Limnol. Oceanogr., 50(5), 2005, 1473–1479

Recruitment of intertidal invertebrates and oceanographic variability at Santa Cruz Island, California

Bernardo R. Broitman
Department of Ecology, Evolution, and Marine Biology, and Marine Science Institute, University of California, Santa Barbara, Santa Barbara, California 93106

Carol A. Blanchette
Marine Science Institute, University of California, Santa Barbara, Santa Barbara, California 93106

Steven D. Gaines
Department of Ecology, Evolution, and Marine Biology, and Marine Science Institute, University of California, Santa Barbara, Santa Barbara, California 93106

Abstract

To examine geographical variation in oceanographic forcing on larval delivery, we studied spatial and temporal variability in larval recruitment of mussels and barnacles in a key oceanographic region around Santa Cruz Island, California. Larval recruitment patterns differed among sites located on the eastern and western shores of the island associated with differences in oceanographic regimes. Western sites had low but variable sea surface temperatures, whereas eastern sites were warmer (1–1.5°C higher) and less variable. Larval arrival was extremely low at western sites relative to eastern sites. Mussels and barnacles differed in the duration and seasonality of larval recruitment. Mussel recruitment occurred over a long period between winter and summer, whereas barnacle recruitment occurred in pulses in spring–summer. Mussel recruitment was not correlated with sea surface temperature anomalies, whereas barnacle recruitment was significantly and positively correlated with temperature anomalies, with time lags ranging from 0 to 3 months across all sites. Oceanographic and larval recruitment patterns suggest that western sites are dominated by an energetic flux of cold, recently upwelled water depleted of larvae, whereas eastern sites receive high numbers of larvae associated with the influx of warmer surface water, likely originating outside the Santa Barbara Channel.

Persistence of marine populations with planktonic development depends on the recurrence of circulation processes suitable for delivering larvae back to adult habitats (Shanks 1995; Caley et al. 1996). Although a wide range of larval transport processes have been examined, upwelling and downwelling circulation are among the more intensively studied processes in temperate coastal habitats (Connolly et al. 2001; Garland et al. 2002). These mesoscale circulation processes are the dominant sources of variability in many nearshore habitats (Largier 2002). Upwelling delivers cold, nutrient-rich seawater to the surface layers, whereas downwelling sinks surface water and its biota to deeper ocean layers. Larvae entrained in the surface layer are hypothesized to be swept offshore by Ekman transport, where they can be collected in offshore frontal regions (Roughgarden et al. 1988; Menge et al. 1997; Poulin et al. 2002). Onshore transport can take place through the shoreward movement of the bottom layer during upwelling or by onshore advection of the coastal front during relaxation (downwelling) events (Wing et al. 1995; Grantham 1997; Shanks et al. 2000; Poulin et al. 2002). These cross-shore patterns of movement can also be coupled to alongshore transport by a number of means (e.g., during the relaxation process [Wing et al. 1995] or through the alongshore advection component of meandering coastal jets), which might play key roles in connecting distant populations.

Although connections between oceanographic forcing and larval transport are typically studied at a single location, there is growing recognition that these connections can vary greatly among locations. Spatial variability in transport processes bears large implications for persistence of coastal benthic populations (Wing et al. 1995; Grantham 1997), the management of marine resources, and the design of marine reserve networks (Gaines et al. 2003; Kinlan and Gaines 2003).

Acknowledgments

We gratefully acknowledge comments by Libe Washburn and two anonymous reviewers, which greatly improved the final manuscript. A large number of people were involved in the arduous collecting and processing of the information presented in the manuscript. We especially thank the University of California Natural Reserve System, Lyndal Laughrin, The Nature Conservancy, Channel Islands National Park, Dan Richards, Derek Lerma, and Jack Engle for site access and field assistance. The following people greatly contributed to field data collection: Tiffany Jenkins, Chris Krenz, Ben Miner, Pete Taylor, Clara Svedlund, Catrina Mangiardi, John Kovach, and Alex Wyndham. AVHRR regional subsets were generated by The Institute of Computational Earth Science Systems at the University of California, Santa Barbara.

B.R.B. gratefully acknowledges financial support from The A. W. Mellon Foundation and the Coastal Environmental Quality Initiative.

This is contribution 182 from The Partnership for Interdisciplinary Studies of the Coastal Ocean (PISCO): A Long-Term Ecological Consortium funded by the David and Lucille Packard Foundation.

Latitudinal variation in the intensity of coastal upwelling, or the frequency of relaxation events, has been suggested to determine geographical patterns of abundance of benthic invertebrate populations in the northeast Pacific (Connolly and Roughgarden 1998; Connolly et al. 2001). The nearshore region of the U.S. West Coast along Washington and Oregon experiences markedly seasonal upwelling with frequent relaxation events. South of the California–Oregon border (Cape Blanco, 42°N) and along much of the central California coast, the occurrence of upwelling-favorable winds intensifies and relaxation events become less frequent (Huyer 1983; Strub and James 2000). At Point Conception, California, the coast changes from a north–south orientation, along which wind-driven upwelling predominates, to an east–west orientation, along which other mesoscale circulation processes are important. In this region south of Point Conception, strong westward flow in late summer drives a counterclockwise eddy in the Santa Barbara Channel. The spring months are typified by eastward flow, strong upwelling, and brief current reversal events (westward flow) resulting from relaxation from upwelling (Huyer 1983; Hickey 1992). Thus, this coastline is characterized by two sharp oceanographic transitions that should alter patterns of larval recruitment: Cape Blanco and Point Conception.

The predicted consequences of oceanographic transitions on larval recruitment have generally been borne out for the region from Washington to central California. The recruitment of several filter-feeding invertebrates with planktonic larvae is dramatically higher along the Washington–Oregon coast than in north-central California (Connolly and Roughgarden 1998; Connolly et al. 2001). The transition between these two recruitment regimes is abrupt, and the temporal dynamics of recruitment at sites within the region are generally consistent with the hypothesized role of variation in upwelling dynamics as a key driver (e.g., Farrell et al. 1991; Wing et al. 1995). By contrast, little is known about the patterns of larval recruitment in the neighborhood of the other sharp oceanographic transition at Point Conception.

Here, we explore the associations between oceanographic variability and larval recruitment patterns in the region just south of Point Conception. We focus on Santa Cruz Island, California, which lies southeast of Point Conception and at the center of a highly oceanographically mixed and biogeographically diverse region. The location of the island at the center of this region provides an ideal opportunity to examine hypotheses regarding oceanographic forcing of larval recruitment. The abundance of benthic invertebrates and algae are correlated with a gradient in sea surface temperature around the island, and a tight relationship between adult abundance and larval supply suggests that invertebrate populations on the island are recruitment limited (Blanchette et al. unpubl. data). To evaluate the strength of oceanographic forcing on larval recruitment, we examine the spatial and temporal relationships between patterns of larval recruitment and sea surface temperature around Santa Cruz Island.

Methods

Physical setting—Santa Cruz Island is the largest of the Northern California Channel Islands and is located in a region of high oceanographic variability in the Santa Barbara Channel. A persistent thermal gradient exists along the channel, with higher sea surface temperatures in the southeastern portion associated with the influx of warmer subtropical water and the topographic deflection of equatorward, upwelling-favorable winds at Point Conception in the northwestern opening of the channel (Hickey 1992; Winant et al. 2003; Otero and Siegel 2004). The northwestern part of the Southern California Bight experiences much colder conditions because of the intense advection of cold water from the nearby Point Conception and Point Arguello upwelling centers (Hickey 1992; Winant et al. 1999; Winant et al. 2003). Over the course of a 5-yr study, we surveyed mussel and barnacle recruitment patterns at six sites around Santa Cruz Island (Fig. 1): three sites on the northwest shore of the island (Fraser, Forney, and Trailer), two on the southeastern shore (Willows and Valley), and one on the northeastern shore (Prisoners). The number and locations of sites were limited by accessibility and other logistical constraints, and sites were selected to be as similar as possible in terms of geomorphology, wave exposure, and habitat type.

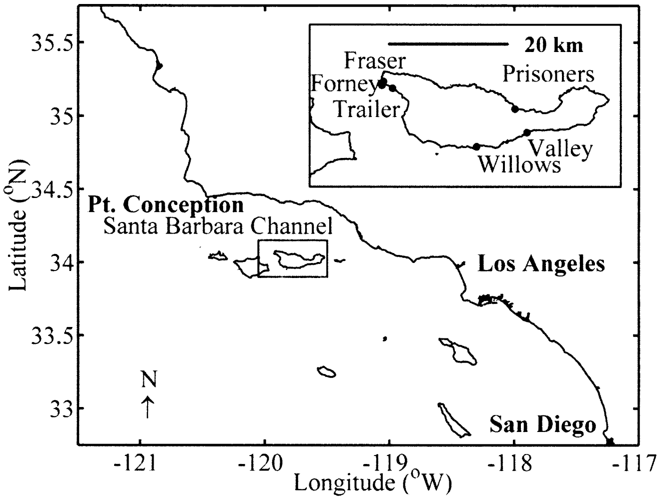

Fig. 1. Map of the Southern California Bight and the California Channel Islands. The western part of the Santa Barbara Channel is under the influence of the large upwelling center located at Point Conception. The inset shows Santa Cruz Island and the location of the intertidal monitoring sites.

Patterns of larval recruitment—Using larval collectors placed in the rocky intertidal zone of each site, we monitored recruitment of two important genera of intertidal invertebrates: mussels (*Mytilus* spp.) and acorn barnacles (*Chthamalus* spp.) We present data for all sites for barnacles from January 1997 to February 2000 ($n = 38$) and all sites except Forney for mussels from March 1996 to September 2000 ($n = 55$). Mussel recruitment rates were quantified with the use of standardized plastic mesh ball collectors, or Tuffys™, whereas barnacle recruitment rates were quantified with the use of ceramic plates (10 × 10 cm; Menge et al. 1997). Five replicate collectors were fastened to the rock in the midzone of each site and replaced roughly every 2–3 months. In the laboratory, mussel recruits were detached from the mesh and counted, whereas recently metamorphosed barnacles and cyprids were counted directly on the plates under a dissecting microscope. Mussel recruitment rates were standardized to number of individuals per Tuffy (~100 cm^3), barnacle recruitment rates were standardized to number of individuals per plate (100 cm^2), and both are expressed as monthly averages of the number of individuals per collector per day.

For a compact visualization of data, we used ordinary kriging to interpolate patterns of larval recruitment in time and space. Kriging is an exact interpolator (i.e., it preserves the original data), allowing the use of empirical decorrelation length scales in the interpolation (Deutsch and Journel 1998; Kyriakidis and Journel 1999). We calculated temporal and spatial length scales from the larval recruitment geographic time series. Temporal scales ranged from 1 month for barnacles to 2 months for mussels, and spatial scales were approximately 20 km for both groups. We limited the interpolation to the region where most of our sites were located, westward from Prisoners Harbor (Prisoners), southward around the western end of the island, and eastward to Valley Anchorage (Valley; Fig. 1).

Remote sensing of sea surface temperature—We characterized oceanographic conditions through spatial and temporal patterns of sea surface temperature from the Advanced Very High Resolution Radiometer (AVHRR) with a nominal resolution of 1.1 km averaged over 5 d. The data set examined here comprises 438 observations spanning 6 yr, from January 1997 to December 2002. From the AVHRR data set, we selected pixels corresponding to the location of our field sites and averaged the first three cross-shelf pixels to obtain a time series with 80–97% of valid observations. Cross-shelf averaging was imposed to improve temporal coverage; missing pixels were common in the nearshore.

Statistical analyses—We used the temporal autocorrelation function of AVHRR sea surface temperature as an index of changing oceanographic conditions. The time-lagged autocorrelation function indicates how observations located at increasing intervals of time become dissimilar (Legendre and Legendre 1998). Preliminary analyses showed that individual time series of sea surface temperature anomaly followed a clear geographic pattern. On the basis of this spatial pattern, we grouped temporal autocorrelation estimates into eastern and western regions to test for first-order differences in temporal variability between regions. These differences were examined after removing annual and semiannual harmonics to generate time series of sea surface temperature anomalies. We examined differences between regions using temporal autocorrelation estimates with a lag of 5 d (from AVHRR temperature averaging) for individual time series with an analog of the two-sample Student's t statistic (Buishand and Beersma 1993). Similarly, temporal autocorrelation functions were plotted with the average of the autocorrelation estimates for individual time series at each lag for each region. To test the hypothesis of a time-lagged dependency of larval recruitment with sea surface temperature, we computed monthly averages from the 5-d temperature data and calculated the cross-correlation between larval recruitment and both the lagged monthly sea surface temperature and sea surface temperature monthly anomalies for each location. Monthly anomalies were calculated by subtracting the long-term mean for each month. Significant correlations were estimated with the Bonferroni correction for multiple comparisons ($\alpha = 0.05$), adjusting the degrees of freedom for the number of comparisons at each lag (Legendre and Legendre 1998).

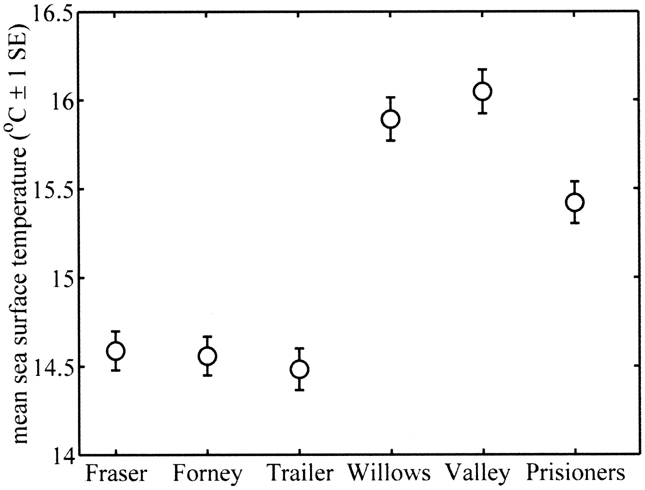

Fig. 2. Long-term mean (±1 SE) of sea surface temperature derived from 1-km resolution AVHRR satellite imagery between 1996 and 2002. Note the large thermal gradient between the three easternmost sites (Fraser, Forney, Trailer) and the others located less than 40 km away alongshore.

Results

Oceanographic regimes—A large thermal gradient between western (Trailer, Forney, Fraser) and eastern (Prisoners, Valley, Willows) sites is evident in the long-term mean sea surface temperature around the island (Fig. 2). East–west sea surface temperature differences ranged between 1°C and 1.5°C, with the coldest and the warmest sites lying less than 40 km alongshore (Trailer and Valley, respectively). The spatial pattern of sea surface temperature was particularly striking during the strong 1997–1998 El Niño event, in which the magnitude of the east–west thermal gradient persisted (not shown) regardless of the regional depression of the thermocline registered during the event (Bograd and Lynn 2001). High temporal autocorrelation of sea surface temperature suggests that the thermal gradient might be linked to contrasting oceanographic regimes around our study sites. Sites located on the eastern side of the island appear to experience thermal fluctuations over different time scales than sites located on the western end of the island (Fig. 3). Temporal autocorrelation of sea surface temperature anomalies at a lag of 5 d across the western sites was significantly different from the eastern sites ($p = 0.0025$, $n = 4$, $t = 5.5826$).

Patterns of larval recruitment—Patterns of larval arrival differed greatly between western and eastern sites. The former collected small numbers of larvae, whereas the latter

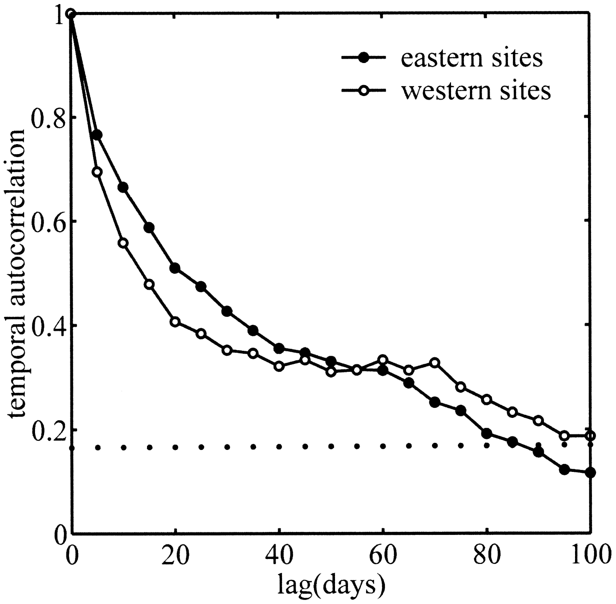

Fig. 3. Mean temporal autocorrelation of the time series of all eastern (filled circles) and western (open circles) sites. The dotted line is the significant correlation ($p < 0.05$) corrected for the degrees of freedom at each time lag.

received almost all the larvae collected over the course of the study (Fig. 4). The spatial differences in magnitude were accompanied by differences in temporal patterns. Western sites received larvae in constantly low numbers, whereas eastern sites received a few large pulses of larvae. Larval recruitment events showed distinct temporal and spatial patterns between groups. Mussels showed a seasonal pattern in which recruitment lasted 4 to 6 months and occurred between winter and summer (Fig. 4b). Barnacle larvae arrived in pulses lasting from 1 to 3 months and were concentrated in a narrow season between spring and summer. Distinct recruitment events for both groups were observed only on the eastern sites (Fig. 4a). The largest event for mussels occurred at the northeastern site (Prisoners) during winter 1998. The largest events for barnacles took place in two successive pulses during summer 1997 in the two southeastern sites (Willows and Valley).

Oceanographic forcing of larval recruitment—Cross-correlation of rates of larval recruitment and monthly mean sea surface temperature showed differences across island sides and between mussels and barnacles (Table 1). Barnacle recruitment showed an immediate and coherent geographic response to positive changes in temperature (Table 1, Barnacles). Almost all sites responded to thermal variability and showed maximal significant correlations with the sea surface temperature at lag 0, at 1 month before (lag 1), and even 2 months before (lag 2). The only site that did not exhibit significant cross-correlations (Willows) was still positively correlated to temperature. Mussel recruitment showed a heterogeneous thermal association across the island (Table 1, Mussels). Significant positive correlations with sea surface temperature were observed at lag 0 only at sites on the western end of the island, where larval recruitment was lowest when the thermal gradient across the island was minimal. Arrival of mussel larvae was not significantly correlated to

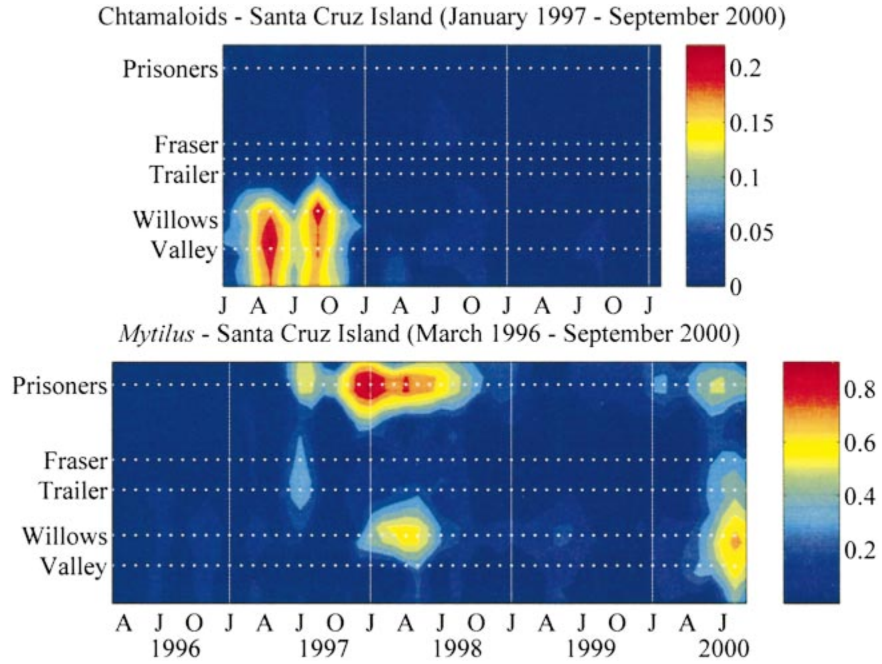

Fig. 4. (A) Spatial time series of log-transformed larval recruitment rates around Santa Cruz Island between 1997 and 2000 for chthamaloid barnacles and (B) between 1996 and 2000 for mytilid mussels. The dotted horizontal line indicates the months data were collected at each site. Vertical reference lines indicate January of each year. The vertical color bars indicate recruitment rates as log(individuals/collector/day). *See text for details.*

Table 1. Cross-correlations of larval recruitment rates with raw sea surface temperature and sea surface temperature anomalies from the annual cycle. The lagged sea surface temperature corresponds to the mean monthly temperature for the same month, 1 month or 2 months before the observation of larval recruitment rate. All Bonferroni-corrected significant correlation coefficients are indicated in boldface ($p37 < 0.0167$ for barnacles and $p54 < 0.0167$ for mussels, n.d. = no data).

	Raw sea surface temperature						Sea surface temperature anomalies					
	Barnacles			Mussels			Barnacles			Mussels		
Lag (months)	0	1	2	0	1	2	0	1	2	0	1	2
Prisoners	**0.4576**	**0.6063**	**0.6269**	0.0104	−0.0208	0.0632	**0.4474**	0.3732	0.35459	0.3367	0.3145	0.4169
Valley	**0.6304**	**0.4483**	0.3709	0.2260	0.1568	−0.0235	**0.5685**	0.4123	**0.4615**	−0.1002	−0.1826	−0.2679
Willows	0.3349	0.3347	0.2389	0.1552	0.0511	−0.1051	**0.5385**	**0.5227**	0.3551	−0.0589	−0.0272	−0.0080
Trailer	**0.5703**	**0.6215**	**0.5886**	**0.5465**	0.3357	0.1083	**0.4646**	0.3298	0.2881	0.1533	−0.0203	−0.0418
Forney	**0.5739**	**0.5899**	**0.4592**	n.d.	n.d.	n.d.	**0.5514**	**0.4425**	0.3566	n.d.	n.d.	n.d.
Fraser	**0.6584**	**0.4956**	0.1949	**0.4696**	0.2675	0.0152	0.4004	0.1823	0.0146	0.1191	0.0600	0.0299

temperature in any of the eastern sites. Cross-correlations of patterns of recruitment and sea surface temperature anomalies (Table 1, Barnacles) indicated that barnacle recruitment was significantly correlated to temperature anomalies at lag 0 at all sites except Fraser. A significant correlation at lag 1 was observed at Forney and Willows and at lag 2 only in Valley. No significant correlations where observed between mussel recruitment and sea surface temperature anomalies (Table 1, Mussels).

Discussion

Our results document the existence of a steep gradient in larval recruitment and oceanographic conditions between the eastern and western shores of Santa Cruz Island. Eastern sites experienced higher rates of larval recruitment of barnacles and mussels than western sites. This gradient in larval recruitment was associated with a thermal gradient across the island. Western sites were subject to cold and variable water temperatures relative to eastern sites, where warmer temperatures persisted longer. Sites located on the western shore of Santa Cruz Island likely experience the persistent influx of cold, recently upwelled water from below the euphotic zone that is apparently devoid of larvae. Sites on the eastern side of the island received the regular influx of warm water potentially rich in larvae.

Across the island, larval recruitment occurred in distinct events distributed across space and time. Barnacle larvae tended to settle in events that were well localized in time and spread in space, whereas mussel larval recruitment was widely distributed in time and very localized in space. During May–September 1997, a similar geographically widespread peak in barnacle recruitment was reported for central California (Connolly and Roughgarden 1999). The concomitance of this and the Santa Cruz Island recruitment events documented here suggest that our observations of synchronous recruitment of barnacles across the island shores (~40 km) might extend across longer distances (~200 km).

The differences in larval recruitment patterns between barnacles and mussels are also reflected in their contrasting responses to sea surface temperature. Barnacle recruitment was strongly and positively correlated to temperature at lag 0 and up to 2 months before as larval recruitment peaked in late summer. Moreover, significant correlations with temperature anomalies at lag 0 at almost all sites hint that barnacle recruitment events might be associated with intrusions of warm water masses. Mussel recruitment only showed a significant response to lag 0 temperature at the low-recruitment sites because the largest larval recruitment events recorded at those locations took place during a narrow window in summer months. The association between mussel recruitment and temperature disappeared when mussel recruitment was correlated to temperature anomalies, suggesting that mussel recruitment events might not be correlated to warm water intrusions. The different responses to monthly patterns of sea surface temperature across larval groups suggest a connection between oceanographic regime and larval biology. The larvae of chthamaloid barnacles remain in the water column for up to 3–4 weeks and have an extended competency period, whereas the larvae of *Mytilus californianus*, the dominant intertidal mussel, spend approximately only 9 d in the plankton (Strathmann 1987). This dichotomy is enhanced by adult reproductive behavior. Barnacles show a markedly seasonal spawning, whereas mussels spawn year-round in Southern California (Hines 1978, 1979). As in our study, larvae from mussels tend to arrive heterogeneously in space and time and have not been successfully related to particular oceanographic mechanisms elsewhere. Our interpretation of this pattern of recruitment variability around Santa Cruz Island is that eastern sites receive a large influx of larvae advected from distant populations, possibly from the mainland coast. The western sites might receive larvae only associated with seasonal intrusions of warm water and a reduction in the east–west thermal gradient, although no clear relationship was detected in the cross-correlation analyses. Barnacle larvae arrive at all island sites synchronously and in larger numbers because of the seasonal release of larvae by adults and possibly because of their accumulation in oceanographic features through their long planktonic period. The end of the summer, the only period when larval recruitment was observed in the western sites, corresponds to the period when stratification in the Santa Barbara Channel is maximal. Stratified conditions have also been related to favorable oceanographic conditions for larval delivery through internal tidal bores in a number of locations around the world (Pineda 1991; Vargas et al. 2004). Alternatively, larvae can be delivered to shore by wind transport (McQuaid and Phillips 2000; Garland et al. 2002) associated with poleward flow events during summer months (Hickey et al. 2003).

The intensive oceanographic field studies in the Santa Barbara Channel over the past 20 yr provide support for results and interpretations of oceanographic conditions that here we derived exclusively from remote sensing information (Winant et al. 2003). Our study suggests the possibility of linking remote sensing assessments of sea surface temperature dynamics to coastal ecology, particularly when deployment of instruments in the field is logistically difficult. Currently, the California Channel Islands are a test piece for the development of marine protected areas (Airame et al. 2003). This marine management problem stresses the critical need for the objective assessment of oceanographic regimes promoting larval delivery to benthic habitats. One important conclusion from this study is that spatial variability in larval recruitment of intertidal invertebrates around Santa Cruz Island is associated with variability in the temporal dynamics of sea surface temperature. Consistent with the results from other studies along the U.S. West Coast, we find that recruitment of species with planktonic larvae, and ultimately population abundance, could be limited in areas of persistent upwelling, even where upwelling is relatively weak.

References

AIRAME, S., J. E. DUGAN, K. D. LAFFERTY, H. LESLIE, D. A. MCARDLE, AND R. R. WARNER. 2003. Applying ecological criteria to marine reserve design: A case study from the California Channel Islands. Ecol. Appl. **13:** S170–S184.

BOGRAD, S. J., AND R. J. LYNN. 2001. Physical–biological coupling in the California Current during the 1997–99 El Niño–La Niña cycle. Geophy. Res. Lett. **28:** 275–278.

BUISHAND, T. A., AND J. J. BEERSMA. 1993. Jackknife tests for differences in autocorrelation between climate time series. J. Clim. **6:** 2490–2495.

CALEY, M. J., M. H. CARR, M. A. HIXON, T. P. HUGHES, G. P. JONES, AND B. A. MENGE. 1996. Recruitment and the local dynamics of open marine populations. Annu. Rev. Ecol. Syst. **27:** 477–500.

CONNOLLY, S. R., B. A. MENGE, AND J. ROUGHGARDEN. 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. Ecology **82:** 1799–1813.

———, AND J. ROUGHGARDEN. 1998. A latitudinal gradient in northeast Pacific intertidal community structure: Evidence for an oceanographically based synthesis of marine community theory. Am. Nat. **151:** 311–326.

———, AND ———. 1999. Increased recruitment of northeast Pacific barnacles during the 1997 El Niño. Limnol. Oceanogr. **44:** 466–469.

DEUTSCH, C. V., AND A. G. JOURNEL. 1998. GSLIB geostatistical software library and user's guide. Oxford Univ. Press.

FARRELL, T. M., D. BRACHER, AND J. ROUGHGARDEN. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California, U.S.A. Limnol. Oceanogr. **36:** 279–288.

GAINES, S. D., B. GAYLORD, AND J. L. LARGIER. 2003. Avoiding current oversights in marine reserve design. Ecol. Appl. **13:** S32–S46.

GARLAND, E. D., C. A. ZIMMER, AND S. J. LENTZ. 2002. Larval distributions in inner-shelf waters: The roles of wind-driven cross-shelf currents and diel vertical migrations. Limnol. Oceanogr. **47:** 803–817.

GRANTHAM, B. A. 1997. Coastal upwelling, larval recruitment, and the dynamics of upper intertidal barnacle communities. Ph.D. thesis, Stanford Univ.

HICKEY, B., E. L. DOBBINS, AND S. E. ALLEN. 2003. Local and remote forcing of currents and temperature in the central Southern California Bight. J. Geophys. Res., C **108** [doi: 10.1029/1200JC000313].

HICKEY, B. M. 1992. Circulation over the Santa Monica–San Pedro basin and shelf. Prog. Oceanogr. **30:** 37–115.

HINES, A. H. 1978. Reproduction in 3 species of intertidal barnacles from central California. Biol. Bull. **154:** 262–281.

———. 1979. Effects of thermal discharge on reproductive cycles in *Mytilus edulis* and *Mytilus californianus* (Mollusca, Bivalvia). Fish. Bull. **77:** 498–503.

HUYER, A. 1983. Coastal upwelling in the California Current System. Prog. Oceanogr. **12:** 259–284.

KINLAN, B. P., AND S. D. GAINES. 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. Ecology **84:** 2007–2020.

KYRIAKIDIS, P. C., AND A. G. JOURNEL. 1999. Geostatistical space–time models: A review. Math. Geol. **31:** 651–684.

LARGIER, J. L. 2002. Linking oceanography and nearshore ecology: Perspectives and challenges, p. 207–239. *In* J. C. Castilla and J. L. Largier [eds.], The oceanography and ecology of the nearshore and bays in Chile. Ediciones Univ. Catolica de Chile.

LEGENDRE, P., AND L. LEGENDRE. 1998. Numerical ecology, 2nd ed. Elsevier Science.

MCQUAID, C. D., AND T. E. PHILLIPS. 2000. Limited wind-driven dispersal of intertidal mussel larvae: In situ evidence from the plankton and the spread of the invasive species *Mytilus galloprovincialis* in South Africa. Mar. Ecol. Prog. Ser. **201:** 211–220.

MENGE, B. A., B. A. DALEY, P. A. WHEELER, E. DAHLHOFF, E. SANFORD, AND P. T. STRUB. 1997. Benthic–pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proc. Natl Acad. Sci. USA **94:** 14530–14535.

OTERO, M. P., AND D. A. SIEGEL. 2004. Spatial and temporal characteristics of sediment and phytoplankton blooms in the Santa Barbara Channel. Deep-Sea Res., Topical Stud. Oceanogr. **51:** 1129–1149.

PINEDA, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. Science **253:** 548–551.

POULIN, E., AND OTHERS. 2002. Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in central Chile. Limnol. Oceanogr. **47:** 1248–1255.

ROUGHGARDEN, J., S. GAINES, AND H. POSSINGHAM. 1988. Recruitment dynamics in complex life cycles. Science **241:** 1460–1466.

SHANKS, A. L. 1995. Mechanisms of cross-shelf dispersal of marine invertebrates, p. 323–367. *In* L. R. McEdward [ed.], Ecology of marine invertebrate larvae. Marine Science Series. CRC Press.

———, J. LARGIER, L. BRINK, J. BRUBAKER, AND R. HOOFF. 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnol. Oceanogr. **45:** 230–236.

STRATHMANN, M. F. 1987. Reproduction and development of marine invertebrates of the northern Pacific coast. Univ. of Washington Press.

STRUB, P. T., AND C. JAMES. 2000. Altimeter-derived variability of surface velocities in the California Current System: 2. Seasonal circulation and eddy statistics. Deep-Sea Res., Topical Stud. Oceanogr. **47:** 831–870.

VARGAS, C. A., D. A. NARVÁEZ, A. PIÑONES, R. M. VENEGAS, AND S. A. NAVARRETE. 2004. Internal tidal bore fronts and settlement of invertebrates in central Chile. Estuar. Coast. Shelf Sci. **61:** 603–612.

WINANT, C. D., D. J. ALDEN, E. P. DEVER, K. A. EDWARDS, AND M. C. HENDERSHOTT. 1999. Near-surface trajectories off central and southern California. J. Geophys. Res., C **104:** 15713–15726.

———, E. P. DEVER, AND M. C. HENDERSHOTT. 2003. Characteristic patterns of shelf circulation at the boundary between central and southern California. J. Geophys. Res., C **108** [doi: 10.1029/2001JC001302].

WING, S. R., J. L. LARGIER, L. W. BOTSFORD, AND J. F. QUINN. 1995. Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnol. Oceanogr. **40:** 316–329.

Received: 13 July 2004
Accepted: 2 May 2005
Amended: 11 May 2005