, $r^2 = 0.24$, $P = 0.035$), both parameters were positively correlated with the number of small individuals (<40 mm TL) present in the populations (Fig. 7). Average pool surface area was negatively correlated with the log-transformed

Table 3. Effects of climate period (El Niño, normal, and La Niña) on tidepool intertidal height, depth, and surface area of fishes. *F* statistics, *P* values, and *r*² are presented for ANOVAs for each species at False Point (FP) and Ocean Beach (OB); *df* = 14 for all species at FP, 17 for *C. analis* and *G. rhessodon* at OB, and 13 for *G. nigricans* and *H. gilberti* at OB.

Variable	False Point			Ocean Beach		
	<i>F</i>	<i>P</i>	<i>r</i> ²	<i>F</i>	<i>P</i>	<i>r</i> ²
<i>C. analis</i>						
Intertidal height	0.14	0.871	0.02	0.70	0.513	0.09
Depth	2.25	0.148	0.27	0.39	0.739	0.04
Surface area	4.39	0.037	0.42	3.31	0.065	0.31
<i>G. nigricans</i>						
Intertidal height	0.41	0.674	0.06	1.13	0.370	0.20
Depth	5.31	0.022	0.47	0.07	0.932	0.01
Surface area	2.90	0.094	0.33	0.68	0.530	0.12
<i>H. gilberti</i>						
Intertidal height	1.08	0.370	0.15	1.44	0.283	0.22
Depth	13.34	0.001	0.69	10.86	0.003	0.69
Surface area	4.16	0.043	0.41	7.62	0.010	0.60
<i>G. rhessodon</i>						
Intertidal height	0.01	0.990	<0.01	3.40	0.061	0.31
Depth	3.86	0.051	0.39	0.02	0.981	0.01
Surface area	0.31	0.736	0.05	0.37	0.700	0.05

number of small fish (FP: *n* = 15, *r*² = 0.52, *P* = 0.002; OB: *n* = 18, *r*² = 0.33, *P* = 0.013), as was average tidepool depth (FP: *n* = 15, *r*² = 0.17, *P* = 0.005; OB: *n* = 18, *r*² = 0.24, *P* = 0.061). *C. analis* exhibits ontogenetic habitat shifts (Davis 2000); therefore, seasonal trends in habitat use may be driven by the seasonal influx of smaller individuals. Unlike *C. analis*, use of pool depth and surface area by *G. nigricans*, *H. gilberti*, and *G. rhessodon* did not have a seasonal pattern. Neither average depth nor surface area for these species was correlated with water temperature (regression analysis: *P* ≫ 0.05).

Despite El Niño-induced changes in water temperature, air temperature, and sea level that might be expected to alter habitat use and interfere with seasonal relationships to the tidepool parameters, the El Niño did not disrupt most of the fishes' use of tidepool intertidal height, depth, or surface area. Average intertidal height was not different for any species when compared among El Niño, normal, and La Niña months (Table 3). Use of pool size was different between climate periods only for *C. analis*, which occupied larger pools during the El Niño at both sites, and for *H. gilberti*, which occupied larger and deeper pools during the La Niña (Table 3, Fig. 8). *C. analis*'s occupation of larger tidepools during the El Niño was not simply due to the lack of young fish, which are found in smaller pools (Davis in press), and presence of mainly large fish during the El Niño. Average size of tidepools occupied by large *C. analis* (≥40 mm TL) was significantly greater during the El Niño as well (*t*-tests, FP: *t*₁₄ = 2.91, *P* = 0.012; OB: *t*₁₇ = 2.48, *P* = 0.025), suggesting that individuals had changed pools.

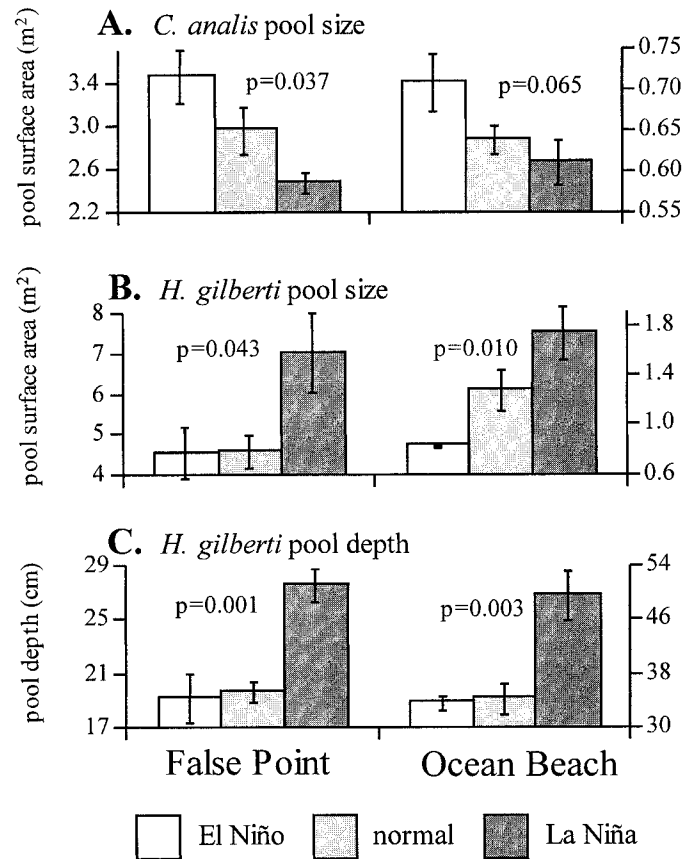


Fig. 8. Habitat differences among El Niño, normal, and La Niña periods. (A) Tidepool surface area of *C. analis*, (B) tidepool surface area of *H. gilberti*, and (C) tidepool depth of *H. gilberti*.

Discussion

Several aspects of the San Diego rocky intertidal fish assemblage changed with season and during the 1997–1998 El Niño event, and several aspects did not change on those scales. Use of some habitat parameters was observed to have a seasonal component, suggesting that environmental fluctuations are directly or indirectly important to habitat use. However, with the exception of *C. analis*'s and *H. gilberti*'s use of tidepool size, environmental changes associated with the El Niño event did not affect species' habitat patterns. Although habitat use was not greatly altered during the El Niño, changes in assemblage structure were observed during this period. Because the study spanned only one El Niño and therefore no replication was possible, these changes cannot be directly attributed to El Niño-induced environmental forces. However, the changes are consistent with those observed and predicted by studies of other El Niño events (Arntz and Tarazona 1990). Assemblage changes in the present study were not long-ranging; the assemblage returned to pre-El Niño conditions almost immediately after the El Niño period.

Species assemblage—Two main changes occurred within the rocky intertidal fish assemblage during the 1997–1998 El Niño: a decrease in abundance of *C. analis*, the assem-

blage dominant, and an increase in *P. Integripinnis* abundance. The latter attained levels only approaching those of *G. elegans*, one of the least common assemblage members, and therefore most likely had little effect on the community. Results are consistent with those of two California intertidal algal studies, in that some species changed in abundance during an El Niño, but the majority did not (Gunnill 1985; Murray and Horn 1989).

It has not been established which of the various El Niño signals contributed to the changes observed in intertidal fish assemblage. Other works have attributed El Niño assemblage changes to increases in water temperature, which can lead directly to mortality of certain dominant species and the release of resources to other species, can lead indirectly to mortality by allowing warm-tolerant species to better compete, or can prompt certain dominant species to migrate poleward, freeing resources for use by other species (Arntz and Tarazona 1990; Urban 1994; Palomarez-Garcia and Gomez-Gutierrez 1996). As in the present study, species evenness in Peruvian rocky intertidal systems increased during the 1982–1983 El Niño because of the mortality of dominant mytilid species and the release of space to less common species (Arntz and Tarazona 1990). In nonintertidal assemblages as well, El Niño-induced temperature change has been partially implicated in the replacement of dominants by warmer-water species, including Peruvian nearshore fishes (Santander and Zuzunaga 1984; Arntz and Tarazona 1990), copepods in a Mexican bay (Palomarez-Garcia and Gomez-Gutierrez 1996), soft-sediment bivalves (Arntz et al. 1987; Urban 1994), and zooplankton off Oregon (Peterson 1999).

In the present study, species composition shifts were consistent with temperature-regime affinities and ancestry. *C. analis*, which declined in abundance during the El Niño period, is a member of the cold-temperate Cottidae (Graham 1970). San Diego (32.8°N) falls within the southern third of the species' latitudinal range (from 28.5°N to 40°N), and its family's center of distribution is in the north Pacific (Graham 1970; Miller and Lea 1972). Ancestral temperature affinities may explain the maintenance of extremely high abundance during 1999, a La Niña period. However, post-El Niño population size began to recover during normal conditions, before the La Niña phase began.

The other five common species all belong to warm-temperate or tropical to warm-temperate families. *P. integripinnis*, which increased in abundance at both sites during the El Niño, is a member of the tropical to warm-temperate Labrisomidae (Stepien et al. 1993). *H. gilberti*, which increased at OB during El Niño and declined during La Niña, is a member of the tropical to warm-temperate Blenniidae (Stepien et al. 1993). *G. nigricans*, *G. elegans*, and *G. rhessodon*, unchanged in abundance at both sites, belong to the warm-temperate Girellidae, warm-temperate Clinidae, and tropical to warm-temperate Gobiesocidae, respectively (Briggs 1955; Johnson and Fritzsche 1989; Stepien et al. 1993; Nelson 1994).

The decrease in *C. analis* population size during the El Niño in the present study (Fig. 3), due mainly to a decrease in the number of new recruits (Fig. 2), may have been caused by events during the planktonic larval phase. Females carried eggs throughout the El Niño period (Davis, unpubl.).

Unless spawning behavior was affected, the instigation of the population decrease occurred between the egg phase and recruitment. Coastal waters were warmer, possibly serving to increase metabolic rates, food requirements, and therefore starvation potential of *C. analis* larvae. Recruitment also may have been diminished because larvae were not transported to intertidal settling areas. Although recruitment of some nearshore species is enhanced during El Niño events because of relaxation of upwelling, which normally induces offshore advection of surface water and larvae (Brodeur et al. 1985; Ebert et al. 1994; Connolly and Roughgarden 1999), El Niño conditions can negatively affect recruitment of other species (Dayton and Tegner 1984; Gunnill 1985; Milligan et al. 1999). The recruitment mechanism of *C. analis* larvae, which are epibenthic (Barnett et al. 1989; Feeney 1992), may be the onshore transport of bottom waters from features like internal tidal bores, similar to the mechanism for barnacle larvae (Pineda 1991, 1994). During El Niño periods, deepening of the thermocline (McGowan 1985; Philander 1990) may prevent bores, which depend on stratification (Pineda 1994), from reaching the shore.

The mechanisms causing *P. integripinnis* to increase in abundance also may be related to temperature or transport. Temperature changes may have induced migration from lower latitude regions, as San Diego (32.8°N) is near the northernmost extent of its along-shore distribution (Almejas Bay [24.5°N] to Santa Cruz Island [34°N], Miller and Lea 1972). Fish may have also colonized the study pools from subtidal or low intertidal areas below the study area, induced by the sea level increase associated with El Niño. Finally, transport of new recruits to the study area from Baja California may have increased. During the El Niño event, the northward California Countercurrent increased in velocity, transporting more water (Norton et al. 1985; Lynn et al. 1998), and perhaps *P. integripinnis* larvae, from the south.

Assemblage shifts occurring during El Niño did not persist after the El Niño period. Instead, the assemblage returned quickly to pre-El Niño conditions. Arntz and Tarazona (1990) describe low-latitude South American intertidal and nearshore communities that were severely perturbed by the 1982–1983 El Niño and had not returned to normal several years after the El Niño. Three explanations could account for the lack of similar ENSO-induced severe changes in north Pacific rocky intertidal communities. First, the effects of El Niño (and La Niña) may be diminished at these latitudes (Paine 1986). Second, natural variability may mask or make more difficult measurements of ENSO-induced changes in these systems (Paine 1986; Murray and Horn 1989). Third, El Niño environmental signals may counterbalance each other in rocky intertidal pools. For example, the rise in sea level, which increases submergence time of tidepools, may counter the temperature effects of warmer El Niño air and water. All three mechanisms may dampen rocky intertidal community change in higher latitudes.

Habitat use—Motile intertidal organisms, unlike their sessile counterparts, are able to alter their habitats in response to seasonal and climatic changes. Seasonal changes in intertidal height were probably the result of migration by individuals, and not the result of seasonal input of recruits with

different intertidal height preferences. Although some species show ontogenetic differences in intertidal microhabitat (Nakamura 1976; Yoshiyama 1981; Prochazka and Griffiths 1992; Davis 2000), timing prevents the acceptance of recruitment as an explanation of seasonal vertical shifts. Heaviest recruitment of *C. analis* and *G. nigricans* juveniles, which tend to settle in pools higher than those occupied by older fish, occurs in late spring, when sea level is low, and in midsummer, when sea level is close to its annual mean, respectively (Davis 2000). However, average intertidal height of both species was greatest in the fall when sea level is highest, not during recruitment season.

Few intertidal studies have examined vertical habitat changes and their potential relationship to ENSO-induced or seasonal changes in sea level (Zander et al. 1999). Paine (1986) measured the upper limits of one species of algae and two species of mussels, and concluded that none responded to changes in sea level associated with El Niño. Two studies have reported seasonal vertical habitat shifts for intertidal fishes. Along the New England coast, *Pholis gunnellus* abandoned the intertidal zone during winter, possibly to avoid freezing temperatures (Sawyer 1967). In central California, *Xerperes fucorum* was found highest in the intertidal zone in summer and lowest in spring, possibly due to springtime downshore spawning migration (Burgess 1978). Neither temperature nor spawning migration explains shifts observed in the present system, as winter temperature is not extreme and spawning occurs from fall through spring (Davis unpubl.). Instead, individuals may migrate vertically on a seasonal cycle, matching sea level changes, to keep constant the amount of time spent isolated from the subtidal zone and its predators. Shifts in intertidal height may not be in direct response to sea level changes, but may be an innate seasonal response. During the El Niño fall of 1997, when the sea level anomaly was greatest, none of the species occurred higher in the intertidal zone than during the previous or subsequent fall.

Unlike seasonal intertidal height shifts by fishes, seasonal changes in tidepool depth and surface area for *C. analis* were apparently not directly related to adult selection for specific environmental conditions, but to the number of small *C. analis* present in the population during each sampling month. Small individuals are often more abundant in smaller, shallower tidepools than larger individuals (Richkus 1981; Davis 2000), thereby influencing the average depth and surface area values during months when they are prevalent.

The shift to larger tidepools during the El Niño event by *C. analis* cannot be explained by a lack of small fish during this period; large fish exhibited an increase in average pool size when analyzed alone. Although individuals may have moved to larger tidepools during the warm El Niño period to combat the temperature increase, they would have been expected to move to deeper tidepools as well, since tidepool depth is more important in preventing daytime rises in tidepool temperature than is surface area (Davis unpubl.). Alternatively, differences in pool size for both *C. analis* and *H. gilberti* among climate periods may simply have been a function of tidepool occupancy probability. During the El Niño, there were fewer *C. analis* and fewer pools contained *C. analis* individuals. During most of the La Niña period,

especially at OB, there were fewer *H. gilberti*. Because average pool surface area was calculated on the basis of presence or absence of fish, the chance that a pool lost all of its fish and was therefore excluded from the calculation was greater for a smaller pool, which had fewer fish initially, than a larger pool. Finally, it is possible that when fewer fish are present, a larger proportion of them may be found in optimal habitats, which may be larger pools.

Conclusions—Expectations of answers to the four questions addressed in this study were partially met. Family affinities of the study species ranged from cold-temperate (*C. analis*) to warm-temperate (*G. nigricans* and *G. elegans*) to tropical/warm-temperate (*P. integripinnis*, *H. gilberti*, and *G. rhessodon*). During the El Niño, the cold-temperate family member decreased in abundance. Neither of the two warm-temperate family members changed in abundance. Of the tropical/warm-temperate family members, one increased at both sites, one increased at only one site, and one did not change. The changes that occurred were consistent with expectations, but not all predicted changes occurred.

Expectations of seasonality and ENSO-scale changes in fish habitat use were also partially met. Seasonal patterns in all four common species' use of intertidal height were identified, and seasonal use of pool depth and surface area was observed for *C. analis*. However, few habitat changes occurred as a result of the El Niño event. Upper intertidal fishes did not move lower and lower intertidal fishes did not move higher in the intertidal zone as predicted. The prediction that fishes would move to deeper, larger tidepools during El Niño to avoid warming was supported only by *C. analis*, whose distribution shifted to larger tidepools.

The greatest influence of ENSO events on intertidal organisms may not take place in the intertidal zone at all, but may be concentrated in the relatively short offshore, planktonic larval stage. Such offshore disturbances, whether affecting larval survivorship or larval transport, result in differences in recruitment, as was observed for *C. analis*. Events affecting larval stages outside of the intertidal realm have potential to affect species dominance patterns and structure of the entire intertidal assemblage. The use of rocky intertidal organisms to study seasonal- and ENSO-scale climate variation may enhance understanding of climate-related changes in various oceanographic realms.

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Received: 26 November 1999

Accepted: 12 April 2000

Amended: 3 May 2000