Title

Rocky Intertidal Community Structure on Different Substrates

Author

Osborn, Dawn A.

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ROCKY INTERTIDAL COMMUNITY STRUCTURE ON DIFFERENT SUBSTRATES

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Dawn Alexandra Osborn

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The Dissertation of Dawn Alexandra Osborn
is approved:

Professor John S. Pearse, Chair

Robert E. Garrison

Professor Robert Garrison

Fiorenza Micheli

Professor Fiorenza Micheli

Professor Peter Raimondi

Robert C. Miller
Vice Chancellor for Research and
Dean of Graduate Studies

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DISSERTATION ABSTRACT

ROCKY INTERTIDAL COMMUNITY STRUCTURE ON DIFFERENT SUBSTRATES

Dawn Alexandra Osborn

The extensive anthropogenic armoring of the shoreline changes the substrate available to settling invertebrate larvae and algal spores that are passively distributed in the ocean currents. A variety of rock types are used, including basalt, sandstone, granite, limestone, and concrete. Much research has been done examining the mechanisms that determine intertidal community patterns, but the role of rock type has been largely neglected (overview of the problem Chapter 1). The interactions between intertidal organisms and substrate type might play a significant role in structuring benthic communities influencing not only initial settlement, but also subsequent species assemblages.

My goals were to: 1) determine the community structure on different rock types, 2) examine the mechanisms responsible for any differences, and 3) link the community structure patterns to life history characteristics of selected species. I conducted two studies – the first comparing intertidal communities at two sites with armored, rip-rapped shorelines (Chapter 2) and the second, monthly monitoring of deployed settlement plates of four different rock types at two sites with different bedrock (Chapters 3 and 4). For three years (April 2002 to April 2005), every 45 days (approximately), I compared recruitment on the plates and on the native bedrock, and

sterilized a subset of plates for the next recruitment period. In addition, I examined post-settlement survival and compared the relationship between the density of settlers and the density of subsequent adults.

Canonical discriminant analysis in Chapter 2 showed significant differences in community structure on different rock types. Analysis of variance in Chapter 3 and 4 indicated that recruit and adult acorn barnacle abundances were significantly different on different substrates. The recruitment pattern on the deployed settlement plates (Chapter 3) did not match the rip-rap community structure (Chapter 2), nor did the post-settlement/adult community (Chapter 4). Regression analysis used in Chapter 4 to test the relationship between settlers and adults with two barnacle species showed a density-independent relationship, aligning with model predictions when recruitment is low, for *Balanus glandula*. *Chthamalus dalli/fissus* adults and recruits showed an initial density-independent relationship that changed to a density-dependent relationship over time.

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Chapter 1.

Rocky intertidal community structure on different substrates: Overview of the problem

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Rocky intertidal community structure on different substrates: Overview of the problem

Dawn Alexandra Osborn

ABSTRACT

The extensive anthropogenic armoring of the shoreline in California changes the substrate available to settling invertebrate larvae and algal spores that are passively distributed in the ocean currents. Rock types available to settlers likely influences community structure in the intertidal, as rock characteristics have been shown to favor or inhibit settlement. Much research has been done examining the mechanisms that determine intertidal community patterns, but the role of rock type has been largely neglected. My goals are to: 1) determine the structure of community assemblages occurring on different rock types, 2) examine the mechanisms responsible for any differences, and 3) link the community structure patterns to life history characteristics of selected species. I have conducted two studies – the first comparing two sites with armored, rip-rapped shorelines (Chapter 2) and the second using settlement plates at two sites with different bedrock within Monterey Bay, California (Chapters 3 and 4). The intertidal community structure on the armored rocks and settling plates shows different patterns for certain species distributions that warrant further examination. These studies will help in predicting how continued armoring of the shoreline will affect species assemblages, as well as enhancing our understanding of variation in intertidal community assemblages at different sites along the coast.

INTRODUCTION

Coastal armoring, adding boulders to fortify the shoreline, is increasing along our coastline to prevent erosion. These rip-rap boulders are rock types that are harder and more erosion resistant than the native rock and add a different substrate to the intertidal, sometimes completely covering up the native substrates. I am interested in the effects coastal armoring, changing the native substrate, will have on the intertidal community structure. Following are the ecological and geological overviews explaining the background issues related to this question.

Ecological Overview

Community structure of the rocky intertidal varies from place to place based on physical and biological factors, including the severity of wave action, the shoreline profile, salinity, oxygen availability, heat stress, competition, predation and the substrate (Lewis, 1964; Caffey, 1985; Foster et al, 1988; Bell, 1995). The presence of algae and animals themselves is a major cause of variation from place to place *i.e.*, some attached species retain water and modify the habitat for other species; some dense, tall species reduce the amount of light falling on underlying species (Lewis, 1964; Dayton, 1975). Direct interactions between the environment and organisms contribute to the abundance and distribution of species due to behavioral and physical adaptations.

Community structure refers to the physical and biological structure of the community (Krebs, 1994). The physical structure of an intertidal marine community is influenced by factors such as shore topography, wave exposure, and rock type (Lewis, 1964). The biological structure of a community includes components such as species distribution, species composition and abundance, species sizes, and trophic relationships (Lewis, 1964; Menge and Branch, 2001). Community structure can be influenced by the effect of higher trophic levels on those below ("top-down" effects) and by effects of lower trophic levels on those above ("bottom-up" effects) (Little and Kitching, 1996; Underwood, 2000). The biological structure of a community is influenced by and even depends on its physical structure (Krebs, 1994). To study community structure, the physical environment (*e.g.*, rock type) and the species present need to be examined.

Much work has been done measuring the influence of the physical environment on rocky intertidal organisms. The importance of water flow and settlement cues to larvae has been demonstrated (Mullineaux and Butman, 1991; Boxshall, 2000), tide and wave fluctuations and exposure (Colman, 1933; Seapy and Littler, 1978; Denny, 1995; Denny and Paine, 1998), temperature (Mathieson and Burns, 1971; Wethey, 1983), and desiccation (Dayton, 1971; Wethey, 1984), have been measured in the field and related to species distributions. Differences between aspect and topography on different shores (Lewis, 1964), geographic location (Wethey, 1983; Caffey, 1985; Raimondi, 1988), and larval availability (Grosberg, 1982; Shanks, 1983; Gaines and Roughgarden, 1985; Underwood, 2000) may also produce different patterns of community structure. The physical environment is difficult to assess however, since the above listed factors all have cumulative effects.

Two prominent patterns of community structure have been frequently studied – the segregation of species into vertical zones (Lewis, 1964; Paine, 1966, 1974; Grosberg, 1982; Foster et al., 1988; Raimondi, 1988; Stillman and Somero, 1996) and the gradients in wave exposure that impact community structure (Connell, 1972; Dayton, 1975; Menge, 1976; Gaylord et al., 2001; Davis et al., 2002). However, the importance of rock or substrate type on community structures has been studied infrequently (*e.g.*, Moore and Kitching, 1939; Caffey, 1982; Raimondi, 1988). Rock type (basalt, mudstone, granite) could be a key factor determining differences in the intertidal community from place to place by causing variable micro-climates for intertidal species, *e.g.*, water retention, surface temperature, surface texture. The interactions between intertidal organisms and substrate type might play a significant role in structuring benthic communities, influencing not only initial settlement, but also subsequent species assemblages (Bavestrello et al., 2000).

Studies in other systems provide good examples of substrate having a profound effect on community structure. Soil type has been studied for terrestrial communities (Rejmánek, 1971, Bending et al., 2002) and sediment type for soft-substrate communities (Butman, 1987) or infaunal species of invertebrates (Butman et al., 1988). However, the importance of rock type on community ecology of the rocky intertidal is difficult to study in the field because geologic differences generally occur over large spatial scales and transplantation studies are difficult. In the few marine examples that exist, Moore and Kitching (1939) showed that in Great Britain the barnacle *Chthamalus stellatus* preferred hard, rough rocks unless sheltered from wave action. Moreover, the larvae of another barnacle, *Balanus balanoides,* did not settle on smooth rock unless there were depressions or scratches (Hatton, 1938 in Moore and Kitching, 1939). In contrast, Caffey (1982) found no trends for settlement density or survival on different rock types for an intertidal barnacle, *Tesseropora rosea.* Some extracts from oil shale inhibited the settlement of *Balanus balanoides*, while metalloporphyrins induced settlement on oil shale in Great Britain (Hill and Holland, 1985). In the Gulf of California, Raimondi (1988) did reciprocal transplant experiments, measured rock temperature with an electronic thermistor, and determined that there was consistently more recruitment of *Chthamalus anisopoma* on granite versus basalt shores, correlated with the thermal capacity of the rocks.

Factors influencing settlement and post-settlement processes of rocky intertidal larvae and algal spores have been examined frequently. McGuinness and Underwood (1986) found that the rock structure of the habitat (surface texture and material) significantly affected the number and/or abundance of species present. Surface texture is an important factor in algal spore settlement (Harlin and Lindbergh, 1977; Fletcher and Callow, 1992) and in larval settlement (Mullineaux and Butman, 1991); rougher surfaces create more surface area for settlement, higher water retention (Fletcher and Callow, 1992), and disrupted boundary layer effects (Mullineaux and Butman, 1991). Settlement in barnacle larvae has been correlated with surface texture (Barnes, 1956) and surface contour (Crisp and Barnes, 1954). Larval habitat selection may also be a behavioral response to chemical cues (Crisp and Meadows, 1962; Butman et al., 1988) along with a response to shear stress in rock depressions (Mullineaux and Butman, 1991). Mussels (*Mytilus edulis*) have been shown to preferentially grow in pitted and creviced hard surfaces (Pulfrich, 1996). Settling behavior of *Mytilus* species is a critical factor in determining their distribution and abundance in the intertidal (Petersen, 1984). Grazing efficiency by a periwinkle (*Littorina littorea*) depended on rugosity of the substrate, attributable to a mismatch between radula dimensions and surface structures, influencing recruitment by a barnacle (*Balanus improvisus*) and a polychaete (*Polydora* sp.) (Wahl and Hoppe, 2002). All of these studies indicate that rock type could have a profound effect on community structure, yet that has not been well documented by critical comparisons of community structure on different rock types at the same site and between sites.

The rocky shores of Monterey Bay, California have a very diverse and productive intertidal region (Ricketts et al., 1985). In Monterey Bay, conditions exist that facilitate the comparison of intertidal communities on different rock types at the same site and at nearby sites with different bedrock. Such comparisons will allow me to determine the effects of variation in substrate type on community composition and on settlement and post-settlement processes that determine community composition and structure. The unique, historical, geological events that have occurred in the Monterey Bay area, along with the addition of rip-rap and boulders to the coastline for stabilization, allow studies on different rock types in large and small spatial scales. Igneous, metamorphic and sedimentary rocks are right next to each other within sites that have been armored with rip-rap and shorelines on the two sides of the Bay have different types of bedrock.

Geological Overview of Monterey Bay

Between about sixty million and a million years ago, the area of the present Sierra Nevada was a volcanic arc system where andesite volcanoes were underlain and intruded by granitic magmas. Sediment eroding from the Santa Cruz mountains was deposited in the Central Valley, which was covered by a shallow sea. These sediments formed thick beds of sedimentary rocks. About thirty million years ago, a transform fault developed as the Pacific Plate and the North American Plate collided, and rocks on the Pacific Plate have been moving north along the San Andreas Fault since that time. The developing transform fault cut into the granitic rocks of southern California and of the Sierra Nevada, slicing off a chunk that was carried north on the Pacific Plate. This chunk of crust, which Monterey Bay sits upon, is called the “Salinian block”. Most of the exposed rocks of the Salinian block today are sedimentary but the majority of the rocks that lie beneath, the so-called “basement rocks”, are granitic (Clark, 1981; Bergeron, 1997).

The central California coast is composed of numerous different rock types. The shoreline of Santa Cruz County consists of uplifted marine terraces composed mainly of sedimentary mudstone, which has been undergoing rapid erosion for centuries. Each terrace consists of remnants of a wave-cut platform and a sea cliff cut into Tertiary sedimentary rocks (Clark, 1981). The rock formations exposed in the coastal cliffs of Santa Cruz are: Purisima Formation (very thick bedded diatomaceous siltstone, forming the high seacliffs and terrace deposits, of Miocene and Pliocene age); below that, the Santa Cruz Mudstone (diatom-rich biosiliceous units composed of mudstones, Upper Miocene); below that, Santa Margarita Sandstone (thick bedded sandstones deposited in a shallow marine environment, early Upper Miocene) (Clark, 1981). The main bedrock in northern and western Santa Cruz County is the Santa Cruz Mudstone, which, in general, is relatively easily eroded by waves and currents.

Because these rocks along the coastline of Santa Cruz County are soft and easily eroded by heavy wave action, since 1990, the County has spent hundreds of millions of dollars to prevent erosion by armoring. Granite, basalt and other hard rock boulders are used to armor the shorelines, and these "introduced" rocks are from quarries in central California (Griggs and Savoy, 1985). The geology of the coastline changes since rip-rap adds a mixture of metamorphic and igneous rock to the mudstone cliffs. About 20% of the rocky shoreline in Monterey Bay is armored with concrete seawalls and blocks, and particularly boulder rip-rap. Without this human intervention, much of the coast along Santa Cruz would retreat a few inches to a few feet per year (Griggs and Patsch, 2004 a and b). Houses built too close to the shore run the risk of falling into the sea. It costs from $10 to $30 million dollars a mile to build sea walls with rip-rap in California (G. Griggs, UC Santa Cruz, pers. comm., 2002). In San Diego Bay, to the south, 74% of the total shoreline is now armored with artificial hard substrate (Davis et al., 2002). Armoring is a significant, expanding business, and with global climate changes and a potential sea level rise, armoring may continue to be a prevalent practice. From an ecological perspective, armoring provides an unusual opportunity to determine the effect of different rock types on intertidal community structure on small spatial scales.

At the southern end of the bay in Monterey County, granodiorite dominates the coastline (*e.g.* Point Lobos and the Monterey Peninsula) and there is less addition of rip-rap due to the natural occurrence of a harder, more erosion-resistant rock. This igneous rock-body was formed during Late Cretaceous time under high temperature and/or high-pressure conditions (Skinner and Porter, 1987). The great difference in bedrocks on the two sides of Monterey Bay sets the stage for field experiments examining settlement and post-settlement processes that could be determining the resultant community structures.

METHODS

Two Studies

I conducted two studies at different spatial scales looking at the effect of rock type on intertidal community structure. The first involves the study of communities on rip-rap boulders adjacent to each other at two separate sites in Santa Cruz County (Chapter 2). The second is an experiment comparing plates of different rock types at two sites on either side of Monterey Bay, California. This latter experiment addresses how settlement (Chapter 3), post-settlement, and community development processes (Chapter 4) of sessile intertidal algae and invertebrates are affected by different substrates. I am interested in determining if there are different community assemblages at different sites along the coast when the rock type varies. The goal of my research is to determine how variation in substrate type affects patterns of intertidal community structure. I believe this project is important because as the rock type along our coastline continues to change due to coastal armoring, there could be changes in the intertidal community structure over time as a response to the altered substrate.

Comparative study on rip-rap

While our coastlines have been altered considerably by the addition of rip-rap, little consideration has been paid to the ecological consequences of such disturbance. To better understand how armoring influences the native invertebrate and algal community structure in the intertidal zone, I carried out a field study in Santa Cruz County on a small spatial scale, eliminating variables due to the different rocks being far apart and experiencing different oceanic regimes.

I chose 2 sites for my first study, both with rip-rap of introduced basalt and sandstone boulders (Chapter 2). The native rock is clay rich sedimentary mudstone, some of which was left undisturbed by the armoring. At one site, Rockview Drive (RD), I examined intertidal communities growing on three substrates – introduced basalt and sandstone boulders, and native mudstone. At the second site, Merced Avenue (MA), the only mudstone was a vertical cliff protected by introduced basalt and sandstone boulders, which were used for the study (Figure 1). At each site, I chose boulders similar in size in the mid-intertidal zone. Rocks were chosen with the same aspect, or orientation to the incoming waves. For sample collection, three distinct boulders of each introduced rock type were selected along with three different outcrops of native mudstone. Nine samples on each rock type were collected. Invertebrate and algae samples were gently scraped into plastic bags, preserved in 70% ethanol, and analyzed in the lab.

Discriminant analysis of the samples taken from these different rock types revealed similar community structures on the different rock types at the two sites. Barnacles (*Chthamalus dalli/fissus*) and finger limpets (*Lottia digitalis*) were more abundant on basalt, and rough limpets (*Lottia scabra*), nori (*Porphyra* spp., a red alga), and scouring pad algae (*Endocladia muricata,* a red alga) were more abundant on sandstone. Even more dramatic, very different species characterized the community structure on the native mudstone, with a high abundance of fly larvae (*Limonia marmorata*), tanaid crustaceans (*Pancolus californiensis*), and green algae (*Ulva* spp.). A pattern of substrate type affecting intertidal communities was confirmed, but the different mechanisms that could contribute to this pattern are difficult to sort out experimentally because of the heterogeneity of the rip-rap environment (Chapter 2). Consequently, I designed experiments using settling plates made of different rock types that could be put out in replicate blocks on contrasting native bedrock: the mudstone on the north side of Monterey Bay, and the granite on the south side (Chapters 3 and 4). Having the different bedrocks should provide information about whether differences seen among the settling plates were influenced by the surrounding bedrock. Also, comparing community patterns at sites with different offshore oceanic conditions may show differences in larval recruitment rates that could be distinguishable from rock type differences.

Experimental studies on settling plates

Two sites were chosen on the two sides of Monterey Bay for settling plate experiments – Terrace Point (TP) below Long Marine Laboratory (UC Santa Cruz), an intertidal bench with mudstone as bedrock in the north, and Point Cabrillo (PC) at Hopkins Marine Station (Stanford University), a granitic outcrop in the south (Figure 1). Both sites have restricted access to the public so field experiments will not be disturbed by people. These sites were chosen to diminish unwanted variances and to be as similar as possible with respect to 1) height in the intertidal region and relatively flat areas where settling plates can be placed in replicate blocks, 2) site accessibility during low tides, 3) logistically feasible to get equipment to, and 4) wave exposure (one faces the open ocean to the southwest and the other to the northwest.) These two sites will allow for comparisons of community structure on settlement plates between shores with different bedrock and offshore, oceanic conditions.

Plates of cut basalt, granite, sandstone and shale 10x10x2cm were attached to the native substrate by stainless-steel screws drilled into the bedrock in March 2002. I assessed settlement of all species of animals and algae that settled monthly on the plates by counting all species with a 10-power field microscope. Half of the plates were cleared of life approximately every 46 days in order to document recruitment patterns. Organisms were counted regularly on all plates but otherwise left undisturbed in the field until March 2005. A species diversity index will be used as a measure of community structure because it is sensitive to both the number of species in the sample and the relative abundances of the species. In addition, multivariate analysis to look at relative abundances of species on the different rock types at the sites will be done.

Preliminary results show that for a barnacle (*Chthamalus dalli/fissus*) at both Terrace Point and Point Cabrillo, sandstone is the preferred substrate, then the native bedrock, then granite and basalt. The least amount of recruitment occurs on shale, the mudstone bedrock mimic. It is interesting that this relationship is the same at these two sites on either side of Monterey Bay. In the rip-rap study, however, this barnacle was more abundant on basalt rather than sandstone.

Preliminary results also indicate differences in recruitment intensity on the two sides of the Bay, being much higher at Terrace Point than Point Cabrillo, and probably reflecting differences in larval supply (Connolly and Roughgarden, 1999). Moreover, there have been considerable differences among the replicate blocks of settlement plates, probably due to fine scale differences in the intertidal, temporal and spatial variables (Denny et al., 2004). As the experiment progressed I continued measuring settlement and post-settlement survival, as well as physical parameters associated with the different rock types at each site; my following thesis chapters will explore the differences in distribution and abundance and some reasons for these differences.

DISCUSSION

My studies thus far reinforce earlier work showing that substrate is important for determining community structure in the rocky intertidal. My comparative study on rip-rap eliminated most confounding factors and left rock type as the underlying cause of the differences seen. Substrate available to settling larvae influences patterns of zonation and community structure on rocky shores (Moore and Kitching, 1939; Caffey, 1982; McGuinness and Underwood, 1986; Raimondi, 1988). Substrate characteristics have been shown to attract or repel invertebrate larvae and algal spores (Harlin and Lindbergh, 1977; Butman et al., 1988; McGuinness, 1989; Fletcher and Callow, 1992). A species assemblage that is more attracted to a particular substrate type could affect succession by its subsequent interaction with later assemblages (Bavestrello et al., 2000). Settlement and post-settlement mortality are affected by specific local physical conditions such as coastal morphology, currents, available space, wave action, and by the abundance of predators (Connell, 1985). More work needs to be done examining differences in community patterns with respect to substrate type.

My results also reinforce the conclusions of other studies about how difficult it is to do comparative studies in the intertidal where there are many factors working in concert (Denny and Wethey, 2001). My experimental results thus far reinforce how variation on several different scales can complicate interpretation of small-scale experiments *i.e.,* differences on the two sides of the Bay and differences between the replicate blocks of plates. The challenges in discerning if/how intertidal community structure differs from shore to shore due to rock type are numerous. It is difficult to tease out biological factors (settlement, recruitment, larval supply) versus physical factors (rock type, thermal capacity of rock, hardness, wave action). The bedrock may change latitudinally along a shoreline, again complicating patterns. Also, there is rarely any record of when placement of rock for coastal reinforcement occurred, information necessary to determine how long an intertidal community has been developing. Santa Cruz City records dates when boulders were added; dates I can use to calculate intertidal community development time (Brian Evers, Santa Cruz City Public Works Inspector, pers. comm., 2000). With sound experimental design, I want to address the factors affecting community structure with respect to rock type. Despite the problems above, my experiments show that rock substrate has an impact on what settles and: 1) following it further should reveal more about how rocks influence the resulting community structure by differentially favoring settlers and 2) my measurement of thermal characteristics and other rock properties may reveal more about the mechanisms involved.

Implicit in studies of attached epibenthic organisms is the importance of larval settlement site on later survival. When armoring of the coastline occurs, added boulders provide new space for intertidal organisms to invade. Once sessile organisms have settled on a specific substrate, there is little chance to move to a different substrate. Site selection is almost irreversible after metamorphosis onto hard substrate. Site selection strongly influences post-settlement mortality (Roegner et al., 1995). There are several models that explain sequences of species when there is new space to invade (Connell and Slatyer, 1977) and these sequences will be important to follow as the geology of the coastline changes. Competition, predation, facilitation and other interactions between species are critical to the course of succession. Intertidal organisms have been found to enhance recruitment of other species by direct and indirect benefits to the secondary settler, for example by reducing herbivore pressure or desiccation stress. In my dissertation, I plan to investigate settlement and post-settlement processes that could affect intertidal community structure on different substrates.

There are consequences to countering the natural erosion by adding boulders and stabilizing structures, *e.g.* sand production decreases and beaches down-current shrink. Intertidal communities are increasingly important from an environmental and from a political standpoint. Environmentally, these communities are in great jeopardy because of the concentration of human populations near the coast and from the increasing public access to the shoreline. Public concern is growing about the impacts to the shoreline that result from anthropogenic input. The effects of these changes are now being documented by a number of groups, including the Monterey Bay National Marine Sanctuary with their rocky intertidal monitoring program (Osborn et al., 2005).

This study has a bearing on ecological changes due to human activities—coastal armoring. The coast may experience unanticipated ecological effects from armoring, and these effects should be documented by careful monitoring programs. In particular, this study demonstrates that the choice of rock used for armoring leads to different community structures, and these findings may be taken into consideration in future armoring projects. In addition, concrete, another material used for armoring is likely to support yet another community structure. This project will be the first to characterize the effect of shoreline fortification on associated intertidal communities. There is an immense amount of interest in maintaining intertidal areas, hence the importance of this project is in its contribution to the understanding of how to manage and maintain these areas.

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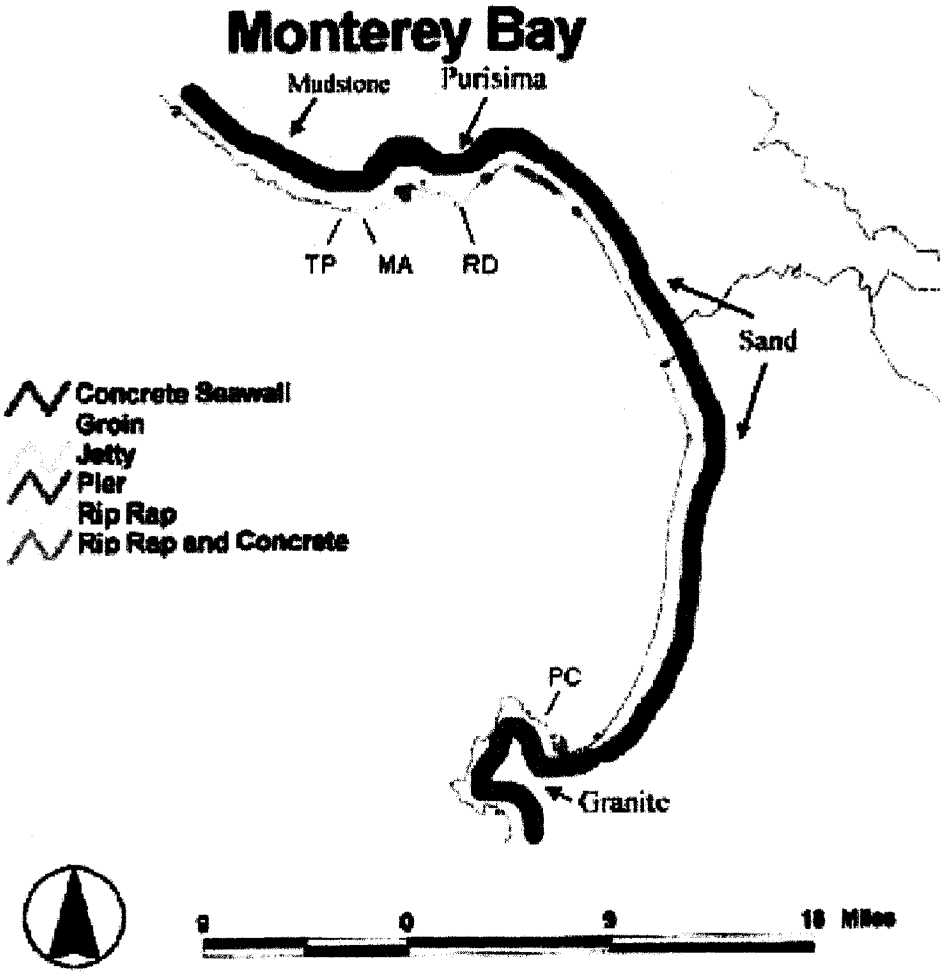
Figure 1. Map of the Monterey Bay in central California (centered at approximately 36° 50' N, 121° 55'W) showing locations of coastal armoring and man-made structures at the land-sea boundary (concrete seawalls, groins, jetties, piers and rip-rap). In addition, the dominant substrate in the intertidal is shown - Santa Cruz Mudstone in red, Purisima in dark blue, Sand in turquoise, and Granite in green. The study sites are also labeled – Terrace Point (TP), Merced Avenue (MA), Rockview Drive (RD), and Point Cabrillo (PC). (Map adapted from K. Patsch, pers. comm., 2005.)



Chapter 2.

Rocky intertidal community structure on different substrates: Comparisons of community assemblages on boulders used for coastal armoring

Rocky intertidal community structure on different substrates: Comparisons of community assemblages on boulders used for coastal armoring

Dawn Alexandra Osborn

ABSTRACT

The extensive anthropogenic armoring of the California shoreline provides an unusual opportunity to determine the effects of substrate type on rocky intertidal community structure. Armoring is a disturbance, covering up native rocks and associated organisms with foreign, introduced hard boulders or concrete. As time passes after the disturbance, new intertidal communities develop on the boulders. A variety of rock types are used, including basalt, sandstone, granite, and limestone. These different rock types are placed side by side in the intertidal, creating excellent conditions for direct field comparisons. Temperature loggers on the different rocks revealed that temperature was significantly warmer on basalt rocks on hot days and mudstone was much cooler. I show that intertidal assemblages on introduced boulders (basalt and sandstone) differ from each other and from those on native mudstone at two sites in Santa Cruz County, California. All organisms were removed, identified and quantified from replicate areas at two sites. Canonical discriminant analysis showed significant differences in community structure among these rock types. There are a series of species that drive the differences in community structure on the different rock types. At both sites *Porphyra* spp. and *Endocladia muricata* distinguished sandstone, and *Lottia austrodigitalis/digitalis* distinguished basalt. *Pancolus californiensis* and *Limonia marmorata* were important in discriminating the

soft, native mudstone at one site. *Chthamalus dalli/fissus* was important in discriminating basalt at one site and *Littorina plena/scutulata* was important in discriminating basalt at the other. These community patterns are probably the result of differences in larval settlement, juvenile recruitment, growth, or survival caused by differences in surface texture, thermal properties, and moisture retention among the different rocks, and these differences demonstrate that the rock substrate itself has a role in determining community structure.

INTRODUCTION

Substrate type is an important yet understated factor structuring rocky marine communities (Moore and Kitching, 1939; Caffey, 1982). The composition of the substrate and the number of microhabitats it contains are two key substrate characteristics and, McGuinness and Underwood (1986) indicated that further investigation is needed to determine the effects of these and other characteristics of substrates on natural communities. In addition, an early species assemblage that is supported by a particular substrate type could affect succession by its subsequent interaction with later assemblages (Bavestrello et al., 2000). Settlement and post-settlement mortality are affected by specific local physical conditions such as coastal morphology, currents, available space, wave action, and the abundance of predators and competitors (Connell, 1985), but little is known with respect to how substrate type influences intertidal assemblages. Moreover, much work has been done examining the mechanisms that determine intertidal zonation patterns (Connell, 1972), but the differences in these patterns with respect to substrate type between shores have been largely neglected. Substrate type varies along the coastline and could be a major factor explaining differences in intertidal community structure and zonation between sites.

Substrate composition and roughness can create different microhabitats (Foster et al., 1988). It has been generally observed that smooth rocks are not as favorable for settlement as irregular ones (Feldman, 1937; Moore and Kitching, 1939; Wethey, 1986; Crisp, 1990). Harlin and Lindbergh (1977) found that surface relief can regulate settlement and growth of marine algal communities. They also noted that patterns in the distribution of algal populations correlated with the size of the graded particles on acrylic settling plates; macroalgae colonized areas with greater surface relief. Den Hartog (1959) found that the upper vertical limit of algal zones was higher on limestone than on basalt. Raimondi (1988) investigated the barnacle *Chthamalus anisopoma* on basalt and granite shores in the northern Gulf of California. He found that its upper vertical limit was 25 cm lower on basalt than on granite, probably because of greater post-settlement mortality on basalt than on granite at the upper limit. This could be due to the thermal capacity of each rock type; basalt was hotter (and darker) than granite. It could also be due to the roughness of the rocks, as he found that basalt, with little surface texture, had significantly higher temperatures during the day than did granite, which had more texture (Raimondi, 1988).

To prevent the effects of coastal erosion, introduced (not naturally occurring in that location) hard substrates have been used to stabilize and armor naturally soft coastlines for centuries. Davis et al. (2002) studied community structure on rip-rap in San Diego Bay where 74% of the natural shoreline is armored with artificial hard substrate (USDON/SWDIV and SDUPD, 2000). They found open-coastal, rocky intertidal species on the granite rip-rap seawalls in the bay, extending the influence of the open coast into the bay. However, they compared these armored sites within the bay to two open coast sites of smooth and conglomerate sandstone 10 and 18 km north of the bay mouth (Davis et al, 2002). No comparison was done on community structure on armored sites and nearby non-armored sites within the bay or on the open coast. Comparing substrate effects is a problem in field observations because substrate variation usually occurs on a large scale, over which other factors also vary. Different rocky substrates rarely occur adjacent to each other where they can be readily compared.

In the present study, two types of hard substrates (boulders of basalt and sandstone) had been placed adjacent to each other and to native mudstone for the purpose of coastal armoring, offering the opportunity to examine how substrate type affects community structure in one location. The main goals of the present study are to: 1) determine if there is a difference in community assemblages relating to different adjacent rock types used to armor a rocky intertidal coastline and if so, 2) to characterize the differences.

METHODS

In April 2001, two rocky intertidal sites were chosen in Santa Cruz County, California. The sites are referred to by the name of the road that dead ends into the ocean leading down to the rocky intertidal. Rockview Drive (RD) is off East Cliff Drive near Soquel Point. Merced Avenue (MA) dead ends onto West Cliff Drive near Natural Bridges State Beach (Figure 1). These sites are to the east and to the west side of the city of Santa Cruz, respectively. The two sites are 6.6 km apart (point to point) and both face south into Monterey Bay. The natural rock substrate at RD is the Purisima Formation of Pliocene age, while MA is Santa Cruz Mudstone of late Miocene age (Clark, 1981). Rocks of the Purisima Formation are slightly "coarser grained" (*i.e.*, contain a bit more sand and silt size grains), typically softer and more porous than the Santa Cruz Mudstone, but both are easily eroded mudstones (Robert Garrison, UC Santa Cruz, pers. comm., 2005).

Basalt and sandstone were introduced as rip-rap boulders approximately 15 years ago to protect these sites (Brian Evers, Santa Cruz Public Works Inspector, pers. comm., 2003) (Figure 2). Native mudstone forms the bedrock at both sites but is not found as boulders. The boulders were placed in the high intertidal zone and had high cover of the alga *Endocladia muricata* and the acorn barnacle *Balanus glandula,* which are distinctive of the high zone in the NE Pacific (Glynn, 1965; Ricketts et al., 1985). I sampled intertidal communities in the *Endocladia-Balanus* zone at both sites. The tidal height of the samples on the boulders was 2.7 m, on average. Three separate basalt and sandstone boulders with a median diameter of about 1 m and similar aspect or orientation to the sea and slopes of approximately 160° were selected for sub-sampling.

At RD, three large outcrops of native mudstone with the same aspect and same tidal height as the rip-rap boulders were selected. The only mudstone at the MA site was a vertical cliff that was not comparable with respect to aspect and slope to the introduced boulders. Therefore, at RD, basalt, sandstone, and mudstone surfaces were compared and at MA, basalt and sandstone were compared.

I removed all algae and invertebrates from three, circular, 15-cm diameter (0.018 m^2) plots on each boulder with a putty-knife and tweezers and put the contents into sealed, labeled Ziploc® bags. The invertebrates and algae collected were immediately brought to the lab and preserved in 70% ethanol. All invertebrates were later identified and counted under a dissecting scope. The algae were separated, identified, oven dried, and weighed. The cleared plots in the field were as similar as possible with respect to position on the different boulders. The circular shape minimized edge effects (Farrell, 1989) and the 15 cm size was similar to algal patch size in the area. In an attempt to simulate a natural disturbance, such as a boulder rolling or banging log (Dayton, 1971), scraping left areas that were barren except for the calcareous barnacle bases and remnants of encrusting algae.

Some species of algae, barnacles, snails and limpets were very difficult to distinguish morphologically and these were not separated (two species indicated by a "/"). For example, *C. fissus* is visually indistinguishable from *C. dalli,* so adults were identified to the genus level only and referred to as *Chthamalus dalli/fissus* (Farrell et al, 1991; Connolly and Roughgarden, 1999). The animal taxa identified and counted were *Balanus glandula* and *Chthamalus dalli/fissus* (common acorn barnacles), *Mytilus californianus* (sea mussel), *Littorina plena/scutulata* (littorine snails), *Lottia austrodigitalis/digitalis* and *Lottia scabra* (limpets), *Lasaea cistula* (small hermaphroditic bivalve), *Limonia marmorata* (dipterid marine fly larva), and *Pancolus californiensis* (tanaid crustacean).The algal species were *Endocladia muricata* (red alga), *Porphyra* spp. (red alga), and *Ulva* spp. (green algae) (Hayden et al., 2003).

Data used for analysis were the counts of invertebrates and the dry weight (grams) of algae. A multivariate technique canonical discriminant analysis (CDA), was used to evaluate which species were driving the differences in community structure. CDA analyzes relationships between sets of variables, with rock type as a grouping variable and all the recorded observations as independent variables. New functions were created that were combinations of the original variables which best discriminate among groups (Tabachnick and Fidell, 1996). The best combination of these variables allowed discrimination between rock types by community structure. In addition, species richness and Shannon-Weiner species diversity function were calculated for each replicate on the different rock types; calculated values were averaged for each rock type and reported. ANOVAs were done for each site separately with rock type as the factor and species richness and diversity as dependent variables.

For comparison of temperature regimes adjacent to the rocks, 9 temperature sensors, called i-buttons®, were deployed at RD on basalt, sandstone, and mudstone where taxa collections were done (average tidal height 2.7 m). The temperature loggers were insulated in a thin layer of z-spar, a marine epoxy resin, and attached directly onto the rocks. One mudstone i-button corrupted in the salt water or was damaged by a direct hit by a rock/log. Temperature data from i-buttons on three basalt, three sandstone and two mudstone boulders were logged every 10 minutes for 44 days (Julian day 63-106) in 2002 for a spring estimate of rock temperature during a time when temperature extremes would be modest. These temperature data were downloaded from the i-buttons with a laptop computer in the field.

Upon first analysis of the temperatures, it was apparent that there was no difference between the different rock types because of the over riding ocean temperature signal when the loggers were underwater (average ocean temperature during these 44 days was 11.9°C). But this could also be the case when the low tide was at night, exposing i-buttons to the same air temperature. Therefore, the exact time of day for each logged temperature was matched with the tidal height so temperature data taken during darkness, 1600-0900, and when i-buttons were underwater (tidal level 2.5 and higher) were omitted from the analysis. Only temperature data logged during daytime low tides were considered.

RESULTS

The invertebrate species found on different rock types at RD and MA were similar. Most of the invertebrates were observed on all rock types but their abundances varied. The most abundant invertebrate taxa were *Balanus glandula* and *Chthamalus dalli/fissus, Mytilus californianus, Littorina plena/scutulata, Lottia austrodigitalis/digitalis, L. scabra, Lasaea cistula, Limonia marmorata,* and *Pancolus californiensis.* The most abundant algal taxa were *Endocladia muricata, Porphyra* spp., and *Ulva* spp. Other species were observed but not abundant enough for the statistical analysis - these include *Syllis* spp., *Lottia gigantea, Lottia paradigitalis,* little black limpets, *Cladophora columbiana, Ralfsia* spp., crustose corallines, and diatoms.

ANOVAs showed the only significant differences between the rock types at either site were with the diversity and richness of algae at RD ($p<0.05$) (Table 1). Otherwise, there were no significant differences between the rock types. The species diversity and species richness of invertebrates and algae was highest on the sandstone at both sites. At RD, the mudstone had the second highest diversity of invertebrates but only one species of algae (*Ulva* spp.), so the algal diversity was zero. Mudstone had the lowest species richness. At MA, the diversity of invertebrates on sandstone and basalt was nearly the same, but sandstone had one additional species.

Canonical discriminant analysis (CDA) led to a high degree of classification and the identity of the substrate from the community structure was highly significant at both sites (MANOVA, Rockview Drive $p<0.001$, Merced Avenue $p<0.01$). Certain species were important in discriminating between rock types and species can be ranked by their order of importance. Loadings are the relationship between the raw data and the factor scores and allow the species driving the differences in community structure on different rock types to be discerned. The discriminant function loadings for the species at each site are shown in Table 2 and 3.

Table 1. The species diversity and richness (invertebrates and algae, separate and combined) for each site, Rockview Drive (RD) and Merced Avenue (MA). There was a significant difference in the diversity and richness of algae between the rock types at RD.

RD	**Diversity Invertebrates**	**Diversity Algae**	**Richness Invertebrates**	**Richness Algae**	**Richness Combined**
Basalt	1.285868855	0.126419367	8	3	11
Sandstone	1.772615064	0.513550924	11	3	14
Mudstone	1.633409792	0	8	1	9
MA					
Basalt	1.540965824	0.384073979	9	2	11
Sandstone	1.564922099	0.66644265	9	3	12

Table 2. These are the discriminant function loadings between the discriminant scores and the original variables for species at Rockview Drive. Loadings represent Pearson correlation coefficients.

Species	**Score 1**	**Score 2**
Balanus glandula	-0.276	0.198
Chthamalus dalli/fissus	-0.638	-0.492
Mytilus californiensis	-0.272	0.150
Littorina plena/scutulata	-0.357	0.225
Lottia scabra	-0.209	0.439
Lottia austrodigitalis/digitalis	-0.208	-0.495
Lasaea cistula	-0.208	0.348
Limonia marmorata	0.509	0.104
Pancolus californiensis	0.627	0.030
Endocladia muricata	-0.602	0.422
Porphyra spp.	-0.311	0.402
Ulva spp.	0.185	0.346
Other algae	0.143	0.012

Table 3. These are the discriminant function loadings between the discriminant scores and the original variables for species at Merced Avenue. Loadings represent Pearson correlation coefficients.

Species	**Score 1**
Balanus glandula	-0.063
Chthamalus dalli/fissus	-0.091
Mytilus californiensis	0.167
Littorina plena/scutulata	-0.349
Lottia scabra	-0.201
Lottia austrodigitalis/digitalis	-0.378
Lasaea cistula	0.153
Limonia marmorata	0.288
Pancolus californiensis	0.224
Endocladia muricata	0.446
Porphyra spp.	0.450
Ulva spp.	0.285
Other algae	0.427

Canonical scores plotted for RD show 95% confidence ellipses for factor 1 vs. factor 2 for nine plots on each rock type from the CDA done on the abundance of all invertebrates and the dry weight of algae (Figure 3). The discriminant function analysis for RD indicated that rock type could be clearly distinguished by community assemblage (Pillai's trace = 1.661; Approx. F = 4.892; df = 26, 26; p=0.0001). The intertidal community on basalt could be correctly identified 89% of the time, on sandstone 100% of the time and on mudstone 100% of the time, for a total of 96% correct classification.

Sandstone, basalt and mudstone communities were significantly different and specific species were important in discriminating between the different rock types. The abundances of species on each rock type are shown in Figure 3. The mudstone community was most distinct from those on the hard, introduced rocks and was characterized by high abundance of *P. californiensis* and *L. marmorata*. The algae *Porphyra* spp. and *E. muricata* and limpet *L. scabra* were associated with sandstone rocks while *L. austrodigitalis/digitalis* and *C. dalli/fissus* were associated with basalt. The algae *E. muricata* and *Porphyra* spp. were not found on mudstone at all. *B. glandula*, *M. californianus* and *L. plena/scutulata* and *L. cistula* showed no particular substrate pattern between sandstone, basalt and mudstone, although they were all slightly more abundant on sandstone. *Ulva* spp. did not discriminate between substrates but was more abundant on mudstone and sandstone. *P. californiensis* was almost exclusively seen on mudstone (Figure 4).

CDA also revealed a high degree of classification of community structure related to rock type at the MA site (MANOVA, $p<0.01$). CDA was done on the abundance of all invertebrates and the dry weight of algae. Canonical scores plotted for MA show the frequency distribution of scores grouped by rock type (Figure 5). The discriminant function analysis for MA indicated that rock type (sandstone and basalt) could be clearly distinguished by the species present (Pillai's trace = 0.855; Approx. F = 6.612; df = 8, 9; p = 0.0052). The intertidal community on both basalt and sandstone could be identified 100% of the time.

Three species showed the same substrate abundance pattern at MA and RD – *Porphyra* spp. and *E. muricata* were associated with sandstone and *L. austrodigitalis/digitalis* was associated with basalt (Figures 3 and 5). In addition, *L. marmorata* was important in discriminating sandstone and *L. plena/scutulata* and *L. scabra* were important in discriminating basalt at MA. *B. glandula*, *C. dalli/fissus*, *M. californianus*, and *P. californiensis* were not significantly associated with a particular rock type at MA (Figure 6). Although the associations were not significant, *M. californianus* was more abundant on sandstone at both sites while *B. glandula* was more abundant on sandstone at RD and almost equal on the rock types at MA. *C. dalli/fissus* was a discriminating community member on basalt at RD and although not significant, more abundant on basalt at MA as well (Figures 4 and 6). *P. californiensis* was a distinguishing community member on mudstone at RD and at MA was seen on the coolest rock type, the sandstone. Two species that were distinguishing community members on a rock type at one site switched patterns and were distinguishing community members on a different rock type at another site. *L. scabra* distinguished sandstone at RD and basalt at MA; *L. marmorata* distinguished mudstone at RD and sandstone at MA (Figures 4 and 6).

Analysis of the temperature data from the i-buttons adhered to the different rock types using a GLM model showed that there was a significant interaction between day and rock type ($F = 2.445$, $df = 78$, $p < 0.001$)(Figure 7). On cold days the temperatures were similar on all rock types. However, on warm days, the basalt was significantly warmer than the other 2 rock types; sandstone was the second warmest. Mudstone was almost always the coolest rock. On cold days, the mudstone was much cooler that the other 2 rock types (Figure 8). The average temperature on the basalt rocks was 25.5°C (±5.5°C), on sandstone 22.1°C (±5.3°C), and on mudstone was 20.5 °C (±4.0°C).

DISCUSSION

The high intertidal zone along the central California coastline is usually dominated by an *Endocladia muricata - Balanus glandula* assemblage (Ricketts et al., 1985). Over 90 species of plants and animals have been found in the *Endocladia-Balanus* assemblage at sites in Monterey Bay, CA (Glynn, 1965). The present study shows a pattern of distinct rocky intertidal communities on different rock types examining only $0.26m^2$ of area on three rock types, consisting of approximately 20 species in this assemblage. This pattern could be due to differences in the settlement and survivorship capabilities of intertidal plants and animals on different rock types with varying surface temperatures, water retention capabilities, and surface roughness.

The limpets *L. austrodigitalis/digitalis* and *L. scabra* were distinguishing community members with different abundance patterns on the different substrates. *L. austrodigitalis/digitalis* was important in discriminating basalt at both sites and *L. scabra* was significant in discriminating sandstone at RD and to a lesser degree, basalt at MA. *L. austrodigitalis/digitalis* and *L. scabra* are mobile animals frequently present on the open rock surface; *L. digitalis* is thought to be more abundant on vertical rock surfaces while *L. scabra* more dominant on horizontal rock surfaces (Haven, 1973). However, the samples in this study were all taken from rocks with the same aspect so this vertical vs. horizontal preference would not explain the limpets living more abundantly on different rock types. Consequently, this pattern of *L. austrodigitalis/digitalis* on basalt and *L. scabra* on sandstone may not be related to a species association or the aspect of the rock but a preference for a specific rock type. Interestingly, *L. digitalis* has a higher vertical distribution than *L. scabra* (Haven, 1973), and therefore may be able to tolerate higher temperatures and more desiccation stress. I found *L. austrodigitalis/digitalis* more abundantly on basalt rocks, which get hotter than the sandstone rocks on hot days. *L. scabra* was more abundant on sandstone. The physiological capabilities of *L. digitalis* have not been examined however, *L. scabra* was shown to produce a highly complex group of low molecular weight stress proteins (heat shock proteins, HSPs) and many isoforms of Hsp60 to handle heat stress better than *L. pelta* (Sanders et al., 1991). In addition, *L. scabra* may be able to hide in/under moist algae that are more abundant on the sandstone than basalt. *L. austrodigitalis/digitalis* could be physiologically more able to tolerate the higher temperatures of basalt rocks than *L. scabra* or *L. pelta* by synthesizing HSPs upon exposure to higher heat conditions. Further research should examine the heat shock response in *L. austrodigitalis/digitalis* measuring the heart rate as temperature increases.

Dayton (1971) believed that the major space consuming animal species have a greater ability to withstand desiccation stress than algal species, suggesting that the distribution of sessile animals is less likely to be determined by physiological stress than is the distribution of algal species. In Monterey Bay, the algal species were distinguishing residents of the intertidal community on sandstone and mudstone, the coolest rock types. Algae were not an abundant community member on the basalt at either site, the hottest rock. At both RD and MA, *Porphyra* spp. and *E. muricata* were distinguishing community members discriminating sandstone, the rock type that is cooler than the basalt but not as cool as mudstone. Tolerance to dehydration in *Porphyra perforata* has been correlated with tidal height at sites near Monterey. *P. perforata* was shown to be more tolerant of high temperature, low temperature and dehydration treatments when compared to other low tide algal species (Smith and Berry, 1986). *E. muricata* was also important in discriminating sandstone rocks which may have to do with its longevity; it is not an ephemeral alga and sandstone is more stable than mudstone over time. *Ulva* spp. was associated with sandstone at RD and more abundant on the coolest rock types compared to basalt, mudstone and sandstone, at RD. *Ulva* spp. has been seen to die out faster when exposed to harsh, dry, physical conditions, such as low tides in the afternoon (Sousa, 1979). *Ulva* spp. and *Porphyra* spp. are ephemeral algae and may be found on the coolest substrate in the area. Environmental factors have been shown to influence photosynthesis rates and recovery after heat/desiccation stress and ultimately, to affect the distributional patterns of marine algae in the intertidal. In addition, algal species may be more sensitive to desiccation stress than invertebrate species.

The smaller acorn barnacle, *C. dalli/fissus*, was a distinguishing member of the intertidal community on basalt rocks, the hottest substrate. *B. glandula* was not important in discriminating any of the rock types. It was found on all rock types at both sites. In Scotland, Connell (1961) studied competition between a species of *Chthamalus*, the upper intertidal zone species, and *Semibalanus balanoides*, the lower zone resident, testing the hypothesis that interspecific competition for space was the reason behind the zone partitioning. He found that *Chthamalus* was tolerant of a much greater degree of emersion than it normally encounters but probably was not found lower because of lack of initial settlement or poor survival of recruits because of competition with *Semibalanus.* Connell concluded that in the upper limits of distribution, *Chthamalus* exists higher than *Semibalanus* as a result of its greater tolerance to heat and/or desiccation. *Chthamalus* is more resistant to thermal stress and desiccation and, therefore, better adapted for survival on hotter rocks, like basalt. Connell's findings match this study's results showing that *C. dalli/fissus* was more tolerant of and more abundant on the hotter rock type, although this species was found on all rock types examined. *B. glandula* was able to survive on all the rock types fairly equally at both sites. However, the two barnacle genera were not found in the same abundance – *C. dalli/fissus* adults were three times more abundant overall at RD and twice as abundant as *B. glandula* at MA.

At Santa Cruz sites, *Limonia marmorata* (crane fly, dipterid) was a distinguishing community member on sandstone at MA and mudstone at RD. In Monterey, Glynn (1965) found *L. marmorata* larvae most often present in the dense holdfasts of *E. muricata*. These larvae were probably able to find refuge in *E. muricata* on sandstone at MA and with *Ulva* spp. on mudstone at RD. At both sites, *L. marmorata* larvae were found on the coolest substrate associated with algae they could potentially find refuge in and their abundance pattern on different rocks may be due to a necessary association for survival. *P. californiensis* was also important in discriminating mudstone at RD, however, very little is known about this species. *P. californiensis* is usually common in the high intertidal associated with *Cladophora* spp. (Smith and Carlton, 1975) and that fits with its abundance on the coolest substrate where *Ulva* spp. was abundant in this study. *Littorina plena/scutulata* were distinguishing community members on basalt at MA. These snails are commonly found on bare rock or in close association with *B. glandula* and *E. muricata* holdfasts (Glynn, 1965). Other species of littorines have been shown to withstand temperatures as high as 32°C (Cannon and Hughes, 1992) and the average temperature of the basalt, the hottest rocks, was 25.5°C, well below their thermal limits. In addition, littorines thermal tolerance has been shown to vary extensively between populations and seasonally, suggesting that the species has the ability to adapt to different thermal regimes (Clarke et al., 2000).

We do not know the life spans or turnover rates for most of the species in the *Endocladia-Balanus* assemblage (Foster et al., 2003). Glynn (1965) saw little seasonal variation and year to year variation in assemblage structure. Foster et al. (2003) concluded that the *Endocladia* assemblage along the coast of California differed in species richness and relative abundance from site to site but showed little seasonal (spring-fall) or year to year variation in the abundances of common species. It seems reasonable then to examine this collection of species from one time period at Santa Cruz sites and compare the community structure on the different rock types. These communities have been maturing for at least 15 years since the rip-rap rocks were added.

Coastal armoring is increasing as the shoreline continues to erode from the scouring of incoming waves. Although biominerology has been determined to influence marine assemblages (Faimali et al., 2004; Guidetti et al., 2004), it is still poorly known how the nature of substrates regulate settlement patterns of invertebrate larvae. Rocky intertidal animals and algae collected on three different substrates showed important discriminating patterns of abundance. The species diversity and species richness of invertebrates and algae was highest on the rip-rap sandstone at both sites, even compared to the native mudstone. Based upon my results, there is a strong likelihood that different community structures will develop on the different rocks used for armoring. If that is the case, the communities that exist on native rocks may be replaced by communities that favor the rip-rap rocks as that substrate increases along the shoreline. Over time, species assemblages and communities would not be the same as they are today. Some reasons for the emerging pattern of intertidal species preferring certain rock types have been discussed above, however experiments transplanting plates of different rock types side by side in the intertidal examining assemblages settling over time would help resolve whether these differences are due to larval recruitment or post-settlement growth, survival, and succession. Future work should explore community structure on different rock types in the field.

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Figure 1. Map of the Monterey Bay in central California (centered at approximately 36° 50' N, 121° 55'W) showing locations of coastal armoring and man-made structures at the land-sea boundary (concrete seawalls, groins, jetties, piers and rip-rap). In addition, the dominant substrate in the intertidal is shown - Santa Cruz Mudstone in red, Purisima in dark blue, sand in turquoise, and granite in green. The study sites are also labeled – Merced Avenue (MA) and Rockview Drive (RD) (Map adapted from K. Patsch, pers. comm., 2005.)

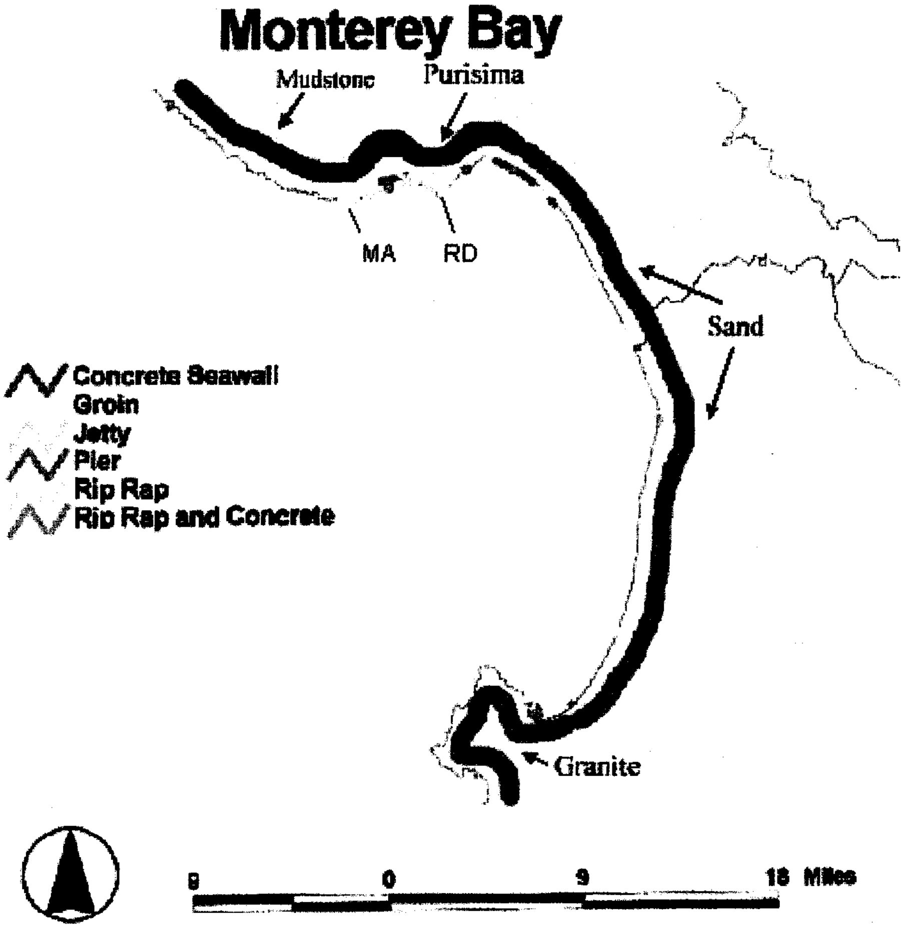
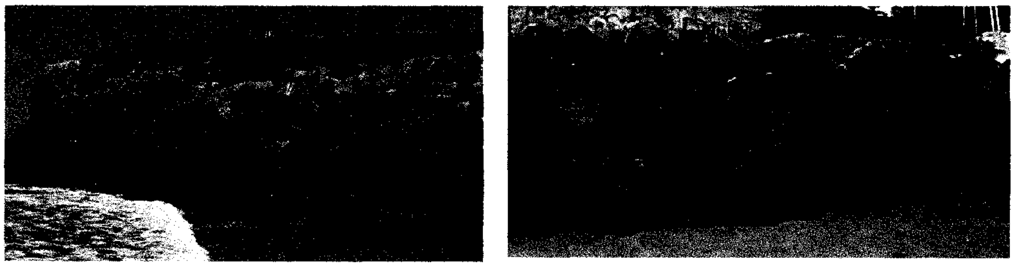


Figure 2. Photographs of the sites and an example of the cleared plots on a sandstone boulder. Cleared plots were 15-cm diameter (0.018 m^2).



Merced Avenue

Rockview Drive

Clearings

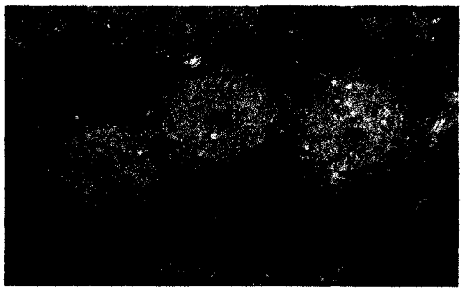


Figure 3. The relationship of the nine plots sampled on each rock type at RD and the scores from the canonical discriminant analysis. Within the groups, rock type is coded by color – sandstone is green, basalt is red and mudstone blue. The communities are different and species that strongly discriminate between rock types were placed on the axes and ranked in order of their importance. The classification matrix had 96% accuracy. The * indicates species that were significantly more abundant on that rock type at both RD and MA.

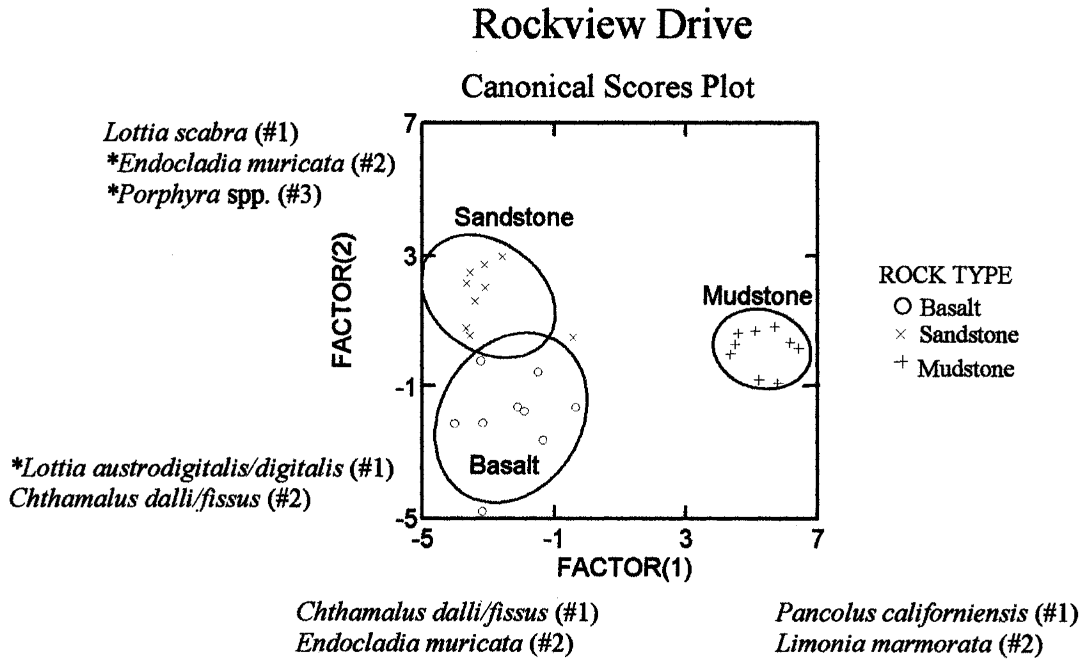


Figure 4. The abundance of each species on the three different rock types at RD. The species with an "S*" above sandstone were important in discriminating ($p<0.05$) sandstone, the species with a "B*" above basalt were important in discriminating basalt, the species with an "M*" were important in discriminating mudstone. The bottom row includes species that did not show a particular association with a substrate. Error bars are standard error, indicating within group variability. Note: the y-axis is scaled differently for each species; count for invertebrates and dry weight (grams) for algae.

Rockview Drive

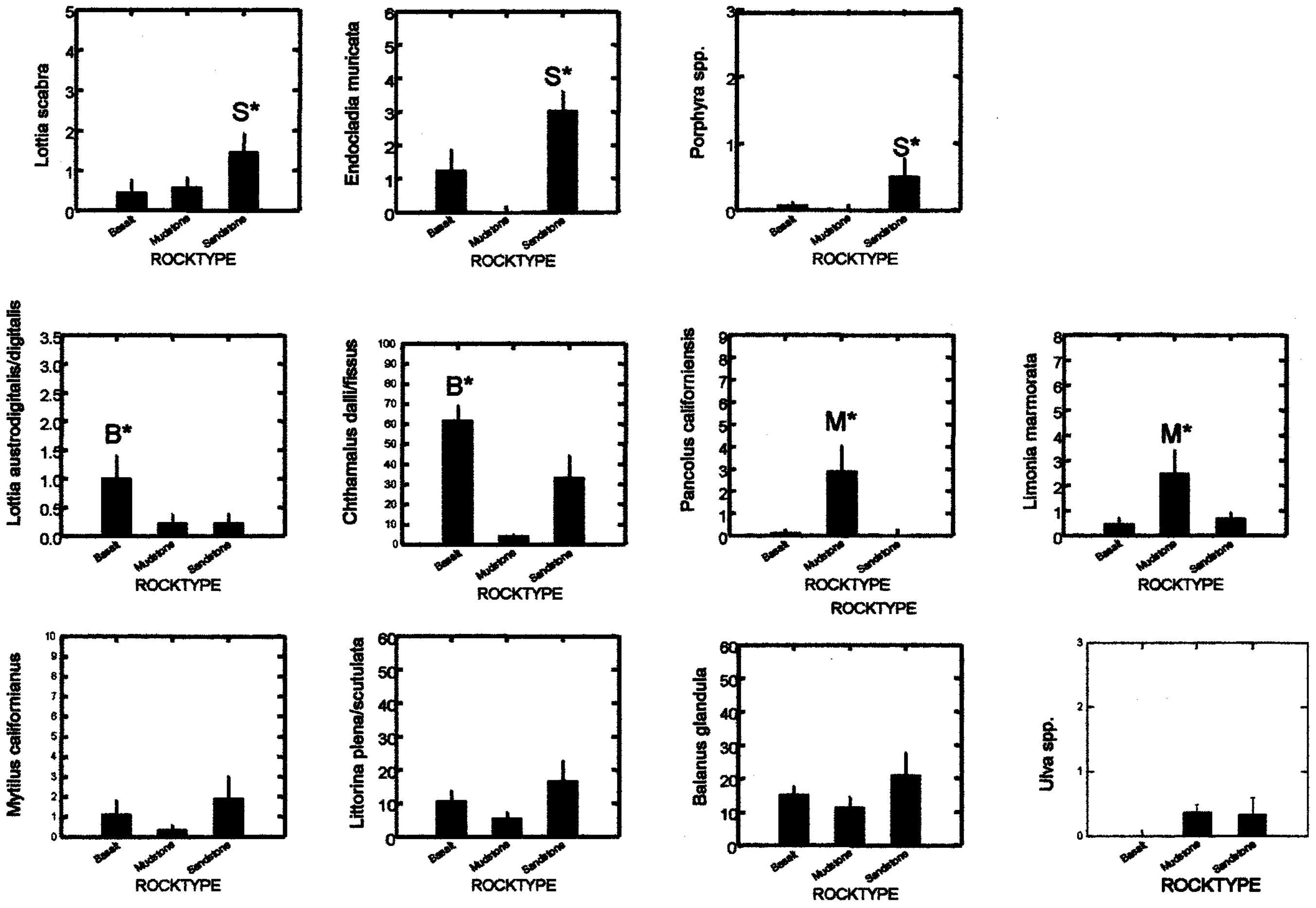
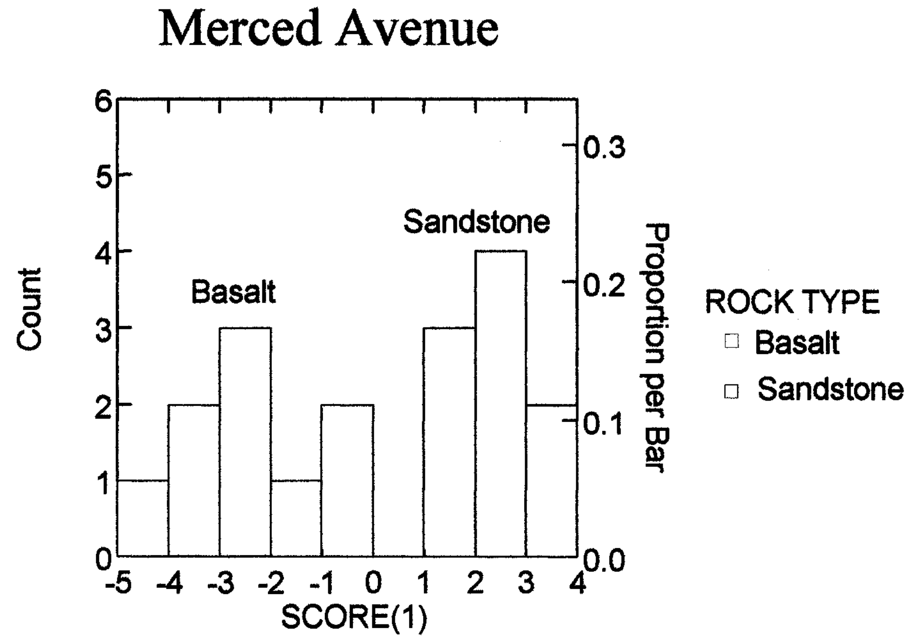


Figure 5. The frequency distribution of scores for nine plots sampled on each rock type at MA. Within the groups, rock type is coded by color –basalt is red and sandstone is blue. Species that strongly discriminate between rock types are specified on the axes and ranked in order of their importance. The classification matrix had 100% accuracy. The * indicates species that were significantly more abundant on that rock type at MA and RD.



**Lottia austrodigitalis/digitalis* (#1)
Littorina plena/scutulata (#2)
Lottia scabra (#3)

**Porphyra spp.* (#1)
**Endocladia muricata* (#2)
Limonia marmorata (#3)
Ulva spp. (#4)

Figure 6. The abundance of each species on two different rock types at MA. The species with an "S*" above sandstone were important in discriminating sandstone ($p<0.05$) and the species with a "B*" above basalt were important in discriminating basalt. The bottom row includes species that did not show a particular association with a substrate. Error bars are standard error, indicating within group variability. Note: the y-axis is scaled differently for each species; count for invertebrates and dry weight (grams) for algae.

Merced Avenue

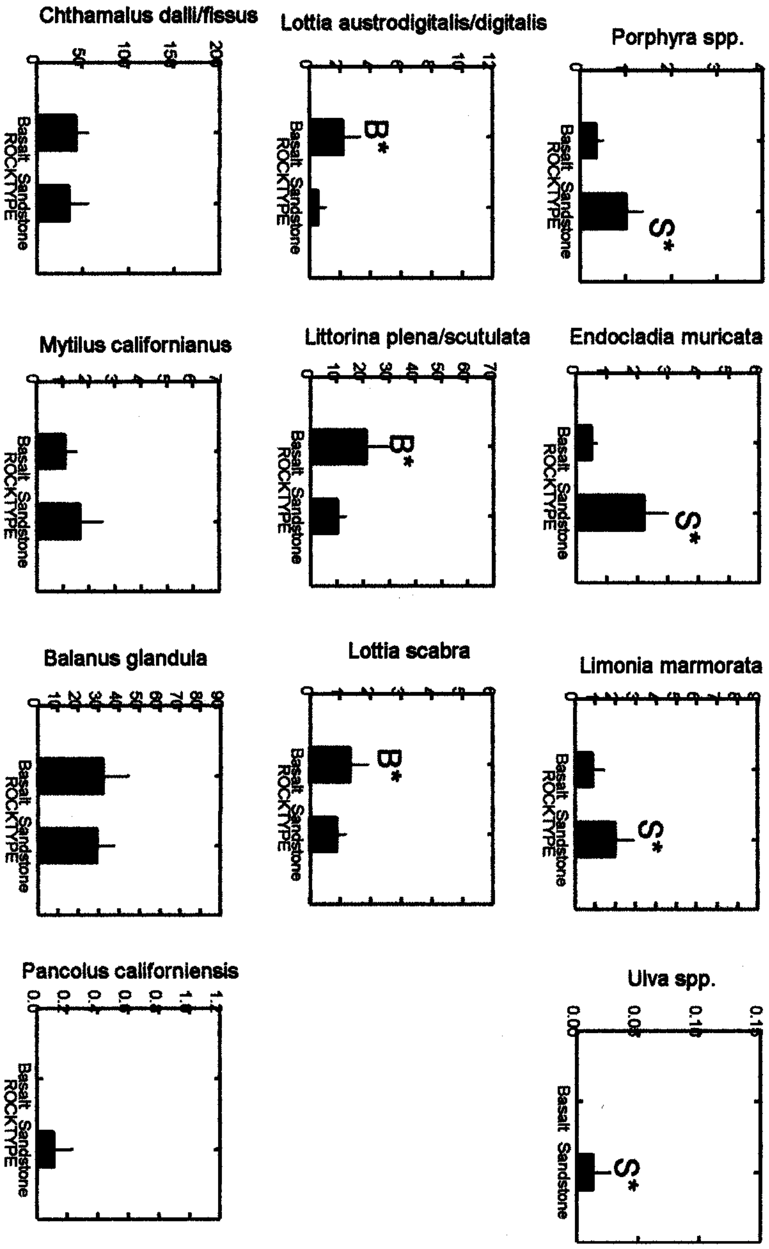


Figure 7. Exposed day time temperature (°C) between March 5 and April 15 on three different rock types. Basalt is shown as a solid red line, mudstone a dotted blue line and sandstone, a dashed green line. Basalt temperatures are warmer on warm days, while on colder days, basalt and sandstone are similar. Mudstone does not get as cold or as warm as the basalt or sandstone. There was a significant rock type by day effect ($p<0.05$).

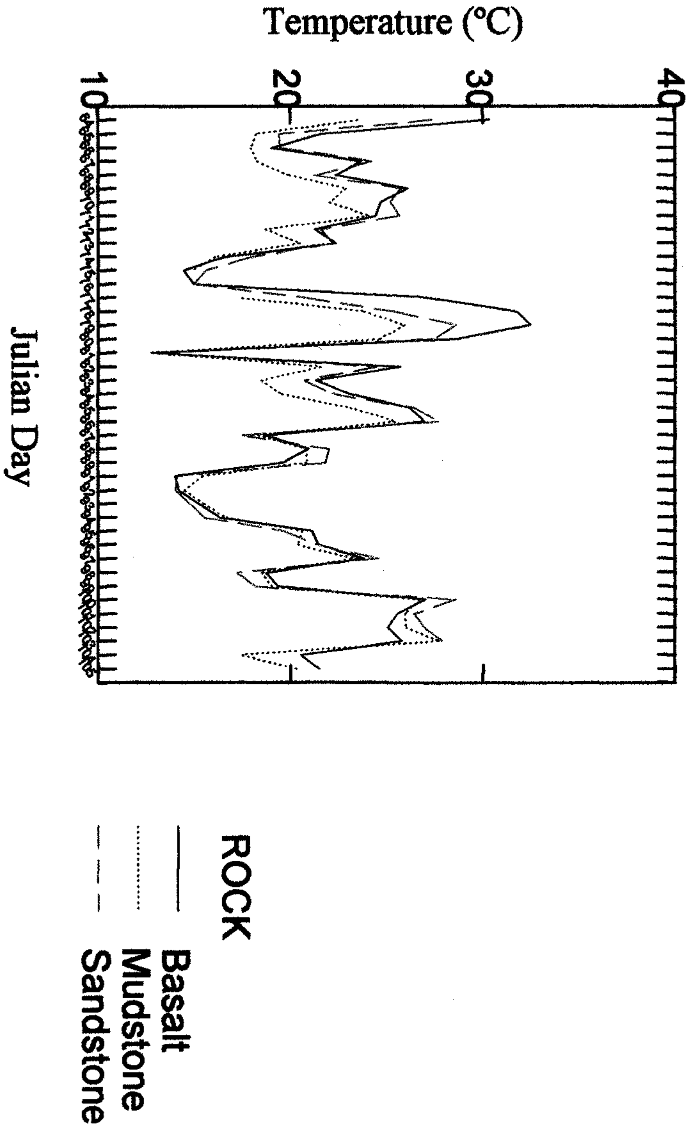
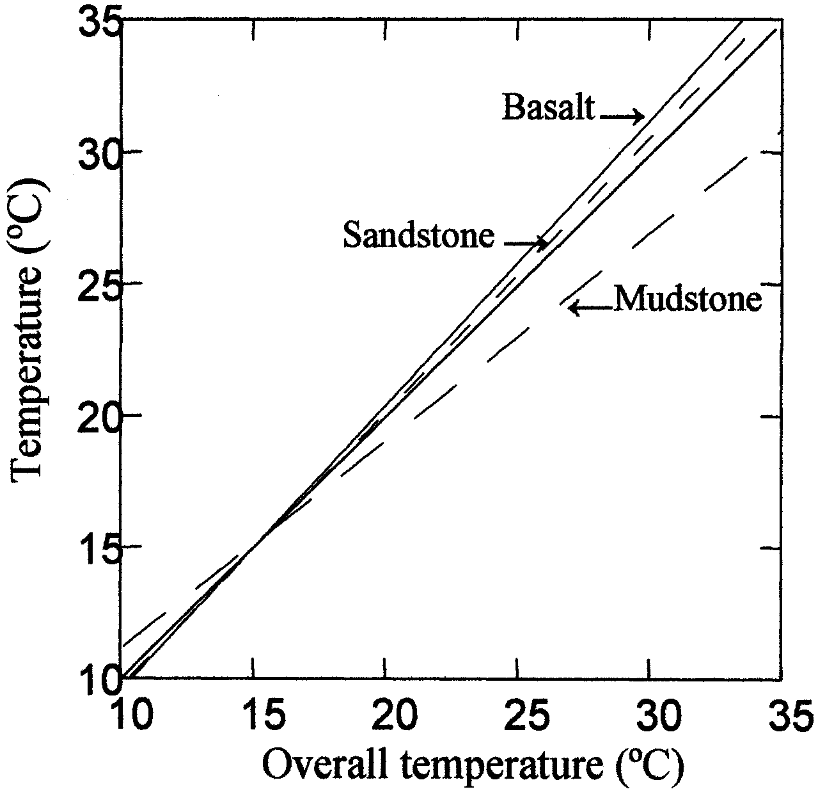

Temperature (°C)
10
20
30
40
Julian Day
ROCK
Basalt
Mudstone
Sandstone

Figure 8. The temperature (°C) of each rock type showing the deviation from the expected temperature calculated across all rock types. The solid black line is the expected temperature – the average temperature across all three rock types. Basalt is the solid blue line, sandstone the short-dashed blue line, and mudstone the long-dashed blue line. Basalt and sandstone are warmer than the overall composite expected temperature and mudstone is cooler than the overall temperature. The equations of the lines are: basalt temperature = 1.08 overall + -1.24; sandstone temperature = 1.04 overall + -7.0; mudstone temperature = 0.787 overall + 3.29.



Chapter 3.

Rocky intertidal barnacle recruitment on different substrates: An experimental test of recruitment on different rock types

Rocky intertidal barnacle recruitment on different substrates: An experimental test of recruitment on different rock types

Dawn Alexandra Osborn

ABSTRACT

Coastal armoring changes the rock substrates available to pelagic larvae settling in the intertidal. It is still poorly known how the nature of substrates regulate invertebrate larval recruitment patterns. To examine the effects of different substrates on recruitment, I deployed plates of four different rock types (basalt, granite, sandstone, slate) in a randomized block design at northern and southern sites in Monterey Bay, California, and compared recruitment on the plates and on the native bedrock at each site (mudstone in the north and granite in the south) from April 2002 to April 2004. Approximately every 45 days for two years, I counted barnacle recruits in the field and every 90 days, on average, I sterilized the plates for the next recruitment period. Analysis of variance indicated that the recruitment of acorn barnacles, *Balanus glandula* and *Chthamalus dalli/fissus*, showed significant differences on different substrates. *B. glandula* recruits were significantly more abundant on native bedrock at both sites; *C. dalli/fissus* recruits were significantly more abundant on sandstone and native mudstone at the northern site. Both species had significantly lower recruitment onto slate. In addition, mean *C. dalli/fissus* recruitment was more than five times greater at the northern site than at the southern site per recruitment period; whereas *B. glandula* had similar but much lower recruitment at the two sites. Examination of temporal trends of recruitment revealed several synchronous peaks for each species during the two years monitored but much variation, especially with *C. dalli/fissus*, which showed more extended recruitment. This study indicates that coastal armoring, which changes the rock type available to settling invertebrate larvae, may change intertidal acorn barnacle recruitment and potentially affect intertidal community structure.

INTRODUCTION

Differences in the composition and surface texture of rock substrates on different shores have been shown to influence intertidal community structure (Raimondi, 1988; Fletcher and Callow, 1992; Davis et al., 2002). In a previous study, I found that different intertidal community assemblages exist on rocks of varying mineralogical composition that were placed adjacent to each other (Chapter 2), supporting the hypothesis that the rocks themselves have a role in determining community structure. There were a series of species that drove the differences in community structure on the different rock types. At one site in Monterey Bay, California, *Chthamalus dalli/fissus* was significantly more abundant on basalt than on mudstone or sandstone while *Balanus glandula* did not show a substrate preference. At both sites, *Porphyra* spp. and *Endocladia muricata* distinguished sandstone, and *Lottia austrodigitalis/digitalis* distinguished basalt. These community patterns probably are the result of differences in larval settlement, juvenile recruitment, growth, or survival caused by differences in surface texture, thermal properties, and moisture retention among the different rocks, and the community patterns demonstrate that the rock substrate itself has a role in determining community structure. One possibility explaining why community structure varies on different rock types is that the different rocks are affecting recruitment (*i.e.,* settlement and early post-settlement survival) differently.

Substrate characteristics have been shown to attract or repel invertebrate larvae and algal spores (Harlin and Lindbergh, 1977; Butman et al., 1988; McGuinness, 1989; Fletcher and Callow, 1992; Hadfield, 1998). Most sessile intertidal organisms have pelagic, dispersive larvae that find new habitats and substrates suitable for settlement. A proper settlement site is key to survival and the first step in settlement is attaching to the appropriate substrate. Settling marine larvae are exposed to numerous chemical, physical and biological cues as they near the substrate. Cues may be color (Yule and Walker, 1985), surface texture or rugosity (Crisp and Barnes, 1954; Barnes, 1956; Crisp, 1990) bioorganic films (Keough and Raimondi, 1995; Lau et al., 2002; Dahms et al., 2004), thermal capacity (Raimondi, 1988), mineralogy (Cerrano et al., 1999) or the presence of adult conspecifics (Raimondi, 1988; Jensen and Morse, 1990; Toonen and Pawlick, 1996, 2001; Zhao and Qian, 2002). Barnacle larvae in particular have been shown to have strong preferences in their choice of settlement surfaces (Wethey, 1986; Holmes et al., 1997). For example, cyprids of *Chthamalus* and *Balanus* species have been shown to prefer pits and grooves on the surface of a substrate compared to smooth surfaces (Huxley et al., 1984; Crisp, 1990). This paper examines the recruitment of rocky intertidal barnacles on five different substrates in the field, including native rocks and substrates used for coastal armoring.

What substrate larvae settle on is critical for their subsequent growth and survival. The process of settlement begins when larvae disseminating through the ocean currents contact a solid object. Larvae interact with surface properties and choose or reject the substrate. If the substrate is selected, the organisms must adhere sufficiently to survive the wave action. For barnacles, the adhesion process includes the cyprid larvae walking on two antennules which adhere temporarily by attachment organs (Crisp et al., 1985). Minute hairs and sense organs open to the surface and at fixation, a larval bioadhesive is discharged from a cement gland through pores in the attachment disc and embeds the cyprid ventral surface. Up to a week after this metamorphosis the basal area adheres to the substratum and as the adult develops, secondary cement glands are formed whose ducts open through the base of the barnacle spreading rings of cement between the base and substrate for attachment (Crisp et al., 1985). Larvae are not able to change substrates after settlement so their growth and survival is dependent on appropriate habitat choice.

Groppelli et al. (2003) showed that for sessile marine tunicates, the selection of a suitable substratum by the larvae was a critical factor determining the distribution of species. They examined the role of the mineral content of the substratum in the settlement of the ascidian *Phallusia mammillata*, using siliceous and carbonaceous stones in the laboratory. Larvae could discriminate between the substrata on the basis of the silica content. In addition, larvae that attached to siliceous stones grew faster and had a wider area of contact with the substratum than those that grew on carbonaceous stones. They concluded that silica is a mineral factor that can be discriminated by chemosensory palps of ascidian larvae during the choice of substratum and suggest that the mineral composition of the habitat can contribute, with other environmental factors, to regulating the spatial distribution of tunicate communities.

This and other recent work indicates that larvae respond to biomineralogy and biofilms when choosing a substrate for settlement (Cerrano et al., 1999; Zhao and Qian, 2002), and certain rocks/substrates might enhance different biofilms (Faimali et al., 2004). The settlement of a *Balanus* species significantly differed among substrates and the developmental pattern of biofilm assemblages changed with substrate. In addition, the attractiveness of the different substrates to larvae tended to disappear with biofilm age (Faimali et al., 2004). Cerrano et al. (1999) introduced the term 'biomineralogy' to refer to the relationship between mineralogical features of a substrate and biological systems (cell, organism, species, community). Mineralogical features of substrates were observed to influence infaunal colonization in marine soft bottom communities (Cerrano et al., 1999), hydroid settlement and epibenthic community structure in marine sublittoral rocky substrates (Bavestrello et al., 2000), and barnacle larval settlement (Faimali et al., 2004) to name a few. No direct experimental evidence has been provided yet to describe the specific mechanisms through which rock type may affect marine organisms (*e.g.,* composition, texture, microtopography, epibiotic cover), however, there is increasing evidence that mineralogical properties of rocks could affect marine communities both directly and indirectly (Bavestrello et al., 2000; Cattaneo-Vietti et al., 2002; Guidetti and Cattaneo-Vietti, 2002; Guidetti et al., 2004). For example, the presence of quartz grains in sediments has inhibited animal colonization in marine benthic communities (Cerrano et al., 1999). For some time the negative biological effects of quartz have been known to be due to the oxidant properties of the crystal surface that generate silicon-based radicals and to the formation of –OH radicals in the surrounding environment, increasing the biological reactivity of the crystals (Marasas and Harington, 1960; Vallyathan et al., 1988; Cerrano et al., 1999).

It is important to characterize the intertidal community structure on different rock types because 86% of California's 1,770 km coastline is actively eroding (Griggs, 1999). To counter this erosion, armoring of the coastline is increasing. Armoring alters the substrates encountered by settling larvae from the native rock types to harder, more erosion resistant boulders. Approximately 165 km or 14% of the state's more developed 1,160 km coastline from Marin County to the US/Mexico border are presently armored; 93 km (56%) of this armoring protects back beach development, harbors, low bluffs, and dunes while the remaining 72 km (44%) of the armoring protects seacliffs (Runyan and Griggs, 2003). Although little attention is generally paid to the ecological consequences of armoring, changing the substrate available to settling larvae does affect intertidal community structure (Raimondi, 1988; Davis et al., 2002; Chapman, 2003; Osborn, Chapter 2). Ecologists and environmental planners must work together to minimize the effects of altering the substrate on rocky intertidal communities.

This chapter experimentally examines the possibility that different rocks affect rocky intertidal communities through their effects on recruitment. Settlement plates of four different rock types (basalt, granite, sandstone, slate) were deployed in the intertidal on two sides of Monterey Bay, California with different bedrocks, mudstone and granite. Although the recruitment of several invertebrate and algal species were recorded on the different substrates, this chapter focuses on the recruitment of the two most abundant species – the barnacles *Balanus balanoides* and *Chthamalus dalli/fissus*. *C. dalli/fissus* produce larvae throughout the year with a lull in the winter, while *B. glandula* produces larvae in winter and spring (Hines, 1978). Larval concentrations vary both spatially and temporally (Gaines et al., 1985). This recruitment study was performed over a two year period to encompass several settlement cycles.

METHODS

Sites and rock substrates

Recruitment plates were deployed at two sites, one on each side of Monterey Bay, California (Figure 1). These sites have different bedrock and exposure. The northern site is Terrace Point (TP), below Long Marine Laboratory (UC Santa Cruz). TP is an intertidal bench with Santa Cruz Mudstone as the main bedrock, which has a low stability and is easily eroded. This intertidal bench faces southwest, away from the predominantly northwesterly swells. The southern site is Point Cabrillo (PC) at Hopkins Marine Station (Stanford University), a granitic outcrop and a harder, more erosion-resistant rock. It faces northeast and is more directly exposed to the northwesterly swells. Both sites have limited access to the public so settlement plates are less disturbed by people visiting the intertidal than elsewhere. These sites were chosen to diminish unwanted variances and to be as similar as possible with respect to: 1) relatively flat areas for settling plates to be placed in replicate blocks at the same height in the intertidal, 2) site accessible during low tides, 3) logistically feasible to get equipment to, 4) moderate wave exposure and, 5) minimal human disturbance (Figure 2). These two sites allow for comparisons of community structure on settlement plates between shores with different bedrock and offshore oceanic conditions.

I used settling plates that were made of the exact rock types as the rip-rap boulders used for coastal armoring in Santa Cruz, CA. Fragments of basalt, granite and sandstone rocks broken off from the original large rip-rap boulders were collected and cut into10 x 10 x 2 cm settling plates. The plates were cut flat on the bottom but the top surface texture was left in the original state for each rock. Therefore, settling larvae and spores were exposed to the same surface roughness, specific to each rock type that they would encounter in the intertidal. Unfortunately, it was impossible to cut the native Santa Cruz Mudstone into plates because it is so friable; therefore, slate was purchased from a rock quarry and used as a substitute for the closest mimic to the native bedrock in Santa Cruz, the Santa Cruz Mudstone. The granite plates cut mimicked the granite bedrock at the PC site. After the rocks were cut, a small hole was drilled into the center in order to bolt them into the intertidal bedrock. In summary, there were 4 different rock types cut into 10 x 10 x 2 cm settling plates – sandstone, basalt, slate (mimic for the TP bedrock) and granite (mimic for the PC bedrock) – placed at two contrasting sites in Monterey Bay. In addition, I cleared 10 x 10 cm plots at the 2 sites to compare the plates with the native substrates. At TP, the clearings were on the mudstone bedrock and at PC the clearings were on the granite bedrock.

Deployment of settlement plates

In March 2002, holes were drilled in the bedrock at TP and PC and settlement plates were attached by 6" stainless-steel screws, a washer, nut, and marine epoxy. A layer of neoprene was placed under the plates to dampen the wave shock and cracking and z-spar epoxy was added around the base of the plates. The plates were not removed from their position in the intertidal once they were deployed. Plates were installed on the bedrock so their aspect, or angle to the ocean, was similar. The tidal height of the plates (mean and range above MLLW: 1.3 m, 1.2-1.5 at TP, 1.6 m, 1.2-1.9 at PC) placed them within the *Endocladia-Balanus* zone (Glynn, 1965). I had to clear this assemblage from the rocks before securing the plates. At both sites, the plates were arranged in a randomized block design with 6 blocks. Each block was composed of 2 basalt, 2 granite, 2 sandstone, and 2 slate plates. Two clearings on the bedrock (a 10 X 10 cm plot) were also included in each block. The clearing treatment was added to 1) compare recruitment on a raised plate to a flat surface and 2) examine recruitment on the native substrate at each site. Clearings on the bedrock were marked on four corners with z-spar epoxy so it was possible to repeatedly find the correct plots. The clearings are treated as another rock type, "clearing."

The experiment began in April 2002. Initially, clearings and the plates were sterilized. Sterilization in all cases included scraping the surface with a metal spatula, scouring with a wire brush, examining with a 10-power hand lens and removing any organism with a dissecting needle, then spraying with Easy Off® oven cleaner. The rigorous sterilization method was used because barnacle cyprid settlement has been shown to increase due to the presence of part of its species or an extract from the species (Crisp et al., 1985; Crisp, 1990). After the experiment began, one replicate plate in each block was counted for recruitment and then routinely sterilized to remove any settlers or residues of past settlers. In contrast, one of the paired plates in each block was left undisturbed the entire duration of the experiment to analyze continuous settlement and community development (Chapter 4). The subset of plates that were routinely cleared after being counted in the field is referred to as the recruitment plates. Including the clearings then, 30 recruitment plates at each site were counted and analyzed, 5 in each of 6 blocks.

Settlement includes the larva's initial contact with the substrate, attachment, and metamorphosis, and is defined as the number of larvae attaching. Recruitment is the number present at some point after attachment – what is counted in the field since some could have died since settlement (Connell, 1985). I counted recruitment of all intertidal species that settled on the plates using a 10-power hand lens in the field every 45 days, on average, for 2 years at both sites. This chapter focuses on the recruitment of the common acorn barnacles *Balanus glandula* and *Chthamalus dalli/fissus*. The two species of *Chthamalus* cannot be distinguished morphologically in the field so they are referred to as *Chthamalus dalli/fissus*, following Farrell et al., 1991 and Connolly and Roughgarden, 1999. In the text, the species are referred to simply as *Balanus* and *Chthamalus*.

Data analysis

The organism counts done on the plates that were microscopically examined for recruits, cleared, and sterilized (process described above) at both sites are considered the recruitment data. During the 700 days of the experiment, I counted recruits on the plates 15 times and cleared recruits 6 times. On average, the plates were counted every 45 and cleared every 90 days. Counting and clearing plates was done within two days of each other at the two sites. Because of the irregular intervals between sterilizing the plates, temporal effects of recruitment were not statistically addressed.

To guard against inflating the degrees of freedom in the statistical analyses, I followed the logic of repeated measures analysis by using the mean value for recruitment per replicate substrate as the variate of interest. That is, the mean value for *Balanus* and *Chthamalus* recruitment for each plate over the entire sampling period at each site was used to determine differences. The count data were not normal (log normally distributed) hence, they were log transformed. For the purpose of this analysis, I was interested in site, substrate and block effects. With the series of data, I examined recruitment on five different substrates at each site in six different blocks. Recruitment on five rock types at two sites was compared using ANOVAs with site (2 levels: TP and PC) and rock type (5 levels: basalt, granite, sandstone, slate and clearing) as fixed factors and block as a random factor nested within site.

In addition, the temporal trends in recruitment dynamics were evaluated for mean *Balanus* and *Chthamalus* recruitment per day per substrate at each site. Plates were sampled on a particular day and abundances reflect the recruitment since the last count. The mean number counted on a rock type per sampling period was divided by the number of days since the last clearing. Therefore, a high recruitment count on day 111, for example, reflects higher recruitment during the previous 45 days, approximately. In addition, if a recruitment event was followed by high mortality, it could have been missed due to the time intervals between sampling.

<u>RESULTS</u>

Balanus glandula

There was no site effect in the analyses of average *Balanus* recruitment from April 2002 through April 2004 (Table 1). That is, the number of *Balanus* recruits was not different between the northern and southern sites in Monterey Bay, Terrace Point (TP) and Point Cabrillo (PC), over the two-year period. There was a significant substrate effect, however, showing that *Balanus* recruitment was significantly different on different rock types. In a Tukey post-hoc test, pair-wise comparison, significant differences in recruitment were between the clearings and the slate – clearings had the highest recruitment and slate had the lowest ($p<0.05$) (Figure 3). In terms of average numbers (untransformed data), there were approximately three *Balanus* recruits on the clearings, two recruits on the sandstone, less than one recruit on the basalt and granite, and 0.1 *Balanus* recruits on the slate per recruitment period. There was no significant difference in recruitment between basalt, granite and sandstone, and recruitment on these three substrates was not significantly different from that on either the clearings or the slate. At TP, the clearings were on the native mudstone and at PC the clearings were on granite. Although the clearing substrate was different at each site, *Balanus* recruits were significantly more abundant on clearings than slate at both sites.

There was no evidence of an interaction effect between site and substrate, indicating that results for substrate preferences were robust across the two sites. There was a significant block effect at PC, however. In a Tukey pairwise comparison, the block effect was driven by block 5, which had significantly higher recruitment than did the other four blocks ($p<0.05$). At TP, there was no block effect ($p>0.05$). Thus, the spatial variability of *Balanus* recruitment varied on a small scale, within a site, and not between sites.

Temporal trends in mean *Balanus* recruitment per day, per substrate, at each site are shown in Figure 4. When comparing the two sites, there were some synchronous peaks in recruitment (day 111 on all substrates except slate at both sites;

day 139 on sandstone at both sites; day 341 on all substrates)(Figure 5). High recruitment to the clearings and sandstone at PC was seen from the counts on day 111 (August 11, 2002). High recruitment to the clearings and sandstone at TP was seen from the counts on day 341 (March 29, 2003). In fact, it appears there was synchrony in recruitment at TP on day 341 across substrates. There was slightly more recruitment on most substrates at PC on day 341 as well. At both sites, there was generally low recruitment onto slate over time.

Table 1. ANOVA table for *Balanus* recruitment from April 2002 through April 2004 at Point Cabrillo and Terrace Point on five different rock types. Site effects were tested using block nested within site as the error term. (Transformation log(x+1))

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Site	0.000549	1	0.000549	0.009562	0.924033
Substrate	0.310074	4	0.077519	5.479842	0.001294
Sub*Site	0.018450	4	0.004613	0.326063	0.858817
Block(Site)	0.574009	10	0.057401	4.057711	0.000686
Error	0.565845	40	0.014146		

Chthamalus dalli/fissus

There was a strong site effect, a strong substrate effect, and a significant substrate by site interaction in mean *Chthamalus* recruitment across all time periods from April 2002 through April 2004. In addition, there was a significant block effect for *Chthamalus* (Table 2). In contrast to *Balanus*, *Chthamalus* recruitment showed two levels of significant spatial variation, 1) between sites and 2) within a site.

There was generally more *Chthamalus* recruitment at TP than at PC. Mean *Chthamalus* recruitment during these two years was more than five times greater at TP than at PC per recruitment period. There were approximately twenty-five *Chthamalus* recruits overall at TP and less than five recruits at PC per recruitment period.

There was a significant interaction between substrate and site, indicated by substrate effects that differed by site. There was no general substrate pattern for recruitment across both sites. In a Tukey pairwise comparison at PC for the different substrates, there was no significant difference in recruitment between the substrates ($p>0.05$). Therefore, at PC recruits respond similarly to the different substrates. There were differences in recruitment on substrates at TP, however (Figure 6). There was significantly more recruitment onto sandstone than onto basalt, granite or slate, but the recruitment on clearings and sandstone plates were not different ($p>0.05$). About fifty *Chthamalus* recruited on sandstone plates per recruitment period at TP, and less than five onto slate plates. At both sites, slate had very little *Chthamalus* recruitment, the same pattern as seen for *Balanus* recruitment.

There was a significant block effect at both sites. A Tukey pairwise comparison showed the only two blocks that differed at PC were block 5 and 6. Block 5 had significantly more recruitment than block 6 ($p<0.05$). At TP, block 6 was significantly different from block 2 and 4 ($p<0.05$). Block 6 had the lowest recruitment and blocks 2 and 4 had the most. *Chthamalus* recruitment per day on each substrate is shown in Figure 7. Comparing sites, there were some synchronous high recruitment counts (Figure 8). At PC, there was high *Chthamalus* recruitment on all substrates except slate in counts from day 139 (September 9, 2002) and day 551 (October 25, 2003). There was high recruitment from counts at TP on day 224 (December 12, 2002) onto most substrates except for slate, and synchronous recruitment on day 341 (March 29, 2003) and day 551 on substrates except slate at TP.

Table 2. ANOVA table for *Chthamalus* recruitment April 2002 through April 2004 at Terrace Point and Point Cabrillo on five different rock types. Site effects were tested using block nested within site as the error term. (Transformation log(x+1))

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Site	2.50878	1	2.5087	9.938148	0.010289
Substrate	2.25716	4	0.5642	8.594525	0.000042
Sub*Site	0.92165	4	0.2304	3.509355	0.015114
Block(Site)	2.524403	10	0.2524	3.844827	0.001063
Error	2.626285	40	0.0657		

DISCUSSION

There was more recruitment of *Chthamalus* (but not *Balanus*) at the northern site in Monterey Bay, TP, than at the southern site, PC. Sites to the north of Monterey Bay tend to have higher long-term mean amounts of barnacle recruitment than sites to the south (Grantham, 1997; Connolly and Roughgarden, 1999). During El Niño years, this pattern has been linked to increased onshore transport of larvae due to anomalous onshore and poleward winds, onshore current flow and downwelling (Connolly and Roughgarden, 1999). In general, when upwelling occurs, larvae are transported offshore before they settle and do not get back to the nearshore environment before they die so recruitment rates are low (Roughgarden et al., 1988). However, in the northern part of Monterey Bay, Graham (1993) characterized an upwelling shadow during spring and summer months, a warm patch of water nearshore where upwelling is absent. This warm, buoyant surface water is retained inshore of upwelled water and a front, visible at the sea surface, is the boundary between these two water bodies. The water in the upwelling shadow has an increased residence time in the northern part of the bay, about 12 days, and nearshore flow is slow and/or recirculating (Graham, 1993), thereby promoting recruitment.

The timing of larval production has shown larvae of *Chthamalus* to be present throughout the year while those of *Balanus* to be restricted to winter and spring (Hines, 1978). This study showed recruitment peaks for *Balanus* in the fall and spring and for *Chthamalus* in the fall, winter, and spring (Figures 5 and 8). Consequently, in all cases, larvae of *Chthamalus* may become entrained in this spring-summer upwelling shadow and not get transported far from the adult population before they are able to settle in the northern part of the bay after approximately 2-3 weeks in the plankton. This upwelling shadow may then be partly responsible for the increased *Chthamalus* recruitment at the northern site in Monterey Bay. In addition, recruitment of *Balanus* at the southern site has been found to be negatively correlated with the upwelling index so when upwelling is high, recruitment is low at PC (Roughgarden et al., 1988). This may also explain the low *Balanus* recruitment overall.

Balanus recruitment strength has also been influenced by the extent of the offshore kelp forest, which reduces water flow and provides habitat for planktivorous juvenile rockfish that feed on barnacle larvae (Gaines and Roughgarden, 1987). Although it was not examined in this study, the kelp forest off both Monterey Bay sites could have been extensive during the spring when *Balanus* larvae are present, preferentially decreasing *Balanus* nauplii through fish predation. In addition, in the early 1980's, Gaines noticed a negative correlation between *Balanus* and *Chthamalus* recruitment – when *Balanus* recruitment was low, *Chthamalus* was high. Due to increased nutrients in the water during upwelling periods, kelp beds tend to be larger. These times are typically bad for barnacle larvae and for *Balanus*, recruitment was low. However, for *Chthamalus*, recruitment was high during upwelling periods and when the kelp forest was larger, opposite of the *Balanus* pattern (Steve Gaines, UC Santa Barbara, pers. comm., 2005). It is unclear why this pattern emerges, however, it could be due to the timing of recruitment influencing abundance of the barnacle larvae at different sites.

The temporal analysis for *Balanus* recruitment showed higher recruitment in the months before August 2002, especially on clearings and sandstone (Figure 4). This summer recruitment is not consistent with larval production in winter and spring. The temporal analysis of *Chthamalus* recruitment showed synchronous recruitment on substrates throughout the year (9/2002, 12/2002, 3/2003, 10/2003), consistent with continuous larval production, however, the pattern was not the same at both sites (Figure 8). There was high recruitment for both species at TP, the northern site, in the spring (3/2003) that was not seen in the southern site, PC. This is consistent with the notion of the upwelling shadow in the spring in northern Monterey Bay increasing the residence time of the water and potentially entraining larvae. The upwelling shadow may be increasing recruitment for both species in northern Monterey Bay, with *Chthamalus* being more abundant than *Balanus*. The temporal trends in recruitment showed that when a larval pool comes into the region of Monterey Bay, larval transport is not the same in the northern and southern regions – offshore of TP and PC are very different oceanic regimes.

The recruitment of *Balanus* and *Chthamalus* differed on spatial and temporal scales. Spatially, *Balanus* recruitment varied on a small scale, within a site, and not between sites. In contrast to *Balanus*, *Chthamalus* recruitment showed two levels of spatial significance, a large and small scale difference, 1) between sites and 2) within a site. Block 5 at PC accounted for the within site differences for both species. Block 5 received more splash and was slightly lower in the intertidal than the other 4 blocks. This within site variability due to block 5 might be related to a longer emersion time allowing more potential recruitment or decreased desiccation stress leading to higher survival of settlers. In addition, for *Chthamalus* only, block 6 at TP was different; it is slightly higher in the intertidal and showed less recruitment. It is difficult to generalize from these results, however, because of the multiple possibilities of explanations due to the underlying scales of relevant interactions. Moreover, these significant differences among the replicate blocks of settlement plates could be due to fine scale differences in the intertidal (Denny et al., 2004).

The recruitment abundance pattern for *Balanus* was the same for the different rock types at both sites. At both the northern and southern Monterey Bay sites, *Balanus* recruitment was greater on the native substrate, mudstone at TP and granite at PC, compared to the plates. There was no statistical difference, however, in recruitment between the bedrock, basalt, granite, and sandstone (Figure 3). Although the native bedrock was different at each site, *Balanus* preferred to settle on the substrate native to each shore. There was significantly lower recruitment on slate plates compared to the bedrock at TP and with this opposite abundance pattern, slate was obviously not a good mimic for the TP mudstone. In a previous study examining adult distributions on rip-rap rocks in Santa Cruz, (Chapter 2), *Balanus* was numerically more abundant on sandstone at one site, although the association was not statistically significant, and almost equal on basalt and sandstone rock types at a second site. In essence, *Balanus* did not show a strong adult distribution on a particular rock type. The current study also shows that *Balanus* recruit onto all available substrates rather equally, and recruitment was not significantly different on any substrate from all others. However, the pattern of *Balanus* recruiting more significantly on the native bedrock than on slate at both sites, even when the bedrock is different, is interesting, and so is the fact that there was significantly lower recruitment on slate for both species as compared to some of the other substrates. The native rocks could facilitate more biofilm growth enhancing recruitment compared to the slate, which was smoother and more easily eroded than granite.

The *Chthamalus* recruitment abundance pattern was different at each site on the different rock types. Recruitment was very low and not different among any of the substrates at PC (Figure 6). On the other hand, at TP, *Chthamalus* had significantly more recruitment onto sandstone than onto other plates, while slate had the lowest recruitment, significantly lower than both sandstone and the clearing (Figure 6). Because recruitment was significantly lower on the slate than the cleared bedrock for both species, slate was not a good mimic for the mudstone bedrock at TP for either *Balanus* or *Chthamalus*. In a previous study examining adults on rip-rap boulders in Santa Cruz County (Chapter 2), *Chthamalus* was more abundant on basalt rip-rap than sandstone rip-rap or native mudstone at one site, but there was no difference in the abundance of *Chthamalus* on basalt and sandstone rip-rap at a second site. The greater *Chthamalus* recruitment on sandstone compared to adult abundance on basalt rip-rap could result from settlement preference or from greater post-settlement survival. Temperature, porosity and water retention differences between sandstone and basalt could lead to these different abundance patterns. The developmental pattern of biofilm assemblages on certain rocks/substrates might also explain the results seen here. The larval attractiveness to different substrates with different biofilms may influence adult distribution patterns as well (Faimali et al., 2004). In addition, biofilm growth on slate may be very different from that on any other rock type as I noticed slate was more easily eroded than the other rock types and the diatom cover on slate was much lower than on any other rock type.

It is possible that having the plates raised above the substrate led to artifacts in recruitment response. Raised plates could affect the near surface water flow or attract/repel grazers and predators. The best indication of recruitment being an artifact of a raised plate is the comparison of granite and clearings on granite at PC. This comparison cannot be done at TP because the slate was not an appropriate mimic for the native mudstone so there is no comparable plate. For both *Balanus* and *Chthamalus*, there is no significant difference in recruitment on the clearings and on the granite at PC ($p>0.05$) indicating that the plates act like rock and the raised nature of the plates does not affect recruitment.

This study has a bearing on ecological changes due to human activities—especially coastal armoring. The coastline may experience unanticipated ecological effects from armoring, and these effects should be documented by careful monitoring programs. In particular, the current study demonstrates that the choice of rock used for coastal armoring may lead to different recruitment patterns and over time, to different biotic communities. When examining barnacle recruitment on different rock types, *Balanus* significantly preferred the native rock type (whether it was mudstone or granite) over slate; recruitment was not different on any of the other introduced substrates. *Chthamalus* showed a recruitment difference at TP only and numbers were significantly higher on sandstone than any other substrate except the native mudstone clearings (Figure 6.) Whether such slight recruitment preferences are related to the differences found in community structure in the rip-rap study (Chapter 2) is not known, but from the present study, that seems unlikely. That in itself is important to know and might be taken into consideration in future armoring projects along with the finding that rocks similar to slate are not substrates conducive to acorn barnacle recruitment. Matching the type of rip-rap rock used for armoring with the native rock would then be important to maintain an intertidal community that is similar to the original community structure. However, the rip-rap armoring is usually occurring to fortify softer native rock. Therefore, it seems reasonable to suggest using sandstone rock for armoring mudstone shorelines (those most often in need of armoring) for the least amount of community disruption and to completely avoid any slate-like rocks, as there was significantly less recruitment to that rock for both species. Slate is also more friable than most alternatives. In addition, concrete, another material used for armoring, is likely to support yet another community structure derived from different recruitment/post-settlement survival; however, concrete was not examined in this study. This project is one of the first to characterize the effects of shoreline fortification on associated intertidal communities. The public has shown an interest in maintaining intertidal areas with normal diversities and communities, hence the importance of this project is in its contribution to the understanding of how to manage and maintain these areas.

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Figure 1. Map of the Monterey Bay in central California (centered at approximately 36° 50' N, 121° 55'W) showing locations of coastal armoring and man-made structures at the land-sea boundary (concrete seawalls, groins, jetties, piers and rip-rap). In addition, the dominant substrate in the intertidal is shown - Santa Cruz Mudstone in red, Purisima in dark blue, Sand in turquoise, and Granite in green. The study sites are also labeled – Terrace Point (TP) and Point Cabrillo (PC). (Map adapted from K. Patsch, pers. comm., 2005.)

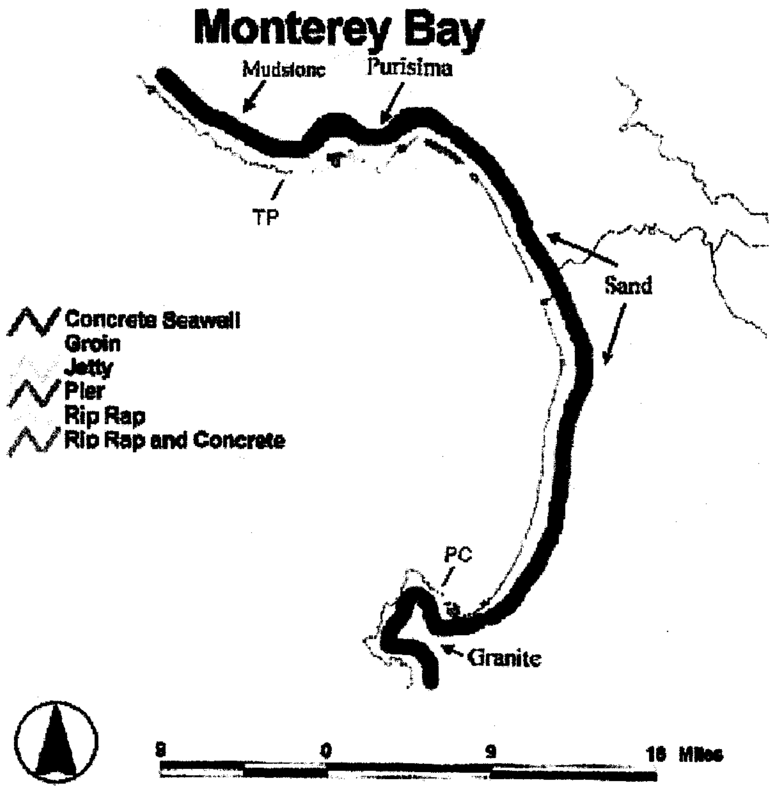


Figure 2. Photographs taken at low tide of the areas where plates were installed at Terrace Point and Point Cabrillo. Red box shows the area where the blocks are located. A close-up photograph of one of the six blocks at each site is also shown. Each block consists of 10 plates.

Terrace Point

Point Cabrillo

Block at TP

Block at PC

Figure 3. The mean number of *Balanus* recruiting on each substrate. The means of the untransformed data are shown and within treatment error bars (standard error). Different coding letters (a, b) indicate differences among treatments ($p<0.05$) generated from log transformed data (Table 1).

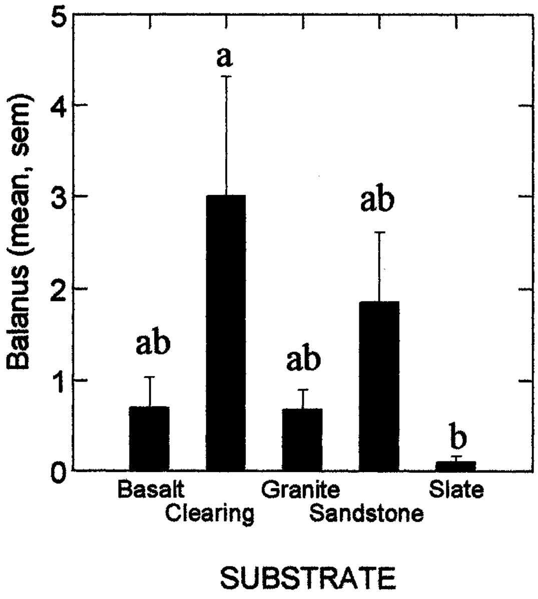


Figure 4. The temporal dynamics of *Balanus* recruitment on each substrate at both sites. The best fit line was drawn between data points on the days the plates were sampled. Day 1 is 4/23/02, day 350 is 4/7/03, and day 700 is 3/20/04. Note the y-axis is scaled differently for the two sites.

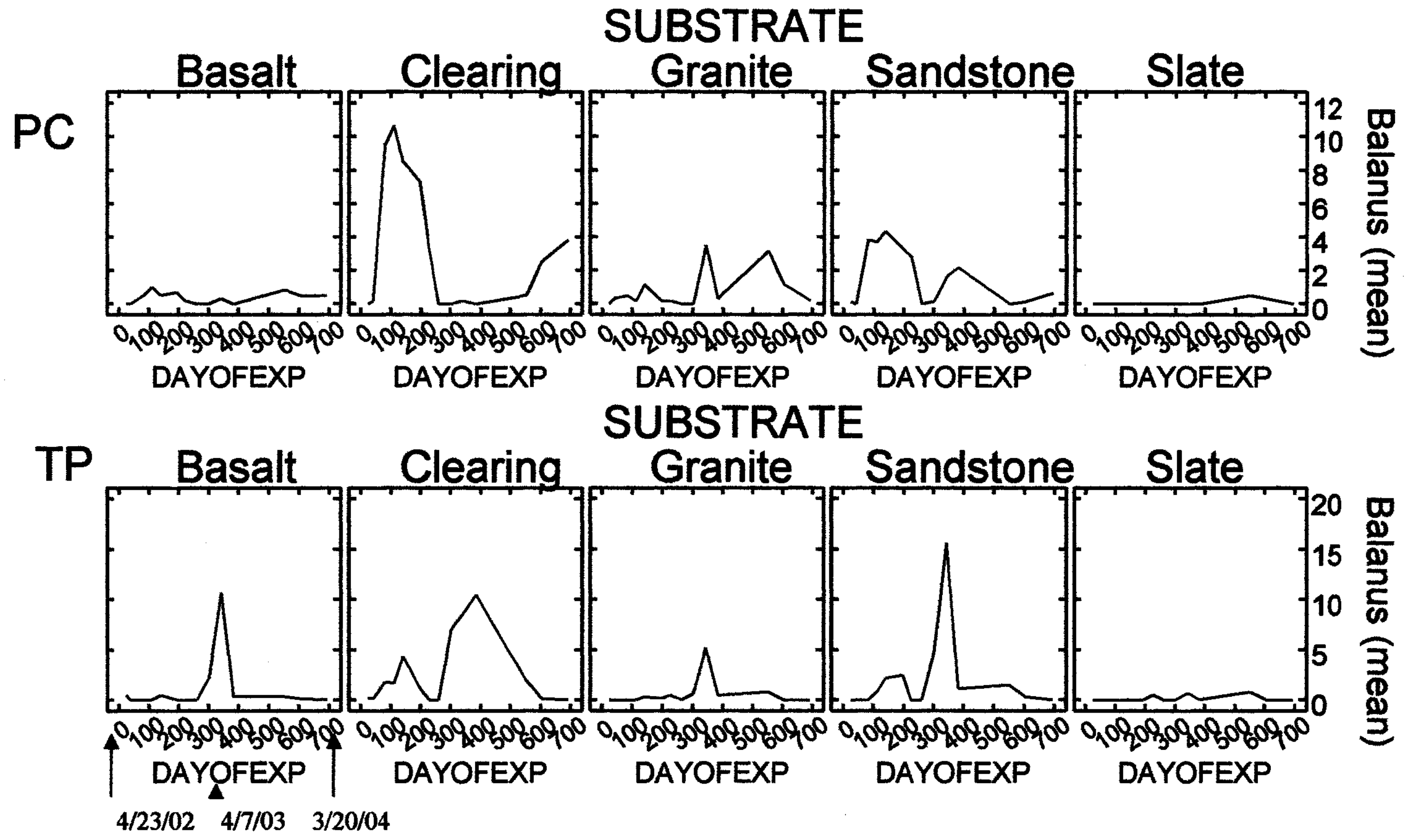

SUBSTRATE
PC
Basalt
Clearing
Granite
Sandstone
Slate
Balanus (mean)
0
2
4
6
8
10
12
DAYOFEXP
0
100
200
300
400
500
600
700
SUBSTRATE
TP
Basalt
Clearing
Granite
Sandstone
Slate
Balanus (mean)
0
5
10
15
20
DAYOFEXP
4/23/02
4/7/03
3/20/04

Figure 5. The temporal dynamics of *Balanus* recruitment at each site. Arrows show recruitment peaks at one or both sites on day 111 (August 11, 2002), 139 (September 9, 2002), and 341 (March 29, 2003).

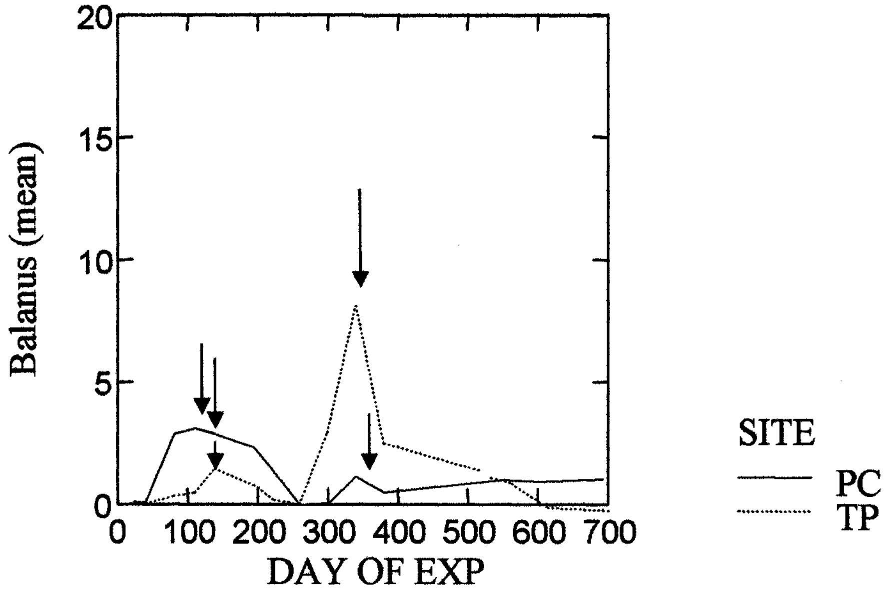


Figure 6. The mean number of *Chthamalus* recruiting on each substrate at Point Cabrillo (PC) and Terrace Point (TP). The means of the untransformed data are shown and within treatment error bars (standard error). Different coding letters (a, b, c) indicate differences among treatments ($p<0.05$) generated from log transformed data (Table 2).

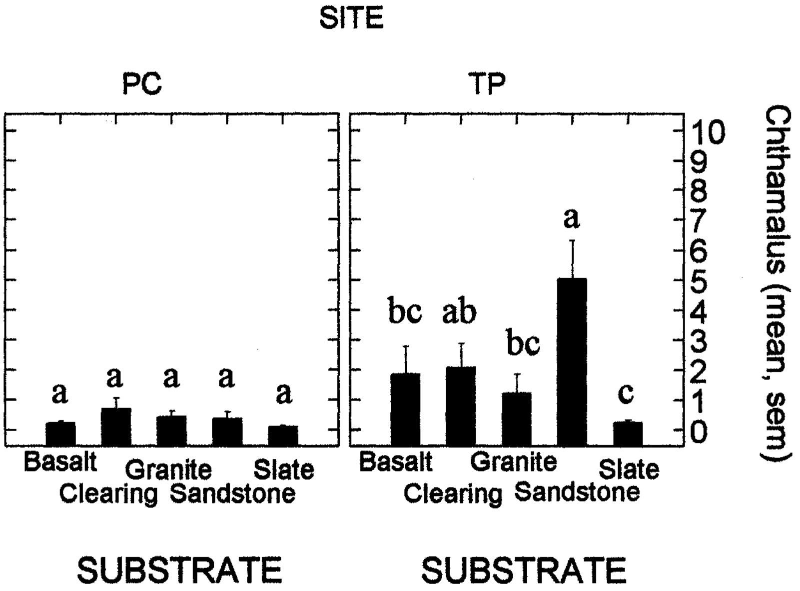


Figure 7. The temporal dynamics of *Chthamalus* recruitment on each substrate at both sites. Day 1 is 4/23/02, day 350 is 4/7/03, and day 700 is 3/20/04. Note the y-axis is scaled differently for the two sites.

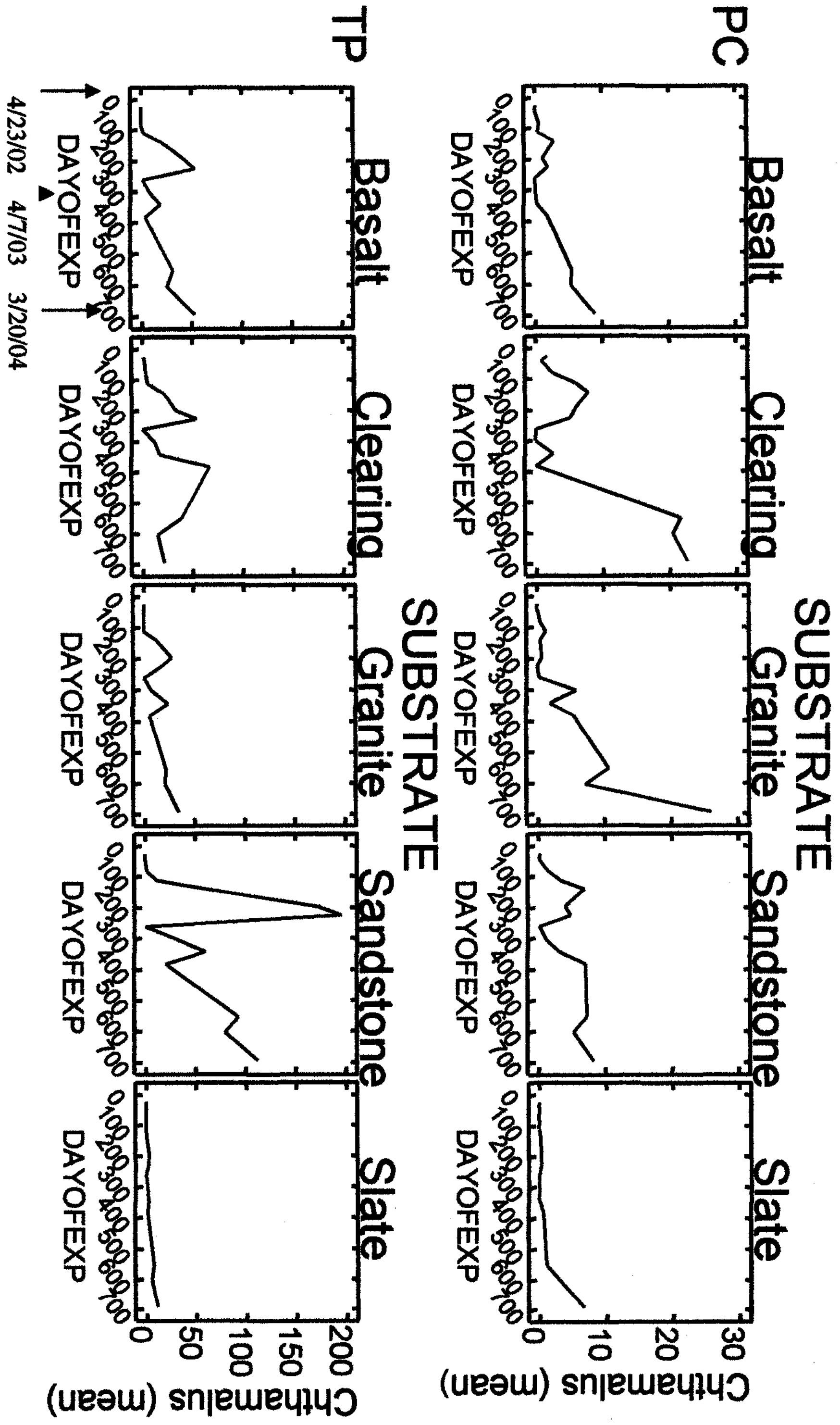
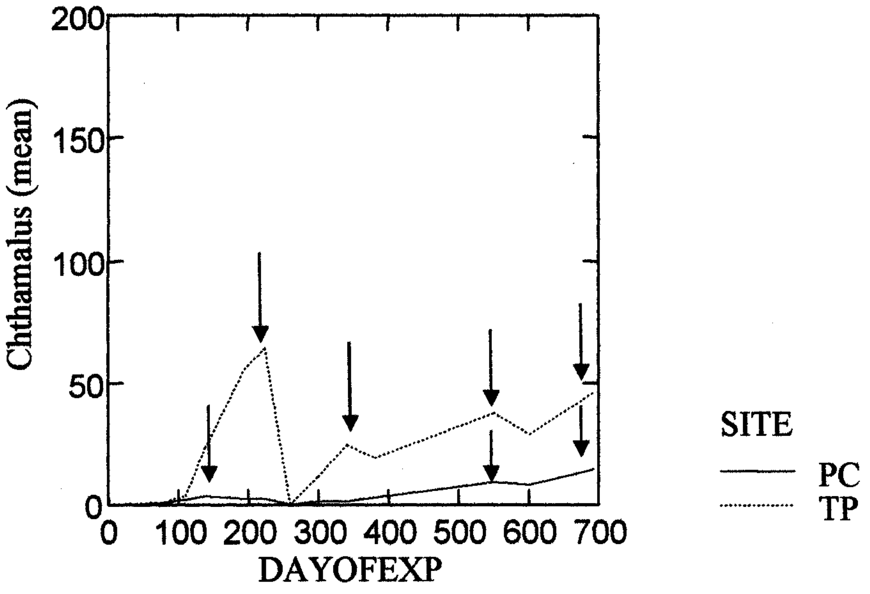

PC
TP
SUBSTRATE
Basalt
Clearing
Granite
Sandstone
Slate
DAYOFEXP
Chthamalus (mean)
0
10
20
30
0
50
100
150
200
4/23/02
4/7/03
3/20/04

Figure 8. The temporal dynamics of *Chthamalus* recruitment at each site. Arrows show recruitment peaks at one or both sites on day 139 (September 9, 2002), 224 (December 12, 2002), 341 (March 29, 2003), 551 (October 25, 2003), and 693 (March 14, 2004).



Chapter 4.

Rocky intertidal community development on different substrates: An experimental test of post-settlement survival on different rock types

Rocky intertidal community development on different substrates: An experimental test of post-settlement survival on different rock types

Dawn A. Osborn

ABSTRACT

This work examines changes in post-settlement survival as a function of the rock type recruits settle on and compares the relationship between the density of settlers and the density of adults. Plates of different rock types were deployed in the intertidal and species were counted and cleared for three years at two sites in Monterey Bay, California. Analysis of variance indicated that *Balanus glandula* adults were more abundant on the native rock at each site compared to any of the introduced rock types. For *Chthamalus dalli/fissus*, the more northern site had significantly more adults after three years time and abundances were higher yet statistically the same on the native rock, granite and sandstone plates. Adult abundance of *B. glandula* never reached a level that competitively excluded individuals of *C. dalli/fissus* on any of the rock types. However, adult abundance of *C. dalli/fissus* did reach levels where intraspecific competition inhibited further recruitment. *B. glandula* adults and recruits showed a linear relationship, density-independent, aligning with what models predict when recruitment is low. *C. dalli/fissus* adults and recruits showed an initial linear relationship that was density-independent which changed to a density-dependent relationship over time. These results suggest that recruit density is an important driver of subsequent population processes for *C. dalli/fissus* and may not be as important for *B. glandula.*

INTRODUCTION

In the last 20 years, California's population has increased forty five percent to approximately 36 million people. Eighty percent of these people live within 50 kilometers of the shoreline and over four million live within five kilometers of the shoreline (Griggs and Patsch, 2004). As urbanization of coastal areas increases, artificial or non-native structures are becoming more common in the intertidal and near-shore oceanic environments. In addition to urbanization of the coast, coastal erosion continues and may be increasing. Sea level has been rising for the past 18,000 years and will continue to rise as global temperatures increase. The average annual cliff erosion rate in California is approximately 10 to 30 cm (Griggs and Patsch, 2004). At a presentation for the California League of Conservation Voters in 2003 Professor Inman, from Scripps Institution of Oceanography, stated that "California's beaches face a critical imbalance as global warming threatens to increase the rate of sea level rise. In the absence of wide beaches, waves attack the base of the sea cliffs. Studies show that 86% of California's coast is actively eroding" (Inman, 2003). To counter coastal erosion and protect structures along the coast, coastal armoring with rip-rap of boulders and concrete has become increasingly prevalent. In some areas, natural cliffs cannot be seen because they have been completely armored.

There is increasing concern about the impacts of fortifying structures on the shorelines (Griggs and Patsch, 2004). Despite this, few studies have focused on the ecological impact of these structures or have attempted to assess the extent to which they can act as surrogates for natural habitats (Bulleri, 2005). The substrate that larvae settle on is critical for their subsequent growth and survival. The physical characteristics of the substrate, for example, can affect the population dynamics within and among species (Moore and Kitching, 1939; McGuinness and Underwood, 1986; Lohse, 1993; Osborn, Chapter 2). How and under what circumstances settlement and early survival of juveniles vary on different substrates and what consequences this variation has for populations and communities is particularly important (Caffey, 1985; Fletcher and Callow, 1992; Hadfield, 1998; Cattaneo-Vietti et al., 2002; Groppelli et al., 2003; Osborn, Chapter 3). Site selection strongly influences post-settlement mortality (Roegner et al., 1995). There are several models that explain sequences of species when there is new space to invade (Connell and Slatyer, 1977), and these sequences will be important to follow as the geology of the coastline changes when new substrates are added. Competition, predation, facilitation and other interactions between species are critical to the course of succession. Certain intertidal species have been found to enhance recruitment of other species by direct and indirect benefits to the secondary settler, for example by reducing herbivore pressure or desiccation stress (Connell and Slatyer, 1977).

Bulleri (2005) investigated whether colonization of space can determine the occurrence of different intertidal assemblages on rocky shores and sandstone seawalls in Sydney Harbour (New South Wales, Australia). Areas were cleared on rocky shores and seawalls at 3 different locations to test hypotheses from 2 alternative models: (1) patterns of distribution and abundance of organisms on the 2 types of structure are the direct result of different patterns of recruitment and (2) early stages of development of assemblages are the same on the 2 types of structure, but later processes (post-recruitment) differ between structures, producing different older assemblages. Furthermore, the model that assemblages developing in clearings on each structure would converge toward mature assemblages found on the same type of structure was tested. Assemblages in clearings differed between seawalls and rocky shores from the early stages of succession and differences persisted through time. Although there was variability among locations, these assemblages tended to converge toward mature assemblages on the same type of structure. These results support the model that intrinsic differences (e.g. topography, weathering, shape and extent of surfaces) between seawalls and rocky shores could affect the recruitment of algae and invertebrates, leading to the establishment of distinct assemblages. This knowledge improves our ability to design artificial structures that more closely mimic natural habitats, potentially mitigating some effects of loss and fragmentation of coastal habitats in urban areas (Bulleri, 2005).

Connell (1985) reviewed literature from many studies and used data for numerous species to investigate the relationship between densities of settlement and recruitment. He found that initial settlement of planktonic propagules may affect the structure of intertidal communities in some circumstances but not in others. He was interested in determining if the initial variation in settlement affects the distribution and abundance of the populations living on the substratum. He found that for intertidal barnacles, mortality between juvenile and adult stages was independent of initial density when recruitment was light, but was density-dependent when recruitment was heavy. As a consequence, adult density was positively correlated with recruit density when recruitment was light, but uncorrelated when recruitment was heavy. He concluded that models of community structure probably apply mainly to sites with high rates of settlement or recruitment, not those where these rates are low.

Larval supply, settlement or post-settlement mortality can all affect the distribution of species on different rock types. As individual larvae settle and grow on different rocky intertidal substrates, a community of adults develop over time showing different growth and survival on different substrates. On south west Irish shores, post-settlement mortality, rather than larval supply, was deemed to be the more significant factor in determining the characteristic patterns of two chthamalid species (*Chthamalus montagui* and *C. stellatus*) (Delaney et al., 2003). In contrast, at Cape Banks, Australia, larval processes primarily determined the numbers of *C. tasmanica*. Settlement was found to be integral to the demography of barnacles and the alternative model that post-settlement mortality determined the distributions and abundance of juveniles and adults was discounted by experimental tests. In addition, spatial patterns of post-settlement mortality of juveniles did not match spatial patterns of adult mortality (Jeffery, 2003).

I examined rocky intertidal community structure after three years of development on settlement plates made from five different substrates. The experiment separated substrate preferences (settlement plates), small-scale (experimental blocks), and large-scale effects (sites) for the two most abundant species, the barnacles *Balanus glandula* and *Chthamalus dalli/fissus*. In Chapter 2, I showed that these species have different abundances both on different adjacent rocks used for coastal armoring and on the native rock. In Chapter 3, the recruitment of *B. glandula* was shown to be significantly higher on native bedrock at both sites, while *C. dalli/fissus* recruits were significantly more abundant on sandstone and native bedrock at the northern site; both species had significantly lower recruitment onto slate. In this chapter, I focus on post-settlement survivorship and the adult abundances and distributions after three years of development. In addition, the relationship between recruitment and adult abundances on different substrates over time was examined for each species to determine if it was density-dependent or density-independent.

METHODS

Sites and rock substrates

Recruitment plates were deployed at two sites, one on each side of Monterey Bay, California (Figure 1). These sites have different bedrock and exposure. The northern site is Terrace Point (TP), below Long Marine Laboratory (UC Santa Cruz). TP is an intertidal bench with Santa Cruz Mudstone as the main bedrock, which has a low stability and is easily eroded. This intertidal bench faces southwest, away from the predominantly northwesterly swells. The southern site is Point Cabrillo (PC) at Hopkins Marine Station (Stanford University), a granitic outcrop and a harder, more erosion-resistant rock. It faces northeast and is more directly exposed to the northwesterly swells. Both sites have limited access to the public so settlement plates are less disturbed by people visiting the intertidal than elsewhere. These sites were chosen to diminish unwanted variances and to be as similar as possible with respect to: 1) relatively flat areas for settling plates to be placed in replicate blocks at the same height in the intertidal, 2) site accessibility during low tides, 3) logistically feasible to get equipment to, 4) moderate wave exposure, and 5) minimal human disturbance. These two sites allow for comparisons of community structure on settlement plates between shores with different bedrock and offshore oceanic conditions.

I used settling plates that were made of the exact rock types as the rip-rap boulders used for coastal armoring in Santa Cruz, CA. Fragments of basalt, granite and sandstone rocks broken off from the original large rip-rap boulders were collected and cut into10 x 10 x 2 cm settling plates. The plates were cut flat on the bottom but the top surface texture was left in the original state for each rock. Therefore, settling larvae and spores were exposed to the same surface roughness, specific to each rock type that they would encounter in the intertidal. Unfortunately, it was impossible to cut the native Santa Cruz Mudstone into plates because it is so friable; therefore, slate was purchased from a rock quarry and used as a substitute for the closest mimic to the native bedrock in Santa Cruz, the Santa Cruz Mudstone. The granite plates cut mimicked the granite bedrock at the PC site. After the rocks were cut, a small hole was drilled into the center in order to bolt them into the intertidal bedrock. In summary, there were 4 different rock types cut into 10 x 10 x 2 cm settling plates –

sandstone, basalt, slate (mimic for the TP bedrock) and granite (mimic for the PC bedrock) – placed at two contrasting sites in Monterey Bay. In addition, I cleared 10 x 10 cm plots at the 2 sites to compare the plates with the native substrates. At TP, the clearings were on the mudstone bedrock and at PC the clearings were on the granite bedrock.

Deployment of settlement plates

In March 2002, holes were drilled in the bedrock at TP and PC and settlement plates were attached by 6" stainless-steel screws, a washer, nut, and marine epoxy. A layer of neoprene was placed under the plates to dampen the wave shock and cracking and z-spar epoxy was added around the base of the plates. The plates were not removed from their position in the intertidal once they were deployed. Plates were installed on the bedrock so their aspect, or angle to the ocean, was similar. The tidal height of the plates (mean and range above MLLW: 1.3 m, 1.2-1.5 at TP, 1.6 m, 1.2-1.9 at PC) placed them within the *Endocladia-Balanus* zone (Glynn, 1965). I had to clear this assemblage from the rocks before securing the plates. At both sites, the plates were arranged in a randomized block design with 6 blocks. Each block was composed of 2 basalt, 2 granite, 2 sandstone, and 2 slate plates. Two clearings on the bedrock (a 10 X 10 cm plot) were also included in each block. The clearing treatment was added to 1) compare recruitment on a raised plate to a flat surface and, 2) examine recruitment on the native substrate at each site. Clearings on the bedrock were marked on four corners with z-spar epoxy so it was possible to repeatedly find the correct plots. The clearings are treated as another rock type, "clearing."

The experiment began in April 2002. Initially, clearings and the plates were sterilized. Sterilization in all cases included scraping the surface with a metal spatula, scouring with a wire brush, examining with a 10-power hand lens and removing any organism with a dissecting needle, then spraying with Easy Off® oven cleaner. The rigorous sterilization method was used because barnacle cyprid settlement has been shown to increase due to the presence of part of its species or an extract from the species (Crisp et al., 1985; Crisp, 1990). After the experiment began, a subset of plates in each block was counted for recruitment and then routinely sterilized to remove any settlers or residues of past settlers (Chapter 3 data used for sum of barnacle recruitment calculations). In contrast, one of the paired plates in each block was left undisturbed the entire duration of the experiment to analyze continuous settlement and community development. These plates are referred to as the post-settlement plates. The intertidal community on the post-settlement plates was left to develop in the field for 34 months. Post-settlement plates were microscopically assessed 16 times for recruits and adults at both sites. On average, these plates were counted every 45 days, except for the last count which was done 300 days after the prior one. Counting was done within two days of each other at the two sites. Including the clearing plots, 30 post-settlement plates at each site were counted and analyzed, 5 in each of 6 blocks.

Settlement includes the larva's initial contact with the substrate, attachment, and metamorphosis, and is defined as the number of larvae attaching. Recruitment is the number present at some point after attachment – what is counted in the field since some could have died since settlement (Connell, 1985). I counted recruitment and the adult community of all intertidal species that settled on the plates using a 10-power hand lens in the field after 3 years at both sites. This chapter focuses on the adult community of the common acorn barnacles *Balanus glandula* and *Chthamalus dalli/fissus*. The two species of *Chthamalus* cannot be distinguished morphologically in the field so they are referred to as *Chthamalus dalli/fissus*, following Farrell et al., 1991 and Connolly and Roughgarden, 1999. In the text, the species are referred to simply as *Balanus* and *Chthamalus*.

Data analysis

Community structure

Canonical discriminant analysis (CDA) (Chapter 2), was used to evaluate if there were differences in community structure among the post-settlement plates and if so, which species were driving the differences. Data used for the analysis were counts of invertebrates and the percent cover of algae on the different substrates at each site. CDA analyzes relationships between sets of variables. Separate CDA was done for each site, with rock type as a grouping variable and all the recorded observations as independent variables. New functions are created that are combinations of the original variables which best discriminate among groups (Tabachnick and Fidell, 1996). The best combination of these variables allows discrimination between rock types by community structure.

Comparison of two barnacles

I examined the most common species on the plates, the barnacles *Balanus glandula* and *Chthamalus dalli/fissus*, to determine 1) if their abundance differed as a function of substrate, block, or site and 2) if their adult distribution patterns mimicked recruitment patterns found on the plates (Chapter 3). This latter comparison determined if there was a relationship between adult abundances and cumulative recruitment on the cleared plates.

1. Effect of substrate, block, and site on the two most abundant species

For the first analysis, I examined *Balanus* and *Chthamalus* on five different substrates in six blocks at each of the two sites. Post-settlement numbers on five rock types at two sites were compared using ANOVAs with site (2 levels: TP and PC) as one factor, rock type (5 levels: basalt, clearing, granite, sandstone, and slate) as fixed factors and block as a random factor nested within site. Tukey pairwise comparisons were done to determine where the differences were for the different rock types and blocks. For *Balanus* and *Chthamalus*, the count data were not normal (log normally distributed) hence, they were log transformed.

2. Recruit and adult relationship

In order to compare the relationship between the adult population and total recruitment, I created a variable: sum of recruitment to day X (S(day)). This was done by summing recruitment to plates that were regularly cleared. As an example, S24 was the number of recruits found on day 24 of the experiment, and S40 was the sum of the recruits that occurred on day 24 and day 40 (plate was cleared on day 24). Hence, sum of recruitment is an estimate of potential recruitment on the plates to day X. I then compared this value (*e.g.*, S40) to the number of adults on plates on day 40 that were never cleared. The mean recruitment over all recruitment plates and the mean adult number for all non-cleared plates on a given date were used as the variates of interest. For each site there were 6 dates where recruitment and adult numbers were measured. I was interested in the following specific questions:

1) Is there a relationship between adult number and potential recruitment?
2) Does adult number vary by site?
3) Does the relationship between adult number and recruitment vary by site?

This set of questions follows the logic of Analysis of Covariance (ANCOVA). I first tested question 3, which tests for the homogeneity of slopes assumption (Winer et al., 1991). All slopes were homogeneous, accordingly, I then ran reduced models to assess questions 1 and 2 (Winer et al., 1991). In addition, in order to more completely characterize the relationship between adult number and recruitment I used regression approaches (linear and non-linear) to derive the function describing the relationship.

RESULTS

Community structure

Canonical discriminant analysis (CDA) led to a weakly significant separation of community structure on the different substrates (MANOVA Pillai's trace = 0.769; Approx. F = 1.517; df = 32, 204; p=0.0456). However, the community structure on the plates did not converge with the adult abundance patterns found on different substrates in the rip-rap intertidal community which had been developing for 15 years (Chapter 2). This may have been because the species found on the rip-rap vs. the plates were somewhat different and the substrates compared were different. In addition, the methods used to count the species were different. The rip-rap communities were scraped from the rocks and examined using a microscope in the lab (methods described in Chapter 2). Small species were easily found and identified in the lab. In the current study, the plates were left in the field and counted *in situ* with a hand lens. Many species that strongly separated the rip-rap rock types were so small they were not seen in the field, such as the tanaid *Pancolus californiensis* and the dipteran *Limonia marmorata*. In addition, some species may not have had enough time to mature on the plates, such as *Endocladia muricata*. Because of these differences, there were no obvious ways to compare the results from Chapter 2 and Chapter 4.

Effect of site, substrate and block on the two most abundant species

Balanus glandula

There was no significant difference in abundance of *Balanus* between the sites on the last sampling day (Question 2). There was a significant substrate effect but not a substrate by site interaction nor a block effect (Table 1). The clearings at both sites had significantly more *Balanus* than did the granite, sandstone or slate plates. There was not a significant difference in the count of *Balanus* between the clearings and the basalt plates. In addition, the numbers on basalt, granite, sandstone, and slate plates were not significantly different from each other (Figure 2). There was no significant difference in adult abundance at PC on granite and on the granite clearings (ANOVA, p=0.323) (Figure 3), indicating that there were no effects on settlement from the raised plates. In addition, the granite plates were good mimics for the granite bedrock. Because the slate and mudstone are different rocks, I cannot test for effects on settlement between slate and mudstone bedrock at TP and conclude from the PC comparison, that there were no effects on settlement from characteristics of the plates (raised, surrounded by z-spar epoxy, etc.).

Table 1. ANOVA table for *Balanus* adults from April 2002 through February 2005 at Point Cabrillo and Terrace Point on five different rock types. Site effects were tested using block nested within site as the error term. (Transformation log (x+1))

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Site	0.185596	1	0.185596	1.44917	0.256382
Substrate	2.335729	4	0.583932	4.56644	0.003931
Sub*Site	0.278104	4	0.069526	0.54370	0.704559
Block(Site)	1.280700	10	0.128070	1.001527	0.458681
Error	5.114992	40	0.127875		

Chthamalus dalli/fissus

There was a significant difference between sites and across substrates, and a marginally significant block effect in adult *Chthamalus* abundance on the different rock types on the last sampling day but not a significant substrate by site interaction (Table 2). Significantly more adults overall were at TP compared to PC (Figure 4; Question 2). The adult number on the different substrates did not vary as a function of site. The abundance of *Chthamalus* adults was not significantly different on the clearings, granite, and sandstone but was higher than on either basalt or slate (Figure 5).

There was a significant difference between the six blocks at each site (Table 2). Using a Tukey post-hoc test, the separation among blocks was uncertain given the large numbers of comparisons. The adult numbers of *Chthamalus* were not significantly different on granite and the clearings at PC (ANOVA, p=0.711) showing that like *Balanus*, there was no effect of the raised plates for *Chthamalus.* The granite plates were good mimics for the granite bedrock.

Table 2. ANOVA table for *Chthamalus* adults from April 2002 through February 2005 at Point Cabrillo and Terrace Point on five different rock types. Site effects were tested using block nested within site as the error term. (Transformation log (x+1))

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Site	8.555775	1	8.555775	15.52495	0.002774
Substrate	8.069100	4	2.017275	8.369869	0.000053
Sub*Site	2.272727	4	0.568182	2.357441	0.069833
Block(Site)	5.510791	10	0.551079	2.286480	0.031368
Error	9.640652	40	0.241016		

Recruit and adult relationship

Although they are both barnacles, *Balanus* and *Chthamalus* had very different recruitment patterns. *Balanus* recruited in small numbers and *Chthamalus* in large numbers. For example, on plates that were left in the field for 1,022 days, the total count of *Balanus* adults at PC was 83 and at TP was 43 while for *Chthamalus* adults, the counts were 1,137 and 5,129 respectively.

For both species, the relationship between recruitment and adult number (averaging across all substrates) did not vary between the two sites (Question 3, interaction between recruitment and site *Balanus* p=0.3967, *Chthamalus* p=0.2688). A reduced model was run (dropping the interaction term; Winer et al., 1991) and there were no site effects, indicating that adult number was not different at the two sites. For both species there was a significant effect of the covariate, recruitment, indicating that adult number was strongly associated with recruitment (*Balanus* Table 3, *Chthamalus* Table 4). Using regression analyses, the best fit for *Chthamalus* was provided by an asymptotic power curve (Figure 6), while for *Balanus* the best fit was provided by a linear approximation (Figure 7). The r^2 for *Chthamalus* was 0.98. On day 341, there was high *Balanus* count, a count immediately after a large recruitment pulse (Chapter 3, Figure 4). The r^2 with day 341 was 0.35 versus without day 341 was 0.58, indicating that adults and recruits are more tightly linked if day 341 is excluded (Figure 7).

Table 3. ANOVA table for the sum of *Balanus* recruitment. Sum of recruitment is the total number of recruits counted on plates that were regularly cleared. Sum of recruitment is an estimate of potential recruitment on the plates to day X.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Sum of Bal. Rec.	76.267306	1	76.26730	5.969721	0.037163
Site	5.352704	1	5.35270	0.418976	0.533609
Error	114.98121	9	12.7756		

Table 4. ANOVA table for the sum of *Chthamalus* recruitment. Sum of recruitment is the total number of recruits counted on plates that were regularly cleared. Sum of recruitment is an estimate of potential recruitment on the plates to day X.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Sum of Ch. Rec.	3278.100023	1	3278.100	73.721759	0.000013
Site	7.971145	1	7.971145	0.179264	0.681944
Error	400.192569	9	44.46584		

DISCUSSION

Canonical discriminant analysis (CDA) showed that the adult community patterns that emerged on the plates after exposure for 3 years was different from those found on the different rip-rap rocks (Chapter 2). There are several possibilities for this finding – 1) the methods used to count the species and the rock types examined were different, 2) not enough time had passed for the plates to develop similar communities (15 years for the rip-rap and 3 years for the plates and succession is temporally likely to take longer), 3) the plates were too small to allow adequate community development. Since adult species of *Balanus* and *Chthamalus* were the species driving the differences seen on the different substrates, I focus below on these species.

Overall, *Balanus* adults were not as abundant as *Chthamalus,* which follows the recruit abundance pattern discussed in Chapter 3. Proposed reasons for this include the more limited timing of larval production in *Balanus,* which 1) place more of their larvae in the upwelling season making them more likely to be swept offshore (Hines, 1978; Breaker and Broenkow, 1994) and, 2) if and when larvae do come ashore, they likely need to pass through the seasonally thick kelp beds where they face larval predation (Gaines and Roughgarden, 1987). *Balanus* adult abundances did not vary as a function of site, nor did *Balanus* recruits (Chapter 3). *Chthamalus* recruits and adults, however, were significantly more abundant at TP (Figure 4). For both species, the recruits and adults showed a significant substrate preference. Adult *Balanus* showed a similar substrate preference pattern (Figure 2) to *Balanus* recruits

(Chapter 3, Figure 3). At both the northern and southern Monterey Bay sites, *Balanus* adults were significantly more abundant on the native substrate at that site as compared to the plates. In addition, *Balanus* was also abundant on basalt and there was no difference between the findings on basalt and clearings. *Balanus* adults were significantly less abundant on granite, sandstone and slate rocks. Thus, *Balanus* recruits and adults were more abundant on the native rock at each site than on the plates. In contrast, *Balanus* adults were more abundant on sandstone rip-rap than on either basalt or native rock (mudstone) in northern Monterey Bay sites similar to TP (Chapter 2).

Interestingly, I noticed a high abundance of limpets sheltering around the sides of the plates during low tides. There was no such refuge around the clearings on the native rock. Dayton (1971) found that limpets affect initial recruitment of barnacles, interfering with barnacle recruitment by eating, pushing, and dislodging the cyprid or newly metamorphosed barnacle from the substrate. However, Dayton stated that the survival of *Chthamalus* was significantly increased at all sites in the presence of limpet disturbance because the limpets had a disproportionately strong negative effect on the populations on the competitively superior *B. glandula* and *B. cariosus*. He found this to be true, despite the fact that limpet activity reduced the success of initial *Chthamalus* recruitment. *Balanus* species very quickly dominated most available substrates in the absence of limpets. Limpet interference on the plates due to the plates providing a sheltering habitat could explain the high recruitment of

Balanus on the clearings. In addition, residual microbial films that may have remained on the clearings could enhance settlement.

Chthamalus adults were significantly more abundant on the native rock, granite and sandstone compared to basalt and slate at both sites (Figure 5). Recruits were more abundant on native rock and sandstone (Chapter 3) which helps explain the adult abundance pattern. However, 15 years after rip-rap was added to one site, *Chthamalus* adults were significantly more abundant on basalt than on sandstone and the native mudstone (Chapter 2), which does not fit with the pattern observed on the plates after three years. The reason for this discrepancy is not clear, and merits further investigation. Individuals of *Chthamalus* tend to be more tolerant of temperature stress and desiccation than those of *Balanus* (Connell, 1961), and when they are in a competitive situation, *Balanus* displaces *Chthamalus*, leaving individuals of the latter in less favorable habitats. On the other hand, without competition, *Chthamalus* does better in more favorable habitats (Connell, 1961). It is possible that the density of *Balanus* did not reach densities that would exclude *Chthamalus* from the most favorable plates during my experiment, while *Balanus* did on the rip-rap boulders. Indeed, the average *Balanus* abundance on the sandstone (more favorable habitat) rip-rap was 1,495/m^2, exceedingly greater than the density on the sandstone plates, 1.2/m^2.

An important issue in ecology surrounds the question of whether the survivorship of juveniles in a population is density-dependent or density-independent. Connell (1985) proposed that survivorship is initially density-independent but as the number of settlers of the same species increases, it changes to density-dependent. Settlers and adult numbers are tightly linked when there are small numbers of settlers; as the number of settlers increases there is not an increase in the number of adults. The results from the current study show that for *Chthamalus* at both sites, the relationship between adults and recruits is a non-linear power curve and the effects of recruitment diminish in a non-linear way as recruitment increases (Figure 6), this is consistent with the model Connell predicted (Figure 8). For *Balanus* at both sites, the relationship between adults and recruits changes as a function of time and is a linear approximation, which is consistent with the models when the recruitment is low (Figure 7). The linear relationship for *Balanus* shows the bottom of Connell's curve, the density-independent portion. Connell (1985) found that variation in settlement density of *B. glandula* among different habitats is more likely to be a function of larval supply than of characteristics of either the local water column or substratum. To assess the overall relationship between settlement and adult numbers, the counts examined looked at all the different substrates together. The relationship might not be so tight if one examined settlement on the slate alone, which was very low, and may be tighter and stronger on the native rock, where the numbers were highest.

Connell (1985) was interested in determining if the initial variation in settlement affects the distribution and abundance of the populations eventually living on the substratum. He looked at the relationship between adults and settlement and found that at low levels of recruitment survivorship is density-independent and there is a direct relationship between the number settled and the adult numbers. As the number of settlers increases, survivorship becomes fully density-dependent and adult number does not vary as a function of settlement. The system becomes saturated and post-settlement mortality reduces the adult numbers. Although the relationship Connell discusses is settlement as a daily census I was not able to count that. Instead, I examined recruitment, which is the survival several days to weeks after settlement. However, the relationship should hold true for recruitment.

After settlement, the number of benthic organisms, like solitary sessile barnacles is affected by mortality. If mortality occurring between initial settlement and some later stage (juvenile or adult) is independent of the density of settlers, then the numbers of the later stages will be a direct reflection of the numbers of settlers. However, mortality may act in a density-dependent way, with different consequences (Connell, 1985). That is, if density-dependent mortality occurs prior to sampling, one would see no relationship between adults and recruits. If density-dependent mortality occurs after sampling, the experiment is more robust and one can see a relationship between adults and recruits. In this experiment, if density-dependent mortality occurs early, there would have been no relationship between adults and recruits. However, these results for *Balanus* and *Chthamalus* show an explicit relationship between adults and recruits following the predicted models for low levels and high levels of recruitment, respectively.

The strength of the relationship between settler input and surviving adults can be determined by examining the slope of the curve for the settlers and adult relationship; a high slope indicates high correspondence between the recruits coming in and the adult number that result. When the plates were initially installed and assessed, the slope was high indicating a strong relationship between recruits and adult numbers ($p<0.05$). Over time, as recruitment builds up, the slope decreases for *Chthamalus*. This progression in slopes shows an initial tight relationship between recruits and adults that decreases over time. Therefore, as recruitment increases, the adult population of *Chthamalus* is less influenced by recruits. Even though more recruits are available, they become less important to the adult population. Over time, the system becomes saturated and post-settlement mortality is more important in structuring the adult population. Initially, settlement affects stability and population regulation because settlement affects local abundance and is unrelated to local production (no lack of feedback, acting like an open system). After some amount of time, settlement variability has no effect on local populations and only local processes affect local populations (behaving like a closed system) (Connell, 1985). This relationship could be driving the differences seen in community structure between the rip-rap and plates. These comparisons allow one to examine how recruitment and adult number are linked and if the relationship diminishes in importance over time and for *Chthamalus*, it does. Over time, the adult numbers become less dependent on recruitment and post-settlement mortality and density-dependent factors become more important in structuring the adult community.

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Figure 1. Map of the Monterey Bay in central California (centered at approximately 36° 50' N, 121° 55'W) showing locations of coastal armoring and man-made structures at the land-sea boundary (concrete seawalls, groins, jetties, piers and rip-rap). In addition, the dominant substrate in the intertidal is shown - Santa Cruz Mudstone in red, Purisima in dark blue, Sand in turquoise, and Granite in green. The study sites are also labeled – Terrace Point (TP) and Point Cabrillo (PC). (Map adapted from K. Patsch, pers. comm., 2005.)

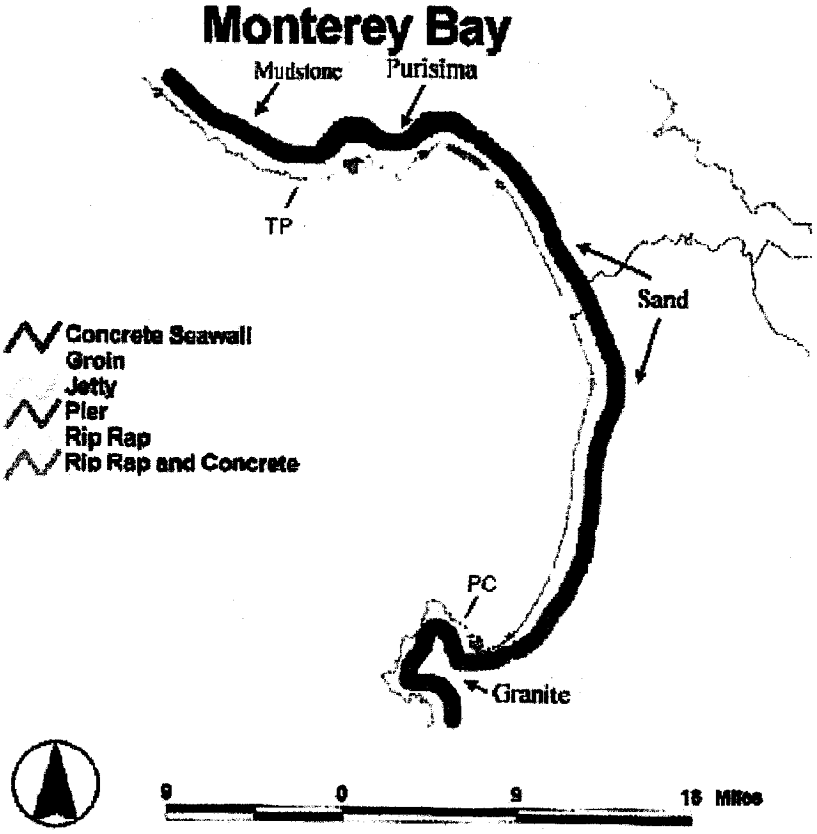


Figure 2. The mean number of *Balanus* settling on each substrate after 1,022 days. The means and within treatment error bars (standard error of the mean) shown are based on log transformed data. In addition, letters indicate differences among treatments generated from log transformed data (Table 1). For convenience, the y-axis is shown in untransformed units and groups that are significantly different ($p<0.05$) are represented with different coding letters (a, ab).

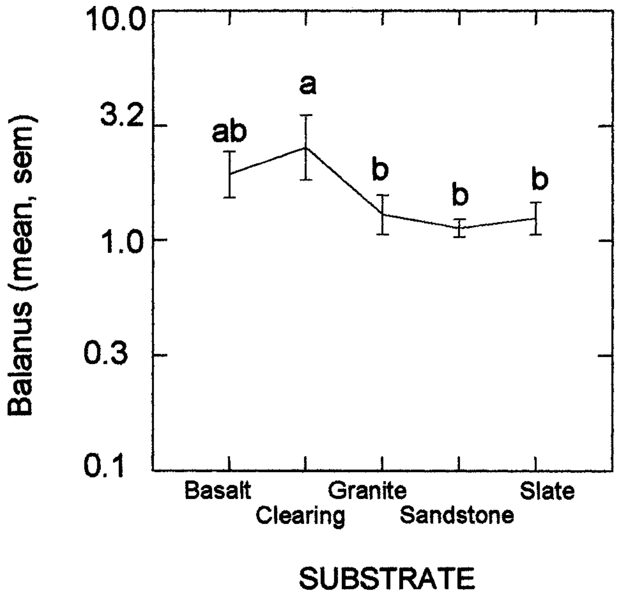


Figure 3. The abundance on *Balanus* at PC on the granite clearings and granite plates was not significantly different. Therefore, the characteristics of the plate (raised, surrounded by z-spar epoxy, etc.) did not affect settlement. For convenience, groups that are not significantly different ($p<0.05$) are represented with same coding letters (a).

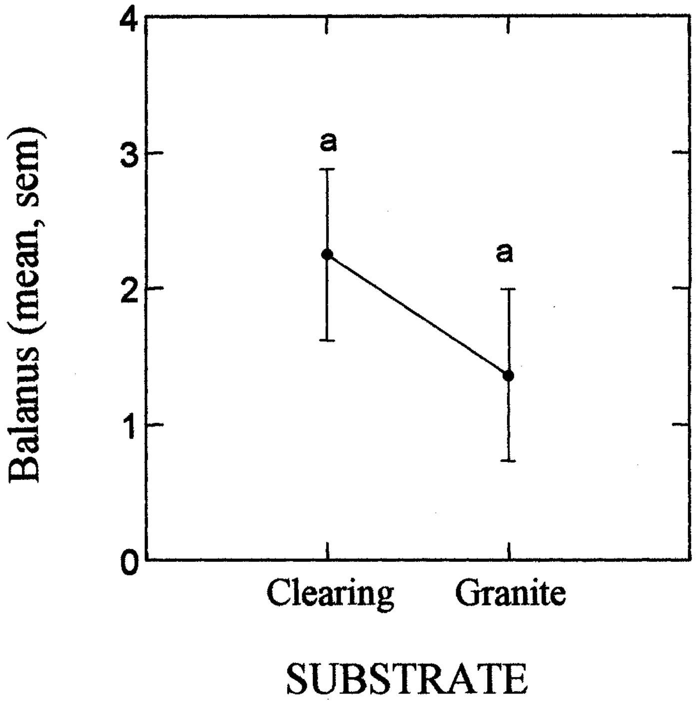


Figure 4. The mean number of *Chthamalus* that settled at Point Cabrillo (PC) and Terrace Point (TP) after 1,022 days. The means and within treatment error bars (standard error of the mean) shown are based on log transformed data. In addition, letters indicate differences among treatments generated from log transformed data (Table 2). For convenience, groups that are significantly different ($p<0.05$) are represented with different coding letters (a, b).

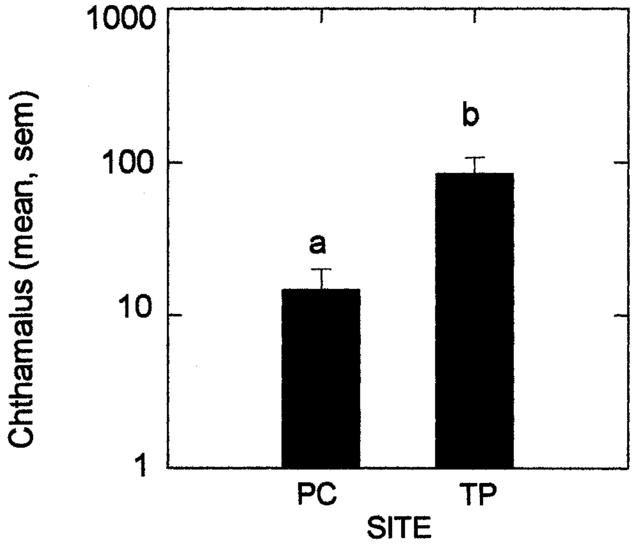


Figure 5. The mean number of *Chthamalus* settling on each substrate after 1,022 days. The means of the untransformed data are shown and within treatment error bars (standard error of the mean). In addition, letters indicate differences among treatments generated from log transformed data (Table 2). For convenience, the y-axis is shown in untransformed units and groups that are significantly different ($p<0.05$) are represented with different coding letters (a, b).

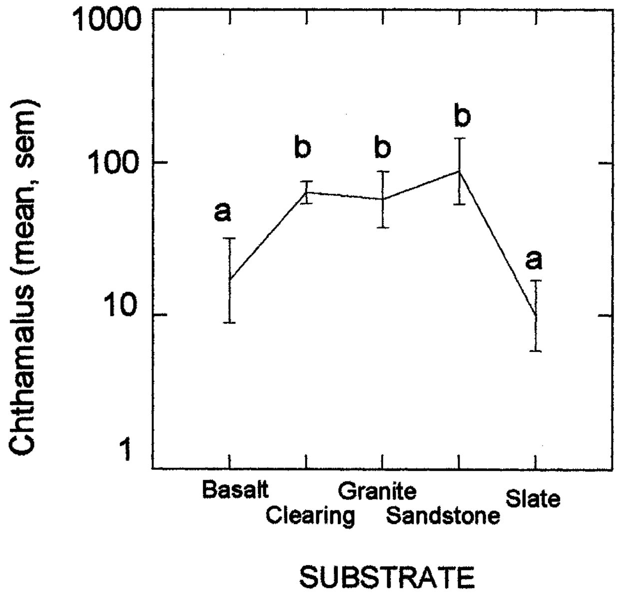


Figure 6. The relationship between the adult *Chthamalus* and the recruits. This relationship was non-linear. The equation of the line was $y = a + b(x)^c$. The r^2 value was 0.98, a=-3.44, b= 4.54, c=0.53.

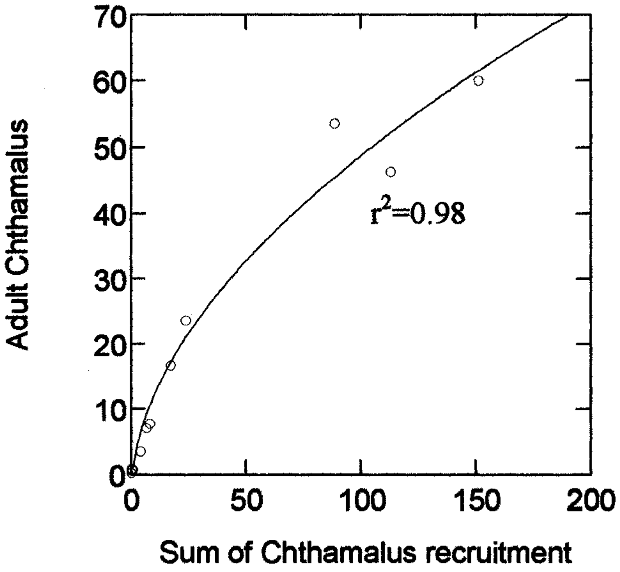


Figure 7. The relationship between the adult *Balanus* and the recruits was linear. Two lines are shown, one with day 341 and one without day 341. The r^2 for the data with day 341 was 0.35, p=0.025, b or slope=0.71, a=0.46. Day 341 was a count potentially very soon after a large recruitment pulse. The r^2 without day 341 was 0.58, p=0.0004, b or slope=0.20, a=0.29.

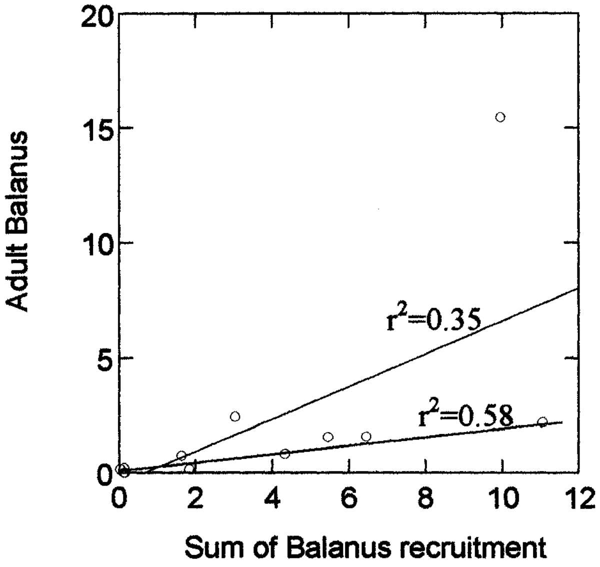
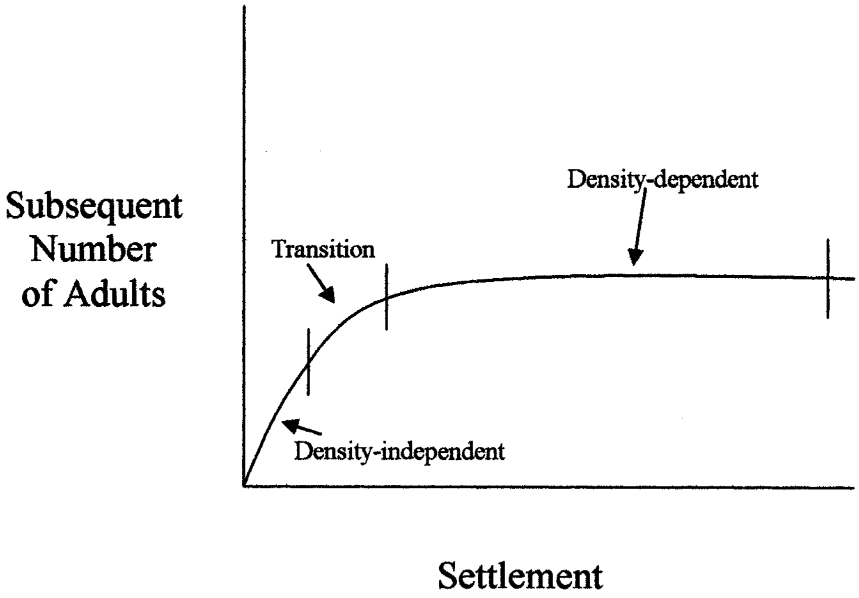


Figure 8. Connell's (1985) hypothetical relationship between settlement (x) and adult numbers (y). There are three areas to the curve – a linear portion that is density-dependent (low levels of recruitment), a transitional portion (as recruitment increases), and then a flat line, fully density-dependent (as recruitment increases, adult numbers are not affected).



Appendix 1

ROCK ANALYSIS

In my thesis chapters, I examined intertidal community structure on different rock types. Numerous studies (see Chapter 1 for references) have shown that rock type (surface texture/rugosity, water retention, chemical cues, and material) can significantly affect the number and/or abundance of species present, yet that has not been well documented by critical comparisons of community structure on different rock types. My goal was to compare the rock substrates upon which I had evaluated community structure. For the analyses, I examined both rock composition (XRD, thin section petrography) and physical properties (porosity, rugosity). These are characteristics that I believe could affect the biology.

METHODS

Collection of samples

There were 6 different rocks tested in these analyses. A slab of the bedrock at Terrace Point, the Santa Cruz Mudstone, was collected in the field (see Chapter 1 for map) for analysis. A hunk of granite from Point Cabrillo was collected in the field, the bedrock at that site. In addition, the settling plates I cut from collected rock from armored shorelines in Santa Cruz County - basalt, granite and sandstone - and a purchased slate rock, were also tested. These are the rock types I used and tested in the experiments (Chapters 3 and 4).

Rock Composition

X-ray diffraction methods were used to identify minerals and other crystalline phases from interatomic spacings. Samples of the rock were finely pulverized and mounted in back-filled powder mounts prior to X-ray diffraction analysis. A Phillips Norelco 3KW X-ray generator fitted with a vertical goniometer was used to determine the overall mineralogic compositions of the rocks in this study. All scans used CuKα X-radiation and a curved graphite monochromator radiation generated at 40 kv and 20 ma. The size of the divergence slit was 1 degree and the receiving slit 0.2 degree. Routine scans were made to determine the overall composition of these rocks at steps of 0.02° two-θ and count times of 1 second per step.

Physical Properties

The **porosity** is the measure of empty space in the rock and therefore, how much water a rock can hold in the pore spaces/cavities. Thin sections of the rock (30 microns) were cut and mounted on slides for this calculation. Estimates of the porosity were determined by examining the crystals in the 2D thin sections using polarized light (travels in one plane) transmitted thru the thin sections so pore spaces appear as bright spots. Porosity was estimated by the percent of empty spaces present in the rock. Under cross-polarized light, empty spaces are black. Using cross polarized light, the pores appear dark where the light is not diffracted; the crystals appear white where light is diffracted. Overlapping the two pictures and combining them with a filter in an image analysis program (Photoshop) allows the estimation of the area of black space (pores) compared to the area of white space, yielding the percentage of pore space in a rock.

The **rugosity** (or micro-rugosity, <1 cm) was assessed with image analysis of weathered surfaces. Weathered surfaces of the rock samples were placed under a dissecting microscope and digital scans/photographs were taken with a transparent ruler for scale. Four digital pictures (camera setting for high contrast reflected light) were taken with a fiber optics cable at 1.5" from surface and at ~10° angle for shading in the 4 orientations relative to the microscope (0 - north, 1- east, 2 - south and 3- west). A total of 6 plates and of 24 photos were examined and pictures saved in jpg format. These images were then imported into Photoshop for image processing. To import pictures taken from the 4 angles (0 to 3), a new document was created and the 4 pictures were imported in 4 separate layers. A filter 'Overlay' was applied and the picture was changed from RGB to grayscale after flattening layers. The pictures were saved as jpegs (8 bits). Images were then imported and converted into 32 bit format and analyzed with ImageJ with plugin SurfCharJ. Grayscale correction was applied with an auto-contrast black and white filter. The picture was scaled with scale tool and micro-rugosity parameters were run with the plug-in SurfCharJ at four different resolutions: for the entire picture, and for areas of the pictures having 0.5, 0.2, 0.1, and 0.01 cm, respectively. Roughness statistics measure R-values on the whole surface and give roughness values according to the ISO 4287/2000 standard: arithmetical mean deviation, root mean square deviation, Kurtosis of the assessed profile, skewness of the assessed profile, lowest valley, highest peak, and the total height of the profile. Micro-rugosity data are reported as Rku, Kurtosis of the assessed profile at 1 cm resolution.

RESULTS

Rock Composition

The mineralogy for each rock type is described below.

Santa Cruz Mudstone (Terrace Point bedrock): The specimen comes from a porcelanite layer composed of biosilica (diatoms) clay and silt to very fine sand. Color is pale brown with darker/ dark-red clay and Fe-oxide spots. Silica frustules are visible in normal light while they disappear in polarized light due their amorphous composition (opal-A and opal-CT). Under the microscope the sample is composed of ~30% silt (mostly angular grains of quartz and secondarily feldspars), with the resting 70% of the mass ground being composed of mixed clay and fine biosilica.

Slate (plate): The specimen of slate is mostly composed of clay minerals: illite, kaolinite and chamosite. There is some quartz and a few percent of plagioclase (anorthite).

Sandstone plate: This specimen is probably from the Franciscan Formation. It consists of poorly sorted, fine to medium sandstone. Matrix is about 50% of the sample (greywacke). The dominant framework minerals are: quartz, feldspars (mostly plagioclases) and lithic fragments (mostly cherts). Sutured contacts between framework minerals and clasts indicate metamorphic conditions after deposition (which is typical of the Franciscan Fmt.).

Basalt (plate): This specimen is 95% sodium plagioclase (albite). Also noted was a lack of porosity, the very fine texture, and complete interlocking between minerals.

Granite (Point Cabrillo bedrock): This specimen is not true granite but a granodiorite, since the two most important minerals are plagioclases and quartz. It is composed of quartz, plagioclase (albite), K-feldspar (microcline), and biotite. One of the main differences between granites and granodiorites is that the latter are usually more prone to weathering and erosion due to the lower quartz content.

Granite (plate): This sample is typical granite. The rock is composed mainly of quartz, although feldspars and black biotite (mica) also occur. This sample differs from the previous in that 1) the granite has less plagioclase (albite) and more K-feldspars (both microcline and orthoclase) and 2) for a very extensive microfracturing of the minerals. However, the microfractures (a few hundred microns) look sealed with secondary precipitation of quartz.

Physical Properties

Table 1. Summary of the results from the rock analyses.

Rock	**Type**	**Porosity**	**Rugosity**
SC Mudstone (native rock TP)	Sedimentary	5-10%	4.82
Slate (plate)	Metamorphic	<1%	24.92
Sandstone (plate)	Slightly metamorphic	<1%	1.39
Basalt (plate)	Metamorphic	<1%	0.57
Granodiorite (plate)	Igneous	<1%	6.61
Granite (native rock PC)	Igneous	<1%	2.16

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