

## Increased recruitment of northeast Pacific barnacles during the 1997 El Niño

**Abstract**—Recruitment of intertidal barnacles was markedly higher in May–September 1997, just after the apparent onset of El Niño conditions in the waters off California, than over the same period during the previous year. This increase was geographically broad, spanning five degrees of latitude, and was unusually large, relative to interannual differences in barnacle recruitment previously documented for this region. Increased onshore transport associated with El Niño events probably caused high recruitment in 1997. This explanation accords with the findings of previous, smaller scale studies in central and northern California and indicates that oceanographic transport anomalies associated with El Niño can strongly affect benthic communities in the northeast Pacific.

The catastrophic effects of the El Niño–Southern Oscillation on the productivity of marine ecosystems in South America are well known (Cushing 1971; Barber et al. 1985). Although El Niño events are largely tropical, they have also been linked to substantial changes in temperature, salinity, and circulation patterns in the California Current System of the northeast Pacific (Enfield and Allen 1980; Chelton and Davis 1982; Simpson 1983, 1984; Emery and Hamilton 1985; Huyer and Smith 1985; Norton et al. 1985; Simpson 1992; Jacobs et al. 1994; Lynn et al. 1995; Ramp et al. 1997; Liu et al. 1998). These large and widespread changes affect planktonic communities at multiple trophic levels (Chelton et al. 1982; Graybill and Hodder 1985; Miller et al. 1985; Mysak 1986; Pearcy and Schoener 1987; Brodeur et al. 1992; Ainley et al. 1995). Because many animals that inhabit benthic communities have a planktonic larval phase, one might expect these changes in planktonic communities to affect recruitment rates to benthic populations. However, evidence for such effects is mixed. In some cases, recruitment is higher than normal (Paine 1986; Roughgarden et al. 1988; Ebert et al. 1994), but, in other cases, recruitment is below levels seen in prior or subsequent years (Tegner and Dayton 1987; Ebert et al. 1994; Shkedy and Roughgarden 1997).

If large scale environmental changes induced by El Niño cause these changes in recruitment rates, as is often proposed (e.g., Paine 1986; Tegner and Dayton 1987; Roughgarden et al. 1988; Ebert et al. 1994), then El Niño events should have geographically broad effects on recruitment. However, most of these studies were confined to one or a few sites in close proximity to one another, so it is difficult to verify whether the observed changes in recruitment were due to El Niño-related regional environmental changes or to changes in more local factors. The exception, a recruitment study at several sites in northern California and the Southern California Bight, did not find a significant change in recruitment across sites in either region (Ebert et al. 1994). Thus, while large changes in planktonic communities occur during El Niño years, evidence for effects on recruitment to benthic populations at the regional scale is lacking.

From 3 May 1996–18 September 1997, we monitored re-

ruitment of the intertidal barnacles *Balanus glandula*, *Chthamalus dalli*, and *Chthamalus fissus* at nine sites spanning approximately five degrees of latitude in central and northern California. These sites extended from Cape Mendocino (40°24'N) to San Simeon (35°35'N) (Fig. 1). Serendipitously, this period included the onset of warm sea surface temperatures, anomalously weak upwelling, and a strengthening of the Aleutian low-pressure system in May 1997, presumably associated with the 1997–1998 El Niño (Liu et al. 1998; CoastWatch, West Coast Regional Node, National Marine Fisheries Service, La Jolla, California; <http://cwatchwc.ucsd.edu/cwatch.html>). To investigate a possible effect of El Niño on intertidal barnacle populations in the northeast Pacific, we compared recruitment during May–September 1997 with recruitment during the same months in 1996. Because the sites span a large region, they provide an opportunity to determine whether changes in recruitment during an El Niño year occur over a broad scale.

Recruitment was monitored by bolting five 50-cm<sup>2</sup> styrene plates covered with safety walk tape (3M) to the substrate at each site (Farrell et al. 1991). Plates were arranged haphazardly in the midintertidal (mussel) zone on the most wave-exposed rocks accessible. Approximately once a month, we collected plates and deployed fresh ones in the same locations. Sampling intervals varied in length from 26 to 31 d because collection dates were constrained to occur when there were daytime negative tides for several days in a row (allowing us to visit all sites during consecutive days). *C. fissus* is visually indistinguishable from *C. dalli*, so recruits were identified to the genus level only (cf. Farrell et al. 1991). From these data, we calculated mean monthly recruitment for May–September 1996 and May–September 1997. Recruitment data for August 1996 were lost due to equipment failure, so we calculated mean monthly recruitment rates for 1997 both with and without August 1997. All differences reported as significant in this paper were significant in both cases. Exact recruitment rates and *P*-values reported here correspond to the first case described above. Because the data did not meet parametric assumptions, we tested for significant differences between years with a non-parametric Friedman's test modified for within-site replication (Gibbons 1985).

Overall, recruitment increased highly significantly across the sampled region from 1996 to 1997 for *Balanus* ( $Q = 17.7$ ,  $P < 0.001$ ) and *Chthamalus* ( $Q = 18.3$ ,  $P < 0.001$ ). When sites were tested individually, recruitment was significantly higher at a majority of the sites for both *Balanus* and *Chthamalus* (Fig. 2). However, at Pescadero Beach and Sobranes Point, *Balanus* recruitment actually decreased in 1997 (Fig. 2), suggesting that El Niño studies restricted to one or a few sites will not necessarily detect a change in recruitment that occurs over a geographically broad scale, even when that change is highly significant.

Earlier studies indicate that the presence of a statistically

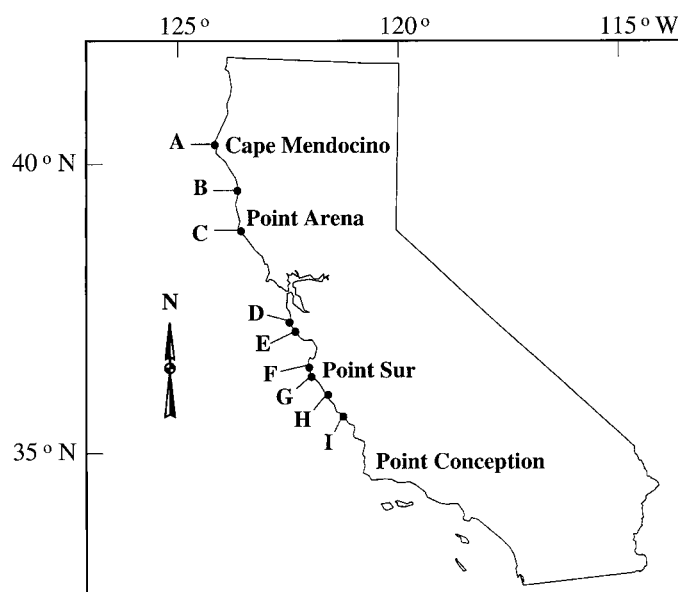


Fig. 1. Map of California showing locations of study sites. Major headlands are shown in bold. Sites are indicated by letters as follows: (A) Devil's Gate (40°24'N); (B) Westport (39°36'N); (C) Saunders' Reef (38°52'N); (D) Pescadero Beach (37°16'N); (E) Waddell Beach (37°06'N); (F) Soberanes Point (36°27'N); (G) Molera Point (36°17'N); (H) Mill Creek (35°58'N); (I) San Simeon (35°35'N).

significant interannual trend across geographically distant sites is uncommon for *Balanus* and *Chthamalus* in the study region. For example, in 1989 and 1990, 12 sites spanning approximately 200 km in central California showed no consistent trend between years: *Balanus* and *Chthamalus* showed higher recruitment in 1989 at half of the sites and higher recruitment in 1990 at the other half (Miller 1992). Further, standard errors of recruitment overlapped at all but one site, implying that interannual differences at individual sites were insignificant in most cases. Similarly, a 24-month study of four sites in the same region from 1993 to 1995 also found that half of the sites showed higher recruitment in the first year, while the other half showed higher recruitment in the second year (Grantham 1997).

In addition, the differences found here appear to be large, relative to interannual differences reported in the past for this region. Recruitment of *Balanus*, *Chthamalus*, or both taxa is more than five times greater in 1997 at two-thirds of the sites (six of nine) and more than one order of magnitude greater at nearly half (four of nine). Interannual differences of this magnitude have been recorded previously in this region, but they are unusual. At 11 of 12 sites studied in 1989–1990 and three of four sites studied in 1993–1995, recruitment of both *Balanus* and *Chthamalus* differed by less than a factor of three between years (Miller 1992; Grantham 1997). At a single site near the southern edge of Monterey Bay, *Balanus* recruitment from 1982 to 1986 differed among years by less than a factor of four, with only one exception (Roughgarden et al. 1988). Thus, the increases in recruitment observed in this study are unusual, both because they are large at several sites and because the overall trend is signif-

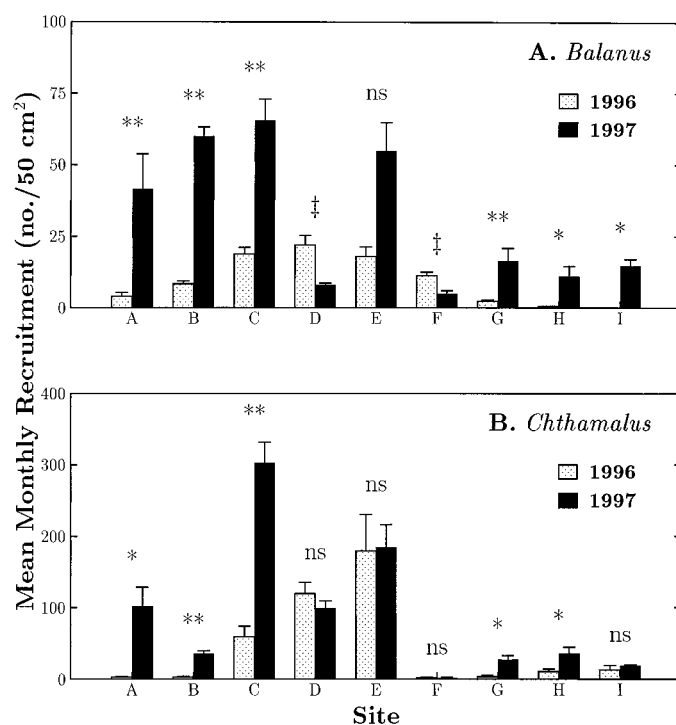


Fig. 2. Mean monthly recruitment in 1996 and 1997 for (A) *Balanus*, and (B) *Chthamalus*, with standard errors. Sites are arranged from north to south along the horizontal axis (see Fig. 1 for exact locations). One asterisk above the bars indicates significantly higher recruitment in 1997 within a particular site (5% level); two asterisks indicate significance at the 1% level; and a double dagger indicates significantly higher recruitment in 1996 (5% level). ns means that interannual differences were not significant for that particular site. Individual sites were tested for significant differences with a Wilcoxon signed-ranks test. Overall, recruitment was significantly higher in 1997 than in 1996 for both species (see text).

icant across a broad region, suggesting that large-scale environmental changes are responsible.

A likely cause of high recruitment in 1997 is increased onshore transport of larvae. Onshore flow, downwelling, and onshore displacement of the California Current have been documented during previous El Niño events and attributed to a teleconnection between El Niño and a strengthening of the Aleutian low-pressure system in the northeast Pacific (Chelton and Davis 1982; Simpson 1983, 1984; Emery and Hamilton 1985; Simpson 1992; Ramp et al. 1997). Preliminary evidence indicates that this occurred in 1997. Large onshore and poleward wind anomalies, characteristic of a strengthened Aleutian low, occurred during the summer of 1997 (Liu et al. 1998). According to weather summaries from the National Marine Fisheries Service (CoastWatch), this phenomenon was associated with periods of anomalously weak equatorward winds near the coast. Thus, winds were less upwelling favorable, on average, during 1997 than during 1996 (Table 1). A strengthened Aleutian low also tends to push the California Current inshore (Chelton and Davis 1982; Simpson 1983, 1984; Emery and Hamilton 1985; Simpson 1992). Because meroplankton accumulate at the inshore boundary of the California Current, this will dis-

Table 1. Mean upwelling indices for northern and central California in May–September of 1996 and 1997 for three buoy stations spanning the study region. Numbers in parentheses are standard errors.

| Year | Upwelling index*<br>(m <sup>3</sup> ·s <sup>-1</sup> per 100 m of coastline) |         |         |
|------|--|---------|---------|
|      | 42°N   | 39°N    | 36°N    |
| 1996 | 86 (6)   | 130 (8) | 112 (5) |
| 1997 | 51 (6)   | 100 (8) | 106 (5) |

\* Calculated from mean daily upwelling indices provided by the Pacific Fisheries Environmental Laboratories of the National Marine Fisheries Service.

place larvae toward shore and thereby promote recruitment (Farrell et al. 1991; Roughgarden et al. 1991; Wing et al. 1995; Alexander and Roughgarden 1996; Grantham 1997).

Larval distributions and recruitment during previous El Niño events accord with this explanation. Meroplankton have been found unusually close to the central California coast during El Niño events (Roughgarden et al. 1988; Yoklavich et al. 1996). Barnacle recruitment was high near Monterey during the spring of 1983 (Roughgarden et al. 1988), when an intensified Aleutian low produced anomalous onshore flow along the California coast (Simpson 1983, 1984; Emery and Hamilton 1985; Simpson 1992). Ebert et al. (1994) found increased recruitment of sea urchins at one site in northern California during early 1992, when a strengthened Aleutian low increased onshore flow (Ramp et al. 1997). In contrast, barnacle recruitment near Point Sur was not unusually high later that same year, when offshore flow was normal, despite prevailing El Niño conditions elsewhere (Shkedy et al. 1995; Shkedy and Roughgarden 1997). Finally, an onshore transport hypothesis explains why effects of El Niño on recruitment are larger in northern than in southern California (e.g., Ebert et al. 1994), since offshore transport during normal years is much more significant north of Point Conception than in the Southern California Bight (Parrish et al. 1981).

Alternative explanations for increased recruitment in 1997 are increased larval production by adults, enhanced larval survivorship, and increased early postsettlement survival on settlement plates. Increased early postsettlement survival on settlement plates could result from reduced exposure to desiccation associated with anomalously high sea levels, which have been reported for central and northern California during previous El Niño events (Enfield and Allen 1980; Chelton and Davis 1982; Simpson 1983, 1984; Emery and Hamilton 1985; Huyer and Smith 1985; Norton et al. 1985; Simpson 1992; Jacobs et al. 1994; Lynn et al. 1995). However, increased larval production or larval survivorship seems unlikely, given the reduced plankton abundances (i.e., food availability for larval and adult barnacles) associated with El Niño conditions (Chelton et al. 1982; Miller et al. 1985).

It is not clear why Soberanes Point and Pescadero Beach, in particular, are exceptions to the overall trend. We suspect that, in these cases, interannual differences in more local processes swamped the effects of regional-scale increases in onshore transport. For example, the coast near San Francis-

co, just north of Pescadero Beach, is in the lee of a jet of cold, recently upwelled water extending south from Point Reyes (Schwing et al. 1991), a situation in which upwelling can actually promote nearshore retention of larvae (Graham et al. 1992). If a large proportion of the recruits to Pescadero Beach come from this area, a weakening of upwelling (and thus the Point Reyes jet) during El Niño may have actually reduced nearshore retention of larvae in this region, thereby causing lower recruitment in 1997.

This study shows that increased barnacle recruitment accompanied the onset of the 1997 El Niño in central and northern California. This increase was statistically significant across a broad region, and unusually large increases occurred at several sites. The increases occurred during a period of anomalous onshore and poleward winds in the northeast Pacific, suggesting that high recruitment was caused by increased onshore transport of larvae. These results indicate that El Niño can have large and widespread effects on recruitment to benthic communities.

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## Acknowledgments

We are grateful to I. C. Kaplan for field assistance; E. P. Bjorkstedt, J. Huisman, E. K. Nelson, L. Rosenfeld, M. A. Palmer, and two anonymous reviewers for helpful comments on the manuscript; and B. A. Grantham, D. M. Gordon, P. M. Vitousek, J. Koseff, C. Knight, S. Ptak, J. K. Pritchard, and N. Garfield for assistance with various stages of the project. We also thank the Pacific Fisheries Environmental Laboratories of the National Marine Fisheries Service, for making upwelling indices available, and the California Department of Fish and Game (permits 803003-01 and 803072-02), the California Department of Parks and Recreation, and the Monterey Bay National Marine Sanctuary (permit MBNMS-07-97) for permission to conduct this study. We gratefully acknowledge financial support from the National Science Foundation (grant OCE-9115876 and a predoctoral fellowship), the American Museum of Natural History Lerner Gray Fund for Marine Research, and the Northern California Phi Beta Kappa Association.

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Received: 16 June 1998

Accepted: 15 September 1998

Amended: 10 November 1998