SPATIAL PATTERNS OF INTERTIDAL COMMUNITY STRUCTURE ACROSS THE CALIFORNIA CHANNEL ISLANDS AND LINKS TO OCEAN TEMPERATURE

CAROL A. BLANCHETTE[1], PETER T. RAIMONDI[2] and BERNARDO R. BROITMAN[3]

[1]Marine Science Institute, University of California, Santa Barbara, CA 93106 USA
(blanchette@msi.ucsb.edu)
[2]Department of Ecology and Evolutionary Biology, University of California, Long Marine Lab,
100 Shaffer Road, Santa Cruz, CA 95060
[3]National Center for Ecological Analysis and Synthesis, Santa Barbara, CA 93106 USA

Abstract—We evaluated the spatial patterns in rocky intertidal community structure through surveys of rocky intertidal communities at the CA Channel Islands. We sampled (22) sites spread across 7 CA Channel Islands: San Miguel (2), Santa Rosa (5), Santa Cruz (6), Anacapa (3), San Nicolas (2), Santa Barbara (2) and Santa Catalina (2) over a 5-year period from 2001 to 2006. We used non-metric multidimensional scaling analyses to examine spatial patterns of community similarity among island sites. We found strong evidence for spatial variation in community similarity across the islands. Sites on Santa Catalina Island were most similar to each other and had very little similarity to all other island sites. In some cases, nearby sites within the remaining 6 islands formed groups most similar to each other, however, in many cases similarity was higher among distant sites, than among sites on the same island. Nearshore oceanographic conditions, as indexed by sea surface temperature (SST), were highly correlated to the overall pattern of community similarity. Similar to findings from a smaller-scale study at Santa Cruz Island, we observed strong associations between SST and patterns of community structure. Invertebrate abundance was highly correlated with SST across all sites, while macrophyte abundance showed the opposite response. The spatial patterns of community similarity found here and the strong links to ocean temperature are strikingly similar to those recently described for intertidal communities along the mainland Pacific coast of North America and the coast of Chile. We suggest that similar oceanographic dynamics and ecological interactions may drive patterns of community structure across these large spatial scales.

Keywords: Channel Islands, intertidal, community structure, biogeography, species similarity

INTRODUCTION

A major goal of ecology is to understand the factors contributing to the distribution and abundance of organisms at a variety of spatial scales. As broad scale questions are increasingly dominant in conservation and management, marine ecologists have been pressed to examine linkages between patterns and processes operating at spatial scales larger than individual sites (Dayton and Tegner 1984, Polis and Hurd 1996, Schiel et al. 2004, Schoch et al. 2006). In marine systems, this ‘scaling-up’ has resulted in a significant conceptual shift in our understanding of the connections among populations and communities and the importance of benthic–pelagic linkages. Benthic communities are inextricably linked to the oceanic environment through the delivery of food, nutrients, propagules and larvae. The oceanographic processes driving the delivery of these constituents span large spatial scales and thereby connect distant onshore communities (Gaines et al. 1985, Roughgarden et al. 1988, Bustamante et al. 1995, Menge et al. 1997b, Schiel 2004).

Recent ecological studies from eastern boundary upwelling ecosystems around the world support a strong coupling between coastal oceanography and nearshore benthic community structure. In South Africa, it has been established that large-scale patterns of nearshore community structure covary with gradients of productivity and wave exposure (Bustamante and Branch 1996). Along the coast of Chile, several studies provide evidence that oceanographic variability is strongly correlated with the abundance of dominant intertidal functional groups (Broitman et al. 2001, Nielsen and Navarrete 2004). Around New Zealand, rocky intertidal structure and dynamics vary with large-scale oceanographic conditions in nearshore environments (Menge et al. 1999, Menge et al. 2003). On the U.S. west coast, nearshore oceanographic conditions have been shown to determine community structure along the coast of Oregon (Menge et al. 1997a, Menge et al. 1997b) and more recently, along the entire Pacific coast of North America (Blanchette et al. 2008).

Along the US Pacific coast, two major water masses meet at Point Conception, California – the southward flowing California current, and the westward flowing southern CA countercurrent (Hickey 1993). This region is one of the most important biogeographic and oceanographic discontinuities on the west coast of North America (Valentine 1966, Doyle 1985, Burton 1998). The northern region is typified by consistently strong coastal upwelling bringing cold, nutrient-rich waters to the surface resulting in both cold sea surface temperatures along the coast and high nutrient concentrations. The Santa Barbara Channel, immediately south/east of Point Conception is typified by weak seasonal upwelling, which tends to occur in the winter months (Blanchette et al. 2002, Winant et al. 2003). The California Channel Islands are located just offshore from Point Conception and lie within this highly diverse oceanographic region (see Fig. 1). The broad range of sea surface temperatures and oceanographic variability found across the entire Point Conception region are found at a much smaller geographic scale within this island group (see Fig. 2). These islands experience variable mixing between the cold waters of the California current and the warm, nearshore waters of the Southern California Countercurrent (Huyer 1983, Hickey et al. 2003).

The Channel Islands are known to contain an incredibly diverse assemblage of marine species (Neushul et al. 1967, Murray and Littler 1981). This great diversity is due largely to: 1) their location near the boundary of two major biogeographic provinces (the Oregonian and the Californian); 2) their diversity of habitat types and exposure to varying oceanographic conditions; and 3) their high productivity resulting from upwelling of cold nutrient-rich water off Pt. Conception. Oceanographic conditions are known to strongly influence the structure of nearshore biological communities via delivery of nutrients and larvae, and direct influences on growth, productivity and reproduction. Ocean temperature is probably one of the best single correlates of environmental variability in the nearshore environment in cold-temperate regions of the world. Low ocean temperatures at the mesoscale are associated with nutrient influx and increase abundance of primary producers (Nielsen and Navarrete 2004, Broitman and Kinlan

2006). In contrast, elevated temperatures have also been shown to affect rates of foraging and growth (Sanford 2002, Blanchette et al. 2007). Increased temperature is also associated with ocean circulation patterns favoring larval delivery and invertebrate recruitment (Connolly et al. 2001, Broitman et al. 2008).

The biogeographical significance of the exposure of the Channel Islands to different oceanographic temperature regimes was recognized early by Hewatt (1946a) who was among the first to describe the marine invertebrate faunas around Santa Cruz Island and their intermediate biogeographical affinities with the faunal elements characteristic of mainland habitats north and south of Point Conception. Although this early documentation was mainly descriptive and contains only single point measures of seawater temperature, Hewatt (1946a) noted the potential importance of ocean temperature differences across the island to variability in community patterns around the island. More recently, we found that the structure of intertidal communities around Santa Cruz Island was strongly linked to oceanographic conditions as indexed by long term mean ocean temperature (Blanchette et al. 2006). Warmer temperatures were associated with invertebrate-dominated sites and high invertebrate recruitment (Broitman et al. 2005). Cooler temperatures were associated with macrophyte-dominated sites with high algal growth and productivity and reduced invertebrate growth, similar to findings from a range of sites spanning a similar oceanographic gradient around Point Conception (Blanchette and Gaines 2007, Blanchette et al. 2007).

The location of the California Channel Islands provides a unique opportunity to examine the relationship between nearshore oceanographic conditions and biological community structure across a relatively small spatial scale. Here we describe the biogeographic patterns of intertidal rocky shores across the California Channel Islands and examine patterns of species similarity relative to both geographic distance and oceanographic conditions.

MATERIALS AND METHODS

Study Region and Biological Sampling Design

We conducted quantitative surveys at 22 rocky intertidal sites distributed across 7 California Channel Islands: San Miguel, Santa Rosa, Santa Cruz, Anacapa, San Nicolas, Santa Barbara and Santa Catalina over a 5-year period from January 2001 to January 2006. (Fig. 1, Table 1). These sites were all gently sloping (0°-20°) rocky benches and were selected to be as similar as possible in terms of geomorphology, wave exposure, and habitat type (see Blanchette et al. 2008 for more detail). Sites were chosen based on accessibility and to be generally representative of the intertidal flora and fauna of that island region. Sites were also chosen to overlap with existing data collection efforts by several major research groups (PISCO, MARINe, and CINP).

We used a stratified point-intercept sampling method to quantify percentage cover of sessile invertebrate and macrophyte species at each site. A representative shore section 30 m long was designated as the site. A 30-m baseline tape was laid out along the upper edge of the highest intertidal barnacle zone, parallel to the shore. A point-intercept transect was then surveyed perpendicular to the horizontal tape at each 3-m interval, for a total of 11 transects per site. These vertical transects extended from the upper edge of the barnacle zone to about the 0.0 m MLLW level predicted by the tide tables (generally the surfgrass zone). Along each vertical transect the species or taxon located under each point at a pre-determined interval along the tape was scored sequentially. The distance between transects at each site depended on the size and topography of the bench and was calculated to provide at least 100 points sampling points per transect. For example, if a vertical transect extended 20 m, the sampling interval would be 20 cm. For each point, we sampled the taxa directly under the point, then additionally the two nearest taxa within a radius equivalent to half the sampling interval from that point. Percentage cover estimates reported here are based on the primary taxa attached to rock located directly under each point.

Mobile invertebrate taxa (e.g., limpets, snails, whelks) were scored by direct counts within 33 0.25-m^2 quadrats along each of the vertical transects. At each transect, the vertical distribution of high, mid and low zones were assessed visually, and quadrats were randomly placed within each of these zones. Because the predatory seastar (*Pisaster ochraceus*) is much larger than most other intertidal invertebrates, and primarily occurs in channels and crevices, we counted the number of seastars within a 2-m swath centered along each of 11 vertical transects.

Sea Surface Temperature Analyses

We followed the approach of Broitman et al. (2005) and Blanchette et al. (2006) and characterized oceanographic conditions at each site through spatial and temporal patterns of sea surface temperature (SST) from the Advanced Very-High Resolution Radiometer (AVHRR) of a nominal resolution of 1.1 km averaged over 5 days. From the AVHRR dataset we selected the pixels corresponding to the locations of our 22 intertidal sites and averaged the first 3 cross-shelf pixels since missing pixels were common in the nearshore. Long-term means were derived directly from the resulting time series from 1996-2005 (Fig. 2). We chose to use satellite-based SST for this analysis due to the availability of long-term data for all of our study locations. One of the great advantages of using remotely sensed observations is that one can explore biophysical relationships in many parts of the world where satellite-based data are available, but long-term data from in-situ physical instrumentation are not. Long-term satellite data also provide a much better index of the persistence of oceanographic regimes over the extended periods of time and across broad spatial scales.

Data analysis

To examine geographic patterns of community similarity, we used the multivariate methods of Clarke (1993) and the PRIMER 6.1.3 (Plymouth Routines in Multivariate Ecological Research) software package. The data matrix of taxon abundances was square root transformed to reduce the contribution of very abundant species and increase that of rare species. A similarity matrix was constructed using the Bray–Curtis similarity coefficient and cluster analysis was performed using a hierarchical method with group-average linking. We used 2-dimensional, non-metric multidimensional scaling (nMDS) to examine regional segregation among communities (Kruskal and Wish 1978). A SIMPROF test using 10000 permutations was run for the dendrogram to indicate significant group structure at the 0.1% level. For sites sampled in multiple years, we found temporal variability in community structure to be extremely small relative to spatial differences among sites. Based on these findings and in order to focus on spatial patterns, we averaged species abundances across sampling years for all sites. For those groups that differed significantly based on the SIMPROF test, characteristic taxa were then identified using similarity percentage breakdown analyses (SIMPER).

We used Mantel tests to examine the correlation between the matrices of community similarity and coastal distances among sites and differences in long-term mean SST among sites (Legendre 1993, Legendre and Legendre 1998, Legendre et al. 2005). The results of these analyses enabled us to test the prediction that community similarity is correlated with both geographic distance and oceanographic climate (Blanchette et al. 2008). However, two variables may appear to be correlated simply because they are both linked to a third, common variable, such as location in space. Thus, in the presence of autocorrelation, it is necessary to remove the effect of this third variable before concluding that the original two variables are indeed correlated, similarly to a partial correlation. This can be done with the partial Mantel test (Smouse et al. 1986, Legendre and Troussellier 1988, Fortin and Payette 2002). A significant coefficient of correlation (r) for the partial Mantel test (with spatial effects removed) indicates that the relationship that exists between the two variables is not related to a common spatial structure (Legendre and Fortin 1989). We used a partial Mantel test to examine the correlation between community similarity and SST while controlling for the effects of geographic location. The Mantel and partial Mantel tests were based on 10,000 random permutations with a Pearson correlation coefficient at a significance level of $\alpha=0.05$. All Mantel tests were done using zt software (Bonnet and Van de Peer 2002).

RESULTS

Cluster analysis and Non-Metric Multidimensional Scaling

Hierarchical cluster analysis and two-dimensional nMDS ordination were used to explore community similarity among sites across the Channel Islands. The two-dimensional structure among sites and the relative spatial separation among sites coded by islands are revealed in the nMDS plot (Fig. 3). Sites located on the same island sometimes cluster close together; however, there is a high degree of scatter among same-island sites. The nMDS is useful for determining which sites form the most cohesive groups (e.g., sites CI-BR and CI-LH). The general geographic configuration of sites from northwest to southeast is apparent in the nMDS plot, going from left (northwestern sites) to right (southeastern sites). The dendrogram illustrates the spatial patterns of island site groupings (Fig. 4). The SIMPROF test identified 6 significantly different groups of sites and 4 sites (sites SR-NT, SM-CP, SR-EP and SC-PH) as outliers. Apart from these outliers, groups of sites generally corresponded to the spatial pattern of ocean temperature, and did not cluster by island (Fig. 5).

Characteristic taxa

Characteristic taxa for each of the island groups are shown in Table 1. The cold water sites of San Miguel, Santa Rosa, San Nicolas and western Santa Cruz Island (blue and green groups) were characterized by relatively high abundance of the seaweeds *Chondracanthus canaliculatus, Endocladia muricata*, coralline algae, the surfgrass *Phyllospadix torreyi* as well as the colonial tubeworm, *Phragmatopoma californica* and the limpets *Lottia scabra* and *L. conus*. Warm water sites at Catalina and Santa Barbara Island (orange and red groups) were characterized by relatively high abundance of the mussel, *Mytilus californianus*, the barnacles *Tetraclita rubescens* and *Chthamalus* spp. and the seaweeds *Halidrys dioica* and *Silvetia compressa*. The geographical and thermal 'intermediate' site groups at southern Santa Cruz Island and Anacapa Island (purple and yellow groups) were characterized by a mixture of taxa from both the colder and warmer regions (Table 1).

Geographic and environmental correlates of community similarity

We used the Mantel and partial Mantel tests to explore the relationships between community similarity and geographic distance and ocean conditions. Community similarity among sites decreased significantly with geographical distance (Mantel r=-0.4995, p<0.0001) and with long-term mean SST (Mantel r=-0.5908, p<0.0001). Due to the strong effects of geographically persistent ocean currents in driving spatial patterns of ocean temperature, we used a partial Mantel test to examine the relationship between community similarity and ocean conditions while controlling for the effect of geographic distance. We found community similarity to be significantly correlated with long-term mean SST independent of geographic location (Partial Mantel r=-0.3656, p<0.0005). Furthermore, when removing the dominant environmental gradient (ocean temperature) from the geographic gradient, we found that distance among sites (while controlling for ocean temperature) was no longer correlated with community similarity (Partial Mantel r=-0.0347, p<0.3593)

DISCUSSION

The overall results of this study implicate temperature as a factor of great importance in determining the composition of intertidal communities at the Channel Islands intertidal species. This finding is generally consistent with ideas developed by others working in this system over time (Hewatt 1946b, Neushul et al. 1967, Murray and Littler 1981). Here we are able to quantitatively describe the correlations between species similarity and both geography and oceanography while accounting for spatial autocorrelation. The strength of the relationship between community similarity and SST was highly significant, even after accounting for the high degree of spatial autocorrelation in patterns of SST. Although a decay of community similarity with geographical distance may result from other, unmeasured environmental factors that are spatially autocorrelated (e.g. daylength, rainfall, etc.), long-term mean SST provides a reasonable index of oceanographic conditions known to influence benthic community structure (Broitman et al. 2005, Blanchette et al. 2006).

Despite the strong correlation between species similarity and spatially-detrended ocean temperature, one must be cautious in interpretation of temperature, per se, as the driving factor in determining species distributions and community composition. In terms of oceanography, temperature is a useful proxy for the movement of water masses. Patterns of ocean circulation are complex here, and cold and warm water current systems collide in this region of the Channel Islands. Thus temperature as a proxy for oceanographic conditions can have important effects on the distribution of organisms through processes linked to larval and propagule dispersal. Temperature can also have direct effects on critical biological functions such as growth, survival and reproduction. Although the spatial patterns of species similarity described here are highly correlated with ocean temperature, we are unable to distinguish the processes underlying these patterns; however, this is a subject of future research in this system.

In addition to finding a strong link between species similarity and temperature, we also note a strong northwest to southeast pattern in similarity revealed in the pattern of site clustering (see Fig. 5). This spatial pattern seems to be largely driven by the relative abundance of particular functional groups across the island region. Blanchette et al. (2006) report similar findings at a smaller spatial scale across Santa Cruz Island. They found the abundance of sessile invertebrates to be greatest at the southeastern warm water sites, and macrophytes to be dominant at the colder water northwestern sites. Interestingly, we note a similar pattern across the larger island region. We found the abundances of sessile invertebrates (mainly barnacles and mussels) to be greatest at the warm water sites and the relative abundance of macrophytes to be highest at the cool water sites. This spatial pattern was also reflected in the abundance of mobile consumers, where herbivores (chitons, limpets, snails) tended to be more abundant at cool water sites, and carnivores (mainly whelks and seastars) were more abundant at warm water locations, suggesting that these bottom-up influences of temperature may propagate to higher trophic levels.

The identification of distinct benthic marine biogeographic regions has important implications for conservation, particularly to ensure that representative sites and their characteristic assemblages within regions are protected (Sink et al. 2005). This is particularly true for the Channel Islands, where marine reserves are becoming an important tool for conservation, and among many goals, are intended to protect the biodiversity and ecosystem functions as well as individually targeted species (Airame et al. 2003, McGinnis 2006). The community-based approach to understanding biogeographic pattern is particularly relevant to conservation planning because regional differences in abundance of some taxa may reflect important ecological differences, such as contrasting trophic patterns that may indicate important ecosystem processes. The inclusion of different community assemblages in marine protected areas is likely to include the distinct smaller and or more rare taxa, which are usually not well sampled or studied. Furthermore, understanding the processes underlying spatial patterns of species similarity is also essential to forecasting the impacts of climate change. This study provides evidence that ocean conditions and likely temperature play a key role in the observed biogeographic patterns, and future changes in sea surface temperatures may alter the structure of these communities in unpredictable ways. Many climate change scenarios predict geographically patchy temperature changes (IPCC 2001, Helmuth et al. 2006) and may act to further divide biogeographic regions or alternatively to homogenize large regions. The knowledge gained from the present study of the distribution and abundance of intertidal species across the Channel Islands will help to provide a baseline against which the potential anthropogenic and natural changes of the future may be assessed.

Conclusions

Our findings reveal a high degree of spatial structure in the similarity of rocky intertidal communities of the Channel Islands, and are generally consistent with those of previously described biogeographic regions based on intertidal macrophytes. The strong correlations between similarity in community composition and both geographic position and SST suggest that both geography and oceanographic conditions act to drive spatial patterns. However, our results suggest that nearshore oceanographic conditions are the most important contributor to spatial patterns of species similarity across these islands.

ACKNOWLEDGMENTS

We appreciate the support of the UC Natural Reserve System, Lyndal Laughrin, The Nature Conservancy, and Channel Islands National Park. The following contributed greatly to field data collection: C. Engel, R. Gaddam, A. Kendall, J. Kovach, K. Kusic, D. Lerma, H. Livingston, E. Maloney, C. Mangiardi, C. Palazzo, D. Richards, C. Svedlund, K. Walters, M. Williams, and A. Wyndham. R. Core and C. Jones provided database assistance. This is contribution 314 of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO): A Long-Term Ecological Consortium funded by the David and Lucille Packard Foundation.

REFERNCES

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. Ecological Applications **13**:S170-S184.

Blanchette, C. A., B. R. Broitman, and S. D. Gaines. 2006. Intertidal community structure and oceanographic patterns around Santa Cruz Island, CA, USA. Marine Biology **149**:689-701.

Blanchette, C. A. and S. D. Gaines. 2007. Distribution, abundance, size and recruitment of the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. Journal of Experimental Marine Biology and Ecology **340**:268-279.

Blanchette, C. A., B. Helmuth, and S. D. Gaines. 2007. Spatial patterns of growth in the mussel, Mytilus californianus, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. Journal of Experimental Marine Biology and Ecology **340**:126-148.

Blanchette, C. A., B. G. Miner, and S. D. Gaines. 2002. Geographic variability in form, size and survival of Egregia menziesii around Point Conception, California. Marine Ecology-Progress Series **239**:69-82.

Blanchette, C. A., C. M. Miner, P. T. Raimondi, D. Lohse, K. E. K. Heady, and B. R. Broitman. 2008. Biogeographic patterns of rocky intertidal communities along the Pacific coast of North America. Journal of Biogeography **35**:1593-1607.

Bonnet, E. and Y. Van de Peer. 2002. zt: a softtware tool for simple and partial mantel tests. Journal of Statistical Software **7**:1-12.

Broitman, B. R., C. A. Blanchette, and S. D. Gaines. 2005. Recruitment of intertidal invertebrates and oceanographic variability at Santa Cruz Island, California. Limnology And Oceanography **50**:1473-1479.

Broitman, B. R., C. A. Blanchette, B. A. Menge, J. Lubchenco, C. Krenz, M. Foley, P. T. Raimondi, D. Lohse, and S. D. Gaines. 2008. Spatial and temporal variability in the recruitment of intertidal invertebrates along the West coast of the United States. Ecological Monographs **78**:403-421.

Broitman, B. R. and B. P. Kinlan. 2006. Spatial scales of benthic and pelagic producer biomass in a coastal upwelling ecosystem. Marine Ecology-Progress Series **327**:15-25.

Broitman, B. R., S. A. Navarrete, F. Smith, and S. D. Gaines. 2001. Geographic variation of southeastern Pacific intertidal communities. Marine Ecology-Progress Series **224**:21-34.

Burton, R. S. 1998. Intraspecific phylogeography across the Point Conception biogeographic boundary. Evolution **52**:734-745.

Bustamante, R. H. and G. M. Branch. 1996. Large scale patterns and trophic structure of southern African rocky shores: The roles of geographic variation and wave exposure. Journal of Biogeography **23**:339-351.

Bustamante, R. H., G. M. Branch, S. Eekhout, B. Robertson, P. Zoutendyk, M. Schleyer, A. Dye, N. Hanekom, D. Keats, M. Jurd, and C. McQuaid. 1995. Gradients of Intertidal Primary Productivity around the Coast of South-Africa and Their Relationships with Consumer Biomass. Oecologia **102**:189-201.

Clarke, K. R. 1993. Nonparametric Multivariate Analyses Of Changes In Community Structure. Australian Journal Of Ecology **18**:117-143.

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.

Dayton, P. K. and M. J. Tegner. 1984. Catastrophic Storms, El-Niño, And Patch Stability In A Southern-California Kelp Community. Science **224**:283-285.

Doyle, R. F. 1985. Biogeographical studies of rocky shores near Point Conception, California. PhD dissertation. University of Californa, Santa Barbara, California.

Fortin, M. J. and S. Payette. 2002. How to test the significance of the relation between spatially autocorrelated data at the landcape scale: A case study using fire and forest maps. Ecoscience **9**:213-218.

Gaines, S., S. Brown, and J. Roughgarden. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, Balanus glandula. Oecologia (Berlin) **67**:267-272.

Helmuth, B., N. Mieszkowska, P. Moore, and S. J. Hawkins. 2006. Living on the edge of two changing worlds: Forecasting the responses of rocky intertidal ecosystems to climate change. Annual Review of Ecology Evolution and Systematics **37**:373-404.

Hewatt, W. G. 1946a. Marine ecologica studies on Santa Cruz Island, California. Ecological Monographs **16**:185-208.

Hewatt, W. G. 1946b. Marine ecological studies on Santa-Cruz Island, California. Ecological Monographs **16**:185-208.

Hickey, B. 1993. Physical Oceanography. Page 926 *in* M. D. Dailey, D. J. Reisch, and J. W. Anderson, editors. Ecology of the Southern California Bight. University of California Press, Berkley.

Hickey, B., E. L. Dobbins, and S. E. Allen. 2003. Local and remote forcing of currents and temperature in the central Southern California Bight. Journal of Geophysical Research-Oceans **108**:[doi:10.1029/1200JC000313].

Huyer, A. 1983. Coastal Upwelling in the California Current System. Progress in Oceanography **12**:259-284.

IPCC. 2001. Climate Change 2001: Synthesis Report. A Contribution of Working Groups I, II, and III to the Third Assessment Report of the Integovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Kruskal, J. B. and M. Wish. 1978. Multidimensional Scaling. Sage Publications, Beverly Hills, CA.

Legendre, P. 1993. Spatial Autocorrelation - Trouble Or New Paradigm. Ecology **74**:1659-1673.

Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing beta diversity: Partitioning the spatial variation of community composition data. Ecological Monographs **75**:435-450.

Legendre, P. and M. J. Fortin. 1989. Spatial Pattern And Ecological Analysis. Vegetatio **80**:107-138.

Legendre, P. and L. Legendre. 1998. Numerical Ecology. 2nd Edition edition. Elsevier, Amsterdam.

Legendre, P. and M. Troussellier. 1988. Aquatic Heterotrophic Bacteria - Modeling In The Presence Of Spatial Auto-Correlation. Limnology And Oceanography **33**:1055-1067.

McGinnis, M. V. 2006. Negotiating ecology: Marine bioregions and the destruction of the Southern California Bight. Futures **38**:382-405.

Menge, B. A., B. A. Daley, J. Lubchenco, E. Sanford, E. Dahlhoff, P. M. Halpin, G. Hudson, and J. L. Burnaford. 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. Ecological Monographs **69**:297-330.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997a. Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proceedings of the National Academy of Sciences USA **94**:14530-14535.

Menge, B. A., B. A. Daley, P. A. Wheeler, and P. T. Strub. 1997b. Rocky intertidal oceanography: An association between community structure and nearshore phytoplankton concentration. Limnology and Oceanography **42**:57-66.

Menge, B. A., J. Lubchenco, M. E. S. Bracken, F. Chan, M. M. Foley, T. L. Freidenburg, S. D. Gaines, G. Hudson, C. Krenz, H. Leslie, D. N. L. Menge, R. Russell, and M. S. Webster. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences of the United States of America **100**:12229-12234.

Murray, S. N. and M. M. Littler. 1981. Biogeographical analysis of intertidal macrophyte floras of southern California. Journal of Biogeography **8**:339-351.

Neushul, M., W. D. Clarke, and D. W. Brown. 1967. Subtidal plant and animal communitiues of the southern California Islands. Pages 37-55 *in* Proceedings of the symposium on the biology of the California Islands, Santa Barbara Botanic Garden, Santa Barbara, CA.

Nielsen, K. J. and S. A. Navarrete. 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. Ecology Letters **7**:31-41.

Polis, G. A. and S. D. Hurd. 1996. Linking marine and terrestrial food webs -allochthonous input from the ocean supports high secondary productivity at small islands andcoastal land communities. American Naturalist **147**:396-423.

Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. Science **241**:1460-1466.

Sanford, E. 2002. The feeding, growth, and energetics of two rocky intertidal predators (Pisaster ochraceus and Nucella canaliculata) under water temperatures simulating episodic upwelling. Journal of Experimental Marine Biology and Ecology **273**:199-218.

Schiel, D. R. 2004. The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. Journal of Experimental Marine Biology & Ecology:309-342.

Schiel, D. R., J. R. Steinbeck, and M. S. Foster. 2004. Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. Ecology **85**:1833-1839.

Schoch, G. C., B. A. Menge, G. Allison, M. Kavanaugh, S. A. Thompson, and S. A. Wood. 2006. Fifteen degrees of separation: Latitudinal gradients of rocky intertidal biota along the California Current. Limnology and Oceanography **51**:2564-2585.

Sink, K. J., G. M. Branch, and J. M. Harris. 2005. Biogeographic patterns in rocky intertidal communities in KwaZulu-Natal, South Africa. African Journal Of Marine Science **27**:81-96.

Smouse, P. E., J. C. Long, and R. R. Sokal. 1986. Multiple-Regression And Correlation Extensions Of The Mantel Test Of Matrix Correspondence. Systematic Zoology **35**:627-632.

Valentine, J. W. 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. LO **11**:198-211.

Winant, C. D., E. P. Dever, and M. C. Hendershott. 2003. Characteristic patterns of shelf circulation at the boundary between central and southern California. Journal of Geophysical Research-Oceans **108**:doi: 10:1029/2001JC001302.

FIGURE CAPTIONS

Figure 1
Map showing locations of Channel Islands rocky intertidal sites. Sitecodes are as listed in Table 1.

Figure 2
Long-term mean Advanced Very High Resolution Radiometer Sea Surface Temperature (AVHRR SST) from 1996 to 2005.

Figure 3
Non-metric multidimensional ordination plot (stress = 0.17) using Bray-Curtis similarity based on the square-root transformed taxon abundance data for each of the 22 sites across the 7 islands.

Figure 4
Dendrogram depicting Bray-Curtis similarity in species composition among island sites. Islands are coded by colored symbols. Solid lines indicate significant group structure at the 0.1% level. Color bars to the left of site codes indicate the clusters of sites represented in each of the 6 groups (Group 1 – green, Group 2 – blue, Group 3 – yellow, Group 4 – purple, Group 5 – orange, Group 6 – red).

Figure 5

Colored dots overlaid on a regional image of Sea Surface Temperature (NOAA image from August 31, 1998) to illustrate the relationship between community similarity and oceanographic conditions. The dots are color coded to represent the site grouping colors used in Figure 4.

Table 1

Characteristic taxa (top ten) for each of the island site groups shown in Figure 4 as determined by SIMPER analysis. The ranking is determined by S_i, the average contribution of each species to the overall similarity of the zone in each region. %Av indicates the average percentage cover of each species from all sites. $\Sigma\%S_i$ is the cumulative percentage contribution of each species to the overall average similarity (S).

Characteristic taxa	%Av	S_i	$\sum\%S_i$
Group 1 - green (S = 72.16)			
Littorina keenae	0.79	8.98	12.44
Bare rock	0.5	5.72	20.36
Lottia scabra/conus	0.32	3.23	24.84
Corallina spp	0.26	2.47	28.27
Phyllospadix torreyi	0.25	2.39	31.59
Chondracanthus canaliculatus	0.25	2.35	34.85
Littorina plena/scutulata	0.24	2.24	37.96
Endocladia muricata	0.2	2.23	41.05
Phragmatopoma californica	0.24	2.2	44.1
Lottia paradigitalis/strigatella	0.21	2.11	47.03
Group 2 – blue (S = 65.32)			
Bare rock	0.54	5.57	8.53
Littorina keenae	0.53	5.41	16.81
Lottia austrodigitalis/digitalis	0.41	4.11	23.09
Lottia scabra/conus	0.3	3.14	27.9
Phragmatopoma californica	0.28	2.96	32.43
Corallina spp	0.27	2.86	36.81
Lottia paradigitalis/strigatella	0.2	2.13	40.07
Littorina spp	0.32	1.95	43.05
Chondracanthus canaliculatus	0.22	1.92	45.98
Littorina plena/scutulata	0.23	1.91	48.91
Group 3 – yellow (S =71.96)			
Littorina keenae	0.78	9.87	13.71
Bare rock	0.48	5.15	20.86
Mytilus californianus	0.35	3.73	26.04
Chthamalus spp	0.3	3.71	31.21
Corallina spp	0.29	3.53	36.12
Littorina plena/scutulata	0.29	3.49	40.97
Encrusting coralline	0.29	3.12	45.3
Lottia scabra/conus	0.24	2.85	49.26
Tetraclita rubescens	0.21	2.31	52.47
Halidrys dioica	0.19	2.11	55.39
Group 4 – purple (S = 72.55)			
Littorina keenae	0.88	11.81	16.28
Bare rock	0.39	4.69	22.75
Littorina plena/scutulata	0.32	3.89	28.1
Chondracanthus canaliculatus	0.29	3.25	32.58
Chthamalus spp	0.27	3.14	36.91
Endocladia muricata	0.22	2.81	40.78
Lottia scabra/conus	0.19	2.16	43.76
Mazzaella affinis	0.16	2.05	46.59
Silvetia compressa	0.19	1.89	49.19
Balanus glandula	0.12	1.57	51.35
Group 5 – orange (S = 72.20)			
Littorina keenae	0.78	8.97	12.42
Mytilus californianus	0.48	5.48	20
Bare rock	0.5	5.32	27.37
Lottia scabra/conus	0.31	3.62	32.39
Corallina spp	0.29	3.04	36.6
Tetraclita rubescens	0.2	2.1	39.51
Lottia pelta	0.23	1.98	42.25
Mazzaella affinis	0.17	1.92	44.9
Chthamalus spp	0.16	1.7	47.26
Lottia paradigitalis/strigatella	0.17	1.65	49.55
Group 6 – red (S = 65.61)			
Littorina keenae	0.78	7.17	10.93
Bare rock	0.4	3.8	16.72
Littorina plena/scutulata	0.33	2.85	21.07
Halidrys dioica	0.27	2.76	25.27
Tetraclita rubescens	0.24	2.45	29.01
Corallina spp	0.29	2.43	32.72
Chondracanthus canaliculatus	0.24	2.38	36.34
Silvetia compressa	0.24	2.11	39.56
Lottia scabra/conus	0.28	1.97	42.55
Chthamalus spp	0.25	1.76	45.23

Figure 1

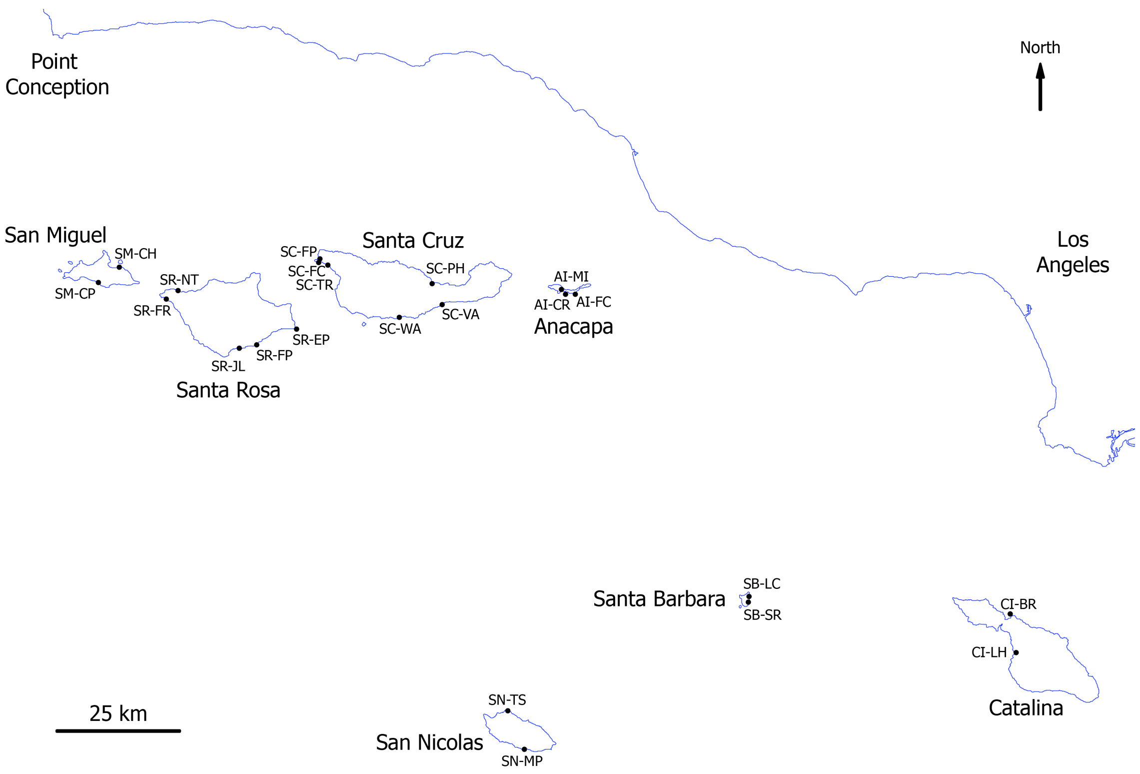

Point Conception
North
San Miguel
SM-CH
SM-CP
SR-NT
SR-FR
SC-FP
SC-FC
SC-TR
Santa Cruz
SC-PH
SC-VA
SC-WA
SR-EP
SR-FP
SR-JL
Santa Rosa
AI-MI
AI-CR
AI-FC
Anacapa
Los Angeles
Santa Barbara
SB-LC
SB-SR
CI-BR
CI-LH
Catalina
25 km
SN-TS
San Nicolas
SN-MP

Figure 2

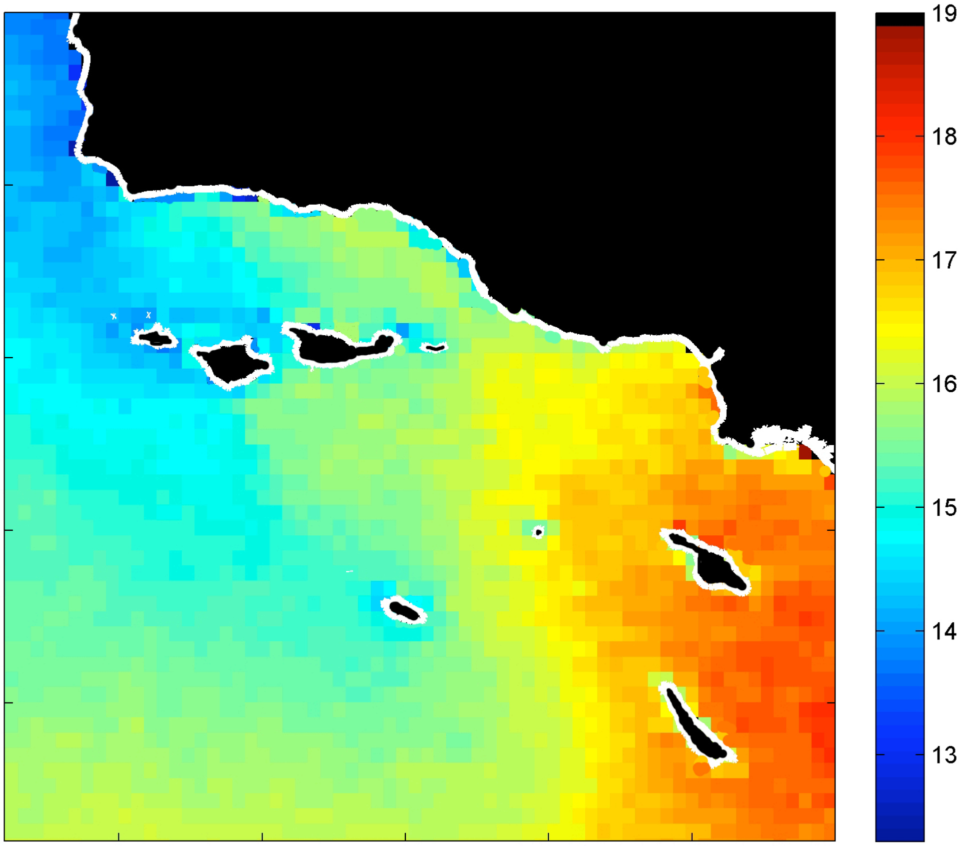


Figure 3

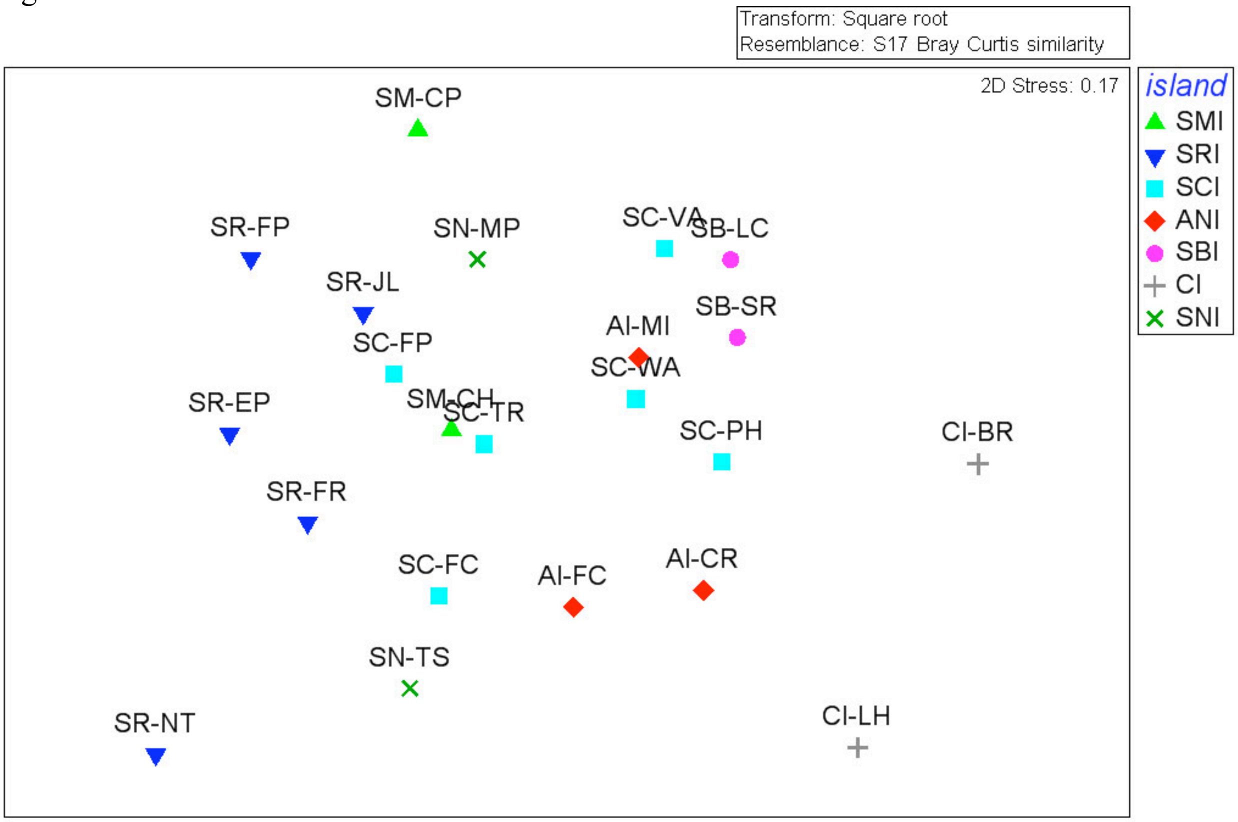
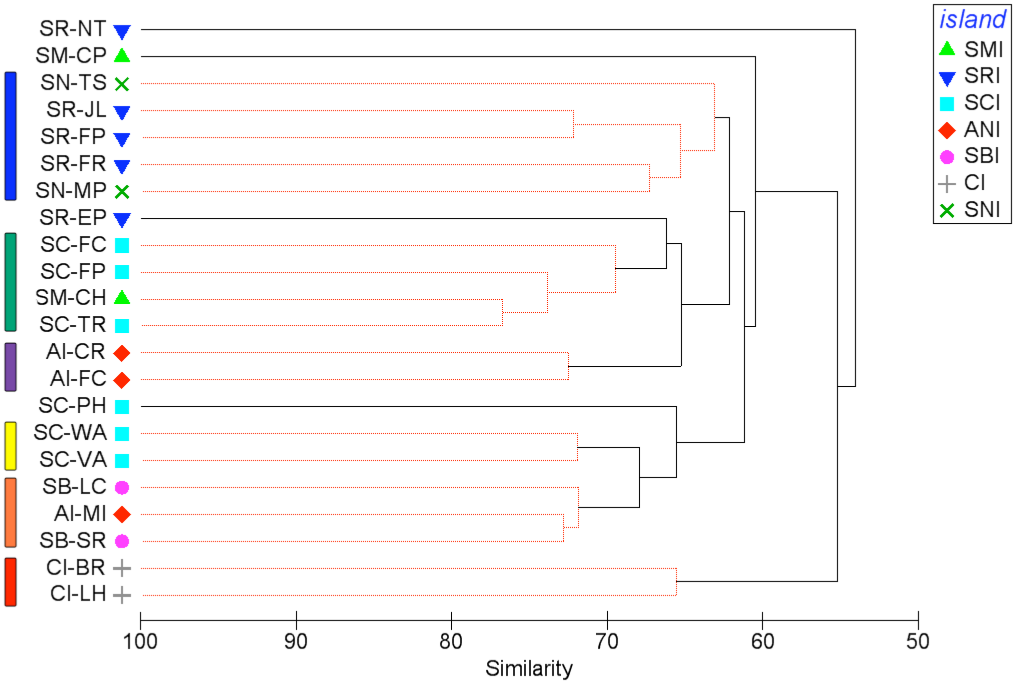
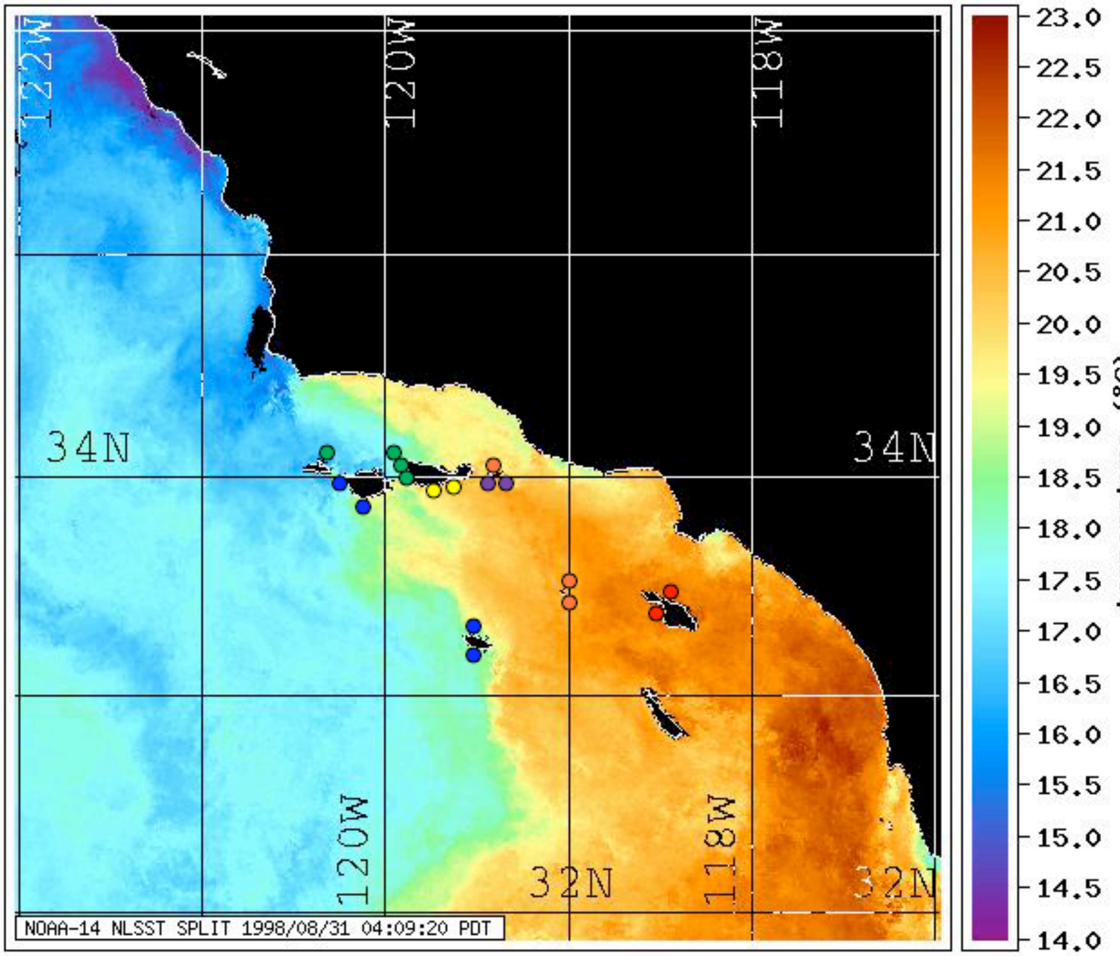

Transform: Square root
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.17
island
SMI
SRI
SCI
ANI
SBI
CI
SNI
SM-CP
SR-FP
SN-MP
SC-VA
SB-LC
SR-JL
SC-FP
AI-MI
SB-SR
SC-WA
SR-EP
SM-CH
SC-TR
SC-PH
CI-BR
SR-FR
SC-FC
AI-FC
AI-CR
SN-TS
SR-NT
CI-LH

Figure 4



island
SMI
SRI
SCI
ANI
SBI
CI
SNI
SR-NT
SM-CP
SN-TS
SR-JL
SR-FP
SR-FR
SN-MP
SR-EP
SC-FC
SC-FP
SM-CH
SC-TR
AI-CR
AI-FC
SC-PH
SC-WA
SC-VA
SB-LC
AI-MI
SB-SR
CI-BR
CI-LH
100
90
80
70
60
50
Similarity

Figure 5


122W
120W
118W
34N
34N
120W
32N
118W
32N
NOAA-14 NLSST SPLIT 1998/08/31 04:09:20 PDT
23.0
22.5
22.0
21.5
21.0
20.5
20.0
19.5
19.0
18.5
18.0
17.5
17.0
16.5
16.0
15.5
15.0
14.5
14.0
temperature (°C)