SCALES OF VARIABILITY IN LARVAL SETTLEMENT WITHIN THE CHANNEL ISLANDS NATIONAL MARINE SANCTUARY AND ALONG THE MAINLAND COAST

STEPHEN C. SCHROETER,[1] HENRY M. PAGE,[1] JENIFER E. DUGAN,[1] CAROLYNN S. CULVER,[1] BRUCE STEELE,[2] RICK GUITERREZ,[3] JOHN B. RICHARDS,[1] AND DAVID KUSHNER[4]

[1]*Marine Science Institute, University of California, Santa Barbara, CA 93106; schroete@lifesci.ucsb.edu*
[2]*1570 W. Highway 246, Buellton, CA 93427*
[3]*722 Dolores Drive, Santa Barbara, CA 93107*
[4]*Channel Islands National Park, 1901 Spinnaker Drive, Ventura, CA 93001*

Abstract—We explored variability in the settlement rates of sea urchins (*Strongylocentrotus franciscanus*, *S. purpuratus*), and rock crabs (*Cancer spp.*) across different spatial (hundreds of meters to 90 km) and temporal (biweekly to decadal) scales in nearshore waters off Santa Cruz, Santa Rosa, and Anacapa islands and along the Santa Barbara mainland coast. Here, we refer to "settlement" as a best estimate of the abundance of small stages of invertebrates recently settled from the plankton. Settlement was measured using two types of collectors: wood-handled scrub brushes and "tuffy" scrub pads attached 1 to 2 m off the bottom either on buoyed mooring lines at stations inside and outside of two marine protected areas (MPAs) at the islands or suspended from piers, one of which is located inside an MPA at Anacapa Island. Benthic recruitment of urchins was also measured at the Anacapa Island station. Larval settlement varied dramatically on a scale of hundreds of meters within and across MPA boundaries. For both red and purple urchins, average settlement at the Santa Cruz and Santa Rosa island sites in 2006 was an order of magnitude higher than average settlement at mainland sites in 2006 and also higher than the historical mainland average (based on a 16-year time series). Comparisons of settlement relative to benthic recruitment at the Anacapa Island station were suggestive of a link for red urchins, but no relationship was evident for purple urchins. Although more data are needed, our results suggest that local and regional scale variability in larval settlement could have important implications for population dynamics, fishery management, MPAs and sampling design. For example, areas with lower settlement rates may take longer to recover depleted populations or be less suitable for restoration efforts based on natural replenishment than areas with greater settlement. Settlement data could provide a fishery-independent measure of stock health and a means for evaluating the role of larval supply in regulating adult populations of economically and ecologically valuable benthic invertebrates.

INTRODUCTION

Shallow rocky reefs are critically important nearshore coastal ecosystems in southern California. These ecosystems support giant kelp (*Macrocystis pyrifera*), understory macroalgae, seagrasses, and populations of ecologically, commercially, and recreationally important fishes and invertebrates. Many of the benthic invertebrate species of rocky reef ecosystems (e.g., sea urchins, rock crabs) have a distinctive two phase life cycle, with a planktonic larval phase and a benthic adult phase. For those species with a larval phase of short duration, most larvae may be retained in the vicinity of the source adult population; however, as the larval phase increases in duration, there can be extensive dispersal of larvae by currents away from the source adults (see reviews by Morgan 2001; Underwood and Keough 2001; Mitarai et al. 2008). For example, red and purple sea urchin adults are sedentary and likely move no more than a few kilometers and as little as tens to hundreds of meters during a lifetime. In contrast, larvae of these species remain in the plankton for several weeks (Strathmann 1978; Cameron and Schroeter 1980) and may be carried hundreds or thousands of

kilometers from their source population before settlement (Ebert et al. 1994; Miller and Emlet 1997). One consequence of this two-phase life cycle is that the availability of settlers is a potential driver of the dynamics of benthic invertebrate populations and communities along with larval behavior, habitat quality, and post-settlement mortality (e.g., Connell 1985; Roughgarden et al. 1987; Raimondi 1990; Morgan et al. 2000).

The two-phase life cycle of many benthic invertebrates has implications for managing reef populations inside marine protected areas (MPAs) at the Channel Islands and elsewhere. Benthic adult populations inside and outside of MPAs are potentially linked through the passive transport of planktonic larvae by ocean currents (Shanks et al. 2003). Since larvae may spend days to weeks feeding in the plankton, larvae produced by benthic adults within an MPA probably recruit to populations at distance from the MPA. Conversely, populations of these species within an MPA may be maintained by larvae produced outside of the MPA. In addition, settlement rates can vary among different species, affecting the recovery time and resilience of benthic populations. Information on spatial and temporal variation in larval settlement is needed to better understand the factors responsible for regulating the distribution and abundance of benthic invertebrates and to evaluate the potential efficacy of MPAs.

Larval settlement of sea urchins has been monitored at a number of locations in southern and northern California since 1990 (Ebert et al. 1994; Schroeter and Dixon 2006), but few data are available from the Channel Islands. Data from a single station (Landing Cove) on Anacapa Island indicates that sea urchin (*Strongylocentrotus* spp.) settlement occurs primarily from March through September (Schroeter and Dixon 2006). Although there is very little information on settlement for rock crab populations (CDFG 2004), Page et al. (1999) documented benthic recruitment of brown rock crabs (*Cancer antennarius*) into a subtidal mussel community during the late spring and early summer on an offshore oil platform 4.7 km from Ellwood Pier in Goleta.

In this study, we compared the settlement rates of reef invertebrates across various spatial and temporal scales. Here, we refer to "settlement" as a best estimate of the abundance of small benthic stages recently settled from the plankton. Settlement may be a proxy for "larval supply" or the abundance of pre-settlement larvae in the plankton (Miller and Emlet 1997). Specifically, we explored variability in settlement: 1) at three spatial scales ranging from comparisons among stations within (hundreds of meters) and across (<1 to 10 km) MPA boundaries to stations at the Channel Islands versus the mainland (48–94 km); 2) across temporal scales ranging from biweekly to decadal; 3) among species; and 4) relative to benthic recruitment of young-of-year sea urchins (which is likely affected by post-settlement mortality) at a single station located within an MPA. We targeted benthic invertebrate species of commercial and ecological importance: purple and red sea urchins (*Strongylocentrotus purpuratus*, *S. franciscanus*) and brown and red rock crabs (*Cancer antennarius, C. productus*).

MATERIALS AND METHODS

Study Design and Sampling Sites

We measured spatial and temporal variability in the settlement of red and purple sea urchins and brown and red rock crabs at three spatial scales. At the smallest scale (hundreds of meters to kilometers), settlement was compared among four stations each at Santa Cruz Island (SCI) and Santa Rosa Island (SRI) from May through September 2006 (Fig. 1). At SCI, two stations were located inside and two outside of the Gull Island MPA. At SRI, two stations were located inside and two outside of the Skunk Point MPA. At a larger scale for island sites (tens of kilometers), settlement was compared among the SCI and SRI stations and at a single station (Landing Cove) on Anacapa Island (AI), a long-term site that is located inside an MPA (Fig. 1). There were no outside MPA data available for the Anacapa Island station. Finally, during 2006 we compared settlement at our island stations to three mainland stations in the Santa Barbara Channel 50 to 90+ km distant (Gaviota Pier, Ellwood Pier, Stearn's Wharf). We also placed results from the SRI and SCI island stations in the context of results of a much larger regional long-term monitoring program, which has been in place since the early 1990s. This long-term program measures larval settlement from a network of brush
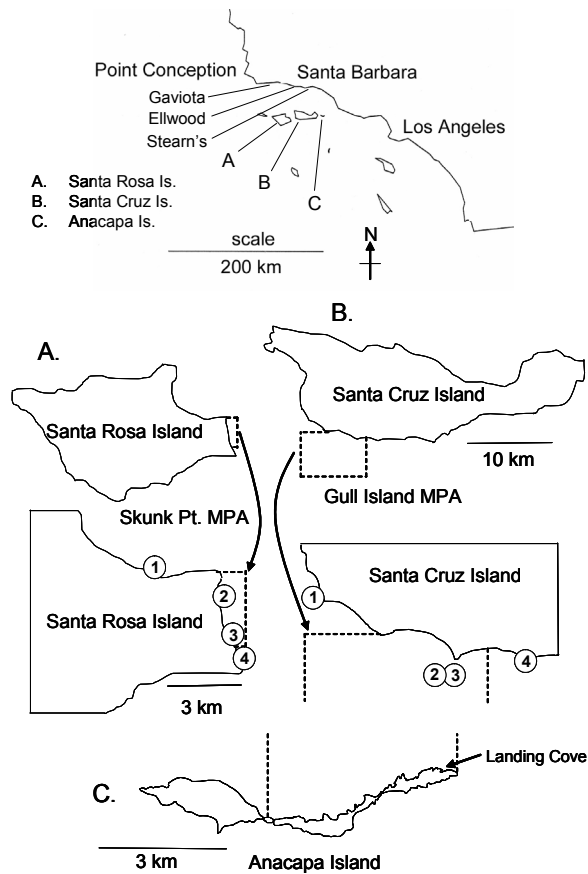
Figure 1. Map showing the location of stations used in the study, including our temporary stations moored inside and outside of A) Skunk Point MPA at Santa Rosa Island (SRI 1-4) and B) Gull Island MPA at Santa Cruz Island (SCI 1-4), and pier stations on the mainland coast and at C) Landing Cove, Anacapa Island. Dashed lines indicate MPA boundaries.

collectors along the mainland coast, including the three stations in the Santa Barbara Channel used in this study (Schroeter et al., unpublished). The sampling station at AI is located ~100 m from a station used by the Channel Islands National Park Service (CINP) to routinely monitor recruitment of selected species of benthic invertebrates (Fig. 1), which is also within the MPA.

Measurement of Settlement and Benthic Recruitment

We measured settlement at SCI and SRI using two types of collectors: wood-handled scrub brushes and "tuffy" scrub pads. At these stations, four brushes and two tuffys were attached to a buoyed mooring line 1 to 2 m off the bottom in 8 to 10 m water depth following the methods of Ebert et al. (1994). Brushes and tuffys were retrieved and replaced using a casing apparatus we developed for this study that allowed surface-based retrieval. Brush and tuffy collectors were retrieved and replaced with fresh collectors at two-week intervals to minimize the potential effects of post-settlement mortality on estimates of settlement. After retrieval, the brushes and tuffys were placed on ice for transport and processing at UCSB following methods in Ebert et al. (1994). The settlement of urchins on brushes and tuffys was highly correlated (total urchins—r^2=0.75, No. tuffy^{-1} = 1.32•(No. brush^{-1}) + 1.86). A similar pattern was found for crabs (total crabs—r^2 = 0.68, No. tuffy^{-1} = 2.76•(No. brush^{-1}) - 0.06); therefore, we present only the data from the brushes here. At the mainland and AI stations, four brushes were attached to a line 1 to 2 m above the bottom suspended from a pier (Schroeter and Dixon 2006).

The relationship between settlement and benthic recruitment was examined at AI using data collected by the CINP from artificial recruitment modules (ARMs). These modules consist of a wire cage made of 5 x 10 cm plastic coated mesh wire filled with 20 bricks made by cutting a concrete cinder block in half longitudinally, which produces two bricks each with a cross section shaped like a lower case "m." The ARMs are taken apart and the animals inside of them (including red and purple sea urchins but not rock crabs) are collected and measured once a year. Between three to seven ARMs were sampled at the Landing Cove site in a given year. Counts of red and purple urchins 30 mm in test diameter, considered to be less than two years old based on previous growth studies (Ebert et al. 1999; CDFG 2004), were used as a measure of recruitment. Comparisons were made for 1994 through 1998, years in which more than 50% of biweekly samples were collected.

Data Analysis

We investigated similarity in patterns of settlement among stations within SCI and SRI, and for grouped stations between these island sites, using Pearson correlation analysis. We compared mean settlement values with ANOVA. In addition, we used commonality analysis to estimate the amount of variability in settlement rates accounted for by three different spatial scales: 1) among

stations within areas (within MPAs or adjacent areas outside of MPAs); 2) between areas (inside versus outside of MPAs); and 3) between islands (Santa Rosa versus Santa Cruz) (Siebold and McPhee 1979; Rowell 1991). We examined the relationship between settlement and recruitment first by plotting yearly averages of recruits per ARM and settlers per brush as a function of year. In addition, we conducted linear regression analysis of recruitment in a given year versus settlement one or two years earlier.

RESULTS

Spatial and Temporal Patterns in Settlement at Island Sites

There was considerable small-scale variability (across hundreds of meters to a few kilometers) in the settlement of purple and red sea urchins and brown rock crabs within sites (Santa Cruz and Santa Rosa islands); there was no settlement of red rock crabs at our island stations during the study. Settlement rates of purple and red urchins and brown rock crabs were generally higher at stations 1 and 4 compared with 2 and 3 at SCI, and stations 2 and 3 compared with 1 and 4 at SRI. No consistent pattern with respect to MPA boundaries was detected in settlement. Variability among stations was particularly noticeable for purple urchins on June 11 at SCI when settler density was 3.1 times

higher at station 3 compared to the next highest station (station 4) located 1.5 km distant (Fig. 1).

Although the abundance of purple sea urchin settlers varied among stations at SRI, patterns in settlement were highly correlated among stations over time (Table 1; Fig. 2). However, this correlation was not evident for red urchins or brown rock crabs, both of which exhibited much lower settlement intensity. The temporal correlations observed in settlement among stations were weaker for purple urchins at SCI, with a significant correlation only between SCI stations 2 and 4 (Table 1). No correlations were detected in settlement over time among the SCI and SRI sites for any species (maximum $r^2 = 0.4$). As a consequence of variability in settlement among stations and over time, no significant difference in average settlement was found between SCI and SRI sites ($P > 0.1$).

Commonality analysis indicated that differences among stations (smallest scale) accounted for most of the variation in settlement observed for all three species, followed by differences between SCI and SRI (sites), and finally by status with regard to MPAs (inside versus outside) (Fig. 3).

Settlement at Island and Mainland Sites

In 2006, the settlement of purple urchins was higher on average at SCI and SRI (mean = 1.47 settler brush^{-1} week^{-1}) than at the mainland (mean = 0.22 settler brush^{-1} week^{-1}) or at AI (mean = 0.04

Table 1. Matrices of simple correlation coefficients (r) in pairwise comparisons of larval settlement onto brushes over time between stations at Santa Cruz Island (SCI) and at Santa Rosa Island (SRI) for purple and red urchins and brown rock crab in 2006. Significant correlations indicated with asterisks: *P < 0.05, **< 0.01, ***< 0.001. Missing data indicated by ----.

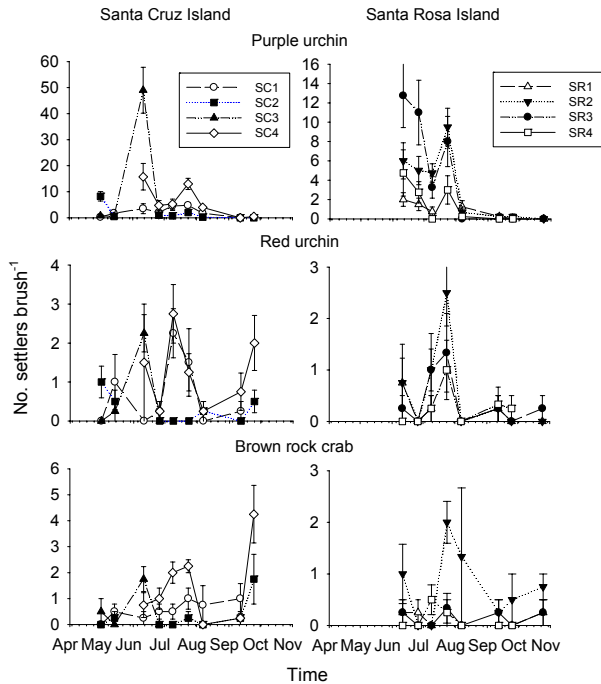|	SCI 2	SCI 3	SCI 4		SRI 2	SRI 3	SRI 4
			Purple urchin				
SCI 1	-0.281	0.818	0.711	SRI 1	0.833*	0.877**	0.869*
SCI 2		-0.192	0.946**	SRI 2		0.810*	0.745
SCI 3			-----	SRI 3			0.960***
			Red urchin				
SCI 1	-0.409	-0.343	0.793	SRI 1	0.740	0.318	-0.123
SCI 2		-----	0.149	SRI 2		0.925***	0.853*
SCI 3			-----	SRI 3			0.803*
			Brown rock crab				
SCI 1	0.582	-0.812	0.834	SRI 1	0.066	0.417	-0.316
SCI 2		-----	0.333	SRI 2		0.524	-0.050
SCI 3			-----	SRI 3			-0.03

Figure 2. Settlement of purple and red sea urchins and brown rock crabs onto brush collectors sampled at approximately two-week intervals at stations nearshore of Santa Rosa and Santa Cruz islands. Open symbols are data for station located outside MPAs and closed symbols are for station located inside MPAs. Note differences in scale of the y-axis among figures.

Figure 3. Percent of variation in settlement on the brushes attributable to differences among stations, stations inside and outside of MPAs, and sites (island versus mainland).

settler brush^{-1} week^{-1}) (Fig. 4). Similarly, settlement of red urchins was higher at SCI and SRI (mean = 0.22 settler brush^{-1} week^{-1}) than at the mainland (mean = 0.03 settler brush^{-1} week^{-1}) or at AI (mean = 0.01 settler brush^{-1} week^{-1}). However, there was no difference in settlement of brown rock crabs between SCI and SRI (mean = 0.10 settler brush $^{-1}$ week^{-1}) and the mainland (mean = 0.10 settler brush^{-1} week^{-1}). Settlement of brown rock crabs at AI (mean=0.03 settler brush $^{-1}$ week^{-1}) was lower than at SCI, SRI, or the mainland. Settlement of red rock crabs occurred only at our mainland stations and was very low.

Examining our data from 2006 within the context of the 16-year data set, indicates that relative settlement between the island and mainland sites varied among three of the four target species. Settlement of red rock crabs, which was very low at the mainland stations, was not considered. Settlement of purple urchins at mainland and AI stations was generally much lower in 2006 compared to the long-term average settlement at those stations, and this was the trend as well on SCI and SRI with the exception of stations 3 and 4 on SCI (Fig. 4). The patterns of settlement were very different for red urchins, where settlement at the AI and mainland stations in 2006 was either lower or similar to long-term averages. However, the 2006 settlement at SCI and SRI stations (with the exception of station 1 on SRI) was generally much higher than the long-term averages at mainland and AI stations (Fig. 4). With a single possible exception of station 4 on SCI, brown rock crab settlement on SCI and SRI was either similar to or lower than the long-term averages at the mainland and AI stations (Fig. 4).

Settlement versus Benthic Recruitment

We explored the relationship between settlement and recruitment into the benthic population using data from 1994 through 1998 on the availability of settlers from the brushes and the
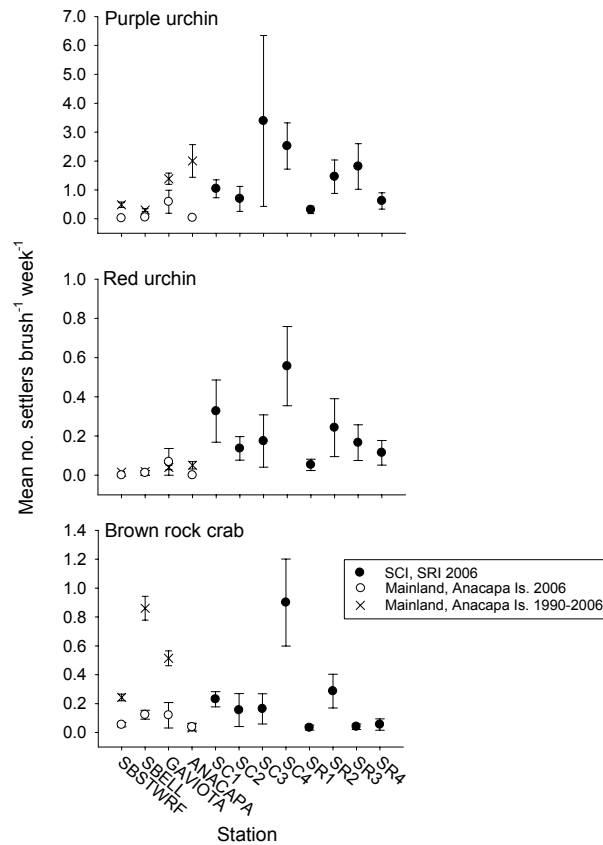
Figure 4. Comparison of settlement rate of purple and red urchins and brown rock crab onto brush collectors among island and mainland stations in 2006, between SCI and SRI stations in 2006 and historical data from Anacapa Island and the mainland averaged from 1990 through 2006. Note differences in scale of the y-axis among figures.
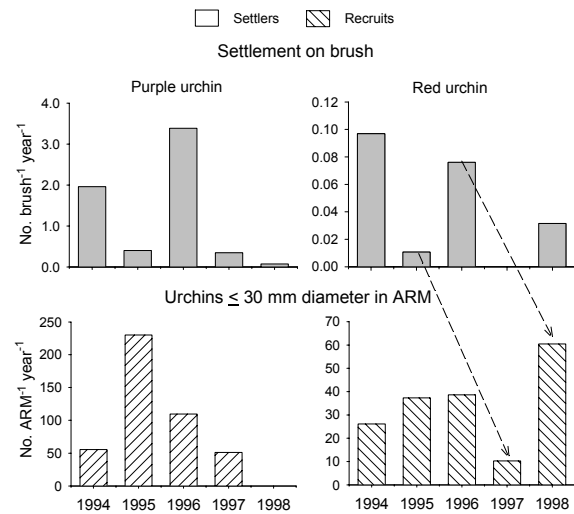

Figure 5. Relationship between the mean number of urchin settlers on the brush collectors and the number of urchins < 30 mm in the ARMs at the Landing Cove station on Anacapa Island, 1994 through 1998. Note differences in scale of the y-axis among figures. Arrows indicate two year time lag between settlement and benthic recruitment for red urchins.

abundance of purple and red urchins ≤ 30 mm diameter in the ARMs located at the Landing Cove station on AI (Fig. 5). Growth of purple and red urchins following settlement is reported to range from ~10 to 30 mm in one year (Ebert 1968; Kenner 1992; Ebert et al. 1999); therefore, an urchin of ≤ 30 mm likely recruited into the benthic population within the previous 1 to 2 years. To account for variability in growth and settlement, time lags of 1 and 2 years were used to explore relationships between settlement and benthic recruitment.

For purple urchins, there was no relationship between settlement on the brushes and the abundance of urchins ≤ 30 mm in the ARMs at time lags of either 1 ($r^2 = 0.02$) or 2 years ($r^2 = 0.10$) (Fig. 5). For red urchins, there was also no relationship between settlement and the abundance of urchins ≤

30 mm at a time lag of 1 year ($r^2 = 0.42$); however, there was a positive relationship ($r^2 = 0.60$) between settlement and the abundance of urchins ≤ 30 mm with a time lag of 2 years (Fig. 5).

DISCUSSION

The abundance of settling larvae can strongly influence benthic recruitment and the dynamics of marine invertebrate populations (reviews by Morgan 2001; Underwood and Keough 2001; Wahle 2003). The spatial scale across which settlement rate varies may thus have important implications to the sustainability of populations and their rate of recovery following a disturbance. Much of the work on spatial variation in settlement has centered on intertidal species, particularly barnacles and mussels, which are amenable to sampling and experimental manipulation (e.g., Connell 1985; Raimondi 1990; McQuaid and Phillips 2006). Our study shows that for two urchin and one crab species, settlement rates can vary appreciably across spatial scales on the order of hundreds of meters (station scale) to tens of kilometers (Island/ Mainland scale). We also found significant

temporal variation in settlement across our shortest (biweekly) time scale and among years.

Although absolute settlement rates varied among stations and over time, correlation analysis revealed coherence in the temporal patterns of settlement for purple and red urchins among some stations, most notably at SRI. However, on SCI the timing of settlement peaks generally differed among stations, some of which were quite close spatially (< 500 m: Fig. 1). Oceanographic conditions, such as the direction and speed of prevailing alongshore currents and upwelling, which influence cross shelf transport, can regulate larval supply and the magnitude and timing of settlement across large spatial scales (e.g., Roughgarden et al. 1987; Gaines and Bertness 1992; Miller and Emlet 1997; Shanks and Roegner 2007). These larger scale oceanographic conditions, which differ between the northern Channel Islands and mainland (Otero and Siegel 2004), could have contributed to the dramatically lower settlement of urchins observed at AI, and our two most easterly mainland stations, compared to SRI and SCI in 2006 and relative to the 16-year average. However, if such a large-scale current pattern were important, one would expect to see similar patterns among the three species (whose larvae have similar planktonic duration) over the long term. This was clearly not the case, as the spatial pattern in 2006 and long-term averages were similar for red sea urchins (indicating a west to east decline in settlement rates) but not for purple urchins and brown rock crabs. For these species the long-term settlement at AI and two mainland stations was either similar to or exceeded settlement at SCI and SRI, and differed from the patterns seen for red sea urchins. Our findings suggest that hydrographic conditions that modulate larval delivery to subtidal reefs at much smaller spatial scales (e.g., local eddies or variability in water flow created by bottom topography) may be as or more important than large-scale current patterns.

Of potentially greater importance to benthic populations is the total number of settlers that arrive on a reef during the year. Annual variability in settlement could influence benthic recruitment and ultimately the abundance of adults within a year class. Such population level effects were postulated to occur following unusually high settlement rates of red urchins in northern California after the 1992 and 1993 El Niño events (Ebert et al. 1994; Morgan

et al. 2001; Schroeter and Dixon 2006). The absence of a correlation between settlement and benthic recruitment would suggest the importance of early post-settlement mortality (e.g., from predation) in limiting recruitment. Because continuous data were available for only a few years, we were unable to adequately characterize the relationship between the availability of settlers (as measured by settlement on brushes) and the abundance of benthic recruits (as measured in the ARMs) from the Landing Cove station on Anacapa Island. Our data are suggestive of a link between settlement and recruitment for red urchins, a harvested species, but no relationship was evident for purple urchins which are not harvested. A longer time series is needed to better evaluate the importance of pre- and post-settlement processes to the population dynamics of purple and red urchins in the Santa Barbara Channel.

It is important to note that our study focused on spatial and temporal patterns of settlement as a proxy for larval supply, and for sea urchins, on the possible effects of this variability on abundances of 1- to 2-year-old recruits. We did not examine possible stock-recruitment relationships for several reasons. First, the data on abundance of adult stocks of the target species are lacking from most of our study sites. Second, while the spatial scales we examined allow a comparison of settlement rates inside and outside of MPAs, our work focused on variations of larval inputs to MPAs rather than the possible effects of MPAs on larval supply. There are at least two reasons for this. First and foremost, even if MPAs affect stocks and ultimately the larval supply, our study was conducted too soon after MPA establishment to detect any possible effects. Second, all of our target species have long-lived (> 3 weeks to months) planktonic larvae, making the detection of any stock-to-recruitment signal problematic.

Variability in settlement within and/or between sites poses problems for making comparisons of annual settlement among, for example, spatial gradients from the inside to the outside of an MPA or among MPAs. This is dramatically illustrated by our data from station SC3 inside of Gull Island MPA. During our study most of the settlement occurred in a single sample date in June 2006 (Fig. 2). We did not anticipate this high station-to-station asynchrony in settlement, as previous studies found

relatively high station-to-station synchrony among even more widely spaced stations (Ebert et al. 1994; Schroeter and Dixon 2006). Understanding the degree of synchrony in settlement is important to the design of monitoring programs (e.g., determining how many study sites to include in a program). Even though our study was unable to provide an estimate of the number of stations necessary to adequately estimate differences in settlement inside and outside of MPAs, the results indicate that single stations are certainly insufficient and could result in an under- or overestimate of yearly settlement within a particular area.

Our results indicate that some areas may consistently experience low larval settlement, which may have important implications for evaluating the performance of MPAs as well as various management actions. Stations receiving much lower larval supplies may take longer to recover depleted populations, or be less suitable for restoration efforts based on natural replenishment, than areas with greater settlement. Thus, data on settlement rates can serve as important covariates in evaluating the performance of MPAs (or other management practices), allowing sites to be compared based on the magnitude of larval input.

Finally, studies of settlement rates can be useful in fisheries management. To our knowledge, the management of nearshore invertebrate fisheries in California relies almost exclusively on fishery-dependent data (e.g., harvest in pounds, species landed, fishing effort, individual size, and sex ratio measurements). Settlement data provide a fishery-independent measure of stock health and a means for evaluating the role of larval supply in regulating adult populations of economically and ecologically valuable benthic invertebrates. Maintaining a long-term data set on settlement and oceanographic conditions also provides a robust measure of stock condition in the face of changes in large scale, long-term oceanographic-related features and climate.

In conclusion, despite the seemingly extensive design suggested by results of the present study (i.e., unbroken strings of biweekly sampling at all sites of potential interest), we argue that monitoring settlement can be both an informative and cost-effective approach to acquiring estimates of stock condition and evaluating MPAs. While many sampling events are required, each event requires relatively little effort. We have maintained such a design for 14–16 years as proof of the feasibility of our approach. A key element in maintaining the scope of such a study has been the participation of fishing partners for both funding and in-kind support.

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