

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

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Abstract--We explored variability in the settlement rates of sea urchins (*Strongylocentrotus franciscanus*, *S. purpuratus*), and rock crabs (*Cancer spp.*) across different spatial (100's of m to 90 km) and temporal (biweekly to decadal) scales adjacent to Santa Cruz and Santa Rosa 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 2 marine protected areas (MPAs) at the islands or suspended from piers. Island samples (brushes and tuffys) were retrieved and replaced using methods that we developed enabling surface-based retrieval. Larval settlement varied dramatically on a scale of 100's 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). Although more data are needed from the islands, our results suggest that local and regional scale variability in larval settlement could have important implications for MPAs and for sampling design. 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.

Keywords: invertebrate settlement, sea urchin, rock crab, spatial and temporal variability, channel islands, benthic recruitment

INTRODUCTION

Shallow rocky reefs are critically important nearshore coastal ecosystems of the California Channel Islands. 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 (reviews by Morgan 2001 and Underwood and Keough 2001, Mitarai et al. 2008). Red and purple sea urchin adults, for example, are sedentary and confined to particular reefs, likely move no more than a few kilometers and as little as 10's to 100's 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). Under some circumstances larvae may be retained in the vicinity of the source population as a result of local oceanographic conditions or larval behavior (Keough, 1988). 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 a MPA probably recruit to populations at distance from the MPA. Conversely, populations of these species within a MPA may be maintained by larvae produced outside of the MPA. In addition, settlement rates can vary among different species and affect the recovery time of 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 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 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 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 (100's 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 bi-weekly to decadal, 3) among species, and 4) relative to benthic recruitment (which is likely affected by post-settlement mortality) at one station. We targeted 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 (*Strongylocentrotus franciscanus*, *S. purpuratus*), and brown and red rock crabs (*Cancer antennarius*, *C. productus*) at three spatial scales. At the smallest scale (100s of meters to kilometers), settlement was compared among 4 locations 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 Pt. MPA (Fig. 1). At a larger scale for island sites (10's of kilometers), settlement was compared among SCI, SRI, and at one station (Landing Cove) on Anacapa Island. Finally, we compared settlement at our island stations to three mainland stations (Gaviota Pier, Ellwood Pier, Stearn's Wharf) (50 to 90⁺ km) for 2006. We also placed data from the island stations in the context of a much larger regional long-term monitoring program, which has been in place since the early 1990's. This long-term program measures larval settlement from a network of brush collectors along the mainland coast, including the three stations in the Santa Barbara area used in this study (Schroeter et al., in progress). The sampling station at Anacapa Island 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).

Measurement of settlement and benthic recruitment

We measured settlement at SCI and SRI using two types of collectors: wood-handled scrub brushes and "tuff" scrub pads. At these stations, four brushes and two tuffs 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 tuffs were retrieved and replaced using methods we developed for this study that allowed surface-based retrieval. Brush and tuff 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 tuffs were placed on ice for transport and processing at UCSB following methods in Ebert et al. (1994). At the mainland and Anacapa Island 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 Anacapa Island 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 2 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 bi-weekly 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 among sites with ANOVA. We assessed variability in settlement across spatial scales ranging from stations, inside and outside of MPAs, and between islands using commonality analysis, which decomposes the squared multiple correlation into the proportion of the explained variance of the dependent variable (e.g., settlement rates) associated the different spatial scales (Siebold and McPhee 1979, Rowell 1991). We examined the relationship between settlement and recruitment first by simply 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

The settlement of urchins on brushes and tuffys was highly correlated (total urchins-- $r^2=0.75$, No. tuffy $^{-1} = 1.32 \cdot (\text{No. brush}^{-1}) + 1.86$). A similar pattern was found for crabs (total crabs-- $r^2 = 0.68$, No. tuffy $^{-1} = 2.76 \cdot (\text{No. brush}^{-1}) - 0.06$). For this reason, we present only the data from the brushes here. Although there was no settlement of red rock crabs at the island stations during our study, there was considerable small-scale variability (across 100s of meters to a few kilometers) in the settlement of purple and red sea urchins and brown rock crabs within the Santa Cruz and Santa Rosa Island sites. Some stations experienced generally higher settlement of these three species than others during our study (Fig. 2), with settlement 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. Variability among stations was particularly noticeable for purple urchins on June 11 at SCI when settler density was 3 to 4x higher at station 3 compared to the next highest station (station 4).

While the abundance of settlers varied among stations, settlement for purple urchins at SRI was highly correlated among stations over time (Table 1, Fig. 2). This pattern was not evident for red urchins or brown rock crabs, both of which had much lower settlement. Correlation in settlement among stations was weaker for purple urchins at SCI than SRI with a significant correlation only between SCI stations 2 and 4 (Table 1). There was no correlation in settlement over time between 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, there was no difference in average settlement 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. 4).

Island vs. 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 the mainland (mean = 0.22 settler brush $^{-1}$ week $^{-1}$) and Anacapa Island (mean = 0.04 settler brush $^{-1}$ week $^{-1}$) (Fig. 3). Similarly, settlement of red urchins was higher at

SCI and SRI (mean = 0.22 settler brush⁻¹ week⁻¹) than the mainland (mean = 0.03 settler brush⁻¹ week⁻¹) and Anacapa Island (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 red rock crabs occurred only at our mainland stations and was very low (about an order of magnitude lower than brown crabs--data not shown).

Examining our data from 2006 within the context of the 16-year dataset indicates that relative settlement between the island and mainland sites varied among these three species (Fig. 3). Settlement of purple urchins at the mainland and Anacapa Island stations was generally much lower in 2006 compared to the long-term average settlement at those stations (Fig. 3). The general patterns of settlement were very different for red urchins. Settlement at Anacapa Island and mainland stations in 2006 was similar to long term averages, whereas settlement at SCI and SRI stations (with the exception of station 1 on SRI) was generally much higher than the long-term averages at the mainland and Anacapa Island. The pattern of brown rock crab settlement was similar to that found for purple urchins for the Anacapa Island and mainland stations (i.e., 2006 values generally lower than the long-term averages, with the exception of the Anacapa Island station). Settlement of brown rock crabs at SCI and SRI stations in 2006 was generally similar to values at the mainland and Anacapa Island stations, with the exception of station 4 at SCI, where settlement was much higher (Fig. 3). Comparisons between 2006 and long-term settlement patterns were more complicated. Long-term averages at the Gaviota and Ellwood pier stations were similar to settlement at station 4 on SCI, but were much higher than at any of the other stations.

Settlement vs. benthic recruitment

We explored the relationship between settlement and recruitment into the benthic population from 1994 through 1998 using the brush data and the abundance of purple and red urchins ≤ 30 mm diameter in the ARMS located at the Landing Cove station on Anacapa Island (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. We explored the relationship between settlement and benthic recruitment at the Landing Cove, Anacapa Island, using the mean abundance of settlers on brushes and the abundance of urchins ≤ 30 mm in the ARMS at time lags of 1 and 2 years to account for variability in growth and settlement.

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 100's of meters (station scale) to 10's of kilometers (Island/Mainland scale). We also found significant temporal variation in settlement across our shortest (bi-weekly) 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. For our other island site (SCI), however, the timing of settlement peaks generally differed among stations, some of which were quite close to one another (< 500 m; Fig. 1). Oceanographic conditions, such as the direction and speed of prevailing alongshore currents and upwelling, which influences cross shelf transport, 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 Channel Islands and mainland (Otero and Siegel. 2004) may have contributed to the dramatically lower settlement of urchins observed at our two most easterly mainland stations compared to SRI and SCI in 2006 and relative to the 16 average. Our findings suggest that local hydrographic conditions (e.g., local eddies or variability in water flow created by bottom topography) may be important as well in modulating larval delivery to subtidal reefs at much smaller spatial scales.

Of potentially greater importance to benthic populations than short-term variability in the magnitude and timing of settlement pulses, however, is the total number of settlers that arrive on the 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 following the 1992 and 1993 El Ninos (Ebert et al. 1994, Schroeter and Dixon 2006, Morgan et al. 2001). 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 are 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, but no relationship was evident for purple urchins. 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 at our study sites.

Variability in settlement within and/or between sites raises difficult practical problems for making comparisons of annual settlement among spatial categories of interest; for example, along 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. Here, most of the settlement measured during our study occurred in a single survey in June 2006 (Fig. 2). We did not anticipate this high station-to-station asynchrony in settlement as results from earlier work that included stations more widely spaced geographically, showed relatively high station-to-station synchrony (Ebert et al. 1994; Schroeter and Dixon 2006). Understanding the level of

synchrony in settlement is important for designing monitoring programs (e.g. determining how many study sites to include in a program). Even though our study is unable to provide an estimate of the number of stations necessary to adequately estimate differences between the insides and outsides of MPAs, the results indicate that single stations are certainly insufficient and could result in an under or over estimate of yearly settlement within a particular area.

In addition to providing information useful in sampling and experimental design, our results, which indicate that some areas may consistently experience low larval settlement, have important implications for evaluating the performance of MPAs and 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 one to potentially adjust comparisons among sites 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., data derived from catch such as pounds and species landed, fishing effort, and catch characteristics such 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. Maintaining a long-term data set on settlement and oceanographic conditions provides a robust measure of stock condition in the face of changes in large scale, long-term oceanographic forcing features.

In conclusion, despite the seemingly extensive design suggested by results of the present study (i.e. unbroken strings of bi-weekly sampling at all sites of potential interest), we argue that monitoring settlement can be both informative and cost effective. 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 such a study has been the participation of fishing partners for both funding and in-kind support.

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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. Significant correlations indicated with asterisks: *P < 0.05, **< 0.01, ***< 0.001. Missing data indicated by ----.

Purple urchin							
	SCI 2	SCI 3	SCI 4		SRI 2	SRI 3	SRI 4
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			-0.033

FIGURE LEGENDS

- Figure 1. Map showing the location of our temporary stations moored inside and outside of Gull Island MPA at Santa Cruz Island (SCI) and Skunk Point MPA at Santa Rosa Island (SRI), and stations at Anacapa Island and the mainland coast.
- Figure 2. Settlement of purple and red sea urchins and brown rock crab onto brush collectors sampled at approximate two week intervals. Note differences in scale of the y-axis between figures.
- Figure 3. Comparison of settlement rate onto brush collectors of purple and red urchins and brown rock crab among island and mainland stations in 2006 and between SCI and SRI in 2006 and historical data from Anacapa Island and the mainland averaged from 1990 through 2006. Note differences in scale of the y-axis between figures.
- Figure 4. Percent of variation in settlement on the brushes attributable to differences among stations, stations inside and outside of MPAs, and sites (island versus mainland).
- Figure 5. Relationship between the mean number of urchin settlers on the brushes and the number of urchins < 30 mm in the ARMS at the landing cove, Anacapa Island 1994 through 1998. Data from the brushes averaged from -- month to month. Note differences in scale of the y-axis between figures.

Figure 1

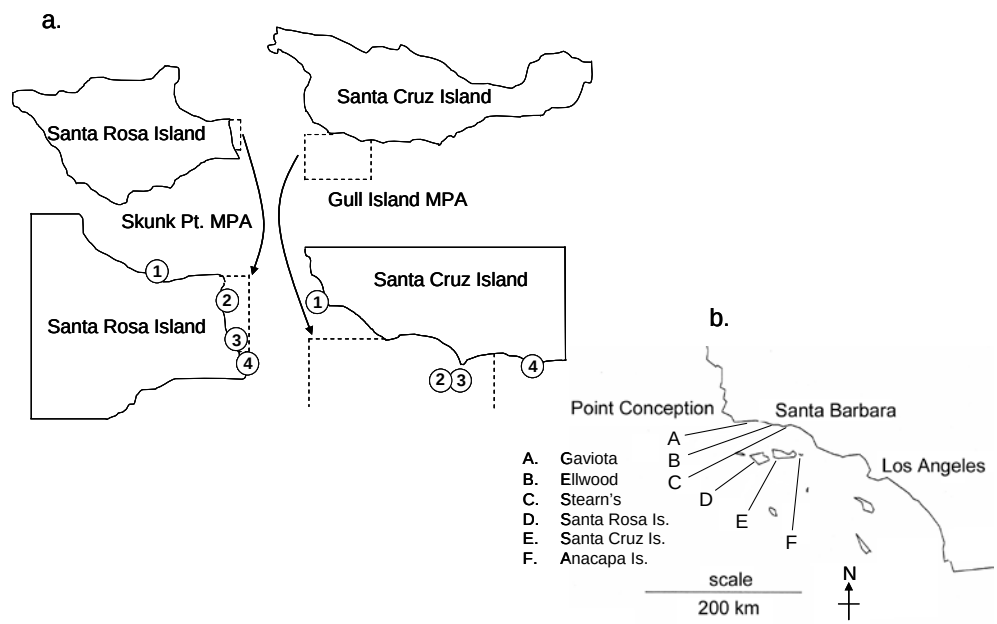


Figure 2.

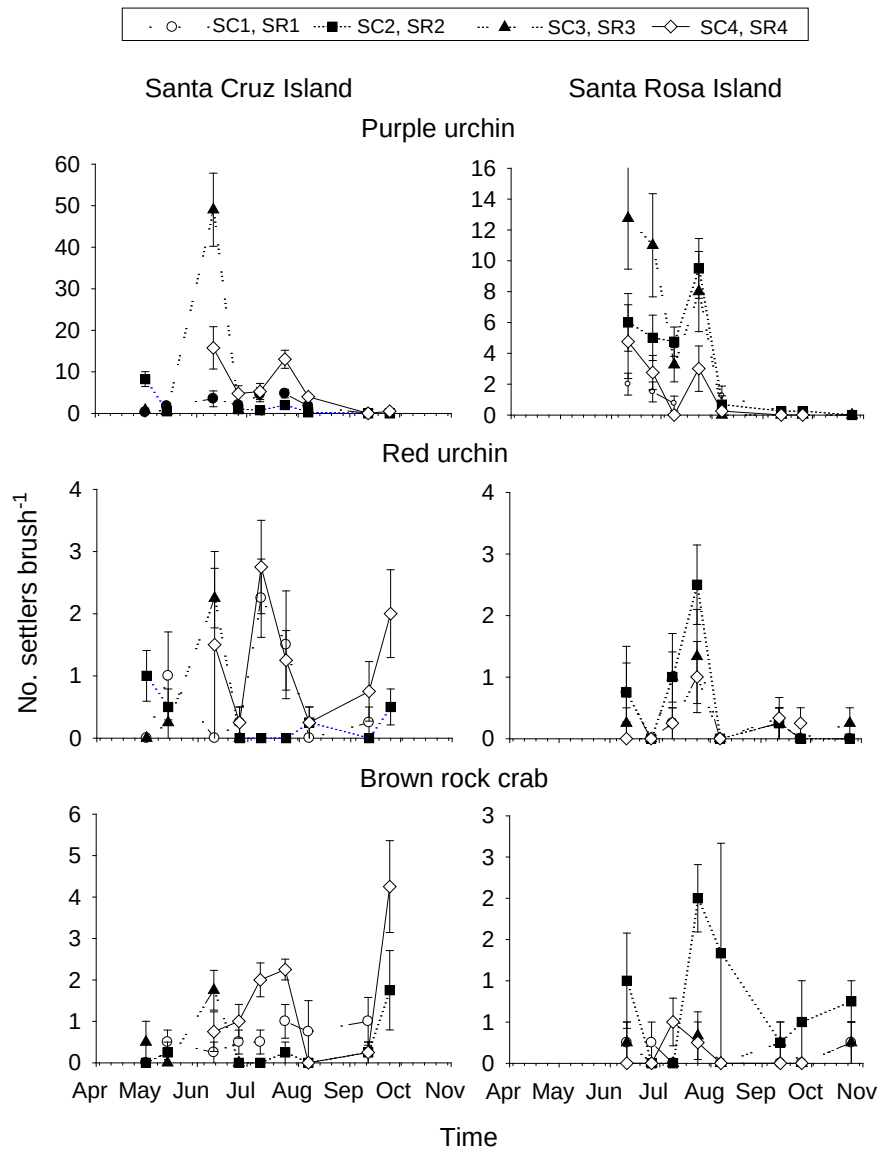


Figure 3

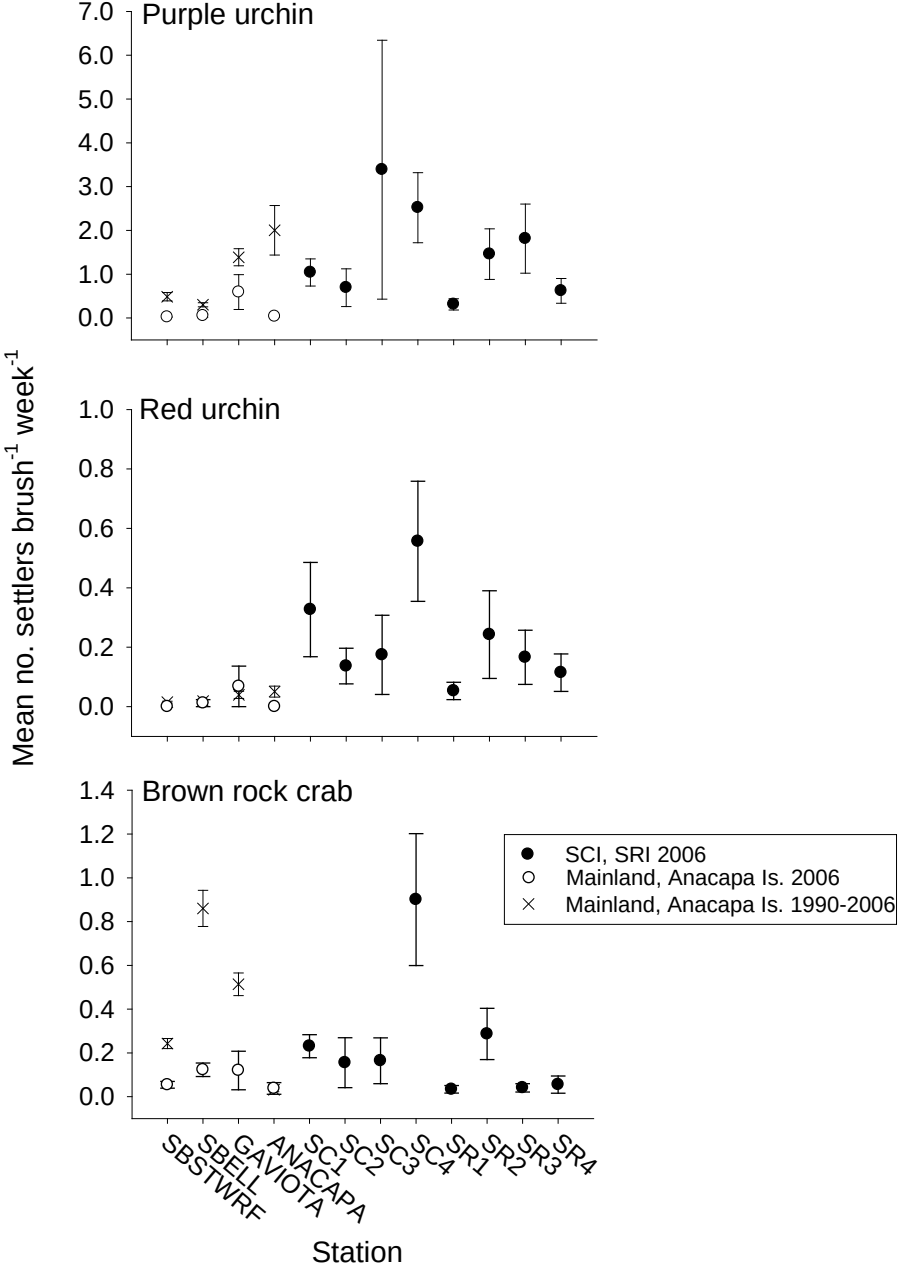


Figure 4

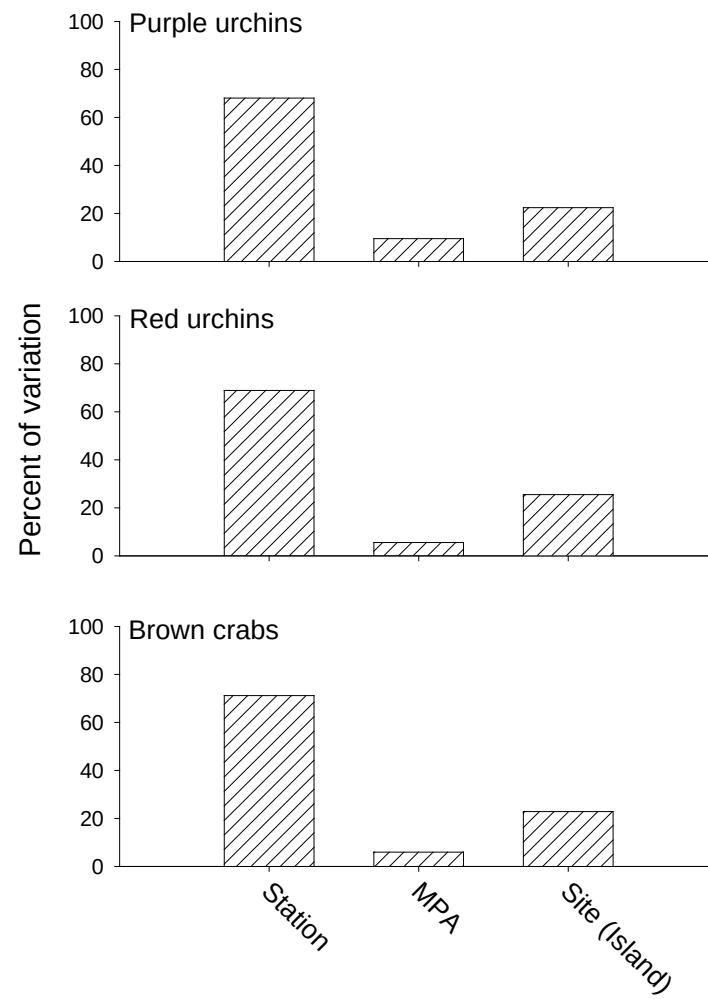


Figure 5

