REGIME SHIFTS, COMMUNITY CHANGE AND POPULATION BOOMS OF KEYSTONE PREDATORS AT THE CHANNEL ISLANDS

CAROL A. BLANCHETTE[1], DANIEL V. RICHARDS[2], JOHN M. ENGLE[1], BERNARDO R. BROITMAN[3] AND STEVEN D. GAINES[1, 3]

[1]Marine Science Institute, University of California, Santa Barbara, CA 93106
blanchet@lifesci.ucsb.edu
[2]Channel Islands National Park, 1901 Spinnaker Drive, Ventura, CA 93001
[3]Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106

Abstract—The ochre seastar (*Pisaster ochraceus*) is a common inhabitant of rocky intertidal shores from Alaska to Baja. It is the quintessential "keystone" predator, and it has been shown to have an inordinately large influence on the diversity and structure of rocky shore communities. For this reason, it has been a focal species in the monitoring programs of the Channel Islands National Park, the Channel Islands Research Program and the Partnership for Interdisciplinary Studies of Coastal Oceans. Here we combine data from these monitoring programs to evaluate the time series of abundance of this predator at several rocky, intertidal sites around the northern Channel Islands. Densities of seastars were lowest at all sites in 1997/1998 coincident with a moderately strong El Niño period and an outbreak of wasting disease affecting multiple seastar species. Sharp population increases have occurred at many island sites (particularly the south-facing sites) beginning in 1999, and in most cases are continuing to increase at present. Here we correlate seastar abundances over time at the Channel Island sites with temperature data from a seven-year time series of satellite-based sea surface temperature to evaluate one of the major bio-physical drivers affecting population abundance. We also present pre- and post-population boom data on the vertical zonation of mussels (the primary prey of the seastar) at three sites on Santa Cruz Island to evaluate the potentially large effects of these population booms on the structure of these rocky intertidal communities.

Keywords: intertidal, Pisaster ochraceus, population size, predation, regime shift, Santa Cruz Island, seastar

INTRODUCTION

The California Channel Islands have seen dramatic changes in the structure of terrestrial biological communities in the last decade as a result of introductions of non-native species and shifts in the structure of food webs (Roemer et al. 2001, Roemer et al. 2002). The marine communities of the Channel Islands have also been greatly altered over the last several decades due to various causes such as over-fishing, disease epidemics and changing climatic regimes. One of the most conspicuous population-level changes in the marine environment of the Channel Islands in recent years has been the near extinction of the black abalone, *Haliotis cracherodii* (Tissot 1988, Davis 1993, Lafferty and Kuris 1993, Vanblaricom et al. 1993, Friedman et al. 1997). Prior the 1980s, abalone were extremely abundant at the Channel Islands and occupied so much space in the low rocky intertidal zone that they were found stacked on top of one another (Douros 1987). The 'withering foot' disease spread through populations of abalone that were apparently stressed from the extremely warm water temperatures during the 1982/1983 El Niño event (Tissot 1988, Lafferty and Kuris 1993, Friedman et al. 1997). Most of the abalone populations of the Channel Islands collapsed to near extinction by the early 1990s (D. Richards and B. Tissot unpubl. data). The space vacated by abalone in these low zone communities has been colonized by a variety of sessile invertebrates and algae, and only recently has a large mobile species, the ochre seastar (*Pisaster ochraceus*), become common.

The ochre seastar is a widely distributed, dominant forcipulate asteroid of the intertidal and shallow subtidal on the west coast of North America, ranging from Alaska to Baja California (Morris et al. 1980). It is well known for the important ecological role it plays in community dynamics. It is a keystone predator and has a great influence on the structure and diversity of intertidal communities through preferential predation on the competitive dominant in the system, the California mussel (*Mytilus californianus*; Paine 1966, Dayton 1971, Paine 1974, Menge et al. 1994, Navarrete and Menge 1996). In the last decade we observed a gradual increase in the densities of *P. ochraceus* at several sites throughout the Channel Islands.

Here we document the increase of *P. ochraceus* in rocky intertidal communities of the northern California Channel Islands from 1994 to 2003. We compare *Pisaster* population trends with a seven-year time series of satellite-derived sea surface temperature indicating an oceanographic regime shift. Finally, we address the community-level consequences of increased *Pisaster* densities at three sites on Santa Cruz Island where seastar densities have recently increased.

MATERIALS AND METHODS

We collected data on seastar abundances at 17 rocky intertidal sites throughout the northern Channel Islands (see map in Fig. 1). Data on seastar densities at sites throughout the northern Channel Islands were compiled from three rocky intertidal monitoring programs: the Channel Islands Research Program, the National Park Service and the Partnership for Interdisciplinary Studies of Coastal Oceans. Although many different observers have collected data over time, we analyzed only data based on a standardized protocol. Seastar counts at each site reflect the number of seastars enumerated by a single observer in a thirty-minute period. We used the timed search method because it is difficult to accurately assess seastar densities using fixed plots on flat surfaces, as seastars primarily occur in channels and crevices. As the vast majority (>95%) of intertidal seastars found at each site were *P. ochraceus,* we include data for this species only. We counted seastars at each site in spring and fall each year from 1994 to 2003; however many gaps in the dataset exist due to poor weather conditions, large swells or lack of personnel.

To characterize site-scale patterns of sea surface temperature (SST), we analyzed a seven-year time series (from 1996 to 2002) of SST from the Advanced Very High Resolution Radiometer (AVHRR) using the version 4 AVHRR Pathfinder algorithm plus erosion filters for cloud masking in

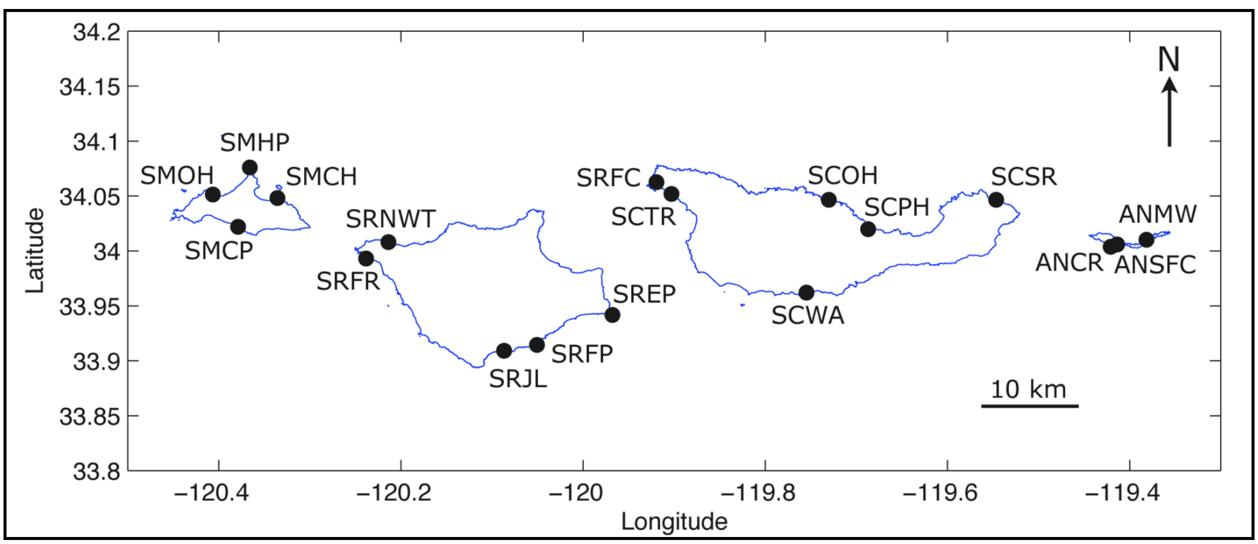

Figure 1. Map of intertidal monitoring sites at the Channel Islands. ANCR = Cat Rock, ANMW = Anacapa-Middle West, ANSFC = Anacapa-South Frenchy Cove, SMCH = San Miguel-Cuyler Harbor, SMCP = San Miguel-Crook Point, SMHP = San Miguel-Harris Point, SMOH = San Miguel-Otter Harbor, SCFC = Santa Cruz-Fraser Cove, SCOC = Santa Cruz-Orizaba Cove, SCPH = Santa Cruz-Prisoner's Harbor, SCSR = Santa Cruz-Scorpion Rock, SCTR = Santa Cruz-Trailer, SCWA = Santa Cruz-Willows Anchorage, SREP = Santa Rosa-East Point, SRFP = Santa Rosa-Ford Point, SRFR = Santa Rosa-Fossil Reef, SRJL = Santa Rosa-Johnson's Lee, SRNWT = Santa Rosa-Northwest Talcott.

the vicinity of cloud edges (Casey and Cornillon 1999). We used only the pixels lying immediately offshore from the coastal study sites around SCI and calculated the long-term temporal mean as a simple approximation to oceanographic conditions.

To evaluate the potential community-level effects of seastar increases, we examined shifts in the zonation of the primary prey and competitive dominant, *M. californianus* (sensu Paine 1974). We utilized data from a related intertidal monitoring project at three Santa Cruz Island sites (Prisoners, Willows and Fraser; Fig. 1). As part of the monitoring we recorded species identification at pre-determined intervals along 11 vertical (i.e., perpendicular to shore) transects at each site. At the Willows site we conducted these surveys in 2000 and 2003. At Prisoners and Fraser sites we conducted surveys in 2002 and 2003. To estimate vertical and elevational mussel bed shifts we calculated the average difference between the lowest limit of mussels along each transect between years.

RESULTS

Although seastars have generally increased in abundance at the Channel Islands over the last decade, the magnitude of this increase is extremely variable among islands and among sites. At Anacapa Island, *Pisaster* increased only at the middle-west but not the west island sites (Fig. 2a). At San Miguel Island, *Pisaster* seem to have increased only temporarily in late 1999 at Crook Point, with a subsequent decline in density following 1999, although densities have remained higher than the period prior to 1999 (Fig. 2b). Densities at the three other sites on San Miguel Island have remained relatively constant over time. At Santa Cruz Island, the largest of the Channel

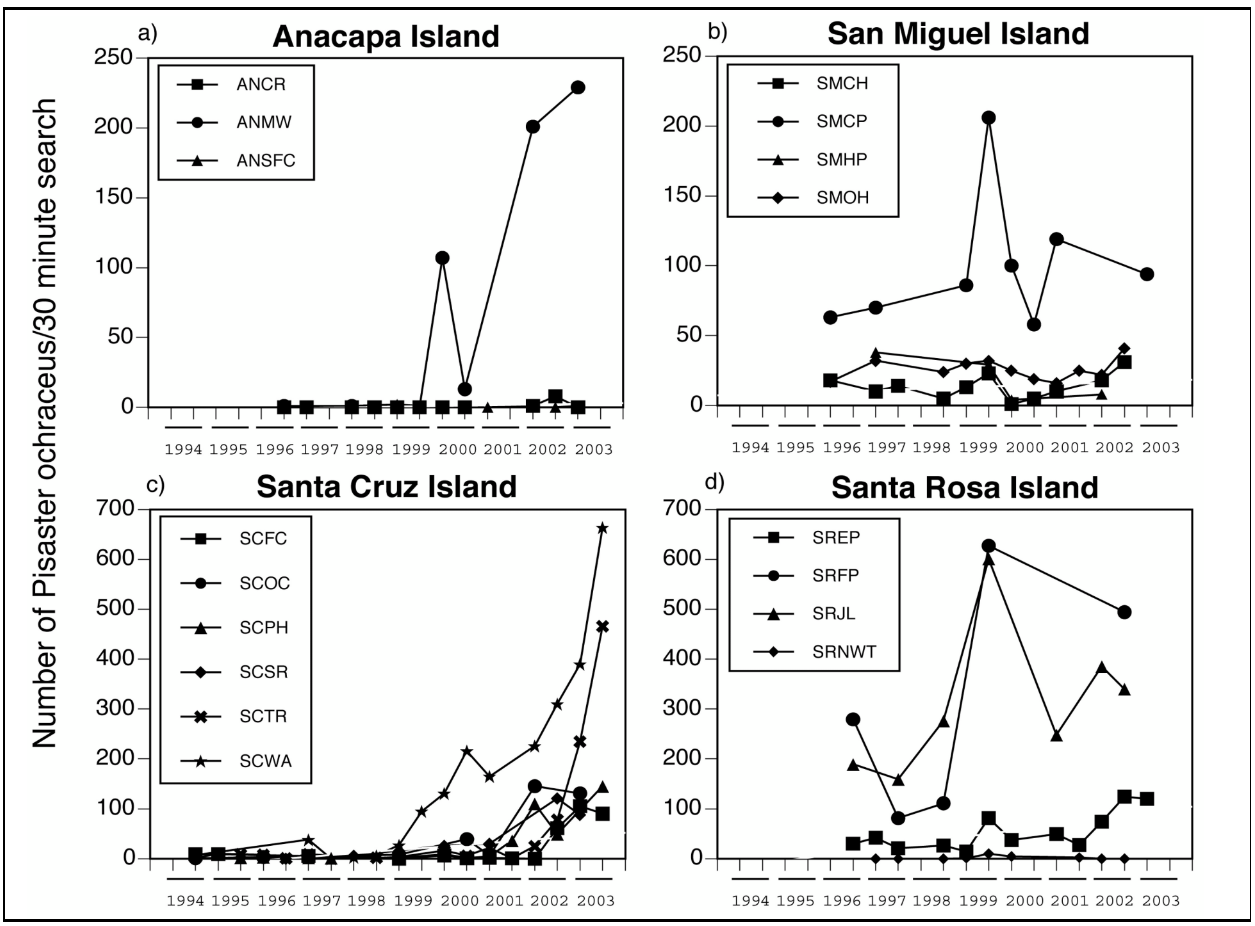

Figure 2. Number of *Pisaster ochraceus* counted in a 30-minute search per site. Counts are biannual (spring and fall) at each site. Site abbreviations are as in Fig. 1.

Islands, the population increases of *Pisaster* were most apparent (Fig. 2c). *Pisaster* densities at all sites collapsed to nearly zero in 1998. Densities increased rapidly at Willows, from zero in 1999 to nearly 700 in 2003. *Pisaster* increases at most other Santa Cruz Island sites occurred following fall 2001. *Pisaster* abundances increased dramatically at the two southernmost sites on Santa Rosa Island in late 1999 (Fig. 2d). Seastars increased more slowly at the easternmost site in 2002. In all cases, seastar abundances were at their lowest point during the 1997/1998 El Niño period and increased at all sites following 1999. In general, *Pisaster* increases were most apparent at southeastern sites.

Long-term mean sea surface temperatures highlight the great variability among years (Fig. 3). The intensely warm temperatures during the 1997/1998 El Niño are apparent, and the effects of the warm temperatures persist even through the winter period of 1997/1998. A strong west to east gradient is apparent in temperature profiles consistent with regional oceanographic patterns.

We observed significant upward shifts in mussel abundance and zonation at the Prisoners and Willows sites, but not at the Fraser site (Table 1). At both these sites we observed “fronts” of foraging seastars and swaths of bare space along the lower edge of the mussel bed. Empty mussel shells littered the beaches near both these sites. Although, seastars also increased at the Fraser site, the magnitude of the increase occurred later and was not as great as those at the other sites. We also did not observe foraging fronts of seastars at the Fraser site.

DISCUSSION

Pisaster densities have increased at several rocky intertidal sites throughout the northern Channel Islands in the last five years; however, these changes were not observed at all island sites and were most apparent only at southern/eastern sites. In general, the southern/eastern sites tend to be warmer and are oceanographically linked to southern California countercurrents. Although we have no information on larval sources, we suspect that larvae have been delivered to the islands from the southeast due to the relatively high increases in populations only at the southeastern island sites. *P. ochraceus* have planktotrophic larvae with a relatively long larval period. Strathman (1978) reports that the time from fertilization to settlement can be between 76 and 228 days. It is difficult to estimate potential larval sources with such a huge window of larval competency. Sewell and Watson (1993) observed a major recruitment of *P. ochraceus* in a semi-enclosed bay on Vancouver Island, and suggested that recruits there resulted from local retention due to the restricted flow in the embayment. The Channel Islands intertidal sites are all relatively open coast sites with high flow rates, and we have no reason to suspect high retention in this system. Although we do not have

Table 1. Mean vertical and elevational shifts over time in the lower limit of the mussel beds at Fraser, Prisoners and Willows sites on Santa Cruz Island. The *t* statistic and *P* values are based on a non-parametric Wilcoxon Signed-Rank test against a hypothesized zero mean shift.

	Mussel Bed Site		
	Fraser	Prisoners	Willows
Distance (m) across shore			
mean	-0.511	-0.518	-3.821
SD	2.266	0.504	2.334
t statistic	-0.677	-3.413	-4.330
P value	0.517	0.006	0.005
Elevation (m) above MLLW[a]			
mean	-0.153	0.136	0.291
SD	0.221	0.132	0.276
t statistic	-0.208	3.421	2.786
P value	0.840	0.006	0.031

[a] MLLW: mean lower low water.

data on size frequencies of *Pisaster* from all sites over time, most of the seastars that we have recently observed at these intertidal sites are relatively large. It is very rare to find small *Pisaster*, and we think that they may recruit to cryptic habitats (such as mussel beds or deep in crevices) where we are not able to count them.

At all sites the increases in seastar densities occurred during or after 1999, following the strong El Niño of 1997/1998. Eckert et al. (1999) report widespread mortality of several species of seastars, including *P. ochraceus* during the 1997/1998 El Niño period. They concluded that the elevated temperatures during this event facilitated the spread of a bacterial infection termed “wasting disease”. The extremely warm temperatures of the 1997/1998 El Niño across all the island sites are evident in the temperature time series (Fig. 3). We observed very few *Pisaster* during the 1997/1998 period most likely due to this El Niño event and mortality due to the reported seastar wasting disease. The sharp increases in density at some sites occurred immediately following this El Niño period. We hypothesize that the increased temperature stress during the El Niño may have caused a mass spawning event. The recruitment and subsequent population boom may reflect the result of both this mass spawning and appropriate oceanographic conditions at southeast facing sites for delivery of competent larvae to shore.

These recent seastar population booms follow the population collapse of the black abalone. Seastars and abalone both occupy similar habitat: low zone rocky intertidal cracks, crevices and channels. It is conceivable that the decline of the black abalone indirectly facilitated the population increase of seastars due to reduced competition for space in the appropriate habitat. Black abalone have been abundant at the Channel Islands for thousands of years (Arnold and Tissot 1993) and have only become effectively extinct from this system in the last decade. We have no quantitative information on seastar abundances over long time periods; however, there are no reports of high

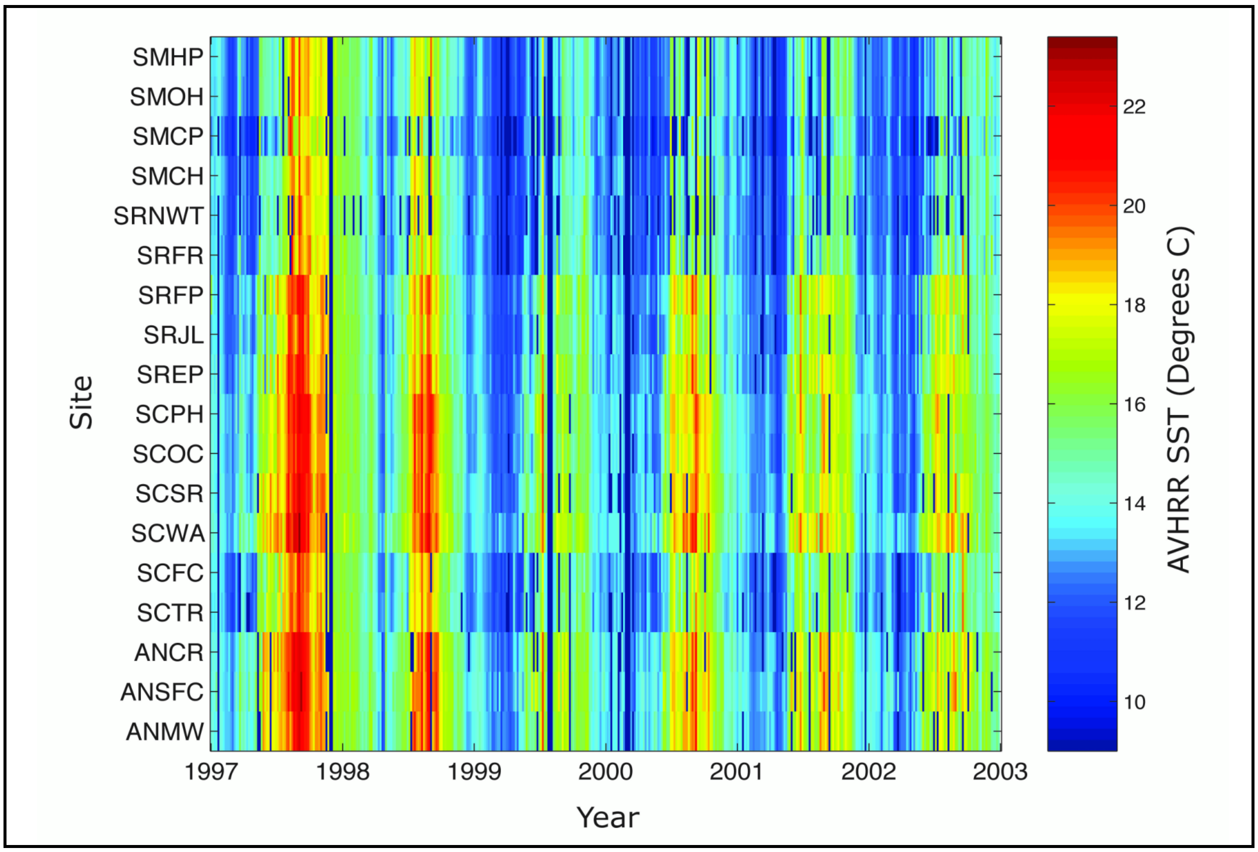

Figure 3. Daily mean Advanced Very High Resolution Radiometer Sea Surface Temperature (AVHRR SST) from September 1996 to September 2002. Site abbreviations are as in Fig. 1. The bar at the right depicts the water temperature legend.

seastar abundances at any of the Santa Cruz Island sites as far back as 1946 (Hewatt 1946). We hypothesize that the recent declines in black abalone across the Channel Islands may have indirectly facilitated seastar population booms triggered following the strong 1997/1998 El Niño.

It is clear from our observations that the recent large increases in seastar densities have had a dramatic effect on community structure at many island sites. The greatest visible effect has been the virtual clearing (and near elimination at some sites) of low- to mid-zone mussels. Along the Washington coast Paine's (1974) experimental removal of *Pisaster* resulted in a measurable downward shift in mussel zonation and a consequent decrease in species diversity. The recent Channel Islands *Pisaster* increases provide a natural experiment—does *Pisaster* "addition" result in an upward shift in mussel zonation? Although the evidence is truly observational and not experimental, we think that the *Pisaster* increases have had a large community effect at some Santa Cruz Island sites. We observed a significant shift upward of the mussel bed at both the Willows and Prisoners sites on Santa Cruz Island over the period of large *Pisaster* increases. At both sites, we observed high rates of seastars foraging on mussels and unusually high numbers of empty mussel shells in the subtidal and on beaches surrounding these sites. Swaths of bare rock with mussel byssal threads and solid advancing fronts of *Pisaste*r composed the low zones at these sites at the time of our last survey. We did not observe significant shifts in mussel zonation at the Fraser site, but we also did not observe foraging fronts of *Pisaster* or unusually high numbers of empty mussel shells along adjacent beaches. Although *Pisaster* densities have increased slightly at the Fraser site, the densities there were still relatively low and have only increased in the last year. We do not know how long *Pisaster* densities can remain elevated if prey recruitment is inadequate. We intend to continue monitoring these populations of predators and prey to understand the factors controlling the structure of these communities.

CONCLUSIONS

The predatory seastar, *Pisaster ochraceus*, has increased greatly in abundance since 1999 at sites throughout the northern Channel Islands, particularly south/eastern facing sites. Population trajectories are currently continuing to increase at most sites. The primary increase seems to be due to a massive recruitment event following the 1997/1998 El Niño. At high density sites, *Pisaster* has taken over space in the low rocky intertidal zone formerly occupied by the black abalone, now effectively extinct at most island sites. The consequence of this massive population boom of seastar predators has been a significant increase in mussel predation and a significant upward shift of the lower limits of mussel beds at two Santa Cruz Island sites.

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