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2 Regional variation in the colonization of experimental substrates by sessile marine
3 invertebrates: Local vs. regional control of diversity

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ABSTRACT

The degree to which local factors interact with a broader regional pool of species to control species diversity on various spatial scales continues to be debated. For marine systems, recruitment has been identified as a critical element uniting local communities within regions. Most studies have addressed this question over large biogeographic scales encompassing multiple regions. Regional species pools are usually defined as fixed and the degree to which this pool is found on a local scale is often used as a measure of regional influence. Usually the degree to which local communities vary temporally and how this relates to the regional pool is not examined. Given that recruitment links local sites within regions and is a temporally dynamic process, it is important to include temporal variation in the regional vs. local control debate; especially given that regional pools themselves are changing much more rapidly with the invasion of new species. Here the results of a study of the colonization of experimental panels at 28 sites within a region encompassing 200 km of the California coast are used to address this question. This study examined experimentally the temporal and spatial variation in species and contrasted intraregional and local factors. At 22 of these sites, all within 15 km of each other, identical colonization experiments were followed for as long as 3 years. Results of these experiments demonstrated that there was some regional control through the seasonal variation in recruitment, but that strong local effects greatly altered the regional input. Substrates of the same size at the same station usually accumulated the same number of species, but among stations mean diversity ranged from 10 to 50 species per substrate. Differences between sites

were a function of more localized recruitment than expected and normal post-recruitment processes of competitive dominance, disturbance, and predation that affected the rates at which species were lost. The colonization of most substrates resulted in their attaining an asymptotic or equilibrium diversity maintained by a balance between species immigration and local extinction. Nevertheless, on most substrates diversity fluctuated much more than predicted by an equilibrium model. The similarity in species richness on substrates at the same site regardless of initial exposure time, the large differences among substrates from different sites, the similar pattern of differences among the sites for panels of different sizes, and the resilience of communities to disturbance and their return to the diversity characteristic of a site all argue for strong local factors controlling the diversity within the region.

1. Introduction

Understanding the links between regional and local species richness continues to be a challenging problem in ecology (Ricklefs 1987, Caley and Schluter 1997, Harrison and Cornell 2008). These links underlie issues of community assembly (Tilman 2004), latitudinal variation in diversity (e.g. Rivendiera et al. 2002, Hillebrand 2004 a, b, Mittelbach et al. 2007), and the degree to which local diversity is controlled or enriched by regional diversity (Karlson et al. 2004, Witman et al. 2004, Russell et al. 2006). Harrison and Cornell (2008) identified several areas in need of study, including: (1) regional-scale causes of variation in species richness; (2) effects of regional richness on local richness; and (3) environmental influences on regional and local species. Recruitment is one link between a regional metacommunity with a defined pool of species and local communities of subsets of the regional pool (Harrison and Cornell 2008). If recruitment ties local communities together, either strongly or weakly, the availability and use of local resources should affect the local success of recruits and the degree to which they squeeze into the community (Tilman 2004). The scale of local interactions, governed to some degree by local environmental constraints may control the level of influence of the regional pool of species on local richness (Russell et al. 2006). On a global scale Karlson et al. (2004) demonstrated the regional enrichment of local communities in which local communities in regions of higher richness also exhibited higher richness. Witman et al. (2004) suggested the regional enrichment of local communities increases with latitude but in the sense that local communities incorporate a greater proportion of the regional pool as latitude increases.

As Harrison and Cornell (2008) have suggested, how local communities,

richness, and processes vary within a region are critical, yet understudied, elements in linking local and regional richness. In an attempt to address these questions the data from a three year colonization study conducted at 28 southern California coastal sites in 1978-1981 are examined. In the study panel substrates were exposed at every site for 1-3 years and repeatedly analyzed at 6 week intervals. As such, the panels represent identical local habitats within a single regional metacommunity with a defined species pool. Although environmental conditions varied among the sites, the substrates themselves were both physically identical and colonized over almost identical time periods. A comparison of the development of communities contrasts the influences of regional and local parameters in the context of temporal change as local resources (space) become utilized. Thus these data frame the regional – local comparison in the context of colonization and change at the local level.

The colonization of new habitat such as an experimental panel is a dynamic process influenced by both regional elements of recruitment such as seasonality in reproduction as well as local variation in populations producing recruits. Local elements of competition, predation, environmental change and disturbance will impact the success of recruits and how the community develops or changes. As such examining how this process varies within and among sites within a region can be used to contrast regional and local controls. If the regional species pool dominates local processes then we would expect sites to be similar in their rates of species accumulation. Regional control in the timing of reproduction such as seasonality in climate could be expected to produce some similarities among sites in recruitment. Stochastic differences among sites would be expected but consistent differences among the sites should not occur

unless there are local controls.

Also, if there is seasonal or any other temporal variation in recruitment, then substrates deployed at different times within a site should have different recruitment histories. Unless there is some local control, species composition, would be expected to differ but diversity (species richness) would be expected to be similar given the identical sizes of the habitats (experimental panels).

Finally, without any strong local effects the diversity would also be expected to be similar among sites. This should be reflected in both the rate at which species accumulate during the colonization process as well as any asymptote or equilibrium in species richness (MacArthur and Wilson 1963, 1967) on a panel.

In order to address the variation of local richness within a region as a dynamic process, the variability in diversity among panel substrates at the sites throughout the colonization process will be contrasted. Any differences in recruitment among the sites, the rates at which species turnover in terms of the losses (local extinction) and gains (immigration) of species, and the resilience of communities among the sites in terms of the recovery of diversity after disturbances will also be examined. Given the extensive nature of the data, only a fraction of the data can be presented in detail. However, a set of graphical appendices that present all of the data are included.

2. Methods

2.1 Sites

The majority of data presented were collected as part of a study investigating regional variation in the development of epifaunal invertebrate communities along the

coast of southern California. A principal objective of the overall study was to determine the effects of the release of cooling water from the San Onofre Nuclear Generating Station (no longer in operation) on community processes. Because of this, 10 of the 28 stations were located on two transects away from the site of release at that time. These transects were parallel to the coast, one north and one south of the outfall (Figure 1). Permanent stations were located at 50, 100, 200, 400, 800, and 1600 m north and 50, 100, 800, and 1600 m south of the discharge. Another two stations were 50 m north and south of the water intake which was approximately 200 m offshore of the discharge. In general these stations were in 6-9 m of water in areas of mixed muds and sands. Sparse patches of cobbles and boulders occurred along the north transect and in the vicinity of the discharge.

Another 13 stations were located in or near three *Macrocystis pyrifera* kelp forests arranged along 15 km of coastline (Figure 1). At the start of the study, at least 3 stations were established in each forest, one inside the forest, one on the edge, and one 500 m outside at depths of 12-15 m. Changes in the spatial extent of the forests led to some distortion and to the establishment of additional stations. Within 3 months of the start of the study, sediment movement and regression of the southern forest (Barn) resulted in all three stations being located outside. In October 1979 (16 mo into the study) a fourth station was established inside the forest. The original three stations were in areas eventually covered by sediments and the fourth station was on a low-profile reef.

In the middle forest (San Onofre) growth and regression of the kelp forest caused the inshore edge and outside stations to fluctuate between edge and outside. A fourth

station was included in this forest at a site on the offshore edge. This station was in an area of very small cobble which were unsuitable for large kelp plants. Thus this station was unaffected by fluctuations in the size of the forest. In August 1979 (14 mo into the study), two stations were added near northern border of the kelp forest. Substrate within the San Onofre kelp forest was mixed cobble, sand, and boulders.

The northern kelp forest (San Mateo) included three stations all whose characterization remained stable throughout the study. This kelp forest was on a stable rock reef and fluctuated little in size. The inside station was on the reef, the outside station was in muddy-sand, and the edge station was at the permanent boundary between these two substrate types.

The three remaining stations were located in kelp forests at Santa Catalina and Santa Cruz Islands (Figure 1) at depths of 12-15 m. Two sites were at Habitat Reef in Big Fisherman's Cove, Santa Catalina Island. One station was located within the kelp forest on stable reef and the other was approximately 100 m outside on coarse sand substrate. The Santa Cruz Island station was in Fry's Harbor and located on stable reef within the kelp forest.

2.2 Experiments

Four identical colonization experiments were conducted at the 22 original stations. A fifth experiment was conducted at these stations and the 3 stations that were added later. Because they could not be sampled as frequently, the experiments conducted at the three Channel Islands stations were similar but not identical in design. The design for these experiments will be discussed separately.

In all the experiments artificial substrates were used to mimic naturally occurring

hard substrate. The five main experiments consisted of the continuous exposure of identical substrates for the length of the study. Experiments were initiated during the first week of June, September, and December 1978, and March and November 1979. Substrates were square panels of asbestos-concrete (Transite). These were attached to flexible field racks that held them 0.5 - 1.0 m above the bottom. In all the experiments, only the surface of the panel facing the seafloor was analyzed. Two sizes of panels were used in the June and December experiments (103 cm² and 15 cm²). In the remaining three experiments only the large panels were used. A minimum of three replicate panels was used in all experiments at all sites.

All sampling was nondestructive. Panels were collected by divers, placed in coolers of aerated seawater, and transported to the laboratory. In the laboratory panels were held in a 2000 l closed seawater system, usually for 2 days but as long as 7 days when weather prevented re-deployment. During this time each panel was photographed, carefully surveyed for all species present, and then the abundances of dominant sessile species were estimated using a randomly placed grid of evenly spaced points (1 cm² for large and 2 cm² for small panels) and counting the number of points falling on each species. Laboratory analyses were done using a dissecting microscope. After the panels were analyzed they were returned to the field racks. Panels were nominally sampled every 6 weeks. After the first 6 sampling periods, the large number of panels made it impossible to sample all substrates this frequently. The frequency of sampling was reduced for some experiments and stations, but most substrates were analyzed every 6-10 weeks. All panels remained in the field at least 6 weeks between sampling times.

In addition to the main colonization experiments, several other types of experiments were conducted:

1. Recruitment was measured by exposing clean panels for each 6 week sampling period at each site. Two replicates of each of the two substrate sizes were used at each station, 103 and 15 cm².

2. At five inshore transect stations panels were suspended 1 m below the water surface as well as 1 m above the bottom. These surface experiments were designed to test whether recruitment differences existed between the surface and bottom waters and whether these differences would have any effect on diversity. Because most larvae were expected to be near the seafloor when they were ready to attach, recruitment was hypothesized to be lower in surface waters.

3. The three Channel Island stations were visited approximately every 3 months. Because panels were usually sampled and returned to the mainland for analysis, a destructive sampling design had to be used. At each station 32 large panels were initially exposed and four of the replicates were sampled every 3 months. In addition, one set of four panels was always sampled and replaced by four clean panels which were subsequently sampled and replaced the following period. These panels were used to measure recruitment over the three-month sampling period.

4. A number of additional experiments designed to investigate specific processes were conducted for short periods at a small subset of sites. The methods used for these will be described along with their results.

During this study 327 species of sessile invertebrates, 30 species of small motile invertebrates, and 39 genera of macroscopic algae were recorded on the experimental

substrates. The sessile invertebrates were represented by 10 different phyla with colonial groups such as sponges, hydroids, bryozoans, and ascidians generally being spatial dominants. Based on taxonomic literature it was estimated that approximately 650 sessile invertebrate species occurred in the region which could have colonized the panels and have been identified.

2.3 Analyses

Analyses are presented which address: (1) temporal patterns of both recruitment and colonization and the causes of variation among substrates, (2) the spatial variation in recruitment and the colonization process, (3) the influence of habitat differences on colonization, and (4) the general ability of immigration and extinction rates to predict the variation in colonization. Two appendices are given which summarize the colonization, recruitment, and immigration - extinction data for all the stations. Because it is impossible to discuss or demonstrate the ranges of variation and similarity of all stations, selected data are necessarily presented below. The appendices present the data as fully as possible and place the selected results presented in the context of the complete study.

Temporal patterns in recruitment and colonization are compared initially as graphical descriptions of colonization and recruitment within and among sites. Statistical analyses addressing specific questions or hypotheses will be described as the results are presented.

For recruitment, analyses were conducted to examine first the degree to which recruitment in terms of both species number and number of recruits varied consistently among sites as an indication of local rather than regional control. Temporal patterns

were contrasted among the sites. Because large temporal differences in recruitment occurred at most sites, the frequency at which species were sampled at all the sites was also used as a test of local control. If a significant number of species recruited more frequently at certain sites this would suggest more local control of recruitment.

For colonization, the change in species richness over time is the main parameter contrasted. Analyses focus on the rate at which species accumulate during the initial stages (~ the first 10 months) and the degree to which diversity reaches an asymptote or equilibrium between species gains (immigration) and losses (extinction) after this time. If regional controls were strong then colonization curves and the equilibrium diversity should have been the same among sites. If series of panels at the same site reached similar equilibrium diversities but these differed among sites or sets of sites, this would argue for stronger local control.

Finally, the immigration and extinction rates on panels were also contrasted among series and sites. In part, these analyses test whether differences among sites were a function of recruitment of new species or the loss of species already present.

3. Results

3.1 Description of General Patterns

3.1.1 Temporal Patterns

3.1.1.1 Recruitment

As can be seen in Appendix 1, recruitment in terms of number of species colonizing clean substrates was quite variable at all stations over the length of the study. Both seasonal and annual differences in larval production are factors that could

exert region-wide control of recruitment. However, differences among stations may result from variation in the success of recruitment, including both local availability of larvae and differences in post-settlement mortality. An examination of recruitment using a 3-way ANOVA design (Season X Year X Station) indicated that each of these factors did contribute to the variation in recruitment (Table 1), but that these variables also interacted significantly with one another and together explained only 54% of the overall variation in the number of species recruiting onto clean substrates.

3.1.1.1.1 Effects of Season

To examine whether any predictable seasonal variation in the timing of reproduction produced consistent patterns across stations, the rank order of sampling times in terms of the number of species/panel and total abundance/panel were determined for each station. A correlation analysis of the rankings for sampling times among the 6 stations sampled in all sampling periods showed that there was a significant concordance (Kendall's tau = 0.406, $p < 0.001$ for species number and 0.410, $p < 0.001$ for total abundance rank) among sites. A similar analysis of the 19 stations that were sampled in all of the first 10 sampling periods yielded similar results (Kendall's tau = 0.361, $p < 0.001$ for species number and 0.139, $p < 0.01$ for total abundance).

Figure 2 shows the change in the rank sum for the different sampling times. An underlying seasonal pattern is evident in this figure. Recruitment exhibited consistent peaks in the late autumn and late spring followed by decreases in the winter and summer.

3.1.1.1.2 Annual Variation

In addition to the seasonal pattern, Figure 2 also shows a general increase in

recruitment over the three year period. This is most evident for those months that were sampled in more than one year. In all cases the rank order of these samples was 1978 < 1979 < 1980. These differences were attributed to normal year to year variation in reproductive rates. Also, given the lack of a significant Year X Station term in the recruitment analysis (Table 1), it appears that this pattern of annual variation was similar at all stations. Increased local recruitment produced from communities on the increasing number of colonization panels at each site could be an alternate explanation for the annual pattern. However, only 12 panels (6 of each size) were <1 m from the recruitment panels and all others were >5 m away. This coupled with the significant number of species producing long-lived planktotrophic larvae suggest that annual variation is the most parsimonious explanation.

3.1.1.2 Colonization

The colonization curve is simply a graph of the temporal change in the number of species in some area or habitat, in this case on an individual panel. The expected pattern is an increase in the number of species as an empty panel is colonized, ultimately approaching an asymptote as resources are utilized and the immigration of new species is balanced by the loss or extinction of the species present (MacArthur and Wilson 1963, 1967). This general pattern assumes that background recruitment rates are constant over time and that losses are not greatly influenced by disturbances or other environmental changes. As shown above recruitment varied seasonally and as will be shown below disturbances to some panels did result in high losses. However, if the colonization curves of most panels display some asymptotic behavior then the differences among sites in asymptotes as well as the rate at which they are approached

can be used to contrast local diversity and regional influences.

Colonization curves were plotted for individual substrates (Figures 3-4) and for each seasonal series (Appendix 1) at each station. Several general features can be seen by comparing these graphs:

1. The number of species on most panels continually increased over the first 6-10 months with the rate of increase decreasing after this time and appearing to approach an asymptote. The diversity on most panels followed this temporal pattern. Figure 3 demonstrates this pattern for large and small panel series at the four main sites in the San Onofre Kelp Forest. Although there is some variability among replicates, seasonal series, and sites, the two panel sizes, as expected, show the greatest difference. Figure 4 shows similar patterns for large panels at four sites at the opposite ends of the inshore transects. However, there were exceptions to this general pattern and these exceptions, whether species number commonly reached an asymptote, and whether the considerable variation around a mean asymptotic diversity was consistent with an equilibrium model are examined below.

2. Panels of the same size and from the same station, regardless of seasonal series, had very similar colonization patterns and accumulated the same number of species. This can be seen for individual panels in Figures 3 and 4 and for seasonal series in Appendix 1. This pattern was almost without exception, even though there was substantial temporal variation in recruitment and the species present on the different substrates, including dominants.

3. Differences in diversity between some stations were very large, with panels at some locations having 2-3 times the number of species as panels at other locations.

There were two distinct regional patterns; species diversity on panels reached higher numbers inside the kelp forests and was higher near the power plant discharge when compared to more distant locations. Although some site differences can be seen in Figures 3 and 4 these differences are more evident in comparing all the sites (Appendix 1).

4. Although general patterns appeared to exist, variation was quite high. Exceptions were found for almost every generality.

The primary questions regarding temporal patterns in diversity (species richness, S) addressed were the commonness of an asymptotic increase in species during the colonization of the panels, the variation in the consistency of the asymptotic mean within and among sites, and the similarity within and among sites in the rate of colonization. Regression analyses of the initial and asymptotic portions of the colonization curves were conducted.

Based on an examination of the colonization curves, it was assumed that an asymptote was approached after 10 months of exposure. If no change in S occurred after this time period, then the slope of the regression of S vs. time should have been zero. Regression analyses were done for all individual panels with sufficient number of observations and for each series of replicate panels. These analyses (Table 2) indicated that 15% of the 178 panels analyzed had a rate of change in S after 10 months exposure that was significantly different from zero. When panels were grouped by location (inshore vs. offshore) or size, there was little difference between the percentages of significant regressions for the groups. This suggests that the significant regressions were not characteristic of particular locations or types of panels. When

replicate panels in each seasonal series were pooled, the analyses showed greater variability. Of the 71 series analyzed 31% were found to exhibit significant changes in S after 10 months of exposure. Even though S appeared to remain constant on a majority of panels (85%) or seasonal series (69%), the number of panels and series that exhibited significant temporal change in S was much larger than would be expected by chance.

In addition, these analyses do not indicate whether S really reached an equilibrium that could be attributed to a long-term balance in the rates of immigration and extinction. For an equilibrium to be attained the fluctuation around the mean S should be relatively small (Keough and Butler 1983) and defined *a priori*. A coefficient of variation of 15% was used (Osman and Dean 1987) and 52% of the regressions exceeded this level of variation. Therefore, a large number of panels that showed no change in S after the initial period of rapid colonization fluctuated in diversity more than expected under equilibrium conditions.

There are several conditions and processes that could contribute to these departures from equilibrium and result in temporal patterns differing from the hypothesized pattern (i.e. the typical asymptotic colonization curve). Certainly, some panels could have reached an asymptote and an equilibrium S only after a longer time than the arbitrarily defined 10-month period of initial colonization. Potentially more important were physical and biological processes, including seasonal and annual variation in recruitment which would affect immigration and dominance and disturbance which would affect extinction.

A second feature of colonization is the initial increase in diversity as species

accumulate. If there is strong regional control of recruitment, the rates of increase within and among sites should be similar for panels of the same size. All panel series at all sites had significant positive regressions showing increases in species richness over the first 10 months of exposure (mean $r^2 = 0.82$, range 0.46 – 0.99). However, the rates of increase (slopes) differed between panel sizes and among most seasonal series within sites (Table 3). Within each site the rate of increase for large panels was always significantly greater than for small panels. At the inshore sites with panels near the surface the rate of increase on the surface panels was always less than for large panels and equal to or greater than the small panels near the bottom. When seasonal series were contrasted the most common pattern was for the rate of increase to be lower on the summer and higher on the fall and spring series, similar to the pattern for recruitment.

3.1.1.3 Competitive Dominance

Both seasonal and annual variation in larval availability and recruitment were external factors affecting immigration and thus the temporal pattern of colonization. A second type of nonequilibrium process resulted from the interplay between the internal, deterministic biological process of spatial dominance by particular species and unpredictable physical disturbance. This pattern was evident in panels from the Barn and San Onofre Kelp Forests (Figure 5) and from all inshore panels exposed near the water surface (Figure 6). However, it was most clearly seen in substrates exposed within the San Mateo Kelp Forest (Figure 7). Dominance (in terms of area covered) by one of more than 40 species was observed on most if not all panels. However, this dominance could only be correlated with a decline in species number below the

predicted equilibrium S on panels dominated by the colonial polychaete *Salmacina tribranchiata*, the mussel *Mytilus edulis*, the colonial corallimorph *Corynactis californica*, or occasionally the bryozoan *Parasmittina* sp. When dominant, each of these species eventually occupied almost 100% of the panel surface and in the case of the aggressive *Corynactis* actively killed other species.

Substrates dominated by *Mytilus* and *Corynactis* were not sampled after complete dominance had occurred and diversity had declined. *Corynactis* dominance occurred at the end of the study, generally developing over the last 6 - 12 months of exposure. At the main station outside of the Barn kelp forest, diversity varied between 20 and 25 species for the 1-2 years prior to *Corynactis* dominance. On those panels on which *Corynactis* dominance developed, the number of species declined to <10 species (Figure 5). This decline in diversity never occurred on those substrates without *Corynactis*. *Corynactis* also became abundant on several substrates transplanted inside the kelp forest as well as on some panels at the San Onofre kelp forest offshore site. However, *Corynactis* did not achieve more than 70% cover on any of these panels and no decline in S was observed (Figure 5). This suggests that even for this very aggressive species, 90-100% cover of the substrate was necessary before diversity was affected.

All the inshore surface panels became dominated by *Mytilus* after less than one year. Figure 6 compares this dominance and its effect at two of the five stations with surface panels. For all such panels a rapid decline in the number of species (from >15 to <5 species) was correlated with the development of this dominance. The biomass of

mussels on these panels (> 1 kg wet weight/panel) was sufficient to sink the surface racks and the experiment was halted before any additional data could be collected.

The effects of dominance and disturbance on colonization patterns were most obvious at the station inside the San Mateo Kelp Forest. Dominance by both *Salmacina* and *Parasmittina* occurred on panels at this station. All large summer and autumn series panels were colonized by *Salmacina*, a species that was fairly rare on panels. On 5 of the 6 panels *Salmacina* came to occupy almost 100% of the available space with a simultaneous decline in the number of species from >40 to 10-25 species/panel. On the sixth panel the bryozoan *Celleporaria brunnea* was also colonized by a mutualistic hydroid *Zanclaea* sp. and together these species were able to prevent the dominance by *Salmacina* (Osman and Haugsness 1981). The number of species on this panel did not decline (Figure 7). The bryozoan *Parasmittina* came to dominate all of the large winter panels at this station, which correlated with a slight decline in S or a failure to increase beyond 30 species/panel (Figure 7). These three panel series were all physically disturbed during the winter of 1979-80 resulting from entanglement of racks with drift kelp during storms. Subsequent to these disturbances the dominants (as well as other species) were reduced in abundance and the number of species increased to the same level as that observed on panels without a strong dominant (~45 species/panel). This return to the same S as observed prior to dominance and observed on panels without the dominating species demonstrates the potential resilience of these communities.

3.1.2 Spatial Patterns

Two general scales of spatial pattern were distinguished. First, there were the

broad intraregional patterns in differences among stations in the mean S attained by similar substrates. These differences can be seen by comparing the colonization curves in Appendix 1. There were two important parts to the regional patterns. First, panels of identical size at the same station usually reached the same mean S while panels of identical size from different stations often attained very different diversities. The mean S on large panels varied between 10 and 50 species. Although small panels had fewer species, their pattern of variability among stations was very similar to the large panels. Secondly, there were spatial patterns within stations relating to differences in size of the substrate, differences in habitat (e.g. surface vs. bottom panels), or differences in microhabitat (e.g. orientation of the substrate, the complexity of its physical structure, exposure to predators).

3.1.2.1 Regional Patterns

3.1.2.1.1 Recruitment

Given the substantial temporal variation among sites in the total number of recruits as well as underlying differences for individual species, regional control might be seen as a similarity in the frequency at which species recruit at sites with local processes altering the actual number of recruits. The cumulative frequency that each species was found on all recruitment panels at each site over the length of the study was calculated (number of panels recruiting on/total number of panels sampled). The sites were compared using Bray Curtis similarities and hierarchical clustering analysis (Primer 6.0). The results (Figure 8) show that recruitment was most different at the 3 most distant Channel Island sites and to a lesser degree recruitment at the kelp forest sites was different from the inshore transect sites. Analysis of similarity (Primer

Anosim) supports the differences in recruitment between these 3 groups of sites (Figure 8). To test whether there was greater regional influence on phyla with generally long-lived planktotrophic larvae (crustaceans, molluscs, cnidarians, annelids) and those with short-lived lecithotrophic larvae (bryozoans, ascidians, porifera) these groups were analyzed separately. Results (Figure 8) were similar to those for all invertebrates. Strong regional control was evident only when crustaceans (mostly barnacles) were analyzed separately (Figure 8). From these analyses it appears that both distance (Channel Islands) and habitat (Inshore vs. kelp forests) can result in the reduction in the degree to which sites within a region are linked by recruitment.

3.1.2.1.2 Colonization

3.1.2.1.2.1 Kelp Forests

The most consistent pattern within the region was the increased diversity on substrates inside kelp forests compared to those at nearby stations on the edge of kelp forests or immediately outside of them. The most obvious trend was exhibited by the three San Mateo kelp forest stations (Figure 9). If the effects of dominance and disturbance at the station inside the kelp forest are ignored, a clear trend of decreasing diversity can be seen. Colonization curves for large substrates inside the forest reached means of 45-50 species/panel, compared to means of 25-30 species/panel at the edge, and 18-20 species/panel outside the forest. A similar pattern of decreasing diversity with distance was also evident for small substrates. This trend could not be seen as clearly in stations associated with other kelp forests, partly because of an inability to establish an unambiguous inside-edge-outside transect in any of the other forests.

Because of the change in habitat at the original edge and inside Barn kelp forest (see Methods), only outside stations existed until a fourth station was later established inside the forest. New substrates were exposed at this station and some substrates from two of the original stations were transplanted to this site. The remaining substrates from these two stations were transplanted to the remaining outside station as a control for the transplantation. Ignoring the confounding effects on diversity of the dominance by *Corynactis* (Figure 5), the number of species on new and transplanted panels inside the Barn kelp forest rose to approximately 40 species/panel, while those panels outside the kelp forest maintained a mean S of 20 species/panel (Figure 10). Even though the Barn and San Mateo kelp forests were separated from one another by almost 15 km, the stations in the same position along the inside-outside transect were more similar to each other in diversity than they were to adjacent stations on the transect. Also the transplant experiment suggested that the location of the station relative to the kelp forest was more important than past history in determining the diversity of a substrate.

The pattern in the San Onofre kelp forest was much less clear (Figure 11). The cobble and boulder substrate was much more scattered than in the San Mateo or Barn kelp forests and the stations could not be established relative to a clear central reef area. Large substrates at the station inside the kelp forest reached a diversity of 30-35 species/panel. The two stations outside or on the inshore edge of the kelp forest accumulated 20-30 species/panel, but these were not followed long enough to determine whether they had reached an asymptote. Some panels were transplanted from the two inshore kelp bed stations to an inside station near the northern edge. The mean S of these substrates increased to 30-40 species/panel (Appendix 1). From these

data it would appear that there was a small increase in the mean S from the inshore outside stations to the station inside the kelp forest. However, all stations clearly overlapped in their mean S values.

The stations at Santa Catalina and Santa Cruz Islands (Figure 12) were not established in any transect, but results support the general pattern of higher diversity inside kelp forests. For both islands, panels at stations inside kelp forests had accumulated 30-40 species while panels at the Catalina Island station outside the forest only reached 10-15 species in the time those inside reached 25 to 30 species (these panels were lost early in the study). Unfortunately the sampling at all three stations was limited and there were insufficient data to determine whether S had reached an asymptote. However, it was clear that the rates of species accumulation were similar to those seen in other kelp forests.

The rates at which new species colonize or immigrate onto panels and species present are lost (extinction rate) indicate the degree to which gains from recruitment and losses from more local processes such as predation, competition, or other environmental factors contribute to the observed patterns. As can be seen in Appendix 2, the expected significant decreasing immigration and increasing extinction rates were observed at almost all sites, although in many cases the immigration r^2 was very low with some curves not being significant. Extinction rate regressions generally had higher r^2 's and were significant.

To analyze the contribution of immigration and extinction rates to the patterns observed in kelp forests each of the three main kelp forests were compared using analysis of covariance (Table 4). Immigration rate decreased from inside to outside the

San Mateo forest for both large and small panels. In part this resulted from significantly shallower slopes for large panels at the station inside the kelp forest. The other forests exhibited a similar pattern but the differences among the sites were not significant. For all three kelp forests there was little difference in extinction rates among the sites. The slope for extinction rate regression for large panels at the outside station in the Barn kelp forest was significantly higher and the extinction rate was significantly lower for the edge station in the San Mateo Kelp forest. Thus, overall there were no consistent patterns for extinction and variation in recruitment and resultant immigration rates contributed most to variation among kelp forest sites.

3.1.2.1.3 Inshore Transects

Another regional colonization pattern that was correlated with differences among stations in immigration and extinction was the general increase among inshore stations in mean S as the distance to the site of the discharge for the power plant decreased (Appendix 1, 2, Figure 13). As with the kelp forest pattern, regressions of immigration rate as a function of the number of species present were fairly weak. An analysis of covariance among stations along the North and South transects (Table 4) showed a significant increase in immigration rate near the discharge for both transects which also had higher mean S's. On the South transect the slopes for the immigration rate regressions were significantly higher for the most distant sites contributing to a more rapid decline in immigration as species colonized. The higher immigration rates could have resulted from the increased abundance of boulder substrate in the discharge area acting as a source area of larvae or from the operation of the discharge. A study of recruitment of epibenthic motile species (Kastendiek et. al. 1981, 1982) clearly

demonstrated that the operation of the discharge was a factor in the elevated recruitment possibly from increased water flow and upwelling by entraining bottom water and moving it to the surface. Substrates placed near the discharge would then be exposed to an increased volume of water per unit time and thus a greater number of larvae. No differences in extinction rate were found for South transect and only two sites differed on the North transect.

3.1.2.2 Local Patterns

Several local or within site patterns in diversity can be examined. How these local patterns differ from regional or between site patterns indicate the degree to which any regional control of diversity is modified locally.

3.1.2.2.1 Surface vs. Bottom Within Sites

The lower mean S on panels exposed near the surface compared to those near the seafloor was consistent for each of the 5 stations where both surface and bottom panels were deployed (Figure 13, Appendix 1). As hypothesized, recruitment rates were lower for the surface panels (Appendix 1) and resulted in significantly lower immigration rates (Table 4) and the extinction rate for surface panels was significantly higher than bottom panels. The higher extinction rates correlated with the loss of species resulting from dominance by *Mytilus* (Figure 6).

3.1.2.2.2 Substrate Size

Comparing the diversity on the small and large panels is a direct measure of the effect of local resource availability on the observed regional patterns. With an increase in substrate size, the recruitment and immigration rates should increase simply because a larger substrate should sample a larger number of recruits. The extinction rate should

decrease because population sizes should be larger and thus reduce the average probability of local extinction for any species. These predictions were generally supported (Figure 14, Appendices 1, 2) at all stations where both large and small substrates were exposed. Large substrates always attained a higher mean S than small panels at the same station. The recruitment for small substrates usually showed the same temporal variation as the large, but the number of species recruiting was reduced (Appendix 1). Immigration and extinction rates were also consistent with the predictions of the model. Immigration rate curves for small substrates generally had lower intercepts than those for comparable large panels (Appendix 2) and the immigration rate was significantly greater for large panels at all sites (Table 5). The extinction rate curves for small panels were steeper than for large but this difference was significant for only 8 of the 22 sites and extinction was significantly higher at 13 of the 22 sites. (Figure 13, Table 5).

3.1.2.2.3 *Substrate Orientation*

Another local habitat parameter that was manipulated was the orientation of the panels. At several kelp forest stations two sets of large panels were exposed in the winter 1979-1980, one set was oriented with the panel surface facing the seafloor (the normal panel orientation) and the other set was oriented facing the water surface (face-down versus face-up substrates). At least two environmental factors were expected to vary between the two treatments; both sedimentation and light exposure should have been higher on the face-up panels. These experiments were done to examine the effect of sedimentation on the species composition of the sessile invertebrate community. However, the effect of orientation on diversity was examined,

even though the panels were not studied long enough to ascertain whether equilibria were reached.

For sessile invertebrates, there were significant differences in mean S that resulted from substrate orientation (Figure 15). At 3 of the 4 stations where the orientation experiments were conducted significant differences in diversity were found between face-up and face-down panels, with the face-down panels having a higher number of species. The species composition and dominant species were quite different (Figure 15) between the two treatments, possibly resulting from differences in sedimentation or effects of increased algal diversity on face-up panels with greater exposure to light.

3.1.2.2.4 Physical Structure of the Substrate

Another type of measurable local difference was the structural complexity of the panels. Natural cobble, boulder, and bedrock substrates can vary over a variety of spatial scales in their structural complexity; e.g. from caves to crevices to grooves to scratches. On panels, however, the major contributors to structural (= habitat) complexity were the organisms themselves (Dean 1981).

A principal group of structure producers are barnacles. As they grew, barnacles increased the surface area of the panel and produced vertical relief. When they died, their tests remained attached to the substrate and the vacant interior provided additional habitat. To examine the effects of barnacles on colonization, panels with 3-6 month old barnacles covering 40-90% of their surface were dried and then placed in a 10% chlorine bleach solution to remove all organic material. These panels were then washed in seawater and exposed along with clean normal panels inside the San Mateo

and San Onofre kelp forests. As with the orientation experiments, these panels were not followed long enough to establish whether equilibria were reached; the panels in the San Mateo kelp forest were lost after one sampling period.

Regardless, after exposure for 3 months the diversity on barnacle panels was 1.5 times higher in the San Onofre kelp forest (14.17 vs. 23.25 species/panel, $t = 4.35$, $p < 0.01$) and 3 times higher in the San Mateo kelp forest (30.06 vs. 10.83 species/panel, $t = 9.09$, $p < 0.001$). Based on their average dimensions, barnacles increase the available surface area of a substrate 2 - 2.5 times and assuming the theoretical area-species relationship, this should have resulted in an increase in diversity of 1.2 to 1.25 times that on flat panels. Therefore, it is not clear whether the increased diversity on the barnacle treatments resulted from more than an increase in surface area. After a year the diversity on the San Onofre barnacle panels increased little and was actually lower than the panels that had no structure initially.

3.1.2.2.5 Inshore vs. Offshore Habitats

A larger scale habitat difference possibly existed between inshore and offshore (kelp forest) stations. One major difference between these areas was an increase in the average turbidity at the shallower stations and a correlated difference in the relative abundances of certain groups of species (Osman et. al. 1981). Comparisons of the colonization curves for the two groups (Appendix 1) did not show any obvious differences in mean S . To examine whether the observed differences in species composition affected immigration and extinction rates and the resulting diversity, reciprocal transplanting of panels between an inshore and offshore station was done. Unfortunately, the inshore panels transplanted offshore were lost. The offshore panels

were from the station inside the San Onofre kelp forest and outside the Barn kelp forest.

These panels were moved to the 1600 m South station. Before transplantation the mean S for the San Onofre kelp panels was 33 species, for Barn kelp was 23 species, and for the inshore station was 18 species. Panels at all three stations which were not moved served as controls.

Transplanted panels were only followed for 6 months and showed no significant change in mean S, or immigration rate, but the panels transplanted from the San Onofre kelp forest displayed a significant increase in extinction rate. The mean S on these transplanted San Onofre panels did decrease from 33 to 24 species but this change was not significant. The change in habitat seems to have resulted in an increased extinction rate on some panels, but this increase did not result in a measurable change in S over the 6 month time period. The increased extinction probably resulted from a differential mortality among species intolerant to turbidity (Osman et. al. 1981).

3.1.2.2.6 Predation

Predation has been shown to have a significant impact on the species composition (e.g. Osman and Whitlatch 1996, 2004, Janiak and Osman 2012) and diversity (e.g. Freestone et al. 2011, 2013) in other fouling communities. At several of the sites in this study seastars were shown to affect the relative abundances of bryozoan species (Day and Osman 1981). In the present study the effects of predators on local diversity was examined in a very limited experiment contrasting panels inside tubes with those in the open. The tubes prevented predation by larger fish predators but allowed access to smaller invertebrate and fish predators. These experiments were conducted at the Channel Island sites. Little difference in diversity was observed inside

the two kelp forests but panels inside tubes outside of the Catalina kelp forest attained a much higher diversity than open panels over the first 6 months of deployment (Figure 12). The open panels were lost at the outside site after 6 months but the diversity of panels inside tubes remained at around 30 species, similar to panels inside tubes inside both kelp forests. Species composition did differ significantly between tube and open panels at the three sites.

4. Discussion

The degree of influence of the regional species pool on local diversity is continuing to be debated (e.g. Cornell and Harrison 2013, Witman 2013). As Witman (2013) has stated, the regional species pool must have some influence in that it sets the limits of the source of species for any local site. Simple logic dictates that a local habitat in a region of 1000 species has the potential of attaining a higher diversity than a similar habitat in a region of 10 species. Nevertheless, it remains an open question as to the degree which regional and local processes control local diversity. For marine systems the distribution of propagules, or recruitment, has been seen as a critical link among sites within a region and thus an important component in the degree of regional control (e.g. Roughgarden et al. 1985, Caley et al. 1996, Connolly and Roughgarden 1999, Ellien et al. 2000, Hixon et al. 2002, Morgan et al. 2009). Recruitment was an essential component of the experiments comprising this study. As such, how it links sites is one measure of regional control. On the other hand, the degree to which sites within the region maintain consistent differences in diversity can be a measure of local control.

The need for experiments addressing regional and local controls of diversity has

692 been seen as a priority (e.g. Cornell and Harrison 2008, 2013, Witman 2013). The
693 contrast of recruitment and colonization on experimental panels among 28 sites within a
694 region across spatial scales of meters to >100 km, addresses this need, at least in part.

695 The data presented were collected solely using experimental panels deployed in a
696 similar manner at all field sites. The use of panels enabled: 1) comparing identical
697 habitat (admittedly artificial) within and among all sites within the region, 2) examining
698 diversity within the dynamic process of colonization that incorporates immigration of
699 new species and local extinction of species present, 3) measuring directly recruitment
700 as a key process connecting sites within the region, 4) measuring temporal changes in
701 abundance of all species present, and 5) knowing or controlling key habitat properties
702 such as location, size, time when exposed, length of exposure, or orientation. All of
703 these properties combine to make the comparison of diversity among sites more
704 straightforward by eliminating many, but not all, of the unknown differences among
705 sampling units of natural habitat. Principally among these are knowing and to some
706 degree controlling, the history of the community on each substrate and being able to
707 observe many processes or at least their consequences. Contrasting local diversity
708 among sites in such a dynamic and historical context acknowledges that local
709 communities are not static and if they can be characterized in terms of their diversity it
710 must be in the context of change

711 Before considering the experimental data presented it is important to consider
712 several aspects of the epifaunal communities of the southern California region that were
713 studied. First, the region is relatively diverse with >650 sessile species that could
714 colonize panels and 327 of these observed on panels in this study. The limit set on

local and panel diversity by the regional species pool was thus fairly high. Secondly, at the local level of a panel the communities are very dynamic, continually gaining and losing species even after total coverage is >90% of the panel surface (e.g. Appendix 2). Thirdly, the 6-10 months that open space remained >10% on panels (Figures 5-7, Appendix 1) and over which diversity continued to increase suggest that communities developed relatively slowly when compared to the >90% cover in one month found in similar New England communities (Stachowicz et al. 1999, 2002, Osman and Whitlatch 2007). These slow rates are also reflected in generally low recruitment rates of often <200 individuals for all species recruiting onto panels during a 6 week sampling period (Appendix 1) compared to 100-1000 individuals per week for single species in New England (Osman 1978, Osman et al. 1992), Delaware (Dean and Hurd 1980), or North Carolina (McDougall 1943, Sutherland and Karlson 1977). Also, individual and population growth rates were low as can be seen in the 6-12 months for populations of some species (Figures 5-7) to dominate panel habitat. Thus the combination of a diverse pool of available species that form locally dynamic communities and the slow rates at which spatial resource is utilized provide the opportunity for recruitment to provide broad regional control.

Within this context, the degree of propagule dispersal among local habitats is a key parameter in the degree of regional control (e.g. Cornell and Harrison 2008, 2013, Witman 2013). A well-mixed propagule bath of larvae (Cornell and Harrison 2013) based on classic barnacle supply-side models (e.g. Gaines and Roughgarden 1987, Roughgarden et al. 1985) with broad dispersal of long-lived planktotrophic larvae certainly argues for strong regional control within marine systems. However, 54% of the

sessile species on the panels and the bulk of the most common taxa (bryozoans, ascidians, and sponges) have short-lived lecithotrophic larvae that may disperse locally within short distances of source populations (Olson 1985, Davis and Butler 1989, Osman and Whitlatch 1998). In addition, numerous studies (Hunt and Scheibling 1997, Osman and Whitlatch 1996, 2004, Sams and Keough 2007) have demonstrated that predation on newly-settled recruits can be sufficient to eliminate the recruitment of prey taxa locally. Local variation in predation on larvae (e.g. Young and Gotelli 1988, Young and Cameron 1989, Navarrete and Wieters 2000) can have a similar effect, especially if certain taxa are preferred or rejected.

Thus the potential exists for a regional bath of larval propagules to be modified by larvae released locally and the local loss of propagules to post-settlement predation. The results presented here demonstrate both regional influence and local modification of recruitment. The temporal patterns reflected in Figure 2 show seasonal and annual variation in recruitment across the region. The temporal patterns of higher recruitment in the spring and autumn and annually increasing recruitment over the 3 years of the study were found for both the number of species and the cumulative abundance of recruits. However, when the similarity in the community of species recruiting at the different sites was contrasted, local influences based on habitat (offshore kelp forests vs. inshore sites) and distance (Channel Islands vs. coastal sites) were strong (Figure 3). Surprisingly, the hypothesis that local influences should be reduced for species with planktotrophic larvae was largely rejected. A similarity in species recruiting across the region was seen only for crustaceans, i.e. barnacles.

Beyond differences in recruitment, the contrasts of colonization curves and

companion immigration/extinction curves test the longer-term temporal and spatial aspects of regional and local control of diversity. With increasing species invasions in epifaunal and other marine communities (e.g. Carlton 1989, Ruiz et al. 1997, 2013) not even the regional species pool cannot be seen as static. At smaller local scales, whether a habitat such as a kelp forest or an individual panel, diversity will vary temporally and it is important to examine regional control in a temporal/spatial context. The analyses of the colonization of individual panels and means for series of panels showed that there was significantly more variability than expected in the initial increase of species richness and the asymptotic or equilibrium diversity when the spatial resource became limiting on the panels. Measured immigration and extinction rates also varied within as well as among sites. As shown, seasonal and annual variations in recruitment, dominance, disturbance, and other processes contributed to this variability. Despite this variability several general patterns did emerge:

1. Replicate panels at each site initially deployed at the same time had very similar colonization curves. Some exceptions to this were seen, mostly resulting from dominance on some panels by particular species.

2. Seasonal panel series at the same site generally reach the same asymptotic or equilibrium diversity regardless of some differences in initial rates of colonization. Again, dominance resulted in a few exceptions to this general pattern.

3. Asymptotic diversity differed significantly among sites with panels at some sites having 2-3 times the diversity than panels at other sites.

4. The total number of species sampled at each site correlated well with the asymptotic diversity on panels. Of the 327 epifaunal species sampled, sites inside kelp

forests had the highest number of species (137-183 species for the 6 sites inside the 5 kelp forests), those on the edge or outside the forests (80-126 species for 10 sites) and along the inshore transects (85-128 species for 12 sites) had fewer, and the surface panels at 5 sites had the lowest number of species (41-106 species). The regional influence can be seen in that 75% of the species colonized panels at the coastal sites as well as panels at one or more of the three Channel Island sites. Of the 56 species found at only one site 18 were associated with one of the coastal kelp forests, 9 were at an inshore site, 24 were from Catalina Island, and 11 from Santa Cruz Island. The latter suggests the impact of distance on local diversity. Even though the Channel Islands were represented by only three sites with many fewer samples, they nonetheless had 40 species (including 5 on both islands) not found at any of the 25 coastal sites.

5. For those sites at which two panel sizes were deployed, the small panels, as expected, consistently attained a lower diversity than the large. With less spatial resource the small panels sampled fewer recruits and had lower immigration rates. The reduced space also led to higher extinction rates. Beyond demonstrating that within a site resource availability can influence diversity, the similarities in the patterns of diversity among sites for both large and small panels is a measure of the consistency of the differences among sites. The sites with highest and lowest diversity exhibited these differences for all series of panels both large and small.

6. For those sites with both bottom and surface panels, the surface panels with generally lower recruitment rates, reached lower diversities than panels exposed near the seafloor. Although the dominance of the surface panels at all sites by mussels was the principal cause of declines in their diversity, these panels were colonized at a lower

rate and reached lower diversities than bottom panels prior to the decline with mussel dominance. As with the small panels, these surface panels demonstrate that processes such as recruitment can vary within a site and create differences in diversity similar to that among sites.

7. Immigration and extinction rates varied more than expected but they followed similar patterns as found in the analyses of recruitment and colonization. The general trend was for the immigration rate to be highest inside kelp forests and at inshore stations nearest the power plant discharge. Patterns for extinction rates were more variable and weaker but overall extinction rate tended to be lower inside kelp forests and near the discharge. Similar patterns were seen for both large and small panels as well as the surface panels.

Given the suite of patterns observed, there is clear evidence that the size of the regional species pool has an impact on local species richness but that this is greatly modified by local processes. Beyond the large regional species pool allowing a high upper limit for local diversity, 46% of the epifaunal species found on panels produce long-lived planktotrophic larvae which would be unlikely to recruit locally. Recruitment by these species must certainly link sites within the region. Even though those remaining species with short-lived lecithotrophic larvae can, and likely do, recruit locally, it is also likely that some larvae are exported to other sites. That 75% of the species were found throughout the region, on both the mainland and distant Channel Island sites also argues for some degree of regional influence. However, the clear differences found in both the fauna and recruitment at the Channel Island sites as well as the recruitment differences between the coastal kelp forest and inshore sites demonstrate

that any regional control is modified locally. The finding that these differences in recruitment existed for both lecithotrophic and planktotrophic species suggests that distance plays a significant role in that the linkage among sites will be stronger for those closest to one another.

Another aspect of regional control is the relatively low overall rates of recruitment, growth, and resultant colonization. Except for barnacle recruitment of >4000 individuals/panel at two San Mateo kelp forest sites during one sampling period, recruitment over 6 weeks never exceeded 1000 individuals/panel for all species at any site. At all but 7 sites, recruitment never exceeded 500 individuals/panel for any 6 week sampling period. The generally low growth rates are reflected in the open space on panels. At most sites a reduction in open space to <10% of panel surface did not occur for at least 6 months and at some sites this could take >12 months (Figures 5-7, Appendix 1). Small panels usually required 3 months for open space to be <10%, but this could also take more than 12 months. These low rates were also seen in the colonization process with most panels not reaching an asymptotic diversity until after 6 months (Figures 3, 4, 9-14, Appendix 1). These low rates across the region likely contribute to high site and panel diversities. With spatial resource available for longer periods of time, the opportunity exists for more species to colonize a panel or site. The high regional species pool can provide these species and seasonal variation in species producing recruiting larvae can increase the likelihood of new species being added.

Although there are some regional controls on diversity of the epifaunal communities studied, local control appears much stronger. First, the data presented support a systematic variation among the sites examined. With regional control we

would expect some level of stochastic variation but for most, if not all, parameters measured the sites varied in a consistent manner. This is most easily seen in the colonization data. In general the replicate panels within seasonal series as well as the 4-5 different seasonal series of panels all reached the same equilibrium or asymptotic diversity at each site (Figures 3, 4, 9-14, Appendix 1). Sites, on the other hand, showed significant differences in diversity, both in terms of individual panels and the cumulative number of species found at each site. These data are not static measures of diversity but rather incorporate the change in diversity over time. Given that recruitment varied throughout the study (Figure 2), each seasonal series of panels experienced a different recruitment environment with the colonization sequence of species based on the larvae available during the time of exposure. If recruitment is the main mechanism of regional control we might expect to see more similarity among sites for seasonal series and greater differences within sites among series. The opposite pattern with series within sites reaching the same equilibrium diversity and diversity showing a consistent variation among sites was found.

There is little evidence that differences in recruitment established any priority effects (e.g. Robinson and Dickerson 1987, Almany 2003, Geange and Stier 2010, Irving et al. 2007, Ralston and Swain 2014) in terms of diversity, but rather that local environments produced a similarity among panels in terms of diversity. However, this does not negate the importance of recruitment. The three major habitat patterns observed were decreasing diversity from inside to outside kelp forests, decreasing diversity away from the power plant outfall, and decreased diversity on surface than bottom panels at the same site. In all three patterns there is evidence that recruitment

varied in a similar manner (Figures 9-14). The extensive rocky substrate of kelp forest are a potential source of larvae. The rocky substrate around the outfall as well as its effects on water flow increasing larval abundance (Kastendiek et al. 1981, 1982) likely increase recruitment locally. The abundance of larvae ready to recruit is likely lower in surface waters compared to bottom waters. Given that many of the species within the epifaunal community produce short-lived larvae that are ready to recruit upon release (e.g. Olson 1985, Davis and Butler 1989, Osman and Whitlatch 1998), some local control of recruitment is likely.

Secondly, the immigration and extinction rate measures also support a significant degree of local control of diversity. The pattern of differences among sites, not surprisingly, correlated with those observed for colonization. Patterns for both immigration and extinction were weak but nonetheless showed differences among sites. Immigration rates are influenced by regional recruitment, any local variation in recruitment, and the number of species already present on any panel. Differences in immigration rates resulted from both differences in the Y-intercept (recruitment with 0 species present) and the slope of the curve. Differences in both of these are more likely to result from local differences given that there is no reason why either should vary under regional control. Extinction rate is almost exclusively a local process that is a function of the local physical and biological environment. The regional pool of available predators or region-wide environmental changes (e.g. El Nino events) could modify local extinction rates but such impacts were not observed during this study.

Finally, the differences among panels within sites resulting from dominance, disturbance, panel size, or surface/bottom location all reinforce the importance of local

control. The similarity among sites in the patterns of small and large panels demonstrates that differences observed are robust in terms of resource available (panel space or size) and controlled by conditions at each site. The differences between surface and bottom panels demonstrate that differences within a site such as lower recruitment at the surface can result in overall differences in diversity. In addition, the pattern of higher diversity near the power plant discharge was similar for the surface and bottom panels, both large and small. This consistency reinforces the impact of local conditions on diversity, even as other parameters such as habitat size or type are changed. The higher diversity on panels outside the Catalina kelp in tubes with some predators excluded and the increase in diversity of panels transplanted from outside to inside the Barn kelp forest also indicate local control. Although some panels transplanted from offshore to inshore declined in diversity as would be expected with local control the difference was not significant.

The response of the panel communities to dominance and disturbance are, perhaps, one of the strongest indications of local control of diversity. The dominance of four different species on some panels at several different sites demonstrates the ability of a single species to influence diversity at the very local level of a panel (Figures 5-7). However, it is the recovery of these communities from this dominance after a disturbance that provides the stronger evidence for local control. The panels in the San Mateo kelp forest that became dominated by *Salmacina* declined substantially in diversity. After these panels were disturbed and the dominant species was reduced in abundance, their diversity recovered to previously high levels and was no different than the panels at that site that were not dominated. In addition, the seasonal series also are

an indication of the ability of these communities to recover from disturbance. Each series was started with new panels, equivalent to a complete disturbance and the removal of all species. They thus represent disturbances at different times and of communities of various ages and diversities. The similarity within each site of the equilibrium diversity of all series as well as the recovery of the *Salmacina*-dominated panels after a disturbance demonstrate the resilience of these communities and their ability to return to the same diversity at each local site again and again.

Overall the results of this study demonstrate that any regional control of diversity is greatly modified at the local level. The relationship between regional and local diversity has been examined as one of regional enrichment of local diversity (Ricklefs 1987, Karlson et al. 2004, Witman et al. 2004) as well as the reciprocal phenomenon of local communities enhancing the larger regional metacommunity (Harrison and Cornell 2008) and evolutionary processes (Ricklefs 1987) contributing to regional diversity. Because the present study focused on a single region with a more or less static regional species pool, the study can address only the degree of regional enrichment resulting from ecological processes operating over a few years and not evolutionary processes impacting the size of the regional species pool.

An important element in characterizing the impact of regional diversity on local communities is the degree to which local communities are saturated (Loreau 2000, Russell et al. 2006, Pinto- Sánchez et al. 2014). For this study this is a question of the maximum number of species that can co-exist on a single panel and whether this is achieved. In experiments with terrestrial plant communities this was addressed by adding new species (Tilman 1997) to test whether local diversity could be increased.

This really is an experimental alteration of recruitment or immigration rates. In this study such variation occurred among and within sites and clearly impacted the diversity on panels. The sites inside kelp forests with panels often maintaining diversities >40 species set the minimum level for saturation. Given the much lower diversities at other sites, it would appear that panels at most sites are under-saturated. At the panel level, site differences in immigration and extinction rates suggest that this under-saturation is the result of both differences in recruitment and losses. There are significant regressions between the cumulative number of species found at the sites (or site species pool) and the mean ($r^2 = 0.73$, $p < 0.0001$) or maximum ($r^2 = 0.77$, $p < 0.0001$) species on panels. Thus the under-saturation found on panels would seem indicative of the sites as well. It would appear that at most sites the opportunities provided by a large regional species pool are not realized at the local level based on an inability of recruitment to link sites across even small spatial scales (e.g. in and outside kelp forests) combined with local differences in mortality (extinction rates).

Regional enrichment of local diversity can be a measure of regional control. However, regional enrichment has been characterized in two different ways. Karlson et al. (2004) found that regions of higher diversity resulted in similarly high local diversities. On the other hand, Witman et al. (2004) characterized lower diversity regions (e.g. higher latitudes) as having local communities that are regionally enriched in the sense that they contain a higher percentage of the regional species pool. In addition, Russell et al. (2006) found that regional enrichment, in either sense, breaks down at small local scales where strong species interactions and local environments decrease the potential influence of the regional species pool. The panels in this study certainly represent a

small local scale and exhibit patterns similar to those found by Russell et al. (2006). If we use the cumulative number of species found at each site as a measure of diversity at a larger local scale or as a local species pool, there is a strong linear relationship between these local pools and the diversity on panels. This direct effect of local pool on panel diversity is similar to the regional enrichment observed by Karlson et al. (2004), supports the argument of Russell et al (2006) that enrichment occurs at larger scales, but does not support the greater proportion of the pool being observed at low diversity sites (Witman et al. 2004). Thus the high regional species pool may provide the opportunity for enrichment but panels at most sites are under-saturated and do not reach their potential diversity.

An important aspect in this study is the dynamism represented by the temporal variation in diversity as the panels were colonized. It is clear that at the most local level of individual panels the composition of the community is continually changing as species are lost and new species recruit. This change cannot occur without a supply of new recruits which, given the life histories of the species, implies some level of regional and local input. The communities within a site and outside contribute to a stream of available recruits. However, the equilibration of panels within a site to the same diversity regardless of their history and the differences among sites indicate strong local control. Even when dominant competitors on some panels (Figure 7) resulted in drastic reductions in diversity, the communities on these panels returned to the site diversity after a disturbance. This resilience also demonstrates strong local effects on diversity.

There is no question that the regional pool of species must have some effect on local diversity. The question is the degree to which regional processes dominate

marine coastal systems. Recruitment is certainly an important element linking sites within a region, but it is also coupled with local processes including not only environmental conditions and interactions among the species present, but also local recruitment. Local recruitment can result from both local settlement of larvae produced by the many lecithotrophic species at each site but also post-settlement mortality of larvae arriving from a regional pool. The concept of a regional bath of larval recruits certainly may be applicable to many species, but these species do not necessarily make regional control of diversity more prevalent in marine coastal systems than in others. The data presented argue for fairly strong local control, demonstrate a general under-saturation of communities at most sites, and show a continuous, dynamic turnover of species. Based on the cumulative number of species found at each site, it is clear that a sufficient number of species are available for the diversity on panels to be greater than usually observed. The diversities observed on kelp forest panels suggest that 40-50 species can be maintained on panels while accommodating turnover rates of 5-10 species per 6 week sampling period. Strong local control of both recruitment and post-recruitment processes is the most compelling reason for panel diversities of 20-30 species being observed at most sites.

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- 1184

1185 7. Tables

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SOURCE	DF	SS	F VALUE	PR > F
YEAR	2	1389.29	61.59	0.0001
SEASON	3	467.94	13.83	0.0001
STATION GROUP 11	11	50.01	9.27	0.0001
YEAR * SEASON	4	163.04	3.61	0.0064
YEAR * GROUP	17	294.02	1.53	0.0783
SEASON * GROUP	32	1413.21	3.92	0.0001
YEAR * SEASON * GROUP	30	612.65	1.81	0.0059
ERROR	511	5763.80		
TOTAL	610	12510.50		

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TABLE 1. Three way analysis of variance of the number of species on recruitment panels. Data were classified by year, season, and groups of stations. Years began on 21 June of 1978, 1979, and 1980. Stations were assigned to one of 12 groups determined by geographic location (each kelp forest, the north transect, and the south transect were discrete locations) and by 'habitat' (inside, outside, or on the edge of a kelp forest, or near or far from the power station discharge). $R^2 = 0.539$.

Station	Large NS	Large Pos	Large Neg	Large <15% CV	Small NS	Small Pos	Small Neg	Small <15% CV
Barn Kelp								
Panels	18	4	1	10	2	0	1	0
Series	5	3	0	1	0	0	1	0
San Onof Kelp								
Panels	27	9	0	17	5	1	0	1
Series	6	1	0	4	2	0	0	1
San Mateo Kelp								
Panels	22	3	1	9	2	1	0	3
Series	9	7	0	0	4	0	0	1
Inshore								
North								
Panels	28	3	2	12	9	0	0	3
Series	7	2	1	1	3	0	0	0
South								
Panels	32	0	1	16	6	0	0	1
Series	10	1	2	5	2	0	0	1
Total								
Panels	127	19	5	65	24	2	1	8
Series	37	14	4	10	12	3	1	3
Percent								
Panels	84.1	12.5	3.3	51.2	88.9	7.4	3.7	33.3
Series	67.3	25.5	7.3	27.0	75.0	18.8	6.3	25.0
Inshore								
Panels	90.9	4.5	4.5	46.7	100	0	0	26.7
Series	73.9	13.0	13.0	35.3	100	0	0	20.0
Offshore								
Panels	78.8	18.8	2.4	55.5	75.0	16.7	8.3	44.4
Series	62.5	34.4	3.1	20.0	63.6	27.2	9.1	28.6

Table 2. Number of panels and series with no significant, positive, and negative change in species number after 10 months exposure. The numbers of panels or series with no significant change that had a coefficient of variation <15% are also shown. Data are summarized by offshore kelp forests and inshore transects.

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Station	Size Slope Sig Diff	Size Slope r ²	Size Slope Rel Diff	Series Slope Sig Diff	Series Slope r ²	Series Slope Rel Diff
Barn Kelp Out 1	<0.001	0.757	S<L	0.0002	0.851	1=5=7>3
Barn Kelp Out 2	<0.001	0.845	S<L	<0.0001	0.918	3=7>1, 5=3=7, 5=1
Barn Kelp Out 3	<0.001	0.791	S<L	0.0247	0.849	7>5=3=1
Barn Kelp In						
San Onofre Kelp In	<0.001	0.823	S<L	<0.0001	0.906	7=5>1=3
San Onofre Kelp Edge	<0.001	0.772	S<L	0.0023	0.826	5=3>1, 7=5=3, 7=1
San Onofre Kelp Out	<0.001	0.857	S<L	0.0128	0.889	5=3>1, 7=5=3, 7=1
San Onofre Kelp Off	<0.001	0.844	S<L	0.0002	0.900	7>5=1, 3>1, 3=5, 3=7
San Mateo Kelp In	<0.001	0.828	S<L	<0.0001	0.901	7>1=3=5
San Mateo Kelp Edge	<0.001	0.842	S<L	0.0007	0.922	3>1=5=7
San Mateo Kelp Out	<0.001	0.836	S<L	0.1494	0.853	NS
1600 North	<0.001	0.804	Srf=S<L	0.8880	0.807	NS
800 North	<0.001	0.719	S<L	0.0078	0.805	3=5=7>1
400 North	<0.001	0.780	S<L	0.0039	0.850	5=7>1, 3=1, 3=5=7
200 North	<0.001	0.867	S<L	0.6930	0.867	NS
100 North	<0.001	0.806	S<L	0.0195	0.843	7>5=1, 3>1, 3=5=7
50 North	<0.001	0.878	S<Srf<L	0.0415	0.913	3>1
50 South	<0.001	0.785	S<Srf<L	0.0561	0.855	NS
100 South	<0.001	0.740	S<L	0.0545	0.837	NS
800 South	<0.001	0.785	S<L	0.0077	0.871	3>1
1600 South	<0.001	0.773	S=Srf<L	0.6382	0.803	NS
Intake North	<0.001	0.778	S<Srf<L	0.0003	0.879	3=5>1
Intake South	<0.001	0.815	S<L	0.0485	0.894	5>1

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1213 Table 3. Results of regression analyses of the initial slopes of the colonization curves.

1214 Comparisons were made within each site of panels of different sizes (including surface panels

1215 as a size class) and different seasonal series for large panels. Series identifications are 1=

1216 Summer 1978, 3=Fall 1978, 5=Winter 1978, and 7=Spring 1979.

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	Immigration Large	Immigration Small	Extinction Large	Extinction Small
Stations				
Barn Kelp Forest				
Station Sig Diff	NS	NS	<0.0001	NS
Slope Sig Diff	NS	NS	0.003	NS
Station Diff	In=Out1=Out3=Out2	Out1= Out3= Out2	Out1=Out2=Out3=In	Out1=Out=Out2
San Onofre Kelp				
Station Sig Diff	0.0388	0.0078	0.0008	NS
Slope Sig Diff	0.0002	NS	NS	NS
Station Diff	In=Off=Edge=Out=No1=No2	In>Off	In=Out=Off>No1	Off=Out=Edge=In
San Mateo Kelp				
Station Sig Diff	<0.001	0.0003	0.0071	NS
Slope Sig Diff	0.0198	NS	NS	NS
Station Diff	In>Edge>Out	In>Edge>Out	In>Edge	Edge=In=Out
North Transect				
Station Sig Diff	<0.0001	0.0062	0.0407	NS
Slope Sig Diff	NS	NS	NS	NS
Station Diff	50N=200N>1600N=400N	50N>400N	200N>1600N	NS
South Transect				
Station Sig Diff	<0.0001	NS	NS	NS
Slope Sig Diff	0.0017	NS	0.0075	NS
Station Diff	50S>100S>1600S	No Diff	No Diff	No Diff
Surface vs. Bottom				
Station Sig Diff	<0.0001		<0.0001	
Slope Sig Diff	0.0054		<0.0001	
Station Diff	Bot>Surf		Surf>Bot	

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1221 Table 4. Results of analyses of covariance of immigration and extinction rate curves for the
 1222 three sets of kelp forest stations the inshore transects, and surface vs. bottom panels.

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Site	Immigration		Extinction	
	Size	Slope	Size	Slope
Barn Kelp Out 1	L > S	NS	S > L	NS
Barn Kelp Out 2	L > S	NS	NS	NS
Barn Kelp Out 3	L > S	L > S	NS	NS
San Onofre Kelp In	L > S	NS	NS	S > L
San Onofre Kelp Edge	L > S	NS	S > L	NS
San Onofre Kelp Out	L > S	NS	S > L	NS
San Onofre Kelp Off	L > S	NS	S > L	S > L
San Mateo Kelp In	L > S	NS	NS	NS
San Mateo Kelp Edge	L > S	NS	S > L	S > L
San Mateo Kelp Out	L > S	NS	NS	NS
	L > S	NS	S > L	NS
1600 North	L > S=Surf	NS	Surf=S > L	Surf=S > L
800 North	L > S	NS	NS	NS
400 North	L > S	NS	NS	NS
200 North	L > S	NS	S > L	NS
100 North	L > S	NS	S > L	NS
50 North	L > Surf=S	NS	Surf > L	NS
	L > S	NS	S > L	NS
50 South	L > Surf=S	NS	Surf > L	NS
100 South	L > S	NS	S > L	S > L
800 South	L > S	NS	NS	NS
1600 South	L > S=Surf	NS	Surf > L	Surf>S > L
	L > S	NS	S > L	NS
Intake North	L > Surf=S	NS	NS	NS
Intake South	L > S	NS	S > L	S > L

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1227 **Table 5.** Comparisons of Immigration and Extinction curves for small, large, and surface panels

1228 at each site based on Analysis of Covariance.

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8. FIGURE LEGENDS

Figure 1. Locations of field stations. The Channel Island and mainland kelp forest sites are indicated by ○'s. The two inshore transects are designated N and S. The north transect had stations at 1600, 800, 400, 200, 100, and 50 m from the discharge of a power plant and the south transect had stations at 1600, 800, 100, and 50 m.

Figure 2. Temporal variation in the Friedman 2-way ANOVA rank sums for the number of species recruiting and total recruit abundance at the 6 stations sampled in all 18 sampling periods (■) and the 19 stations sampled in all of the first 10 sampling periods (●). Time is shown as the number of days from 1 - June - 1978. Months on X-axis indicate the beginning of the month. Peaks were in December and June and troughs in September and April. Recruitment was measured over the 6 week period between sampling times.

Figure 3. Colonization of Summer (●) and Winter panels (■) at the three San Onofre Kelp forest sites showing the differences in diversity among the sites for both large and small panels. The X-axes are scaled to the number of days from June 1, 1978 (0).

Figure 4. Colonization of Summer and Winter panels at Inshore Transect stations near and far from the power plant outfall showing the general lower diversity away from the outfall. The X-axes are scaled to the number of days from June 1, 1978 (0).

Figure 5. A comparison of panels with varying levels of dominance by *Corynactis californica*. Data from panels outside and inside the Barn kelp forest and from the offshore station in the San Onofre kelp forest are show. Curves are for individual panels and *Corynactis* abundance (top), % Open space (middle) and species diversity (bottom) from the same panel are represented by the same symbols. The X-axes are scaled to the number of days from June 1, 1978 (0).

Figure 6. A comparison of *Mytilus* abundance, % open space, and species diversity of surface panels from three inshore stations. All curves are for individual panels. The X-axes are scaled to the number of days from June 1, 1978 (0).

Figure 7. A comparison of the abundances of the colonial polychaete *Salmacina tribranchiata* and the bryozoan *Parasmittina* spp. on panels inside the San Mateo kelp forest. The % open space and diversity are also shown for the panels. The two species were dominant on different panels. The one panel on which *Salmacina* did not dominate also did not exhibit any decline in diversity. The X-axes are scaled to the number of days from June 1, 1978 (0).

Figure 8. Regional variation in the frequency of species recruiting. Top: Overall similarity among the 28 sites with sites identified by the north and south inshore transects, the kelp forests sites (BK – Barn Kelp, SOK – San Onofre Kelp, SMK – San Mateo Kelp) and the Channel Island sites. Sites are also categorized in terms of whether they were inside, outside, or on the edge of kelp forests. Bottom: Four ANOSIM analyses for the 5 regions for all taxa, lecithotrophic species, planktotrophic species, and Crustacea.

Figure 9. Comparison of colonization curves for large (left) and small (right) panels at

stations inside, on the edge, and outside the San Mateo kelp forest. Panels initially exposed in the summer (●) are represented by solid lines and winter panels (■) are represented by dashed lines. The X-axes are scaled to the number of days from June 1, 1978 (0).

Figure 10. Comparison of panels from the stations outside the Barn kelp forest (bottom and middle) with panels transplanted from an outside station to the station inside the forest (top). The arrow indicates the time the transfer was made. The X-axes are scaled to the number of days from June 1, 1978 (0).

Figure 11. Comparison of the colonization of panels at the four San Onofre kelp forest sites. The X-axes are scaled to the number of days from June 1, 1978 (0).

Figure 12. Comparison of the number of species on panels from the Channel Islands stations. Both panels on open racks (closed symbols) and inside tubes (open symbol) to exclude predators are shown. Data are means $\pm$ SE. The X-axis is scaled to the number of days from June 1, 1978 (0).

Figure 13. Comparison of colonization curves for selected panel series at the inshore transect stations. Surface panels series are represented by open symbols. Shown are the mean $\pm$ SE. The X-axes are scaled to the number of days from June 1, 1978 (0).

Figure 14. Comparison of the number of species on large and small panels from selected stations. Large panel series are represented by circle or square symbols and solid lines and small panel series are represented by triangle symbols and dashed lines. Data are means $\pm$ SE. The X-axes are scaled to

1297 the number of days from June 1, 1978 (0).

1298 Figure 15. Comparison of panels from the main series with their analyzed surface

1299 facing the seafloor with panels oriented towards the water surface (face-up). The

1300 X-axes are scaled to the number of days from June 1, 1978 (0). Data are means

1301 +/- SE. The MDS plot at the bottom contrasts the communities on the main face-

1302 down panels and the face-up panels.

1303

Figure 1

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Panel Orientation

9. APPENDIX 1

The figures included in this appendix show the colonization curves for each panel series at the 22 main experiment stations and the measured recruitment at each site.

Data are display as means +/- the standard error. Days on the X-axis start at June 1, 1978. Small panels were not included for surface sites, Barn Kelp Inside, and the two San Onofre Kelp North sites. Each figure consists of 6 separate graphs:

Top Left. Large colonization panels for series begun in June, September, and December 1978 and March, November 1979.

Top Right. Small colonization panels for series begun in June and December 1978.

Mid Left. Open space on large panels in cm². Data are for the same series as in the colonization curves above.

Mid Right. Open space on the small colonization panels in cm².

Bottom Left. Number of species recruiting on large and small 6 week recruitment panels.

Bottom Right. Total number of individuals for all species recruiting on large and small 6 week recruitment panels.

The following symbols were used to identify different panel series:

Circle - Summer 1978 Series

Square - Fall 1978 Series

Diamond - Winter 1978 Series

Up Triangle - Spring 1979 Series

Down Triangle - Winter 1979 Series

- 1327 Additional Series (These are also identified by keys in the graphs):
- 1328 Open Circle, Dashed Line – June 1977 Preliminary Study Series
- 1329 Open Square, Dashed Line – September 1977 Preliminary Study Series
- 1330 Open Down Triangle, Dashed Line – Caged Tube Rack Panels
- 1331 Open Circle, Dashed Line - Panels Transplanted from other sites
- 1332 Open Circle, Dashed Line – Summer 1978 Surface Panels
- 1333 Open Square, Dashed Line – Winter 1978 Surface Panels
- 1334 X, Dotted Line – Face-up Panels
- 1335 Open Down Triangle, Dashed Line – Barnacle Panels
- 1336 Catalina and Santa Cruz Island Panels
- 1337 Circle – Main Open Panels
- 1338 Open Circle – Caged Tube Rack Panels
- 1339 Square, Dotted Line – Bottom Caged Panels
- 1340 Up Triangle, Dotted Line – Bottom Open Panels
- 1341 Arrows indicate the time when panels were transplanted from another site
- 1342 The two San Onofre kelp forest north edge stations were plotted on the same
- 1343 graphs and are differentiated by solid and dashed lines.
- 1344

San Mateo Kelp Forest – Inside

San Mateo Kelp Forest – Edge

San Mateo Kelp Forest – Outside

San Onofre Kelp Forest – Inside

San Onofre Kelp Forest – Edge

San Onofre Kelp Forest – Outside

Large

Small

San Onofre Kelp Forest – Offshore

San Onofre Kelp Forest – North

Barn Kelp Forest – Inside

Small

Barn Kelp Forest – Edge

Barn Kelp Forest – Outside 1

Barn Kelp Forest – Outside 2

1600 North

Large

Small

800 North

400 North

Large

Small

200 North

Large

Small

100 North

Large

Small

50 North

50 South

100 South

800 South

1600 South

Intake North

Intake South

Santa Catalina Island

Santa Cruz Island

10. APPENDIX 2

This appendix compares immigration and extinction rate data for all colonization panel series at each of the stations. Immigration (Left) and extinction (Right) plots are shown separately for each panel series. The regression line for the extinction data is included as a dotted line in the immigration plots. The Regressions for large and small panels were done separately with large panels represented in the top two graphs and small panels in the bottom two graphs. Data for the two North San Onofre Kelp sites were combined. The r^2 and regression equation for each curve are shown. Also the estimated equilibrium diversity (S) for the number of species present where the two curves intersect is included in the immigration graphs. Small panels were not included for surface sites, Barn Kelp Inside, and the two San Onofre Kelp North sites.

San Mateo Kelp Inside

San Mateo Kelp Edge

San Mateo Kelp Outside

San Onofre Kelp Inside

San Onofre Kelp Edge

San Onofre Kelp Outside

San Onofre Kelp Offshore

San Onofre Kelp North

Barn Kelp Inside

Barn Kelp Edge

Barn Kelp Outside 1

Barn Kelp Outside 2

1600 North

800 North

400 North

200 North

100 North

50 North

North Surface

50 South

100 South

800 South

1600 South

South Surface

Intake North

Intake North Surface

Intake South