UNIVERSITY OF CALIFORNIA, SAN DIEGO

Impacts of human trampling and periodic sand inundation on Southern California intertidal algal turf communities: Implications for conservation and management of rocky shores

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in
Oceanography

by

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ABSTRACT OF THE DISSERTATION

Impacts of human trampling and periodic sand inundation on Southern California intertidal algal turf communities: Implications for conservation and management of rocky shores

by

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Doctor of Philosophy in Oceanography
University of California, San Diego, 2006
Professor Paul K. Dayton, Chair

Natural and anthropogenic disturbances are important structuring agents in rocky intertidal communities. Here, the impacts of disturbance in the form of human trampling and periodic sand inundation on the invertebrates and algae of coralline algal turf communities were evaluated. First, a preliminary observational study of the turf communities at eight rocky intertidal sites indicated that differences in invertebrate community composition, diversity, and abundances existed among sites and sampling times. Density and diversity were highest in an area that has been closed to public use and lowest at the most heavily visited sites.

In order to quantify the timing and extent of sand inundations to a rocky intertidal area, observations of sand depth were made along a large, permanent grid system for 21 months. Inundations of sediment were relatively rapid and lasted on the order of one to two months, while erosion was equally rapid. The presence of sand was negatively correlated to the maximum significant wave height for that time period.

The use of time-lapse video proved to be an efficient method for collecting vast amounts of data regarding patterns of human visitation to the rocky intertidal. It was observed that the amount of visitation was highly site-specific. Time of day and week were more important predictors of visitation than was the height of the tide.

The coralline turf invertebrate communities exhibited rapid responses to disturbance in manipulative studies, but also appeared to recover rapidly. An acute, or “pulse”, disturbance in the form of controlled sand addition caused an immediate exodus of highly mobile taxa and then a gradual increase in psammophilic (sand-loving) gastropods. A more continuous, or “press”, disturbance in the form of human trampling caused a decrease in density and diversity of coralline turf invertebrates. In both cases, a return to control abundances occurred within one to nine months, indicating a resilient system.

The results of these studies fill an important gap in the knowledge of the natural history of rocky intertidal communities and the processes which shape them. Additionally, the techniques and results presented here will be valuable for future management decisions in protected coastal areas.

CHAPTER 1

Introduction to the dissertation

One of the central themes in community ecology research is an attempt to understand and quantify the processes responsible for patterns of species distribution and abundance. In the rocky intertidal, early research identified biological factors such as competition and predation as important structuring forces (Hatton 1938, Connell 1961a, b, Dayton 1971). Physical forces, such as disturbance, were then also shown to interact with the biological components and strongly influence community structure (eg. Dayton 1971, Sousa 1979). As human populations grow and impose increasing pressures on rocky intertidal ecosystems, it is imperative that we gain a better understanding of both natural and anthropogenic disturbances and their potential interactions.

DISTURBANCE

Disturbance, defined by Sousa (1984) as a "…killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established", has been widely recognized as an important structuring agent in both terrestrial and marine communities (eg. Dayton 1971, Connell 1978, Addessi 1994). In marine habitats, disturbances may be natural such as emersion, wave action, and sand inundation, or anthropogenic such as fishing, pollution, and trampling. Anthropogenic disturbances are often superimposed onto stresses caused by natural environmental factors (Osenberg and Schmitt 1994, Crowe et al. 2000), making them difficult to isolate and quantify.

Both natural and human-induced disturbances may be defined as “press” (chronic) or “pulse” (acute) forces (Bender et al. 1984, Crowe et al. 2000). Press disturbances are more or less continuous stresses while pulse disturbances are variable in time and are followed by periods of potential recovery. It can be difficult to determine whether a disturbance should be viewed as press or pulse, especially with many anthropogenic disturbances. This decision may in turn affect how experiments are designed and what results are seen.

HUMAN INFLUENCES ON THE COAST

Human exploitation of marine resources is one of the most important issues that scientists and resource managers must address today. The rapidly growing human population near our coasts, along with a booming tourist industry in many coastal areas, imposes numerous impacts on marine ecosystems. Disturbances to coastal ecosystems include fishing and collecting, pollution, coastline modification by artificial structures, disturbance of shorebirds, and removal of wetlands. The extensive use of coastal areas also leads to large amounts of foot traffic in intertidal and shallow subtidal areas. Human trampling can affect organisms directly through crushing, dislodgement, or weakening attachment strength (Brosnan and Crumrine 1994). Indirect effects may also occur such as changing patterns of sediment movement as algal cover is altered (Povey and Keough 1991). In order to effectively manage human impacts on coastal communities, the intensity and patterns of public use along with the effects on organisms and habitats must be understood.

ALGAL TURF COMMUNITIES

Large portions of intertidal rocky beaches in southern California are covered by carpet-like mats of small algal thalli referred to as algal turf. These mats are made up of a few anchor species that attach directly to the substrate (usually *Corallina sp.* in southern California) and many epiphytes that attach to these anchor species or to sand grains. The entire mat is an entangled mesh that traps sediment, shell, and algal debris (Stewart 1982). At times large amounts of sandy sediment can be observed within the mat and the presence or absence of this sand is an important factor to be considered when studying this community (Stewart 1983). Sediment may exhibit direct effects on organisms such as physical injury due to smothering or scour (Devinny and Volse 1978), or indirect effects, for example, by removing less tolerant organisms and opening up space for opportunistic settlers (Littler et al. 1983).

These algae and associated sediment provide an important habitat for assemblages of small invertebrates and larvae including bivalves, gastropods, polychaetes, crustaceans, nematodes, and foraminifera. Macrofauna, variously defined as being greater than 1or 2 mm in length (Hicks 1985, Gibbons and Griffiths 1986), are relatively well known and frequently studied because of their convenient size for field observations. Meiofauna, described generally as animals greater in length than 63 um but smaller than 1 mm (Gibbons and Griffiths 1986), are less well known and rarely have been considered in studies of disturbance within these turf communities (Brown and Taylor 1999 for an exception). However, according to Gibbons and Griffiths (1986), meiofauna are always more abundant than macrofauna and they account for 25 percent of total secondary production on rocky shores. Gibbons and Griffiths (1986) also showed that most meiofaunal taxa reach peak densities within mats of algal turf. Failure to incorporate meiofauna into an analysis of this community has lead to a large gap in the understanding of the system.

OBJECTIVES OF THE DISSERTATION

Subsequent chapters of this dissertation describe both mensurative and manipulative experiments that have been conducted in order to gain a better understanding of the invertebrate communities of coralline algal turf and natural and anthropogenic factors that may influence them. Chapter 2 characterizes the structure and dynamics of the invertebrate community of coralline turf in San Diego County. Chapter 3 investigates patterns of periodic sand movement at a small rocky intertidal site near La Jolla, CA. The effects that these shifts in sediment levels may have on the turf communities are then experimentally examined in Chapter 4. Chapter 5 describes the use of a time-lapse video system to quantify human visitation to three San Diego County rocky intertidal sites. The impacts of human trampling on the invertebrate communities of the algal turf were then experimentally investigated in Chapter 6. Insight into the dynamics of these communities helps to fill in a gap in knowledge about the structure and function of rocky intertidal ecosystems.

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CHAPTER 2

Spatial and temporal variation in the invertebrate communities of intertidal coralline algal turf

ABSTRACT

Rich algal assemblages common to temperate rocky shorelines provide habitat for diverse communities of small invertebrates and larvae. In southern California, coralline algal turfs dominate the mid-intertidal zone. The complex mat of turf-forming algae and associated sediment support numerous macro- and meiofauna. Although these animals are numerically and ecologically important, they have received little attention in the literature. This study characterizes the invertebrate community of coralline turf in San Diego County, CA. In order to investigate the spatial and temporal dynamics of this community, monthly turf samples were taken from eight rocky intertidal sites, one of which is closed to public access, from August to December 2002. Significant differences existed among the invertebrate communities from the different sites. Additionally, the trajectory of community change in the site that was closed to public access was different than that from any of the other sites. Several measures of diversity also showed significant differences among the sites, with the fully protected site generally showing the highest levels of diversity. The results indicate that both large- and small-scale physical factors as well as human influences are important in understanding this system.

INTRODUCTION

Macroalgae are a conspicuous element of rocky intertidal communities on temperate shores. In addition to being important contributors to rocky shore biodiversity and food-chain dynamics themselves (Norton 1986), algae also provide important habitat for extremely abundant assemblages of small invertebrates (Hicks 1986). These invertebrates, which include small macrofauna (>1 mm) and meiofauna (<1 mm and >63 µm) (Gibbons and Griffiths 1986), are numerically and ecologically significant players in this system (Coull and Wells 1983, Coull 1988). Despite their abundance and potential roles in the intertidal ecosystem, these animals, especially meiofauna, have received little attention in most regions of the world.

A predominant feature of southern California rocky shores is a visually uniform, carpet-like mat of coralline algal turf that covers the sloping rock benches and boulders. This is in contrast to the classic image of a rocky intertidal community where large fleshy algae form a rich canopy and turf-forming algae function as less dominant understory species. Stewart (1989) performed a series of algal removal experiments over a period of more than three years in San Diego County to test the hypothesis that two *Corallina* species (the main turf-forming species in this area) are able to dominate the substrate because they competitively exclude other species. She found that the abundances of other species did not increase in the absence of *Corallina.* She then presented observational evidence that these species of *Corallina* are adapted to the periodic sand inundations that frequently occur on these shores and hypothesized that it is this ability to withstand sand disturbance that allows them to become spatially dominant.

In San Diego County, the turf consists of a few anchor species that attach directly to the substrate (usually *Corallina pinnatifolia*) and many species of epiphytic algae that attach to the anchor species (Stewart 1982). The complex mat of turf-forming algae and associated sand provides habitat for diverse assemblages of invertebrates and larvae including gastropods, crustaceans, bivalves, foraminifera, polychaetes, nematodes, and oligochaetes (Dommasnes 1969, Neumann et al. 1970, Gibbons and Griffiths 1986, Akioka et al. 1999, Kelaher et al. 2001). Brown and Taylor (1999) found more than 200,000 animals m^{-2} (>500 µm) and personal observations have revealed densities as high as 1.6 million animals m^{-2} (>63 µm). Many of these animals have been shown to be important prey for larger species of gastropods (Gosselfin and Chia 1994), fish (Coull and Wells 1983), and birds (Dierschke 1994).

As stated above, meiofauna have rarely been considered in studies of the turf community. However, according to Gibbons and Griffiths (1986), meiofauna are always more abundant than macrofauna and they account for 25 percent of total secondary production on rocky shores. Gibbons and Griffiths (1986) also showed that most meiofaunal taxa reach peak densities within mats of algal turf on rocky shores. Failure to incorporate meiofauna into an analysis of this community has led to a large gap in the understanding of the diversity, production, and biological interactions of the system.

In this study, I investigated the structure and dynamics of San Diego County algal turf communities, including both macro- and meiofauna. The primary questions were: (1) Do the invertebrate communities of coralline algal turf vary in composition among different rocky intertidal sites within San Diego County? (2) Do diversity and dominance of the turf communities vary among sites? (3) Are there temporal variations in the structure of turf communities? (4) Which species are causing any observed differences among sites?

STUDY AREA

Eight sites along the outer coast of San Diego County were chosen for this study (Figure 2-1). Dike Rock (DR), Marine Room (MR), Cave Shop (CS), Boomer's Cove (BC), and Shell Beach (SB) are spaced from north to south respectively along an approximately 6 km stretch of shoreline near La Jolla, CA (32°87' N, 117°25' W). Cabrillo Zone 1 (Z1), Zone 2 (Z2), and Zone 3 (Z3) are located within Cabrillo National Monument on Point Loma (32°28' N, 117° 11' W), a long peninsula within the city of San Diego (24 km south of La Jolla) that is bordered by the Pacific Ocean to the west and San Diego Bay to the east.

Marine Room, Boomer's, and Shell Beach are all characterized by broad sandstone platforms covered with coralline algal turf, a few large boulders, and sandy beach on either side. These sites experience low to moderate human visitation (Huff 2006 and unpublished data).

The physical setting at Cave Shop is markedly different than the other sites. It is located at the base of a small, steep cliff with limited human access and is characterized by narrow sandstone platforms covered with coralline algal turf and significant amounts of fleshy, non-turf-forming algae. This site is separated from nearby sandy beaches by narrow ocean channels and appears to receive much higher wave energy than the other sites.

Dike Rock is part of the University of California Natural Reserve System. The site consists of a fairly large boulder field and adjacent small sandstone platforms covered with coralline algal turf. It is entirely open to the public and is visited extensively during a relatively wide range of tidal heights (Huff 2006) and is bordered on either side by sandy beaches.

Cabrillo National Monument is a 144-acre urban national park that contains approximately 120 acres of rocky shoreline. The area includes rocky benches that range in width from 10 to 40 meters, many fields of large boulders, and small stretches of sandy beach. The park has been divided into three “zones” based on human accessibility. Zone 1 contains the only access path to the intertidal area and receives an average of more than 200 visitors per day (Huff 2006). Zone 3 has been completely closed to the public since 1996. Zone 2 is located between the other two zones and therefore receives an intermediate amount of visitation.

MATERIALS AND METHODS

Sampling procedure

Six permanent 1.0 m^2 plots were haphazardly established in the mid-intertidal at each of the eight sites. The plots were then sampled monthly between August and December 2002. During each sampling event, a sharpened, circular, metal coring device (6 cm in diameter) was pushed through the algae and associated sediment to the bedrock. A metal spatula was then used to scrape the sample from the rock, taking care to remove all algae, sediment, and animals. According to Gibbons and Griffiths (1988), this method is capable of recovering up to 97 percent of the faunal components of the assemblage. Samples were placed in plastic containers, tightly sealed, and taken to the lab where they were preserved in 70 percent ethanol until analysis.

Each sample was washed on a 63 µm screen and carefully sorted under a dissecting microscope. All invertebrates were removed, identified to the lowest possible taxonomic level, and counted. Warwick (1988) has shown that identification to the species level was not necessary to detect differences in macro- and meio-benthic communities with the sort of multivariate analyses used in this study. Therefore, identification to species was made when possible, but taxonomic resolution of the fauna varied among groups because some species have not been described, others require specialized taxonomic knowledge to identify, and some were juveniles that could not be conclusively identified.

Data analysis

Invertebrate community compositions were compared using matrices of multivariate Bray-Curtis similarity coefficients based on taxon abundances (Clarke and Warwick 2001). The raw data were square-root transformed in order to reduce the dominance of the most abundant taxa in the analyses. These similarity matrices were used in the construction of two-dimensional non-metric multidimensional scaling plots (nMDS, Clarke and Warwick 2001) to visually illustrate biological relationships among the sites. A 1-way analysis of similarities (ANOSIM, Clarke and Warwick 2001) was then used to test for significant differences in community structure among the sites within each sampling period. Additionally, a similarity percentages analysis (SIMPER, Clarke and Warwick 2001) was employed to analyze contributions of different taxa to average dissimilarities between samples. Finally, a second-stage nMDS, based on Spearman rank correlations between multiple similarity matrices, was used to determine if the trajectory of community change through time at each site appeared to be the same as those from other sites. An additional ANOSIM test was used to determine if any differences in time trajectories were significant (Clarke et al. 2006). These analyses were performed using Plymouth Routines in Marine Ecological Research (PRIMER) software v.5.2.9 (Primer-E Ltd. 2002).

Multiple diversity indices were also calculated with PRIMER including total number of individuals (N), total number of taxa (S), the Shannon-Weiner diversity index (H'log *e*), and Pielou's evenness index (J'). Analysis of variance (ANOVA) was then performed to determine if significant differences in diversity existed among the sites within each sampling period. Additionally, the cumulative total numbers of species found at each site over the course of the study were compared.

RESULTS

Community composition

Preliminary analyses showed that the invertebrate community composition at the Cave Shop site was markedly different from that at any of the other sites. This site was initially chosen to determine if different physical characteristics (slope, wave shock, etc.) would be associated with a different invertebrate community. The observed differences in physical setting and community composition were so great, however, that comparisons with the other sites were not meaningful. So, after further consideration, the Cave Shop was not included in subsequent analyses and instead the analyses concentrated on potential differences between communities at physically comparable sites.

Community composition at every site was significantly different from that at every other site within each sampling period with a few exceptions (ANOSIM, df = 42, R > 0.30, p < 0.05). Non-significant comparisons (R < 0.30 or p > 0.05) included: Cabrillo Zone 2 and Zone 3 (Sept., Nov., and Dec.), Shell Beach and Boomer's and Shell Beach and Marine Room (Nov. and Dec.) (Appendix 2-1). A separation among the communities at different sites was also revealed by nMDS plots for each sampling period (Figure 2-2). Additionally, while the individual sites tend to separate, the three Cabrillo sites also group more closely to each other than to those from the La Jolla sites.

A few relatively abundant genera of micro-mollusks and small crustaceans tended to be responsible for most of the dissimilarity among sites (SIMPER). Zones 2 and 3 in Cabrillo consistently had much higher abundances of the gastropod *Caecum californicum* (Figure 2-3a), while Boomer's, Shell Beach, and Cabrillo Zone 1 had greater abundances of gammarid amphipods (Figure 2-3b). Cabrillo Zones 2 and 3, Shell Beach, Boomers, and Marine Room generally had higher abundances of the micro-snails *Amphithalamus* sp. and *Barleeia* sp. (Figure 2-3c). Ostracods and the small bivalve *Lasaea adonsoni* were also significant contributors to the dissimilarity among samples.

Changes through time

Cabrillo Zone 3 showed a significantly different trajectory of community change through time than any of the other sites (second-stage ANOSIM, df = 42, Global R = 0.184, p = 0.004, for between site comparisons with Zone 3 R > 0.30, p < 0.05 in all cases). Figures 2-4a – 2-4c show first-stage nMDS ordinations for three sites from the study. Figures 2-4a and 2-4b are representative of the non-protected sites while 2-4c shows Zone 3 (the protected site). Arrows which indicate the progression of the community in an individual plot through time show relatively large changes between sampling times for Dike Rock and Shell Beach (large distances between points) whereas changes between sampling times appear to be smaller in Zone 3 (small distances between points) until the final sampling event. An assemblage of the time trajectories in a second-stage nMDS plot (which can be thought of as an nMDS plot of the pairwise similarities between the previous nMDS plots from all seven sites (Clarke et al. 2006)) supports the result that the turf community in Zone 3 has a different time trajectory than those from the other sites. If all of the plots had similar time trajectories, points from all sites would be relatively evenly dispersed on the nMDS plot. Instead, we see that points from Zone 3 tend to clump together while there is generally more spread and overlap among the other sites (Figure 2-5).

Diversity

All four measures of diversity (N, S, H'log *e*, and J') were significantly different among sites within each sampling period (ANOVA, $p < 0.05$, Figure 2-6 and Table 2-1). Generally, Dike Rock, Marine Room and Cabrillo Zone 1 had fewer individuals (lower N-values) and fewer taxa (lower S values) while Cabrillo Zone 3 had some of the highest N and S values ($p<0.05$, see Table 2-1). Dike Rock and Zone 1 also generally had higher evenness (higher J' values) ($p<0.05$, see Table 2-1). The Shannon-Weiner diversity index did not appear to have any consistent patterns.

A cumulative total of the number of taxa found at each site over the entire 5-month sampling period showed that Cabrillo Zone 3 had the most taxa with a total of 56 and Dike Rock and Zone 1 had the fewest with 34 and 35 species respectively (Figure 2-7).

DISCUSSION

Data from the Cave Shop indicate that differences in large physical factors such as wave shock and slope appear to be important in explaining differences among rocky intertidal turf communities. Additionally, ANOSIM analyses indicate that sites that are spatially close together are more likely to have similar invertebrate communities. For example, pairs of sites that did not have significantly different invertebrate communities included Cabrillo Zone 2 and 3, Shell Beach and Boomer's, and Shell Beach and Marine Room. All of these pairs of sites are within 2 km of each other. nMDS plots also supported this idea as they repeatedly showed the three Cabrillo sites grouping more closely with each other than with the La Jolla sites (Figure 2-2).

Significant differences among sites with similar physical features and among others in close proximity to one another, however, indicate that these are not the only important influences on the turf assemblage. We must, therefore, consider what other types of factors might be shaping these communities. Algal complexity, density, and biomass have been shown to affect associated fauna (Gibbons and Griffiths 1986, Gibbons 1988, Gee and Warwick 1994, Hull 1997, Kelaher 2002, Chemello and Milazzo 2002). Gibbons and Griffiths (1986) found that meiofauna were most abundant in areas with the richest algal cover. Chemello and Milazzo (2002) found that species of macroalgae that are more complex encourage a more abundant and well-diversified fauna. Sediment has also been shown to be important in structuring the invertebrate communities associated with algae (Gibbons and Griffiths 1986, Gibbons 1988, Kelaher et al. 2001). Kelaher et al. (2001) found that the strength of the relationship between sediment and macrofauna became greater as architectural characteristics of the turf were also incorporated. This indicates that perhaps the sand / turf matrix as a whole may be a key factor influencing these communities. These will be important variables to consider in future studies of this community.

Several patterns in species abundances among the sites were revealed by SIMPER analyses. These patterns are difficult to interpret, however, because the natural history of most of the micro-faunal community is poorly understood. Classic studies of rocky intertidal ecology have revealed that species distributions tend to be affected by particular physical, biological, or temporal variables such as temperature, salinity, moisture, predator / prey interactions, and disturbance (eg. Dayton 1971, Connell 1972). If, with future study, we can begin to better understand the associations of individual turf species with these sorts of variables, then perhaps we can use species abundance patterns as indicators of the status of particular locations.

Cabrillo Zone 3 was shown to have a different trajectory of change in community structure through time than any of the other six sites (Figures 2-4 and 2-5). Zone 3 also consistently showed some of the highest numbers of individuals and taxa per sample and had the highest cumulative number of taxa found throughout the study (Figures 2-6 and 2-7, Table 2-1). This is noteworthy since Zone 3 is also the only area along the coast that has been completely closed to visitation by the public. Dike Rock and Cabrillo Zone 1 generally exhibited the lowest values for total number of individuals and number of species per sample and had the lowest cumulative number of species found throughout the study. These sites also appear to have the highest rates of human visitation among the sites in this study (Huff 2006, in prep). Given these results, it is important that we consider anthropogenic effects in analyses of these communities.

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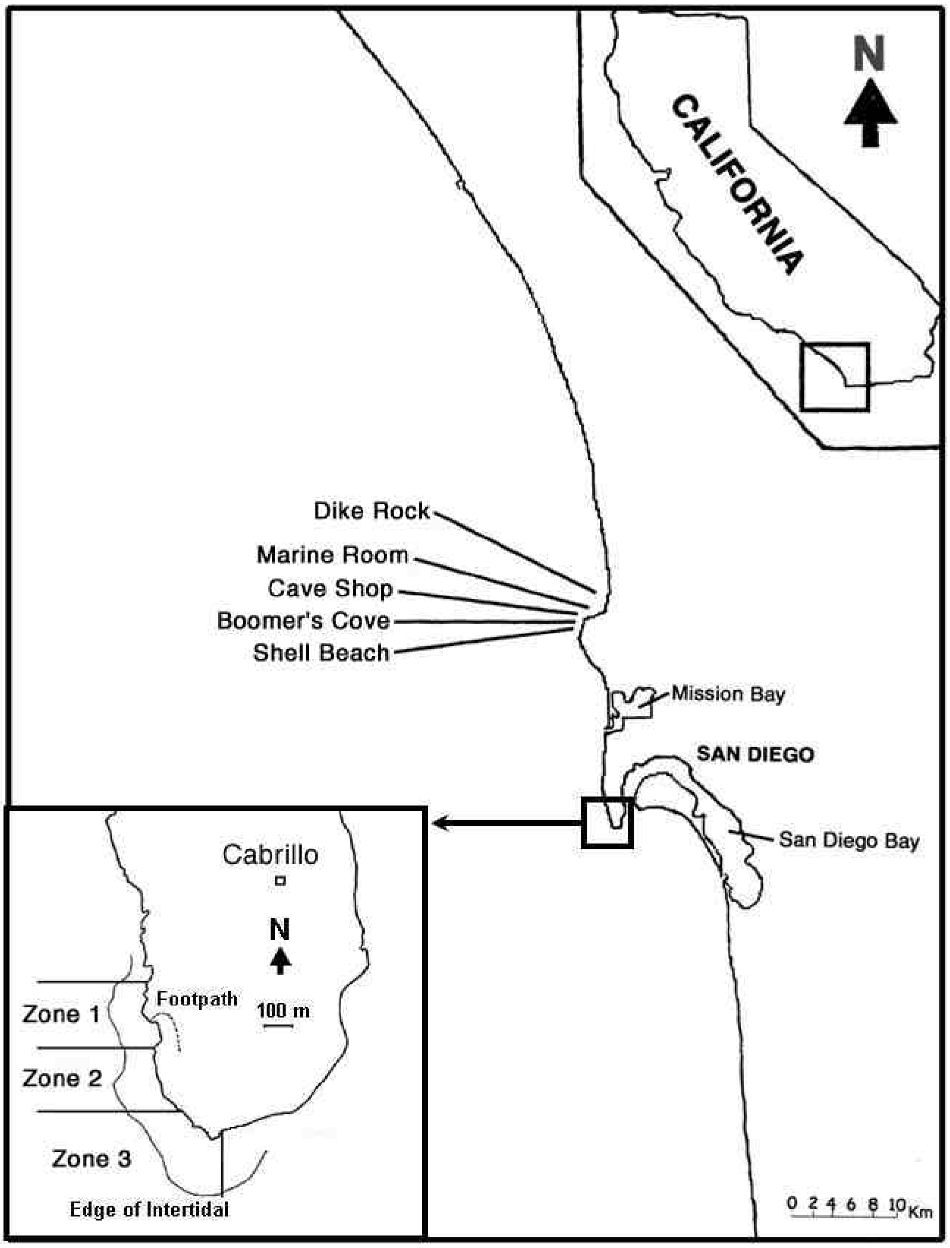


Figure 2-1. Map of the San Diego Region showing the location of the eight study sites (Modified from Schroeter et al. 1996 and a map owned by Cabrillo National Monument).

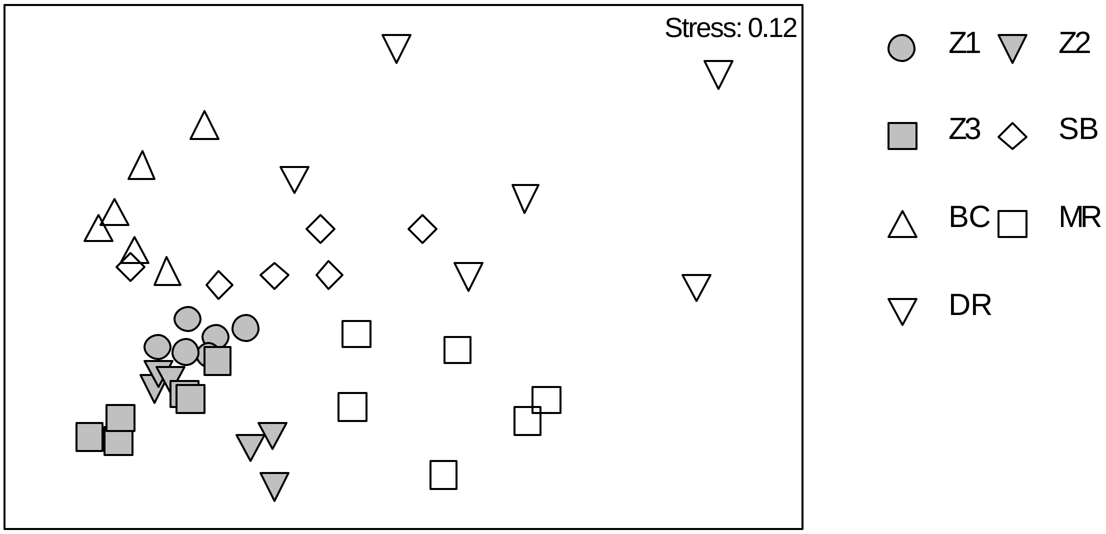
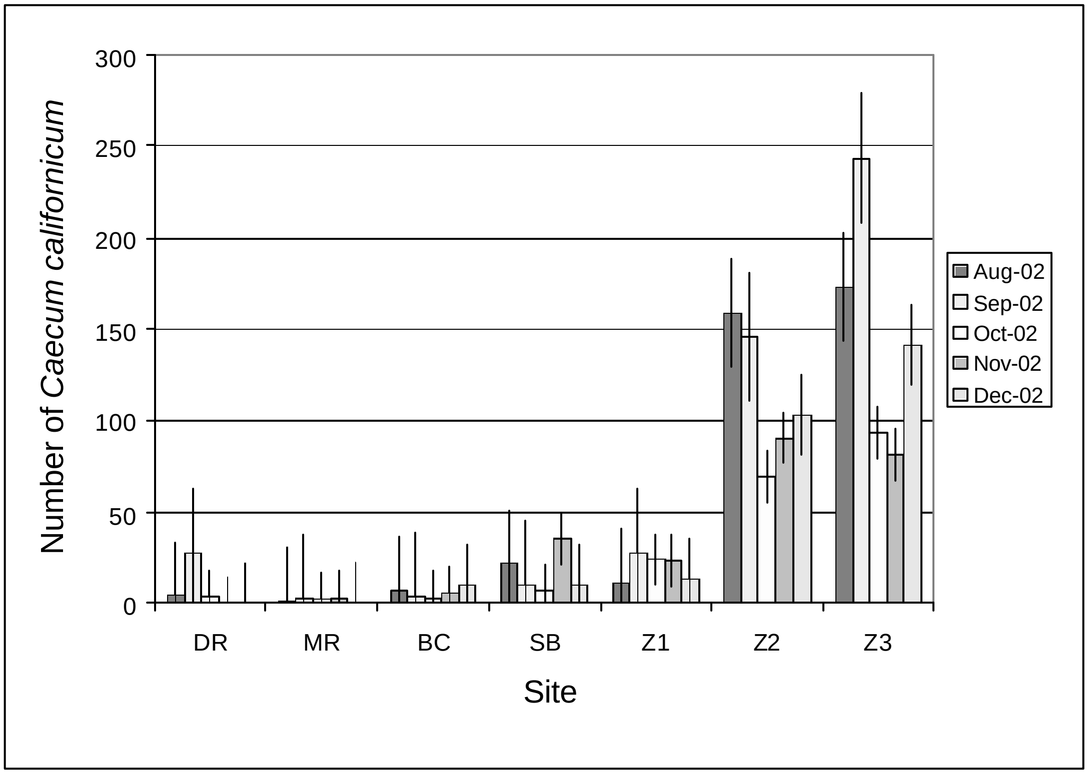


Figure 2-2. Representative nMDS plot of taxon counts from seven sites in September 2002. Z1 = Cabrillo Zone 1, Z2 = Cabrillo Zone 2, Z3 = Cabrillo Zone 3, SB = Shell Beach, BC = Boomer's Cove, MR = Marine Room, and DR = Dike Rock

Figure 2-3. Average number of **a.** *Caecum californicum* **b.** gammarid amphipods and **c.** *Barleeia sp.* per sample at each site for monthly samples taken from August 2002 – December 2002. Z1 = Cabrillo Zone 1, Z2 = Cabrillo Zone 2, Z3 = Cabrillo Zone 3, SB = Shell Beach, BC = Boomer's Cove, MR = Marine Room, and DR = Dike Rock

a.


Number of *Caecum californicum*
300
250
200
150
100
50
0
DR
MR
BC
SB
Z1
Z2
Z3
Site
Aug-02
Sep-02
Oct-02
Nov-02
Dec-02

b.

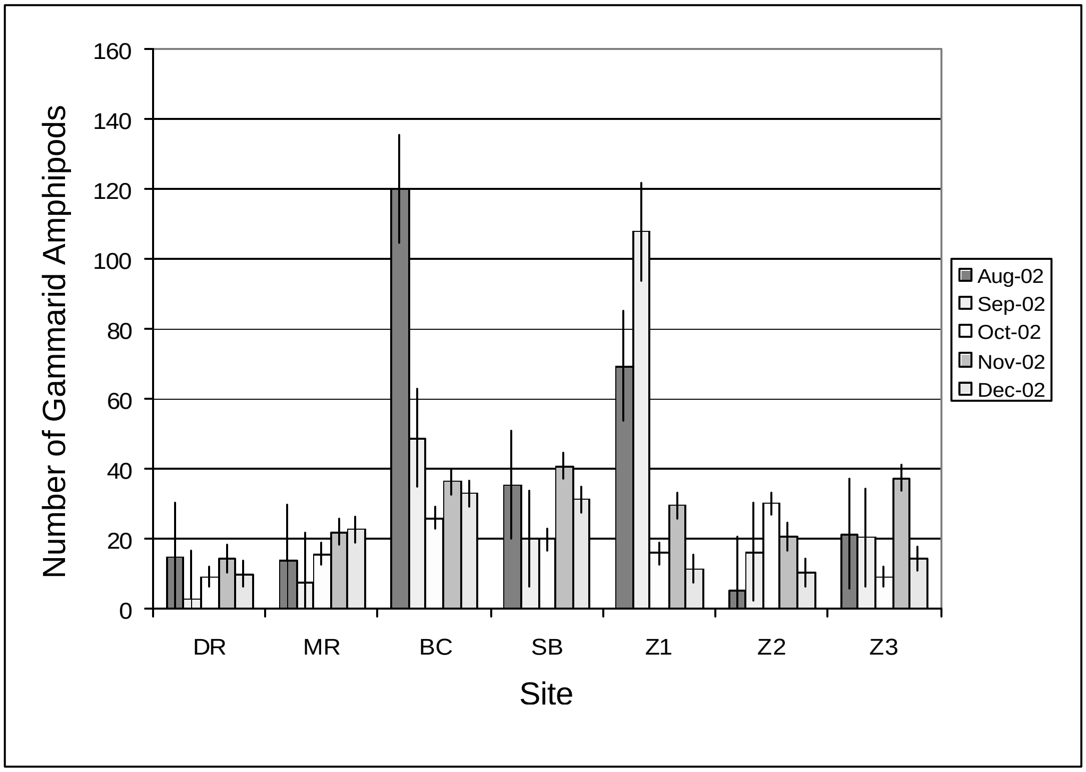

Number of Gammarid Amphipods
160
140
120
100
80
60
40
20
0
DR
MR
BC
SB
Z1
Z2
Z3
Site
Aug-02
Sep-02
Oct-02
Nov-02
Dec-02

Figure 2-3. continued.

c.

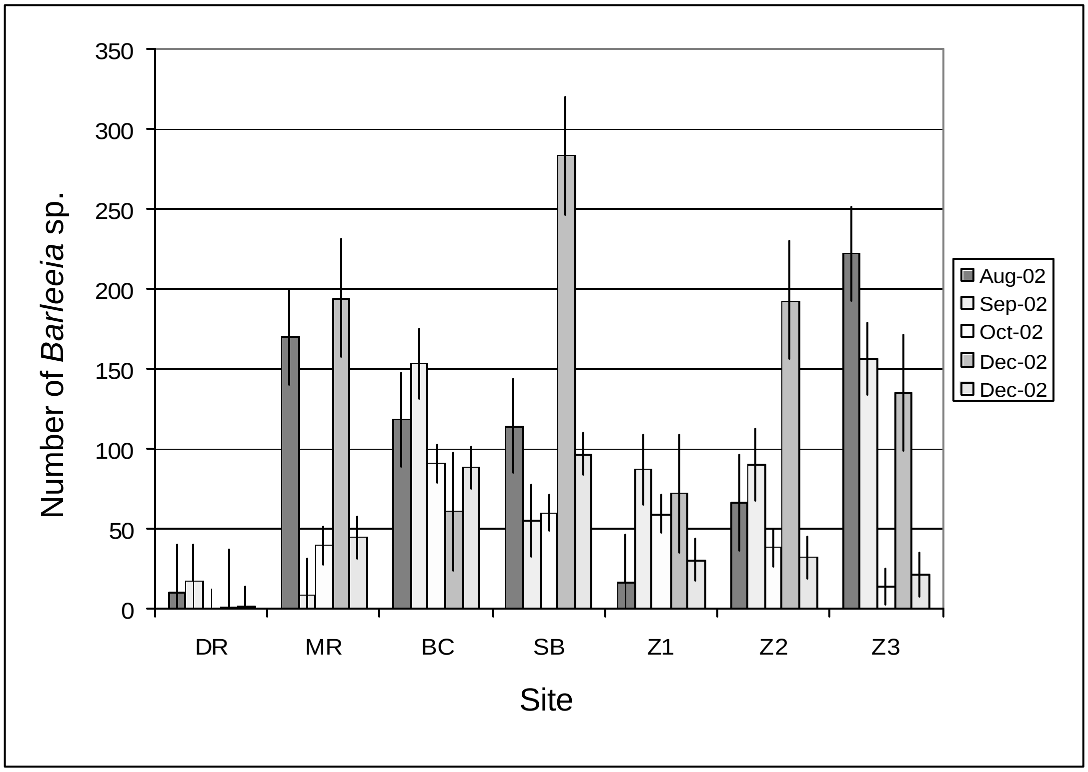

Number of Barleeia sp.
350
300
250
200
150
100
50
0
DR
MR
BC
SB
Z1
Z2
Z3
Site
Aug-02
Sep-02
Oct-02
Dec-02
Dec-02

Figure 2-4. First-stage nMDS ordinations for representative study sites **a.** Dike Rock **b.** Shell Beach and **c.** Cabrillo Zone 3. Arrows indicate the progression of the community from an individual plot through time.

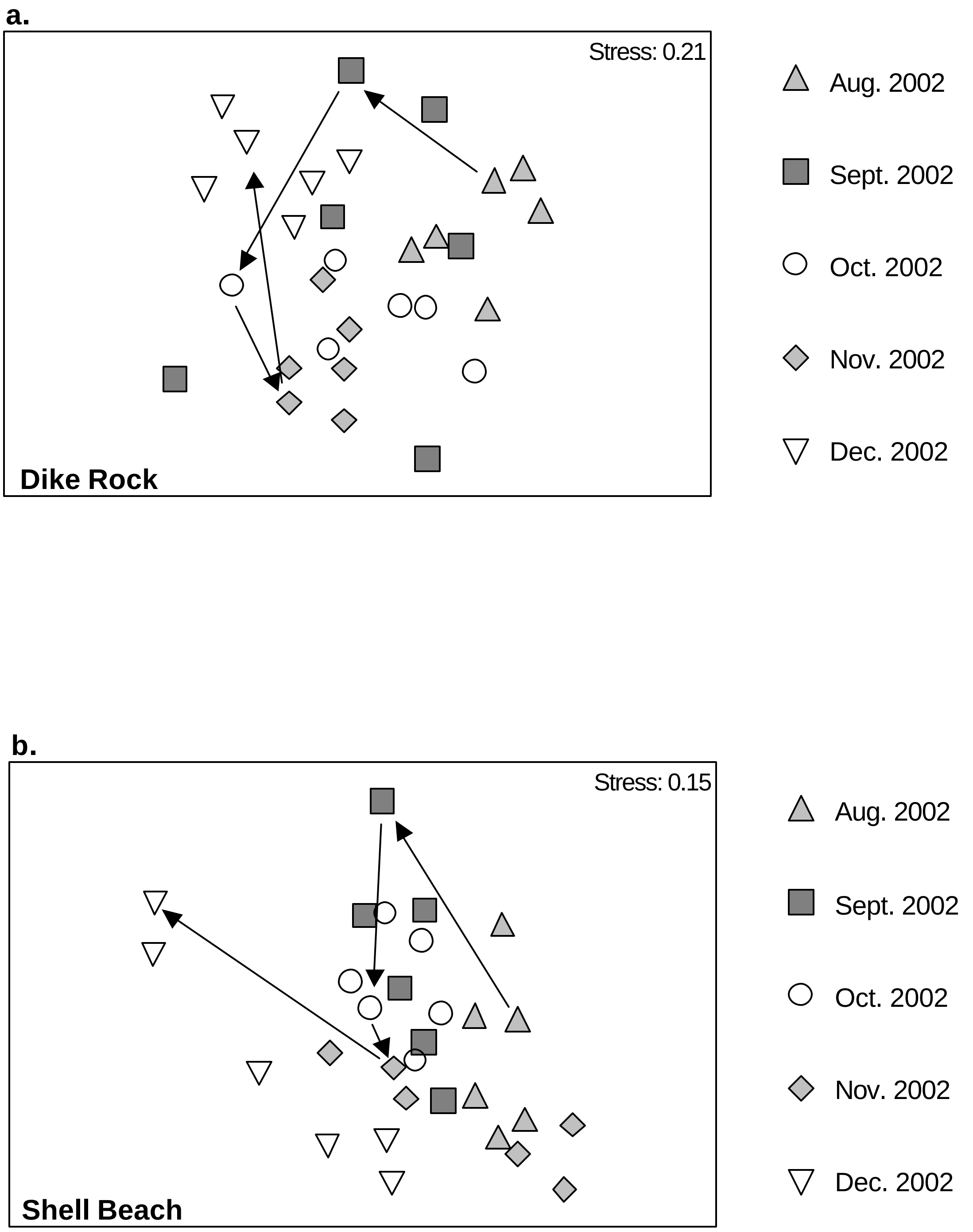
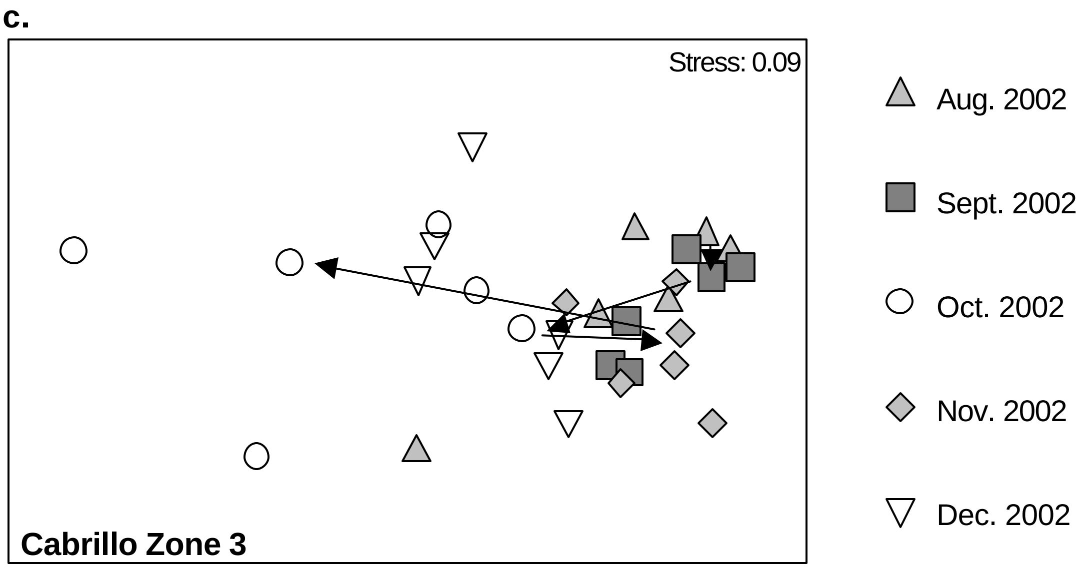

a.
Stress: 0.21
Dike Rock
△ Aug. 2002
■ Sept. 2002
○ Oct. 2002
◆ Nov. 2002
▽ Dec. 2002
b.
Stress: 0.15
Shell Beach
△ Aug. 2002
■ Sept. 2002
○ Oct. 2002
◆ Nov. 2002
▽ Dec. 2002

Figure 2-4. continued.


c.
Stress: 0.09
Cabrillo Zone 3
Aug. 2002
Sept. 2002
Oct. 2002
Nov. 2002
Dec. 2002

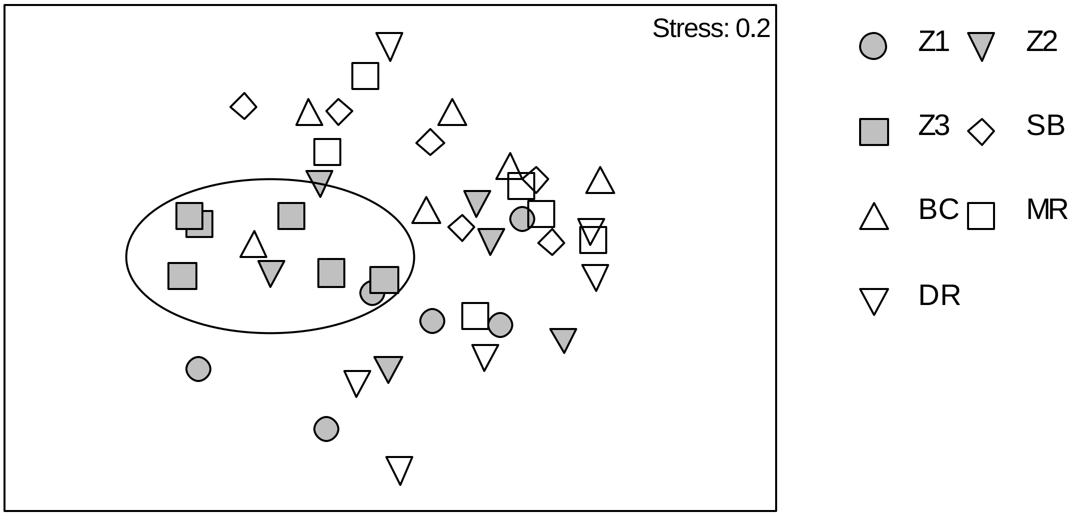
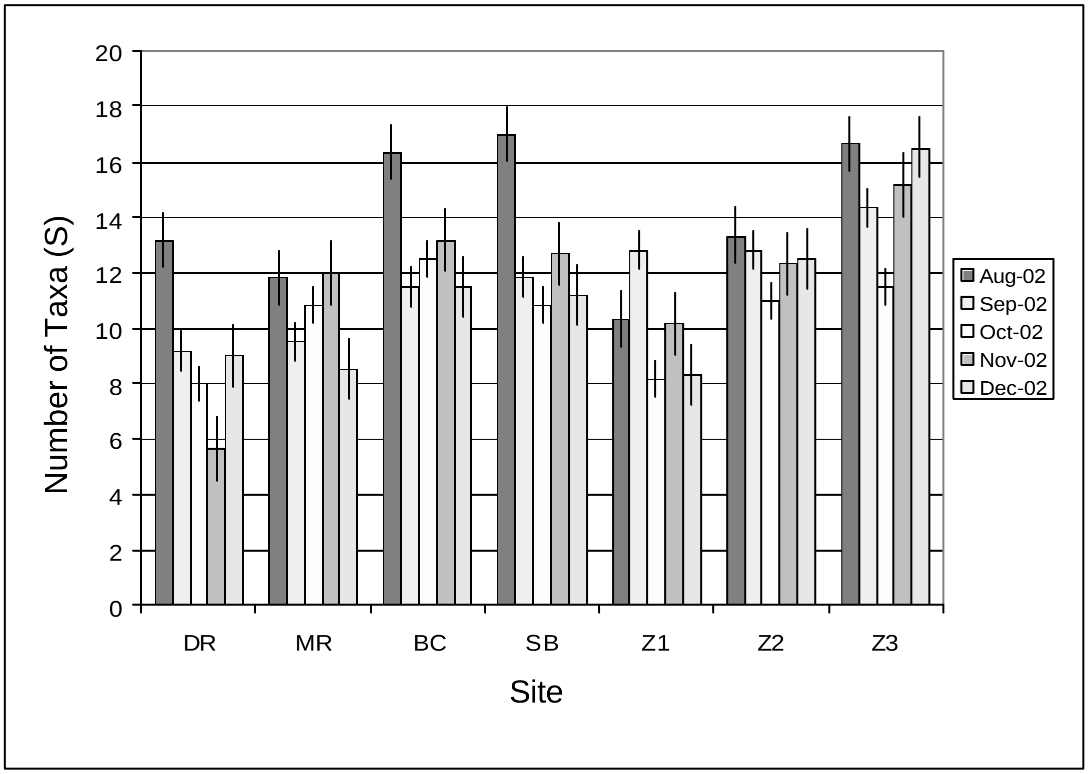


Figure 2-5. Second-stage nMDS plot indicating a difference in trajectory of community change through time between Zone 3 and the other six sites. Note the grouping of points that represent Zone 3. Z1 = Cabrillo Zone 1, Z2 = Cabrillo Zone 2, Z3 = Cabrillo Zone 3, SB = Shell Beach, BC = Boomer’s Cove, MR = Marine Room, and DR = Dike Rock.

Figure 2-6. Mean number of **a.** taxa (S) and **b.** individuals (N) and mean values for **c.** Shannon diversity (H') and **d.** Pielou's evenness (J') for the turf communities of seven rocky intertidal sites August 2002 – December 2002. Z1 = Cabrillo Zone 1, Z2 = Cabrillo Zone 2, Z3 = Cabrillo Zone 3, SB = Shell Beach, BC = Boomer's Cove, MR = Marine Room, and DR = Dike Rock

a.


Number of Taxa (S)
0
2
4
6
8
10
12
14
16
18
20
DR
MR
BC
SB
Z1
Z2
Z3
Site
Aug-02
Sep-02
Oct-02
Nov-02
Dec-02

b.

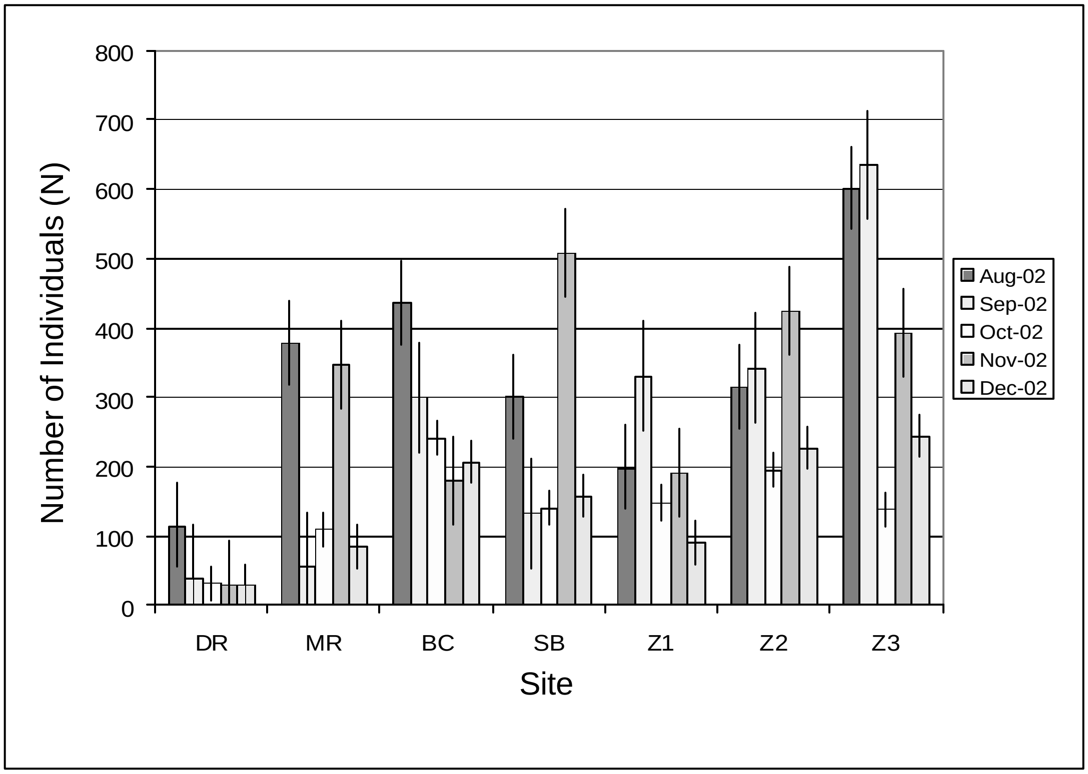
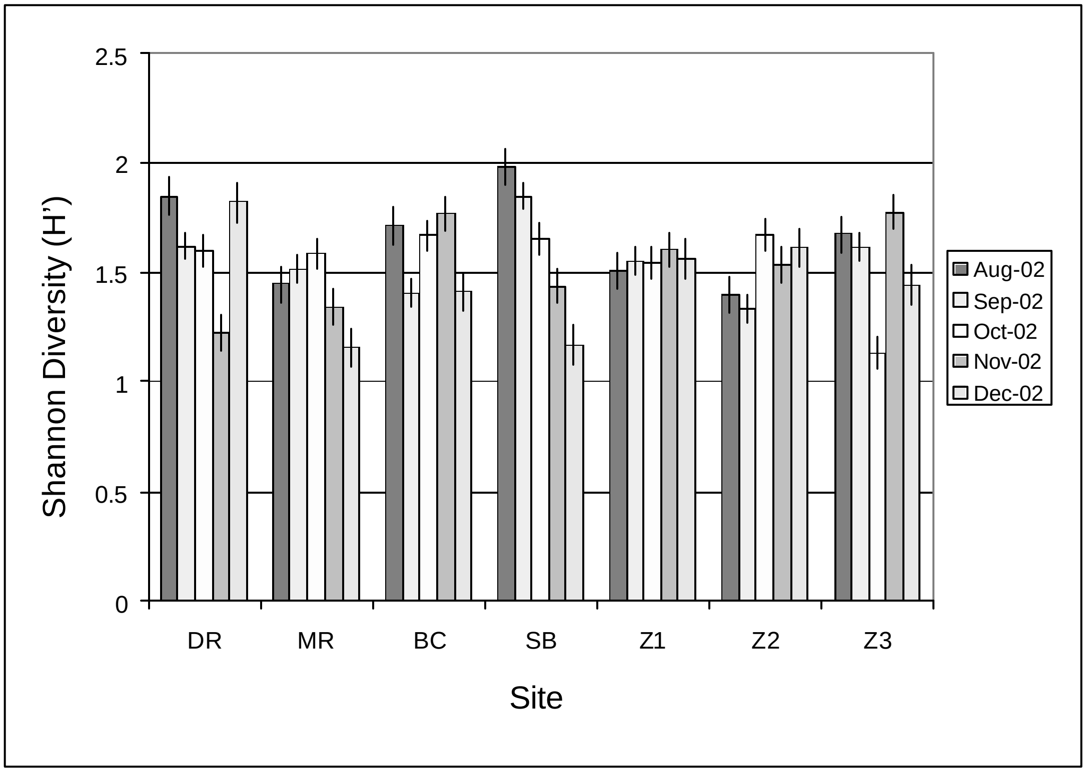
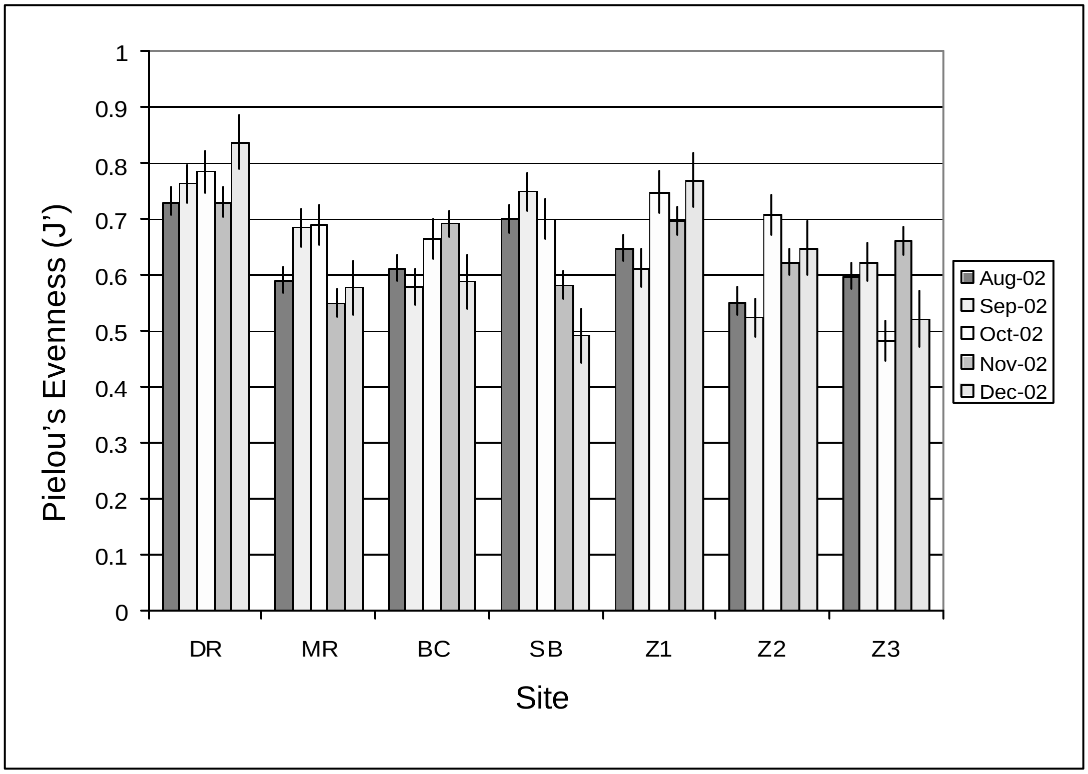

Number of Individuals (N)
0
100
200
300
400
500
600
700
800
DR
MR
BC
SB
Z1
Z2
Z3
Site
Aug-02
Sep-02
Oct-02
Nov-02
Dec-02

Figure 2-6. continued

c.


Shannon Diversity (H')
2.5
2
1.5
1
0.5
0
DR
MR
BC
SB
Z1
Z2
Z3
Site
Aug-02
Sep-02
Oct-02
Nov-02
Dec-02

d.


Pielou's Evenness (J')
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
DR
MR
BC
SB
Z1
Z2
Z3
Site
Aug-02
Sep-02
Oct-02
Nov-02
Dec-02

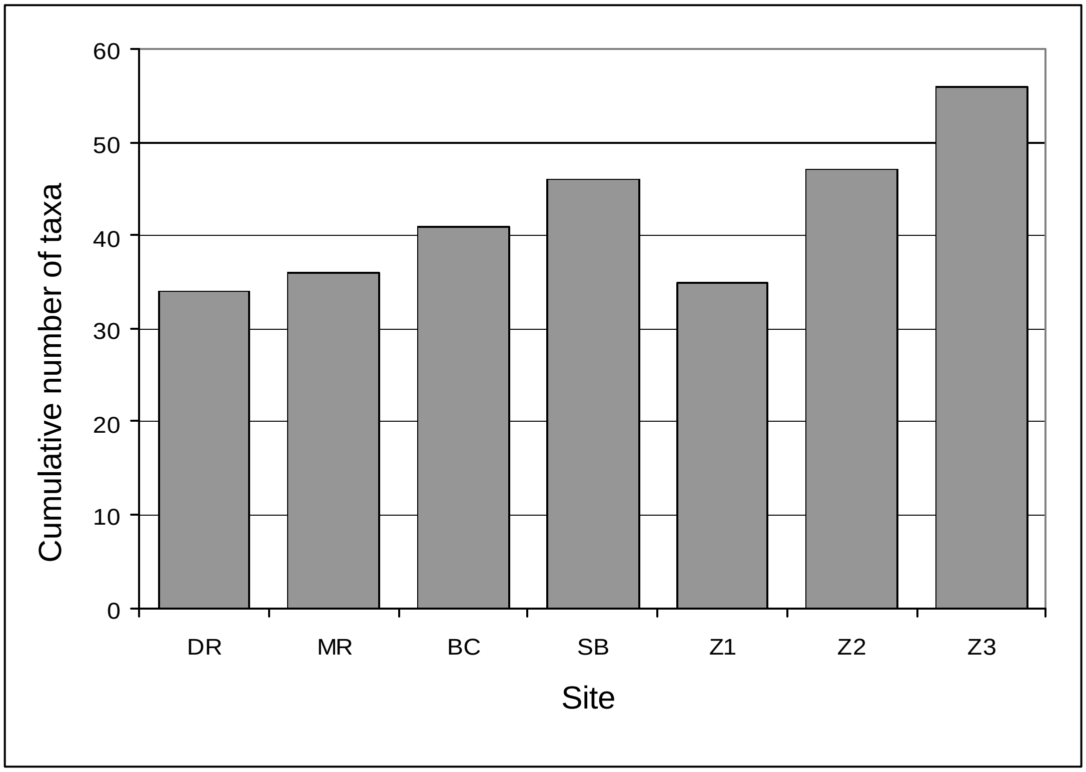


Figure 2-7. Cumulative number of invertebrate taxa found in coralline algal turf samples taken monthly between August and December 2002 from seven San Diego County rocky intertidal sites. Z1 = Cabrillo Zone 1, Z2 = Cabrillo Zone 2, Z3 = Cabrillo Zone 3, SB = Shell Beach, BC = Boomer’s Cove, MR = Marine Room, and DR = Dike Rock

Table 2-1. Results from ANOVA (overall) and Fisher's PLSD (pairwise comparisons) for diversity indices from Boomer's Cove (BC), Dike Rock (DR), Marine Room (MR), Shell Beach (SB), Cabrillo Zone 1 (Z1), Cabrillo Zone 2 (Z2), and Cabrillo Zone 3 (Z3). * indicates significance ($p < 0.05$)

Sampling Time	Diversity index	Sites	df	F-value	p-value
August 2002	S	Overall	6	5.055	<0.001*
		BC, DR			0.058
		BC, MR			0.008*
		BC, SB			0.684
		BC, Z1			0.001*
		BC, Z2			0.072
		BC, Z3			0.838
		DR, MR			0.417
		DR, SB			0.023*
		DR, Z1			0.089
		DR, Z2			0.919
		DR, Z3			0.037*
		MR, SB			0.003*
		MR, Z1			0.361
		MR, Z2			0.361
		MR, Z3			0.005*
		SB, Z1			<0.001*
		SB, Z2			0.030*
		SB, Z3			0.838
		Z1, Z2			0.072
		Z1, Z3			<0.001*
		Z2, Z3			0.047*
	N	Overall	6	5.984	<0.001*
		BC, DR			0.001*
		BC, MR			0.533
		BC, SB			0.156
		BC, Z1			0.014*
		BC, Z2			0.197
		BC, Z3			0.083
		DR, MR			0.007*
		DR, SB			0.051
		DR, Z1			0.376
		DR, Z2			0.038*
		DR, Z3			<0.001*
		MR, SB			0.419
		MR, Z1			0.061
		MR, Z2			0.499
		MR, Z3			0.021*

Table 2-1. continued.

Sampling Time	Diversity index	Sites	df	F-value	p-value
August 2002	N	SB, Z1			0.273
		SB, Z2			0.894
		SB, Z3			0.003*
		Z1, Z2			0.220
		Z1, Z3			<0.001*
		Z2, Z3			0.004*
	J’	Overall	6	3.757	0.032*
		BC, DR			0.028
		BC, MR			0.678
		BC, SB			0.094
		BC, Z1			0.489
		BC, Z2			0.251
		BC, Z3			0.766
		DR, MR			0.010*
		DR, SB			0.573
		DR, Z1			0.121
		DR, Z2			0.001*
		DR, Z3			0.014*
		MR, SB			0.039
		MR, Z1			0.272
		MR, Z2			0.460
		MR, Z3			0.906
		SB, Z1			0.315
		SB, Z2			0.006*
		SB, Z3			0.051
		Z1, Z2			0.070
		Z1, Z3			0.325
		Z2, Z3			0.393
	H’log *e*	Overall	6	3.866	0.003*
		BC, DR			0.366
		BC, MR			0.071
		BC, SB			0.080
		BC, Z1			0.180
		BC, Z2			0.042*
		BC, Z3			0.803
		DR, MR			0.010*
		DR, SB			0.382
		DR, Z1			0.028*
		DR, Z2			0.005*
		DR, Z3			0.251
		MR, SB			0.001*

Table 2-1. continued.

Sampling Time	Diversity index	Sites	df	F-value	p-value
August 2002	H'log *e*	MR, Z1			0.673
		MR, Z2			0.759
		MR, Z3			0.132
		SB, Z1			0.003*
		SB, Z2			<0.001*
		SB, Z3			0.047*
		Z1, Z2			0.468
		Z1, Z3			0.272
		Z2, Z3			0.072
September 2002	S	Overall	6	2.743	0.273
		BC, DR			0.151
		BC, MR			0.217
		BC, SB			0.835
		BC, Z1			0.408
		BC, Z2			0.408
		BC, Z3			0.084
		DR, MR			0.835
		DR, SB			0.103
		DR, Z1			0.027*
		DR, Z2			0.027*
		DR, Z3			0.003*
		MR, SB			0.151
		MR, Z1			0.043*
		MR, Z2			0.043*
		MR, Z3			0.005*
		SB, Z1			0.534
		SB, Z2			0.534
		SB, Z3			0.125
		Z1, Z2			0.989
		Z1, Z3			0.352
		Z2, Z3			0.352
	N	Overall	6	11.775	<0.001*
		BC, DR			0.005*
		BC, MR			0.008*
		BC, SB			0.060
		BC, Z1			0.713
		BC, Z2			0.625
		BC, Z3			<0.001*
		DR, MR			0.843
		DR, SB			0.286

Table 2-1. continued.

Sampling Time	Diversity index	Sites	df	F-value	p-value
September 2002	N	DR, Z1			0.002*
		DR, Z2			0.001*
		DR, Z3			<0.001
		MR, SB			0.382
		MR, Z1			0.003*
		MR, Z2			0.002*
		MR, Z3			<0.001*
		SB, Z1			0.027*
		SB, Z2			0.020*
		SB, Z3			<0.001*
		Z1, Z2			0.903
		Z1, Z3			0.001*
		Z2, Z3			0.002*
	J’	Overall	6	3.618	0.068
		BC, DR			0.008
		BC, MR			0.118
		BC, SB			0.014*
		BC, Z1			0.626
		BC, Z2			0.404
		BC, Z3			0.509
		DR, MR			0.239
		DR, SB			0.823
		DR, Z1			0.027*
		DR, Z2			0.001*
		DR, Z3			0.040*
		MR, SB			0.337
		MR, Z1			0.274
		MR, Z2			0.019*
		MR, Z3			0.358
		SB, Z1			0.044*
		SB, Z2			0.002*
		SB, Z3			0.065
		Z1, Z2			0.190
		Z1, Z3			0.861
		Z2, Z3			0.140
	H’log *e*	Overall	6	1.990	0.094
		BC, DR			0.212
		BC, MR			0.522
		BC, SB			0.013
		BC, Z1			0.402
		BC, Z2			0.654

Table 2-1. continued.

Sampling Time	Diversity index	Sites	df	F-value	p-value
September 2002	H'log *e*	BC, Z3			0.220
		DR, MR			0.536
		DR, SB			0.182
		DR, Z1			0.675
		DR, Z2			0.094
		DR, Z3			0.982
		MR, SB			0.055
		MR, Z1			0.842
		MR, Z2			0.279
		MR, Z3			0.552
		SB, Z1			0.083
		SB, Z2			0.004*
		SB, Z3			0.175
		Z1, Z2			0.202
		Z1, Z3			0.692
		Z2, Z3			0.098
October 2002	S	Overall	6	1.947	0.087
		BC, DR			0.009*
		BC, MR			0.313
		BC, SB			0.313
		BC, Z1			0.011
		BC, Z2			0.363
		BC, Z3			0.543
		DR, MR			0.089
		DR, SB			0.090
		DR, Z1			0.919
		DR, Z2			0.073
		DR, Z3			0.038*
		MR, SB			0.989
		MR, Z1			0.110
		MR, Z2			0.919
		MR, Z3			0.685
		SB, Z1			0.110
		SB, Z2			0.919
		SB, Z3			0.685
		Z1, Z2			0.090
		Z1, Z3			0.048*
		Z2, Z3			0.761
	N	Overall	6	4.373	0.001*
		BC, DR			<0.001*

Table 2-1. continued.

Sampling Time	Diversity index	Sites	df	F-value	p-value
October 2002	N	BC, MR			0.003*
		BC, SB			0.019*
		BC, Z1			0.028*
		BC, Z2			0.259
		BC, Z3			0.017*
		DR, MR			0.068
		DR, SB			0.012*
		DR, Z1			0.008*
		DR, Z2			<0.001*
		DR, Z3			0.014*
		MR, SB			0.459
		MR, Z1			0.369
		MR, Z2			0.048*
		MR, Z3			0.488
		SB, Z1			0.873
		SB, Z2			0.203
		SB, Z3			0.962
		Z1, Z2			0.264
		Z1, Z3			0.835
		Z2, Z3			0.187
	J’	Overall	6	6.087	<0.001
		BC, DR			0.025*
		BC, MR			0.630
		BC, SB			0.486
		BC, Z1			0.113
		BC, Z2			0.397
		BC, Z3			0.001*
		DR, MR			0.071
		DR, SB			0.110
		DR, Z1			0.479
		DR, Z2			0.146
		DR, Z3			<0.001*
		MR, SB			0.828
		MR, Z1			0.262
		MR, Z2			0.713
		MR, Z3			<0.001*
		SB, Z1			0.363
		SB, Z2			0.880
		SB, Z3			<0.001*
		Z1, Z2			0.447
		Z1, Z3			<0.001*

Table 2-1. continued.

Sampling Time	Diversity index	Sites	df	F-value	p-value
October 2002	J’	Z2, Z3			<0.001*
	H’log *e*	Overall	6	3.639	0.004*
		BC, DR			0.609
		BC, MR			0.540
		BC, SB			0.906
		BC, Z1			0.361
		BC, Z2			0.995
		BC, Z3			<0.001*
		DR, MR			0.919
		DR, SB			0.694
		DR, Z1			0.686
		DR, Z2			0.605
		DR, Z3			0.001*
		MR, SB			0.620
		MR, Z1			0.762
		MR, Z2			0.536
		MR, Z3			0.002*
		SB, Z1			0.426
		SB, Z2			0.901
		SB, Z3			<0.001*
		Z1, Z2			0.358
		Z1, Z3			0.004*
		Z2, Z3			<0.001*
November 2002	S	Overall	6	8.374	<0.001*
		BC, DR			<0.001*
		BC, MR			0.418
		BC, SB			0.727
		BC, Z1			0.042*
		BC, Z2			0.562
		BC, Z3			0.168
		DR, MR			<0.001*
		DR, SB			<0.001*
		DR, Z1			0.003*
		DR, Z2			<0.001*
		DR, Z3			<0.001*
		MR, SB			0.642
		MR, Z1			0.205
		MR, Z2			0.816
		MR, Z3			0.032

Table 2-1. continued.

Sampling Time	Diversity index	Sites	df	F-value	p-value
November 2002	S	SB, Z1			0.087
		SB, Z2			0.816
		SB, Z3			0.087
		Z1, Z2			0.136
		Z1, Z3			0.001*
		Z2, Z3			0.054
	N	Overall	6	3.926	0.002*
		BC, DR			0.195
		BC, MR			0.149
		BC, SB			0.007*
		BC, Z1			0.932
		BC, Z2			0.040*
		BC, Z3			0.071
		DR, MR			0.008*
		DR, SB			<0.001*
		DR, Z1			0.168
		DR, Z2			0.001*
		DR, Z3			0.003*
		MR, SB			0.175
		MR, Z1			0.519
		MR, Z2			0.702
		MR, Z3			0.009*
		SB, Z1			0.470
		SB, Z2			0.326
		SB, Z3			0.049*
		Z1, Z2			0.084
		Z1, Z3			0.793
		Z2, Z3			0.244
	J’	Overall	6	2.202	0.054
		BC, DR			0.507
		BC, MR			0.023*
		BC, SB			0.071
		BC, Z1			0.909
		BC, Z2			0.261
		BC, Z3			0.618
		DR, MR			0.004*
		DR, SB			0.016*
		DR, Z1			0.518
		DR, Z2			0.077
		DR, Z3			0.248
		MR, SB			0.606

Table 2-1. continued.

Sampling Time	Diversity index	Sites	df	F-value	p-value
November 2002	J’	MR, Z1			0.017*
		MR, Z2			0.225
		MR, Z3			0.069
		SB, Z1			0.056
		SB, Z2			0.480
		SB, Z3			0.184
		Z1, Z2			0.217
		Z1, Z3			0.514
		Z2, Z3			0.527
	H’log *e*	Overall	6	5.154	0.003*
		BC, DR			<0.001*
		BC, MR			0.002*
		BC, SB			0.012*
		BC, Z1			0.197
		BC, Z2			0.070
		BC, Z3			0.972
		DR, MR			0.355
		DR, SB			0.098
		DR, Z1			0.005*
		DR, Z2			0.018*
		DR, Z3			<0.001*
		MR, SB			0.452
		MR, Z1			0.045*
		MR, Z2			0.135
		MR, Z3			0.001*
		SB, Z1			0.196
		SB, Z2			0.449
		SB, Z3			0.011*
		Z1, Z2			0.584
		Z1, Z3			0.186
		Z2, Z3			0.065
December 2002	S	Overall	6	7.129	<0.001*
		BC, DR			0.168
		BC, MR			0.099
		BC, SB			0.852
		BC, Z1			0.083
		BC, Z2			0.577
		BC, Z3			0.008*
		DR, MR			0.780
		DR, SB			0.230

Table 2-1. continued.

Sampling Time	Diversity index	Sites	df	F-value	p-value
December 2002	S	DR, Z1			0.710
		DR, Z2			0.056
		DR, Z3			<0.001*
		MR, SB			0.142
		MR, Z1			0.926
		MR, Z2			0.030*
		MR, Z3			<0.001*
		SB, Z1			0.119
		SB, Z2			0.458
		SB, Z3			0.005*
		Z1, Z2			0.024*
		Z1, Z3			<0.001*
		Z2, Z3			0.030*
	N	Overall	6	9.453	<0.001*
		BC, DR			<0.001*
		BC, MR			0.003*
		BC, SB			0.204
		BC, Z1			0.004
		BC, Z2			0.599
		BC, Z3			0.313
		DR, MR			0.138
		DR, SB			0.001*
		DR, Z1			0.103
		DR, Z2			<0.001*
		DR, Z3			<0.001*
		MR, SB			0.062
		MR, Z1			0.878
		MR, Z2			0.001*
		MR, Z3			<0.001*
		SB, Z1			0.085
		SB, Z2			0.076
		SB, Z3			0.030*
		Z1, Z2			<0.001*
		Z1, Z3			<0.001*
		Z2, Z3			0.626
	J’	Overall	6	5.920	<0.001*
		BC, DR			0.004
		BC, MR			0.887
		BC, SB			0.237
		BC, Z1			0.030*
		BC, Z2			0.460

Table 2-1. Continued.

Sampling Time	Diversity index	Sites	df	F-value	p-value
December 2002	J’	BC, Z3			0.406
		DR, MR			0.003*
		DR, SB			<0.001*
		DR, Z1			0.406
		DR, Z2			0.024*
		DR, Z3			<0.001*
		MR, SB			0.297
		MR, Z1			0.022*
		MR, Z2			0.397
		MR, Z3			0.493
		SB, Z1			0.001*
		SB, Z2			0.059
		SB, Z3			0.716
		Z1, Z2			0.141
		Z1, Z3			0.004*
		Z2, Z3			0.122
	H’log *e*	Overall	6	6.444	<0.001*
		BC, DR			0.044*
		BC, MR			0.203
		BC, SB			0.223
		BC, Z1			0.448
		BC, Z2			0.307
		BC, Z3			0.877
		DR, MR			0.002*
		DR, SB			0.002*
		DR, Z1			0.196
		DR, Z2			0.302
		DR, Z3			0.061
		MR, SB			0.956
		MR, Z1			0.046*
		MR, Z2			0.025*
		MR, Z3			0.155
		SB, Z1			0.051
		SB, Z2			0.028*
		SB, Z3			0.171
		Z1, Z2			0.789
		Z1, Z3			0.545
		Z2, Z3			0.384

Appendix 2-1. Results of ANOSIM analyses of square-root transformed data to test for differences among the invertebrate communities of seven rocky intertidal sites for **a.** August **b.** September **c.** October **d.** November and **e.** December 2002. Z1=Cabrillo Zone 1, Z2=Cabrillo Zone 2, Z3=Cabrillo Zone 3, SB=Shell Beach, BC=Boomer's Cove, MR=Marine Room, DR=Dike Rock
*Indicates significant value (df = 42, p < 0.05)

a.

Sites	R-value	p-value
Global	0.656*	0.001*
Z1, Z2	0.894*	0.002*
Z1, Z3	0.722*	0.002*
Z1, SB	0.841*	0.002*
Z1, BC	0.933*	0.002*
Z1, MR	0.837*	0.002*
Z1, DR	0.472*	0.002*
Z2, Z3	0.359*	0.013*
Z2, SB	0.704*	0.002*
Z2, BC	0.907*	0.002*
Z2, MR	0.889*	0.002*
Z2, DR	0.743*	0.002*
Z3, SB	0.481*	0.002*
Z3, BC	0.713*	0.002*
Z3, MR	0.606*	0.002*
Z3, DR	0.713*	0.002*
SB, BC	0.315*	0.019*
SB, MR	0.689*	0.002*
SB, DR	0.591*	0.002*
BC, MR	0.750*	0.002*

b.

Sites	R-value	p-value
Global	0.613*	0.001*
Z1, Z2	0.559*	0.002*
Z1, Z3	0.572*	0.002*
Z1, SB	0.683*	0.002*
Z1, BC	0.837*	0.002*
Z1, MR	0.772*	0.002*
Z1, DR	0.739*	0.002*
Z2, Z3	0.276	0.028*
Z2, SB	0.793*	0.002*
Z2, BC	0.843*	0.002*
Z2, MR	0.789*	0.002*
Z2, DR	0.806*	0.002*
Z3, SB	0.741*	0.002*
Z3, BC	0.972*	0.002*
Z3, MR	0.900*	0.002*
Z3, DR	0.813*	0.002*
SB, BC	0.661*	0.004*
SB, MR	0.691*	0.002*
SB, DR	0.417*	0.004*
BC, MR	0.985*	0.002*

Appendix 2-1. continued.

c.

Sites	R-value	p-value
Global	0.577*	0.001*
Z1, Z2	0.317*	0.006*
Z1, Z3	0.550*	0.002*
Z1, SB	0.350*	0.004*
Z1, BC	0.730*	0.002*
Z1, MR	0.376*	0.009*
Z1, DR	0.909*	0.002*
Z2, Z3	0.333*	0.006*
Z2, SB	0.583*	0.002*
Z2, BC	0.887*	0.002*
Z2, MR	0.617*	0.002*
Z2, DR	0.919*	0.002*
Z3, SB	0.722*	0.002*
Z3, BC	0.867*	0.002*
Z3, MR	0.517*	0.002*
Z3, DR	0.831*	0.002*
SB, BC	0.702*	0.002*
SB, MR	0.365*	0.002*
SB, DR	0.956*	0.002*
BC, MR	0.617*	0.002*

d.

Sites	R-value	p-value
Global	0.518*	0.001*
Z1, Z2	0.580*	0.002*
Z1, Z3	0.619*	0.002*
Z1, SB	0.441*	0.002*
Z1, BC	0.507*	0.002*
Z1, MR	0.433*	0.002*
Z1, DR	1.000*	0.002*
Z2, Z3	0.117	0.16
Z2, SB	0.301*	0.041*
Z2, BC	0.615*	0.002*
Z2, MR	0.381*	0.006*
Z2, DR	1.000*	0.002*
Z3, SB	0.454*	0.006*
Z3, BC	0.648*	0.002*
Z3, MR	0.461*	0.002*
Z3, DR	1.000*	0.002*
SB, BC	0.207	0.061
SB, MR	0.263	0.045*
SB, DR	1.000*	0.002*
BC, MR	0.487*	0.004*

Appendix 2-1. continued.

e.

Sites	R-value	p-value
Global	0.627*	0.001*
Z1, Z2	0.296	0.024*
Z1, Z3	0.493*	0.002*
Z1, SB	0.576*	0.002*
Z1, BC	0.83*	0.002*
Z1, MR	0.524*	0.002*
Z1, DR	0.939*	0.002*
Z2, Z3	0.052	0.255
Z2, SB	0.678*	0.002*
Z2, BC	0.893*	0.002*
Z2, MR	0.746*	0.002*
Z2, DR	0.994*	0.002*
Z3, SB	0.744*	0.002*
Z3, BC	0.872*	0.002*
Z3, MR	0.707*	0.002*
Z3, DR	0.994*	0.002*
SB, BC	0.274	0.037*
SB, MR	0.130	0.171
SB, DR	0.843*	0.002*
BC, MR	0.448*	0.006*
BC, DR	0.867*	0.002*

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CHAPTER 3

Quantification of sand movement at a southern California rocky intertidal site

ABSTRACT

It is well known that sandy beaches along the California coastline experience seasonal onshore / offshore movements of sand. Sand movement on neighboring rocky shores, however, has been relatively under-studied despite the fact that sand is thought to be a major factor in structuring rocky intertidal communities. In this study, changes in sand levels were quantified during a 21-month period at Dike Rock, a rocky intertidal area near La Jolla, CA. Two major sand inundations were seen during this period – one in July / August of 2004 and one in August 2005. A smaller influx of sand was also seen in November 2004. The accumulation of sand was not kept at relatively constant levels by the presence of algal turf as had been shown in prior studies of subtidal sediment cycles. The coralline turf at this site, however, proved to be well adapted to sand inundation as the average depth of the turf was not significantly reduced after either of the major sand intrusions. Sediment levels at this site are negatively correlated with the maximum significant wave height for that time period, but no correlation was found between sediment levels and the mean significant wave height. As anthropogenic influences increase on our shorelines, it becomes crucial to establish baseline patterns of sediment transport.

INTRODUCTION

It has long been recognized that sandy beaches along the southern California coastline experience large-scale, seasonal, onshore / offshore movements of sand (eg. Shepard 1950). Extensive work has gone into quantification of the timing, duration, and spatial dynamics of these inundations (Winant et al. 1975, Aubrey 1979, Aubrey et al. 1980, Quick 1991, Morton et al. 1993, Stockdon et al. 2002, Sallenger et al. 2003). However, neighboring rocky shores that experience periodic influxes of sand are relatively under-studied. These mixed rock and sand ecosystems constitute a considerable portion of the world's shorelines (Bally et al. 1984, Brown et al. 1991), and yet only a handful of studies have attempted to quantify sand movement in such areas (Daly and Mathieson 1977, Littler et al. 1983).

A common seasonal pattern of sand movement has been found on most sandy beaches worldwide. A gradual accretion of sand during calm summer months leads to a peak in sand levels in late summer, while winter storm-generated waves rapidly erode the beach and the sediment is transported offshore (Winant et al. 1975, Aubrey 1979). Such a consensus does not exist in the literature concerning sand movement on rocky shores. Stewart (1983) reported increased sand deposition in southern California rocky intertidal habitats in summer during periods of relatively calm weather. Daly and Mathieson (1977) also found that a site in New Hampshire experienced major summer sand intrusions. In contrast, Littler (1980) and Littler et al. (1983)

found that sand burial consistently occurred during the winter months on San Nicholas Island, California, and Prathep et al (2003) reported increased sand levels during the winter at the Isle of Man in the Irish Sea.

Natural cycles of sand movement are being altered by human activities and man-made structures (reviewed in Brown and McLachlan 2002). The construction of jetties, breakwaters, and harbors can deprive down-drift beaches of sand while updrift sand accumulates (Kraus and McDougal 1996). Additionally, beach nourishment transfers sediment from offshore areas to higher levels in order to combat beach erosion (Peterson et al. 2000). This imported sand is then incorporated into the existing sediment cycle.

It is important to recognize these patterns of sand movement and how they are being altered because sediment dynamics are a major structuring agent on rocky shores (Daly and Mathieson 1977, Robles 1982, Seapy and Littler 1982, Taylor and Littler 1982, Littler et al. 1983, Stewart 1983, D'Antonio 1986, Barry 1988, Pineda and Escofet 1989, McQuaid and Dower 1990, Littler et al. 1991, Airoldi 2003, Schiel et al. 2006). Sediment may have negative effects on organisms through physical injury due to scour, smothering due to reduced light, nutrients, or dissolved gases, or detrimental chemical changes of the surrounding interstitial micro-environment (Devinny and Volse 1978). However, sediment may have indirect positive effects for stress-tolerant and opportunistic strategists by removing less tolerant organisms and creating space for settlement and reducing competition (Littler et al. 1983).

Additionally, certain species of non-perennial algae will only attach to the thalli of other algae and to sand grains (Stewart 1983). Finally, at a larger scale, it has been suggested that sand inundation increases the heterogeneity of the environment and therefore increases species richness where sand refuges are available (McQuaid and Dower 1990).

The local distribution and accretion of sediments can be controlled by the biota present on that shore (Airoldi 2003). Turf-forming algal assemblages can bind and stabilize sediments even on exposed coasts (Stewart 1983, Airoldi and Virgilio 1998) and may maintain relatively constant accumulations of sediments despite marked temporal variations in sediment deposition (Airoldi 2003). Furthermore, Airoldi and Virgilio (1998) found that though the growth of the turf was sensitive to accumulation of sediment, the total cover of algal turf was unaffected by sediment burial and scour. As turf-forming algae are a dominant feature of southern California rocky shores that provide habitat for an important community of small invertebrates and larvae (Stewart 1983, Huff 2006), these turf / sand interactions must be considered in a study of this area.

As anthropogenic impacts on patterns of sediment movement increase, we need a better understanding of baseline sediment cycles on rocky shores. The goal of this study was to quantify local changes in sand levels at Dike Rock, a rocky intertidal site in southern California. The primary questions were: (1) What are the timing and extent of sand inundations at Dike Rock? (2)

Does accumulation of sand remain relatively constant in areas where algal turf is present? (3) Is the average thickness of coralline algal turf reduced following an inundation event? (4) Are sand levels correlated with monthly average or maximum significant wave height (H_S)?

METHODS

Study site

This study was conducted in the Scripps Coastal Reserve at Dike Rock, La Jolla, California (32°87’ N, 117°25’). Dike Rock is a small rocky intertidal area bordered on either side by sandy beach. Rugged coastal bluffs rise approximately 100 meters above the reserve. This site is characterized by many large boulders in the high intertidal, broad mud- and sandstone benches covered with coralline algal turf and a few small boulders in the mid-intertidal, and a mixture of larger boulders and algae-covered flats in the lower intertidal area. Neighboring sandy beaches have distinct seasonal sediment profiles, with a peak in sediment found in late summer / fall and minimum sediment levels found in late winter / spring (Winant et al. 1975).

Sampling procedure

In April 2004, four eye-bolts were installed in large boulders to mark the corners of a 10 m (parallel to the coastline) x 30 m (perpendicular to the coastline) grid that spanned the shore from the high to the low intertidal. During each sampling event, measuring tapes were strung tightly between two bolts on each of the long sides of the grid (“vertically”). A third measuring tape was then stretched between them along one short side of the grid (“horizontally”) and fastened with carabiners so that it could slide (Figure 3-1).

Beginning at one corner, we recorded the type of organism or substrate that was found at one-meter intervals horizontally along the grid. Observations generally fit into six main categories: bare boulder (“boulder”), coralline turf (“turf”), coralline turf on boulder (“boulder / turf”), other algae, cobble, or sand. With the exception of boulder / turf, the substrate or organism that was found immediately at the surface was recorded, while subsequent layers were not. So, for example, if sand had completely covered a boulder, the sand would be recorded and the boulder would not. If sand or turf was present, a depth measurement was also taken. When possible, this was done by inserting the depth probe of Vernier calipers through the sand or turf to the bedrock. When the sand was too deep for the calipers, we inserted a long, thin metal rod into the sand and then measured it against a meter stick to determine the depth.

After observations had been recorded for each meter along the width of the grid (eleven measurements), we then slid the tape measure 2 m vertically and again recorded what we observed at one-meter intervals along the shorter tape. This process was repeated until we reached the opposite end of the grid (sixteen times for a total of 176 measurements during each sampling event) (Figure 1). Twenty sampling events were conducted opportunistically (during appropriate tides, after large storms, etc.) during a 21-month period (see figure 3-2 for specific sampling dates).

Data analysis

To create a visual representation of the timing, magnitude, and spatial extent of sand movement, an animation was created using Matlab (v. 7.0 The MathWorks, Inc. 2004). Each of the main categories that had been recorded was assigned a color (boulder = grey, boulder / turf = grey-green, turf = green, other algae = turquoise, and cobble = brown) and sand was divided into four depth ranges that were also assigned colors (< 50 mm = light pink, > 50 mm and < 200 mm = bright pink, > 200 mm and < 400 mm = red, > 400 mm = dark red). A schematic of the grid was then created, with 176 rectangles (11 x 16) that were each colored to represent an individual observation from the first sampling date. This was repeated for every sampling event (Figure 3-2) and each schematic then became one frame in the animation.

To look at patterns of sand inundation in different regions of the intertidal, the grid was divided into four zones: “High”, “High-mid”, “Low-mid”, and “Low” (Figure 3-1). The proportion of each zone that was occupied by turf, cobble, boulder, boulder / turf, other algae, and each of the four sand depths was then calculated for every sampling date. 95% confidence intervals were calculated for the proportion of exposed algal turf in each zone and in the total grid area over all sampling dates to determine whether sand accumulation remained relatively constant in areas where turf was present.

Potential differences in average turf depth before and after the two largest recorded sand inundations were examined with a Mann-Whitney test. Turf-depth data from June 16, 2004 were compared to those from October 15, 2004 and data from July 22, 2004 were compared to October 19, 2005.

Monthly mean and maximum significant wave height (H_S) for April 2004 through December 2005 were obtained from the website of the Coastal Data Information Program (CDIP) at Scripps Institution of Oceanography (http://cdip.ucsd.edu). A Spearman's Rank correlation analysis was then performed to determine if the proportion of total sand cover within the grid was correlated with either mean or maximum H_S for the month during which the sand measurements were taken.

RESULTS

The sand grid animation highlighted two major sand intrusions (July / Aug. 2004, Aug. 2005) and one less extensive inundation (Nov. 2004) during the 21 months covered by the study (Figure 3-2).

The proportion of each of the main substrate types and sand depths was similar across sampling dates among the low, low-mid, and high-mid zones with the exception of cobble and sand < 50 mm in depth ($p > 0.05$ in all cases except cobble and sand < 50 mm, results in this section are from ANOVA unless otherwise noted). The high-mid zone had significantly more cobble than either the low or low-mid zones ($p < 0.0001$) and the low-mid zone had significantly more sand < 50 mm deep than low or high-mid ($p < 0.0001$). The high zone had significantly more boulders, more cobble, less sand < 50 mm, less boulder / turf, and less turf than any of the other three zones ($p < 0.0001$ in all cases). There were no significant differences among any of the four zones in the proportion of sand > 50 mm, > 200 mm, or > 400 mm in depth ($p > 0.05$ for all comparisons) (Figure 3-3).

The proportion of exposed turf (“turf” plus “boulder / turf”) varied significantly in each of the zones during the course of the study. During the two largest sand inundations, all four zones had significantly less exposed turf. Additionally, the high and high-mid zones had significantly less exposed turf in October and November 2004 during the smaller influx of sand (< 95% CI in all cases).

The average thickness of algal turf was not significantly different after the first large sand influx at Dike Rock than it was before the sand inundation occurred (June 2004 vs. October 2004) (Mann-Whitney test, $p = 0.761$). The second large sand influx also did not affect the thickness of the turf. Average turf thickness in July 2005 was not significantly different from that in October 2005 (Mann-Whitney test, $p = 0.111$).

There was a significant negative correlation between the total proportion of the grid that was covered by sand (the sum of all four depth ranges) and the maximum significant wave height during that period (Spearman Rank correlation, ? = -0.484, $p = 0.044$) (Figure 3-4). Mean significant wave height and the presence of sand were not significantly correlated (Spearman Rank correlation, ? = -0.389, p = 0.090).

DISCUSSION

Maximum accumulations of sand in the rocky intertidal area at Dike Rock appear to occur during the summer months (July and August during this study). At nearby sandy beaches, maximum sand levels have been recorded later in the year in October and November (Winant et al. 1975, Aubrey 1979). The difference in observations between these two systems could merely be the result of the timing of sampling events. In September and early October in southern California, tidal levels are not particularly low. Because of this, we were unable to collect measurements of sediment levels for either year during these times. So, sediment levels may have continued to increase after July and August but were unrecorded in this study. It is also possible that there are inherent physical differences between rocky intertidal areas and stretches of sandy beach that affect the accumulation and erosion of sand.

While there were no statistically significant differences among the four zones of the study region in proportion of area covered by sand except in the shallowest depth range, sediment was generally observed to accumulate more extensively in the lower three zones as illustrated in Figure 3-4. The “low-mid” region of our study grid seemed to be most affected by the influx of sand, especially relatively shallow accumulations. This is probably because this zone has very few large boulders as compared to the other three zones, and the small boulders and benches are more easily covered with sand.

Previous studies of sand inundation on rocky shores have shown that generally, sand deposits are patchy and “refuge” areas exist for those organisms that are able to crawl or swim away from the sediment accumulations (Littler et al. 1983, McQuaid and Dower 1990). This appears to be the case for the Dike Rock algal turf community as well. Even during the largest sand inundation events, patches of algal turf found on large boulders were left unburied.

In subtidal areas, turf-forming algae can maintain relatively constant accumulations of sediments despite temporal variation in sediment load (Airoldi 2003). This was not the case in the intertidal region at Dike Rock. The proportion of exposed algal turf was significantly lower during times of sand inundation. Sediment levels were so much deeper during these times, even in areas dominated by turf, that the turf was completely covered.

The results of this study suggest, however, that coralline algal turf is well adapted for sand burial. Airoldi and Virgilio (1998) found that sediment reduced the “vertical growth” (length) of filamentous algal turf. The coralline turf at Dike Rock did not show a similar pattern as the average depth (length) of the coralline turf did not change after either major sand inundation. Coralline turf may be more resistant to sand scour than filamentous turf because of its rigid structure and densely packed fronds.

At Dike Rock, the maximum significant wave height is more important than the mean significant wave height in the regulation of sand levels. In other words, storms that cause large waves have a greater effect on sediment levels than the general, daily wave regime. This is significant for organisms that live in this environment as they must be adapted to relatively sporadic and rapid changes in sediment levels.

As was discussed above, sediment can be a major structuring factor in rocky intertidal assemblages. Studies such as this one that help us to gain a better understanding of the timing and extent of sand inundations to rocky shores are crucial to our understanding of these communities. Additionally, as anthropogenic structures increase along our coastlines, it is becoming urgent that we gain a better understanding of baseline patterns of sediment movement on rocky shores so that better management decisions can be made.

ACKNOWLEDGEMENTS

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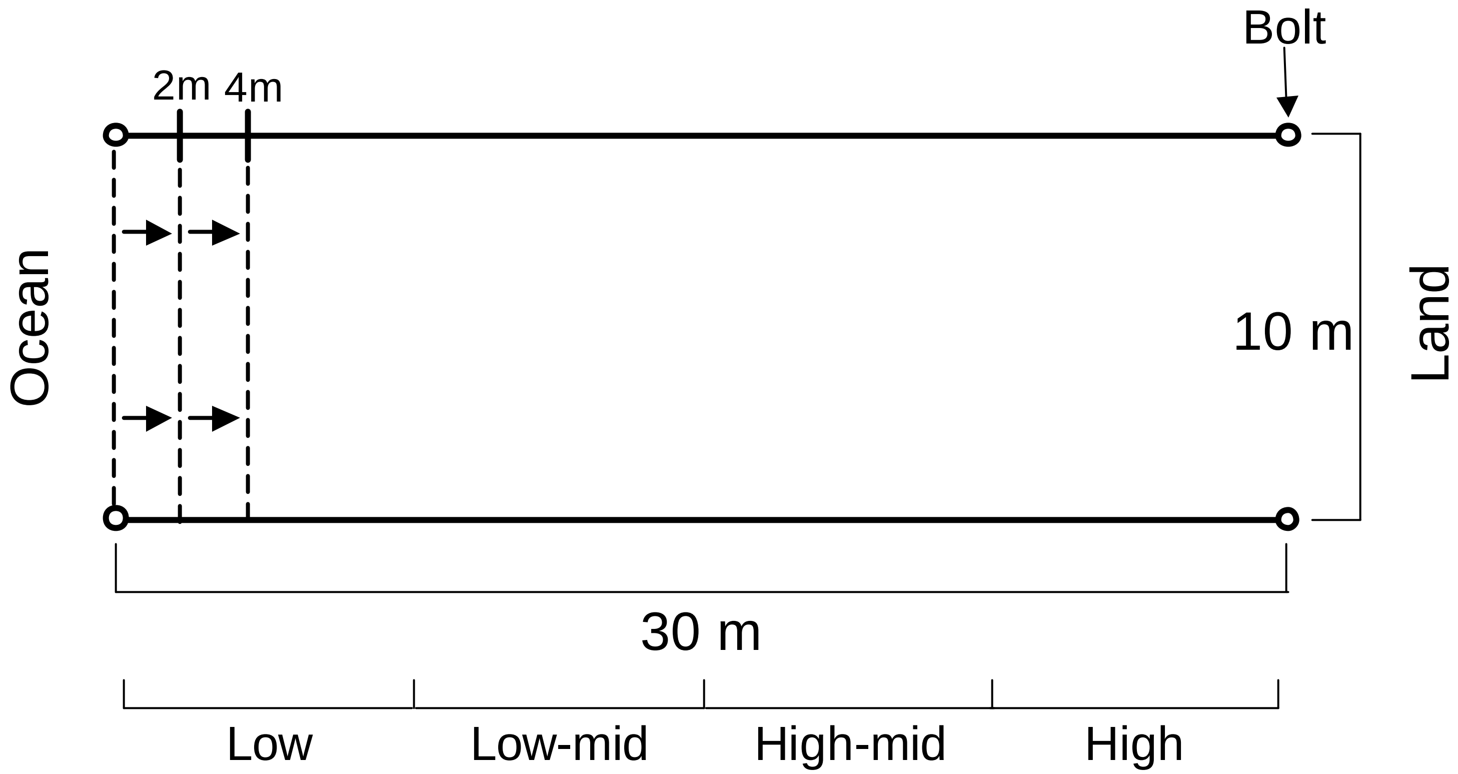


Figure 3-1. Diagram of sand grid layout and sampling scheme.

Figure 3-2. Individual frames from an animation depicting the change in sediment levels at Dike Rock from April 2004 – December 2005. Note sand intrusions in July / August 2004 (**e, f**), November 2004 (**h**), and August 2005 (**o**).

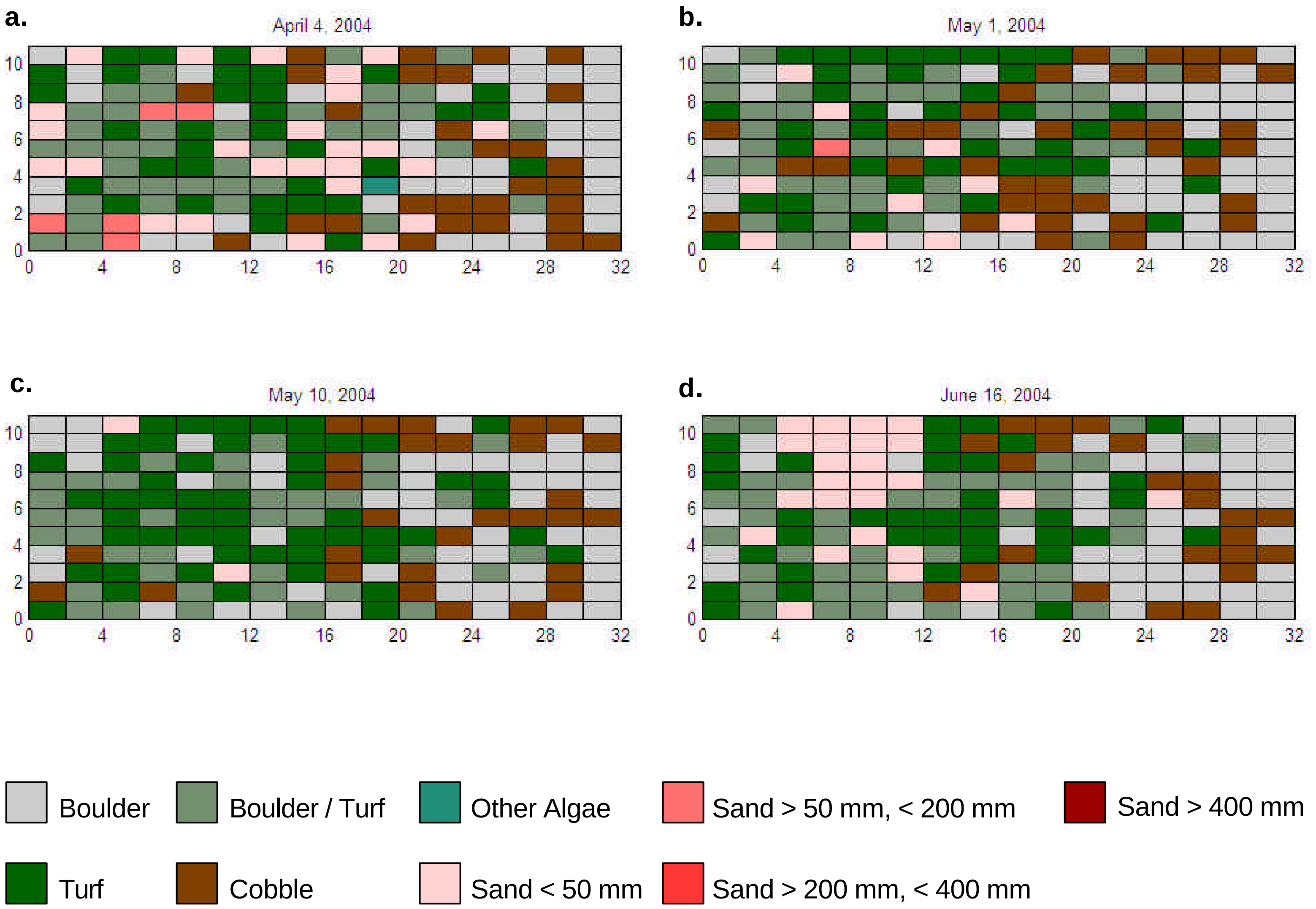

a.
April 4, 2004
b.
May 1, 2004
c.
May 10, 2004
d.
June 16, 2004
0
2
4
6
8
10
0
4
8
12
16
20
24
28
32
Boulder
Boulder / Turf
Other Algae
Sand > 50 mm, < 200 mm
Sand > 400 mm
Turf
Cobble
Sand < 50 mm
Sand > 200 mm, < 400 mm

Figure 3-2. continued.

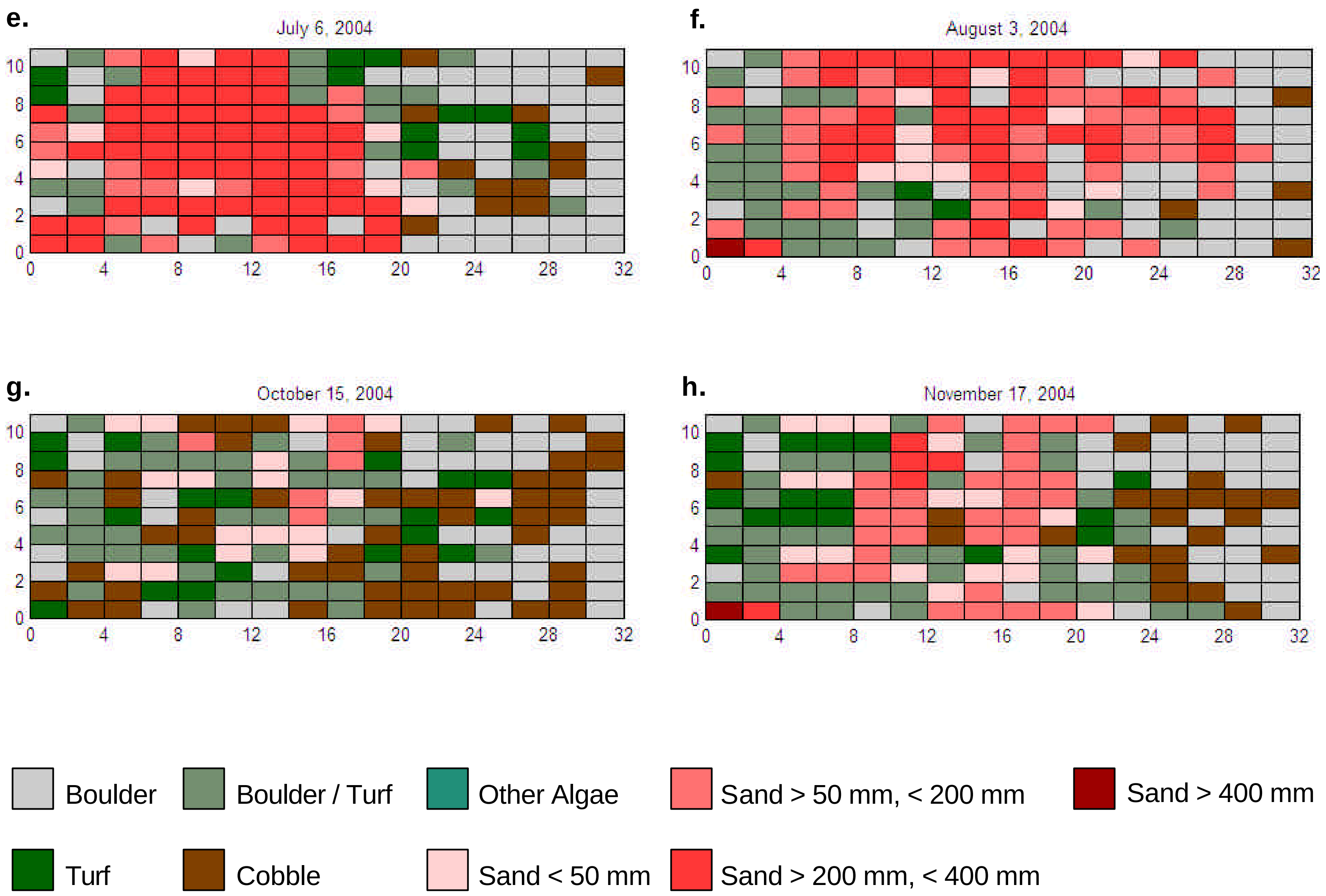

e.
July 6, 2004
f.
August 3, 2004
g.
October 15, 2004
h.
November 17, 2004
0
2
4
6
8
10
0
4
8
12
16
20
24
28
32
Boulder
Boulder / Turf
Other Algae
Sand > 50 mm, < 200 mm
Sand > 400 mm
Turf
Cobble
Sand < 50 mm
Sand > 200 mm, < 400 mm

Figure 3-2. continued.

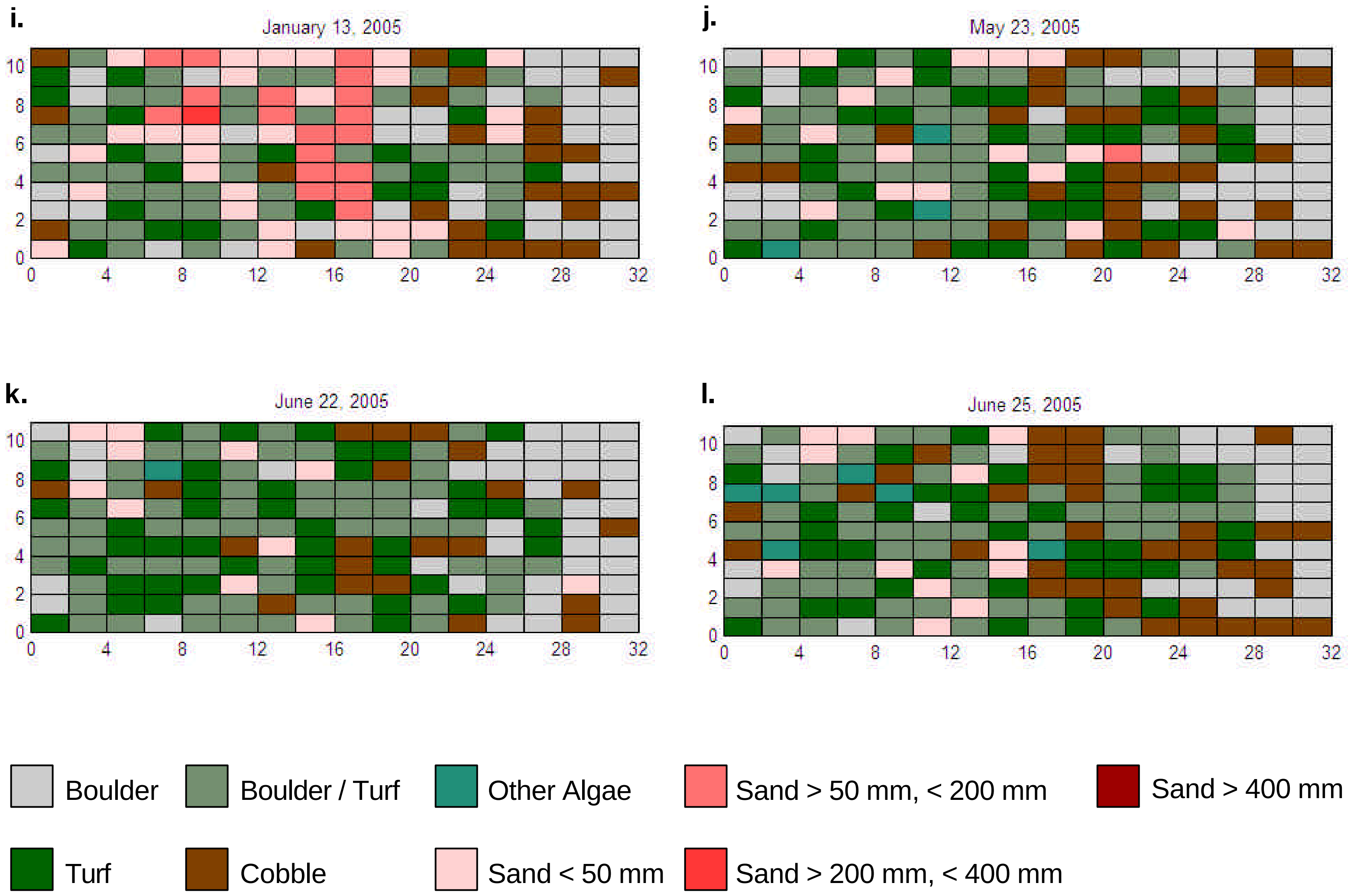

i.
January 13, 2005
j.
May 23, 2005
k.
June 22, 2005
l.
June 25, 2005
0
2
4
6
8
10
0
4
8
12
16
20
24
28
32
Boulder
Boulder / Turf
Other Algae
Sand > 50 mm, < 200 mm
Sand > 400 mm
Turf
Cobble
Sand < 50 mm
Sand > 200 mm, < 400 mm

Figure 3-2. continued.

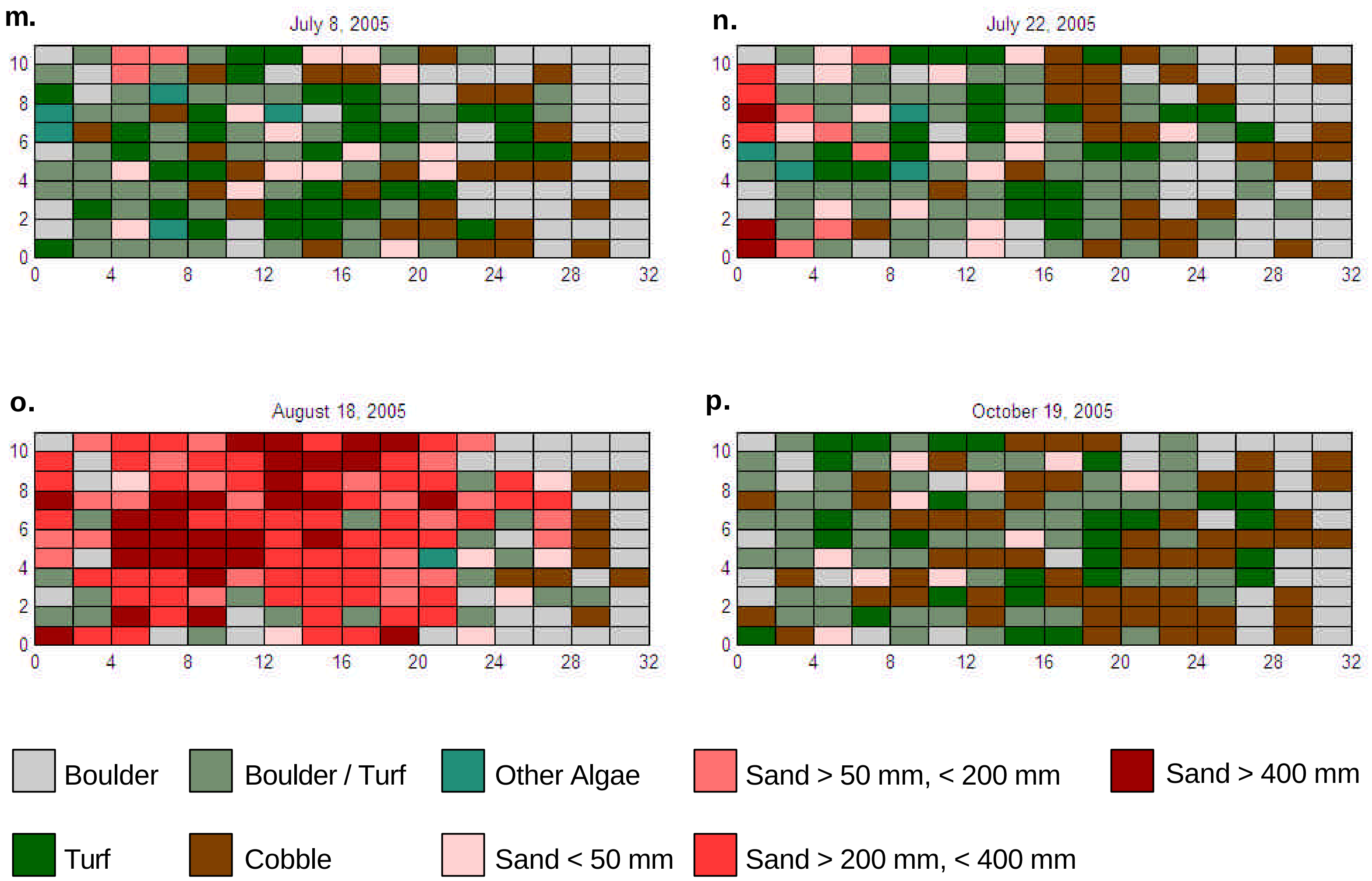

m.
July 8, 2005
n.
July 22, 2005
o.
August 18, 2005
p.
October 19, 2005
0
2
4
6
8
10
0
4
8
12
16
20
24
28
32
Boulder
Boulder / Turf
Other Algae
Sand > 50 mm, < 200 mm
Sand > 400 mm
Turf
Cobble
Sand < 50 mm
Sand > 200 mm, < 400 mm

Figure 3-2. continued.

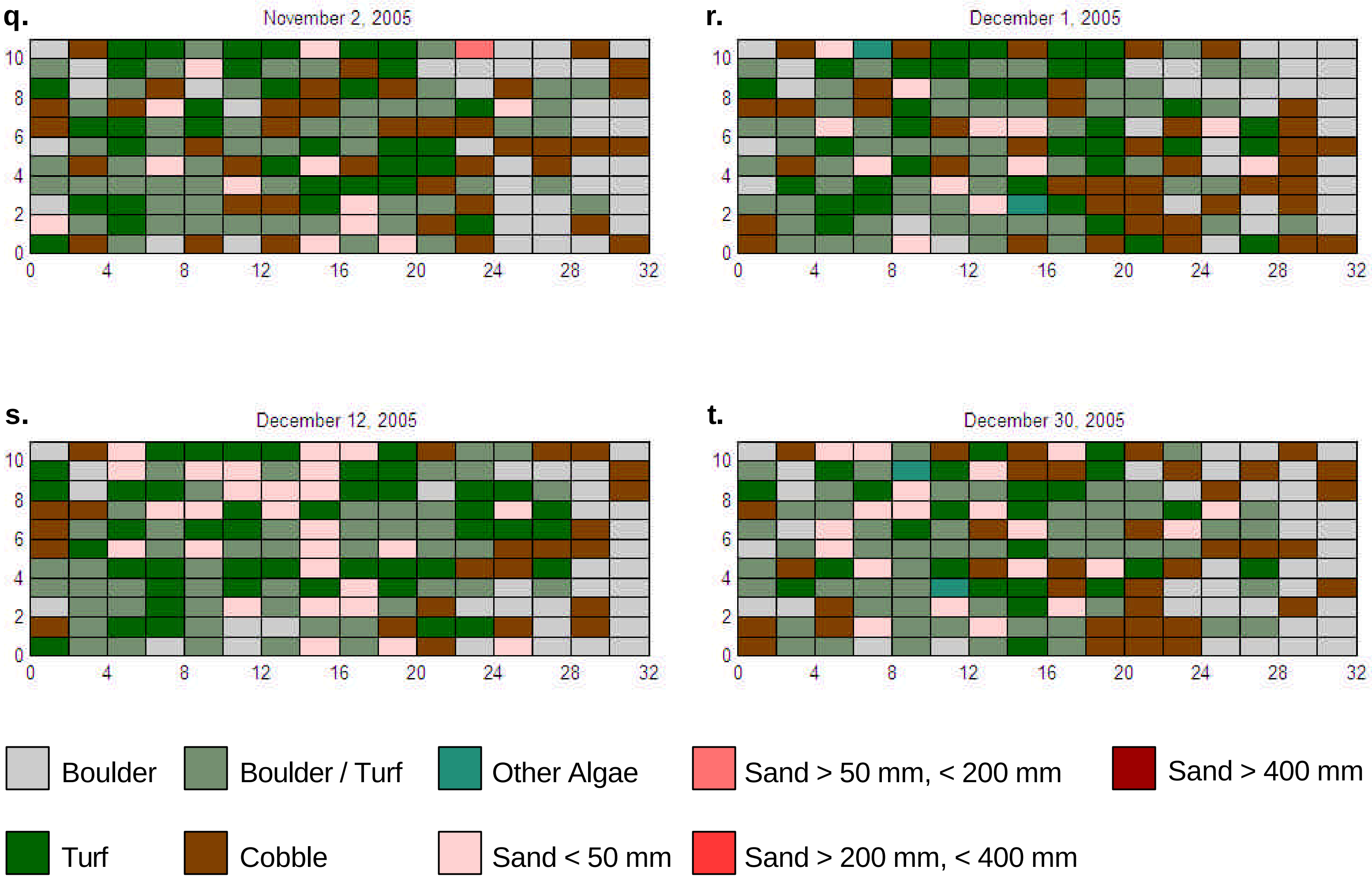
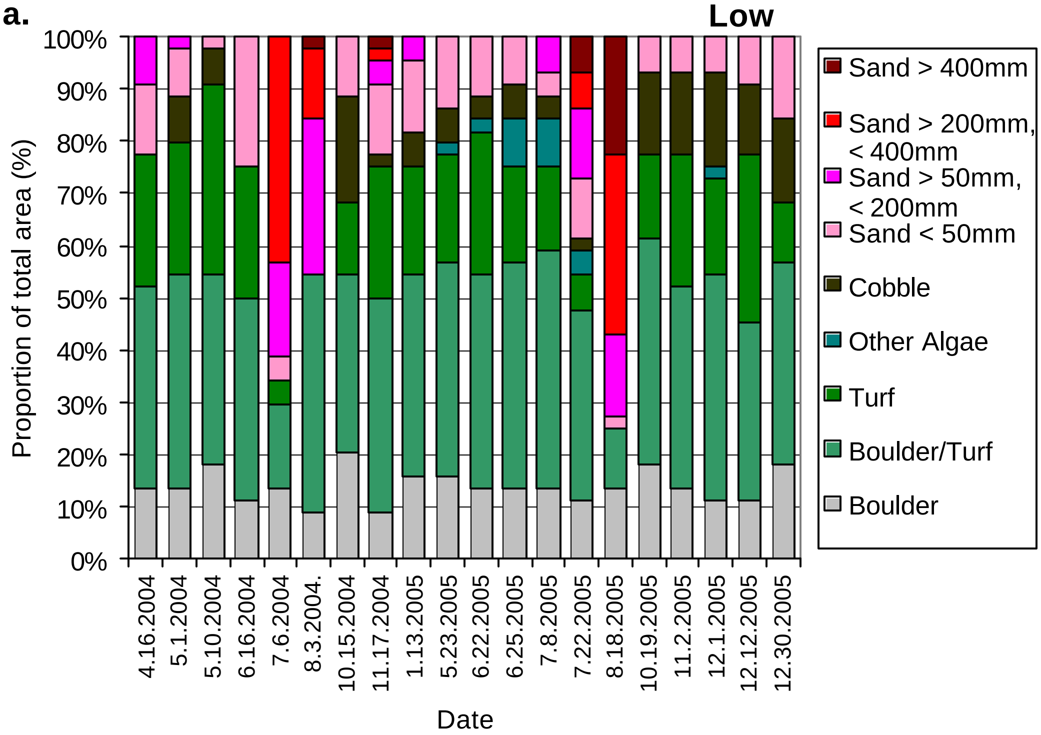

q.
November 2, 2005
r.
December 1, 2005
s.
December 12, 2005
t.
December 30, 2005
0
2
4
6
8
10
0
4
8
12
16
20
24
28
32
Boulder
Boulder / Turf
Other Algae
Sand > 50 mm, < 200 mm
Sand > 400 mm
Turf
Cobble
Sand < 50 mm
Sand > 200 mm, < 400 mm

Figure 3-3. Proportion of each of the main substrate types found in the **a.** low **b.** low-mid **c.** high-mid and **d.** high zones of the study area from April 2004 to December 2005


a.
Low
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Proportion of total area (%)
4.16.2004
5.1.2004
5.10.2004
6.16.2004
7.6.2004
8.3.2004.
10.15.2004
11.17.2004
1.13.2005
5.23.2005
6.22.2005
6.25.2005
7.8.2005
7.22.2005
8.18.2005
10.19.2005
11.2.2005
12.1.2005
12.12.2005
12.30.2005
Date
Sand > 400mm
Sand > 200mm, < 400mm
Sand > 50mm, < 200mm
Sand < 50mm
Cobble
Other Algae
Turf
Boulder/Turf
Boulder

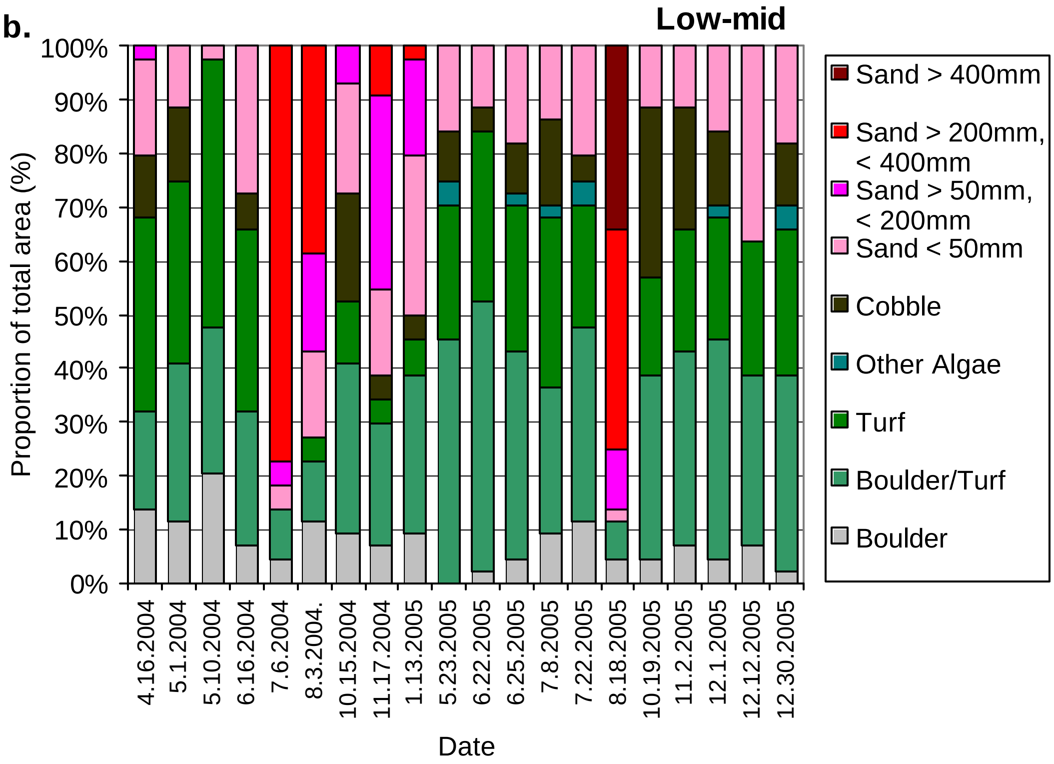
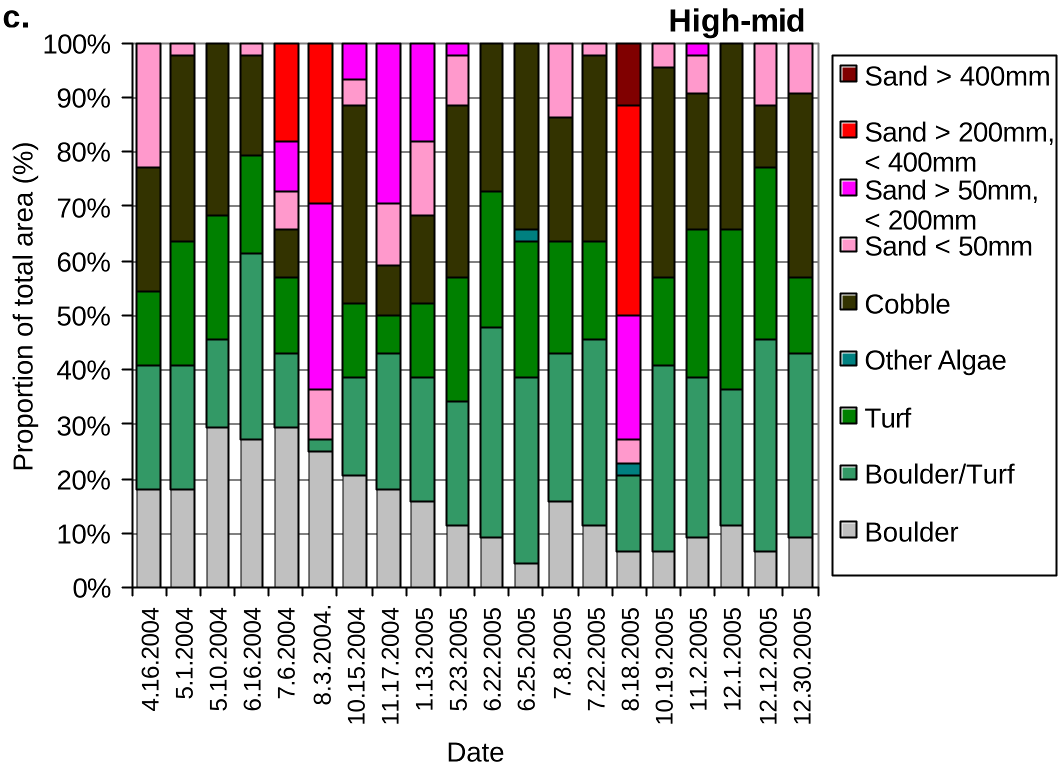
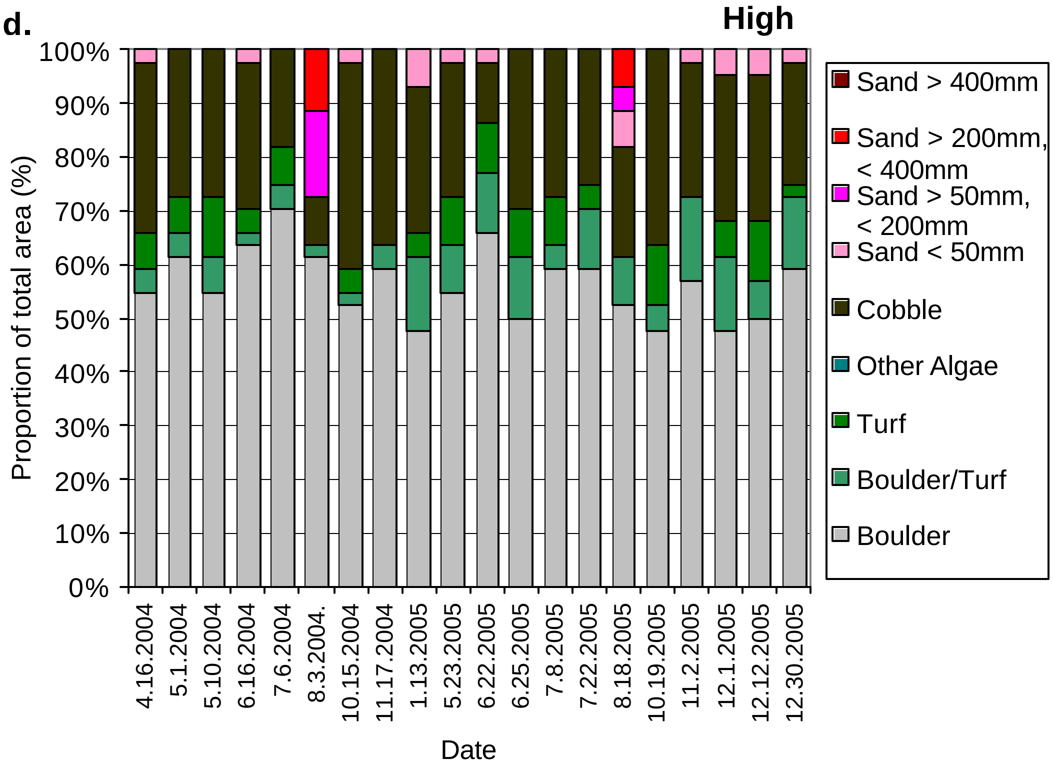

b.
Low-mid
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Proportion of total area (%)
4.16.2004
5.1.2004
5.10.2004
6.16.2004
7.6.2004
8.3.2004.
10.15.2004
11.17.2004
1.13.2005
5.23.2005
6.22.2005
6.25.2005
7.8.2005
7.22.2005
8.18.2005
10.19.2005
11.2.2005
12.1.2005
12.12.2005
12.30.2005
Date
Sand > 400mm
Sand > 200mm, < 400mm
Sand > 50mm, < 200mm
Sand < 50mm
Cobble
Other Algae
Turf
Boulder/Turf
Boulder

Figure 3-3. continued.

c.


High-mid
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Proportion of total area (%)
4.16.2004
5.1.2004
5.10.2004
6.16.2004
7.6.2004
8.3.2004.
10.15.2004
11.17.2004
1.13.2005
5.23.2005
6.22.2005
6.25.2005
7.8.2005
7.22.2005
8.18.2005
10.19.2005
11.2.2005
12.1.2005
12.12.2005
12.30.2005
Date
Sand > 400mm
Sand > 200mm, < 400mm
Sand > 50mm, < 200mm
Sand < 50mm
Cobble
Other Algae
Turf
Boulder/Turf
Boulder

d.


High
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Proportion of total area (%)
4.16.2004
5.1.2004
5.10.2004
6.16.2004
7.6.2004
8.3.2004.
10.15.2004
11.17.2004
1.13.2005
5.23.2005
6.22.2005
6.25.2005
7.8.2005
7.22.2005
8.18.2005
10.19.2005
11.2.2005
12.1.2005
12.12.2005
12.30.2005
Date
Sand > 400mm
Sand > 200mm, < 400mm
Sand > 50mm, < 200mm
Sand < 50mm
Cobble
Other Algae
Turf
Boulder/Turf
Boulder

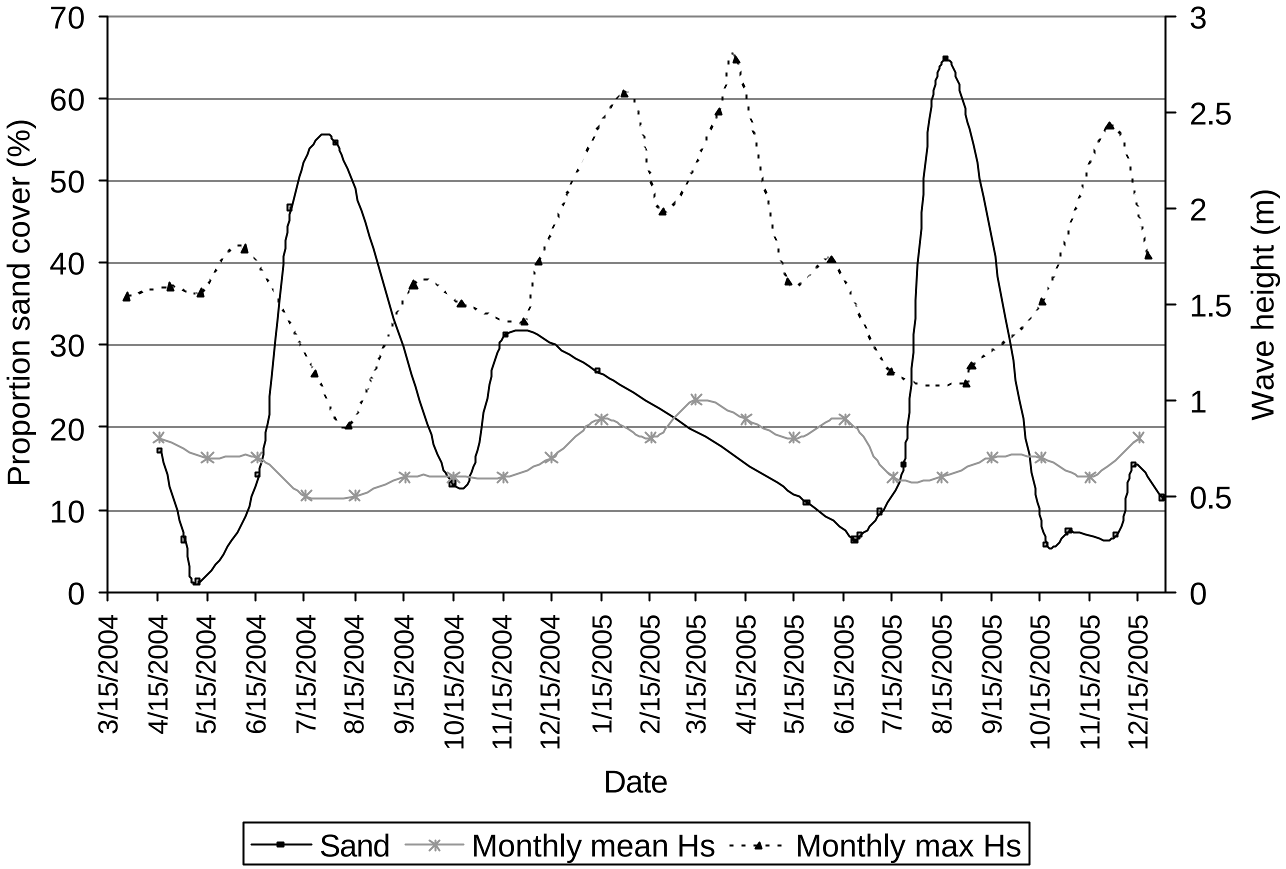


Figure 3-4. Change in proportion of total sand cover at the Dike Rock study site between April 2004 – December 2005 as compared to monthly mean and maximum significant wave heights for the same period. Sand cover and maximum significant wave height were negatively correlated (? = -0.484, p = 0.044).

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CHAPTER 4

Sand addition alters the invertebrate community of Southern California intertidal coralline turf

ABSTRACT

Southern California rocky intertidal areas are subject to periodic sand inundations due to a natural cycle of sand movement that is being altered and intensified by human activities. Though sand is thought to be a major structuring force in intertidal communities, little experimental research has been done to investigate its effects on intertidal organisms. Assemblages of meio- and macrofauna that inhabit intertidal coralline algal turf have been especially neglected. In this study, sand was added daily to coralline turf plots to maintain depths of either 3 cm or 6 cm for one month. Within one hour of sand addition, faunal community composition had changed significantly due to a decrease in the abundances of highly mobile animals. Another shift was seen after two weeks when abundances of psammophilic gastropods increased. One month after sand addition had ceased, communities in treatment plots again resembled those of the controls. This experiment demonstrates that turf communities rapidly respond to and recover from local physical disturbances due to sand inundation. Since these species form an important component of the marine food web, these results could be significant for the whole rocky intertidal community.

INTRODUCTION

Large areas of southern California rocky shores are covered by a carpet-like mat of algal thalli referred to as algal turf. In San Diego County, turf is comprised of a few anchor species that attach directly to the substrate (usually *Corallina* spp.) and many epiphytes that attach to the anchor species (Stewart 1982). At times, large amounts of sediment can be observed within the algal mat and the presence or absence of this sand is an important factor to be considered when studying the turf community (Stewart 1983). The complex mat of algae and associated sediment provides habitat for diverse assemblages of small invertebrates and larvae (Dommasnes 1969, Neumann et al. 1970, Edgar 1983, Hicks 1985, Gibbons and Griffiths 1986, Akioka et al. 1999, Kelaher et al. 2001). Abundances in excess of 200,000 animals m^{-2} (> 500 µm) have been previously observed in these turf communities (Brown and Taylor 1999) and personal observations have shown densities as high as 1.6 million animals m^{-2} (> 63 µm).

These invertebrates form an important component of the food chain in the rocky intertidal and hence are significant players in the system (Coull and Wells 1983, Coull 1988). According to Coull (1988), over 50 papers have been published since the early 1970s that document the presence of meiofaunal prey in the stomach contents of marine fish and invertebrate predators. Gut analysis of the intertidal blenny *Helcogramma medium* indicated that amphipods were their primary prey (Coull and Wells 1983) and

Hicks (1984) found that benthic copepods were the dominant prey for young flatfish. Additionally, Gosselfin and Chia (1994) found that juvenile *Nucella emarginata* commonly preyed upon small bivalves such as *Lasaea* spp. and juvenile *Mytilus* spp. Dierschke (1994) also determined that the main prey species of the purple sandpiper *Calidris maritima* included small snails such as *Littorina saxatilis*, small crustaceans, polychaetes, juvenile *Mytilus* spp., and the isopod *Idotea granulosa*. All of these examples include prey species that are often part of the turf community.

Evidence suggests that six thousand years ago, most of the southern California shoreline was rocky habitat. With a rise in sea level, sand that previously may have fallen into the deep sea began to accrete on the ocean shelf and bury much of this rocky environment (Graham et al. 2003). This has resulted in a fragmentation of rocky areas and has caused a shift to an intertidal community that appears to be moderately tolerant of episodic sand burial (Littler et al. 1983, 1991). Currently, many rocky shores experience sand levels that are variable in both space and time. Additionally, these sand cycles are being altered and intensified by human activities such as the building of seawalls and beach replenishment (AMEC 2002).

Though the dynamics of sand movement are thought to be a major structuring agent on rocky intertidal shores (eg. Daly and Mathieson 1977, Taylor and Littler 1982, McQuaid and Dower 1990, Airoldi 2003), there is a need for experimental work to investigate the effects of sand on the organisms that inhabit these shores (but see Kendrick 1991, Airoldi and Cinelli 1997, and Airoldi and Virgilio 1998 for subtidal work). Limited observational studies of the effects of sand inundation on assemblages of meio- and macrofauna in coralline algal turf have been published (Kelaher et al. 2001, Prathep et al. 2003). Kelaher et al. (2001) showed that of four environmental variables, sediment showed the strongest relationship with macrofaunal assemblages in coralline turf. However, experimental work was still needed to follow up on this observation.

The goal of our study was to use experimental techniques to investigate the role of sediment in intertidal coralline turf habitat, particularly in relation to complete burial by sand. Our primary questions were: (1) How does the coralline turf macro- and meiofauna community change with sand burial? (2) Which organisms appear to be sand-tolerant or sand-intolerant? (3) Do thresholds exist in time or depth of burial for turf animals?

METHODS

Study site

This experiment was conducted in the Scripps Coastal Reserve at Dike Rock, La Jolla, California, USA (32°87’ N, 117°25’ W). Dike Rock has many boulders as well as a flat shelf of mudstone covered with coralline algal turf and is bordered on either side by sandy beach. Experimental plots were located on the shelf in the mid- to low-intertidal. Turf in this area consists mainly of *Corallina pinnatifolia* Daws with occasional *C. officinalis* Kütz as anchor species and epiphytic *Ulva californica* Wille, *Gelidium* spp. Lamouroux, *Centroceras clavulatum* Montagne*, Leathesia difformis* Aresch, and *Laurencia pacifica* Kylin.

Much of the rocky area at this site is subject to periodic burial by sand, ranging from a depth of several centimeters to more than a meter (Huff unpublished data). During the duration of this study, however, very little natural sand was present.

Experimental design and sampling procedure

Three sand treatments were applied to a total of fifteen experimental plots: 5 shallow sand addition plots, 5 deep sand addition plots, and 5 control plots to which no sand was added. In order for the desired sand depths to be maintained, plots were haphazardly sited in semi-enclosed circles of boulders where they were protected from the full force of waves and where only trace amounts of natural sand occurred. Sand treatments were then randomly assigned to plots.

Sand of a size typical to natural inundations (mean particle size < 1 mm and > 500 µm) was taken from a nearby beach and placed on plots daily to maintain a depth of 3 cm (shallow sand treatment) or 6 cm (deep sand treatment). The tips of the algal turf remained exposed at the shallow sand depth, while turf was completely covered by the deep sand treatment. Care was taken to cover each plot with sand well outside of its boundaries in order to reduce edge effects.

Each 0.50 m by 0.75 m plot was divided into six 0.25 m by 0.25 m quadrats. Each of these quadrats was sampled at one of six times after initial sand addition: 1 hour, 12 hours, 1 day, 2 days, 2 weeks, or 4 weeks. Samples were also taken immediately before sand addition began ("pre-impact") and one month after sand addition had ceased ("recovery"). Each quadrat within a plot was randomly assigned a sampling time and no quadrat was sampled more than once until recovery samples were taken. Pre-impact samples were taken from the area immediately outside the plot frame and recovery samples were taken randomly from any quadrat inside each plot (Fig. 4-1). During every sampling period, 3 samples were taken randomly from within each plot. In addition to taking algal samples, each plot was watched for 5 minutes after the initial sand addition and animals that emerged were recorded and counted.

Samples were obtained by cutting through the turf mat with a 4.4 cm diameter (13.8 cm^2) metal coring device and carefully scraping the turf from the bedrock with a metal spatula. Samples were placed in tightly sealed plastic containers, taken back to the lab, and immediately preserved in ethanol. They were later rinsed on a 63 µm sieve. Samples were sorted manually with forceps under a 12x dissecting microscope. All invertebrates were removed, identified to the lowest possible taxonomic level, and counted. Although sessile animals that were attached to algal fronds (e.g. bryozoans, serpulorbid snails, sponges, etc.) were commonly found in the turf, these animals were not included in the study because the methods used were not appropriate to quantify them accurately (Kelaher 2002). Once defaunated, the algae and sand were separated, dried in a 60° C drying oven until a constant weight was obtained (at least 24 hours), and weighed.

In order to avoid a bias in our results due to the inadvertent addition of organisms to the study plots directly with the addition of sand, samples of the sand were taken back to the lab and inspected. Invertebrates were removed and counted and those found in large abundances were noted.

Data analysis

For all analyses, data from the three samples taken during each time period from each plot were averaged to give dry weights of sand and algae and average animal abundances. Inspection of the invertebrate community that was found in the sand itself along with comparison of pre- and post-impact species assemblages in the turf revealed one organism, a Platyhelminth, which appeared to be a direct artifact of sand addition. We believe that this was the only abundant organism that was imported to the plots with the sand. Therefore, it was removed from all further analyses.

Because samples contained varying amounts of sand and algae, analyses were performed to determine if standardization of sample size was necessary (e.g. animals per dry weight algae or sand rather than animals per sample). A multiple regression was first completed with dry weight of sand and algae as predictor variables and total number of invertebrates as the response variable. Regression coefficients showed that the number of animals was significantly correlated with amount of algae ($R^2 = 0.287$, $p < 0.001$), but not with sand ($R^2 = 0.017$, $p = 0.080$).

Then, in order to determine if the average amount of algae in each sample was significantly different among the three treatments, an analysis of variance (ANOVA) was performed. Average dry weight of algae was used as the dependent variable and sand treatment (shallow, deep, or control) as a factor. No significant differences were found among the weights of algae in the three treatments ($p = 0.11$, $F = 7.191$, $df = 2$) and consequently no standardization of sample size was done.

Analysis of similarities (ANOSIM) and non-metric multidimensional scaling (nMDS) were used to investigate patterns and quantify changes in the turf communities. Additionally, the similarity percentages method (SIMPER) was used to determine which taxa were contributing to any perceived differences between samples. This type of analysis uses a Bray-Curtis dissimilarity matrix and computes the contribution of each species to the total average dissimilarity between all pairs of inter-group samples. These analyses were performed using Plymouth Routines in Marine Ecological Research (PRIMER) software v.5.2.9 (Primer-E Ltd. 2002).

Multiple diversity indices were also calculated with PRIMER including the Shannon-Weiner diversity index (H’), Pielou’s evenness index (J’) and the

Simpson index (1-?). Diversity indices were used as response variables with time as a factor in additional ANOVAs to look for changes in diversity between treatments and through time within each sand treatment.

RESULTS

Overview

A total of 44,090 invertebrates from 133 taxa were counted (Table 4-1). The taxonomic resolution of the fauna varied among groups because some species have not been described, others require specialized taxonomic knowledge to identify, and some were juveniles that could not be conclusively identified. The use of differing (ie. higher) levels of taxonomic discrimination in these types of multivariate analyses has been shown to have little effect on the outcome (Herman and Heip 1988, Warwick 1988a, b, James et al. 1995).

Animals were observed immediately emerging from experimental plots after sand addition. Counts made during the five minutes after initial sand addition showed that these animals mostly included amphipods, isopods, pycnogonids, hermit crabs, and larger gastropods (Table 4-2).

Time and sand depth

ANOSIM analyses revealed no significant differences among the invertebrate assemblages of control, shallow, and deep treatment plots before sand was added. With sand addition, significant differences were found between both shallow and deep sand treatments and control plots during every sampling interval with two exceptions - no significant difference was found between deep treatment and control plots in the 1 or 2 day samples (Appendix 4-1). nMDS plots also reveal a distinct separation between control plots and plots to which sand had been added (Figure 4-2). There were no significant differences between the communities of shallow and deep sand treatment plots during any sampling period. Recovery samples taken one month after the cessation of sand addition showed no significant differences among the fauna of shallow, deep, and control plots (Appendix 4-1).

ANOSIM analyses also showed significant differences through time within sand addition treatments. Significant differences were seen between pre-impact and other sampling times within both the shallow and deep plots, again with two exceptions – no significant differences were seen between deep pre-impact and 1 or 2 day samples. Additionally, shallow and deep treatment plots showed significant differences between the very short-term samples (1 and 12 hours and 1 day) and the longer-term samples (2 and 4 weeks). Control plots did not show these patterns, however significant differences were detected between earlier samples (pre-impact, 1 and 12 hours, 1 and 2 days) and later samples (4 weeks) (Appendix 4-2).

Community response

In order to determine which taxa were responsible for the dissimilarity between treatments, a SIMPER analysis was performed. Highly mobile taxa including copepods, gammarid amphipods, and ostracods accounted for the majority of differences between treatment and control plots during the early time periods (1 and 12 hours, 1 and 2 days). Abundances of these taxa show a rapid and sustained decrease with sand addition and an increase to near-control levels in recovery samples (Figure 4-3a). A second shift in community composition was seen in the 2 and 4 week samples when abundances of *Barleeia* sp. and *Amphithalamus* spp. began to increase. These snails also decreased to near-control levels in recovery samples (Figure 4-3b).

An ANOVA of diversity indices (H', J' and 1-?) using time as a factor within each treatment showed no significant differences except in the deep sand addition plots. J' and 1-? were both shown to increase significantly through time for the deep treatment plots (F = 4.224, p = 0.002, df = 7 and F = 4.689, p = .001, df = 7).

DISCUSSION

This study has established that the experimental addition of sand to intertidal coralline turf has almost immediate and sustained effects on the associated meio- and macrofauna. Two distinct shifts in community composition were seen with sand inundation – a rapid exodus of mobile sand-intolerant animals and a more gradual increase in psammophilic ("sand-loving") gastropods. As early as one hour after sand addition, significant differences were seen between control and treatment plots. Both observation and statistical analyses suggest that these differences were caused by highly mobile, sand-intolerant animals such as amphipods and ostracods which rapidly dispersed from sand inundated plots. Amphipods and ostracods both tend to live in interstitial spaces of the algal turf (Gibbons 1988, Coull and Wells 1983). It is possible that the addition of sediment clogged the coralline algae, thus eliminating their spatial niche and refuge from predators (Dean and Connell 1987, Coull and Wells 1983). While they have an exoskeleton, these animals are not protected by a hard shell and increased scour associated with sand addition could also be a cause of their decrease in abundance.

A second difference in community composition between treatment and control plots was seen beginning in the 2-week samples when abundances of the snails *Amphithalamus tenuis, A. inclusus* and *Barleeia* sp. showed significant increases in treatment plots. Microgastropods are able to move about and disperse into new habitats as adults within a period of days or weeks (Olabarria and Chapman 2001, Olabarria 2002), so they may respond to habitat changes and move to more preferable areas. *Amphithalamus* spp. are commonly reported to be positively correlated with the presence of sediment (Olabarria and Chapman 2001, Kelaher et al. 2003) and *Barleeia* sp. also tend to have higher abundances when more sediment is present (personal observation).

No significant differences were seen between the communities of the shallow and deep sand addition plots. The two depths and multiple sampling times were employed to determine if perhaps some organisms possess a tolerance threshold for sand depth or time of burial. It appears, however, that sand-intolerant organisms respond almost immediately to even shallow levels of sand inundation. If a sand tolerance threshold does exist for some of these animals, it appears to be at sand levels less than 3 cm.

Within both the shallow and deep sand treatment plots, significant differences in community composition were seen between pre-impact and all other sampling times with the exception of the 1 and 2 day samples from the deep treatment. The control plots, however, showed no significant community changes with time until the recovery samples were taken. This is evidence that although the composition of turf communities may have natural fluctuations with time because of settlement events, disturbance, or other influences, inundation with sand causes a much more rapid change in community structure than would otherwise be seen.

The anomalous non-significant data points seen in the deep treatment plots for 1 and 2 day samples deserve some consideration. A random number chart was employed when plots were assigned a particular sand treatment. In hindsight, we noticed that several of the deep treatment plots were located in more energetic areas with more water flow than the shallow plots. In the short term (ie. 1 and 2 day samples), this may have changed the impact of the sand addition.

For the most part, diversity measures of this community showed little change through time within sand treatments. Evenness (J’ and 1-?), however, was shown to increase significantly through time in the deep sand treatment plots. Since dominant mobile taxa decreased while other more scarce sand-tolerant taxa increased in sand plots as compared to control and pre-impact samples, an increase in evenness in these communities makes sense.

The results of this experiment are significant not only because such dramatic changes were seen in the meio- and macrofaunal communities but also because these shifts will likely be felt up through the marine food chain. As stated previously, meiofauna have been shown to be important prey for many species of fish and invertebrates. Small macrofauna like those found in turf are also frequently reported as prey items for larger predators (Dugan et al. 2002, Gibbons and Griffiths 1986). Additionally, meiofauna may play an important role in making detritus available to macroconsumers either through their enhancement of microbial activity or by ingestion of the meiofauna themselves (Coull 1988).

Many questions still remain unanswered about turf communities in relation to periodic sand inundation. This experiment showed a rapid response of turf fauna followed by a relatively rapid recovery as well. However, our experimental plots were small in scale as compared to the broad areas of habitat that can be covered with sand during a natural inundation event. Recovery of such a large area might take significantly longer since animals may crawl in from the edges of a small experimental plot more easily than they could if a whole stretch of habitat was inundated. Additionally, this study did not examine how the community is affected by anoxia caused by sand burial or by very long-term inundation events. These are likely to be fruitful areas for future research.

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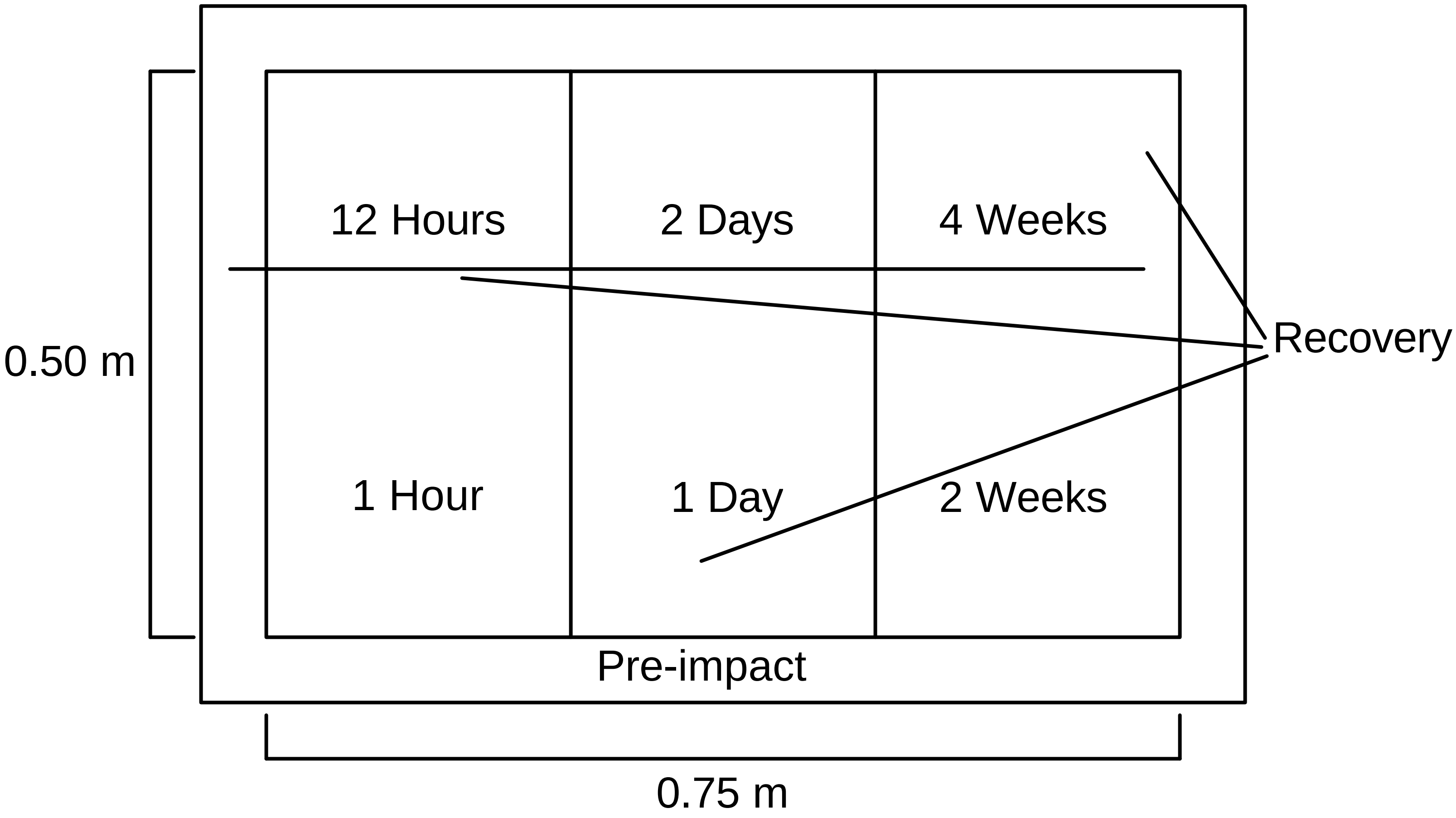


Figure 4-1. Example of 0.5m x 0.75m plot divided into six quadrats. Each quadrat was randomly assigned a sampling time. Pre-impact samples were taken from directly outside of the plot and recovery samples were taken randomly from any quadrat inside the plot.

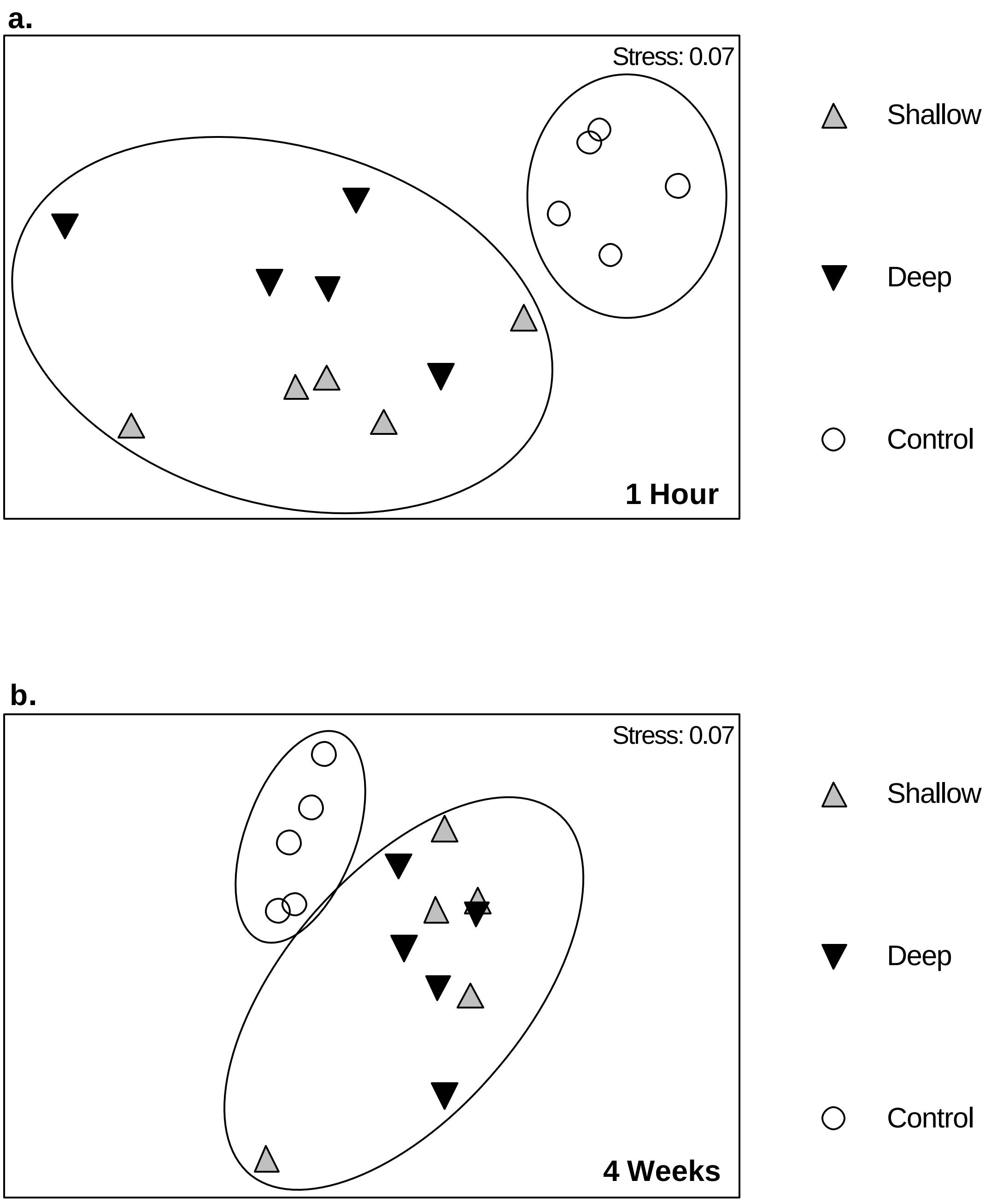
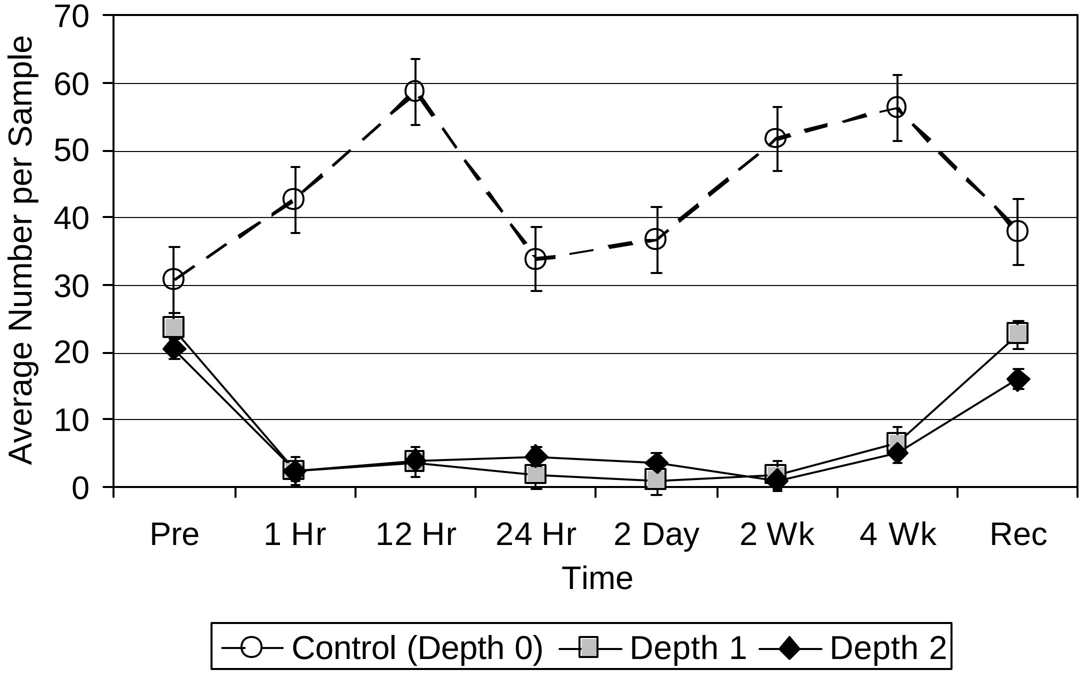


Figure 4-2. Representative nMDS plots of **a.** change in turf community structure 1 hour after sand addition and **b.** change in turf community structure 4 weeks after sand addition. Circles have been added to illustrate the clustering of points representing the different sand treatments.

Figure 4-3. Average abundance of **a.** copepods and **b.** *Amphithalamus inclusus* through time for each sand treatment.

a. Average Copepod Abundance



b. Average *Aphithalamus inclusus* Abundance

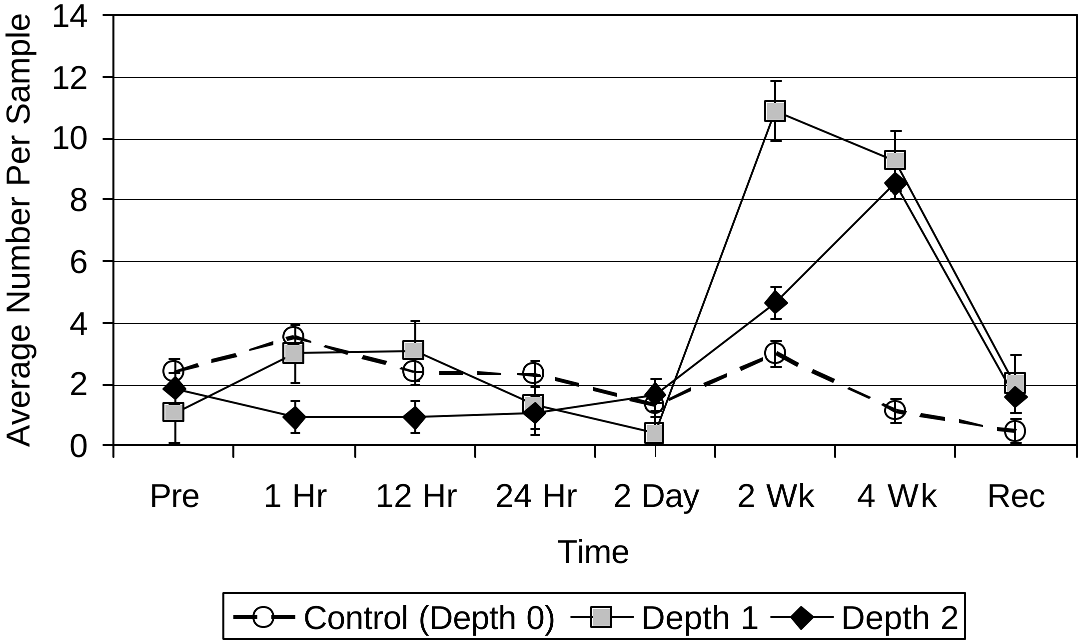


Table 4-1. List of taxa found in coralline turf samples

Phylum	Class or Subclass	# of Taxa	Highest Resolution
Annelida	Polychaeta	10	Family – 8; Genus – 2
	Oligochaeta	1	Family - 1
Arthropoda	Ostracoda	8	Genus – 6; Species – 2
	Copepoda	1	Order – 1
	Cirripedia	3	Genus – 2; Species – 1
	Malacostraca	10	Order – 3; Suborder – 3; Genus – 2; Species – 2
	Cheliceriformes	1	Suborder – 1
	Pycnogonida	1	Class – 1
	Insecta	1	Family – 1
Cnidaria	Anthozoa	1	Genus – 1
Echinodermata	Ophiuroidea	1	Class – 1
	Echinoidea	1	Genus – 1
Mollusca	Polyplacophora	4	Species – 4
	Gastropoda	65	Order – 1; Genus – 9; Species – 55
	Bivalvia	18	Family – 2; Genus – 5; Species – 11
Nematoda	-	1	Phylum – 1
Platyhelminthes	-	1	Phylum – 1
Granuloreticulosa	Foraminifera	4	Family – 4
Sipuncula	-	1	Phylum – 1

Table 4-2. Visual estimates of numbers of invertebrates that migrated out of treatment plots within 5 minutes of first sand addition. S = Shallow sand treatment (3 cm), D = Deep sand treatment (6 cm)

Plot	Depth	*Alia sp.*	Amphipods	*C. californicus*	Fish	Hermit Crabs	Isopods	*P. crassipes*	Pycnogonids	Other	Total
5	S	10	30	1	0	1	0	0	0	0	42
1	S	25	50	0	0	4	0	0	1	1	81
4	S	1	100	1	1	2	0	0	0	0	105
2	S	10	90	1	1	1	5	1	1	1	111
9	S	80	35	0	0	3	1	0	6	0	125
7	D	30	20	0	0	3	1	0	3	0	57
8	D	35	20	1	0	2	2	0	4	4	68
6	D	40	15	0	0	6	3	2	6	1	73
3	D	3	65	0	0	3	0	0	5	3	79
10	D	135	15	0	1	6	3	0	3	0	163

Appendix 4-1. Results of ANOSIM analyses to test for the effect of sand addition. df = 14 for all tests. S = Shallow sand treatment (3 cm), D = Deep sand treatment (6 cm), C = Control. *Indicates significant value (p<0.05)

Time / Treatments	R statistic	p-value
Pre-impact		
S,D	0.056	0.302
S,C	0.292	0.032
D,C	-0.068	0.730
1 Hour		
S,D	-0.04	0.651
S,C	0.768*	0.008*
D,C	0.792*	0.008*
12 Hours		
S,D	-0.036	0.516
S,C	0.896*	0.008*
D,C	0.828*	0.008*
1 Day		
S,D	0.076	0.190
S,C	0.596*	0.008*
D,C	0.096	0.206
2 Days		
S,D	-0.04	0.603
S,C	0.772*	0.008*
D,C	0.292	0.056
2 Weeks		
S,D	0.018	0.365
S,C	0.925*	0.008*
D,C	0.096*	0.008*
4 Weeks		
S,D	-0.068	0.706
S,C	0.588*	0.008*
D,C	0.760*	0.008*
Recovery		
S,D	-0.012	0.484
S,C	-0.088	0.675
D,C	-0.080	0.643

Appendix 4-2. Results of ANOSIM analyses to test for community differences through time within each sand treatment. df = 44 for all tests. Time 0 = control, 1 = 1 hour, 2 = 12 hours, 3 = 1 day, 4 = 2 days, 5 = 2 weeks, 6 = 4 weeks, 7 = recovery. *Indicates significant value ($p < 0.05$)

	Control		Shallow		Deep	
Time	R-value	p-value	R-value	p-value	R-value	p-value
0,1	-0.188	1.000	0.580*	0.016*	0.576*	0.008*
0,2	0.008	0.397	0.596*	0.008*	0.532*	0.008*
0,3	0.056	0.254	0.552*	0.008*	0.140	0.095
0,4	0.016	0.357	0.672*	0.008*	0.272	0.040*
0,5	0.088	0.254	0.776*	0.008*	0.892*	0.008*
0,6	0.244	0.071	0.600*	0.008*	0.688*	0.008*
0,7	0.624*	0.008*	0.500*	0.008*	0.844*	0.008*
1,2	-0.188	0.952	0.100	0.198	-0.096	0.817
1,3	-0.032	0.571	0.168	0.320	-0.024	0.571
1,4	-0.032	0.627	0.156	0.127	-0.020	0.476
1,5	-0.038	0.556	0.280	0.056	0.360*	0.024*
1,6	0.144	0.167	0.288	0.040*	0.424*	0.016*
1,7	0.596*	0.008	0.392*	0.016*	0.462*	0.008*
2,3	0.092	0.230	0.172	0.119	-0.032	0.627
2,4	0.072	0.230	0.316*	0.024*	0.068	0.198
2,5	0.100	0.222	0.236	0.071	0.512*	0.016*
2,6	0.032	0.040*	0.244	0.071	0.320*	0.040*
2,7	0.612	0.008*	0.476*	0.016*	0.484*	0.016*
3,4	-0.100	0.810	0.136	0.135	-0.124	0.913
3,5	-0.081	0.683	0.220	0.087	0.192	0.063
3,6	-0.024	0.484	0.344*	0.024*	0.188	0.056
3,7	0.516*	0.008*	0.404*	0.008*	0.292	0.008*
4,5	-0.006	0.468	0.280	0.024	-0.008	0.460
4,6	0.140	0.135	0.392*	0.032*	0.188	0.111
4,7	0.368*	0.024*	0.620*	0.008*	0.208	0.063
5,6	-0.075	0.532	-0.032	0.532	0.168	0.111
5,7	0.363*	0.056	0.656*	0.008*	0.708*	0.008*
6,7	0.304*	0.024*	0.440*	0.016*	0.736*	0.008*

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The text of Chapter 4, in full, has been submitted and is in review for the journal Marine Ecology Progress Series. The dissertation author was the primary investigator and author of this paper.

CHAPTER 5

Quantification of Human Visitation to Recreational Areas Through the Use of Time-Lapse Video

ABSTRACT

Quantification and proper management of human visitation is crucial to the protection of natural areas used for recreation. To establish the degree and variation of human recreational use, traditional methods have required complicated experimental designs and numerous man-hours in the field. This study utilizes a simple, inexpensive time-lapse video recorder to quantify human visitation to three rocky intertidal sites in relation to both space and time. Frame-by-frame analyses of the video tapes produced detailed visitation data. These data were then evaluated in relation to various physical and temporal factors. More people visited the sites in the afternoon than in the morning and on weekends versus weekdays. Significant variation in visitation also occurred among the sites. Tidal height, however, was not shown to significantly influence visitation. Interactions among several of these factors, particularly “site” and each of “a.m. vs. p.m.”, “weekday vs. weekend”, and “tidal level”, were also shown to be significant in relation to visitation. Knowledge of the intensity and variation of human visitation as it relates to environmental variables is crucial for realistic design of manipulative experiments to determine the effects of the observed human disturbance on

ecological systems. This knowledge can then be employed in the choice and implementation of management strategies such as decisions regarding human access to reserve areas.

INTRODUCTION

Human visitation to and exploitation of natural regions are two of the most important issues that planners and managers of protected areas must address. Visitation to coastal reserves and national and regional parks is often encouraged in order to provide education and a sense of connection to the natural world. However, if this visitation is not carefully managed, it can have a negative impact on the very systems that we are trying to protect. Proper management requires knowledge about how humans affect the system as well as knowledge about the system itself (Underwood and Kennelly 1990). However, quantification of human usage can be a difficult and time-consuming endeavor. Here, I describe the use of a simple, inexpensive time-lapse video system at three coastal sites to gain detailed, long-term data on numbers of visitors, spatial patterns of visitation, and correlation of visitation with physical and temporal variables.

Humans utilize southern California rocky shorelines for many different activities such as fishing, collecting, tidepooling, and educational field trips. These activities can be detrimental to the rocky intertidal ecosystem because of the intense removal of certain organisms (eg. Castilla 1985, Murray et al.

1999), trampling effects (Brosnan and Crumrine 1994, Keough and Quinn 1998, Milazzo et al. 2002), disturbance of shorebirds (Lafferty 2001), and repeated overturning of boulders (Addessi 1994). Management options for protected rocky shore sites include the use of restricted hours of public access, creation of areas that are completely closed to the public, construction of boardwalks, open access but "no-take" regulations, and placement of docents to provide education and enforce rules. It may be difficult, however, to decide which of these management strategies might be most appropriate for a given area without knowing the intensity and patterns of public use.

Past studies of human visitation to rocky shores have relied on visual surveys (Underwood and Kennelly 1990, Kingsford et al. 1991, Addessi 1994, Murray et al. 1999, Alessa et al. 2003). These surveys must be extensive in order to obtain enough information to establish the degree and variation of human recreational use (Altmann 1974). Thus, according to Underwood and Kennelly (1990), "it is inevitable that many variables will cause confounded differences in the data from one place to another; different sites will necessarily be sampled at different times, under different patterns of weather, at different stages of the tide, and so on." They also point out that any sampling procedure that involves only random dates and times will be biased by yearly events such as school holidays unless very long-term sampling is conducted. A method that includes continuous, long-term, time-lapse recording can eliminate many of these sampling issues.

Video monitoring and time-lapse photography have been used in ecology to record the behaviors and activities of animals for more than 30 years. Temple (1972) described one of the first portable time-lapse camera systems that could be installed in the field. Scientists, especially ornithologists, have since continued to use and improve upon these early methods (eg. Jenkins 1978, Beck and Smith 1987). With advances in technology and decreases in price, the use of video systems has become relatively common in recent ecological literature. Study systems have included deep sea sediment communities (Smith et al. 1997), nesting Gyrfalcons (Booms and Fuller 2003), breeding sockeye salmon (Shardlow 2004), nesting American oystercatchers (Sabine et al. 2005), grazing green sea urchins (Lauzon-Guay et al. 2006), and hunting insectivorous bats (Lang et al. 2006). The use of video allows researchers to gain high-frequency, long-term data with little or no disturbance of their subjects.

In this study, I used time-lapse video systems to observe three San Diego, CA rocky intertidal sites. My primary goals were: (1) to quantify human visitation to rocky shorelines in relation to both space and time; (2) to correlate levels of visitation with physical and temporal factors that might be used to guide management decisions; and (3) to design and implement a video system and method for image analysis that can be employed by other scientists and reserve managers to quantify human impact on both marine and terrestrial systems.

METHODS

Study sites

Cameras were placed at three rocky intertidal sites along the coast of southern San Diego County (Figure 5-1). The sites were chosen because of differing levels of accessibility to humans, popularity for recreational activities, management, and enforcement of rules.

The Scripps Coastal Reserve at Dike Rock, La Jolla, California, USA (32°87' N, 117°25' W) is a small rocky intertidal area bordered on either side by sandy beach. Rugged coastal bluffs rise to approximately 100 meters above the reserve. The nearest beach access points are approximately 0.4 km (0.25 miles) to the north and 1 km (0.6 miles) to the south of Dike Rock. The reserve is a popular site for tourists, school groups, and fishermen. Although fishing is permitted, collection of invertebrates and algae is prohibited within reserve boundaries.

The La Jolla Ecological Reserve at Marine Room is located approximately 3.3 km (2 miles) south of Dike Rock. Large coastal bluffs again border this site while sandy beach is found to the north and south. The nearest beach access point is approximately 0.4 km (0.25 miles) north of the rocky area. To the south, topographical barriers deter most human access. Collection of any sort is prohibited within this reserve.

Cabrillo National Monument is a small urban National Park located at the tip of Point Loma, CA, USA (32°28’ N, 117° 11’ W) that contains approximately 1.5 km of rocky shoreline. Human access to the park is restricted from the north by a Naval base and from the south by topography. A single public access path leads from the top of the cliffs to a highly visited rocky intertidal area at the northern end of the park. Access is only allowed from 9 am – 5:15 pm (6:15 pm during summer months). The southern end of Cabrillo’s intertidal area has been completely closed to public use since 1996 and is regularly monitored by volunteer docents and park rangers during low tide. Collection of invertebrates and algae is prohibited at Cabrillo while fishing is allowed.

Camera systems and installation

A Focus Company 1280-hour time lapse recorder (ER1280TN) was used for each of the video systems. This recorder can be set to several recording speeds (frames / s), and provides 8 - 1288 hours of recording time on a single T-160 VHS tape. For this study, the recorders were set to film 0.37 frames / s (1288 hours per tape).

Because of physical differences between the sites and the cost associated with greater zoom capabilities, cameras of different focal lengths were used with each system. At Dike Rock, the camera was mounted at the end of Scripps Pier (located approximately 1 km south) and aimed back toward land. Here, we installed a Crest Electronics CP-6524-H black and white camera with a 5.5 to 82.5 mm lens zoomed out to the maximum focal length. The camera was housed in a Crest Electronics CH-1400 environmental housing and mounted to the top of the small research lab that is located at the end of the pier. The recorder was placed inside the lab and the connecting wires were run through an insulated hole in the lab wall. The system was powered through an AC outlet located in the lab.

The Marine Room camera system was placed in the yard of a private residence that directly overlooks the southern end of the rocky intertidal area. A Supercircuits PC106C black and white camera with an 8mm fixed lens was used at this location. This camera comes pre-enclosed in an aluminum weather-proof housing. The recorder was placed in a water-proof box and hidden under the stairs of the house. Connecting wires were run through an insulated hole in the box, beneath ground cover, and to the camera which was mounted on a wooden stake near the cliff's edge. The system was powered through an extension cord which ran to an AC outlet on the outside of the residence.

The Cabrillo camera was mounted to a fence at the cliff's edge and aimed so that the field of view included the single access path to the beach and the rocky intertidal area to either side of that access point. In this system we used a Crest Electronics CJ-8224-DNH color camera with a 5-15mm lens zoomed out to the maximum focal length. This camera was also housed in a Crest Electronics CH-1400 environmental housing. The recorder was placed in a waterproof box, chained and locked to the fence, and covered with brush for camouflage. Connecting wires were run though a sealed hole in the box to the camera. The system was powered through a heavy-duty extension cord which ran to an AC outlet in a storage facility located about 50 yards from the camera.

A small, portable, black and white video monitor was used to properly orient each camera's view and set the recorder. Once the cameras were in place, the video monitor was removed from the system. Total cost for each of these video systems was $500-$900 depending on camera, cable, and weatherproofing requirements.

Image analysis

Video tapes were collected from the recorders approximately every 50 days, replaced with new tapes, and brought back for analysis. Frame-by-frame counts of human visitation during daylight hours were made for each site. People were counted as they entered the camera's field of view either from the sides (Dike Rock and Marine Room) or from the top (access path at Cabrillo) of the frame. Visitors were counted during 15-minute intervals (ie. the number of people entering the frame between 9:00 – 9:15, 9:15 – 9:30, 9:30-9:45, etc. were counted) and these numbers were summed to get the total number of visitors for each day.

Additionally, I divided the field of view at each site into two or more spatial "zones". These zones were defined by use patterns, tidal height, and accessibility (Table 5-1). At the end of each 15-minute interval (ie. at 9:00, 9:15, 9:30, etc), the number of people that were present in each zone were counted and recorded.

Data analysis

Patterns of visitation among the three sites were compared by plotting the total number of visitors per day against date for each location. Tidal data were also included on this plot in order to look for possible correlations. The lowest predicted tidal level during daylight hours was recorded for each day and plotted on a secondary y-axis of the visitation graph. Tidal information was obtained from http://tbone.biol.sc.edu/tide/tideshow.cgi. Additionally, a spectral analysis was performed to detect possible periodicities in the visitation data (Matlab 7.0 The MathWorks, Inc. 2004).

Monthly averages for numbers of visitors within each 15-minute time interval were calculated in order to determine peak visitation times. The mean number of visitors during each time interval was then plotted against time so that patterns within and among sites could be compared visually.

Daily averages of the number of people located in each “zone” within a site at the end of every 15-minute interval were also calculated. The mean number of visitors to each zone per day was then plotted so that relative visitation to the different zones could be compared.

Formal analyses of log-transformed visitation data were also done using four-factor analysis of variance. In order to look at the effect that time of day might have on the magnitude of visitation, daily visitor totals were divided into "a.m." (6am – noon) and "p.m." (noon – 6pm) before analysis. Factors included in the ANOVA were site, a.m. vs. p.m., weekend vs. weekday, and positive vs. negative lowest daily tidal height (relative to mean low water).

RESULTS

Total daily visitation was much lower at the Marine Room than at either of the other two sites (Figure 5-2a). With the exception of January 2003, visitation was never greater than 100 people per day and was nearly always less than 50 people per day. In contrast, more than 50 people per day were commonly seen at both Dike Rock and Cabrillo and totals of more than 200 people at these sites were not unusual. Visual assessment of the relationship between the number of visitors and the level of the lowest daytime tide revealed that visitation and tidal height generally display opposite but offset sinusoidal patterns (Figure 5-2b). Periodicities in visitation at approximately five, seven and twenty days were indicated by the spectral analyses (Figure 5-3).

Monthly visitation averages for each 15-minute time interval ranged between zero and eight people at Cabrillo, zero and five people at Dike Rock, and zero and two people at Marine Room. In general, greater numbers of visitors were seen in the afternoon than in the morning and a peak in visitation was observed during mid- to late-afternoon for all of the sites (Figure 5-4).

On average, at the end of each 15-minute interval, notably more people were seen in the low zone at Dike Rock than were seen in the high boulder zone (Figure 5-5a). At Marine Room and Cabrillo, however, the patterns were not as clear (Figures 5-5b, 5-5d). With careful examination, one can see that the highest numbers of people were generally seen in the northern zone at the Marine Room (Figure 5-5c). At Dike Rock, the patterns of visitor distribution change with time. In the late summer and fall of 2004, the greatest numbers of visitors were seen on the high platforms and in the small pocket beach. Few people were counted in the lower intertidal areas north and south of the access point during this time. In February and March of 2005, however, average counts of visitors were relatively similar among the four different areas at the Cabrillo site (Figure 5-5e).

Significantly greater numbers of visitors were seen on weekends versus weekdays and in the afternoon versus morning (ANOVA, $p<0.0001$). Significant differences in the numbers of visitors among the three sites were also seen with Cabrillo > Dike Rock > Marine Room ($p<0.0001$). Tidal height was not shown to have a significant effect on the numbers of visitors to these sites ($p = 0.56$). Analyses of interactions among the factors have been summarized in Table 5-2.

DISCUSSION

The magnitude of human visitation to rocky intertidal areas was clearly site-specific. For example, Dike Rock and the Marine Room are located only a few kilometers apart so one might assume that they would receive similar numbers of visitors. However, visitation at Dike Rock was nearly an order of magnitude higher than that at the Marine Room on most days. I am unsure as to why visitation to the Marine Room was so much lower, although it may simply relate to ease of access. As stated earlier, topography limits human access to the Marine Room from the south and parking near the northern access point is extremely limited. Worthy of discussion, however, is the anomalously high visitation at the Marine Room in January 2003. A popular local entertainment guide awarded “Best Tidepooling in San Diego” to the Marine Room, and specifically mentioned that the best tide would be on January 2 of that year. Not only do we see a spike in visitation on that day, but a general increase in visitation was seen for a few weeks after the publication of that article. This indicates that perhaps Dike Rock and Cabrillo are more highly visited because they are more well-known. Since both of these sites are managed by entities that encourage education of the public (National Park Service and University of California), it is likely that they are more visible to people through websites, brochures, and educational materials.

Spatial distributions of visitors were also highly site-specific. Data from Dike Rock showed many more people present in the low zone than in the high boulders. Continuous analysis of the videos showed that this pattern is a result of the sampling methods that were chosen. People in the high zone were nearly always just passing through the area and were therefore not as likely to be caught in the camera’s field of view as visitors to the low zone (who tended to remain at the site for longer stretches of time). These types of observations could be valuable in cases where managers are considering the construction of paths or boardwalks at their sites. If preliminary research is done with the video camera to determine where visitors most heavily impact the area, plans can be made which incorporate these patterns.

Spectral analyses of visitation data indicated periodicities at approximately five, seven and twenty days. Given the results of the analysis of variance, the five and seven day intervals probably correspond to the weekend / weekday cycle. It is more difficult to speculate about the twenty day interval.

Several interactions among the factors in the analysis of variance were shown to be significant in relation to visitation. Of particular interest is the fact that interactions between “site” and all three of the other factors (a.m. vs. p.m., weekday vs. weekend, and tidal level) are significant. This adds more support to the conclusion that many of these observations are site-specific and that individual studies will be necessary for specific management purposes.

An unexpected result of this study is the fact that tidal level is not a significant influence on the number of visitors to the rocky intertidal. I would have expected that tidal level and visitation would be negatively correlated, however visual inspection of graphs and the results from analysis of variance indicated that this is not so. Of course there are times when the intertidal is completely inaccessible to visitors on foot. But, in general, a lower tide does not attract significantly more visitors. After these results were determined, an informal survey of tidepool visitors indicated that the vast majority of people had not checked a tide chart or even considered what the tidal level might be before they decided to visit the site. This is also an important result as it pertains to management concerns. For example, if docents are being used to educate the public and enforce rules, they may be more valuable during afternoons and weekends irrespective of the tides during these times.

This study has shown that the use of time-lapse video recorders is an efficient way to collect vast amounts of data regarding patterns of human visitation to recreational areas. One researcher can collect nearly two months' worth of visitation data in one day of frame-by-frame analysis of the video tapes. Information on the number of visitors to a site, the spatial distribution of these visitors within a site, and the temporal patterns of visitation to a site can all be easily obtained from the videos. This information will be valuable for planning realistic manipulative experiments to determine the effects of human disturbances on natural systems (Underwood and Kennelly 1990, Huff 2006 in prep.). All of the observational and manipulative data can then be examined in relation to physical and temporal factors in order to guide management decisions.

ACKNOWLEDGEMENTS

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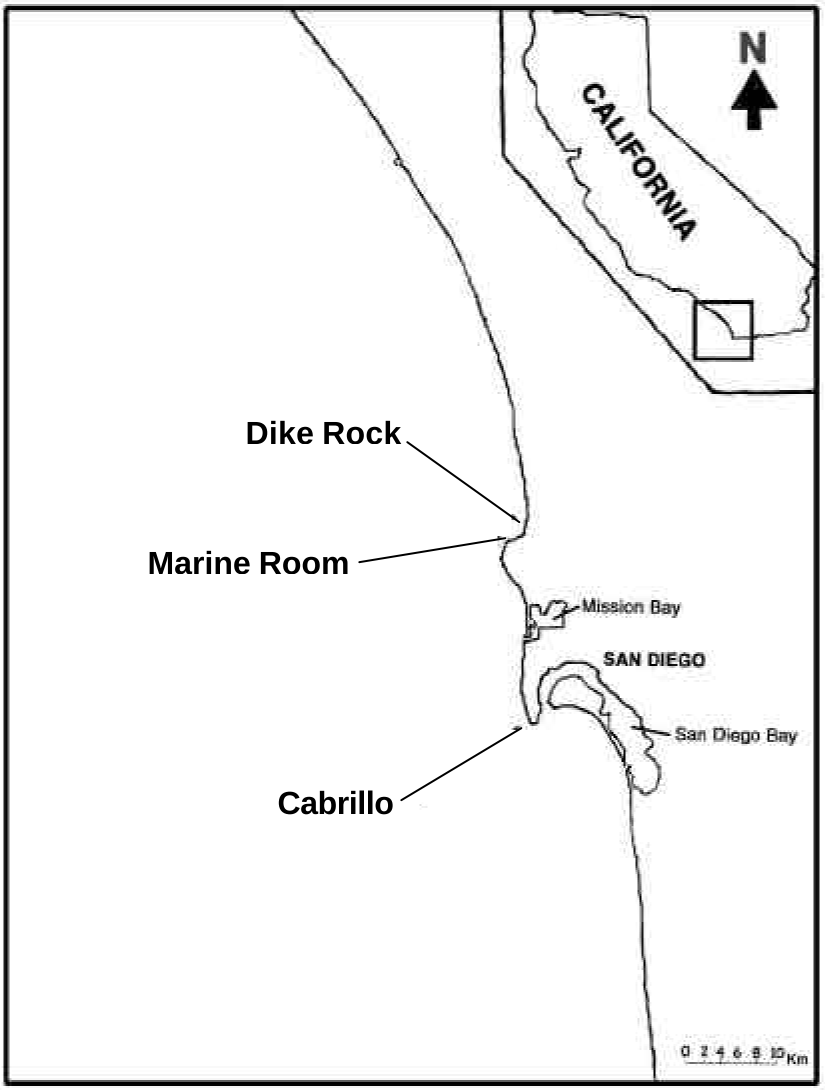
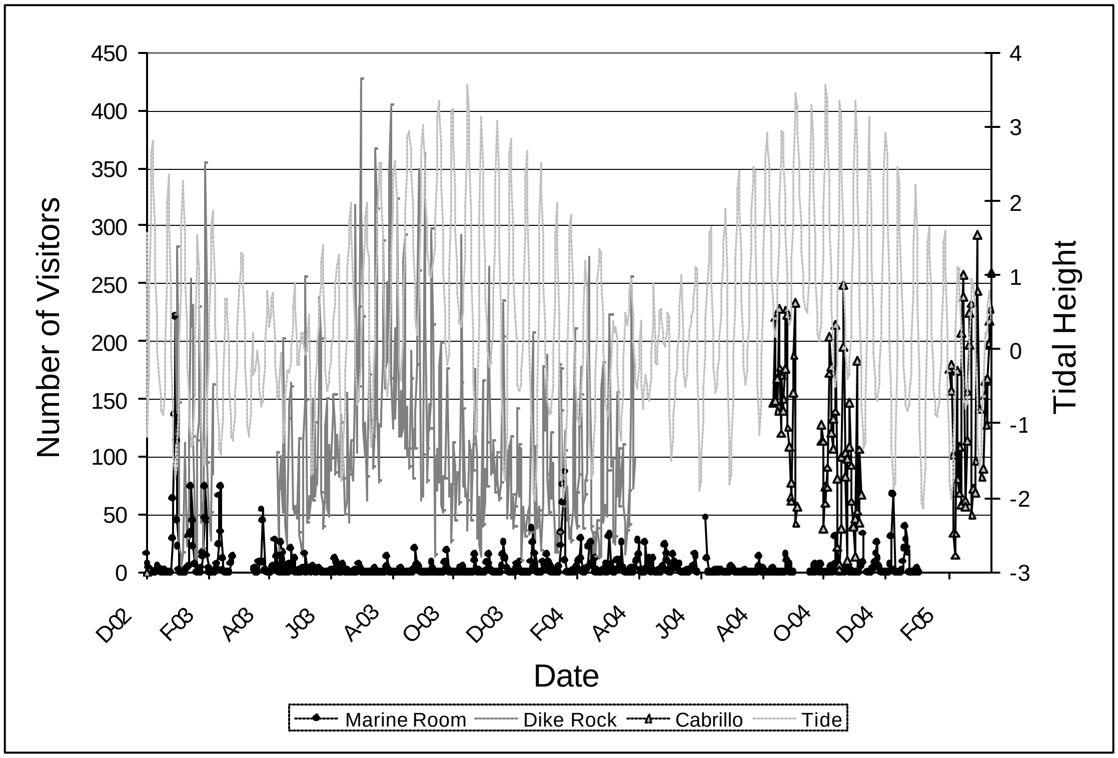


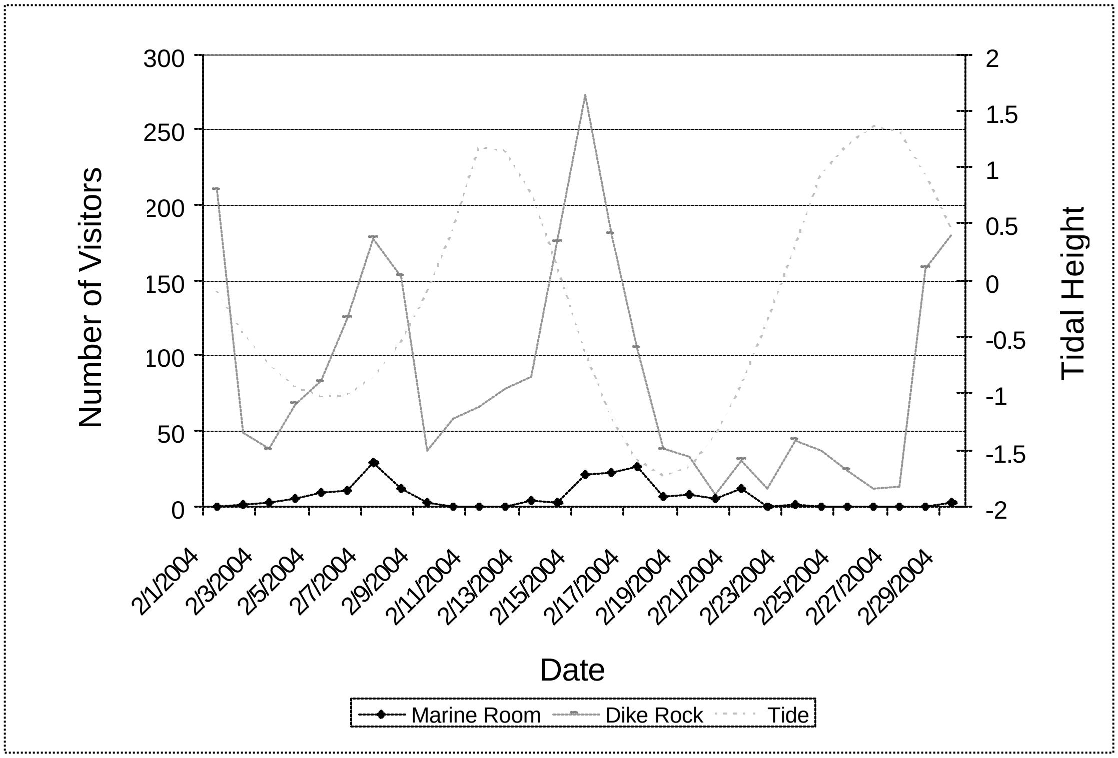
Figure 5-1. Map of the San Diego region showing the location of the three study sites.

Figure 5-2. Total visitation for each study site for **a.** the duration of the study and **b.** a representative month during the study (February 2004).

a.


Number of Visitors
450
400
350
300
250
200
150
100
50
0
Tidal Height
4
3
2
1
0
-1
-2
-3
D-02
F-03
A-03
J-03
A-03
O-03
D-03
F-04
A-04
J-04
A-04
O-04
D-04
F-05
Date
Marine Room
Dike Rock
Cabrillo
Tide

b.


Number of Visitors
300
250
200
150
100
50
0
Tidal Height
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
2/1/2004
2/3/2004
2/5/2004
2/7/2004
2/9/2004
2/11/2004
2/13/2004
2/15/2004
2/17/2004
2/19/2004
2/21/2004
2/23/2004
2/25/2004
2/27/2004
2/29/2004
Date
Marine Room
Dike Rock
Tide

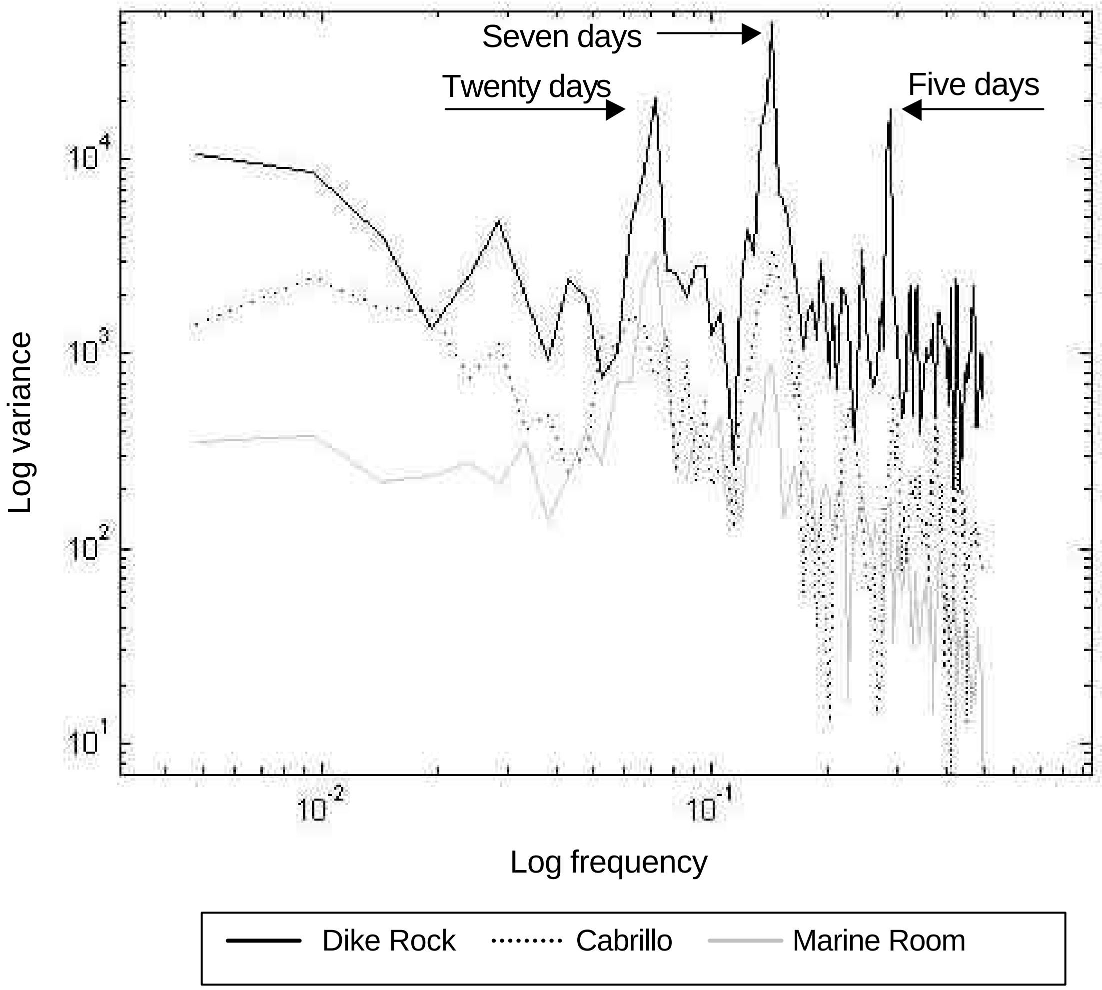
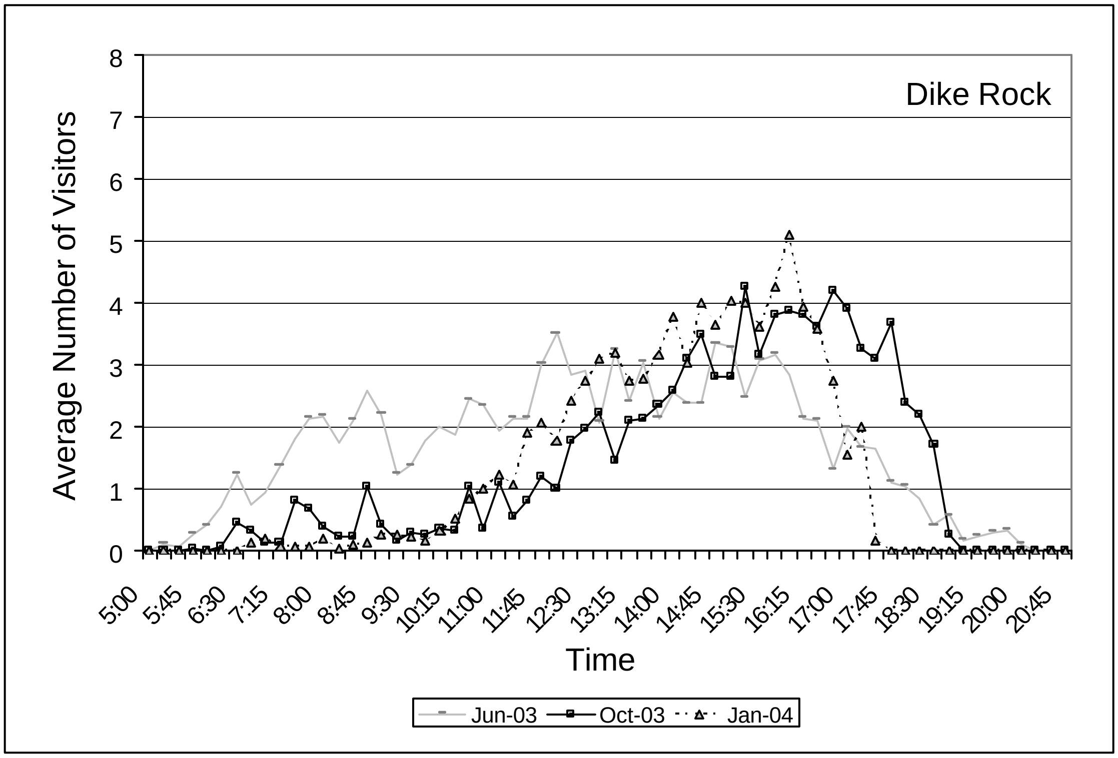


Figure 5-3. Spectral analysis of visitation data from each of the three study sites.

Figure 5-4. Representative monthly visitation averages for 15-minute time intervals during daylight hours for **a.** Dike Rock **b.** Marine Room and **c.** Cabrillo. Note the difference in scale of the y-axis for Marine Room.

a.


Dike Rock
Average Number of Visitors
0
1
2
3
4
5
6
7
8
5:00
5:45
6:30
7:15
8:00
8:45
9:30
10:15
11:00
11:45
12:30
13:15
14:00
14:45
15:30
16:15
17:00
17:45
18:30
19:15
20:00
20:45
Time
Jun-03
Oct-03
Jan-04

b.

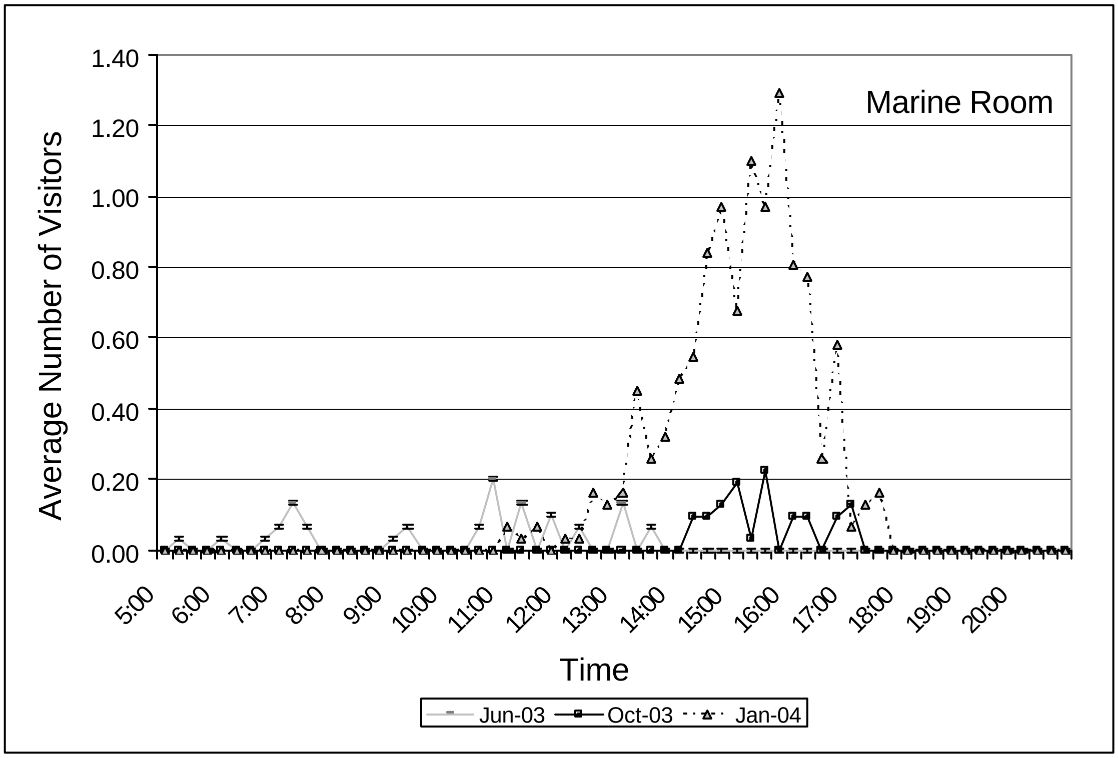
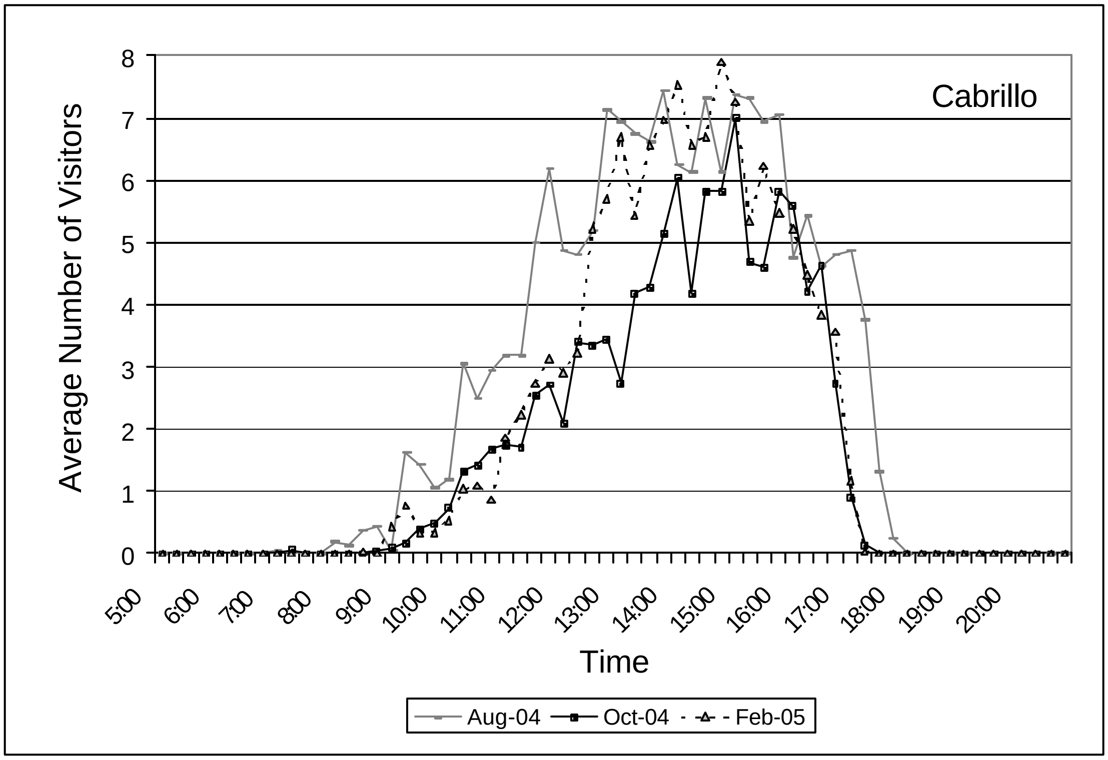

Marine Room
Average Number of Visitors
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
5:00
6:00
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
20:00
Time
Jun-03
Oct-03
Jan-04

Figure 5-4. Continued.

c.


Cabrillo
Average Number of Visitors
0
1
2
3
4
5
6
7
8
Time
5:00
6:00
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
20:00
Aug-04
Oct-04
Feb-05

a.

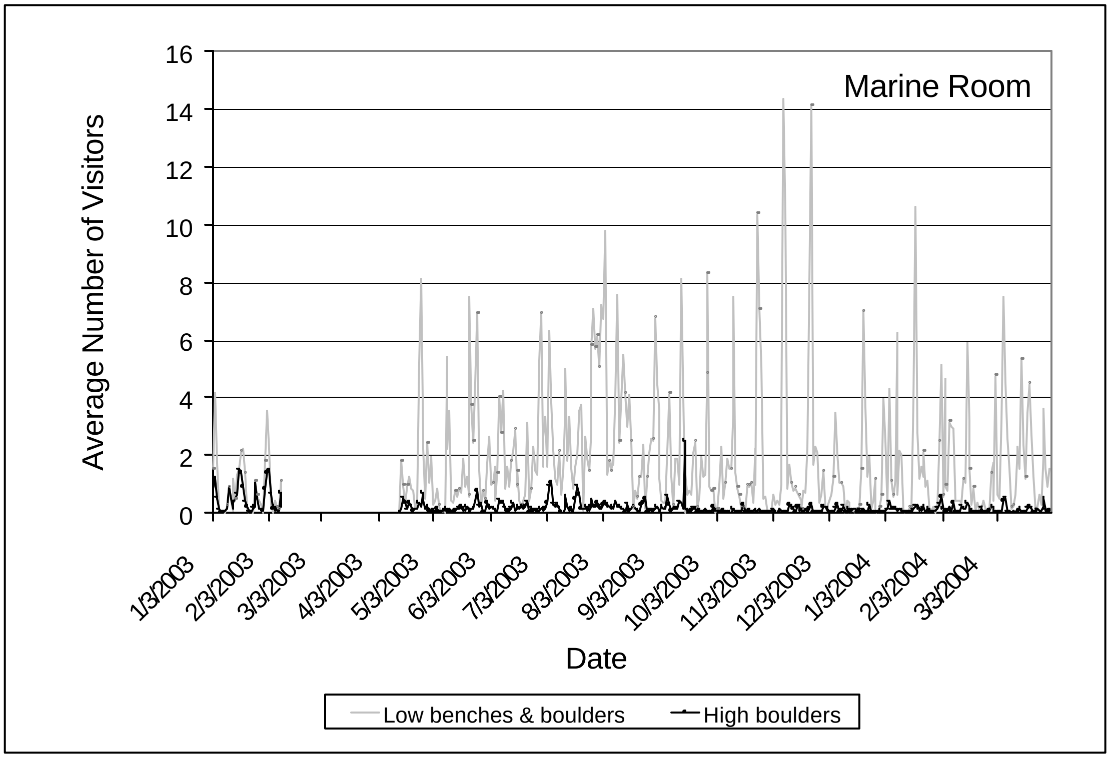
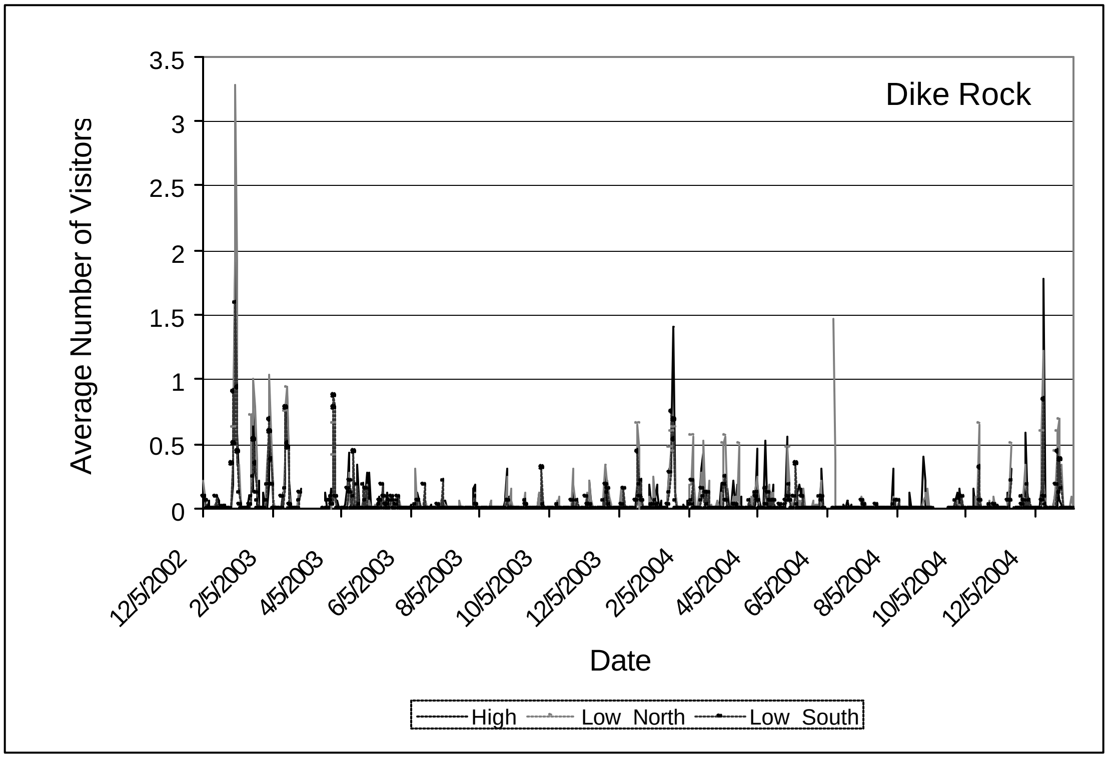


Figure 5-5. Daily averages of the number of visitors found in each zone of **a.** Marine Room **b.** Dike Rock and **d.** Cabrillo. Enlargements of representative months are seen for **c.** Nov. 2003 at Dike Rock and **e.** Feb. 2005 at Cabrillo.

Figure 5-5. continued.

b.


Dike Rock
Average Number of Visitors
3.5
3
2.5
2
1.5
1
0.5
0
12/5/2002
2/5/2003
4/5/2003
6/5/2003
8/5/2003
10/5/2003
12/5/2003
2/5/2004
4/5/2004
6/5/2004
8/5/2004
10/5/2004
12/5/2004
Date
High
Low North
Low South

c.

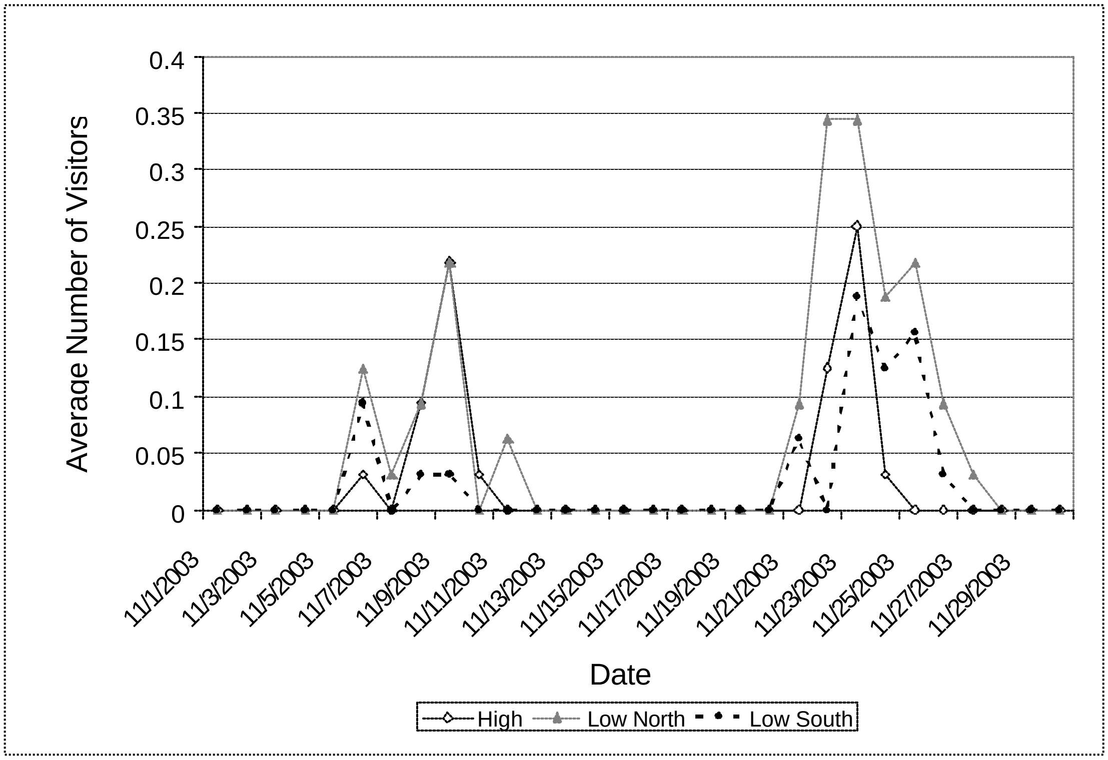
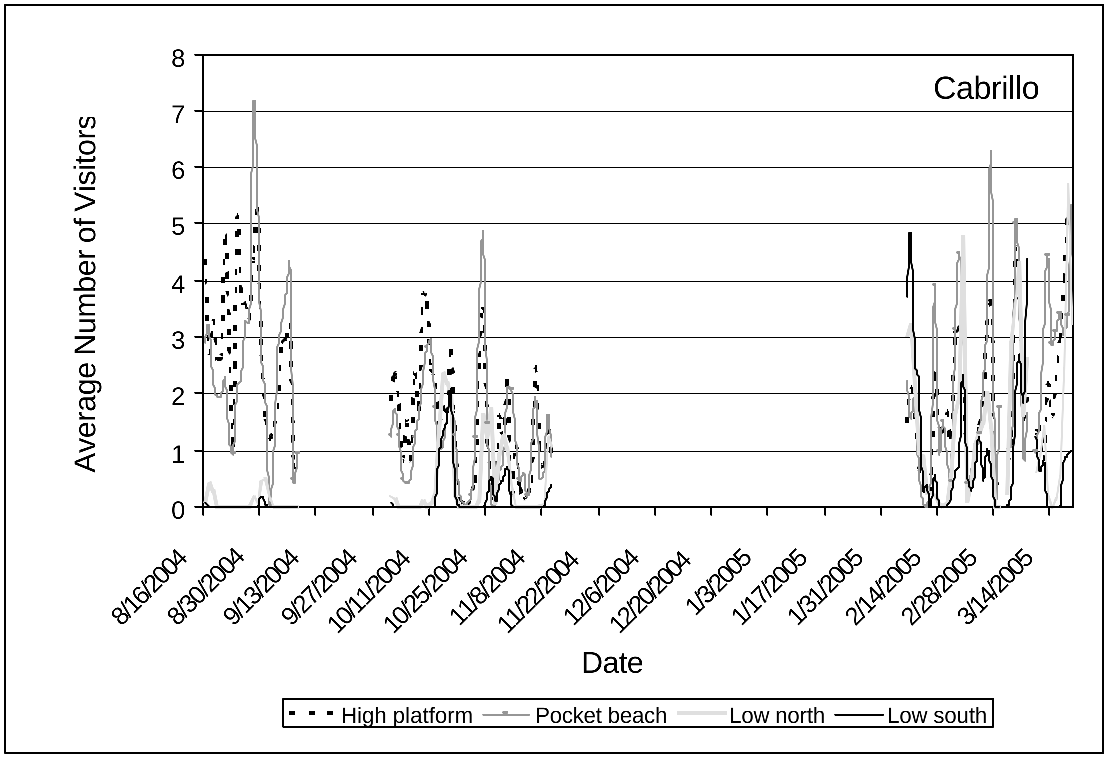

Average Number of Visitors
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
11/1/2003
11/3/2003
11/5/2003
11/7/2003
11/9/2003
11/11/2003
11/13/2003
11/15/2003
11/17/2003
11/19/2003
11/21/2003
11/23/2003
11/25/2003
11/27/2003
11/29/2003
Date
High
Low North
Low South

Figure 5-5. continued.

d.


Cabrillo
Average Number of Visitors
0
1
2
3
4
5
6
7
8
8/16/2004
8/30/2004
9/13/2004
9/27/2004
10/11/2004
10/25/2004
11/8/2004
11/22/2004
12/6/2004
12/20/2004
1/3/2005
1/17/2005
1/31/2005
2/14/2005
2/28/2005
3/14/2005
Date
High platform
Pocket beach
Low north
Low south

e.

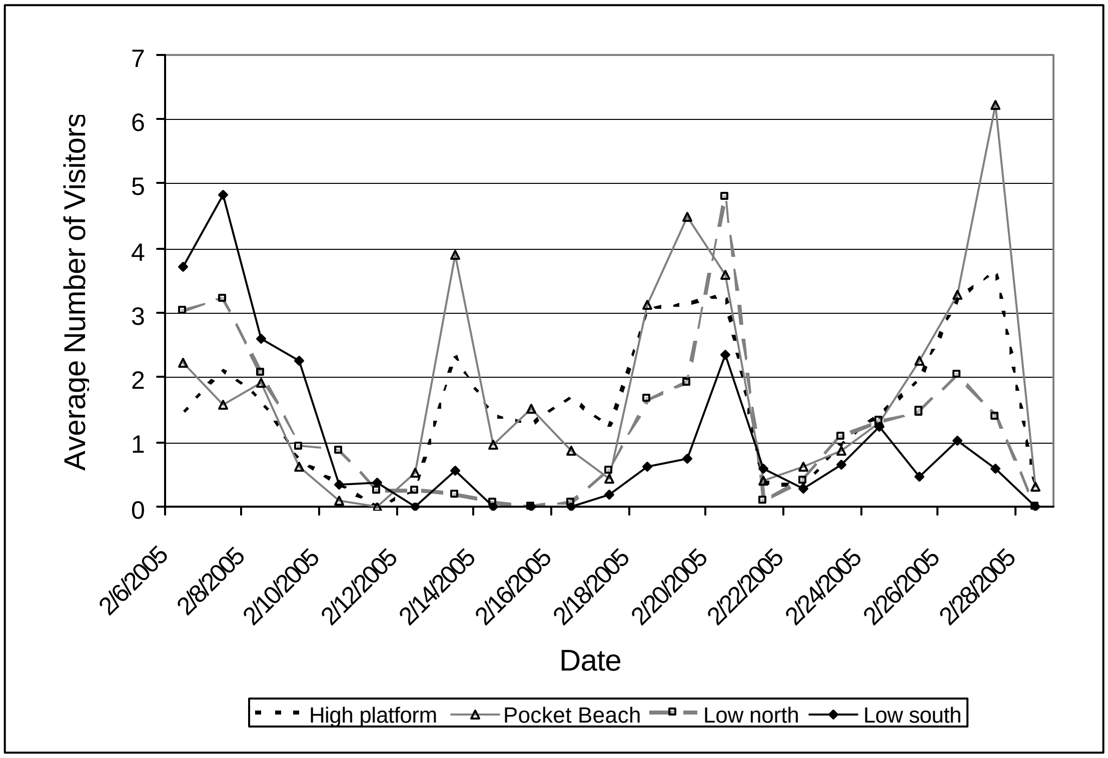

Average Number of Visitors
0
1
2
3
4
5
6
7
2/6/2005
2/8/2005
2/10/2005
2/12/2005
2/14/2005
2/16/2005
2/18/2005
2/20/2005
2/22/2005
2/24/2005
2/26/2005
2/28/2005
Date
High platform
Pocket Beach
Low north
Low south

Table 5-1. Description of spatial zones designated within each study site

Site	Zone	Tidal Height	Accessibility	General Use
Dike Rock	High boulders	High	Ok at relatively high tides	Path to cross site
	Low benches & boulders	Mid / low	Only during minus tides	Tidepooling, fishing
Marine Room	High	High / mid	During medium low tides	Path to cross site
	Low north	Mid / low	Only during minus tides, closer to access point	Tidepooling
	Low south	Mid / low	Only during minus tides, further from access point	Tidepooling
Cabrillo	High platform	High	Ok at relatively high tides	Site-seeing
	Pocket beach	High / mid	During medium low tides	Recreational activities
	Low north	Mid / low	Only during minus tides	Tidepooling
	Low south	Mid / low	Only during minus tides	Tidepooling

Table 5-2. Results from 4-way ANOVA. Visitation data were natural-log transformed.

Source of variation	df	Mean square	F-value	p-value
Weekday / Weekend (W)	1	79.753	84.634	<0.0001
Time of Day (T)	1	430.041	456.384	<0.0001
Site (S)	2	1858.972	1972.760	<0.0001
Tide Level (L)	1	0.320	0.340	0.5599
W *X* T	1	0.009	0.009	0.9235
W *X* S	2	22.515	23.894	<0.0001
W *X* L	1	0.066	0.070	0.7909
T *X* S	2	48.912	51.906	<0.0001
T *X* L	1	62.682	66.519	<0.0001
S *X* L	2	44.771	47.511	<0.0001
W *X* T *X* S	2	0.982	1.042	0.3530
W *X* T *X* L	1	0.006	0.007	0.9340
W *X* S *X* L	2	6.688	7.098	0.0008
T *X* S *X* L	2	0.250	0.265	0.7669
W *X* T *X* S *X* L	2	2.116	2.246	0.1061
Residual	2406	0.942	-----	-----

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CHAPTER 6

Effects of human trampling on intertidal algal turf communities and implications for management of protected areas on rocky shores

ABSTRACT

Rapidly growing populations of residents and visitors are having significant effects on coastal ecosystems. Human trampling causes decreased density and diversity of organisms on rocky shores, especially large, foliose algae. Coralline algal turfs and the invertebrate communities that inhabit them have not been extensively studied in terms of human trampling. Here, a relatively long-term manipulative trampling study based on realistic levels of human visitation was conducted in areas dominated by coralline algal turf. The invertebrate community composition of trampled plots was significantly different than that of protected control plots. Trampled plots had significantly lower numbers of individuals and taxa than protected control plots as well. Additionally, the trajectory of invertebrate community change through time in trampled plots was significantly different than that of both protected and open-access control plots. Bare space increased in trampled plots as compared to pre-impact levels, while percentage of bare rock in control plots did not show significant increases. Nine months after trampling had ceased, the invertebrate communities from trampled plots had similar community structure to that of protected controls and bare space had decreased to pre-impact

levels. However, trampled plots had significantly more taxa and higher Shannon diversity values than controls. These results indicate that in order to manage visitor pressure to rocky shores, “no-access” zones may be as important as “no-take” zones. However, the rapid recovery seen here also indicates that perhaps rotating or seasonal closures might be an effective management strategy for protecting turf communities.

INTRODUCTION

More than half of the population of the contiguous United States lives in a narrow margin along its coasts that comprises only 17% of the total land area. In 2003, approximately 153 million people lived in U. S. coastal counties, and this number is expected to grow to 160 million by 2008 (Crossett et al. 2004). Additionally, tourism to coastal areas continues to become increasingly popular. In 1996, 90% of all tourist spending in the U. S. occurred in coastal states (Houston 1996).

The activities of this rapidly growing population of residents and visitors produce numerous disturbances to coastal ecosystems including the intense removal of organisms by fishing and collecting (Castilla 1999, Murray et al. 1999), pollution (Thompson et al. 2002), repeated overturning of rocks and boulders (Addessi 1994), coastline modification by artificial structures (Thompson et al. 2002), and disturbance of shorebirds (Lafferty 2001). Anthropogenic disturbances are often superimposed onto natural stresses such as emersion, wave shock, and sand inundation, making them difficult to isolate and quantify (Osenberg and Schmitt 1994, Crowe et al. 2000). Carefully controlled, realistic, manipulative experiments are therefore essential to the understanding of human impacts.

This heavy use of coastal areas leads to extensive foot traffic in intertidal and shallow subtidal areas. Trampling can affect marine organisms directly, by removing all or part of an individual through crushing or dislodgement, or by weakening attachment strength. It can also affect marine organisms indirectly by removing other species that interact with them through competition, predation or habitat provision (Brosnan and Crumrine 1994) or through changing patterns of sediment movement as algal cover is altered (Povey and Keough 1991). While studies of human trampling in terrestrial ecosystems date back to Jeffreys (1917) and Bates (1930, 1935, 1938), trampling studies in the marine environment are a more recent phenomenon. Modern studies have found effects of foot traffic on coral reefs (Liddle 1991, Rodgers and Cox 2003), in seagrass beds (Eckrich and Holmquist 2000), in salt marshes (Woolfolk 1999), and on tidal flats (Chandrasekara and Frid 1996, Wynberg et al. 1997).

In the rocky intertidal, researchers have used both mensurative and manipulative studies to investigate the effects of human trampling. Beauchamp and Gowing (1982) were among the first to look at the variations among rocky intertidal sites that differ in degree of human trampling. They found a general pattern of higher density and diversity of organisms at less trampled sites with especially dramatic effects on the fleshy brown alga *Pelvetiopsis limitata* which was entirely absent at their most trampled site. Larger, branching species of algae were also significantly reduced on a heavily visited intertidal ledge in the UK as compared to a ledge that was more isolated from human visitation (Pinn and Rodgers 2005).

Manipulative studies have shown a similar dramatic reduction of large, foliose algae in experimentally trampled plots (Povey and Keough 1991, Brosnan and Crumrine 1994, Fletcher and Frid 1996, Keough and Quinn 1998, Schiel and Taylor 1999, Jenkins et al. 2002, Milazzo et al. 2002, but see Bally and Griffiths 1989 for an exception). Algal turfs have displayed less consistent responses. In various studies, percent cover of turf-forming species in trampled treatments has been shown to increase (Povey and Keough 1991, Brosnan 1993, Brosnan and Crumrine 1994), decrease (Fletcher and Frid 1996, Keough and Quinn 1998, Schiel and Taylor 1999, Brown and Taylor 1999) and remain the same (Bally and Griffiths 1989, Jenkins et al. 2002).

Prior investigations have focused on the effects of human trampling on the algae themselves, with few publications that consider how trampling affects the associated invertebrate community. In New Zealand, densities of macrofauna associated with algal turfs decreased significantly in trampled plots as compared to controls (Brown and Taylor 1999). Additionally, macro- and meiofauna associated with a mixed assemblage of erect algae showed significantly lower abundances in trampled plots than in control areas (Casu et al. 2006). In both of these studies, trampling was treated as a “pulse” (acute) disturbance (Bender 1984). Brown and Taylor trampled their experimental plots once per day for five days, while Casu et al. applied two trampling intensities only once each. In areas like Southern California where visitation to rocky intertidal areas is extensive year-round, it may be more realistic to treat trampling as a continuous “press” (chronic) disturbance. Additionally, invertebrate communities associated with algal turfs are highly variable in both space and time (Huff 2006a). So, in order to determine if realistic, sustained levels of human trampling causes meaningful differences among the invertebrate assemblages of impacted and control locations, extensive replication and multiple control sites are necessary (Underwood 1993).

In southern California, large areas of rocky shores are covered by a thick, carpet-like mat of coralline algal turf. This is in contrast to the classic image of the rocky intertidal where large, fleshy algae predominate and turf forms are mainly found as less dominant understory species. The effects of human trampling in turf-dominated intertidal communities have rarely been considered (see Brown and Taylor 1999 for an exception). Southern California is also one of the most densely populated and highly visited coastal areas of the United States (Crossett et al. 2004), making studies of trampling effects imperative.

This study investigates the effect of human trampling on the algae and associated meio- and macrofauna of coralline algal turf communities in

Southern California. The main questions are: (1) Does relatively long-term human trampling affect community composition of the invertebrates associated with coralline algal turf? (2) Does human trampling cause a difference in the trajectory of invertebrate community change as compared to protected and / or open-access control plots? (3) Which invertebrate taxa are most affected by human trampling? (4) Which specific environmental variables are most correlated with any changes in invertebrate community structure caused by trampling? (5) Does the average percent-cover of dominant turf-forming algal species change with human trampling? and (6) Do both algae and invertebrate communities return to control levels when trampled plots are allowed to recover?

METHODS

Study area

Cabrillo National Monument ("Cabrillo" hereafter) is a small national park located at the tip of Point Loma, CA (32°28' N, 117° 11' W) that contains approximately 120 acres of rocky shoreline. Broad sand- and mudstone benches covered in coralline algal turf dominate the area, with several boulder fields and small stretches of sandy beach spaced intermittently. Human access to the park is restricted from the north by a Naval base and from the south by topography. A single access path leads down from the cliffs to a highly visited intertidal area at the northern end of the park. The southern portion of the intertidal area has been closed to public access since 1996 and is regularly monitored by park rangers and volunteer docents during low tide (Figure 6-1). Plots that would be experimentally trampled ("impact plots") and control plots that were protected from human foot traffic ("protected control plots") were established in this closed zone of the park.

Control plots were also established at several other open-access sites in order to account for natural variations among locations ("open-access control plots"). Plots were established in the high- and mid-use areas of Cabrillo and at three rocky intertidal sites near La Jolla, CA (Figure 6-1). The La Jolla sites, Shell Beach, Marine Room, and Bedrock, all have similar topography to Cabrillo and though they are open to the public, visitation to these sites is relatively low (Huff 2006b and unpublished data).

Experimental design and sampling procedure

Thirty two permanent experimental plots were haphazardly sited on turf-covered benches of the mid-intertidal in December 2003. Sixteen trample plots and six protected control plots were located in the closed area of Cabrillo, and two open-access control plots were located at each of the other five sites (Cabrillo high-use, Cabrillo intermediate-use, Shell Beach, Marine Room, and Bedrock). Each plot was 0.75 m x 0.25 m in size and was divided into three regions – a 0.25 m x 0.25 m square in the center that was marked by bolts in which percent cover measurements would be taken and a 0.25 m x

0.25 m square above and below the center-square from which destructive sampling would occur (Figure 6-2).

Before trampling was initiated, pre-impact sampling was conducted. A random number chart and numbered grid system were used to determine the locations from which measurements and samples would be taken within each plot. Pore water salinity, temperature within the turf, and shear strength of the sand / turf matrix were measured three times per plot. To obtain salinity measurements, small samples of the turf and associated sand were placed into empty syringes and the pore water was pressed through three stacked Whatman filters onto a hand-held refractometer. Temperature was measured by placing a digital temperature probe as far into the turf as possible. And, as a measure of compaction, shear strength was measured with a Slope Indicator Torvane fitted with the standard-sized vane. Three turf samples, 4.5 cm in diameter (15.9 cm^2), were also taken from each of the plots using a sharpened metal coring device which was pushed through the turf to the bedrock below. A metal spatula was then used to scrape all algae and associated sediment from the rock. Samples were placed in tightly sealed plastic containers and brought back to the lab for analysis. Finally, percent cover of dominant algal species was determined by recording the most abundant species for each of 121 small squares within a grid at the center of each experimental plot. The species that was most apparent to the researcher without moving algae aside and looking deeper into the turf was recorded. So, for example, if fleshy red epiphytes were growing on a base of coralline turf (which was often the case), the epiphyte would be recorded rather than the coralline base. The number of squares in which an alga was dominant were then summed and divided by 121 in order to convert to a percentage.

After pre-impact sampling was completed, experimental trampling was begun. Time-lapse video data have shown that visitation to popular rocky intertidal areas like Cabrillo averages approximately 200 people per day and can reach values of more than 400 people per day (Huff 2006b). While not all of these people will walk in exactly the same areas, visitors do tend to take predictable paths through the tidepools. Given these data, I chose 125 trampling passes per appropriate low tide as a realistic but conservative estimation of impact. For each trampling episode, a person of average size passed over each of the impacted plots 125 times, taking care to evenly distribute their footsteps across the plots and into a buffer zone around each plot. Turns were also made outside of the plots so as to standardize impact. Trampling was applied during every daytime tide lower than -0.5 ft. between December 2003 and May 2005.

Post-impact sampling was conducted in May 2004, November 2004, and May 2005 using the same procedure as described for the initial sampling. Trampling was stopped in May 2005, and plots were allowed to recover for nine months. Recovery samples were then taken in February 2006.

Lab procedures

Algal turf samples were brought back to the lab, weighed, rinsed on a 63 µm screen, and preserved in ethanol. They were then manually sorted under a 12x dissecting microscope. Invertebrates were removed, identified to the lowest possible taxonomic level, and counted (Appendix 6-1). Although sessile animals that were attached to algal fronds (e.g. bryozoans, serpulorbid snails, sponges, etc.) were commonly found in the turf, these animals were not included in the study because the methods used were not appropriate to accurately quantify them (Kelaher 2002). In an attempt to strike a balance between gathering as much data as possible and efficient sample sorting, the taxonomic resolution of the fauna varied among groups. Additionally, some species have not been well described, others require specialized taxonomic knowledge to identify, and some were juveniles that could not be conclusively identified. The use of differing levels of taxonomic discrimination in these types of multivariate analyses has been shown to have little effect on the outcome (Herman and Heip 1988, Warwick 1988a, b, James et al. 1995).

Once the samples had been defaunated, the algae were carefully separated from the sand, and the sand was rinsed through a series of sieves (1 mm, 500 µm, and 63 µm) in order to sort it into three size classes. Sand and algae were then placed in a 60°C drying oven and dried until a constant weight was obtained (at least 24 hours).

Data analysis

For all analyses, data from the three measurements of each environmental variable and the three turf samples from each plot were averaged. Invertebrate communities of the impact plots, protected control plots, and open-access control plots were compared using non-metric multi-dimensional scaling (nMDS) and analysis of similarities (ANOSIM). Data were square-root transformed in order to reduce the dominance of the most abundant taxa in the analyses. Second-stage nMDS and an additional ANOSIM test were used to determine if invertebrate communities from impact plots had a significantly different trajectory of change through time than those from either set of control plots (Clarke et al. 2006). Additionally, the similarity percentages method (SIMPER) was used to determine which animals were contributing most to dissimilarities among samples. These analyses were performed using Plymouth Routines in Marine Ecological Research (PRIMER) software v.5.2.9 (Primer-E Ltd. 2002).

The extent to which environmental variables “explain” the biotic assemblages was tested using the BIO-ENV function in PRIMER. For this type of analysis, the multivariate pattern of environmental data is compared to that of the species data. The program then searches for subsets of the environmental data whose pattern best matches that of the species data in order to determine which of those variables are best correlated with the biotic community. Average salinity, temperature, shear, percent water weight, dry weight of algae, and dry weight of the three size classes of sand were considered during this analysis.

Several measures of diversity were also calculated using PRIMER including number of taxa (S), number of individuals (N), the Shannon diversity index (H'log *e*), and Pielou's evenness index (J'). Differences in diversity among the impacted and control plots were then tested using analysis of variance (ANOVA).

In order to analyze potential differences in percent cover, all fleshy red turf-forming algae were lumped into a "fleshy red" category. Then, differences between sampling times in percent cover of the four most common groups (*Corallina pinnatifolia, Ulva californica*, fleshy reds, and bare rock) were investigated using analysis of variance (ANOVA).

RESULTS

Environmental variables

In pre-impact samples, no significant differences were found in any of the measured environmental variables between impact and protected control plots ($p > 0.05$ in all cases). Measurements taken during the period when plots were being trampled (in May 2004, November 2004, and May 2005) consistently showed significantly greater values for dry weight of algae, sand > 1 mm, and sand < 500 mm and > 63 µm in protected control plots than in impact plots ($p < 0.01$ in all cases). Additionally, total percent water by weight was shown to be significantly less for samples from impact plots than for those from protected control plots in samples from May 2004 and May 2005 ($p = 0.0003$, $p = 0.0024$). Samples taken in February 2005, nine months after trampling had ceased, indicated that impact plots had returned to control values for all environmental variables ($p > 0.05$ in all cases).

No combination of the measured environmental variables was significantly correlated with invertebrate community composition. The highest correlation value was given by a combination of the variables salinity, temperature, and dry weight of sand >63 µm and <500 µm (BIO-ENV, ? = 0.180).

Community composition

Pre-impact invertebrate communities of the impact and protected control plots were not significantly different from each other ($R = 0.014$, $p = 0.393$, unless otherwise noted, all results in this section are from ANOSIM, df = 31). Impact plots, however, did begin with significantly different communities than open-access control plots ($R = 0.446$, $p = 0.001$).

After five months of trampling, communities from the impact plots were significantly different than those of the protected controls ($R = 0.645$, $p = 0.001$). Trampled and open-access control plots continued to show significant differences in community composition as well ($R = 0.566$, $p = 0.001$). A separation between the communities of the trampled and control plots was also revealed by nMDS (Figure 6-3). Similar results were seen for November 2004 and May 2005 as were seen for the first post-impact samples, with significantly different community composition in impact plots than in either the protected or open-access control plots (R > 0.35, p < 0.05). Nine months after trampling had ceased (February 2006), the communities of the trampled plots had returned to protected control levels (R = 0.229, p = 0.06) but were still significantly different than the communities of the open-access controls (R = 0.545, p = 0.001).

Before trampling was initiated, the taxa that contributed the most to the dissimilarity between communities from the impact plots and those from the open-access controls were three taxa of foraminifera (*Quinqueloculina* sp., *Rosalina* sp., and Rotaliidae), three species of gastropod (*Caecum californicum, Amphithalamus tenuis*, and *Barleeia* sp.), the ostracod *Cythera* sp., copepods, and gammarid amphipods. Together, these taxa contributed more than 50% of the dissimilarity between impact and non-protected control plots (SIMPER). In each case, abundance was greater in the plots that had been designated as impact plots (Figure 6-4a).

Foraminifera, gastropods, ostracods, copepods, and gammarid amphipods continued to contribute much of the dissimilarity between impact and open-access control plots after trampling was initiated. In May 2004, taxa from these groups again contributed more than 50% of the dissimilarity between these treatments. However, abundances were now greater in the open-access control plots for all taxa except Rotaliidae and *Cythera* sp. Impact plots and protected controls were also distinguished by these groups, and abundances of all contributing taxa were greater in the controls (Figure 6-4b). These patterns of taxon dissimilarity continued through the November 2004 and May 2005 sampling dates.

In recovery samples, slightly different taxa contributed to the dissimilarity between impact and open-access control plots. Ceratopogonid insects, syllid polychaetes, and tanaids, along with three gastropods (*Caecum californicum, Amphithalamus tenuis*, and *Barleeia* sp.), two ostracods (*Cythera* sp. and O. Myodocopa), Rotaliidae, copepods, and gammarid amphipods explained more than 50% of the dissimilarity (Figure 6-4c).

Community changes through time

Impact plots showed a significantly different trajectory of community change through time than either set of control plots (second-stage ANOSIM, df = 31, Global R = 0.433, p = 0.001, trample vs. non-protected controls R = 0.379, p = 0.001, and trample vs. protected controls R = 0.717, p = 0.001). Figures 6-5a – 6-5c show first-stage nMDS ordinations for impact, protected control and open-access control plots. Sampling times distinctly separate for the impact plots, and a circular progression through time can be seen as indicated by arrows. Protected control plots do not demonstrate such a distinct separation among sampling times, and the progression through time appears to be more linear. Open-access controls do not appear to separate well by sampling time and a progression of community change through time is more difficult to ascertain. An assemblage of the time trajectories in a second-stage nMDS plot (which can be thought of as an nMDS plot of the pairwise similarities between the previous three nMDS plots (Clarke et al. 2006)) supports the result that impact plots have different time trajectories than controls. If all of the plots had similar time trajectories, points from all three treatments would be relatively evenly dispersed on the nMDS plot. Instead, we see that points from the impact plots tend to clump together while there is generally more overlap between the two sets of controls (Figure 6-6).

Diversity

Before trampling was initiated, number of individuals (N) and number of taxa (S) were significantly greater and evenness (J') was significantly less in impact plots than in open-access controls. There was no significant difference in Shannon diversity (H'log *e*) (Table 6-1).

All three sets of samples from the trampling period displayed significantly higher numbers of individuals and taxa in the protected control plots than in the impact plots. In May 2005, there were also significantly more individuals and taxa in the open-access control plots than in trampled plots (Table 6-1).

Nine months after trampling had ceased, the invertebrate communities from impact plots had significantly more taxa and higher Shannon diversity than those from either set of controls. There were no significant differences between impact plots and controls in number of individuals or evenness (Table 6-1).

Percent algal cover

Percent cover of *Corallina pinnatifolia* was significantly greater in pre-impact measures than in those from any other sampling time for impact plots and both types of control plots ($p<0.01$ in all cases, unless otherwise noted all results in this section are from ANOVA). In impact plots, fleshy red turf-forming algae had significantly smaller percent cover values in May 2004 and May 2005 than they did in pre-impact measures ($p = 0.002, 0.041$) but were unchanged from initial measurements in control plots during this time. An increase in percent cover of turf-forming fleshy red algae was seen in both sets of control plots in November 2004 as compared to pre-impact ($p < 0.01$ in both cases). For all three treatments, percent cover of *Ulva californica* was seen to increase significantly in May 2004, May 2005, and February 2006 as compared to pre-impact levels ($p < 0.01$ in all cases).

Amount of bare rock in impact plots was significantly greater in all three sets of measurements from the trampling period than in pre-impact measurements (May 2004 $p = 0.006$, Nov. 2004 and May 2005 $p < 0.0001$). However, recovery samples showed a return to pre-impact values for percentage of bare space in impact plots ($p = 0.875$). Open-access controls showed no significant differences in amount of bare rock during any sampling time as compared to pre-impact values ($p > 0.05$ in every case). Protected controls had a significant decrease in the percentage of bare rock in both

November 2004 and February 2006 as compared to pre-impact measurements ($p = 0.043, 0.048$, Figure 6-7).

DISCUSSION

Past studies have come to various conclusions regarding the effect of human trampling on algal turf for several potential reasons. First, authors often use the term “turf” without specifying the type of algae to which they are referring. Turf-forming species include both fleshy and coralline forms, and these different morphologies may be affected differently by trampling. Additionally, manipulative experiments have been of different intensities and durations. Those that were of longer duration or that used higher trampling intensities tended to show greater impact on the turf. Here, a relatively long-term study based on realistic levels of human trampling was conducted to help to clarify conclusions about human impacts on the invertebrates and algae of coralline algal turf communities.

Impact and protected control plots, which began with similar invertebrate community structures, were shown to have diverged after five months of trampling in the impact plots. During each of the post-impact sampling events, invertebrate communities of trampled plots were significantly different from those in the protected control area. These differences appear to be mainly caused by a decrease in abundances of several common invertebrate taxa including three taxa of foraminifera, three species of gastropods, copepods, and gammarid amphipods.

One might have expected the communities of the trampled plots to become more similar to open-access controls as trampling progressed. Instead, trampled plots had significantly different communities than the open-access controls for the duration of the experiment. However, taxa that were responsible for the majority of the dissimilarity tended to be more abundant in impact plots before trampling began but less abundant in impact plots while trampling was occurring. As mentioned in the site descriptions, the three non-protected sites in La Jolla and the intermediate-use zone of Cabrillo do not have particularly high visitation. Visitation to these areas averages tens of people per day rather than the hundreds of people per day found at highly visited sites (Huff 2006b and unpublished data). Since the chosen number of experimental trampling passes was based on video data from highly visited sites, it is not unexpected that the impact to these plots might be greater than that of normal visitation to the open-access controls.

After nine months with no trampling, invertebrate community structure in the trampled plots was seen to be similar to that of control plots located in the protected area. Number of taxa and Shannon diversity, however, were significantly higher in the trampled plots after recovery. Since ANOSIM analyses can be highly influenced by the most abundant taxa, the differences in these results may be due to the numbers of rare species in the trampled plots versus controls.

Impact plots contained significantly less sand and algae (by dry weight) than protected controls during the period when trampling occurred. Impact plots also had significantly less moisture content than protected controls during this time. Consequently, less total habitat was available for the invertebrate community, and the habitat that was present was not as protective against dessication.

None of the environmental variables that were measured in this study were highly correlated with the invertebrate community structure. Past studies have shown that algal complexity, density, and frond length have an effect on the associated invertebrate assemblages (Gee and Warwick 1994, Hull 1997, Chemello and Milazzo 2002, Kelaher et al. 2001, Kelaher 2002 and 2003). In this study, the amount of algae present in the sample was not highly correlated with differences in community structure through time or among treatments. Perhaps dry weight of algae is not an appropriately descriptive measure, and average turf thickness or frond length would have shown higher correlation values. Due to the unevenness of the substrate beneath the turf, however, turf thickness and frond length proved difficult to quantify accurately.

Overall, bare space significantly increased in trampled plots while such increases were not seen in controls. Additionally, although accurate measurements were difficult to obtain, visual evaluation of trampled plots indicated that turf density and thickness were much lower than controls. These results suggest that human trampling decreases the overall amount of algal turf and therefore decreases the amount of available habitat for associated invertebrates. A return to pre-impact values for bare space after nine months with no trampling again indicates a fairly rapid recovery in this community.

Variations in the percent cover of *Corallina pinnatifolia, Ulva californica,* and fleshy reds occurred in both experimental and control plots, indicating that the changes were not due to trampling. Increases in *U. californica* as compared to pre-impact measurements (and associated decreases in the *C. pinnatifolia* and fleshy reds) in May 2004 and 2005 were likely due to the natural seasonality of this species. According to Stewart (1991), *U. californica* is particularly abundant in late spring and early summer in San Diego County.

This study clearly indicates that human trampling affects the community structure of invertebrates in intertidal turf communities. It also indicates that the invertebrate assemblages are relatively quick to recover from trampling disturbance. Questions remain, however, about which specific physical or biological factors are causing the ultimate differences in invertebrate communities. More complete measurements of physical factors along with quantification of biological factors such as predation and dispersal would be beneficial to future studies.

The observed recovery of the invertebrate and algal community is an interesting result in terms of management of visitor pressures on rocky intertidal ecosystems. Potential management schemes include rotating or periodic closure of rocky intertidal regions to allow for recovery from human impacts. Since nine months is approximately the length of the “off-season” in areas that rely on summer tourism, closure of certain areas during this time may be beneficial to the invertebrate and algal communities.

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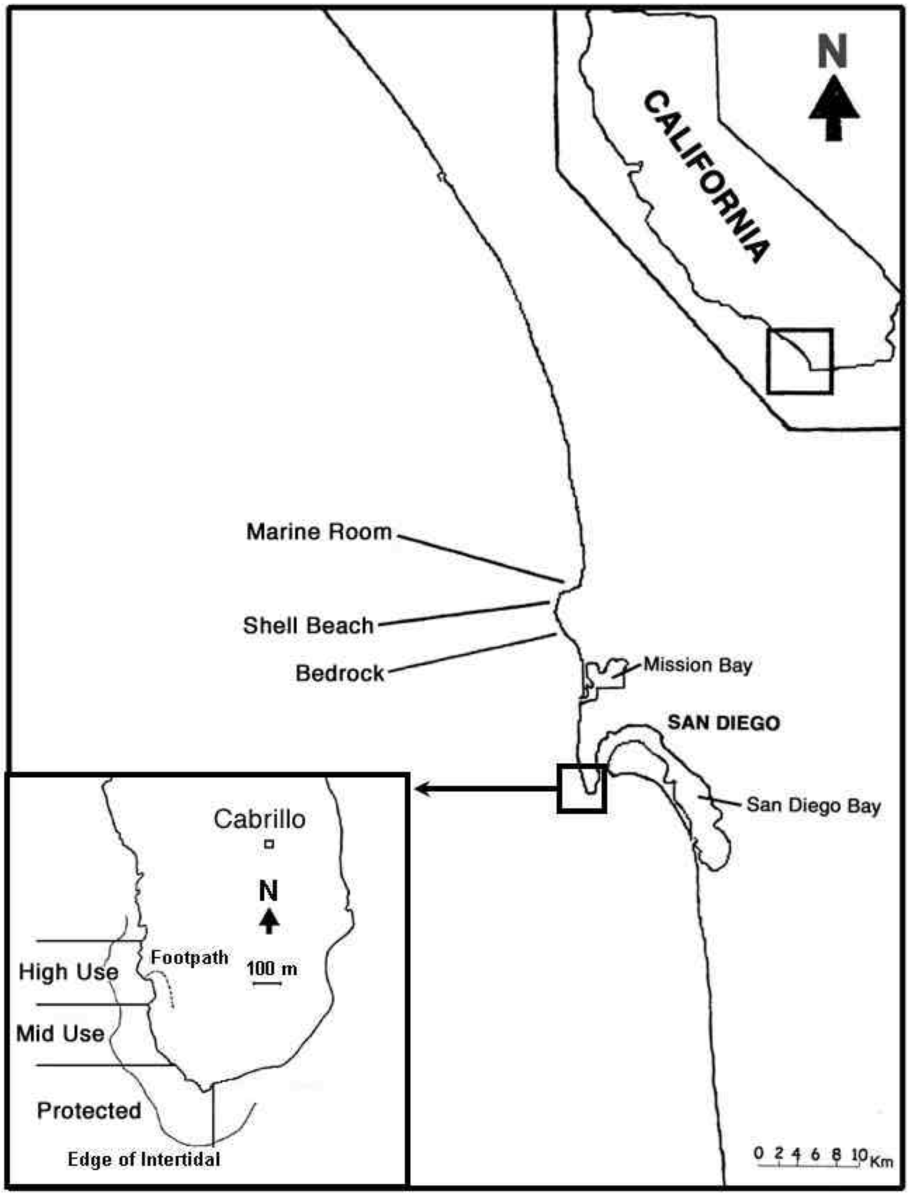


Figure 6-1. Map of the San Diego region showing locations of study sites. Impact and protected control plots were established in the "protected" region of Cabrillo, while open-access controls were established in the "mid-use" and "high-use" areas of Cabrillo and at Marine Room, Shell Beach, and Bedrock near La Jolla.

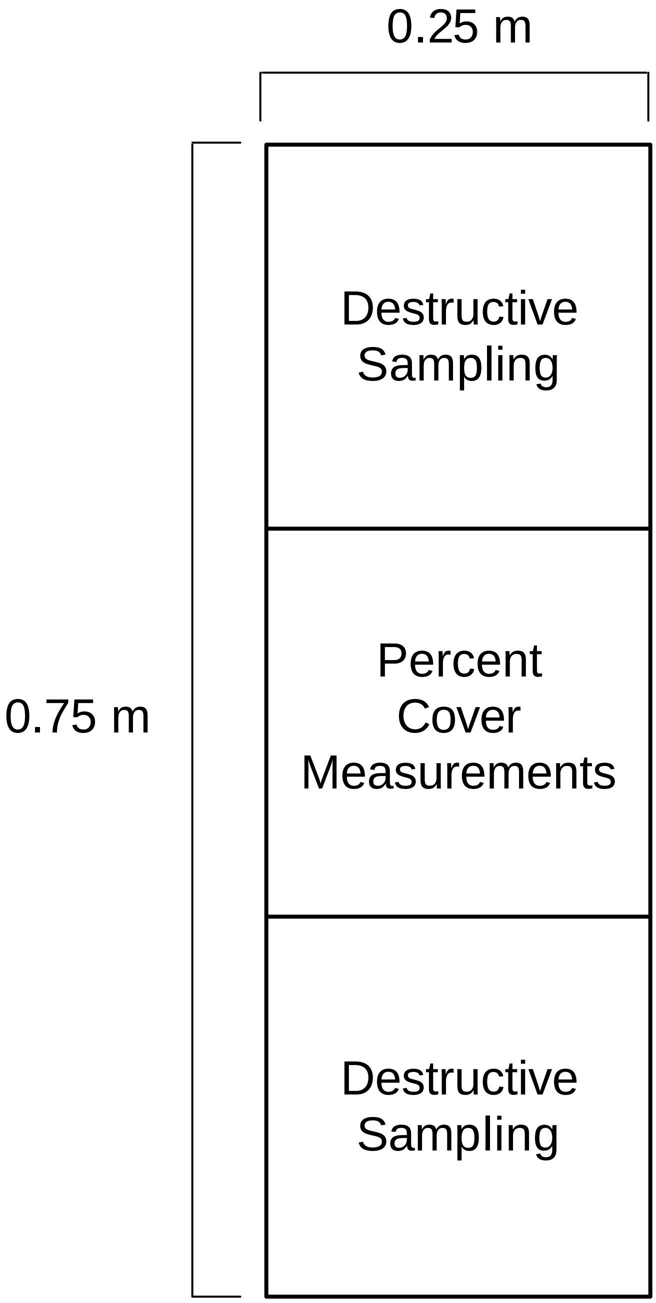


Figure 6-2. Diagram of plot layout and sampling scheme

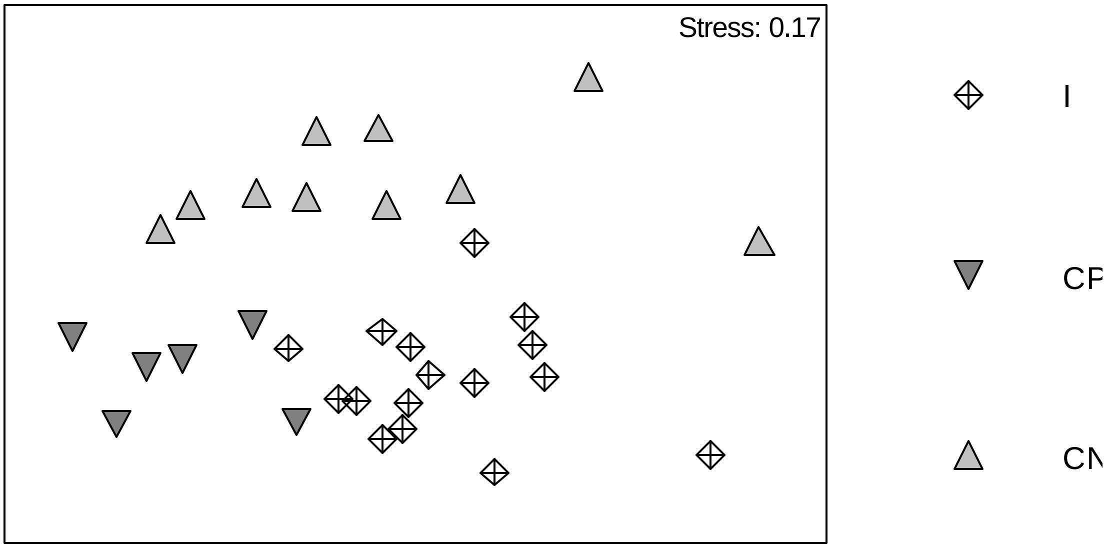
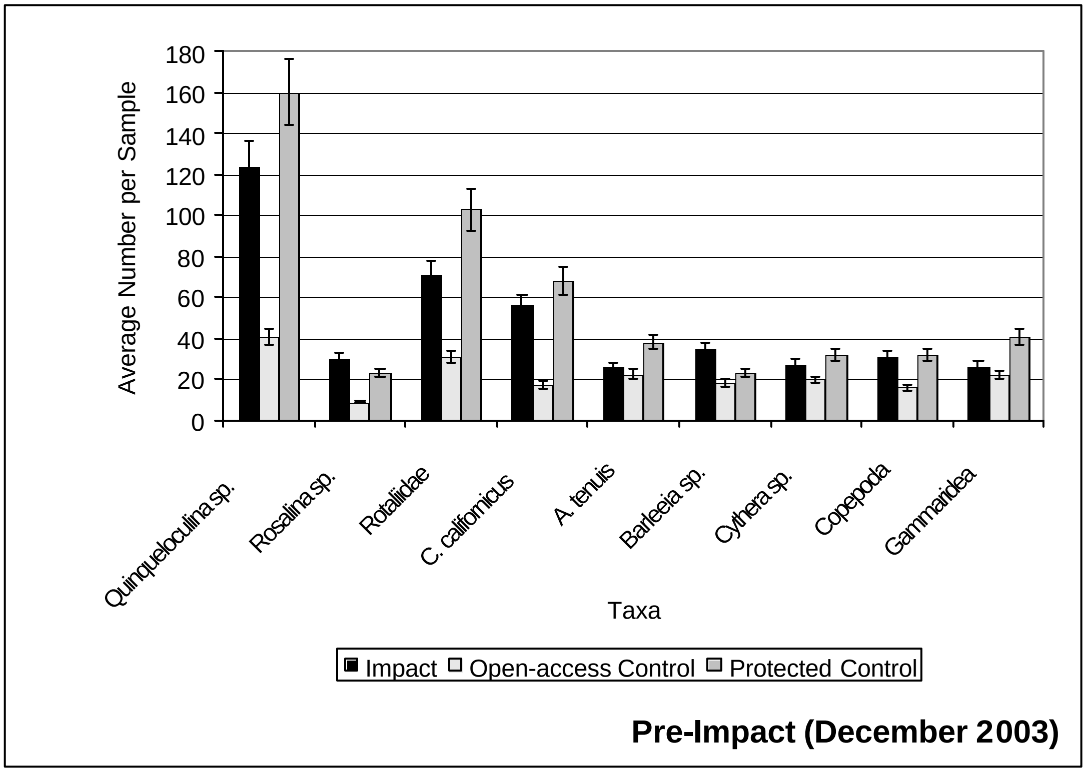


Figure 6-3. nMDS plot of invertebrate community data from May 2004 (five months after trampling had begun) I = Impact, CP = Protected Control, CO = Open-access Control

Figure 6-4. Average abundances of taxa that most contributed toward dissimilarity among treatments (SIMPER) from **a.** pre-impact samples **b.** five months after trampling had begun and **c.** recovery samples.

a.


Average Number per Sample
0
20
40
60
80
100
120
140
160
180
Quinqueloculina sp.
Rosalina sp.
Rotaliidae
C. californicus
A. tenuis
Barleeia sp.
Cythera sp.
Copepoda
Gammaridea
Taxa
Impact
Open-access Control
Protected Control
Pre-Impact (December 2003)

b.

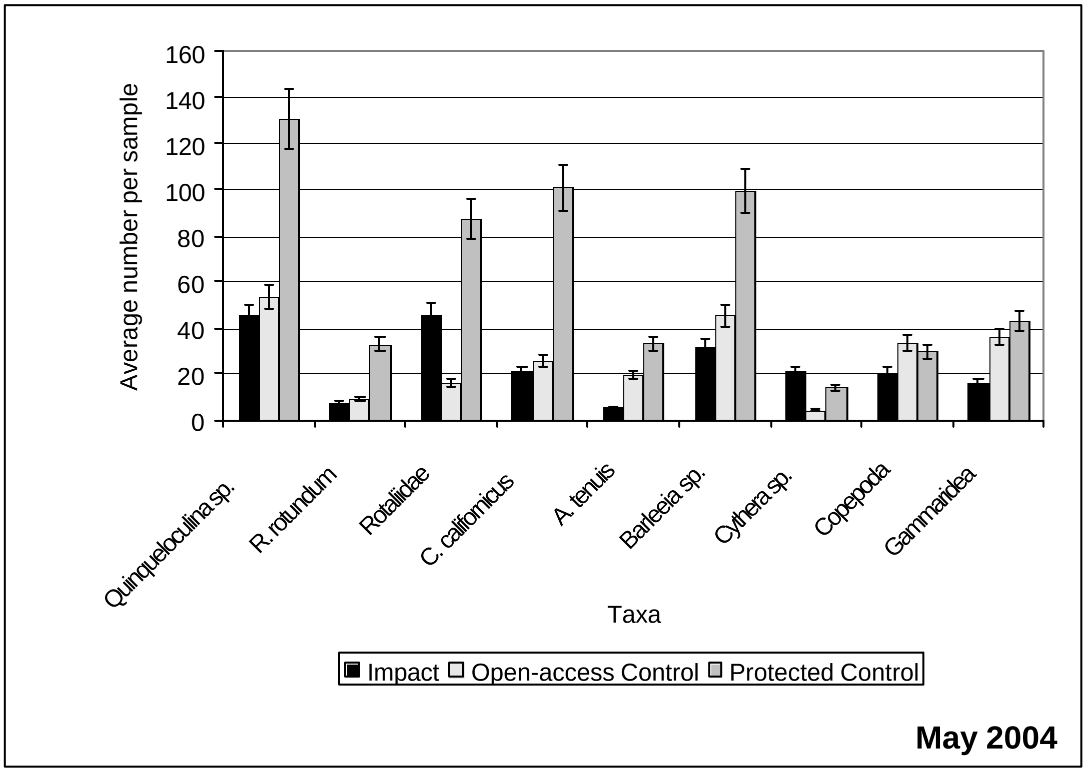

Average number per sample
0
20
40
60
80
100
120
140
160
Quinqueloculina sp.
R. rotundum
Rotaliidae
C. californicus
A. tenuis
Barleeia sp.
Cythera sp.
Copepoda
Gammaridea
Taxa
Impact
Open-access Control
Protected Control
May 2004

Figure 6-4. continued.

c.

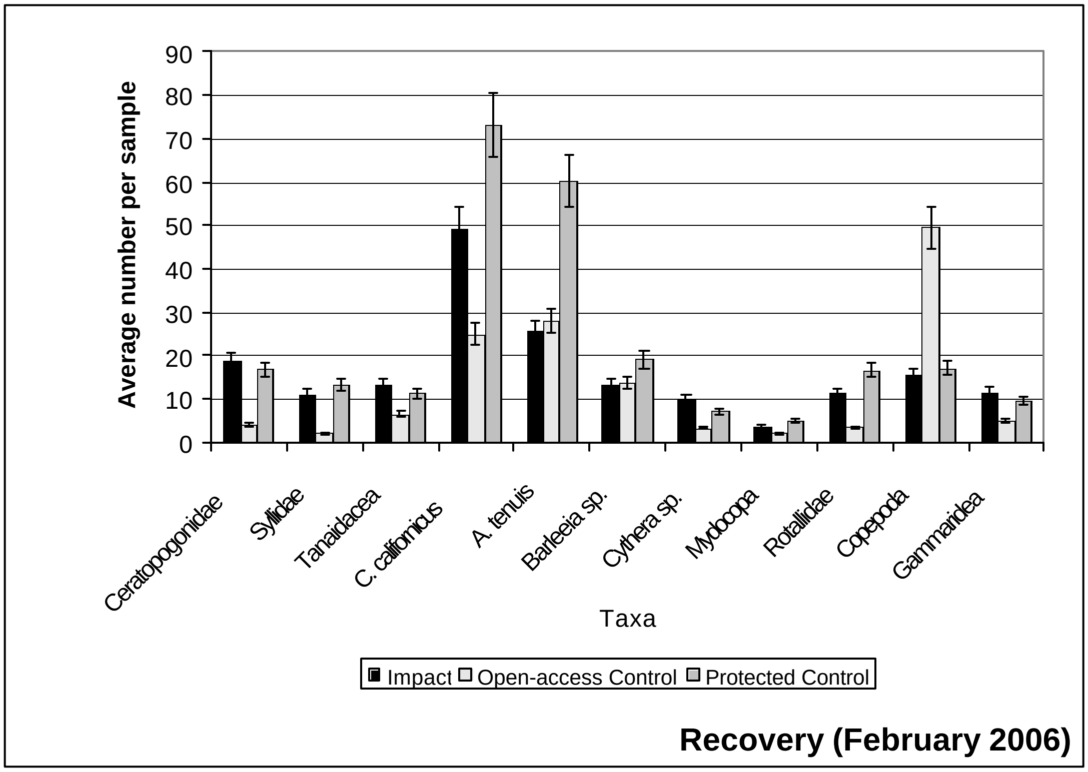

90
80
70
60
50
40
30
20
10
0
Average number per sample
Ceratopogonidae
Syllidae
Tanaidacea
C. californicus
A. tenuis
Barleeia sp.
Cythera sp.
Mydocopa
Rotallidae
Copepoda
Gammaridea
Taxa
■ Impact □ Open-access Control ▨ Protected Control
Recovery (February 2006)

Figure 6-5. First-stage nMDS ordinations for **a.** impact **b.** protected control and **c.** open-access control plots. Arrows indicate the general progression of community change through time. As a clear pattern was not present in the open-access controls, no arrows were added.

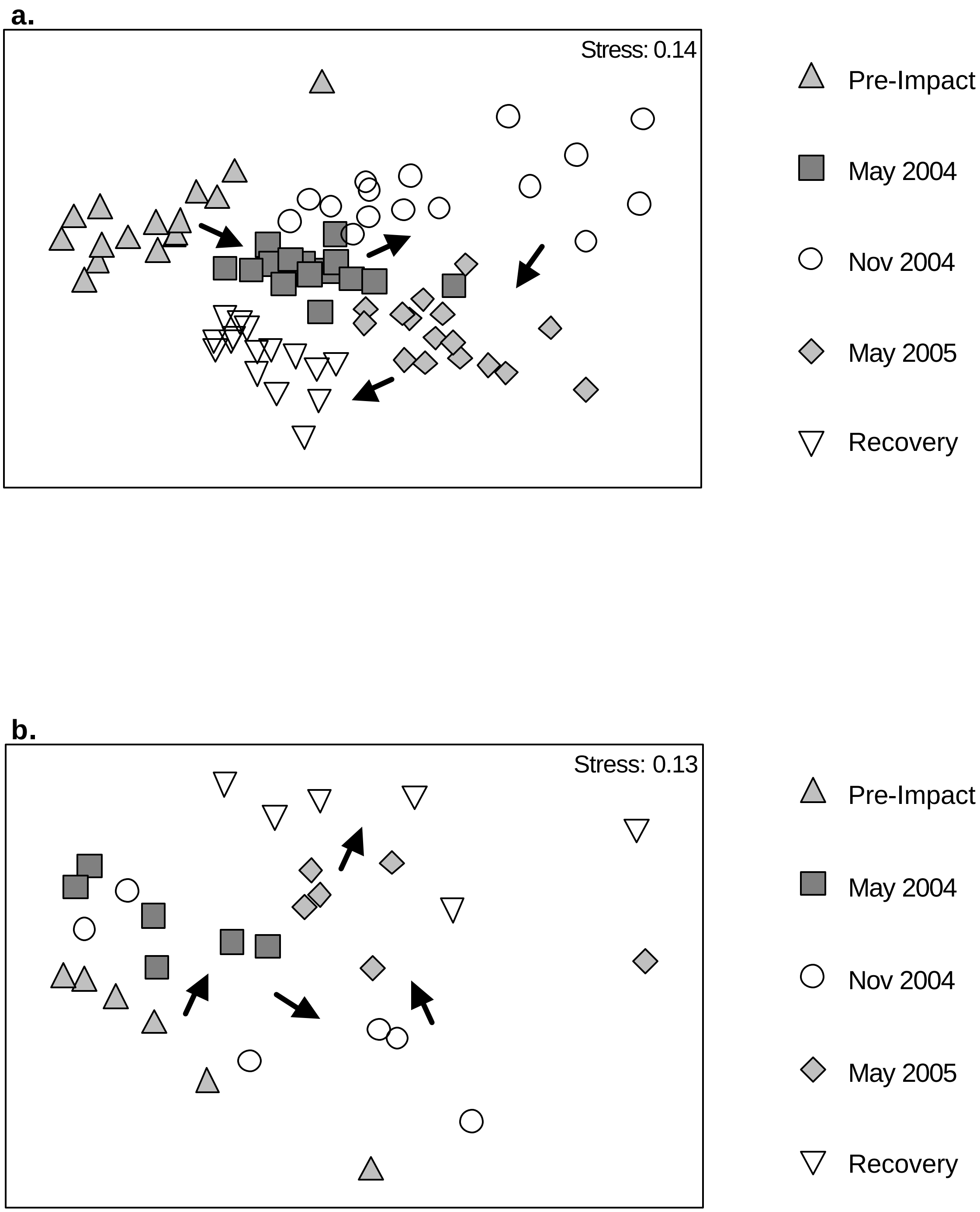
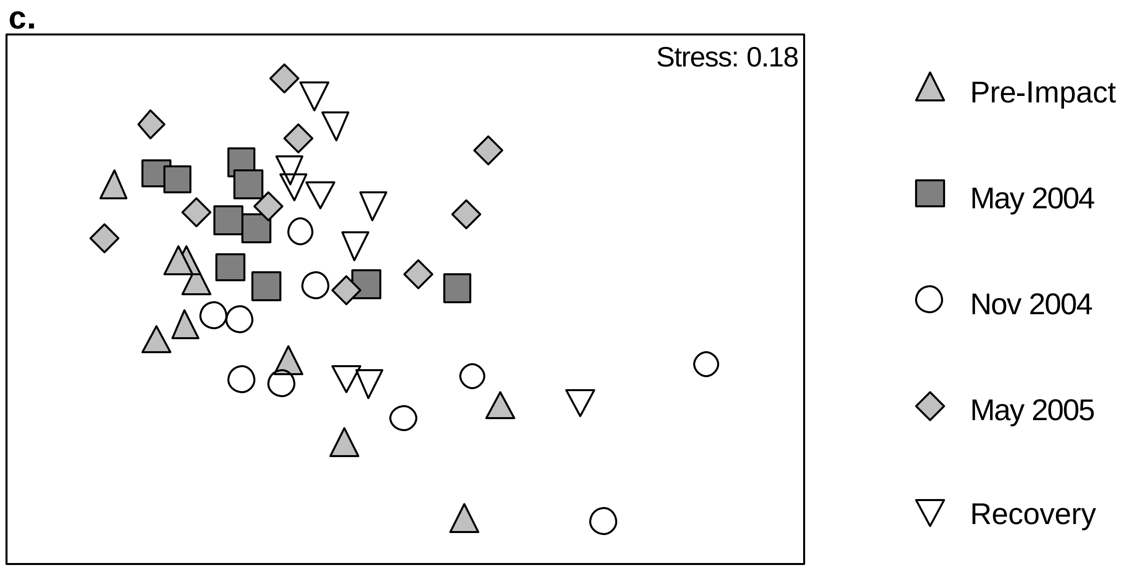

a.
Stress: 0.14
Pre-Impact
May 2004
Nov 2004
May 2005
Recovery
b.
Stress: 0.13
Pre-Impact
May 2004
Nov 2004
May 2005
Recovery

Figure 6-5. continued.


c.
Stress: 0.18
Pre-Impact
May 2004
Nov 2004
May 2005
Recovery

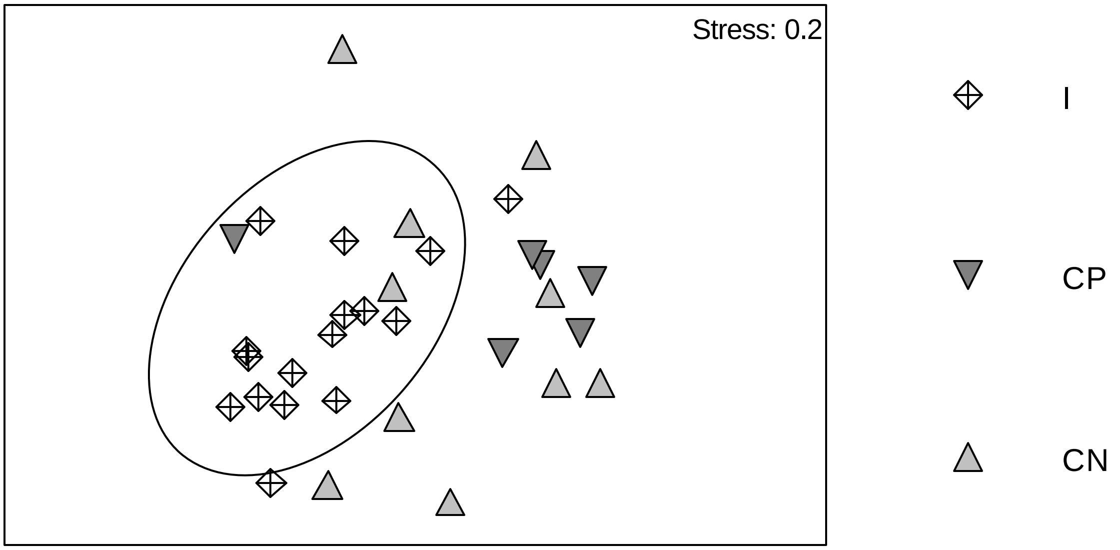


Figure 6-6. Second-stage nMDS plot indicating a difference in trajectory of community change through time between impact and control plots. Circle was added to emphasize the separation of impact plots. I = Impact, CP = Protected Control, CO = Open-access Control

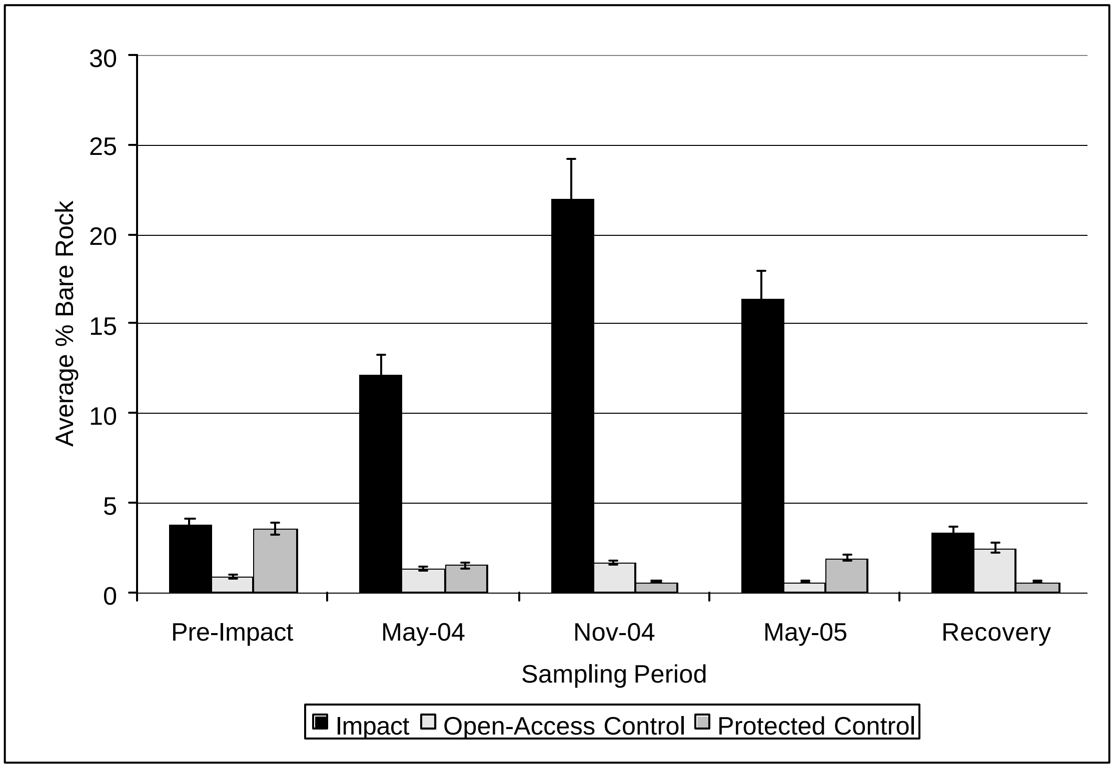


Figure 6-7. Average percent bare rock for impact, non-protected control, and protected control plots from each of the sampling periods

Table 6-1. Results from ANOVA for diversity indices of impacted (I), protected control (CP), and open-access control (CO) plots. * indicates significance ($p < 0.05$)

Sampling Time	Diversity index	Treatments	df	F-value	p-value
Pre-impact (December 2003)	S	Overall	2	5.726	0.008*
		CO, CP			0.114
		CO, I			0.002*
		CP, I			0.284
	N	Overall	2	8.945	0.001*
		CO, CP			0.018*
		CO, I			<0.001*
		CP, I			0.415
	J’	Overall	2	6.888	0.004*
		CO, CP			0.019*
		CO, I			0.001*
		CP, I			0.707
	H’log *e*	Overall	2	0.960	0.395
		CO, CP			0.240
		CO, I			0.246
		CP, I			0.769
May 2004	S	Overall	2	6.063	0.006*
		CO, CP			0.095
		CO, I			0.078
		CP, I			0.002*
	N	Overall	2	20.790	<0.001*
		CO, CP			<0.001*
		CO, I			0.567
		CP, I			<0.001*
	J’	Overall	2	2.881	0.072
		CO, CP			0.691
		CO, I			0.070
		CP, I			0.053
	H’log *e*	Overall	2	0.569	0.572
		CO, CP			0.312
		CO, I			0.809
		CP, I			0.374
November 2004	S	Overall	2	13.503	<0.001*
		CO, CP			<0.001*
		CO, I			0.449
		CP, I			<0.001*
	N	Overall	2	22.370	<0.001*
		CO, CP			<0.001*
		CO, I			0.84
		CP, I			<0.001*

Table 6-1. continued.

Sampling Time	Diversity index	Treatments	df	F-value	p-value
	J’	Overall	2	2.230	0.121
		CO, CP			0.079
		CO, I			0.832
		CP, I			0.066
	H’log *e*	Overall	2	1.992	0.150
		CO, CP			0.075
		CO, I			0.643
		CP, I			0.107
May 2005	S	Overall	2	6.900	0.004*
		CO, CP			0.276
		CO, I			0.015*
		CP, I			0.002*
	N	Overall	2	14.120	<0.001*
		CO, CP			0.753
		CO, I			<0.001*
		CP, I			0.001*
	J’	Overall	2	1.474	0.246
		CO, CP			0.419
		CO, I			0.097
		CP, I			0.579
	H’log *e*	Overall	2	1.019	0.374
		CO, CP			0.227
		CO, I			0.973
		CP, I			0.184
Recovery (February 2006)	S	Overall	2	18.052	<0.001*
		CO, CP			0.063
		CO, I			<0.001*
		CP, I			0.007*
	N	Overall	2	2.300	0.118
		CO, CP			0.041*
		CO, I			0.339
		CP, I			0.146
	J’	Overall	2	1.195	0.317
		CO, CP			0.298
		CO, I			0.636
		CP, I			0.133
	H’log *e*	Overall	2	10.085	0.001*
		CO, CP			0.838
		CO, I			0.001*
		CP, I			0.002*

Appendix 6-1. Classification of invertebrates used in community analyses. Levels of taxonomic resolution that were included in analyses are in bold print (when species-level identification was used, both genus and species are in bold). Classification from Brusca and Brusca (1990), Lee et al. (2000), McLean (1978), and SCAMIT (2001).

Phylum: Annelida
- Class: **Oligochaeta**
  - Family: **Tubificidae**
- Class: **Polychaeta**
  - Family: **Cirratulidae**
    - Genus: **Cirrifornia**
  - Family: **Nerididae**
  - Family: **Oenonidae**
  - Family: **Sabellidae**
  - Family: **Syllidae**
    - Genus: **Odontosyllis**
  - Family: **Nephtyidae**
  - Family: **Maldanidae**
  - Family: **Lumbrineridae**

Phylum: Arthropoda
Subphylum: Cheliceriformes
- Class: **Pycnogonida**

Subphylum: Uniramia
- Class: Insecta
  - Family: **Ceratopogonidae**

Subphylum: Crustacea
- Class: Malacostraca
  - Order: Amphipoda
    - Suborder: **Gammaridea**
    - Suborder: **Caprellidea**
  - Order: Decapoda
    - Suborder: Pleocyemata
      - Infraorder:Anomura
        - Genus: **Pagurus**
      - Infraorder: **Brachyura**
        - Genus: **Pachygrapsus**
          - Species: **crassipes**
        - Genus: **Pugettia**
          - Species: **gracilis**
        - Genus: **Cancer**
  - Order: **Cumacea**
  - Order: **Tanaidacea**

Appendix 6-1. continued.

- Order: **Isopoda**
- Class: Maxillopoda
  - Subclass: Cirripedia
    - Order: Thoracica
      - Genus: **Balanus**
      - Genus: **Chthamalus**
      - Genus: **Pollicipes**
        - Species: **polymerus**
  - Subclass: Ostracoda
    - Order: Podocopida
      - Family: Cytheridae
        - Genus: **Cythera**
        - Genus: **Paradoxostoma**
      - Family: Bairdiidae
        - Genus: **Bairdia**
    - Order: Platycopida
      - Family: Cytherellidae
        - Genus: **Cytherella**
    - Order: **Myodocopida**
      - Family: Sarsiellidae
        - Genus: **Sarsiella**
      - Family: Cylindroleberididae
        - Genus: **Postasterope**
      - Family: Rutidermatidae
        - Genus: **Rutiderma**
          - Species: **rotundum**
          - Species: **judayi**
  - Subclass: **Copepoda**
- Class: Cheliceriformes
  - Order: Acari
    - Suborder: **Acariformes**

Phylum: Cnidaria
- Class: Anthozoa
  - Subclass: Hexacorallia
    - Order: Actiniaria
      - Genus: **Anthopleura**

Phylum: Echinodermata
- Class: **Echinoidea**
  - Subclass: Euechinoidea
    - Genus: **Strongylocentrotus**

Appendix 6-1. continued.

- Class: **Ophiuroidea**

Phylum: Granuloreticulosa
- Class: **Foraminifera**
    - Order: Miliolida
        - Family: Hauerinidae
            - Genus: **Quinqueloculina**
    - Order: Rotaliida
        - Family: Rosalinidae
            - Genus: **Rosalina**
        - Family: **Rotaliidae**
        - Family: **Trichohyalidae**

Phylum: Mollusca
- Class: Bivalvia
    - Subclass: Lamellibranchia
    - Superorder: Filibranchia
        - Family: Mytilidae
            - Genus: **Mytilus**
            - Genus: **Modiolus**
                - Species: **rectus**
            - Genus: **Adula**
                - Species: **falcata**
            - Genus: **Septifer**
                - Species: **bifurcatus**
            - Genus: **Musculista**
                - Species: **senhousia**
        - Family: **Pectinidae**
        - Family: **Ostreidae**
    - Superorder: Eulamellibranchia
        - Order: Veneroida
            - Family: Chamidae
                - Genus: **Pseudochama**
                    - Species: **exogyra**
            - Family: Veneridae
                - Genus: **Chione**
                    - Species: **californiensis**
            - Family: Donacidae
                - Genus: **Donax**
                    - Species: **gouldii**
            - Family: Tellinidae
                - Genus: **Macoma**

Appendix 6-1. continued.

- Genus: **Leporimetis**
  - Species: **obesa**
- Family: Neoleptonidae
  - Genus: **Neolepton**
    - Species: **subtrigona**
- Family: Carditidae
  - Genus: **Glans**
    - Species: **carpenteri**
- Family: Lasaeidae
  - Genus: **Lasaea**
    - Species: **adonsoni**
- Order: Myoida
  - Family: Myidae
    - Genus: **Sphenia**
  - Family: Hiatellidae
    - Genus: **Hiatella**
  - Family: Pholadidae
    - Genus: **Penitella**
- Order: Arcoida
  - Family: Philobryidae
    - Genus: **Philobrya**
      - Species: **setosa**
- Class: Gastropoda
  - Subclass: Prosobranchia
    - Order: Archaeogastropoda
      - Family: Haliotidae
        - Genus: **Haliotis**
          - Species: **fulgens**
      - Family: Scissurellidae
        - Genus: **Sinezona**
          - Species: **rimuloides**
      - Family: Fissurellidae
        - Genus: **Fissurella**
          - Species: **volcano**
        - Genus: **Diodora**
          - Species: **aspera**
      - Family: Acmaeidae
        - Genus: **Collisella**
          - Species: **ocracea**
          - Species: **digitalis**
        - Genus: **Lottia**
          - Species: **conus**

Appendix 6-1. continued.

- Genus: **Maclintockia**
  - Species: **scabra**
- Genus: **Notoacmea**
  - Species: **insessa**
  - Species: **palacea**
- Family: Trochidae
  - Genus: **Calliostoma**
    - Species: **annulatum**
  - Genus: **Tegula**
    - Species: **funebralis**
  - Genus: **Norrisia**
    - Species: **norrisi**
- Family: Skeneidae
  - Genus: **Parviturbo**
    - Species: **acuticostatus**
- Family: Phasianellidae
  - Genus: **Eulithidium**
    - Species: **rubrilineatum**
    - Species: **pulloides**
- Order: Mesogastropoda
  - Family: Lacunidae
    - Genus: **Lacuna**
      - Species: **unifasciata**
  - Family: Littorinidae
    - Genus: **Littorina**
      - Species: **planaxis**
      - Species: **scutulata**
  - Family: Rissoidae
    - Genus: **Rissoella**
    - Genus: **Alvinia**
      - Species: **aequisculpta**
      - Species: **compacta**
      - Species: **cosmia**
      - Species: **oldroydae**
      - Species: **purpurea**
    - Genus: **Amphithalamus**
      - Species: **inclusus**
      - Species: **tenuis**
    - Genus: **Barleeia**
  - Family: Vitrinellidae
    - Genus: **Vitrinella**
      - Species: **eschnauri**

Appendix 6-1. continued.

- Genus: **Teinostoma**
  - Species: **supravallatum**
- Genus: **Omalogyra**
- Genus: **Truncatella**
  - Species: **californica**
- Family: Caecidae
  - Genus: **Caecum**
    - Species: **californicum**
  - Genus: **Fartulum**
    - Species: **occidentale**
- Family: Cerithiidae
  - Genus: **Bittium**
    - Species: **interfossa**
    - Species: **purpureum**
- Family: Cerithiopsidae
  - Genus: **Seila**
    - Species: **montereyensis**
- Family: Triphoridae
  - Genus: **Triphora**
    - Species: **pedroana**
- Family: Epitoniidae
  - Genus: **Epitonium**
    - Species: **tinctum**
- Family: Calyptraeidae
  - Genus: **Crepidula**
- Family: Cypraeidae
  - Genus: **Cypraea**
    - Species: **spadicea**
- Order: Neogastropoda
  - Family: Muricidae
    - Genus: **Ocenebra**
  - Family: Columbellidae
    - Genus: **Nassarina**
      - Species: **penicillata**
    - Genus: **Alia**
      - Species: **carinata**
      - Species: **tuberosa**
    - Genus: **Astyris**
      - Species: **aurantiaca**
  - Family: Marginellidae
    - Genus: **Cystiscus**
      - Species: **jewettii**

Appendix 6-1. continued.

- Genus: **Granulina**
  - Species: **margaritula**
- Genus: **Olivella**
  - Species: **biplicata**
- Family: Conidae
  - Genus: **Conus**
    - Species: **californicus**
- Family: Turridae
  - Genus: **Pseudomelatoma**
    - Species: **penicillata**
- Family: Haminoeidae
  - Genus: **Haminoea**
    - Species: **virescens**
- Family: Scaphandridae
  - Genus: **Acteocina**
    - Species: **culcitella**
    - Species: **harpa**
    - Species: **inculta**
- Family: Pyramidellidae
  - Genus: **Aartsenia**
    - Species: **satura**
  - Genus: **Odostomia**
    - Species: **aepynota**
    - Species: **cincta**
    - Species: **eucosmia**
    - Species: **navisa**
    - Species: **turricula**
    - Species: **virginalis**
  - Genus: **Chemnitzia**
  - Genus: **Pyrgiscus**
- Subclass: Opisthobranchia
  - Order: **Nudibranchia**
- Class: **Polyplacophora**
  - Family: Lepidochitonidae
    - Genus: **Nuttallina**
      - Species: **fluxa**
  - Family: Mopaliidae
    - Genus: **Mopalia**
      - Species: **muscosa**
  - Family: Acantochitonidae
    - Genus: **Acanthochitona**
      - Species: **avicula**

Appendix 6-1. continued.

Family: Ischnochitonidae
Genus: **Callistochiton**
Species: **palmulatus**

Phylum: **Nematoda**

Phylum: **Platyhelminthes**

Phylum: **Sipuncula**

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The text of Chapter 6, in full, is in preparation for submission to the Journal of Experimental Marine Biology and Ecology. The dissertation author was the primary investigator and author of this paper.

CHAPTER 7

Conclusions

The work presented here is important in both theoretical and applied contexts. The composition and dynamics of a relatively under-studied but numerically and ecologically important component of the rocky intertidal ecosystem, the invertebrate community of coralline algal turf, have been described. The response of this community to both natural and anthropogenic disturbances has also been evaluated. The results of these studies help to fill in an important gap in knowledge of the natural history of rocky intertidal communities and the processes which shape them. Additionally, the techniques and results presented here will be valuable for future management decisions in protected coastal areas.

NATURAL HISTORY OF TURF COMMUNITIES

The invertebrate communities of coralline algal turf in San Diego County are spatially and temporally dynamic. Significant differences in community composition, diversity, and abundances existed among sites and sampling times (Chapter 2). Density and diversity were highest in the region of Cabrillo National Monument that has been closed to public use and lowest at the most heavily visited sites.

Abundances of these animals were as high as 1.6 million animals m^{-2}. In all, 146 taxa from nine phyla were identified. Common taxa that were represented in this community include gastropods, bivalves, small crustaceans, polychaetes, nematodes, oligochaetes, and foraminifera.

These invertebrate communities exhibited rapid responses to disturbance, but also appeared to recover rapidly (Chapters 4 and 6). An acute, or “pulse”, disturbance in the form of sand inundation caused two distinct shifts in turf fauna (Chapter 4). Initially, highly mobile animals rapidly exited the impacted area. Then, while the sand inundation continued, psammophilic gastropods slowly increased in abundance. A more continuous, or “press”, disturbance in the form of human trampling also caused changes in the structure of the invertebrate community associated with algal turf (Chapter 6). Trampled plots exhibited lower density and diversity than protected control plots. Also, the change in community composition through time was significantly different in trampled plots than it was in controls.

The turf itself is also relatively resilient to natural disturbance. In the observational study of sand movement in the rocky intertidal, the depth (frond length) of the turf did not change after sand inundation (Chapter 3). Percent cover and density of coralline turf decreased with sustained human trampling, but returned to control levels after a nine-month recovery period (Chapter 6). Perhaps the turf has become naturally adapted to living in areas with large influxes of sand and is therefore resistant to damage from scour or burial.

These types of adaptations may contribute to the relatively rapid recovery of turf after trampling as well.

OBSERVATIONAL STUDIES

Observational studies give us the opportunity to see patterns and processes in real-world conditions. So, although we may not be able to draw strong conclusions about causation, the correlations that we see can give us a clue as to where to concentrate our efforts on manipulative studies and modeling. Chapters 3 and 5 both describe observational studies that gave us quantitative information on the extent and timing of disturbances in the rocky intertidal.

Sand movement at Dike Rock was negatively correlated to maximum significant wave height (Chapter 3). Large inundations of sediment were relatively rapid and generally lasted on the order of a month or two, while erosion of sand was seen to be equally as rapid. All regions of the intertidal were equally affected by sand inundation, however the sand tended to be patchy and “refuges” always existed for animals that were able to move away from the disturbance. These observations were valuable in designing a realistic, manipulative sand experiment with which the responses of the turf community could be quantified.

The use of time-lapse video proved to be an efficient method for collecting vast amounts of data regarding patterns of human visitation to the rocky intertidal (Chapter 5). It was seen that the amount of visitation was highly site-specific. Time of day and weekday vs. weekend were more important predictors of visitation than was the height of the tide. Again, these data were valuable in the design of a realistic, manipulative experiment to determine the effects of trampling on coralline algal turf communities. Additionally, knowledge of real-world patterns of human visitation will be extremely valuable in management decisions.

MANIPULATIVE STUDIES

Manipulative studies allow us to isolate variables and determine causation rather than just correlation. It is important to conduct manipulative experiments on realistic time scales, especially in reference to disturbance. Short-term experiments may be effective for examining pulse disturbances, but longer-term projects may be necessary to see the effects of press disturbances. As described above, manipulative studies were used here to isolate the effects of sand inundation and human trampling.

MANAGEMENT

It is important that scientists continue to form partnerships with resource managers and take advantage of opportunities to do work in places like Cabrillo National Monument. The existence of protected areas is valuable not only for the protection of the resource in question but also so that controlled experiments can be more easily conducted and more knowledge about the system can be obtained. In short, detailed, long-term observational studies give us information so that realistic experimental studies can be designed and implemented. These type of experiments can be used to inform management decisions and subsequently monitor the results of those management strategies.