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COMMUNITY ECOLOGY OF THE INVASIVE INTERTIDAL BARNACLE

CHTHAMALUS PROTEUS IN HAWAII

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ABSTRACT

Chthamalus proteus is the most recent invasive barnacle in the Hawaiian Islands, arriving some time after 1973. A native of the Gulf of Mexico, Caribbean Sea and southwestern Atlantic Ocean, *C. proteus* is now found throughout the main Hawaiian Islands. While still mainly restricted to harbors on neighbor islands, *C. proteus* has spread around the island of Oahu, inhabiting the intertidal zone in open-coast settings and attaining high abundance in wave-protected harbors and bays.

Aspects of the barnacle's life history were investigated at several locations within its home range and in Hawaii. While there were some differences in fecundity and vertical range between locations, there was overall little change in life history characteristics between the native and invaded ranges. We predict that the barnacle will continue to spread throughout the islands and to other areas in the Pacific that receive shipping traffic from Hawaii.

Competitive interactions between *C. proteus* and two other barnacles, an earlier invader, *Balanus reticulatus*, and the native *Nesochthamalus intertextus* were investigated at three locations on Oahu. Competition for space does not appear to be occurring between *C. proteus* and the native barnacle, but the newer invader is able to outcompete *B. reticulatus* via substrate pre-emption. Variation in recruitment between sites appears to be more important than competition in determining barnacle abundance and which barnacle will be the numerical dominant.

Interactions between *C. proteus* and the native limpet *Siphonaria normalis* were also

examined. While the presence of the limpet enhances settlement of the barnacle, limpets prefer barnacle-free areas and move into patches cleared of barnacles. Whether interactions between the barnacle and limpet will be positive or negative may vary with densities of the two organisms.

A “field microcosm” experiment, in which tiles were assembled with one or three species of native bivalves and then placed into the intertidal zone, was used to test the idea that higher diversity leads to invasion resistance. There was no difference due to diversity in the communities of organisms that invaded tiles, but the presence or absence of certain bivalves in the original assembled communities led to differences in invaders.

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CHAPTER 1.

Introduction

With few exceptions, introduced aquatic species have, up until the last two decades, been overlooked by both the public and scientific community. Several of these species, notably the zebra mussel, *Dreissena polymorpha*, and the aquarium water moss or Giant Salvinia, *Salvinia molesta*, have gained public notoriety in the mainland United States because of the extensive damage they have done by clogging water intake pipes and choking waterways. These two species illustrate one of the potential problems of introduced species – freed from their native predators and competitors, these organisms can reproduce without check and by their sheer numbers alter the environment in which they find themselves.

Recent research has identified 343 introduced species in Hawaiian marine and brackish waters, including 287 invertebrates, 24 algae, 20 fish and 12 flowering plants (Carlton and Eldredge in prep). Introduced species (defined here as species moved into new regions purposely or inadvertently by human activities) have been noted in Pearl Harbor and other Oahu ports for many years, and fouling communities, which include many introduced organisms, have been particularly examined (Edmondson 1931, Ingram 1937, Edmondson and Ingram 1939, Edmondson 1940, 1942, 1944, Hutchins 1944, Edmondson 1951, Edmondson 1952, Edmondson 1954, Edmondson 1962, Hurlbut 1990, 1991a, Hurlbut 1991b, Eldredge 1995). In Kaneohe Bay and Malama Bay on the island of Oahu a number of invasive algal species are causing problems by outcompeting native algae for light and by overgrowing coral species (C.M. Smith, personal communication, Woo 2000, Smith 2003). The soft coral *Carijoa riisei*, a native of the Caribbean, has

recently been discovered overgrowing up to 50 percent of black coral (*Antipathes dichotoma*) colonies at depths of 80 to 110 m (S. Kahng, personal communication). Despite a high awareness of the impacts of invasive species in terrestrial ecosystems in Hawaii, comparatively little research has been done on marine invaders and their impacts or potential impacts on native species and ecosystems, and even less on the invertebrates (exceptions are Kinzie 1966, Kinzie 1968, Thomas 1979).

Invertebrate invaders in the intertidal zone have received perhaps the least amount of attention. Despite extensive investigations of coral reef and terrestrial habitats by researchers at the University of Hawaii and various state and federal agencies, the rocky intertidal of Hawaii, like that of many tropical islands, has not been well characterized. Charles Edmondson wrote a children's book about the intertidal zone (1949) and his taxonomic work on intertidal animals, along with that of others, was included in the Reef and Shore series (Edmondson 1946, Devaney and Eldredge 1977, Kay 1979, Devaney and Eldredge 1987, Abbott et al. 1997), but there are no comprehensive accounts of the intertidal fauna and no current plans for surveys or monitoring efforts by any of the local academic researchers or management agencies. A literature search using the Zoological Records and Biosis databases (1978 to current) using the key words "Hawaii AND rocky intertidal OR rocky shores" uncovered 10 journal articles, most of which dealt with taxonomy of a single species or genus. Approximately 20 theses in the archives of the Zoology Department at the University of Hawaii deal with some aspect of the intertidal, but with a few exceptions (*i.e.*, Strasberg, 1953) these generally focus on the taxonomy, life history or behavior of one species or genus. Virtually nothing has been written on the diversity or the community ecology of Hawaii's intertidal (exceptions are Kay 1979, Kay

1987, Smith 1992). Without such work, processes important to the structure of intertidal communities will remain unknown and new invasions or local extinctions of native species will go undetected.

Such is the case of the invasion of the Hawaiian Islands by the intertidal barnacle *Chthamalus proteus*, which arrived some time after 1973, the year of the most recent survey of intertidal barnacles on Oahu (Matsuda) and was not discovered until it had already become abundant and widespread around the islands. Although researchers collected it in Pearl Harbor in 1993 (Brock, personal communication), its identity was not revealed until John Hoover, a local wildlife photographer, collected a sample and sent it to a mainland barnacle taxonomist (Southward et al. 1998). Although this barnacle may have replaced an earlier invader, *Balanus amphitrite*, which was itself once widespread and abundant, the lack of attention to intertidal organisms in the intervening years does not allow us to determine when or how that may have happened.

Other than the mantis shrimp studied by Kinzie (1966), which can be found in the lower intertidal as well as the shallow subtidal, this dissertation represents perhaps the first research on the ecology of an invasive invertebrate in Hawaii's intertidal zone.

Organization of the dissertation

Each of the next five chapters has been written as a stand-alone paper, with its own literature review and introduction. The first of these chapters, which compares aspects of the life history, population biology and ecology of *C. proteus* in the Hawaiian Islands and at three sites in its native range, Curacao, Panama, and Brazil was written with two members of the Kewalo Marine Laboratory, John Zardus and Michael Hadfield; Fabio

Bettini Pitombo, Instituto de Biología, Universidade Federal Rural do Rio de Janeiro; and Vanessa Fread, of the University of Queensland, who worked on this project at Kewalo Marine Laboratory through the Undergraduate Mentoring in Environmental Biology Program. Work on the population structure of *C. proteus* using molecular techniques has also been done (Zardus and Hadfield, in press), but is not included here.

Chapters 3 and 4 examine interactions between *C. proteus* and two other barnacles in Hawaii, *Balanus reticulatus*, which was first reported from Hawaii in the 1920s, and the native *Nesochthamalus intertextus*. Chapter 5 examines competitive and facilitative interactions between *C. proteus* and the native pulmonate limpet *Siphonaria normalis*. Chapter 6 uses a field microcosm experiment to examine the effect of native species diversity on the ability of sessile intertidal organisms to invade established communities. Chapter 7 provides a general conclusion and context to the dissertation.

CHAPTER 2.

A tale of three seas: consistency of natural history traits in a Caribbean-Atlantic barnacle introduced to Hawaii

Introduction

One of the major, and still elusive, goals of invasion biology is to predict which species will arrive in a new area, where and when they will do so, and what impacts they will have. Arrival and establishment involve so many fluctuating factors that reliable predictions seem unlikely, except in rare instances where modes of introduction and the basic physiological requirements of an organism are well-known. But it should be possible to predict how quickly and where an established invader might spread, armed with knowledge of the organism's life history and aspects of the new environment that might aid dispersal, such as prevailing wind or water currents. Indeed, a substantial literature has been devoted to creating such predictive models for invading species (for reviews, see Andow et al. 1990, Grosholz 1996, Higgins and Richardson 1996, Williamson 1996). Models have also been proposed to predict whether introduced algae, plants, birds and mammals will become "invasive" (e.g., Smallwood and Salmon 1992, Tucker and Richardson 1995, Reichard and Hamilton 1997, Pheloung et al. 1999, Daehler and Carino 2000, Nyberg and Wallentinus 2005). These authors defined "invasive" as spreading into natural areas and being perceived as pests or weeds by botanists, wildlife managers and agriculturalists. Here, we use the term "invader" in its

broader sense to mean an organism that has entered a new biogeographic region as the result of human activities.

Models of spread and models that predict pest status are dependent on knowledge of the life history, geographical range, environmental tolerances, and resource requirements of an invader. Unfortunately, an understanding of the basic biology of many invading organisms is lacking, particularly for invertebrate animals of little or no commercial value and no previous history as pests. Even with such knowledge, models may be of limited use if invaders display plasticity in key traits. Shifts in behavior, habitat use, morphology and reproductive biology, and changes in the ecological role of an invader between its home range and new region have been noted frequently in the literature (e.g., Elton 1958, Blaustein et al. 1983, Blossey and Notzold 1995, Carroll and Dingle 1996, Stiling and Simberloff 2000, Torchin et al. 2003). The few comparative studies that have been made on marine invertebrate invaders suggest that changes frequently occur (e.g., Grosholz and Ruiz 2003, who looked at body size in 19 species of decapod crustaceans, molluscs and a sea star, and Torchin et al. 2003, who looked at parasites in 26 species including marine molluscs and crustaceans). Here, we examine aspects of the biology and ecology of an invasive barnacle in its native and new ranges to test the assumption that change is the rule in invasions.

Study organism

The intertidal barnacle *Chthamalus proteus* is native to the western Atlantic Ocean and Caribbean Sea (Dando and Southward 1980). It is the most recent alien barnacle to settle in the Hawaiian Islands, following introductions of *Balanus amphitrite*, *B. eburneus*, and

B. reticulatus (Carlton and Eldredge in prep). The exact date of the arrival of *C. proteus* is unknown. It was not found in a survey of the intertidal zone on the island of Oahu in the early 1970s (Matsuda 1973) and had not been described in earlier Hawaiian barnacle literature (e.g., Pilsbry 1927, Edmondson and Ingram 1939, Edmondson 1946, Gordon 1970). *Chthamalus proteus* was first reported in 1995 by a wildlife photographer who was preparing a book on Hawaii's marine invertebrates (Southward et al. 1998), although a specimen, misidentified as *Euraphia hembeli*, a native barnacle, was collected in Pearl Harbor two years earlier (J. Brock, unpublished report 1993). By the time it was correctly identified, *C. proteus* already occurred in dense aggregations in Kaneohe Bay on the windward side of Oahu. It was subsequently found at several other locations around the island by investigators from the Bishop Museum (Coles 1999) and reported from Kauai and Maui (Southward et al. 1998). It has since been reported from Midway, Guam and the Mariana Islands (Southward et al. 1998), and from Mangareva and Moorea in French Polynesia (A. Southward, personal communication).

The native range of *C. proteus* is reported to be from southern Florida in the Gulf of Mexico to Parana state, Brazil and west to the Caribbean (Dando and Southward 1980). *Chthamalus proteus* was only recently separated from two other *Chthamalus* species, *C. fragilis* and *C. bisinuatus*, by Dando and Southward (1980). These two species co-occur with *C. proteus* in the northern and southern portions of its range, respectively. Observations on the distribution of *C. proteus* in the Gulf of Mexico and the Caribbean suggest that it does not tolerate lowered salinity (<22 ppt) and is found in highest abundance in moderate to low-energy locations with muddy or murky water (Southward

1975, Dando and Southward 1980). Other than these observations nothing was known about the biology and ecology of *C. proteus* prior to the present study.

Although *C. proteus* could potentially spread throughout the Hawaiian Islands via natural larval dispersal (assuming favorable currents and sufficiently long larval life spans), vessel traffic between islands is likely a more efficient mode of interisland transport. *Chthamalus proteus* has been observed heavily fouling the hulls of the interisland barges that travel regularly between the islands (Godwin, personal communication). If barnacles on boat hulls release larvae in port, they are inoculating these areas with a larger and more regular supply of larvae than might be expected via natural dispersal. While vessel traffic may be largely responsible for the spread of this invader around an island, dispersal in the plankton to nearby sites “down current” from established populations may also play a major role. Thus, for both within-island and between-island spread, the barnacle’s reproductive effort and larval life history may be key factors in its invasion, but neither of these had been described for *C. proteus*. Additionally, knowledge of an invading organism’s somatic growth, particularly as it affects fecundity and mortality rates, is potentially useful in understanding the success of an invasion, but had not been investigated in this barnacle.

Study objectives

Our study had five objectives: 1) to describe key life history parameters of *C. proteus* in Hawaii; 2) to map the present distribution of *C. proteus* in the Hawaiian Islands; 3) to compare habitat use, body size, fecundity and population density between Hawaii and sites in the barnacle’s native range; 4) to evaluate whether the Caribbean-Atlantic data, if

known earlier, could have informed us about the basic physiological and ecological limits of the current invasion, and if so, 5) to use these data to make predictions about the future of this invasion in Hawaii and the tropical Pacific.

Materials and Methods

Life history of *Chthamalus proteus* in Hawaii

Larval development. Studies of the larval development of *Chthamalus proteus* were made in the winters of 2002-03 and 2003-04. For each study, several hundred adult barnacles were collected intact with their substratum from various sites around Oahu. Barnacles were kept covered overnight in the laboratory and induced to release larvae by removal of the cover in the morning. Swimming nauplii were concentrated at a light source, drawn out with a pipette, and placed into 2 L beakers of 0.22 μm filtered seawater. Following standard protocols for barnacle culture (Strathmann 1987), antibiotics were added to the water (60 $\mu\text{g/ml}$ penicillin and 50 $\mu\text{g/ml}$ streptomycin) and cultures were adjusted to a density of 1,000 larvae/L. In 2002-03, larvae were fed the flagellate *Isochrysis galbana* (Chrysophyta) at a density of 125,000 cells/ml and incubated at one of two temperatures, 25°C or 28°C. In 2003-04, larvae were fed either *I. galbana* at 250,000 cells/ml or a combination of *I. galbana* and the diatom *Skeletonema costatum* at a total density of 250,000 cells/ml and cultured at either 24°C or 28°C. Water changes were made daily. Individual larvae were reared alongside mass cultures under the same conditions but in 2 ml culture wells to observe stages of molting.

Reproduction and seasonality. Once a month from September 2001 to August 2003, individuals of *C. proteus* were collected from rocks at Keehi Lagoon and near the Hawaii Institute of Marine Biology's Lilipuna Pier in Kaneohe Bay (Fig. 2.1, arrows). Fifty individuals from each site were haphazardly selected each collecting period and removed from the rocks using a thin blade. The rostrocarinal length was measured to the nearest 0.01 mm for each individual and its reproductive status noted. Female reproductive status for each barnacle was categorized as no gonadal development, ovaries present, yolky eggs, embryos with eyes, or nauplii. When eggs, embryos or nauplii (hereafter referred to as "propagules") were present, they were removed from the adult barnacle, placed in a dish under a dissecting microscope and counted. Numbers of swimming nauplii were estimated from random subsamples.

To determine if fecundity is correlated with size in *C. proteus*, the number of propagules was regressed against barnacle size (*i.e.* shell length). An analysis of covariance was used to examine differences in fecundity between sites, using size as a covariate. Length data were log transformed and egg counts were square-root transformed to meet assumptions of homogeneity of variance. To investigate seasonal patterns in fecundity, the proportion of individuals with propagules at each site was plotted against month.

Growth. The growth of individuals of *C. proteus* living on seawalls was tracked over two one-year periods in Hawaii at a site in Waikiki (Kuhio Beach) and over one 13-month and one nine-month period at Kualoa Beach Park on Oahu's windward side (Fig. 2.1, sites 39 and 62). Twenty permanent 12 x 15 cm quadrats were established on a seawall in

the middle of the barnacle zone at each site (approximately 60 cm above zero tide). Individual barnacles were mapped onto acetate sheets and numbered. The rostrocarinal length of the mapped barnacles was recorded every two months from Oct 1999-Oct 2000 and December 2000-December 2001 at Waikiki and from June 2000-July 2001 and July 2001-March 2002 at Kualoa. Measurements were made using Vernier calipers; measurement error was estimated to be ~0.3 mm through repeated measurements of a sample of individuals.

Barnacles were haphazardly selected and thus included some crowded and some uncrowded individuals. In Waikiki, 101 of 200 barnacles survived for the first year, and 93 of 200 survived in the second year. The survivors were used in growth measurements, with mean monthly growth calculated as the difference between final and initial size, divided by 12. At Kualoa, 26 of an initial 40 barnacles survived for five months of the first year, and 10 of these survived for the entire first time period. Growth was calculated for the first five months using the 25 barnacles, and for the 13 month period using the remaining 10. In the second time period, nine out of 23 barnacles survived and were used for growth measurements.

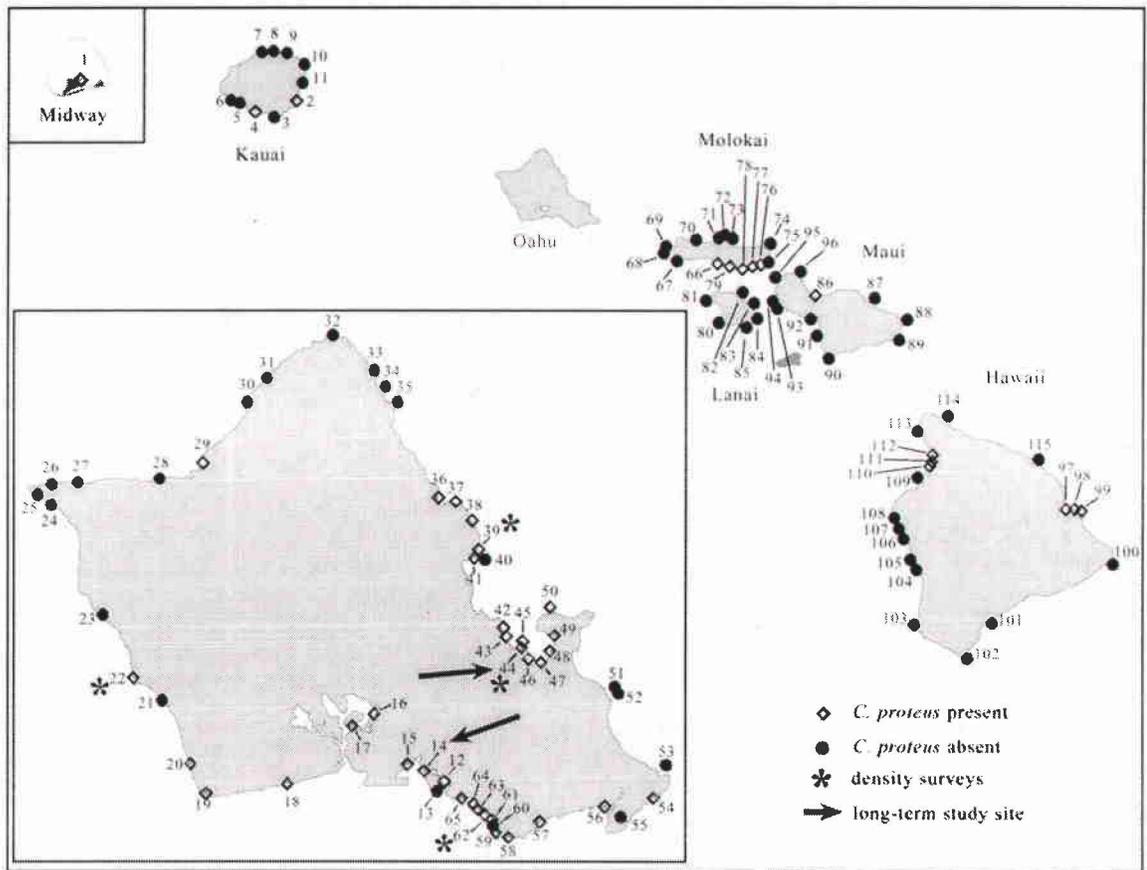


Figure 2.1. Map of main Hawaiian Islands, showing survey and study sites. Sites are numbered for reference in Appendix A.

Additional data on growth of *C. proteus* were gathered from a site in Kaneohe Bay (Lilipuna Pier, Fig. 2.1, site 44). Here, growth was determined by tracking individuals that had settled onto 10 x 10-cm terra cotta tiles attached to pier pilings at approximately 60 cm above the zero tide mark. These plates were photographed bimonthly for 1 year using a Nikonos V camera with a 35 mm lens and a 2:1 framer. Size measurements were made of individual barnacles using these photos and factoring in the magnification. Recruitment of barnacles and oysters to the plates was extremely high, making it difficult to track individual barnacles with certainty over more than about a two month period. Thus, growth was calculated from three sets of barnacles: 18 barnacles on one plate between March 2002 and May 2002; 10 barnacles on another plate between May 2002 and July 2002; and 20 barnacles on a third plate between November 2002 and January 2003. Some of the barnacles tracked during the fall-winter period were new recruits to open patches, but most of the barnacles were growing in already quite crowded conditions. Because new settlers in open patches should grow faster than larger or more crowded barnacles, we calculated mean monthly growth in several ways: the mean difference in length of all the barnacles tracked (N = 48); the mean difference in length of an additional 11 newly settled barnacles; and the mean length of the 18 barnacles on the first plate mentioned above on March 2002, calculated by dividing by the length of time the plate had been in the water (seven months).

Mortality. To determine the overall mortality rate and whether mortality was size dependent, we used the same barnacles tracked for growth in Waikiki and Kualoa. The tests of dead barnacles, when present, were used to determine size at death. Bimonthly

growth at these sites was low (frequently lower than measurement error), so where tests were not present, we were able to use the size recorded two months earlier with confidence that it was a good estimate of size at mortality. The mortality rate was calculated as number of barnacles that had died at the end of each time period over the initial number of barnacles. A chi-square test was used to determine whether there was a difference between expected and observed deaths in 1 mm (rostrocarinal axis) size classes ranging from 4.0 to 11.9 mm at Waikiki and from 4.0 to 7.9 mm at Kualoa. Although smaller and larger barnacles were tracked, there were too few individuals in these groups to include in the analyses.

Comparison of *C. proteus* in Hawaii and native range

Geographic distribution and habitat use. From 1999 to 2003, we surveyed a number of intertidal sites around the island of Oahu for *C. proteus*, returning to many sites several times over the years. Sites included open coast areas, estuarine environments, embayments, stream mouths and channelized river openings to the ocean, and private, military and commercial harbors and marinas (Fig. 2.1 and Appendix A). Sites were selected based on accessibility and the presence of habitats suitable for shore barnacles. We looked for the barnacle on rocks, sea walls, pier pilings, mangrove prop roots and other hard substrata above the zero tide line in intertidal situations and on floating structures in harbors and marinas. Sites were searched for at least 1.5 hour during each survey. The islands of Molokai, Maui, Lanai, Kauai and Hawaii were also surveyed, although less intensively (Fig. 2.1 and Appendix A). Searches on these islands focused on harbors and boat ramps, with additional sites along the open coast. Sites were surveyed

for about 1 hour, unless the barnacle was found sooner. Between all six islands, we surveyed 115 sites. These data were used to map the current geographic distribution of *C. proteus* in Hawaii, with additional sites obtained from discussions with researchers at the Bernice P. Bishop Museum.

Twenty-three sites were surveyed in Curaçao, 23 in Panama and three in Brazil (Fig. 2.2). These sites were selected as above and included a range of habitat types including open-coast rocky intertidal areas and harbors. Additional information on the distribution of *C. proteus* in its native range is contained in Southward (1975, as *C. bisinuatus*), Dando and Southward (1980) and Young (1993, 1995).

In addition to noting the presence or absence of *C. proteus*, sites were qualitatively described in terms of wave exposure (low, medium, high), substrate type, and water clarity. When the barnacle was present, we also noted its vertical distribution, whether other barnacles were present, and the identities of other abundant organisms in the intertidal zone. Where they were available from records and research publications for the region under study, or for specific sites, we also collected data on tidal amplitude, air and water temperatures and salinity.

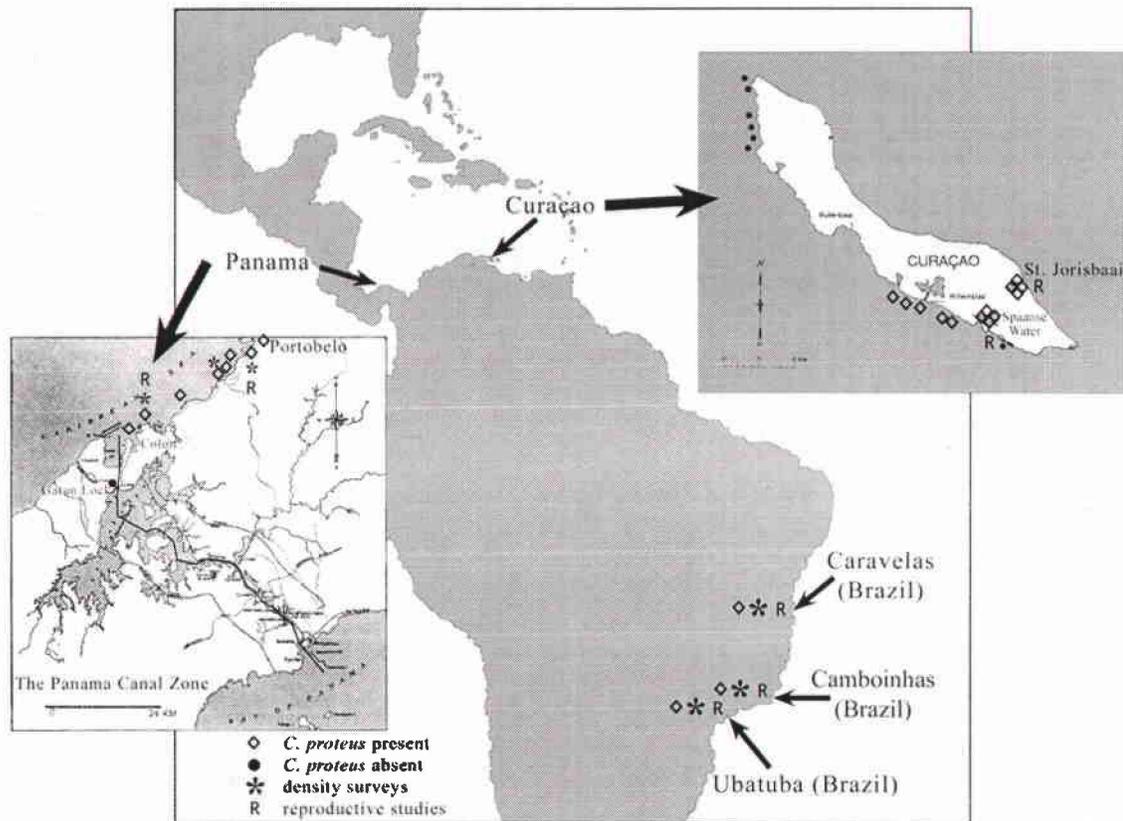


Figure 2.2. Map of Caribbean and Atlantic, showing areas surveyed and study sites.

Reproduction, body size and spatial variation. In addition to the studies at Keehi Lagoon and the Kaneohe Bay site described above, data on reproduction were also collected once from an additional five sites on Oahu from December 2001-February 2002 (Fig. 2.1, sites 22, 41, 44, 58 and 62). At three of these sites, Waikiki (Kuhio Beach), Kaneohe Bay (pier pilings, Lilipuna Pier) and Kualoa Beach Park, where *C. proteus* was abundant, we used a 10 m transect line and randomly placed 12.5 x 15 cm quadrats to select barnacles.

Individuals falling under random points in the quadrats were taken until 50 individuals had been collected. At the sites that were less densely populated with *C. proteus*, *i.e.*, Diamond Head and Maili Point, all individuals found in 20 quadrats were collected.

Fifty individual barnacles were collected from each of two sites in Curaçao and five sites in Panama, and between 12 and 28 individuals were collected from three sites in Brazil (Fig. 2.2, inset). Collections were made one time only at each site, except at one of the Brazil sites, where monthly collections were made from June through September 2003. Where possible, we used the same methods used on Oahu to select barnacles. Where this was not feasible (*e.g.*, on mangrove roots or small stones) an effort was made to collect barnacles representative of the different size classes on that substratum.

Typically, most barnacles at these sites did not vary more than 1 mm in size, with a few smaller new recruits and a few larger individuals present. In an attempt to prevent bias in sampling, most of the barnacles we collected were close to the mean size. At sites where 50 barnacles were collected, we typically also collected 1-2 smaller and 1-2 larger specimens.

Length was measured and reproductive status was noted following the methods described in the section “Reproduction and seasonality” above. The percentage of

individuals with propagules was calculated along with the mean number of propagules per reproductive individual. These numbers were added to the plot of the long-term data collected at Keehi Lagoon and Kaneohe Bay for visual comparison. The relationship between size and number of propagules was plotted for all sites. Analysis of covariance was used as previously described to compare number of eggs per individual between regions.

Population density. Measures of percent cover were also made at three of the Hawaiian sites mentioned above (Fig. 2.1, asterisks), using a transect line placed in the middle of the barnacle zone. The number of 25 randomly placed points in 15 to 20 12.5 x 15 cm quadrats which fell directly over a barnacle was counted to estimate percent cover. Cover was similarly measured at two sites in Panama; in Brazil, Curaçao and three Panama locations where such techniques were infeasible, percent cover was visually estimated using categories of <10 percent, 10-25 percent, 26-50 percent, 51-75 percent, and >75 percent.

Results

Life history of *C. proteus* in Hawaii

Larval development. Seven larval stages were confirmed for *C. proteus*: six naupliar stages followed by a cyprid. The developmental period varied with temperature and diet. At low food concentration (single alga diet) at 28°C, the earliest cyprids were seen on the ninth day, whereas at 25°C they were observed on the 17th day. At high food

concentration (single alga diet) there was no difference between temperature treatments, with the first cyprids seen on the eighth day. Fed a high concentration mixed algal diet, cyprids also appeared on the eighth day at 28°C but two days later at 24°C.

Reproduction and seasonality. Adult barnacles with developing eggs and unhatched nauplii were found in varying abundance at all times of the year (Fig. 2.3). Five distinct peaks of production were observed across a 25-month period at two study sites in Hawaii with a maximum of 72% of the individuals carrying propagules at any given time. The peaks of production were approximately synchronous between the sites. The first peak was observed in the winter of 2001/02 followed by peaks in the spring and fall of both 2002 and 2003. A less distinct peak in the winter of 2002/03 was observed at Keehi Lagoon and was equivocally present at the Kaneohe Bay site. On average, 46% percent of the animals carried propagules during peaks of production (mean calculated across all 5 peaks, both sites).

The mean shell length of barnacles at the Kaneohe Bay site was slightly larger than that at Keehi Lagoon (5.63 mm, SD = 1.26 and 4.93 mm, SD1 = 0.12, respectively). Because barnacles were not selected randomly, these statistics may not be unbiased population estimates, and shell length could not be formally compared.

At both sites, greater numbers of propagules were associated with larger shell size when tested by linear regression: Kaneohe Bay, adj. $r^2 = 0.54$, $P < 0.000001$ (N = 202); Keehi Lagoon, adj. $r^2 = 0.31$, $P < 0.000001$ (N = 207). Comparisons of fecundity between the two sites with shell length as a covariate could not be made by ANCOVA as the test of parallel regression slopes was rejected.

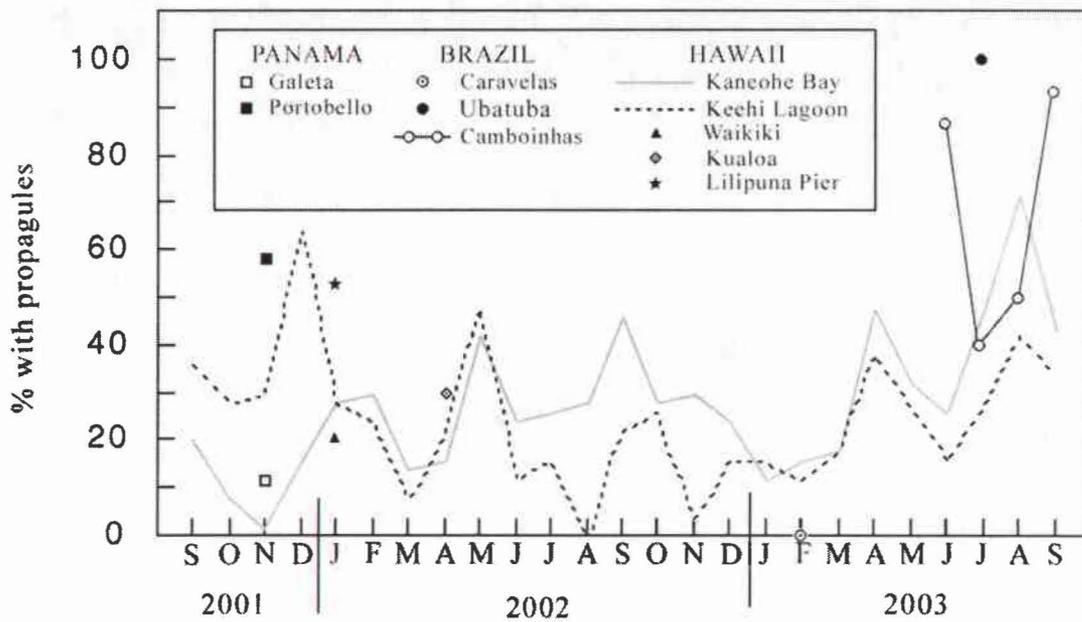


Figure 2.3. Monthly proportion of individuals of *C. proteus* with eggs or unhatched larvae across two annual cycles at two localities in Hawaii. Also included are data for single time-point surveys elsewhere in Hawaii, Panama, Brazil, and a multi-time-point survey in Brazil. Not shown are values taken during September 2000 in Curaçao, Netherlands Antilles: St. Jorisbaai (40%) and Spaanse Water (64%).

Growth. Plots of the ratio of initial to final size vs. initial size indicated that growth of barnacles in our survey was incremental (not proportional). Thus, we were confident in calculating growth as a monthly average across different size classes. Overall, mean growth rates varied by site and by time period, with growth so low at Kualoa in the second time period that it was indistinguishable from measurement error (Table 2.1).

In Kaneohe Bay, mean growth was 0.17 mm/month for all barnacles: 0.37 mm/month for isolated barnacles in bare patches (barnacles ranged from 2 to 4.5 mm at first measured size), and 0.53 mm/month for barnacles growing on plates that had been completely bare seven months earlier. For most of the Kaneohe Bay individuals, growth was by a similar increment across most size classes, but barnacles with initial lengths of <3 mm in bare patches grew faster than those >3 mm, with individuals doubling or tripling in size over a 2-month period. These small barnacles were not included in overall monthly growth estimates.

Mortality. Mortality rates, summarized in Table 2.1, varied both spatially and temporally. In the first year at Waikiki, there was a trend for barnacles in the size class 6.0-6.9 mm to die in higher percentages than other size classes and for barnacles in size classes between 8.0 and 12.9 mm to die in lower percentages than other size classes (Table 2.2A, $\chi^2 = 12.45$, DF = 6, $P = 0.053$). This same trend was seen in the second year in Waikiki, but was clearly not significant (Table 2.2B). There were no differences in mortality between size classes at Kualoa, but there were too few barnacles above 7 mm to detect a trend in larger size classes (Tables 2.2C-D).

Table 2.1 Growth and mortality of *Chthamalus proteus* at three sites in Hawaii.

Site	Initial size (mm)			Growth (mm/month)			Mortality rate (% of total)		
	Min	Max	Mean (SD)	Period I (SD)	N for Period I	Period II (SD)	N for Period II	Period I (N)	Period II (N)
Waikiki	2.6	11.1	6.4 (1.7)	0.13 (0.11)	101	.07 (.07)	93	50 (200)	54 (200)
Kualoa	3.2	7.8	5.5 (1.2)	0.08 (0.12)	26	*	*	75 (40)	61 (23)
Kaneohe Bay	2	7.4	4.4 (1.2)	0.17 (0.74) all barnacles; 0.37-0.53 bare patches	48	N/A	N/A	N/A	N/A

Table 2.2A. Waikiki Year 1 Mortality by size class

Size class (mm)	# alive/expected	# dead/expected	Total
5.0-5.9	15/15	11/11	26
6.0-6.9	12/19	20/13	32
7.0-7.9	26/28	22/20	48
8.0-8.9	29/24	12/17	41
9.0-9.9	19/19	14/13	33
10.0-10.9	18/15	8/11	26
11.0-11.9	9/6	2/4	11
Total	128	89	217

$\chi^2 = 12.449$, DF = 6, P = 0.053

Table 2.2B. Waikiki Year 2 Mortality by size class

Size class (mm)	# alive/expected	# dead/expected	Total
4.0-4.9	6/6	6/6	12
5.0-5.9	10/8	7/9	17
6.0-6.9	7/11	15/11	22
7.0-7.9	14/15	18/17	32
8.0-8.9	15/13	13/14	28
9.0-9.9	16/14	14/16	30
10.0-10.9	13/12	13/13	26
11.0-11.9	7/8	9/8	16
Total	88	95	183

$\chi^2 = 4.203$, DF = 7, P = 0.756

Table 2.2C. Kualoa Year 1 Mortality by size class

Size class (mm)	# alive/expected	# dead/expected	Total
4.0-4.9	9/7	4/6	13
5.0-5.9	8/9	9/8	17
6.0-6.9	7/8	7/6	14
Total	24	20	44

$\chi^2 = 1.632$, DF = 2, P = 0.442

Table 2.2D. Kualoa Year 2 Mortality by size class

Size class (mm)	# alive/expected	# dead/expected	Total
4.0-4.9	3/4	7/6	10
5.0-5.9	7/7	10/10	17
6.0-6.9	8/7	9/10	17
Total	18	26	44

$\chi^2 = 0.684$, DF = 2, P = 0.684

Comparison between Hawaii and native range

Geographic distribution and habitat use. In Hawaii, *C. proteus* was found on five of the six main Hawaiian Islands and at Midway Atoll; Lanai was the only island where it was not found. The barnacle was present at 47 of the 115 sites surveyed (Fig. 2.1, Appendix A). With some exceptions, *C. proteus* appears to be mainly restricted to harbors and sheltered anchorages on most of the Hawaiian Islands. On Oahu, where it has its greatest distribution, it is found in a range of habitat types, including the open coast along the south and west shores (Fig. 2.1). It is particularly abundant in Kaneohe Bay, which is well protected by a fringing reef and receives a high volume of boat traffic.

Habitat use was, in general, similar between sites in the native range and Hawaii (Table 2.3). *Chthamalus proteus* is most abundant in the calm waters of bays and harbors. However, large, fecund individuals were found in semi-protected sites, sometimes in high densities. The barnacle was rarer in truly open-coast settings: we did not find it at any such sites investigated in Curaçao and at only two such sites in Panama. It was present at six high-energy sites on Oahu (site numbers 19, 22, 29, 50, 54, 58), although in such locations it is typically found in low abundance or in protected microhabitats. On Oahu, the one exception to this general pattern is along wave-beaten shores at the Kaneohe Bay

Marine Corps Base (site 50). There it is found in relatively high abundance co-occurring with the native barnacle *Nesochthamalus intertextus* above rocks covered with encrusting coralline algae, the limpets *Cellana spp.* and the helmet urchin, *Colobocentrotus atratus*, a typical high-energy intertidal assemblage. All of these individuals of *C. proteus* were quite small (mean ~4 mm rostrocarinal length), and it remains to be seen whether this is a viable population.

Chthamalus proteus appears to be a substratum generalist; we found it on rocks, metal and cement structures, plastic, mangroves, oysters, whelks, limpets and other barnacles both in Hawaii and in its native range. *Chthamalus proteus* is strictly an intertidal organism: it was never found in the shallow subtidal zone. The upper limits of its vertical distribution varied between sites, generally reflecting the difference in tidal excursion at each location, *i.e.*, higher in Hawaii than in either Caribbean location and higher in wave splashed vs. calm areas. Brazil was an exception to this. At a number of sites there, *C. proteus* was found below *C. bisinuatus* (see below); and at one site at a river mouth, *C. proteus* was restricted to the mid- to low-intertidal range, probably due to the presence of a fairly continuous freshwater lens bathing the high intertidal. Although we did not determine its exact salinity tolerance, the barnacle is conspicuously absent from areas that have continuous freshwater input, both in its native range and in Hawaii. *Chthamalus proteus* appears to tolerate a fairly wide range of water temperatures: extreme highs of 38 C° recorded in shallow waters of the Galeta reef flat of Panama (Cubit 1990) and lows of 16 C° during some upwelling months in southeastern Brazil (Neto 2003). It is also apparently able to survive in both clear and turbid waters and is highly tolerant of disturbed environments, growing well in polluted harbors and lagoons. Numerous

individuals were surviving on an oiled seawall at Galeta, and several individuals were found settled on beach tar covering intertidal rocks in Curaçao.

In Hawaii and at a number of Caribbean locations where *C. proteus* was particularly abundant, it was the only sessile organism in the high intertidal. At eight of 12 sites where *C. proteus* was found at >40 percent cover, no other barnacles were present, and at two sites another species of *Chthamalus* was present. We observed individuals of *C. proteus* crowding each other to the point of hummock formation only once, in a small patch at one location (site 44, Lilipuna Pier). *Chthamalus angustitergum*, a Caribbean native common on exposed coasts, co-occurs with *C. proteus* in more protected environments in the native range. These two barnacles were seen overgrowing each other in Curaçao and Panama. In Brazil, *C. bisinuatus* occurs in the upper strata of the intertidal zone from exposed to protected shores with *C. proteus* below and a wide zone of overlap between the two. *Chthamalus proteus* was frequently overgrown or squeezed into distorted shapes when found with larger barnacles like *Nesochthamalus intertextus* and *Balanus* spp. In Hawaii, individuals of *C. proteus* lower in the intertidal were frequently overgrown by oysters, and in Curaçao the barnacle was, at three locations, found buried but alive under layers of algae, hydroids, sponges and tunicates.

Predatory snails, including *Morula* spp., were found at a number of sites where *C. proteus* was present in Hawaii and Panama and at one site in Curaçao where *C. proteus* was absent, but *C. angustitergum* was present. In Brazil, the whelk *Stramonita haemastoma* is commonly found in the low intertidal zone on exposed shores, and was observed preying on *C. proteus*. Crabs, which might prey on barnacles, were found at nearly every site. Large grazers such as chitons and limpets which might inadvertently

ingest or “bulldoze” young barnacles off the substrata were found at a number of sites in the Caribbean. In Curaçao, these were nearly always present where the barnacle was absent, but in Panama, they co-occurred with the barnacle, although generally lower in the intertidal zone. Hawaii has few chitons and its patellid limpets are generally restricted to high-energy coasts, where *C. proteus* is not usually found, although a small pulmonate limpet does co-occur with *C. proteus*.

Table 2.3. Habitat use and population measures of selected sites in Hawaii, Caribbean and Brazil.

Location	<i>C. proteus</i> habitat comparisons				<i>C. proteus</i> population measures			Mean # eggs, individuals with eggs	Other barnacle species present
	Substrate	Wave exposure	Water clarity	Tidal amplitude	Vertical distribution	Cover	Mean r/c length(mm) ± SD		
Ma'ili Point, Oahu, Hawaii	BR/B	S-P to E	C	1 m	60 cm	<1%	N/A	N/A	<i>Ni</i> 17% cover
Kaneohe Bay, Oahu, Hawaii	PVC	P	T	1 m	N/A	45%	7.8 ± 2.17	544	none
Kaneohe Bay, Oahu, Hawaii	CPP	P	T	1 m	1 m	38-85 %	4.4 ± 1.2	N/A	<i>Br, Be, Ba, C</i> sp.
Kaneohe Bay, Oahu, Hawaii	BR/B	E	C	1 m	1 m	<10%	~4	N/A	<i>Ni</i>
Kualoa, Oahu, Hawaii	CSW	S-P	C	1 m	60 cm	38%	5 ± 1.4	319 ± 282	<i>Ni</i> 4% cover
Diamond Head, Oahu	LB	S-P	C	1 m	~30 cm	0.04%	N/A	0	<i>Ni</i> 5% cover
Waikiki, Oahu, Hawaii	CSW	S-P	C	1 m	1 m	2%	5.75 ±	350	<i>Ni</i> 39%, few <i>Eh</i>
Galeta Marine Lab, Colon, Panama	OCS	S-P	C	59 cm	88 cm	32%	4.9 ± .99	209 ± 117	None
Galeta Marine Lab, Colon, Panama	<i>Rm</i>	P	C	59 cm	~30 cm	N/A	6.6 ± 1.33	600 ± 200	unid <i>B</i>
Galeta Marine Lab, Colon, Panama	CSW	P	C	59 cm	20 cm	58%	5 ± .92	N/A	None
Portobelo Bay, Colon, Panama	SR	P	T	59 cm	N/A	>75%	4.7 ± 1.10	227 ± 30	none
B'tn Portobelo and Galeta (beach)	BR/B	S-P	C	59 cm	N/A	50- 75%	~6	N/A	none
B'tn Portobelo and Galeta (coast)	CSW, VR	S-P to E	C	59 cm	~70 cm	>75%	~6	N/A	none
B'tn Portobelo and Galeta (wall)	R/P, OCS, W	E	T	59 cm	N/A	N/A	N/A	N/A	none
Spaanse Water , Curacao	<i>Rm</i>	S-P	C	30 cm	30 cm	HDP	8 ± 1.44	507 ± 457	<i>Ca</i>
Spaanse Water , Curacao	BH, R/P, OCS, W	P	T	30 cm	30 cm	HDP	N/A	N/A	<i>Ca</i>
Spaanse Water , Curacao	VR	S-P	C	30 cm	30 cm	S	N/A	N/A	<i>B</i> spp., <i>Ca</i>
St. Jorisbaai, Curacao	VR	P	C	30 cm	30 cm	HDP	4.9 ± .72	108 ± 40	none

Table 2.3. (Continued) Habitat use and population measures of selected sites in Hawaii, Caribbean and Brazil.

Location	<i>C. proteus</i> habitat comparisons				<i>C. proteus</i> population measures				
	Substrate	Wave exposure	Water clarity	Tidal amplitude	Vertical distribution	Cover	Mean r/c length(mm) ± SD	mean # eggs, individuals with eggs	Other barnacle species present
mouth of Piscadero Bay, Curacao	BH, OCS, CR, MS	P	T	30 cm	30 cm	S	N/A	N/A	<i>Ba</i>
Barbara Beach, Curacao	VR, OCS, MS	S-P	C	30 cm	30 cm	S	N/A	N/A	none
Willemstad, Curacao	CSW	P	T	30 cm	30 cm	HDP	N/A	N/A	<i>Ba</i>
Spaanse Water, Curacao	<i>Rm</i> , <i>A</i> sp., OCS, MS, VR, BH	P	T	30 cm	30 cm	HDP	N/A	N/A	<i>Ca</i>
Camboinhas, Niteroi, RJ, Brazil	GR, O, B	P	T to C	1.3 m	20 cm	10-25%	4.6 mm ±0.8	422 ±186	<i>Cb, Ba, Ts</i>
multiple dates						10-25%	5.3mm ± 1.1	417 ±142	<i>Cb, Ba, Ts</i>
						10-25%	6.3 mm ±1.6	815 ±426	<i>Cb, Ba, Ts</i>
Caravelas, BA, Brazil	<i>Rm</i> , OCS, O	P	T	2.5 m	80 cm	>75%	6.3mm ±1.6	N/A	<i>Er</i>
Ubatuba, SP, Brazil	GR,	P	C	1.2 m	20 cm	10-25%	4mm ±0.5	245 ±56	<i>Cb, Ts</i>

Table 2.3 (Continued)

Notes: **Substrate:** *Avicennia* sp., *A* sp; boat hulls, **BH**; barnacles, **B**; basalt rocks and benches, **BR/B**; cement pier pilings, **CPP**; cement seawall **CSW**; other cement structures **CS**; coral rocks, **CR**; granite rock, **GR**; limestone benches, **LB**; metal structures, **MS**; oysters, **O**; PVC pipe, **PVC**; Rhizophora mangle, **Rm**; rubber or plastic maritime objects, **R/P**; sedimentary rocks, **SR**; various rock types, **VR**; wood structures, **W**; **Wave exposure:** exposed, **E**; semi-protected, **S-P**, protected, **P**; **Water clarity:** clear **C**, turbid, **T**; **Cover:** highly dense patches, **HDP**, scattered individuals, **S**; **Other barnacle species present:** *Balanus* spp., **B**; *B. amphitrite*, **Ba**; *B. eburneus*, **Be**; *B. reticulatus*, **Br**; *Chelonibia* spp. **C** sp.; *Chthamalus angustitergum*, **Ca**; *Chthamalus bisinuatus*, **Cb**; *Euraphia hemblei*, **Eh**; *Euraphai rhizophorae*, **Er**; *Nesochthamalus intertextus*, **Ni**; *Tetraclita stalactifera*, **Ts**.

Reproduction, body size and spatial variation. Data from single-date surveys of reproduction throughout all sites plotted along with the long-term Hawaii data showed a high degree of variability among sites within a given month (Fig. 2.3). The percentage of reproductive individuals across all sites was within the range seen in Hawaii with the exception of three survey points in Brazil which were well above all others.

Mean shell length was not appreciably different among the three regions (Fig. 2.4). However, an ANCOVA examining fecundity with shell length as a covariate showed that fecundity per body size does vary with region (Fig. 2.5). Significant differences ($F = 89.23$, $P < 0.0000005$) were found among Hawaiian, Caribbean and Brazilian barnacles. Tukey's multiple comparisons revealed that Hawaiian and Caribbean barnacles were similarly fecund relative to shell size, but that Brazilian representatives produced greater numbers of propagules per shell size (Brazil vs. Hawaii and Brazil vs. Caribbean, $P < 0.005$). Subsequent to these findings, average egg-length was compared between 30 individuals each from Camboinhas, Brazil and Pearl Harbor, Hawaii. Eggs in Hawaiian individuals averaged 166 μm (SD 11.4) in length whereas in Brazilian samples they averaged 183 μm (SD 17.9). Using log-transformed variates, this difference proved highly significant in a single-factor ANOVA ($F = 18.644$, $P < 0.00005$).

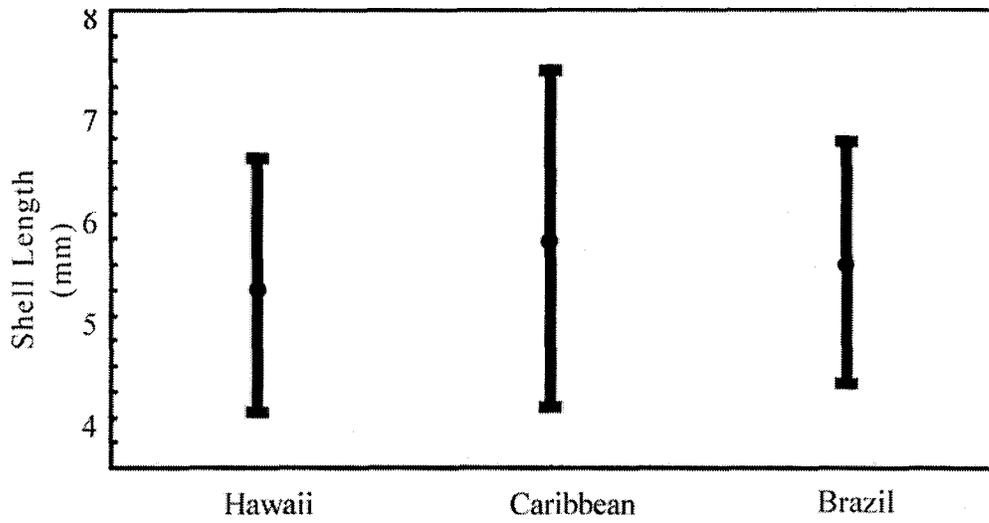


Figure 2.4. Mean rostrocarinal length of barnacles sampled in Hawaii (N = 1896), the Caribbean (N = 291) and Brazil (N = 129).

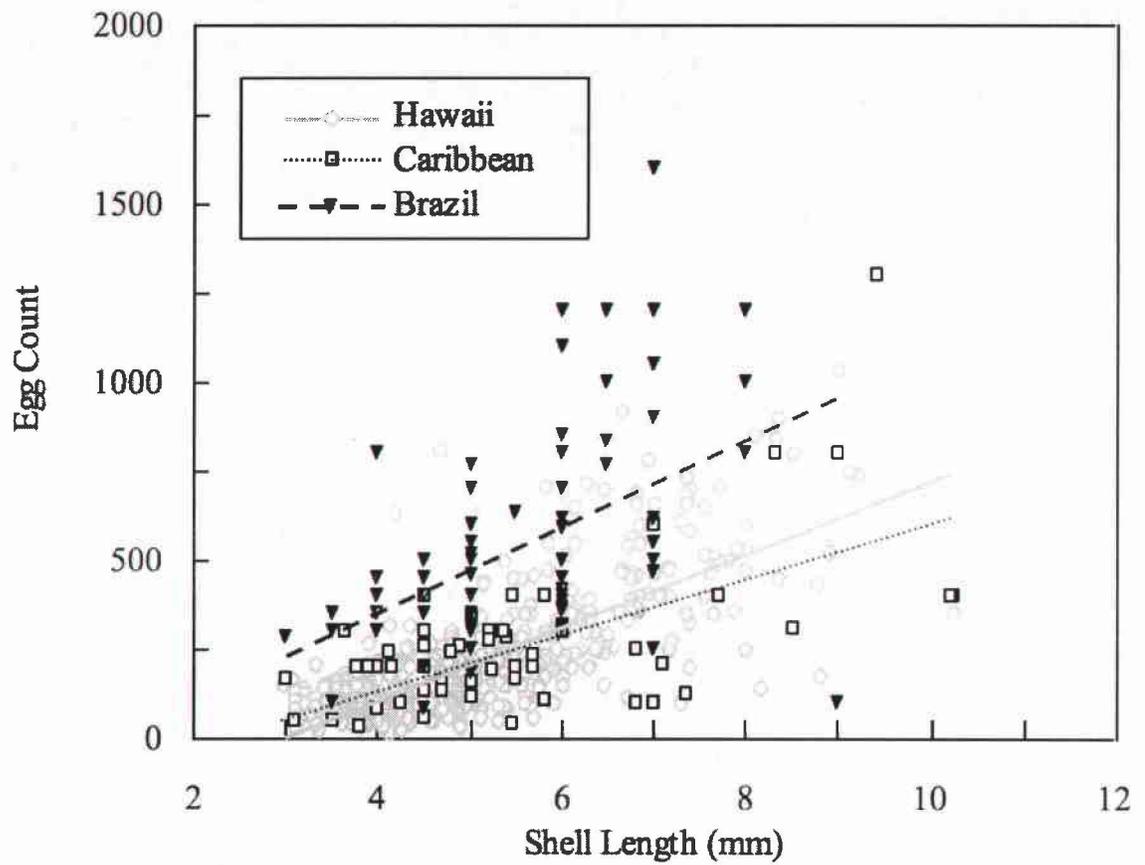


Figure 2.5. Mean number of eggs/individual with eggs for barnacles samples in Hawaii, the Caribbean and Brazil.

Population density. No individuals of *C. proteus* were found at Maili Point using the percent cover method, although the barnacle is present there in low numbers. At other Oahu sites we surveyed, cover by the invader ranged from 0.04 percent to >75 percent (Table 2.3). In Panama, cover ranged from 32 to >75 percent. In Brazil most sites had 10-25 percent cover, with one at 50-75 percent. In Curaçao, *C. proteus* was typically patchy, but there were dense clusters, with cover within a patch in the 50-75 percent range.

Discussion

Status of invasion

Chthamalus proteus is thriving in the Hawaiian Islands. Over the course of this study period new populations have appeared at some of the sites to which we have returned (e.g., Sandy Beach, Maili Point) and the barnacle is increasing in cover at others (e.g., Waikiki). We have found this barnacle over a greater geographic range in Hawaii than had previously been reported. Whether this represents an expansion of range for the barnacle since the findings of Southward et al. (1998) cannot be determined, as they did not survey Molokai and Hawaii Island. *Chthamalus proteus* may also have disappeared at one locality. Southward et al. (1998) reported finding it at Maalaea Harbor, Maui (site 89), but we did not. However, we did find it in Kahului Harbor, Maui, where it had not been reported in 1998. The wider distribution on Oahu compared to its general restriction to harbors on the other islands suggests that *C. proteus* arrived first in Oahu and was subsequently exported, most likely via boat-hull fouling. It is not clear what factors drive

the general pattern of higher cover in harbors and protected waterways: greater opportunity to arrive in these locations via boat traffic, larvae being retained in these areas and recruiting back to parent populations in high numbers, or some physical factor or combination of factors that leads to greater recruitment and/or survival. But the fact that populations are thriving in semi-protected locations and in some high-energy locations suggests that open coast intertidal communities are not immune to this invasion.

Chthamalus proteus has many of the “weedy” life history characteristics that make for a good invader: rapid growth following settlement, early onset of reproduction, year round production of propagules, quick larval development time, and the ability to spread via human mediated pathways. Generation time is also relatively short: we have observed one barnacle, 6 weeks post-settlement, with eggs, and many barnacles with eggs within two months. In addition, *C. proteus* appears to be quite tolerant of at least short periods of lowered salinity, a range of water quality, temperature, and wave exposure, and it will settle on many types of substrata.

Comparison between the Caribbean, Brazil and Hawaii

As far as we were able to determine, little has changed in the life history of *C. proteus* between the sites investigated in the Caribbean, Brazil and Hawaii. Body size, fecundity and percent cover, while varying between sites and dates, all fall within the same general range for both regions, although the Brazilian barnacles appear to be more fecund in terms of the number of individuals with propagules, the number of propagules per individual, and egg size. Habitat use is strikingly similar: protected to semi-protected sites appear to be favored, but some populations are found in open coast settings,

suggesting that wider distribution is ultimately possible in Hawaii. Substrata include manmade materials, natural rocks, and other organisms. Although it appears to be a substrate generalist, at all locations *C. proteus* reaches highest densities on artificial substrata. Such substrata are typically correlated with low- to moderate-energy sites, so the effects of substratum cannot be separated confidently from the effects of wave energy. On the other hand, it was conspicuously absent on old coral or limestone rock. Southward and Newman (1977) commented on the general unsuitability of coral rock for attachment by barnacles with membranous bases, hypothesizing that the porosity of this rock type leads to increased desiccation.

The upper vertical range is generally related to tidal incursion and wave splash. Periodic lowered salinity is tolerated, but the barnacle is missing from areas with constant freshwater input; this has been previously noted (Southward 1975, Dando and Southward 1980).

Without experimental work, it is not possible to confidently describe the fundamental (versus realized) ecological niche of *C. proteus*, but some observations about the barnacle are suggestive: it attains highest densities in a number of sites where it is the only sessile organism in the high intertidal zone. There were no clear “winners” in the Caribbean where *C. proteus* co-occurred with *C. angustitergum*, as it was both overgrowing and being overgrown by its congener. However, *C. proteus* may be displaced from the highest intertidal zone by *C. bisinuatis* in Brazil. Larger barnacles such as *Nesochthamalus intertextus* and *Balanus* spp. appear to be able to overgrow *C. proteus*.

In Hawaii, populations lower in the intertidal were frequently overgrown by oysters, and in Curaçao, where tidal range is very small, the barnacle was, at three locations,

found buried but alive under layers of algae, hydroids, sponges and tunicates. All of these observations suggest that *C. proteus* is not generally a good interference competitor for settlement space, but that it likely survives by being able to live in locations where few other organisms can (like the very high intertidal or turbid waters) and by being the first to arrive on new substrate. It may also be able to withstand periods of overgrowth by other organisms. Overall, it appears that there are fewer potential competitors for space in Panama or Hawaii than in Curaçao or Brazil.

There is some suggestion, at least at the Waikiki study site, of size-dependent mortality, which may result from predation by a common native whelk, *Morula granulata*. The whelk is a generalist, readily consuming *C. proteus*, the native barnacle *N. intertextus* (Fread, unpublished data), and a wide variety of molluscs (Kay 1979). Whelks are present in the open coast intertidal sites we investigated, but were generally absent from the more typical fouling assemblages in harbors and embayments. Fish may also be predators on *C. proteus*, but their importance and differences in fish predation between the sites is unknown. As far we could determine from observations, there is no clear indication of predation as a major control of the barnacle either in its native range or in Hawaii, although its success in fouling assemblages might be attributed to lowered predation in these areas. The grazing of chitons and limpets might be a factor in determining the lower limits of *C. proteus* in open coast settings in its native range; this is not likely important in Hawaii due to the rarity of chitons and the general restriction of patellid limpets to high wave exposure sites.

There appears to be a positive correlation between the pulmonate limpet *Siphonaria normalis* and *C. proteus* at some locations in Hawaii, suggesting a facilitative role played

by the limpet, which keeps rock surfaces clear of encrusting and filamentous algae. However, *C. proteus* is found in locations where *S. normalis* is absent or rare, so it is clearly not dependent on the presence of the limpet. Such relationships might occur with other grazers, such as littorines and nerites, which are found in the Caribbean, Brazil and Hawaii, but these organisms are frequently missing from the fouling assemblages, suggesting that they are not necessary for settlement by *C. proteus*.

Predicting invasions

Chthamalus proteus so far has successfully invaded Hawaii apparently without a major change in its biology or its ecological niche. Thus, with information about the barnacle in its native range, predictions could have been made about the locations in Hawaii most vulnerable to invasion and perhaps the rate or pattern of spread around the islands. The mystery remains as to why *C. proteus* did not arrive earlier; many other Caribbean invaders have been in Hawaii for decades (Carlton and Eldredge in prep). Discussions with representatives from the shipping industry in Hawaii have not revealed any changes in either the frequency or nature of ship traffic between the Caribbean, Brazil and Hawaii that might have affected the timing of this invasion, although this is the most obvious conclusion. Another possible explanation is that *C. proteus* had been a relatively minor component of the fauna in natural settings, but as advantageous habitat in the form of artificial substrate and protected waterways has increased over time in the native range, populations there have built up to some threshold level that makes transport out of the native range more likely. With more individuals and thus more propagules in a given area, the likelihood should be greater that boat hulls would be fouled in sufficient number

to successfully start a new population elsewhere. Similarly, increasing amounts of favorable habitat in Hawaii might have increased settlement chances of colonizing larvae. It is always possible, of course, that *C. proteus* arrived earlier than 1973, but was in such low abundance that it went undetected.

At this point, the conditions under which this invader can successfully be transported long distance are not known. Because of the lack of data between 1973 and the present study, we only know that it took a maximum of 30 years for *C. proteus* to reach achieve its current range within the Hawaiian Islands. With these considerations in mind, we make the following predictions for the future of this invasion:

1. Spread around the Hawaiian Islands. At the moment, except for Oahu, *C. proteus* is primarily, but not exclusively, limited to harbors. Over time, we expect it to increase in density within harbor areas due to continued inoculations from vessel traffic and the relatively long water residence times in these areas that should retain larvae released by resident populations and individuals on boat hulls. From these initial points of establishment, we expect *C. proteus* to spread into adjacent protected and semi-protected waters. Currents in Hawaii are complicated and extremely varied (Firing 1996, Parnell 2000), so it is difficult to predict timelines, but we know that given its life history traits, *C. proteus* is capable of rapid spread.

Considering that *C. proteus* probably attained its present distribution around Oahu in 30 years or less, we predict the barnacle to become widely established in suitable habitats around the other main islands within 2 to 3 decades. Places less often reached by

currents, less visited by boat traffic, areas of high wave exposure, and brackish waterways are at lower risk of invasion by *C. proteus*.

2. *Spread to other Pacific islands.* Boat traffic from Hawaii, Guam and from locations in the Mariana Islands and French Polynesia where the barnacle is established is likely to bring *C. proteus* to additional islands in the Pacific. Vessels most likely to spread the invader are those that have been in residence in infested waters for some periods of time, as these are most likely to have collected high densities of adult barnacles. Given its relatively wide environmental tolerances, we have no reason to believe it would not be able to invade other islands, particularly those without high cover by other sessile intertidal species. In areas with higher numbers of predators, such as fish or crabs that might prey on barnacles, distribution may be restricted to the high intertidal. Because it does not appear to settle readily on old coral rock, distribution may also be limited by the availability of hard substrata on islands lacking other types of shoreline rocks. Thus, we predict that *C. proteus* will first appear on manmade materials in harbors and adjacent mangrove systems that do not receive continuous freshwater input.

3. *Spread to subtropical mainland U.S. and Mexico.* Individuals of *C. proteus* have been found on commercial vessels about to leave Hawaii for the U.S. mainland (S. Godwin, personal communication). Based on the latitudinal range displayed in the Atlantic, and its tolerance of waters at least as cold as 16 C°, we see no reason why this barnacle could not invade areas from approximately San Diego south. Cooler waters may lead to less rapid reproduction and thus slower spread, and high biodiversity in a given intertidal zone

might lead to less rapid colonization of open coast areas. But if *C. proteus* is able to build up populations in harbors, larvae should be available to opportunistically invade whenever open space is available, just as they do in Hawaii. As *Chthamalus* species are frequently hard to distinguish in the field, it is entirely possible that *C. proteus* would go undetected for a period of time on the mainland West Coast, and perhaps is there now. Rate of spread to the mainland is dependent on the amount of ship traffic with barnacle-fouled hulls, their residence time in port, and the perhaps reduced survival of *C. proteus* in cooler waters.

Patterns of change in invading species

Differences between native and invading populations can arise in a number of ways. Changes may occur independently of genetic differences between native and invading populations. These might include ecological shifts that are the differences between potential and realized niches such as the consumption of a broader range of prey species or wider range of habitat. Indeed, one might argue that nearly any invader that undergoes a population boom is able to do so because of release from predators, parasites or competitors that keep its population in check in its native range. Other types of changes may result from genetic differences between populations of a species in its native and introduced ranges due to founder effects, mutations, or differences in selection pressures between regions. For example, populations of Argentine ants invading the United States originated from so few individuals that they are essentially one large colony and do not display intraspecific aggression, as they do in their native area (Suarez et al. 1999). This

change in behavior within the invading populations is thought to be one of the keys to their rapid spread. Additionally, major changes in an invading population may result from hybridization with other species. *Spartina townsendii* and *S. angelica*, cordgrasses that have invaded and dramatically changed estuaries on the West Coast of the United States, are among the better-known examples of this type of change. They are hybrids that resulted from a cross between an invader and a native species in Britain (Raybould et al. 1991) and inhabit a wider range of habitats than do their progenitors. As a broad generalization for invading animals, we should expect changes due to ecological release to be rapid and genetic changes to occur some generations later, assuming genetic isolation between the original population and the invading population and/or strong selection pressure. Where closely related species co-occur with an invader, hybridization also might occur rapidly. An exception to this general chronology will occur in cases where founding populations are small.

That *Chthamalus proteus* appears to have undergone little change between its native and invaded range doesn't preclude the possibility that it might do so, given enough time. A recent genetic study characterized significant population structure for *C. proteus* in its native range and found that representatives of each genetic stock identified occur in transplanted Hawaiian populations (Zardus and Hadfield, in press). Genetic divergence between some of the native stocks was very high suggesting very little migration occurs between them. This raises the possibility that in Hawaii, genetic types which otherwise would remain separated could combine and give rise to new ecological variants in a short period of time.

Little is known about the frequency with which marine invertebrate animals change in their biology or ecological interactions between their native range and places where they have been introduced. This is true in part because most marine invertebrate species have been little studied even in their native range. Exceptions to this have tended to be species with commercial value and a handful of others that have drawn attention by being particularly abundant or otherwise conspicuous, or that make good study animals in laboratories.

In the case studies we were able to find, a number of marine invertebrate species have undergone some type of shift – ecological and/or genetic – that resulted in differences in habitat use, body size, life history and/or ecological interactions. These changes occurred to such a degree that their spread and impact in the places to which they were introduced could not have been predicted based on knowledge of the organism in its native range. Twelve of 19 marine invertebrates investigated by Grosholz and Ruiz (2003) were larger in their new vs. native range; the remaining seven did not undergo size change. Dramatically fewer parasites were found in invading populations of 26 terrestrial and marine animal species when compared to populations in their native ranges (Torchin et al. 2003). Other examples of changes in invaders include: the marine mussel *Mytilus galloprovincialis*, native to the tideless, low-energy Mediterranean, now flourishing in the high-energy rocky intertidal in South Africa (Griffiths et al. 1992); the European green crab, *Carcinus maenas*, growing to significantly larger mean size and not using the full range of habitat types on the West Coast of the United States compared to its native Europe and invading populations elsewhere (Grosholz and Ruiz 1996); the sea anemone *Diadumene lineata* reproducing apparently only asexually in the number of places it has

invaded outside of its native Japan, where it propagates primarily via sexual reproduction (Fukui 1995).

Other species have not significantly changed, at least in the traits that were investigated, and the ecological and biological course of these invasions could have been predicted. Examples include: the Japanese shore crab *Hemigrapsus sanguineus*, which did not change in its body size, habitat usage, range of prey types, or degree of diet overlap (and thus potential competition) with other crab species in its invasion of the East Coast of the United States (Lohrer et al. 2000); and the bivalve *Musculista senhousia*, which is eaten by a wide range of predators including crustaceans and birds in its native Japan and in Southern California, to such a degree that these predators apparently control its populations in both locations (Crooks 1999).

More case studies of invasive species are needed before we can hope for any general patterns to emerge, but multi-continent studies are expensive and logistically difficult. We stress that the globalization of the world economy — leading to increasingly open and rapid exchanges of goods and services between biogeographic regions — increases the need for collaborative studies between scientists and managers in different parts of the world.

Appendix A. Localities and habitat data for sites surveyed among the Hawaiian Islands for the presence of the alien barnacle

***Chthamalus proteus*.**

Island	Site No.	Place Name (area searched)	<i>C. proteus</i> present	Habitat Characteristics			
				Wave Exposure	Substratum	Water Clarity	Boat Traffic
				L = low	C = concrete	C = clear	C = commercial
				M = medium	R = rock	T = turbid	M = military
				H = high	R/F = recr./fishing		
				S = scientific			
Midway	1	Midway Lagoon (wharf)	X	L	C	C	M, S
Kauai	2	Nawiliwili Bay – Niumalu Harbor (breakwater)	X	L	R, C	T	C, R/F
Kauai	3	Kukuiula Bay (wharf)		M	R, C	T	R/F
Kauai	4	Hanapepe Bay - Port Allen (breakwater)	X	L	R, C	T	C, R/F
Kauai	5	Waimea Bay (pier)		M	C	T	R/F
Kauai	6	Kikiaola Boat Harbor (shore & boat ramp)		M	C	T	R/F
Kauai	7	Kee Beach (shoreline)		H	R	C	R/F
Kauai	8	Hanalei Bay (pier)		M	C	C	R/F
Kauai	9	Kalihiwai Bay (shoreline)		H	R	C	R/F
Kauai	10	Anahola Bay - Anahola Beach County Park (shoreline)		M	R	C	R/F
Kauai	11	Wailua Bay - Lydgate State Park (breakwater)		M	R	C	R/F
Oahu	12	Honolulu Harbor - Sand Island (harbor-side seawall)	X	L	R	C	C, R/F
Oahu	13	Sand Island State Park (ocean-side seawall)		M	R	C	R/F
Oahu	14	Keehi Lagoon - Ke'ehi Marina (shore & seawall)	X	L	R, C	T	R/F
Oahu	15	Keehi Lagoon - Lagoon Drive (shore & seawall)	X	L	R, C	T	R/F
Oahu	16	Pearl Harbor - Rainbow Bay Marina (dock & shore)	X	L	R, C	T	M
Oahu	17	Pearl Harbor - Ford Island (wharf)	X	L	C	C	M
Oahu	18	Ewa Beach (shoreline)		M	R	C	R/F
Oahu	19	Kolaeloia - Barbers Point Beach County Park (shoreline)	X	M	R	C	R/F
Oahu	20	Kolaeloia "Barbers Point" Harbor (shore & seawall)	X	L	R, C	C	C, R/F

Appendix A. (Continued) Localities and habitat data for sites surveyed among the Hawaiian Islands for the presence of the alien barnacle *Chthamalus proteus*.

Oahu	21	Nanakuli Beach County Park (shoreline)		M	R	C	R/F
Oahu	22	Maili Point (shoreline)	X	H	R	C	R/F
Oahu	23	Waianae Boat Harbor (dock & seawall)		M	R, C	C	R/F
Oahu	24	Kaena Point site 1 (shoreline)		H	R	C	R/F
Oahu	25	Kaena Point site 2 (shoreline)		H	R	C	R/F
Oahu	26	Kaena Point site 3 (shoreline)		H	R	C	R/F
Oahu	27	Pali Alei gate (shoreline)		H	R	C	R/F
Oahu	28	Waialua Bay – Mokule'ia (shoreline)		M	R	C	R/F
Oahu	29	Waialua Bay - Hale'iwa Harbor (breakwater)		M	R, C	C	R/F
Oahu	30	Pupukea Beach County Park (shoreline)		H	R	C	R/F
Oahu	31	Sunset Beach County Park (shoreline)		H	C	C	R/F
Oahu	32	Kahuku Point (shoreline)		H	R	C	R/F
Oahu	33	Kahuku (shoreline)		H	R	C	R/F
Oahu	34	Laie Bay - Moku Auia "Goat Island" (shoreline)		M	R	C	R/F
Oahu	35	Laie Point County Park (shoreline)		M	R	C	R/F
Oahu	36	Kahana Bay (shore & boat ramp)	X	M	R, C	T	R/F
Oahu	37	Kauhiimakaokalani "Crouching Lion" (shoreline)	X	M	R	C	R/F
Oahu	38	Kaaawa Beach County Park (shore & seawall)	X	M	R	C	R/F
Oahu	39	Kualoa County Regional Park site 1 (shore & seawall)	X	L	R, C	C	R/F
Oahu	40	Mokolii Island "Chinaman's Hat" (shoreline)		M	R	C	R/F
Oahu	41	Kualoa County Regional Park site 2 (shore & seawall)	X	L	R, C	C	R/F
Oahu	41	Kualoa County Regional Park site 2 (shore & seawall)	X	L	R, C	C	R/F
Oahu	42	Kaneohe Bay - Heeia Kea Pier (shore & seawall)	X	L	R, C	T	R/F
Oahu	43	Kaneohe Bay - Heeia Kea fishpond (shoreline)	X	L	R	T	R/F
Oahu	44	Kaneohe Bay - Pohakea Point, Lilipuna Pier (shore & pier)	X	L	R, C	C	R/F
Oahu	45	Kaneohe Bay - Moku o Loe "Coconut Island" (shore & pier)	X	L	R, C	C	R/F, S
Oahu	46	Kaneohe Bay - Kaneohe Beach County Park (shoreline)	X	L	R	T	R/F
Oahu	47	Kaneohe Bay - Waikalua Loke Fishpond vicinity (shoreline)	X	L	R	T	R/F

Appendix A. (Continued) Localities and habitat data for sites surveyed among the Hawaiian Islands for the presence of the alien barnacle *Chthamalus proteus*.

Oahu	48	Kaneohe Bay - Kaneohe Yacht Club (shore & dock)	X	L	R, C	C	R/F
Oahu	49	Kaneohe Bay - Marine Corps Base gate (shoreline)	X	L	R	T	M
Oahu	50	Mokapu Peninsula – Kuaa "Pyramid" Rock (shoreline)	X	H	R	C	R/F
Oahu	51	Lanikai – Moku Lua 1 (shoreline)		M	R	C	R/F
Oahu	52	Lanikai - Moku Lua 2 (shoreline)		M	R	C	R/F
Oahu	53	Kaohikaipu Island (shoreline)		H	R	C	R/F
Oahu	54	Sandy Beach County Park (shoreline)	X	H	R	C	R/F
Oahu	55	Hanauma Bay (shoreline)		L	R	C	none
Oahu	56	Hawaii Kai - Kuliouou (shore & seawall)	X	L	R, C	T	R/F
Oahu	57	Waialae Beach County Park (seawall)	X	L	C	T	R/F
Oahu	58	Diamond Head Beach County Park (shoreline)	X	M	R	C	R/F
Oahu	59	Sans Souçi State Recreation Area (shore & seawall)	X	M	R, C	C	none
Oahu	60	Waikiki - Natatorium (seawall)		M	C	C	
Oahu	61	Waikiki - Queens Surf Beach (seawall)	X	M	R, C	C	none
Oahu	62	Waikiki – Kuhio Beach County Park (seawall)	X	M	C	C	R/F
Oahu	63	Waikiki – Fort DeRussy Beach (seawall)	X	M	R,C	T	
Oahu	64	Ala Wai Harbor (seawall)	X	L	C	C	R/F
Oahu	65	Ala Moana County Regional Park (shore & seawall)	X	L	R, C	T	R/F
Molokai	66	Kaunakakai Harbor (pier & seawall)	X	L	C	T	C, R/F
Molokai	67	Hale o Lono Harbor (shore & pier)		L	C	C	R/F
Molokai	68	Kapukahehu Beach (shoreline)		M	R	C	R/F
Molokai	69	Papohaku Beach County Park (shoreline)		M	R	C	R/F
Molokai	70	Moomomi Bay (shoreline)		H	R	C	R/F
Molokai	71	Kalaupapa (shore & pier)		M	C	C	C, R/F
Molokai	72	Hoolehua Point (shoreline)		H	R	C	R/F
Molokai	73	Kalawao (shoreline)		M	R	C	R/F
Molokai	74	Halawa Bay (shore & breakwater)		M	R	C	R/F
Molokai	75	Kanaha Point (shoreline)		M	R	C	R/F
Molokai	76	Honouli Wai Bay (shoreline)	X	M	R	C	R/F

Appendix A. (Continued) Localities and habitat data for sites surveyed among the Hawaiian Islands for the presence of the alien barnacle *Chthamalus proteus*.

Molokai	77	Pukoo (shoreline)	X	M	R	C	R/F
Molokai	78	Kamalo Harbor (shore & seawall)	X	M	R	T	R/F
Molokai	79	Kanoa Fishpond (seawall)	X	L	R	T	R/F
Lanai	80	Kaumalapau Harbor (shore & wharf)		M	C	C	C, R/F
Lanai	81	Keanapapa Point (shoreline)		H	R	C	R/F
Lanai	82	Lae Hi "White Rock Point" (shoreline)		M	R	C	R/F
Lanai	83	Waiopae Fishpond vicinity (shoreline)		L	R	T	R/F
Lanai	84	Naha Fishpond vicinity (shoreline)		L	R	T	R/F
Lanai	85	Manele Bay (seawall)		M	R, C	T	R/F
Maui	86	Kahului Harbor (seawall)	X	L	R	T	C, R/F
Maui	87	Keanae Point (shoreline)		H	R	C	R/F/
Maui	88	Hana Bay (shore & pier)		M	R, C	C	C, R/F
Maui	89	Kepio Point (shoreline)		H	R	C	R/F
Maui	90	La Perouse Bay (shoreline)		M	R	C	R/F
Maui	91	Kamaole Beach County Park (shore & boat ramp)		M	C	C	R/F
Maui	92	Maalaea Harbor (seawall)		L	C	T	R/F
Maui	93	Lahaina Harbor (seawall)		M	C	C	C, R/F
Maui	94	Mala Wharf (pier)		M	C	C	C, R/F
Maui	95	Kapalua Bay (shoreline)		M	R	C	R/F
Maui	96	Mokolea Point - Olivine Pools (shoreline)		H	R	C	R/F
Hawaii	97	Hilo Bay - Waiakea Peninsula (inside breakwater)	X	L	R, C	T	C, R/F

CHAPTER 3.

Battle of the barnacle *malahini*: shifts in dominance between three invading barnacle species, in Kaneohe Bay, Oahu, Hawaii

Introduction

In natural communities pairs of similar, co-existing species may have evolved in ways that reduce competition between them, such as niche partitioning. Sets of invasive species with similar resource requirements coming from different biogeographical provinces and thus free from the “ghost of competition past” (Connell 1980) would appear to offer a unique opportunity to directly observe competition (Simberloff 1981). Indeed, theory predicts that as more invaders become established in a given area, resistance to further invasion will develop via competitive interactions (*e.g.*, Elton 1958, Moulton and Pimm 1983, Robinson and Dickerson 1984, 1987, Case 1990, Drake 1990, Case 1991, Stachowicz et al. 1999). However, aside from research on weeds and agricultural crops, relatively few studies examining competition between invading species have been done.

A literature review of 7 journals between 1993 and 1997 found 254 papers dealing with some aspect of interactions between non-native species (Simberloff and Von Holle 1999). The vast majority of interactions (156) involved predation (including herbivory). Competitive interactions were relatively minor (10) and just as common as mutualisms (10) and commensalisms (12). It’s hard to know how to interpret the low frequency of studies reporting competitive interactions. Is it possible that invading species rarely have resource requirements similar enough to result in strong competitive interactions?

Perhaps the frequency of studies does not reflect the frequency with which competition occurs. For example, failed invasions, which might result from competitive interactions, are rarely studied.

General ecological theory predicts that species that are the most similar in terms of resource use are most likely to compete (Hutchinson 1959, MacArthur and Levins 1967, May 1973). Thus, competitive interactions might reasonably be expected to occur between sets of invasive species that have strongly overlapping resource requirements (e.g., Diamond and Case 1986). Competition should be most readily observable when both species are in relatively high abundance and resources are limiting.

Chthamalus proteus is the most recent barnacle invader in Hawaii's intertidal zone, having arrived sometime after 1973 (Southward et al. 1998). This native of the tropical and subtropical Atlantic co-occurs in the Hawaiian Islands with 3 other invasive barnacles: *Balanus amphitrite*, *B. reticulatus* and *B. eburneus*. Before the arrival of *C. proteus*, *B. amphitrite*, which has been on the island of Oahu since at least 1902 (Pilsbry 1906), was the most abundant invasive barnacle in intertidal locations around Oahu (Matsuda 1973). In 1973, *B. amphitrite* was found from the high to low intertidal on numerous hard structures in the southern portion of Kaneohe Bay on the island's windward side, forming nearly 100 percent cover in many locations, including the cement pier belonging to the Hawaii Institute of Marine Biology (Matsuda, personal communication). Only a few individuals of *B. reticulatus* were reported from the pier at that time. Today, *B. reticulatus* comprises about 45 percent cover between the 0 and 15 cm tide marks, while *C. proteus* makes up the remainder of the cover on the pilings up to the high tide mark, reaching nearly 100 percent cover in the high intertidal (personal

observation). Only a few individuals of *B. amphitrite* are found. *B. amphitrite* is also almost completely absent from other intertidal structures on Coconut Island (Moku O Loe) where Matsuda had found it in great abundance in the 1970s. *C. proteus* now covers these.

If resources are limited, competitive interactions might be occurring between these three barnacle species in Kaneohe Bay. While occasional specimens of *B. eburneus* can also be found on the pier, this barnacle appears to be mostly limited to protected, low-salinity habitats.

Space appears to be a major limiting factor for barnacles in other locations (Connell 1961a, b, Stanley and Newman 1980, Wethey 1983, 1984). Competition for space between barnacle species can occur after settlement through overgrowth, undercutting and crushing (Connell 1961b, Wethey 1983, 1984). In such interactions, larger, faster growing balanoid barnacles are likely to win over the typically smaller chthamaloid barnacles (Connell 1961b, Stanley and Newman 1980, Wethey 1984). Competition can also occur via pre-emption of space. Barnacles tend to settle near conspecifics (Barnett and Crisp 1979, Denley and Underwood 1979, Underwood and Denley 1984) but also tend not to settle in already crowded conditions (Crisp 1961, Meadows and Campbell 1972, Gaines and Roughgarden 1985, Chabot and Bourget 1988, Raimondi 1990, Minchinton and Scheibling 1993). Thus a barnacle species that arrives first and settles in abundance may have a competitive advantage over a second species that then encounters a crowded substrate and few conspecifics (Barnett and Crisp 1979). Patterns of distribution and abundance of barnacle species that display strong conspecific settlement behavior should be governed at least in part by priority effects (*sensu* Paine 1977), and

succession involving such barnacles might be expected to follow Connell and Slayter's (1977) inhibition model.

Other types of interactions might be occurring between *C. proteus* and other organisms in the intertidal. Direct and indirect effects, both positive and negative, of barnacles on other species have been reported, including mussels (Lively and Raimondi 1987), limpets (Wootton 1993), littorine snails (Kostylev et al. 1997) and algae (Farrell 1991, Hill and Hawkins 1991, Kim 1997). Few studies have examined whether such effects would change if the barnacle species under study were replaced by another barnacle (e.g., Farrell 1991). *C. proteus* is smaller than all of the other intertidal barnacles in Hawaii, and is unique in having a completely membranous (non-calcified) base. The tests of barnacles with calcified or partially calcified bases remain cemented to the substrate for a period of time after individuals die; empty tests of *C. proteus* rarely do so. If the identity of intertidal barnacles in Hawaii is changing, it seems possible that the numerous small organisms that live in and around live barnacles and dead barnacle tests might be affected as well as other intertidal organisms that might compete with, prey upon or be preyed on by barnacles.

The invasion of Oahu by *C. proteus* went completely unnoticed by marine scientists until 1995, at which point the barnacle had already become highly abundant (Southward et al. 1998). No surveys of intertidal barnacles were done in the years between Matsuda's 1973 survey and the present study. As a result, it is impossible to know how and when the shift in dominant barnacle species in Kaneohe Bay occurred.

To determine whether the decline of *B. amphitrite* was due to competition for space with *C. proteus*, I carried out a yearlong experiment in which all settlers of *C. proteus*

were continuously removed from a set of settlement plates. A balanoid barnacle did recruit in higher numbers to these plates relative to unmanipulated controls, reaching high cover, but it was *B. reticulatus*, not *B. amphitrite*. This result suggests that *B. reticulatus* would be abundant on the pier pilings if *C. proteus* were not present.

Study objectives

This study focuses on the interaction between *C. proteus* and *B. reticulatus* and attempts to explain how changes in dominant barnacle cover might have occurred in Kaneohe Bay. Additionally, I wanted to know what effects a shift in the identity of the dominant barnacle might have on other intertidal invertebrate organisms.

Specifically, I address the following questions:

1. Are the invertebrate organisms that live on barnacles and in dead barnacle tests affected by the identity of the dominant barnacle?
2. Could *C. proteus* have become the dominant barnacle if cover of *B. reticulatus* was high when *C. proteus* first invaded (or might some type of disturbance have been needed to facilitate this change)?
3. How does *C. proteus* outcompete the larger, faster-growing *B. reticulatus*?

I attempted to answer these questions by using the above-mentioned set of settlement plates. Following the initial competition experiment, in which settlers of *C. proteus* were removed from 12 of 24 plates for 1 year, I compared the communities of invertebrates on 8 of the plates (4 *C. proteus*-removal and 4 unmanipulated plates). A year-long invasion experiment, with no further manipulations on the remaining plates, was used to determine the ability of *C. proteus* to invade an established community dominated by *B. reticulatus*.

Observations of settlement and early juvenile survival of *B. reticulatus* over a 2-month period during this invasion experiment were used to determine the mechanism by which *C. proteus* excludes *B. reticulatus*.

Methods and Materials

Study species and site

Balanus reticulatus, a putative native of the Indo-Pacific now with a widespread distribution in warm seas, was first reported from Hawaii in 1929 (Carlton and Eldredge in prep). Taxonomic confusion with *B. amphitrite* makes unraveling its origins and chronology of spread difficult. A fouler of boat hulls and other maritime structures, its current distribution includes Japan to the Malay Archipelago; New Zealand; East Asia from the Yellow Sea to the Gulf of Thailand; Malaysia to southeast Africa; Mediterranean Sea; North Sea; West Africa; the southeastern United States through the Gulf of Mexico; and the West Indies (Henry and McLaughlin 1975, Foster and Willan 1979, Kerckhof and Cattrijsse 2001). By the early 1930s it was present on Oahu, at least in Pearl Harbor and Kaneohe Bay (Henry and McLaughlin 1975). In Hawaii, *B. reticulatus* is found in the low intertidal and shallow subtidal zones in fouling situations as well as on mangrove roots and in the rocky intertidal on wave-protected shores. A whitish barnacle with red or purple longitudinal stripes, it can reach 18 mm in length and 10 mm in height (Utinomi 1967). Most individuals of *B. reticulatus* in the intertidal zone in Hawaii are smaller, particularly in crowded conditions, reaching about 6 to 8 mm in length and 3 to 5 mm in height (personal observation).

The native range of *Chthamalus proteus* is from Southern Florida to Brazil (Pitomo, personal communication). The barnacle has been reported from scattered locations throughout the Gulf of Mexico and the Caribbean (Southward 1975, Dando and Southward 1980). The date of its arrival in Hawaii is unknown, but it was not found in a survey in the early 1970s (Matsuda 1973) and not reported until 1995 (Southward et al. 1998), although specimens collected in Pearl Harbor in 1993 were later identified as *C. proteus* (J. Brock, personal communication). *C. proteus* occurs throughout the intertidal zone and reaches greatest densities in harbors and bays, although populations can be found in many protected to semi-protected rocky intertidal areas. It has clearly overtaken *B. amphitrite* as the most widespread invasive barnacle on Oahu (personal observation). Mature individuals are typically 4 to 6 mm in length and 2 to 4 mm high on Oahu, although occasional specimens up to 15 mm in length are seen, and even more rarely some very tall cylindrical individuals can be found growing in highly crowded conditions in still waters (personal observation).

Settlement of *C. proteus* occurs throughout the year on Oahu with spring and fall peaks (Chapter 2). In Kaneohe Bay peaks in recruitment of *B. reticulatus* also occur in the spring and the fall, but recruitment is consistently lower than that of *C. proteus* (Chapter 4), and adults are rarely seen in densities as high as those attained by *C. proteus*.

Kaneohe Bay is the largest sheltered body of water in the Hawaiian Islands. A barrier reef protects the bay from waves. Average depth is 8 m, and circulation in the bay is slow, particularly in the southern portion, where waters may take up to 10 days to flush out (Smith et al. 1981). During storms, the bay is subjected to high freshwater input and siltation from a dozen small streams that empty into the bay (Banner 1974). Major kills of

marine organisms due to flooding occurred in 1965 and 1987. The study site is the cement pier surveyed by Matsuda in 1973, which is located on a shallow reef flat in the southern portion of the bay (Fig. 3.1).

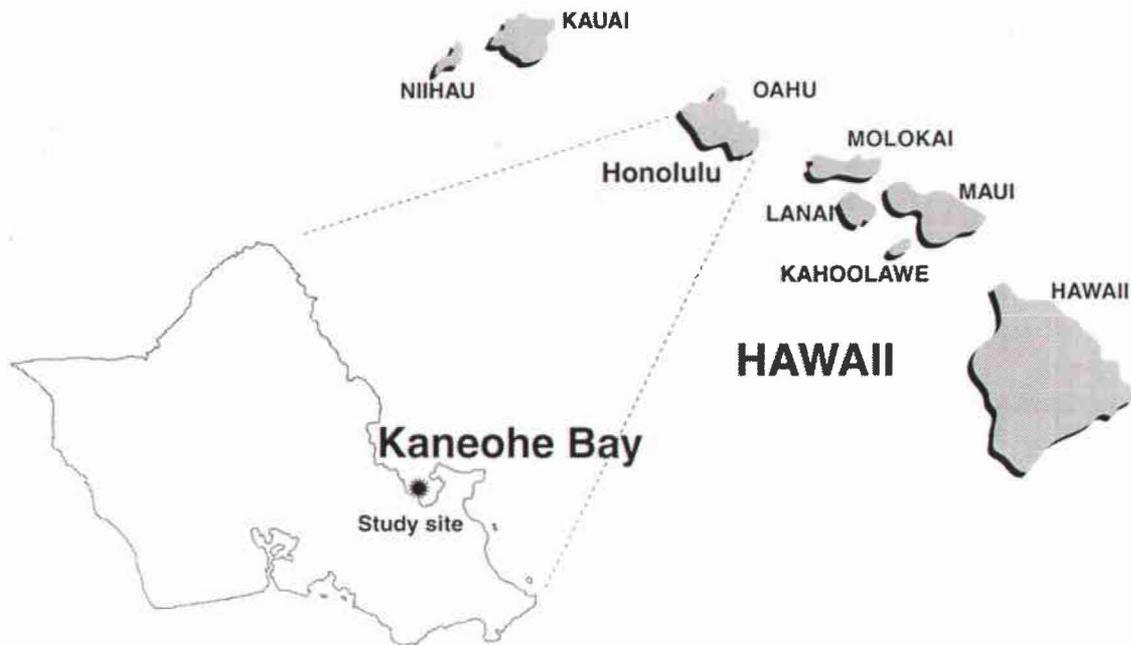


Figure 3.1. The main Hawaiian Islands, inset of Oahu, showing Kaneohe Bay and the location of the pier.

Initial competition experiment

To determine whether the present low cover of *B. amphitrite* is the result of competition for space with *C. proteus*, I attached 24 10 x 10 cm terra cotta settlement plates to the pilings of the Lilipuna Pier near the 0 tide mark. Four plates were placed on each of 6 pilings, 1 plate to each side. All plates were attached at the same tidal height. I had originally intended to examine interactions with a third invader, the Japanese oyster *Crassostrea gigas*, but no settlers of *C. gigas* were observed during the experiment, so for each piling 2 plates became *C. proteus*-removal treatments and 2 served as controls. These were randomly assigned to different sides of the pilings. Pilings were thus considered to be blocks in the experimental design.

Every 2 weeks for 1 year (July 2001-July 2002) during a spring low tide, I removed the plates from the pilings, placed them in plastic tubs and took them to the Hawaii Institute of Marine Biology. I lightly brushed each plate with a toothbrush and rinsed it with seawater to remove debris so that I would be able to identify the barnacle species. Barnacles were closed during the brushing, so this was unlikely to have hurt adults; examination of the plates before and after brushing confirmed that this did not remove new settlers. I examined each plate under a dissecting microscope, using 6X magnification. At this magnification, I was able to distinguish between barnacle species 1 mm in length. On the plates designated as removal treatments, I used a pin to remove settlers of *C. proteus* without harming other invertebrate settlers nearby. Unmanipulated plates were passed under the microscope to mimic any handling effects experienced by the barnacles on the removal plates. Plates were returned to the pilings within 2 hours.

Every 2 months, I photographed the plates in the laboratory, using a Nikonos V camera with a 35 mm lens and a 2:1 framer. I determined percent cover of all sessile organisms by placing an acetate sheet over each photograph, and recording what was underneath each of 45 points marked in a uniform grid pattern on the sheet. The percent cover data were plotted to visually examine the effects of cover of *C. proteus* on cover of other barnacle species. The data were then arcsine-square root transformed to meet the assumptions of normality and analyzed with ANOVA. Treatment (removal of *C. proteus* or unmanipulated) and time period were considered fixed effects; piling and plate (nested in the treatment by piling interaction) were considered random.

Community-effects study

In July 2002, one year after the initial experiment, I removed plates from 3 of the pier pilings. These twelve plates included one set of 4 that had fallen off of the pier before the last time period in the above experiment. This set of plates lost barnacle cover, so they were not used for further study. I placed each of the remaining 8 plates in a separate container of seawater and added MgCl crystals to relax the organisms on the plates overnight. The plates were then fixed in Formalin (35 percent buffered formaldehyde). After 1 week, I rinsed the plates in seawater and scraped all the organisms into jars of 70 percent ethanol. Animals were later sorted and identified. Species lists from the two types of plates (*Chthamalus*-dominated vs. *Balanus*-dominated) were compared after organisms that appeared only once were eliminated.

Invasion experiment

To determine whether *C. proteus* would be able to invade areas dominated by *B. reticulatus*, I left 12 of the plates (6 *C. proteus*-removal treatments and 6 unmanipulated) on 3 of the pier pilings for another year. During this time, none of the plates were manipulated, except for being removed and examined for the settlement-survival study (below) and lightly brushed and photographed 1 year later, in July 2003.

Percent cover was determined as above. Differences in cover of *B. reticulatus* between July 2002 and July 2003 and were first examined with a plot using the raw data. Data were then arcsine-square-root transformed to meet assumptions of normality. I used an ANOVA to determine whether there was a difference in cover of *B. reticulatus* on the former *C. proteus*-removal plates between the first and second years and whether the former *C. proteus*-removal plates were still higher in cover of *B. reticulatus* than the unmanipulated plates after a year.

Recruitment and survival of *Balanus reticulatus*

To determine whether lack of recruitment or lower survival post-settlement of *B. reticulatus* might be the cause of the dominance of space by *C. proteus*, I examined the 12 plates used in the invasion study (above) for 4 2-week periods from Nov. 11, 2002 to Jan. 7, 2003. An ANOVA indicated that there was no difference in empty space between the two treatments (former *C. proteus*-removal and unmanipulated plates) at the beginning of the study period. Every two weeks, I recorded new recruits of *B. reticulatus* (defined as animals between 1-2 mm in rostrocarinal length) on each plate. After the first time period, I also counted small barnacles in the size class 3-5 mm that were presumably

survivors of earlier surveys (these small barnacles could be distinguished from older barnacles also by color, as the older barnacles had a cover of encrusting microalgal growth). The number of barnacles in this category correlated well to the cumulative number of new recruits in the previous time periods. Total numbers of recruits and small size-class survivors over the observation period were calculated per plate. Survivorship rates per plate were calculated as the total number of survivors at the end of the entire period divided by the cumulative number of new recruits. After square-root transforming the recruit counts to improve normality, I used ANOVA to determine whether recruitment and survival were different between the treatment types.

Results

Initial competition experiment

Cover of *B. reticulatus* was clearly higher on the *C. proteus*-removal plates compared to unmanipulated plates within 4 months of the experiment, reaching between 50 and 90 percent. Cover of *B. reticulatus* on the removal plates continued to rise and remained higher than on the unmanipulated plates throughout the course of the experiment (Fig.3.2A). Empty space was greater on the *C. proteus*-removal plates than on the unmanipulated plates after the first two months, but continued to fall until the two treatments became indistinguishable from each other in terms of empty space by the 8th month, or fourth time period (Fig.3.2B). This trend was reversed for a few plates in the last month when one set of plates fell from the pilings before the last time period,

resulting in an increase in empty space on two of the *C. proteus*-removal plates for that period. Empty space on a third *C. proteus*-removal plate also increased in that period due to a large oyster that had died and fallen off the plate. An analysis of variance determined that cover of *B. reticulatus* was significantly different between the *C. proteus*-removal and unmanipulated plates. The time period, treatment x time period interaction, and plate factors were also highly significant (Table 3.1).

Table 3.1. ANOVA table for differences in cover of *B. reticulatus*, competition experiment.

Source	df	MS	F denom.	F	P
Treatment	1	11.21725	0.11589	96.79	<0.0005
Piling	5	0.17607	0.12289	1.43	0.309
Time period	5	1.41149	0.02407	58.64	<0.0005
Piling*Time period	25	0.02407	0.01707	1.41	0.641
Treatment*Time period	5	0.31601	0.01707	18.52	<0.0005
Treatment*Piling	5	0.11589	0.17800	0.65	0.705
Plate (Treatment*Piling)	12	0.17800	0.01707	10.43	<0.0005
Error	85	0.01707			

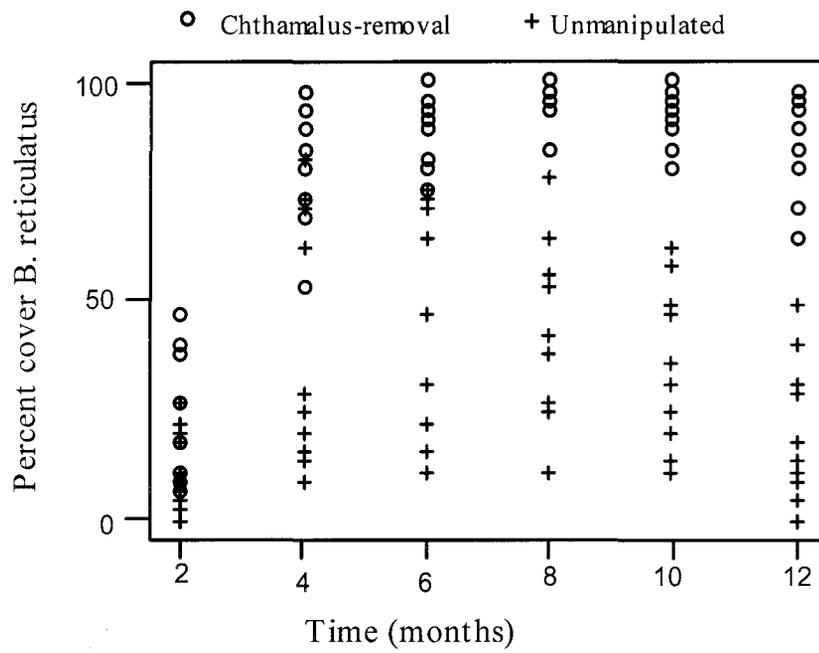


Figure 3.2.A. Percent cover of *Balanus reticulatus* over time, in two month intervals, competition experiment. Each symbol represents one plate.

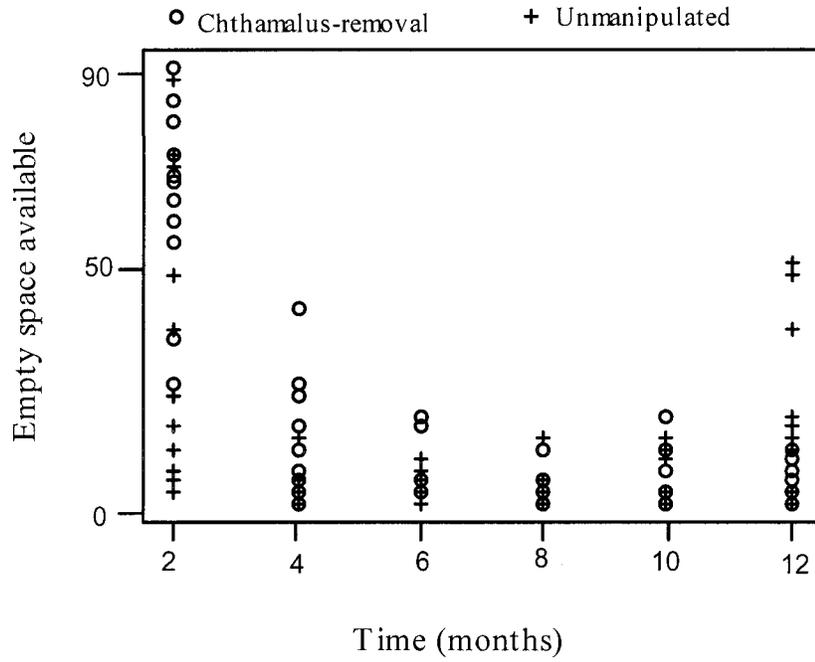


Figure 3.2.B. Percent of empty space over time, in two month intervals, competition experiment. Each symbol represents one plate.

Community-effects study

The plates used for this study consisted of *B. reticulatus*-dominated plates (73 to 96 percent cover) with no *C. proteus* present vs. *C. proteus*-dominated plates (44 to 89 percent cover) that contained some *B. reticulatus* (9 to 30 percent cover). Altogether, 39 taxa were found on the plates (Table 3.2). The most abundant organisms on the plates were a Folliculinid protozoan, an unidentified mite (family Halacaridae), an isopod, *Dynamenella* sp., and the bivalves *Lasaea hawaiiensis* and *Ostrea hanleyana*. When the 18 species that appeared only once were removed, the two types of plates jointly shared 18 species; 3 additional species were found only on the *Chthamalus*-dominated plates.

Phyla	Taxa	<i>Balanus</i> -dominated plates	<i>Chthamalus</i> -dominated plates	Used for comparison
Protozoa	Folliculinid sp.	X	X	Y
Porifera	Unidentified species	X	0	N
Cnidaria	<i>Dynamena</i> sp.	X	X	Y
Annelida	Unidentified Oligochaete	X	0	N
	?Euplanidae	X	0	N
	? <i>Taenioplana</i> sp.	0	X	N
	?Oweniidae	X	X	Y
	<i>Dorvillea</i> cf. sp.	X	X	N
	Eunicid sp. 1	X	0	N
	Eunicid sp. 2	X	0	N
	Neanthes sp.	X	X	Y
	Unidentified Phyllodocid	X	0	N
	Unidentified Serpulid	0	X	Y
	Unidentified Spirobid	X	X	Y
	<i>Typosyllis</i> sp. 1	X	X	Y
	<i>Typosyllis</i> sp. 2	X	X	Y
	? <i>Salmacina dysteri</i> ?	0	X	N
	Unidentified Sabellid	0	X	Y
Mollusca	<i>Siphonaria normalis</i>	X	X	Y
	<i>Hipponix</i> sp.	0	X	N
	<i>Lasaea hawaiiensis</i>	X	X	Y
	<i>Ostrea hanleyana</i>	X	X	Y
	Unidentified clam	X	0	N
	<i>Brachidontes crebristratus</i>	0	X	N
	<i>Isognomon californicum</i>	X	X	Y
	<i>Dendropoma gregaria</i>	X	0	N
Arthropoda	Unidentified Halacarid	X	X	Y
	Unidentified tanaid	X	X	Y
	Unidentified isopod	X	X	Y
	Unidentified copepod	X	0	N
	Xanthid 1	X	X	Y
	Xanthid 2	X	X	Y
	Grapsid 1	X	X	Y
	Grapsid 2	X	0	N
	Crab megalop	0	X	N
Bryozoa	<i>Crisia circinata</i>	0	X	N
	<i>Rhamphostomella argentea</i>	X	X	Y
	<i>Bugula</i> sp.	X	0	N
Echinodermata	Brittle star	X	0	N
Unknown	Unidentified Larva	0	X	Y

Table 3.2 List of species found on the plates dominated by *Balanus reticulatus* vs.

those dominated by *Chthamalus proteus*. An X indicates presence, 0 absence.

Singletons were eliminated before species lists were compared.

Invasion experiment

At the end of this experiment, the former *C. proteus*-removal plates still had higher cover of *B. reticulatus* than the plates that had never been manipulated (Fig.3.3A). This difference was statistically significant (Table 3.3A).

Table 3.3.A. ANOVA table for cover of *Balanus reticulatus* on former removal vs. unmanipulated plates at end of Invasion Experiment.

Source	DF	MS	F denom	F	P
Treatment	1	0.60231	0.03145	19.15	0.048
Piling	2	0.09967	0.03145	3.17	0.240
Treatment*piling	2	0.03145	0.02099	1.50	0.297
Error	6	0.02099			

However, mean percent cover of *B. reticulatus* dropped over the year on the former *C. proteus*-removal plates, from 87 to 45 percent by the end of the year (Fig.3.3B), with a concurrent rise in *C. proteus* cover from nearly 0 to a mean of 32 percent. The difference in cover of *B. reticulatus* on the former *C. proteus*-removal plates between the years and between pilings was statistically significant (Table 3.3B).

Table 3.3.B. ANOVA table for cover of *Balanus reticulatus* on former removal plates, end of Year 1 vs. end of Year 2.

Source	DF	MS	F denom	F	P
Year	1	0.72841	0.02077	35.07	0.002
Piling	2	0.08496	0.00443	19.18	0.020
Plate(piling)	3	0.00443	0.02077	0.21	0.883
Error	5	0.02077			

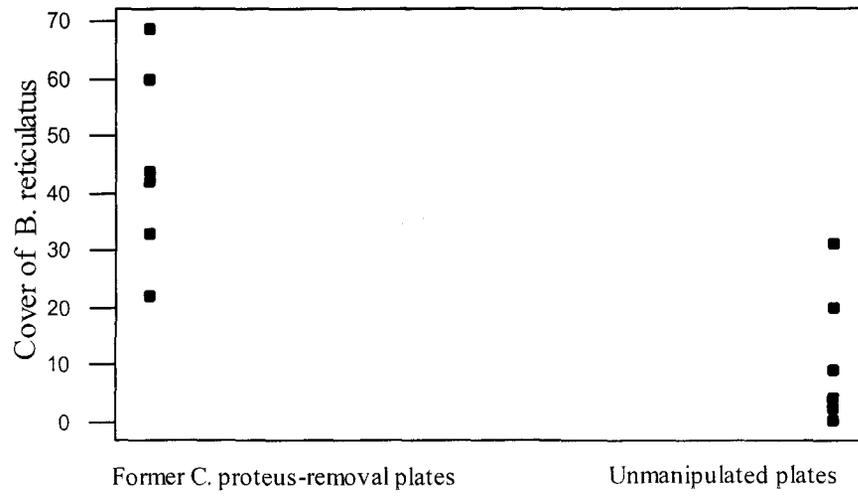


Figure 3.3.A. Cover of *Balanus reticulatus* on the former *Chthamalus proteus*-removal plates vs. unmanipulated plates, end of Invasion Experiment. Each symbol represents one plate.

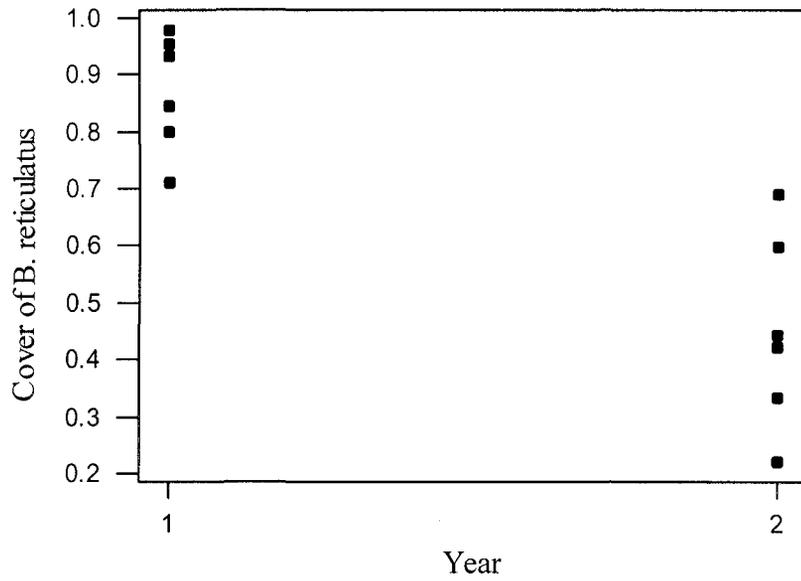


Figure 3.3.B. Percent cover of *Balanus reticulatus* on the former *Chthamalus proteus*-removal plates at the end of Year 1 (Initial Competition Experiment) and Year 2 (Invasion Experiment). Each symbol represents one tile.

Recruitment and survival of *Balanus reticulatus*

B. reticulatus recruited in higher numbers to the former *C. proteus*-removal plates, which were dominated by their conspecifics (Table 3.4A).

Table 3.4.A. ANOVA table for recruitment of *Balanus reticulatus* on plates dominated by conspecifics vs. by *Chthamalus proteus*.

Source	DF	MS	F denom	F	P
Treatment	1	16.794	0.897	18.72	0.049
Piling	2	1.761	0.897	1.96	0.337
Treatment*piling	2	0.897	1.275	0.70	0.531
Error	6	1.275			

The mean number of settlers was 18.2 for *B. reticulatus*-dominated plates and 4.3 for *C. proteus* dominated plates (Fig.3.4). There was no difference between the two types of plates in terms of percentage of settlers of *B. reticulatus* surviving at the end of observation period (Table 3.4B).

Table 3.4.B. ANOVA table for percent of recruits of *Balanus reticulatus* surviving on plates dominated by conspecifics vs. by *Chthamalus proteus*.

Source	DF	MS	F denom	F	P
Treatment	1	0.0041	0.0471	0.09	0.795
Piling	2	0.0221	0.0471	0.47	0.680
Treatment*piling	2	0.0471	0.1285	0.37	0.708
Error	6	0.1285			

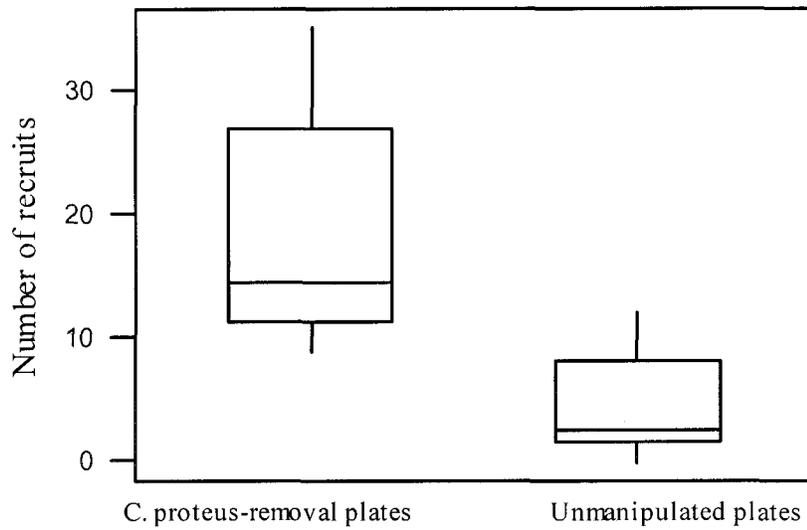


Figure 3.4. Box and whisker plots of recruits of *Balanus reticulatus* on plates dominated by conspecifics and plates dominated by *C. proteus*. The rectangles depict the interquartile range, with a horizontal line at the median; the whiskers depict the high and low values.

Discussion

Cover of *B. reticulatus* on plates in the competition experiment varied temporally, with the effects of removal of *C. proteus* becoming more pronounced over time. Likewise there was variation between individual plates. Nonetheless, the pattern was consistent: cover of *B. reticulatus* was clearly greater on the *C. proteus*-removal plates.

This study demonstrates that *C. proteus* can outcompete *B. reticulatus* for space. Observations of the recruitment and early survival of *B. reticulatus* indicate that the mechanism by which *C. proteus* outcompetes *B. reticulatus* is inhibition of recruitment. Recruits of *C. proteus* inevitably appeared on new substrate in Kaneohe Bay more rapidly and in higher numbers than those of *B. reticulatus* (personal observation), pre-empting space and apparently making surfaces less attractive to *B. reticulatus*.

Settlement of many barnacle species is known to be dependent on chemical cues from adult barnacles. A strong preference for settling with conspecifics has been reported for *B. amphitrite* (Crisp 1990) and *B. balanoides* (Knight-Jones and Moyse 1961, Larman and Gabbott 1975, Barnett and Crisp 1979, Barnett et al. 1979) and this settling pattern appears to hold for *B. reticulatus*. Barnett & Crisp (1979) suggested that one of the ecological consequences of gregarious settlement behavior is dominance via substrate pre-emption: "If the two species are in other respects equally fit, the species occupying the habitat at higher density will always encourage the settlement of the conspecific at the expense of a rival, resulting in cover by the single dominant species." This appears to be

largely true in Kaneohe Bay; although *C. proteus* isn't the only intertidal barnacle species in the bay, it is far and away the most numerous.

Barnett & Crisp (1979) further hypothesized that only a habitat change that favors a second species could lead to a change in dominance. But some barnacle species may be less dependent than others on conspecific cues. There is some indication that *Elminius modestus*, an invasive barnacle in Europe, is less influenced by conspecifics than its native counterpart *Balanus balanoides* (Larman and Gabbott 1975, Barnett et al. 1979). Selection pressure in a newly invading species might be expected to favor phenotypes that are not as reliant on the presence of conspecifics in substrate choice (Larman and Gabbott 1975). It is not clear from this experiment whether *C. proteus* is less dependent than *B. reticulatus* on cues from conspecifics. However, I have observed *C. proteus* among sparsely settled *B. amphitrite* and other barnacle species elsewhere on Oahu and in the Caribbean. Although recruits of *C. proteus* were not counted in this experiment, hundreds of new recruits of *C. proteus* were seen on both types of plates at nearly every time interval. In Kaneohe Bay, *C. proteus* is certainly able to exploit available space rapidly, even in areas dominated by other barnacles. Assuming the processes operating at the small scale of this experiment also operate on larger scales, and I have no reason to believe they would not, this study shows how *C. proteus* could have invaded and come to dominate intertidal structures in Kaneohe Bay even in the absence of physical disturbance of established barnacle communities. Of course, physical disturbances such as changes in salinity or nutrient- and sediment loading due to storm run-off may have expedited the invasion process.

The result of the initial competition experiment raises the question of which barnacle was dominant when *C. proteus* arrived in Kaneohe Bay. In the same manner that *C. proteus* is able to outcompete *B. reticulatus* today, *B. reticulatus* might have replaced *B. amphitrite* in the years following Matsuda's study. *B. reticulatus* was present in the bay in the early 1930s (Henry and McLaughlin 1975), although its abundance appears to have been low for some time. In 1935 Edmondson and Ingram (1939) reported finding "at least two... apparent varieties of *B. amphitrite*" including one with a "slightly curved beak." *B. reticulatus* tends to have more steeply angled radii than *B. amphitrite*, which would give it a curved appearance. This variety was described as numerous in Pearl Harbor, but less common in Kaneohe Bay, where the vast majority of the barnacles recruiting to intertidal and shallow subtidal fouling panels were *B. amphitrite*. This was apparently still the case in 1973 when Matsuda described *B. reticulatus* as rare in the intertidal zone and *B. amphitrite* as the second-most widespread and abundant barnacle in the intertidal on Oahu after the native *Nesochthamalus intertextus*. Earlier studies of Hawaiian barnacles (e.g., Pilsbry 1906, Pilsbry 1927) were not quantitative and do not indicate which barnacles were dominant in Kaneohe Bay before 1939.

In the absence of data on barnacle abundance between Matsuda's study and the present one, it is impossible to know what might have occurred, but a decline in the abundance of *B. amphitrite* credited to competition with another balanoid species has been reported from at least one other location. In Mar del Plata Port, Argentina, where *B. amphitrite* was also introduced, it was once highly abundant on pier pilings and other hard substrate in intertidal harbor areas. Following the invasion of a second barnacle, *B. glandula*, *B. amphitrite* all but disappeared (Vallarino and Elias 1997). It was hypothesized that *B.*

glandula was able to pre-empt settlement space in the harbors by settling in the winter, when space was available due to storm-driven disturbance. *B. amphitrite*, which was reported to have a summer settlement in Argentina, would presumably have little room to settle, and where it did, it could be easily crushed by the already large and fast-growing *B. glandula*. Researchers did not find any *B. amphitrite* even on plots cleared monthly, however, so the mechanism of displacement remained speculative. Intriguingly, *B. reticulatus* appears to have been replaced by *B. amphitrite* in Japanese harbors following World War II, although *B. reticulatus* was reported to still be the dominant barnacle subtidally in some full-salinity settings (Utinomi 1967). An alternate scenario for Kaneohe Bay is that barnacle cover might have been low due to some disturbance when *C. proteus* began its invasion. At the initial stages of the Kaneohe Bay invasion, *C. proteus* cyprids would have been in smaller numbers than they are today, so the rate of change from *Balanus*-dominated communities to *C. proteus*-dominated communities would have been much slower than in the invasion experiment. Any event in Kaneohe Bay that could have reduced the dominant barnacle would have accelerated the process, but it is hard to imagine what kind of event would be harmful to *B. amphitrite* or *B. reticulatus* and not to *C. proteus*. Although both *Balanus* species are highly tolerant of low salinity — *B. amphitrite* more so than *B. reticulatus* (Thiyagarajan et al. 1997) — it is conceivable that floods in 1987 reduced barnacle cover, particularly in the intertidal zone, which would have been bathed in the freshwater lens. If *C. proteus* was introduced to the bay after the floods, or was already present and had some survivors, presumably it could have quickly covered large areas before the population of *Balanus* built back up.

This study suggests that the community of small organisms that live in and around barnacles is unaffected by the change in the dominant barnacle, or by increased barnacle diversity, as the plates dominated by *C. proteus* used in this study also retained some cover of *B. reticulatus*. However, with only four samples from each community type and without enumerating all of the individuals of each taxa, subtle differences in communities might have gone undetected. It certainly should not be concluded that there are no community-level effects resulting from a change in the dominant barnacle — not all organisms that might interact with these barnacle species were examined. In particular, changes in the abundance of larger, mobile organisms would likely have not been detected in such a small-scale experiment.

C. proteus may not be the only relatively new invader to reduce cover of *Balanus* species in Kaneohe Bay. The portion of the Lilipuna Pier pilings in the low intertidal (below 0 tide) is thickly covered with *Gracilaria salicornia*, an invasive red alga introduced to Kaneohe Bay in the 1970s. Settlement plates strapped to the pier pilings on top of this algal cover attracted numerous recruits of *B. reticulatus* and a few individuals of *C. proteus* (personal observation). This suggests that cover of *B. reticulatus* and perhaps *C. proteus* would extend lower into the intertidal than it currently does, at least in some locations, if it weren't for *G. salicornia*.

Changes in abundance in Kaneohe Bay notwithstanding, all three barnacles seem likely to persist in Hawaii. *B. amphitrite* is still the dominant barnacle in certain locations, particularly low-salinity settings such as the Ala Wai canal on Oahu. *B. reticulatus* is numerous on pilings in Pearl Harbor and at the seaward end of the Ala Wai canal and boat harbor, especially in the lower intertidal zone where *C. proteus* is nearly absent.

Although *C. proteus* has the ability to withstand temporary immersion in freshwater, and can tolerate periodic lowered salinity, it does not appear to have as great a tolerance for long-term lowered salinity as *B. amphitrite* (personal observation). *Balanus reticulatus* also appears less tolerant of long-term lowered salinity than *B. amphitrite* (Utinomi 1967, Thiyagarajan et al. 1997). Additionally, while *C. proteus* appears to be restricted to the intertidal zone, both *Balanus* species can live in the shallow subtidal as well. *Chthamalus proteus* has attained a wider distribution than either barnacle around Oahu, being found in open coast settings where wave exposure is moderate such at Diamond Head and Barber's Point and even in some protected micro-habitats on high-energy shores, such as Sandy Beach and Maili Point (Chapter 2).

The invasion of *C. proteus* offers an opportunity to observe competitive interactions between barnacle species. It also demonstrates that despite the fact that larger, faster-growing barnacles nearly always win in interference competition for space, smaller barnacles may sometimes outcompete larger ones via substrate pre-emption. At the site tested, such competition appears to be a major factor in determining the abundance and distribution of barnacle species. This outcome should be interpreted with caution, however. It should not be assumed that competition is a key factor in the structure of intertidal barnacle communities throughout Oahu. Physical factors, larval supply, and predation are likely to be important as well (Chapter 4).

Invasion theory has historically predicted that a community should become increasingly resistant to new invaders as resident species diversity builds up (*e.g.*, Elton 1958, Moulton and Pimm 1983, Robinson and Dickerson 1984, 1987, Case 1990, Drake 1990, Case 1991, Stachowicz et al. 1999). Recently, a second scenario, that of an "invasional

meltdown” where earlier invaders alter communities and facilitate new invasions, has also been proposed (Simberloff and Von Holle 1999). In the case of intertidal barnacles in Hawaii, there is no evidence that either scenario is correct, at least at this point. Settlement of *C. proteus* does not appear to be dependant on the presence of *B. reticulatus* or *B. amphitrite*. The newer invader has successfully settled in locations without *B. reticulatus*, and in places where there are no other barnacle species at all (Chapter 2s). Likewise, although settlement of *C. proteus* on plates dominated by *B. reticulatus* was lower than it would have been on completely empty plates, *B. reticulatus* was not able to exclude the newer invader indefinitely: *C. proteus* settlers rapidly fill up empty space and readily settle on living and dead *Balanus*. Rather, what we seem to be witnessing in Kaneohe Bay, is at least one — and possibly two — near replacements of an earlier invader by a later one. What we are left to wonder is which species will invade next?

CHAPTER 4.

Recruitment levels linked to competition outcomes between pairs of barnacle species

Introduction

Ecologists have long been concerned with determining what factors are important in the abundance and distribution of species. In intertidal ecology, early workers emphasized physical factors such as wave exposure, heat stress, and desiccation as the major forces influencing species distributions (*e.g.*, Colman 1933, Doty 1946, Lewis 1964, Stephenson and Stephenson 1972). Following Connell's landmark study of competition between two barnacle species (Connell 1961b), the emphasis shifted to competition as a major factor affecting community structure (*e.g.*, Connell 1961a, Stimson 1970, Dayton 1971, Menge 1972, Haven 1973, Connell 1975, Lubchenco 1980, for reviews, see Connell 1983, Schoener 1983). The impacts of predation and/or herbivory became a focus shortly thereafter (*e.g.*, Paine 1966, Paine 1969, Connell 1970, Paine 1974, Connell 1975, Lubchenco 1978, Castilla and Duran 1985, for reviews, see Sih et al. 1985, Robles and Desharnais 2002), followed by numerous explorations of the role of disturbance (*e.g.*, Dayton 1971, Sousa 1979a, b, McGuinness 1987, for review, see Sousa 2001) and then an emphasis on the role of larval supply in structuring populations of sessile adults (*e.g.*, Grosberg 1982, Keough and Downes 1982, Underwood and Denley 1984, Gaines and Roughgarden 1985, Roughgarden et al. 1988, Raimondi 1990, for reviews, see Young

1990, Grosberg and Levitan 1992). Several models have been proposed that attempt to integrate all of the above ideas and to predict under what conditions these various factors might be most important (*e.g.*, Menge 1976, Connell 1985, Menge and Sutherland 1987, Menge 1991, Robles and Desharnais 2002).

Despite evidence that competition may not be a strong structuring force in all communities, many studies of the vulnerability of communities to invasion by alien species have either explicitly or implicitly suggested that competition plays a major role in the success or failure of invasions (*e.g.*, Darwin 1859, Elton 1958, Moulton and Pimm 1983, Case 1990, Stachowicz et al. 1999). Along these lines, the success of the intertidal barnacle *Chthamalus proteus* as an invader in the Hawaiian Islands has been attributed to the lack of competition with other intertidal barnacle species (Southward et al. 1998). The Hawaiian Islands have few native intertidal barnacle species, and these tend to occur in cracks and crevices, rarely attaining the thickly settled barnacle bands seen in other intertidal locations around the world. Additionally, native intertidal barnacles tend to favor high energy habitats, while *C. proteus* is characterized as a calm water barnacle, which should further preclude competition with native Hawaiian barnacles (Southward et al. 1998).

However, *C. proteus* is not without at least potential barnacle competitors. At semi-protected sites it co-occurs with native barnacles, and in protected waters it can be found in the fouling community with other invasive barnacle species, which are sometimes highly abundant (personal observation). Cover of *C. proteus* appears generally to be negatively correlated with cover of other barnacle species. This pattern of abundance and distribution is what we would expect to find if competition is important in structuring

barnacle communities in Hawaii. However, without experimental evidence, we cannot rule out other factors.

I used removal experiments to determine whether competition for space was occurring between *C. proteus* and the native barnacle *Nesochthamalus intertextus* at two semi-protected sites where overall barnacle abundance was relatively high. Here, I discuss these experiments and contrast them with a third experiment examining competition between *C. proteus* and another invasive barnacle, *Balanus reticulatus* (Chapter 3). Additionally, in an attempt to determine whether cover of adult barnacles can be explained by recruitment rate, I monitored recruitment of the three barnacle species at three intertidal sites for one year.

Materials and Methods

Study organisms

Chthamalus proteus naturally ranges from Southern Florida to Brazil (Pitomo, personal communication) and has been reported from scattered intertidal locations throughout the Gulf of Mexico and the Caribbean (Southward 1975, Dando and Southward 1980). The date of its arrival in the Hawaiian archipelago is unknown, but it was not found in a survey of intertidal barnacles on the island of Oahu in the early 1970s (Matsuda 1973) and not reported from the islands until 1995 (Southward et al. 1998), although specimens collected in Pearl Harbor in 1993 were later identified as *C. proteus* (J. Brock, personal communication). It is a small barnacle, typically 6 mm in rostrocarinal length, restricted to the intertidal zone and generally found in highest abundances in semi-protected to

protected locations. Recently described in its native range (Dando and Southward 1980), little is known about its ecological role in its native or new range (but see Chapters 2, 3 and 5).

Nesochthamalus intertextus is an intertidal barnacle with a wide Indo-Pacific distribution (Foster and Newman 1987). It is the most abundant and widespread intertidal barnacle on Oahu, being found from the most wave-beaten shores to semi-protected coastlines on basalt and limestone rocks as well as on manmade structures such as seawalls. It does not seem to tolerate lowered salinity well, as it is absent from harbors and canals. It is conspicuously missing from most of Kaneohe Bay, a large, protected waterway on Oahu's windward side. Populations are found only at the edges of the bay where conditions are more oceanic: Kualoa Beach park to the north, and past the airport runway at the Kaneohe Bay Marine Corps Base to the south (personal observation). Little is known about its life history or ecology. In Hawaii, *N. intertextus* is typically 10 mm in rostrocarinal length. Unlike *C. proteus*, it is rarely found blanketing a substrate. At most intertidal sites it is restricted to cracks and crevices, but can be abundant (up to 40 percent cover) on semi-protected rocky shorelines with consistent wave wash.

Competition between *C. proteus* and *N. intertextus*

Neighbor-removal experiments. To investigate impacts of the native barnacle *N. intertextus* on the invasive barnacle *C. proteus*, I removed native barnacles from permanent plots on a cement seawall in Waikiki on the south shore of Oahu (Fig. 4.1). The seawall runs parallel to the beach, creating a wave-protected swimming area for

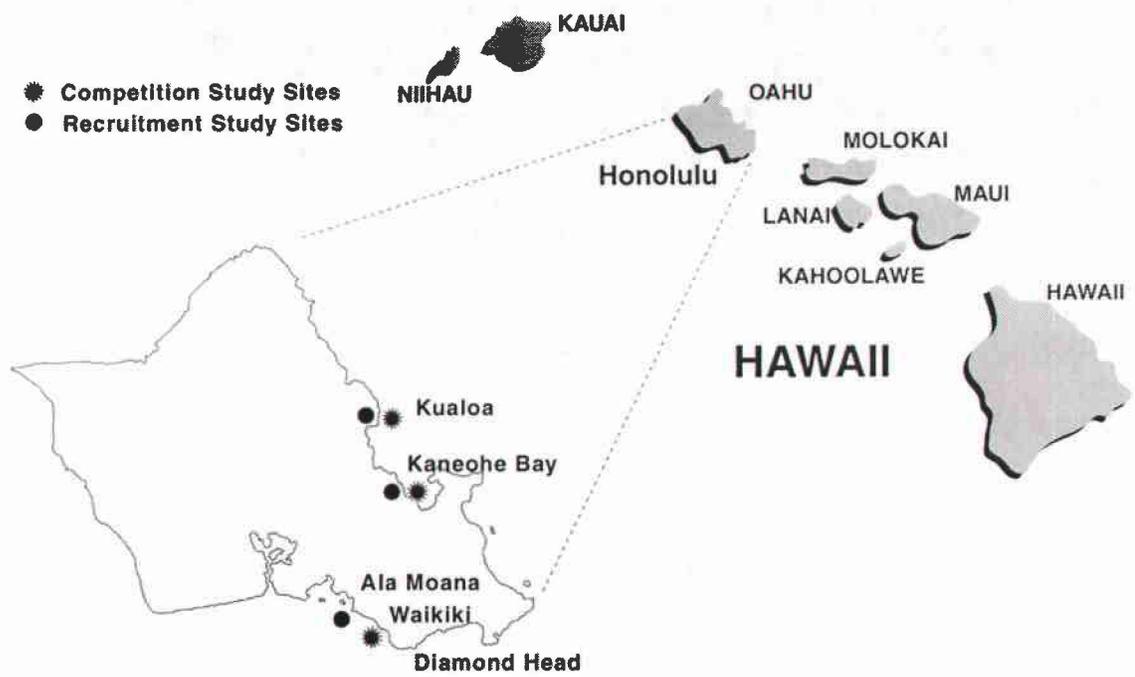


Figure 4.1. Study sites at Waikiki, Ala Moana, Kaneohe Bay and Kualoa.

beachgoers; waves hit the seaward edge of the wall and break over the top, pouring water over the shoreward edge of the wall.

In October 1999, *N. intertextus* comprised about 40 percent cover in the barnacle zone and *C. proteus* about 2 percent (calculated by counting barnacles under 25 random points in 40 12.5 by 15 cm quadrats). Although this level of cover is low relative to intertidal locations elsewhere, it is high for open-coast settings in Hawaii (personal observation). Observations suggested that competition for space might be occurring: first, individuals of *C. proteus* were frequently overgrown by the larger native barnacle. Secondly, the distribution of barnacles was fairly aggregated, which may have been the result of limited microhabitats, *i.e.* pits and grooves in the rocks that remain moist during low tide.

It seemed unlikely that I would have been able to detect an impact of *C. proteus* on *N. intertextus* through a removal experiment at this site, as there were so few invaders relative to natives. Instead, I used a second site, where the invasive barnacle was numerically dominant and *N. intertextus* was relatively rare, to test for impacts of the invader on the native. The site is a seawall at Kualoa Beach Park at the northern edge of Kaneohe Bay (Fig. 4.1). Here *C. proteus* comprised 38 percent cover and *N. intertextus* 4 percent (cover determined as above, surveyed in January 2000). The seawall consists of a series of saw-horse shaped cement blocks that run roughly north to south and enclose a shallow sandy pool on the east-facing side of the beach. This site is generally protected from waves by a fringing reef, but the seawall is frequently washed by small waves. Larger waves that pass over the reef occasionally hit the seawall in winter when large north and west swells occur.

At each site, I used a flattened ball of Z-Spar Splash Zone marine epoxy about the size of a quarter to mark the lower left corner of each of 20 12.5 by 15 cm plots. Plots were placed in the densest portion of the barnacle zone, over a distance of approximately 10 m. At Waikiki, I selected areas to be designated as plots if they had at least 10 individuals of *C. proteus* in them; the plots were then randomly assigned to be treatments or controls. In treatment plots, I removed all individuals of *N. intertextus* within 5 mm of each individual of *C. proteus*; no barnacles were removed in the control plots. I mapped the barnacles in each plot using an acetate sheet of the same size as the plot. These maps were used to locate the plot during subsequent visits and to track the fate of individual barnacles. I maintained the 5 mm space around each tracked barnacle bi-monthly. Settlement was low enough that this time period was sufficient to keep barnacles consistently cleared. The length and width of tracked barnacles were measured bi-monthly, using Vernier calipers. Measurement error was determined to be about 0.3 mm through repeated measures. I used a soft toothbrush to gently brush the barnacles to remove encrusting algae before identifying and measuring the barnacles; barnacles in control plots were also brushed. I noted when barnacles were dead or missing and interactions with neighbors (*i.e.*, overgrown by *N. intertextus*, next to *C. proteus*, etc.) were recorded. These measurements were made over two one-year periods beginning October 1999. When barnacles died, whenever possible, I found new individuals to track in an effort to keep at least 10 barnacles per plot. For example, I started with 197 barnacles in the first year and 185 in the second year, approximately 100 of which were new barnacles.

I used the same protocol at Kualoa, except that I selected plots based on the number of individuals of *N. intertextus* (there had to be at least five), and *C. proteus* within 5 mm of individuals of *N. intertextus* were removed in treatment plots. Experimental set up is summarized in Table 4.1.

Recruitment inhibition experiments. To determine whether the presence of *N. intertextus* was inhibiting recruitment of *C. proteus* at the Waikiki site, I used a removal experiment to examine recruitment of the invasive barnacle in the absence of *N. intertextus*. In March 2000, I established 6 pairs of 12.5 by 15 cm plots. One plot in each pair was completely cleared of all *N. intertextus* and one was unmanipulated and served as a control. Treatments were randomly assigned within each pair. The removal plots were cleared monthly, and new recruits (defined as barnacles <3 mm) of *C. proteus* were counted in each plots in April, June and August 2000. At the Kualoa site, to determine whether recruitment of *N. intertextus* was inhibited by the presence of the in the invader, I cleared 10 plots of all *C. proteus* and compared recruitment to those plots to 10 paired controls in April, July and November 2000.

Experimental set up is summarized in Table 4.1.

Growth, mortality and recruitment of numerically dominant barnacle. At each site, I also measured growth and tracked mortality of the numerically dominant barnacle (*N. intertextus* at Waikiki and *C. proteus* at Kualoa). These observations were made in control plots. Recruits of *N. intertextus* and *C. proteus* at Waikiki and Kualoa,

respectively, were also counted in both treatment and control plots in the Recruitment Inhibition experiment.

The set up of these surveys is summarized in Table 4.1.

Table 4.1 Methods for Waikiki and Kualoa experiments and surveys

Location	Experiment/survey	Treatment/Method	Dates	N
Waikiki	Neighbor-removal: Effect of <i>N. intertextus</i> on growth, mortality of <i>C. proteus</i>	Removal of <i>N. intertextus</i> within 5 mm of <i>C. proteus</i> in treatment plots	October 1999 -October 2000	197 barnacles in 20 plots
			December 2000-December 2001	185 barnacles in 20 plots
Waikiki	Growth, mortality of numerical dominant, <i>N. intertextus</i>	Measured in control plots in above experiment	March 2000-December 2000	25 barnacles in 5 plots
			December 2000-December 2001	41 barnacles in 5 plots
Waikiki	Recruitment inhibition: Effect of <i>N. intertextus</i> on recruitment of <i>C. proteus</i>	Removal of all <i>N. intertextus</i> in treatment plots	March-August 2000	12 plots
Waikiki	Recruitment of numerical dominant, <i>N. intertextus</i>	Counted recruits to removal and control plots in above experiment	March-August 2000	12 plots
Kualoa	Neighbor-removal: Effect of <i>C. proteus</i> on growth, mortality of <i>N. intertextus</i>	Removal of <i>C. proteus</i> within 5 mm of <i>N. intertextus</i> in treatment plots	March 2000-March 2001	127 barnacles in 20 plots
			March 2001-2002	98 barnacles in 20 plots
Kualoa	Growth, mortality of numerical dominant, <i>C. proteus</i>	Measured in control plots in above experiment	June 2000-March 2001	40 barnacles in 5 plots
			March 2001-March 2002	53 barnacles in 5 plots
Kualoa	Recruitment inhibition: Effect of <i>C. proteus</i> on recruitment of <i>N. intertextus</i>	Removal of all <i>C. proteus</i> in treatment plots	April 2000-November 2000	20 plots
Kualoa	Recruitment of numerical dominant, <i>C. proteus</i>	Counted recruits to removal and control plots in above experiment	April 2000-November 2000	20 plots

Growth calculations. When a barnacle was overgrown by other barnacles so that the edges of the test were not visible, I could not be certain of its actual size. Based on my observations of *C. proteus* removed from substrate, it appears that when individuals of *C. proteus* are crowded by other barnacle species, particularly larger, faster growing ones, normal growth ceases and the test shape becomes distorted. Except in one highly sheltered and extremely crowded location (one piling of the Lilipuna Pier, South Kaneohe Bay) I have not observed *C. proteus* to grow tall or form hummocks in response to crowding. Rather, individuals become asymmetrical, growing toward open areas, with tests forming scalloped edges where they come into contact with nearby barnacles. At Kualoa, *N. intertextus* also grew in this manner when in contact with other barnacles. This presented a challenge for accurate measurement of growth, as size measurements could only be made to visible edges. If a barnacle was overgrown on all four sides or was being overgrown faster than it could grow in an uncrowded direction, its size was determined to be decreasing. Thus my calculations of “growth” are really a measure of changes in area free from overgrowth and are probably lower than the actual growth. As overgrowth leads to slowed growth and eventually to death, this measure seemed an adequate descriptor of how well barnacles were faring vis a vis space competitors. In other studies, measurements of apertures have been used as a proxy for total size. This was not a useful measure for this study for two reasons: 1) the ratio of aperture to total size in *C. proteus* changes under different environmental conditions (and in some locations between young and old barnacles) and thus would not be useful for

comparisons between areas; 2) because of the small size of these barnacles, measurement error would likely have been higher than changes in aperture size.

Because of the tendency of barnacles to grow asymmetrically when crowded, I calculated barnacle basal area estimated as an oval, rather than length or width alone, in determining size. Bi-monthly growth at Waikiki and Kualoa was frequently less than measurement error, so I used yearly growth rather than the bimonthly data. Barnacles that died before the end of the year were eliminated from these calculations. Estimates for monthly growth were made by dividing the year's growth by 12.

Statistical analyses. To test for differences in growth of the numerically inferior barnacle (*C. proteus* at Waikiki and *N. intertextus* at Kualoa) between treatment and controls for each year and site, I used ANOVAs with treatment as a fixed factor and plot nested in treatment as a random factor. If barnacles grow at a different rate depending on size, differences in initial size between treatments and controls could affect the results. I plotted initial size vs. the ratio of initial to final size for each species at each site and time period and used Pearson's correlations to determine if there was a relationship between growth and initial size. Where a correlation was found, I used ANOVAs to test whether initial sizes were different between treatments and controls.

I used chi-square tests to determine whether mortality of the numerically inferior barnacle was higher between treatments and controls. For these tests, I used all the barnacles tracked within each one-year period. This was a total of 238 individuals of *C. proteus* for the first year and 306 for the second at Waikiki, and 126 and 178 individuals of *N. intertextus* in the first and second years, respectively, at Kualoa. One possible

explanation for a finding of no difference between treatment and control plots could be too few interspecific interactions in treatment plots. To test for this, I recorded interactions with neighbors at the time of death for each barnacle. I grouped these situations into three categories: 1) barnacles involved in intraspecific interactions (=touching, being overgrown, overgrowth by a conspecific), 2) barnacles involved in interspecific interactions (= touching, being overgrown, overgrowth by another barnacle species), and 3) barnacles without a neighbor within 5 mm. Since my focus was on interspecific competition, I placed any barnacle involved in an interspecific interaction in Category 2 even if it was also involved in an intraspecific interaction. Barnacles from both treatment and control plots were used: because no barnacles in treatment plots were involved in interspecific interactions, they could be placed only into categories 1 or 3. A chi-square analysis was then used to determine whether mortality was higher than would be expected due to chance alone for barnacles in any of these groupings.

Comparison to Kaneohe Bay

An experiment testing for competitive interactions between *C. proteus* and *Balanus reticulatus* was carried out on 24 10 by 10 cm settlement plates from July 2001 to July 2003 in southern Kaneohe Bay (Fig. 4.1). Methods are described in Chapter 3.

To compare growth and mortality of barnacles between this experiment and the Waikiki and Kualoa experiments, I examined photographs taken during the course of the Kaneohe Bay experiment to determine percent cover and growth and mortality rates of both barnacle species at that site. Mean percent cover for the Kaneohe Bay site was estimated by placing a grid of 45 points over photographs taken in July 2002 of the 12

control plates (these had not been manipulated). Growth was determined by measuring the length and width of 50 individuals of *C. proteus* and *B. reticulatus* in the photographs and correcting for magnification. Individuals were tracked for as many months as possible between the period of March 2002 and January 2003; both controls and treatment plates were used. Some barnacles were tracked over the entire period, but high mortality and recruitment to the plates made it difficult to track individuals for more than two months in many cases. Mortality over this time period was estimated for 10 of the settlement plates. The resolution of the photographs was not high enough to determine the specific identities of newly settled individuals, so accurate counts of recruitment could not be made. During the first year of the Kaneohe Bay experiment, I removed hundreds of recruits of *C. proteus* from the treatment plates every two weeks. For the purpose of comparing recruitment to Waikiki and Kualoa I conservatively estimated recruitment of *C. proteus* at 100 individuals per plate per month. Recruitment of *B. reticulatus* to plates was always lower than for *C. proteus*, ranging from a few individuals in some months to about half that of *C. proteus*. I used a conservative estimate of 10 recruits of *B. reticulatus* per plate per month. I then standardized recruitment at Waikiki and Kualoa to number of recruits per 100 cm² to calculate a mean number of settlers per month for the months recorded.

Recruitment study

Because many barnacle species settle preferentially when chemical cues from adult conspecifics are present, I used settlement panels cued with adult barnacle extract to further quantify recruitment rates at three sites. While I was able to set up panels at two

of the earlier study sites, panels set up as part of a pilot study were vandalized at Waikiki, and a less conspicuous site on the south shore, Ala Moana Beach Park, ~4 kilometers west, was used instead (Fig. 4.1). Total barnacle cover immediately adjacent to my study site was less than <1 percent and abundance of *C. proteus* and *N. intertextus* was about equal. Thus, adult barnacle cover was greatest at Kaneohe Bay, intermediate at Kualoa and lowest at Ala Moana. At each site, I set out 10 5 by 10 cm Plexiglas plates covered with Safety-Walk anti-slip tape (3M medium duty gray, catalog no. 7740) in the middle of the barnacle zone. I collected adult barnacles from sites where they are abundant: *N. intertextus* from Diamond Head Beach Park and *C. proteus* and *B. reticulatus* from structures around the Hawaii Institute of Marine Biology. To create a settlement cue from adult barnacles, I ground the barnacles into a paste using a mortar and pestle (Raimondi 1988). The paste was strained through a 300 micron mesh and brushed onto the plates. I used 15 mL of adult barnacles and an equal amount of seawater per five plates. Collecting, grinding and painting implements were kept separate for each species. The plates were allowed to dry overnight and were placed at their respective sites during low tide the next morning: five plates cued with *N. intertextus* and five with *C. proteus* at Kualoa and Ala Moana; five with *C. proteus* and five with *B. reticulatus* at Kaneohe Bay. Plates remained in place for two weeks. Pilot studies indicated that the number of recruits on the plates at the end of two weeks was reflective of cumulative daily recruitment over the same time period and that lesser time periods were frequently not able to capture recruitment events. The plates were put out and collected every two weeks between mid-May and August 2004 and once a month from September 2004 to April 2005. Because it

was difficult to collect *B. reticulatus* in quantity, I only used it as a cue four times during the one year period.

At Ala Moana and Kualoa, panels were collected by peeling the Safety-Walk tape from Plexiglas plate, which was attached to the substrate with marine epoxy. At the Kaneohe Bay site, where plates were attached to pier pilings with plastic ties, plates were cut down and replaced with new plates. By counting numbers of recruits on plates removed this way and then pulling up the Safety-Walk tape and counting a second time, I determined that although some recruits were crushed when the tape was removed, none were lost. Thus I was confident that using different techniques did not affect my results. The plates were examined under a microscope at 20X and the number of each type of recruit was tallied. New recruits of the three species are easy to tell apart: *C. proteus* is white to light brown with an oval shaped operculum; *N. intertextus* is dark blue-grey; settlers of *B. reticulatus* have rudimentary stripes and a more diamond-shaped operculum than the other two.

Results

Competition between *C. proteus* and *N. intertextus*

Neighbor-removal experiments.

1. *Effect of N. intertextus on C. proteus.* Mean yearly growth of *C. proteus* at Waikiki is summarized in Table 4.2. Barnacle growth was not proportional to initial size in the first year (Pearson correlation = 0.138, $P = 0.170$), but it was in the second year (Pearson

correlation = 0.240, $P = 0.023$). However, ANOVA indicated there was no difference in initial size between treatments (*N. intertextus*-removal vs. controls) for either year.

Table 4.2. Mean annual growth (mm²) for *C. proteus* at Waikiki site, years 1 and 2.

Year	Treatment	Growth	Standard deviation	N
1	Control	27	28.2	63
1	<i>N. intertextus</i> -removal	41	30.8	38
2	Control	17.2	23.0	56
2	<i>N. intertextus</i> -removal	16.9	21.1	34

Although there was a trend toward higher growth in the treatment quadrats in the first year, this was not statistically significant (Table 4.3A). The plot effect was highly significant. There was no such trend between treatments in the second year, and the plot effect was not statistically significant (Table 4.3B).

Table 4.3A. ANOVA table for the effect on growth of *C. proteus* of removing *N. intertextus*, Year 1.

Source	DF	Adj SS	Adj MS	F	P
Treatment	1	3156.5	3156.5	1.67	0.210
Plot(treatment)	18	41831.2	2324.0	4.41	<0.0005
Error	81	42710.6	527.3		
Total	100	89272.6			

Table 4.3B. ANOVA table for the effect on growth of *C. proteus* of removing *N. intertextus*, Year 2.

Source	DF	Adj SS	Adj MS	F	P
Treatment	1	76.7	76.7	0.14	0.712
Plot(treatment)	18	10216.9	567.6	1.13	0.346
Error	72	36277.4	503.9		
Total	91	46521.6			

There was no difference by treatment in the proportion of the barnacles that died in first year ($\chi^2 = 1.910$, $df = 1$, $P = 0.167$); in the second year more barnacles in the treatment plots died ($\chi^2 = 4.183$, $df = 1$, $P = 0.041$). There was no difference in terms of mortality for barnacles involved either interspecific or intraspecific interactions or those without a nearby neighbor in the first year ($\chi^2 = 0.384$, $df = 2$, $P = 0.825$); in the second year, there was higher than expected mortality for barnacles involved in intraspecific interactions ($\chi^2 = 12.63$, $df = 2$, $P = 0.002$).

2. *Effect of C. proteus on N. intertextus.* At Kualoa, growth of *N. intertextus* was nearly identical in treatment (*C. proteus*-removal) and control plots (Table 4.4). Growth in the second year was lower than measurement error, making further analysis meaningless. Initial area was correlated with the ratio of initial to final growth in both years, with larger barnacles growing more slowly (Year 1, Pearson correlation = 0.315, $P = 0.002$; Year 2 0.424, $P < 0.0005$), but there was no statistically significant difference in initial size in either year between treatments and controls.

Table 4.4. Mean annual growth (mm²) for *N. intertextus* at Kualoa site.

Year	Treatment	Growth	Standard deviation	N
1	Control	21.1	31.6	45
1	<i>C. proteus</i> -removal	20.4	20.3	52
2	Control	N/A	N/A	42
2	<i>C. proteus</i> -removal	N/A	N/A	47

Analysis of variance confirmed that there was no statistically significant difference in growth between treatments and controls in the first year (Table 4.5).

Table 4.5. ANOVA table for the effect on growth of *N. intertextus* of removing *C. proteus*, Year 1.

Source	DF	Adj SS	Adj MS	F	P
Treatment	1	13.8	13.8	0.03	0.865
Plot(treatment)	18	8012.6	445.1	0.60	0.887
Error	77	56839.0	738.2		
Total	96				

There was no difference by treatment in the proportion of barnacles that died in the first year ($\chi^2 = 0$, $df = 1$, $P = 0.995$) or in the second year ($\chi^2 = 0.346$, $df = 1$, $P = 0.556$). In the first year, there was no difference in mortality between barnacles in interspecific vs. intraspecific interactions, but barnacles that did not have a neighbor within 5 mm died in higher than expected numbers ($\chi^2 = 27.069$, $df = 2$, $P < 0.0005$). There were too few

barnacles involved in intraspecific interactions in the second year to analyze data by the chi-square test.

Recruitment inhibition experiments: 1. Effect of N. intertextus on C. proteus. In Waikiki, recruitment of *C. proteus* was low and there was no difference between cleared (*N. intertextus*-removal) and control plots (Table 4.6).

Table 4.6 Number of recruits of *C. proteus* per set of six plots at Waikiki.

Month	Treatment	
	Cleared of <i>N. intertextus</i>	Control
April	2	2
May	0	2
June	0	0
Total	2	4

Recruitment inhibition experiments: 2. Effect of C. proteus on N. intertextus.

At Kualoa, recruitment of *N. intertextus* was extremely low during the experimental period and nearly identical between treatments and controls (Table 4.7).

Table 4.7. Number of recruits of *N. intertextus* per set of 10 plots at Kualoa.

	Treatment	
Month	Cleared of <i>C. proteus</i>	Control
April	3	1
July	2	0
November	1	5
Total	7	6

Growth, mortality and recruitment of numerically dominant barnacle.

Growth and mortality rates of the numerically dominant barnacle (*N. intertextus* at Waikiki and *C. proteus* at Kualoa) are summarized in Table 4.10.

At Waikiki, recruitment of *N. intertextus* was higher than that of *C. proteus* by an order of magnitude and occurred only in the cleared plots (Table 4.8).

Table 4.8 Number of recruits of *N. intertextus* per set of six plots at Waikiki.

	Treatment	
Month	Cleared of <i>N. intertextus</i>	Control
April	19	0
May	30	0
June	16	0
Total	65	0

At Kualoa, recruitment of *C. proteus* for at least one month was higher than that of *N. intertextus* by an order of magnitude and higher to cleared plots (Table 4.9).

Table 4.9. Number of recruits of *C. proteus* per set of 10 plots at Kualoa.

	Treatment	
Month	Cleared of <i>C. proteus</i>	Control
April	72	0
July	N/A	N/A
November	0	7
Total	72	7

Comparison to Kaneohe Bay

Percent cover, mean monthly growth, recruitment and mortality for each species at each site are summarized in Table 4.10. Percent cover of *C. proteus* was highest at the Kaneohe Bay site, as was total barnacle cover. Growth rates are highest at Kaneohe Bay than at any other site, with the rate for *B. reticulatus* higher than that of any other barnacle species. The high growth of *C. proteus* at the Kaneohe Bay site might be a result of a high percentage of barnacles whose initial length was less than 5 mm in rostrocarinal length; these individuals would be expected to grow more quickly than larger specimens. When these small individuals are eliminated from calculations, growth rate is intermediate between the first year and second years at Waikiki. Recruitment of *C. proteus* in Kaneohe Bay is three orders of magnitude higher than that of any barnacle at the other two sites; recruitment of *B. reticulatus* is an order of magnitude lower than *C. proteus* at the same site, and two orders of magnitude higher than that of any barnacle at

any other site. Mortality was higher for *B. reticulatus* than for the chthamaloids, but also very high for *C. proteus* at Kualoa in the second year.

Table 4.10. Summary of cover, growth, recruitment and mortality for three sites.

Site	Study period	Species	Cover (percent)	Mean growth (mm ² /month)	Recruitment (individuals/100 cm ² /month)	Mortality (percent of total)
Waikiki	1	Cp	2	2.69	0.13	51
Waikiki	1	Ni	42	2.46	0.76	14.9
Waikiki	2	Cp	3	1.49	N/A	49
Waikiki	2	Ni	42	1.53	N/A	55
Kualoa	1	Cp	38	0.83	0.70	41.7
Kualoa	1	Ni	4	1.72	0.12	25
Kualoa	2	Cp	38	0.96	N/A	80
Kualoa	2	Ni	4	N/A	N/A	49
Kaneohe Bay	1	Cp	65	4.88/1.66*	~100**	34.4
Kaneohe Bay	1	Br	25	7.29	~10**	93

*Mean for 20 individuals >5 mm in length at start of study period.

**Estimates. See Methods for further explanation.

Study periods as defined in methods. Cover at beginning of experiment. Mortality of barnacles tracked for entire study period.

Recruitment study

Recruitment varied in time and space, but recruitment of all barnacles was consistently higher at the Kaneohe Bay site than Kualoa or Ala Moana (Fig. 4.2). At each site, *C. proteus* recruited in consistently higher numbers than did *N. intertextus* or *B. reticulatus*.

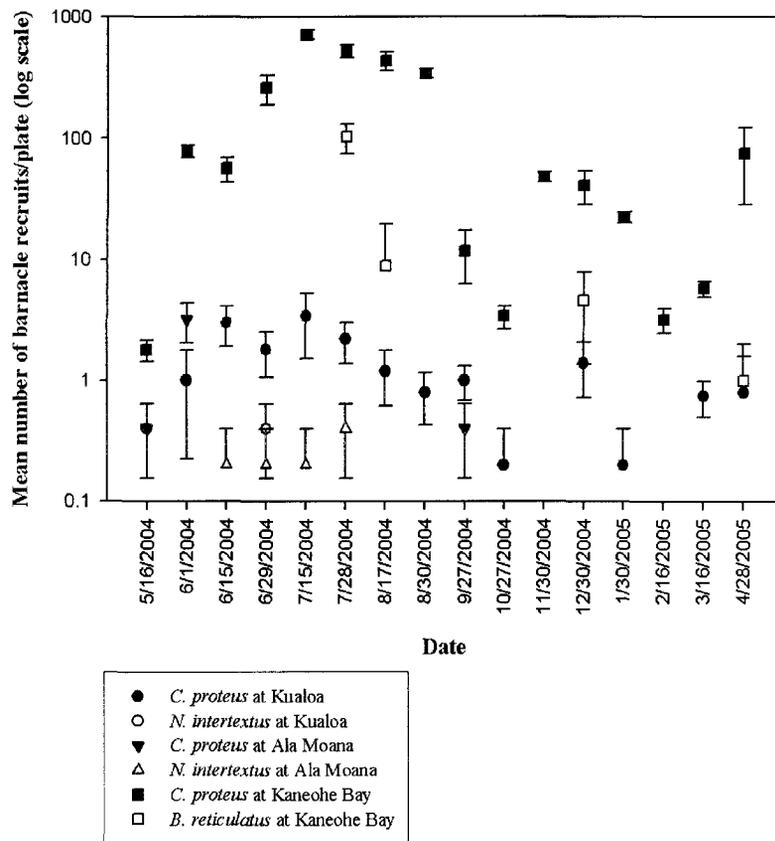


Figure 4.2. Mean number of recruits on plates cued with conspecifics, for each location and time period.

Barnacles did not settle exclusively on plates cued with conspecifics. Both *B. reticulatus* and *C. proteus* settled in higher numbers on plates cued with *B. reticulatus* (Fig. 4.3).

Recruits of *B. reticulatus* increased between 2- and 10-fold on plates with a conspecific cue; recruits of *C. proteus* was about 1/3 more plentiful on plates with *B. reticulatus* cue.

Recruitment of *C. proteus* was about equal on plates cued with *N. intertextus* and with conspecifics. Overall, recruitment of *N. intertextus* was low, with no clear preference for different cues (Figs 4.4, 4.5).

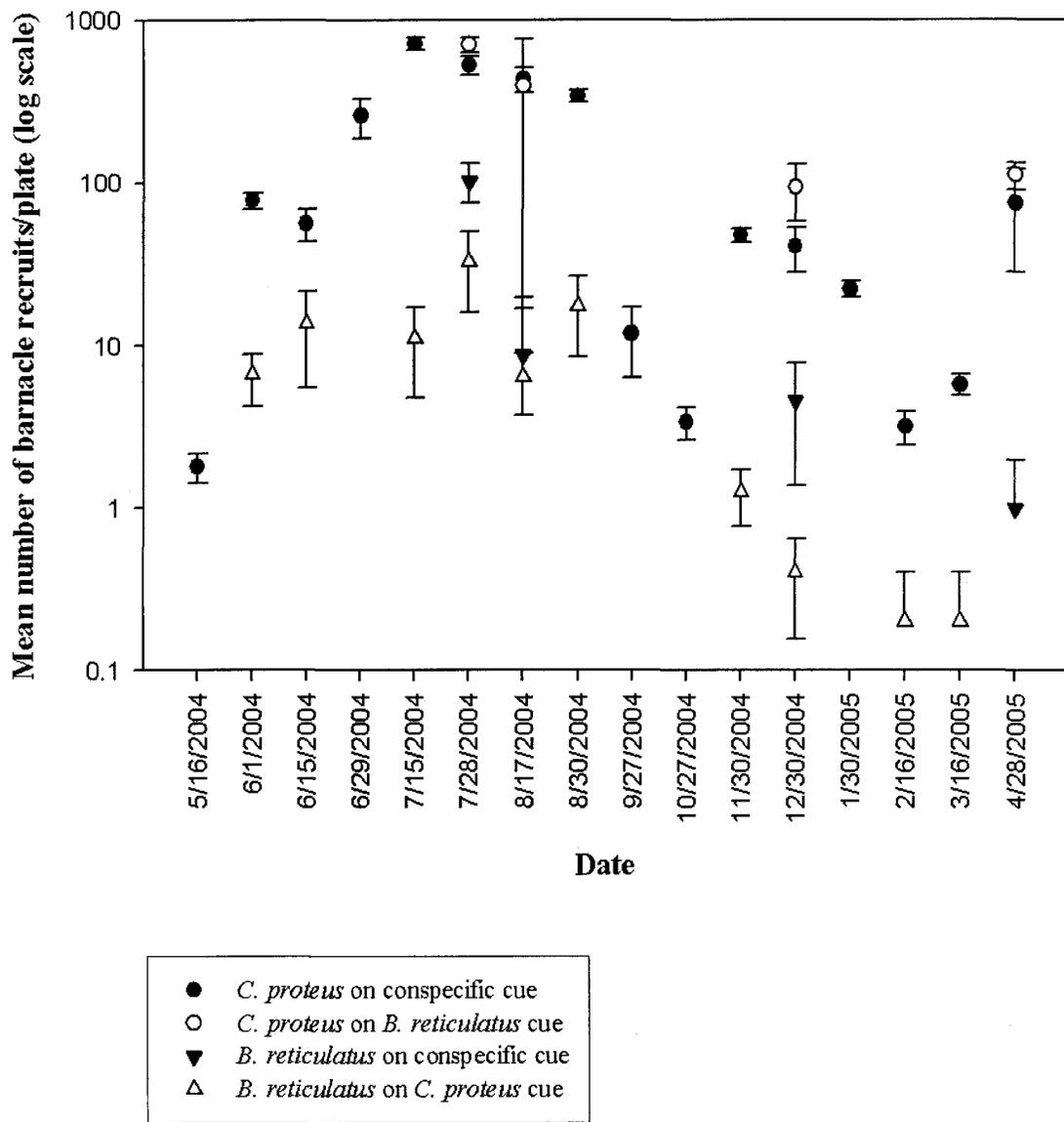


Figure 4.3. Mean number of recruits of *C. proteus* and *B. reticulatus* at the Kaneohe Bay site. *Balanus reticulatus* was only used as a cue four times.

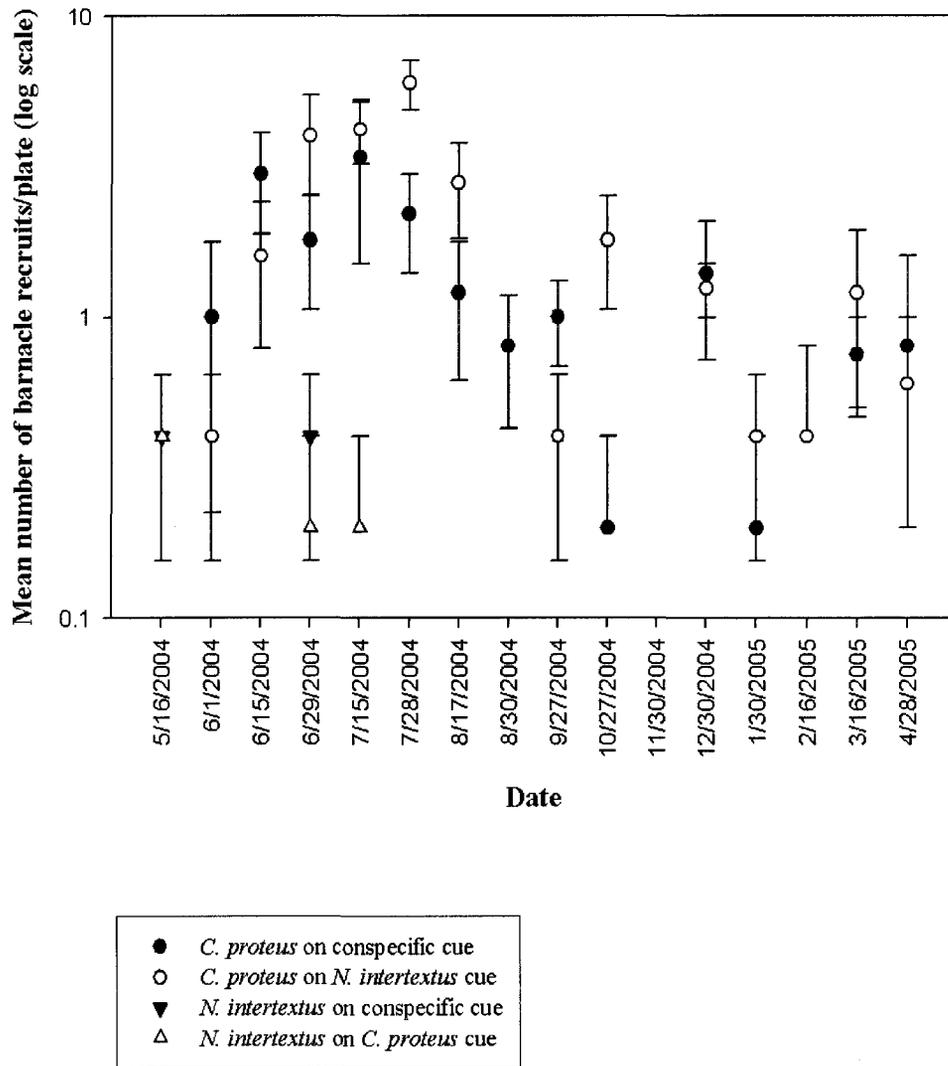


Figure 4.4. Recruitment of *C. proteus* and *N. intertextus* at Kualoa. Note the change in scale from Figure 4.3.

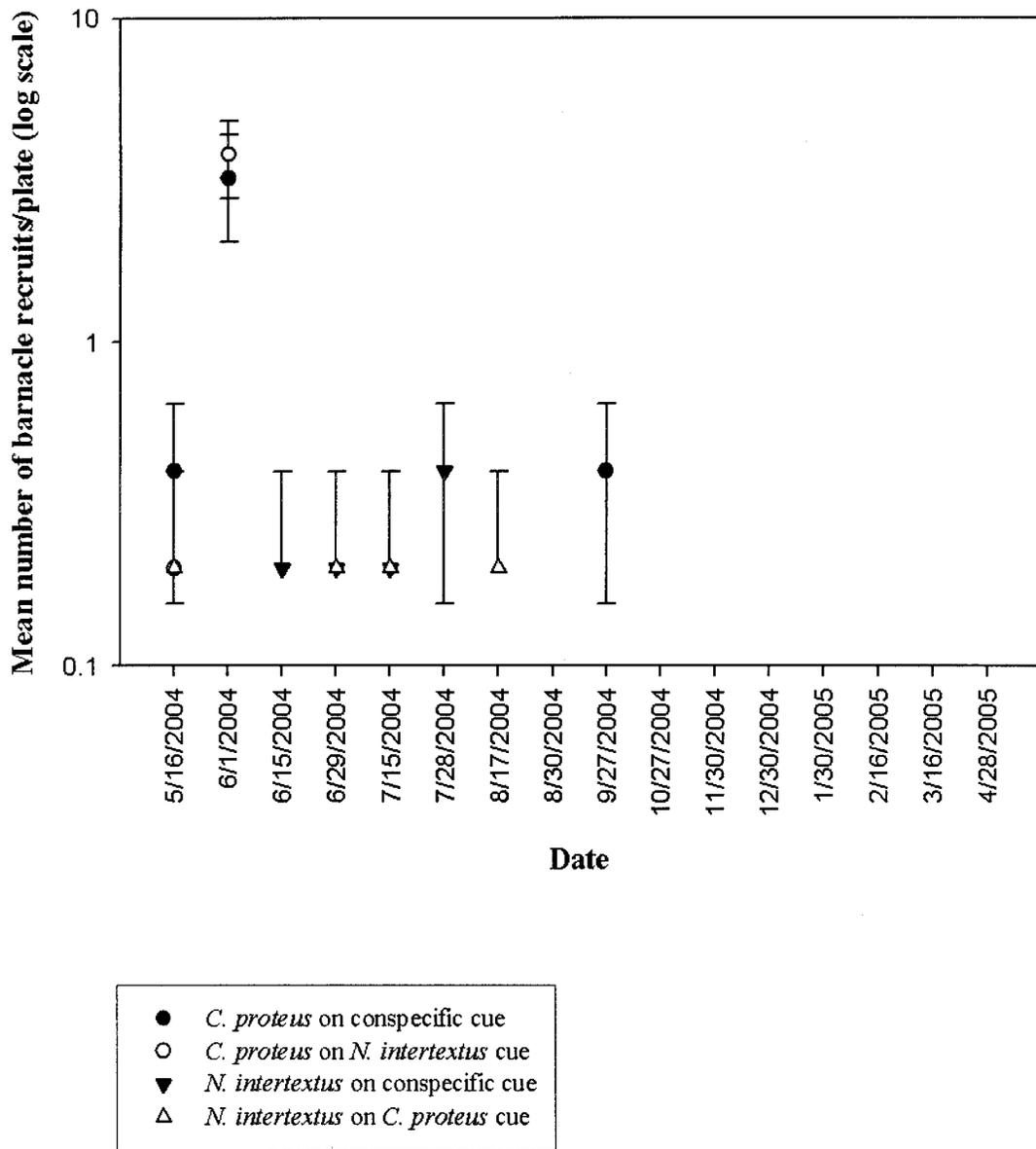


Figure 4. 5. Recruitment of *C. proteus* and *N. intertextus* at Ala Moana. Note that the scale is different from Figure 4.3, same as 4.4. There were no recruits for the last 7 time periods.

Discussion

Importance of competition varies between sites

There was no indication, by any measure – growth, mortality or recruitment – that competition was occurring between *Chthamalus proteus* and *Nesochthamalus intertextus* at either Waikiki or Kualoa. In Waikiki in the first year, there was a trend toward higher growth of *C. proteus* in the neighbor-removal plots, but this was statistically insignificant. There was an effect of plot that year, suggesting that differences in microhabitats affected growth. These differences were apparently not important in the second year, as the plot effect was not significant. Perhaps a difference in climatic factors, such as the shift between El Niño and La Niña conditions that occurred during the duration of this experiment, could nullify the effects of microhabitat, but this is purely speculative.

Although there was no evidence of interspecific competition, intraspecific competition may have been occurring. At Waikiki, where *N. intertextus* was predominant, recruitment of *N. intertextus* occurred only in cleared plots. A similar trend was seen at Kualoa where *C. proteus* was predominant. There, *C. proteus* recruited in higher numbers to cleared plots, but this only happened in one of two months recorded. It is possible that barnacles are facing intraspecific competition for appropriate settlement space. Raimondi (1990) found no further settlement of *Chthamalus anisopoma* to intertidal rocks in the Gulf of California after barnacles had reached 13 percent cover, despite continued settlement to adjacent cleared patches. He surmised that appropriate microhabitats (mainly cracks and crevices) were limited even though total space was not.

It is not clear why, in the second year at Waikiki, disproportionately more barnacles involved in intraspecific interactions died, or why barnacles without a nearby neighbor at Kualoa in the first year died in greater proportion. Because of the way they were categorized (a barnacle involved in both intraspecific and interspecific interactions would be categorized as being involved in interspecific interactions; those categorized as being involved in intraspecific interactions were those interacting only with conspecifics), barnacles in intraspecific interactions tended to have fewer neighbors than those in interspecific interactions. It is possible that having more neighbors can be advantageous (there might be less of a risk of desiccation, for example). However, this was not a consistent finding throughout the study.

In contrast, the experiment in southern Kaneohe Bay found that competition was occurring between *C. proteus* and *B. reticulatus*. Plates kept clear of *C. proteus* developed high cover of *B. reticulatus* relative to controls where *C. proteus* was allowed to settle (Chapter 3). This was the result of fewer settlers of *B. reticulatus* on plates with *C. proteus*, not a difference in post-settlement survival. *B. reticulatus* is a larger and faster growing barnacle that easily overgrows *C. proteus*. This experiment revealed that the presence of *C. proteus* inhibits settlement by *B. reticulatus*.

Possible factors influencing competition

There are several possible explanations for the difference between the outcome of the experiment at the Kaneohe Bay site and that of the Waikiki and Kualoa experiments.

First, there could be some innate, species-specific difference between *B. reticulatus* and *N. intertextus*. For example, *N. intertextus* displays determinate growth (Newman 1961,

Crisp and Bourget 1985) and might be less of a space competitor for that reason. Secondly, it is also possible that *B. reticulatus* may be more dependent than either chthamaloid on cues from conspecifics for substrate selection, and thus is less likely to settle where another species is in high abundance. In the Kaneohe Bay experiment, *C. proteus* settled just as readily on plates dominated with *B. reticulatus* as it did on plates with conspecifics; more settlers of *B. reticulatus* settled on plates dominated by conspecifics than on plates dominated by *C. proteus* (Chapter 3). The data from the Recruitment Study do suggest a stronger attraction for conspecific cue by *B. reticulatus* than for the other species. However, it is hard to know how well a cue painted on a plate mimics cues from settled adult barnacles. Even though the same volume of barnacles was applied to each plate, the paste from *B. reticulatus* remained visible on the plates for longer than that of either *C. proteus* or *N. intertextus*. Chemical components of the adult paste other than species-specific cues might be the cause of the greater settlement on *B. reticulatus* cued plates.

Other possible explanations for the outcomes of the above experiments include differences in predation, growth, total barnacle cover, and recruitment rates between the three sites, any of which should be expected to influence competitive interactions.

While differences in predation rates were not tested in this study, there are some obvious differences between the sites in the abundance of the most common predator of intertidal barnacles, the whelk *Morula granulata*. The whelk is most abundant at Kualoa and least abundant at the Kaneohe Bay site (personal observation). *Morula granulata* hides in crevices during daytime low tides, and the structure of seawall at Kualoa provides more crevices than does the seawall at Waikiki. The pier pilings at the Kaneohe

Bay site would appear to offer little refuge for *M. granulata*. Feeding experiments in which *M. granulata* was offered a choice of *C. proteus* or *N. intertextus* indicated that this predator does not appear to have a preference (Pang, Fread and Zabin, unpublished data), and thus while it might influence overall barnacle cover, it is not likely to influence the abundance *C. proteus* relative to *N. intertextus*. Where *B. reticulatus* might fit in terms of preferences is unknown, but the whelk has been characterized as a generalist predator, whose main diet appears to be vermetid snails (Kay 1979). That fact, along with the results of the feeding trials, suggests that the whelk is unlikely to display a strong preference for a particular barnacle species. The mortality rate of *C. proteus* was lowest at the Kaneohe Bay site (34 percent), but mortality of *B. reticulatus* was quite high (93 percent), so it is not clear whether predation is low there relative to the other sites and thus an influence on barnacle cover and competition.

Growth of *B. reticulatus* was significantly higher than for any other barnacle studied. If high growth was sufficient for competition to occur, one would expect it to happen at the Kaneohe Bay site, but *B. reticulatus* would be the expected dominant. Cover of both barnacle species was highest at the Kaneohe Bay site and recruitment significantly so, and either or both (as they are likely related) may explain why competition occurred there and not at the other two sites.

Recruitment data for 2004-2005 show variability in space and time, but relative abundances of larvae between sites match relative cover of adult barnacles, in terms of total cover and proportions of species. Data from the Recruitment Study are consistent with results from the Recruitment Inhibition studies; the recruits of the most abundant barnacle were an order of magnitude higher than those of the less abundant barnacle at

each site. Unless other post-settlement factors that act on barnacles younger than two weeks of age are different between sites, recruitment appears to be the driver behind percent cover of adults and which barnacle will be most abundant. Where recruitment is high, competition will occur, where it is low, competition is negligible.

That competition would occur at a site with high recruitment and high cover and not occur (or be less important) at sites with lower recruitment and lower cover is intuitive and consistent with results from research elsewhere (*e.g.*, Connell 1985, Gaines and Roughgarden 1985, Sutherland 1990, Menge 1991, but see Raimondi, 1990) and with models of community regulation that take recruitment into account (*e.g.*, Menge and Sutherland 1987).

Importance of recruitment in Hawaii

Two other studies of Hawaiian invertebrates with pelagic larvae have concluded that recruitment is a major influence in the structure of adult populations. After carefully examining available food, adult and juvenile densities, and fecundity of the intertidal snail *Littoraria pintado* on Oahu's east-facing shores, Whipple (1966) showed that these snails were not limited by food, space or adult reproductive effort. Juveniles were rare, and Whipple argued that her study population must be limited by recruitment. A study of shallow subtidal invertebrates in Malama Bay on Oahu's south shore that used larval traps, recruitment tiles, and surveys of adult densities found strong correlations between larval supply, recruitment and adult distributions (Parnell 2000).

Employing a variety of physical and biological measures, Parnell linked the differences in larval supply to heterogeneity of water masses in the bay; some areas appeared to be

consistently bathed by larval-poor waters of pelagic origin and others by coastal waters moving out of bays and harbors and remaining close to shore. Coastal water masses had both higher amounts of larvae and a different larval assemblage from pelagic water masses. Water moving through Parnell's Ala Wai site was typically offshore and larval poor; this is consistent with the recruitment data shown here. The Waikiki site lies between Parnell's Ala Wai and Diamond Head sites. Diamond Head had intermediate amounts of larvae when all taxa were considered, but was consistently low in barnacle recruits.

Parnell found few larvae of the barnacle *Balanus amphitrite* (a calm-water barnacle typical of harbors and bays) in waters of pelagic origin and high numbers in coastal water masses. Similarly, I expect waters of pelagic origin to contain more larvae of *N. intertextus* than of *C. proteus*, as the native barnacle is more abundant and widespread throughout coastal areas in the Hawaiian Islands and the Indo-Pacific. Larvae of *C. proteus* should be more abundant in water masses moving out of harbors and bays where the invader is abundant and the native rare or absent.

Circulation in Kaneohe Bay is sluggish, particularly in the southern portion, where water may take up to 10 days to flush out (Smith et al. 1981). In the laboratory, *C. proteus* larvae have become competent to settle just 9 days after release (Chapter 2). Thus, it is likely that many barnacle larvae are retained in the bay, resulting in high recruitment rates relative to open-coast areas where larval supply is diluted. A similar situation has been noted for Narragansett Bay, Rhode Island, where larval recruitment in the bay is highest in years when flushing rates are low and low in years when flushing rates are high (Gaines and Bertness 1992). If larvae are retained at a high rate in Kaneohe

Bay, larval supply not only determines whether competition will be a structuring factor in adult populations, but the results of competition between adults affects larval supply, creating a feedback loop that may have played a role in the success of *C. proteus* in invading the bay. While no studies have been done of circulation patterns *vis a vis* larval supply at Kualoa, it is likely that its location at the edge of Kaneohe Bay allows for at least periodically heavy input of *C. proteus* larvae from the bay.

Larval retention and invasive species

Because of their potentially long larval lifespan and weak swimming abilities relative to typical current speeds, barnacle larvae are generally thought to be carried away from adult populations. Indeed, larvae of coastal barnacles have been found as far as 85 nautical miles from shore (Roughgarden et al. 1988). Thus, barnacle populations are typically characterized as open and larval supply is generally treated as uncoupled from local larval production. Some studies have shown that small scale eddies and currents can retain invertebrate larvae close to where they are released or that larval behavior insures a return to adult habitat (Ayre and Dufty 1994, Chiswell and Roemmich 1998, Christy and Morgan 1998, Parnell 2000). Until we develop better methods for tracking the paths traveled by larvae, we cannot determine whether or to what degree recruitment is an independent factor. It is likely, however, that in water bodies with relatively low flushing rates, such as Kaneohe Bay and perhaps many harbors and bays, larvae recruit back to adult populations. Characterizing these populations as closed might be more appropriate, at least for ecological studies.

This study suggests that the post-settlement factors that limit an invader and/or an invader's potential impacts on native species may vary with larval supply. Researchers and those concerned with management of invasive species may want to focus their attention on areas that are likely to retain larvae and those that receive large larval input from established populations of invaders.

The forces that determine the abundance and distribution of native species in the intertidal zone are likely to also determine the abundance and distribution of invaders: physical factors, competition, predation, disturbance, facilitation, parasitism and propagule supply. Models like the Menge-Sutherland Environmental Stress Model (Menge and Sutherland 1987), which predicts the relative contributions of abiotic factors, competition and predation over a continuum of physical stress and recruitment levels, might be successfully used as a guide in determining what factors will be important to the success or failure of an invading organism at a given location.

CHAPTER 5.

Taking advantage of aloha: a native limpet may facilitate and then suffer from recruitment of an invasive barnacle in Hawaii's intertidal zone

Introduction

Barnacles and limpets interact strongly in many intertidal ecosystems, often with effects that ripple throughout the community. Interactions may have negative impacts on limpets: dense patches of barnacles attract predators that also prey on limpets (Creese 1982); barnacles have been found to limit the ability of some limpets to graze effectively (Fischer-Piette 1948, Dayton 1971, Lewis and Bowman 1975, Branch 1976, Choat 1977, Creese 1982, Hawkins and Hartnoll 1982, Underwood et al. 1983, Hartnoll and Hawkins 1985, Sutherland and Ortega 1986, Hodgson 1999, Dunmore and Schiel 2003); and barnacles may limit the ability of limpets to maintain firm attachment to substrate (Hawkins and Hartnoll 1982). Barnacles may suffer "bulldozing," crushing or ingestion by limpets as they graze over the substrate (Lewis 1954, Connell 1961b, Stimson 1970, Dayton 1971, Branch 1975b, Denley and Underwood 1979, Paine 1981, Miller and Carefoot 1989, Iwasaki 1993a,b, Safriel et al. 1994). On the other hand, positive interactions have also been recorded: by removing algae from substrate, limpets can facilitate barnacle settlement and survival (Iwasaki 1993b) and because barnacles create a rugose surface, they can increase the survival of small limpets by providing them with protection from desiccation, heat stress, and the grazing activities of larger limpets and

other predators (Lewis and Bowman 1975, Branch 1976, Choat 1977, Creese 1982, Hawkins and Hartnoll 1982).

Until the invasion of *Chthamalus proteus*, a barnacle native to the Caribbean and the Western Atlantic, the Hawaiian archipelago was generally without high cover of intertidal barnacles. The native barnacles *Nesochthamalus intertextus*, *Euraphia hemblei* and *Tessoropora pacifica* tend to be rare and restricted to cracks and crevices in high to moderately wave-exposed areas. With a few exceptions, cover rarely reaches more than 40 percent (personal observation) and is thus low relative to intertidal systems elsewhere. *Chthamalus proteus* arrived in Hawaii some time between 1973 and 1993 and has since spread around the island of Oahu, becoming highly abundant, particularly in low-energy environments. In Kaneohe Bay, on the island's windward side, cover of *C. proteus* can extend from the high to low intertidal zone and reach nearly 100 percent (personal observations). Throughout the islands, the barnacle co-exists with the native pulmonate limpet *Siphonaria normalis*. The propensity of *C. proteus* to settle in high numbers and in quiet waters presents a novel situation for *S. normalis*, which would have rarely encountered native barnacles in these habitats or in such abundance.

No studies of interactions between intertidal barnacles and limpets have been done in Hawaii, or between *C. proteus* and limpets in the barnacle's native range. If strong interactions are occurring between *C. proteus* and *S. normalis*, we might see the results of these interactions reflected in patterns of abundance and distribution of the two species. In fact, a striking small-scale distribution pattern can be seen on a seawall on Coconut Island (Moku O Loe) in Kaneohe Bay, where both species are highly abundant. The seawall is a conglomerate of different rock and cement types supported in places by iron

rebar. *Siphonaria normalis* is present in much higher abundance on light-colored cement and old limestone rocks, while *C. proteus* is more abundant on the dark-colored rocks and rebar. These different materials are present at the same tidal height and shoreline aspect (personal observations). Substrate selectivity by settlers and differential survival across micro-habitats have been demonstrated to be a factor in the abundance and distribution of barnacles (Edmondson and Ingram 1939, Crisp and Barnes 1954, Crisp 1974, Foster 1974, Southward and Newman 1977, Crisp 1985, Chabot and Bourget 1988, Raimondi 1988a, Miller and Carefoot 1989, Minchinton and Scheibling 1993 and many others), while limpets are able to migrate to more suitable micro-habitats after settlement (Hatton 1938, Haven 1966, Bastida et al. 1971, Haven 1971, Vermeij 1971a, Underwood 1979, Creese 1981, Creese and Underwood 1982, Garrity 1984, Levings and Garrity 1984, Branch 1985, Branch et al. 1990, Hodgson 1999, Kay 2002). Substrate effects, pre- or post-settlement, rather than interspecific interactions could be an alternate explanation for the pattern observed on the seawall, as the material types vary in chemical make-up, rugosity and heat conductance and perhaps in the composition of microalgae and biofilms colonizing them. Finally, the distribution pattern could be the result of the combined effects of substrate and barnacle-limpet interactions.

In this study, I used field surveys and experiments in an attempt to disentangle the effects of substrate on recruitment of each organism on the other.

Materials and Methods

Study organisms

Chthamalus proteus is a small (typically 6 mm rostrocarinal length), tan, intertidal barnacle native to the Gulf of Mexico, the Caribbean Sea and the tropical and warm-temperate Atlantic Ocean. It was not found in a survey of Oahu's intertidal barnacles in the early 1970s (Matsuda 1973), and was first collected but misidentified as a native barnacle in Pearl Harbor in 1993 (Brock, personal communication). By the time its identity was discovered, it had already become widespread. It is also present on all the main Hawaiian Islands and has been reported from Guam, Midway, the Marianas and the Society Islands (Southward et al. 1998; Chap 1). The barnacle most likely arrived in the Hawaiian Islands via fouled vessel hulls and is continuing to spread in this manner. It has been noted on the hulls of the interisland barges traveling between the Hawaiian Islands, on ships traveling between California and Hawaii (Godwin, personal communication) and on the hulls of small craft in the Caribbean (personal observation).

Other than observations on the types of locations where *C. proteus* has been found in its native range, little is known about its ecological role or life history there (but see Chapter 2). In Hawaii, it co-exists in some locations with a suite of other native and non-native organisms, including other barnacles, whelks, littorines, nerites, vermetids, bivalves, crabs, algae and limpets. In other locations in Hawaii, it may be the only sessile macro-organism in the high intertidal to mid-intertidal zone, but it is nearly always found with *S. normalis*. Laboratory and field studies in Hawaii have determined that the barnacle has a

continuous breeding season with peaks in late spring and late fall and a larval life of less than a week from release to the cyprid stage (Chapter 2).

Siphonaria normalis is limited to the mid- to upper rocky intertidal zone in Hawaii. It is found in both calm and wave-exposed sites on a wide variety of substrates and has a widespread distribution throughout the Indo-Pacific. It can reach a maximum length of 17 mm, but is typically less than 10 mm, particularly in sheltered locations (personal observation). Shells are dark gray with white ribs. *Siphonaria normalis* lays yellowish gelatinous egg masses on rocks throughout the year in Hawaii. Crawl-away juveniles have been observed to hatch from these masses in seawater tables in the laboratory (M. G. Hadfield, personal communication). The diet of *S. normalis* is not known, although as a group, siphonariids are thought to eat macroalgae such as *Enteromorpha* and *Ulva*, diatoms and algae sporlings (Branch 1981, Creese and Underwood 1982, Hodgson 1999). *Siphonaria normalis* grazes while the substrate is awash during rising or falling tides (Cook 1969, Cook and Cook 1978). Cook (1969) observed limpets to move distances of one to 14 times their body length during a tide change. In between foraging bouts, *S. normalis* return to home scars – depressions in the substrata to which each individual's shell is abraded for an exact fit.

Study site

Coconut Island is located in the southern portion of Kaneohe Bay (Fig. 5.1). The island has been built up over time with dredged materials and many of its shores have been hardened with seawalls. Protected by a barrier reef, Kaneohe Bay is a low-energy environment; intertidal assemblages in the bay are typical of protected areas in Hawaii. In

the high and mid-intertidal zones, *S. normalis* is the only abundant limpet and *C. proteus* is the only abundant barnacle. Abundant high and mid-intertidal grazers include *Nerita picea*, *Nodilittorina hawaiiensis*, *Littoraria intermedia*; other sessile intertidal organisms include vermetids, oysters, and mussels and the non-native barnacle *Balanus reticulatus*, but these are relatively rare at Coconut Island. Foliose macro-algae are abundant only in the lower intertidal, while crusts of cyanobacterial mats, *Ralfsia* sp., and *Enteromorpha* spp. are visible in the high- to mid-intertidal zone.

Experiments were conducted on a seawall and a series of cement blocks on the south side and northwestern sides of the island, respectively. The seawall abuts a sandy reef flat and is ~1.5 m tall. The series of blocks runs perpendicular to the shore over a shallow reef flat and the tops of the blocks are at about the 0 tide level.

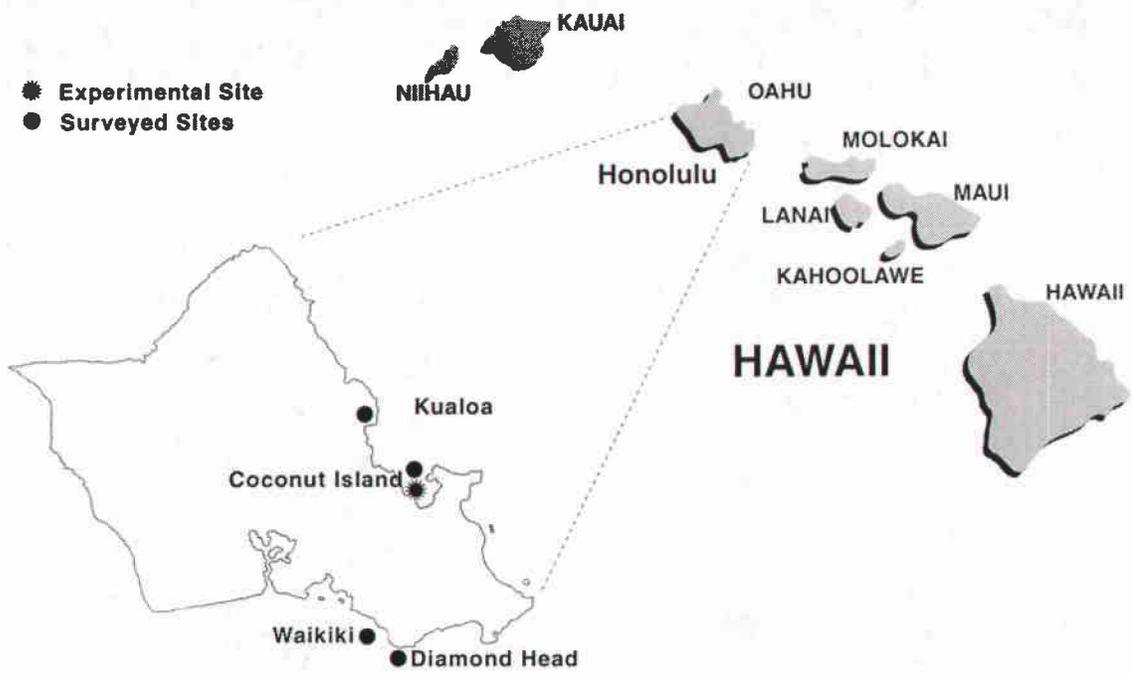


Figure 5.1. Map of Oahu, showing study and survey sites.

Seawall survey

To quantify the distribution patterns on the seawall, I counted barnacles and limpets in 52 randomly placed 7.5 x 5 cm quadrats at approximately 18 cm above 0 tide and noted the color (dark vs. light) of the substrate as well as its rugosity (rough vs. smooth). Substratum was recorded as light if its color value was equal to or lighter than fresh cement; anything darker was considered “dark.” The substratum was recorded rugose if it contained pits or projecting gravel >10 mm in the dimension perpendicular to the wall, otherwise it was considered “smooth.” The effects on the abundance of barnacles of number of limpets and substrate color and texture, as well as interactions between all factors were tested using an analysis of covariance. The effects of barnacles and substrate on limpet abundance were similarly examined. To meet assumptions of normality, numbers of barnacles and limpets were log-transformed after adding 1 to eliminate zeros.

Recruitment preferences

To test for recruitment preferences of *S. normalis*, I made four types of cement tiles: dark/rough, dark/smooth, light/rough, light/smooth. The tiles were made using Quikrete cement mix poured into 6.5 cm by 5 cm rectangular plastic molds to a height of 2 cm. Dark colored tiles were created by adding Quikrete black cement dye and basalt sand to the cement mixture; coral sand was added to the cement to make light-colored tiles. Gravel larger was removed from the cement mixture by sifting it through a screen (5 mm mesh) so that tiles would be of relatively uniform rugosity. To create rough tiles, I used a wooden tongue depressor to make a single line approximately 10 mm wide down the

center of each tile from top to bottom and another from side to side, before the cement had fully hardened. This increased surface complexity by creating a groove of ~10 mm depth with edges that projected above the plane of the tile by about 5-10 mm. The tiles were attached randomly in three rows of eight tiles on three cinderblocks using Velcro strips. The cinderblocks were placed side by side in front of and touching the seawall, with the tiles in a horizontal orientation at ~18 cm above the 0 tide level. These were left in place from May to September, 2002. At the end of the study period, I counted limpets on each tile during a low tide when they were not moving and thus presumably on their home scars. While the intention was to allow limpets to recruit in the absence of barnacles, a small number of barnacles did settle during the course of this experiment. The effect of tile type on limpet abundance was analyzed using an analysis of covariance, with number of barnacles used as a covariate to separate out effects of barnacles on limpets. All data were transformed as above. Tukey's simultaneous pairwise comparisons were used to determine whether there were differences in recruitment between tile types.

Although the above experiment was intended to investigate recruitment preferences of *S. normalis*, the recruitment of *C. proteus* to the tiles offered an opportunity to examine barnacle settlement preferences in the presence of *S. normalis*. Analysis was as above, but with the barnacles as a response variable and limpets as a covariate.

Effects of *S. normalis* on recruitment of *C. proteus*

Cages. To test for the effects of limpets on barnacle recruitment across substrate types, I constructed four types of cement tiles as described above. The only difference in tile construction for this experiment was that tiles were 11 cm by 10 cm, and rugose tiles had

two lines running lengthwise and two side to side. Fences 5 cm high of plastic mesh (3 mm mesh size) were attached using marine epoxy (Splash Zone Z-Spar) around the edges of each tile. One tile of each type was placed on a cinderblock, for a total of eight cinderblocks and 32 tiles. The order of tile placement was random on each block. The cinderblocks were placed in front of the seawall. Four were designated as treatment blocks and four as controls. To match mean limpet density on the seawall, 32 limpets were added to each plate on the treatment blocks. In addition to the fences, plastic turf was attached with marine epoxy around the edges of the tiles to prevent limpets from entering or exiting the plates. In an attempt to prevent sediment from accumulating inside the fenced tiles, the cinderblocks were placed on their sides after 2 weeks so that the tiles had a vertical orientation. Limpets were periodically counted and dead or missing individuals were replaced in an attempt to keep 32 individuals on the treatment tiles. This experiment ran from May to August 2003. Despite the precautions of fencing and plastic turf, some individuals of *S. normalis* migrated onto the control blocks. In addition, one set of blocks was tipped over in a storm and some animals were lost from it. As a result, in some cases there were more limpets on the exclusion tiles than on the inclusion tiles. To address this, I used the number of limpets on the tiles at the end of the experiment as a covariate in an ANCOVA rather than using treatment type as a categorical factor. Because limpets that had migrated onto exclusion tiles were not present as long as those on inclusion tiles, this was a conservative method of determining the effects of limpets on barnacle settlement. I considered tile type a fixed factor and cinderblock a random factor in the analysis. Data were transformed as above to meet assumptions of normality.

Barriers. A second experiment examining the effects of *S. normalis* on *C. proteus* recruitment was set up due to concerns about the possible effects of shading and sediment collection resulting from the fencing in the previous experiment. Four segments of the seawall, all 50 cm in width, and running from the bottom to the top of the *S. normalis* zone were designated as experimental areas. Each segment was divided in half, one side of which was randomly designated as a control and one as a treatment area. A strip of plastic turf 4 cm wide was attached with marine epoxy to the seawall, delimiting the edges of each experimental plot. In each plot, one pair of dark rough and light rough cement tiles was attached to the seawall with marine epoxy. To the degree possible without damaging the substrate, limpets were removed from the treatment areas; dozens of tiny (<2 mm) limpets remained in small holes in the treatment areas as they could not be removed without altering the substrate. Limpets were removed by hand from the treatment plots every 2 weeks from August 2003 until June 2004. Few barnacles recruited to the tiles during this time period. Rather than counting barnacles on the tiles, I counted barnacles on the seawall in 4 by 4 cm randomly placed quadrats along a transect line in the middle of the barnacle zone. This portion of the seawall was made of a single material, thus substrate type could not be tested. Five quadrats were counted inside each area. Despite barriers and the hand-picking, limpets were still present on the removal plots and in some cases in similar abundance to control plots. Thus, as for the previous experiment, I analyzed the data with an ANCOVA, using limpets counted in the small quadrats at the last time period as a covariate and block as a random factor. Counts of barnacles and limpets were square-root transformed to meet assumptions of normality.

Effects of *C. proteus* on *S. normalis*

To examine the effects of the presence of barnacles on limpet abundance and recruitment, I set up a removal experiment on 7 cement blocks in the intertidal zone on Coconut Island. Barnacles were highly abundant on these blocks, at nearly 90 percent cover. On each block, I established three 5 X 10 cm plots. Plots were randomly assigned to one of three treatments: removal, one-time cleared, and unmanipulated. The removal and one-time cleared plots were cleared of all individuals of *C. proteus* on May 4, 2004. Barnacle recruits were continually cleared from the removal plots during a low tide every 2 weeks for 12 weeks, but were allowed to recruit back to the one-time cleared plots. No barnacles were removed from the unmanipulated plots. All plots were marked with a small patch of marine epoxy in the upper right and lower left corners; the perimeter of the plot could then be found by aligning a 5 X 10 cm clear acetate sheet with the two epoxy markers. Because limpets were on their home scars during low tide, individuals could be mapped on the acetate sheets and their fates tracked over time. Limpets were counted in each of the plots every two weeks. The number of limpets in each plot at the beginning of the experiment was subtracted from the final number to calculate net gains or losses. These data were analyzed using an ANOVA with treatment type as a fixed factor and cement block as a random factor.

Results

Seawall survey

Barnacles were found in highest abundances on dark rock (Fig. 5.2A) and were negatively correlated with limpets across all substrate types. Rugosity was not a statistically significant factor. Limpets were found in highest abundance on light-colored rock (Fig. 5.2B); the effect of color was statistically significant when taken alone, but neither color nor rugosity was an important factor when number of barnacles was included in the model. Results are summarized in Tables 5.1A and 5.1B.

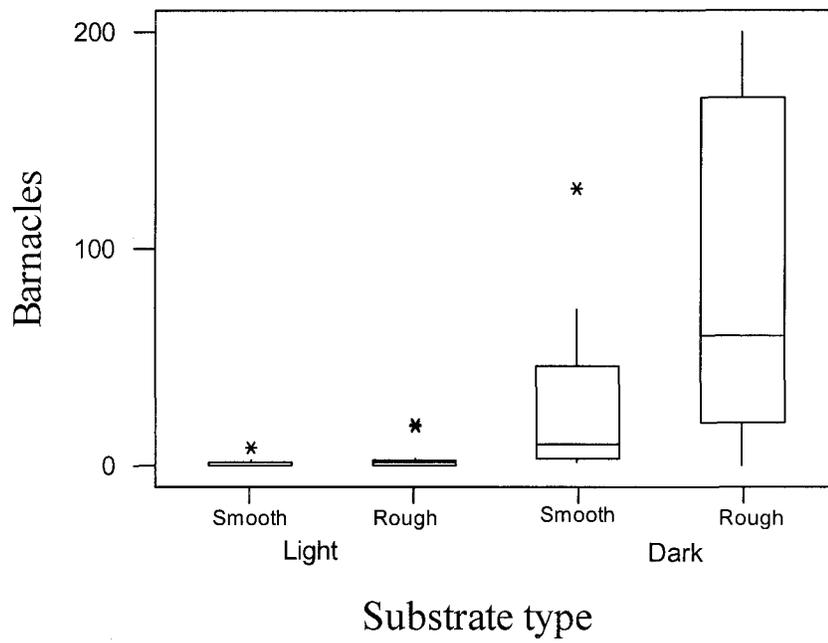


Figure 5.2A. Box and whiskers plots for number of barnacles in quadrats on seawall by substrate type. The horizontal line indicates the median, the edges of the box the first and third quartiles and the bars low and high values. The asterisks indicate outliers.

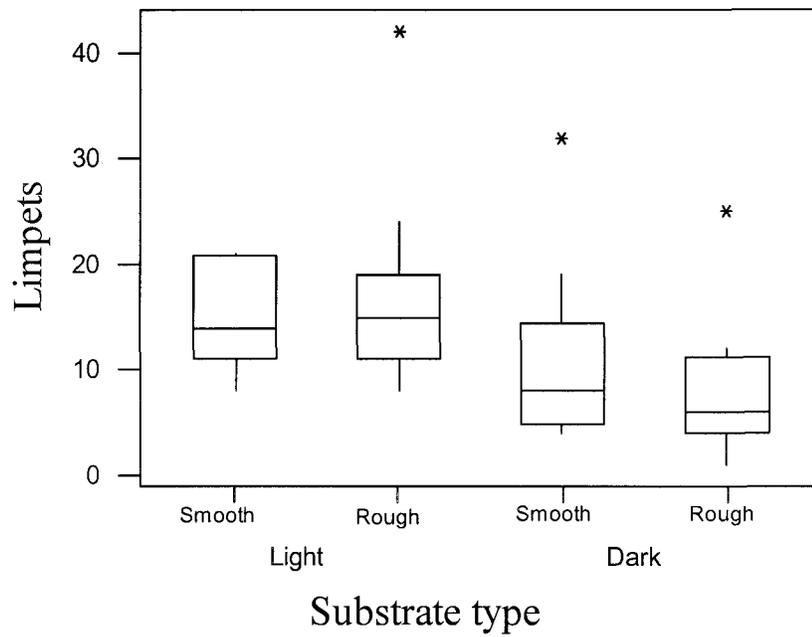


Figure 5.2B. Number of limpets in quadrats on seawall by substrate type. The horizontal line indicates the median, the edges of the box the first and third quartiles and the bars extreme low and high values. The asterisks indicate outliers.

Table 5.1A. ANOVA table for barnacle abundance vs. color, rugosity, and number of limpets on seawall.

Source	DF	Adj SS	F	P
Color	1	1.4809	5.69	0.021
Rugosity	1	0.0184	0.10	0.758
Limpets	1	0.0514	5.46	0.024
Color*rugosity	1	0.1641	0.85	0.361
Color*limpets	1	0.3003	1.56	0.218
Rugosity* limpets	1	0.0893	0.46	0.499
Color*rugosity*limpets		0.1187	0.62	0.437
Error	46	8.6686		
Total	52			

Table 5.1B. ANOVA table for limpet abundance vs. color, rugosity, and number of barnacles on seawall.

Source	DF	Adj SS	F	P
Color	1	0.03040	0.62	0.435
Rugosity	1	0.00005	0.00	0.976
Barnacles	1	0.32530	6.64	0.013
Color*rugosity	1	0.00235	0.05	0.828
Color*barnacles	1	0.4713	2.08	0.156
Rugosity*barnacles	1	0.10187	0.46	0.501
Color*rugosity* barnacles	1	0.02830	0.58	0.41
Error	46	0.02259		
Total	52			

Recruitment preferences

Tile type was a statistically significant factor in limpet recruitment preferences. Although limpets recruited in the highest numbers to the light/rough substrate (Fig. 5.3A), pairwise comparisons showed that this was not significantly different from light/smooth substrate. Barnacles did not affect recruitment. Results are summarized in Table 5.2A.

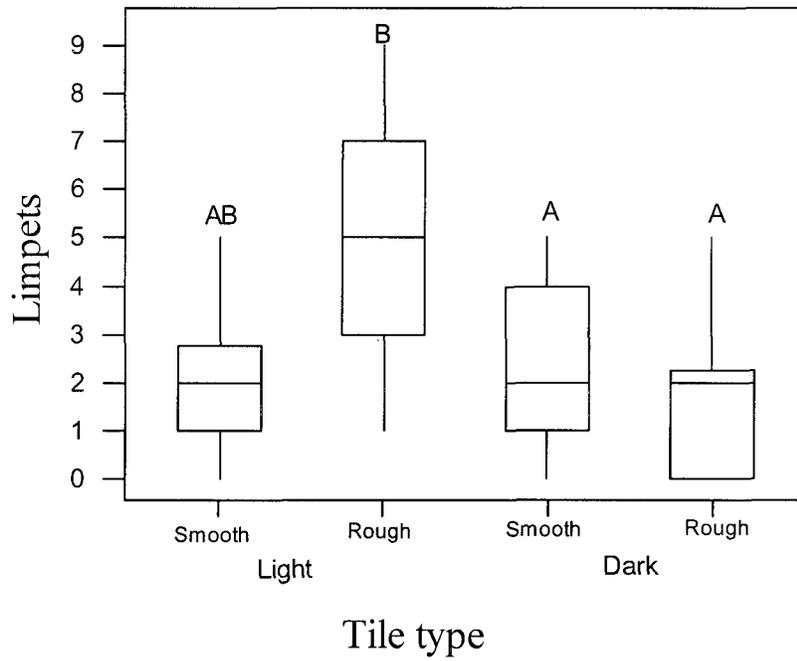


Figure 5.3A. Number of limpets recruiting to different tile types. Letters indicate groups that are significantly different from each other.

Table 5.2A. ANOVA table for limpet recruitment vs. tile type.

Source	DF	Adj SS	Adj MS	F	P
Tile type	3	1.66220	0.55407	8.98	<0.0005
Error	67	4.13236	0.06168		
Total	70	5.79456			

Tile type was a statistically significant factor in barnacle recruitment. Barnacles settled in highest numbers on dark/rough tiles (Fig. 5.3B), but there was no statistical difference between this tile type and the light/rugose tiles. Limpets did not affect recruitment.

Results are summarized in Table 5.2B.

Table 5.2B. ANOVA table for barnacle recruitment vs. tile type and number of limpets.

Source	DF	Adj SS	Adj MS	F	P
Tile type	3	1.7891	0.5964	3.38	0.024
Limpets	1	0.0040	0.0040	0.02	0.881
Tile type*limpets	3	0.9963	0.3321	1.88	0.142
Error	63	11.1150	0.1764		
Total	70				

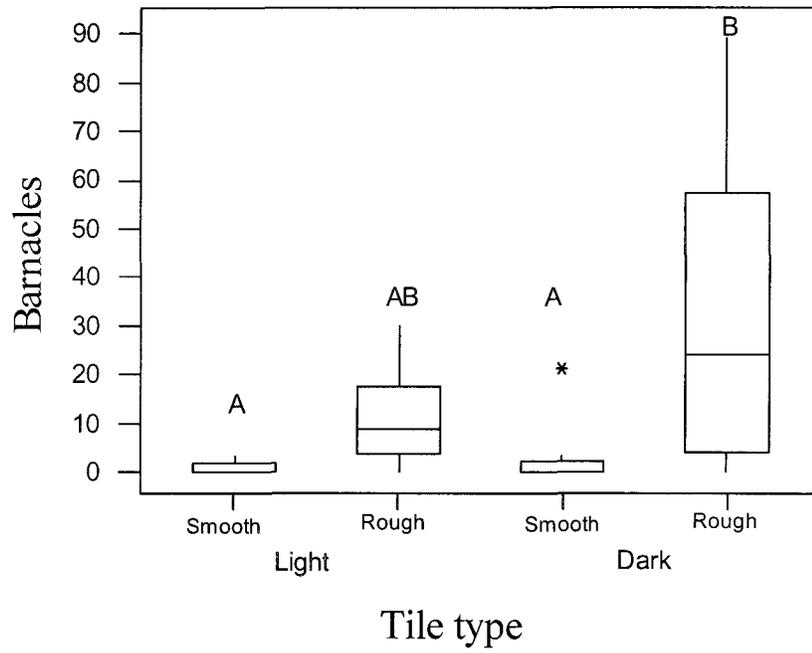


Figure 5.3B. Number of barnacles recruiting to different tile types. Letters indicate groups that are significantly different from each other.

Effects of *S. normalis* on recruitment of *C. proteus*

Cages. Limpets were a significant positive factor in barnacle recruitment to the plates. Barnacles settled in highest numbers on black rough tiles in limpet inclusion treatments and on light rough tiles in limpet exclusion treatments for three of four blocks; on block 3 (the overturned block) recruitment was highest on the dark smooth substrate in the inclusion treatment and about equal on the dark rough and light rough tiles in the exclusion treatment. As a result, tile type was not significant at the $\alpha = .05$ level. No other factors had statistically significant effects (Table 5.3).

Table 5.3. ANOVA table for barnacle recruitment vs. tile type and number of limpets, exclusion cages.

Source	DF	Adj SS	Adj MS	F	P
Limpets	1	1.3423	1.3423	6.11	0.035
Block	3	0.3394	0.1131	0.54	0.667
Type	3	1.8902	0.6301	2.97	0.086
Type*Limpets	3	1.2395	0.4132	1.88	0.203
Block*Limpets	3	0.3912	0.1304	0.59	0.635
Block*Type	9	0.9226	0.1025	0.47	0.864
Error	9	1.9780	0.2198		
Total	31				

A plot of number of barnacles against number of limpets shows a trend of a stronger positive association between limpets and barnacles on the smooth substrate (Fig. 5.4).

Barriers. Barnacle recruitment was positively affected by the presence of limpets. No other factors were significant (Table 5.4).

Table 5.4. ANOVA table for barnacle recruitment on seawall vs. number of limpets, barriers.

Source	DF	Adj SS	Adj MS	F	P
Plot	3	4.721	1.574	0.79	0.510
Limpet	1	17.566	17.566	8.79	0.006
Plot*limpet	3	6.877	2.292	1.15	0.345
Error	32	63.935	1.998		
Total	39				

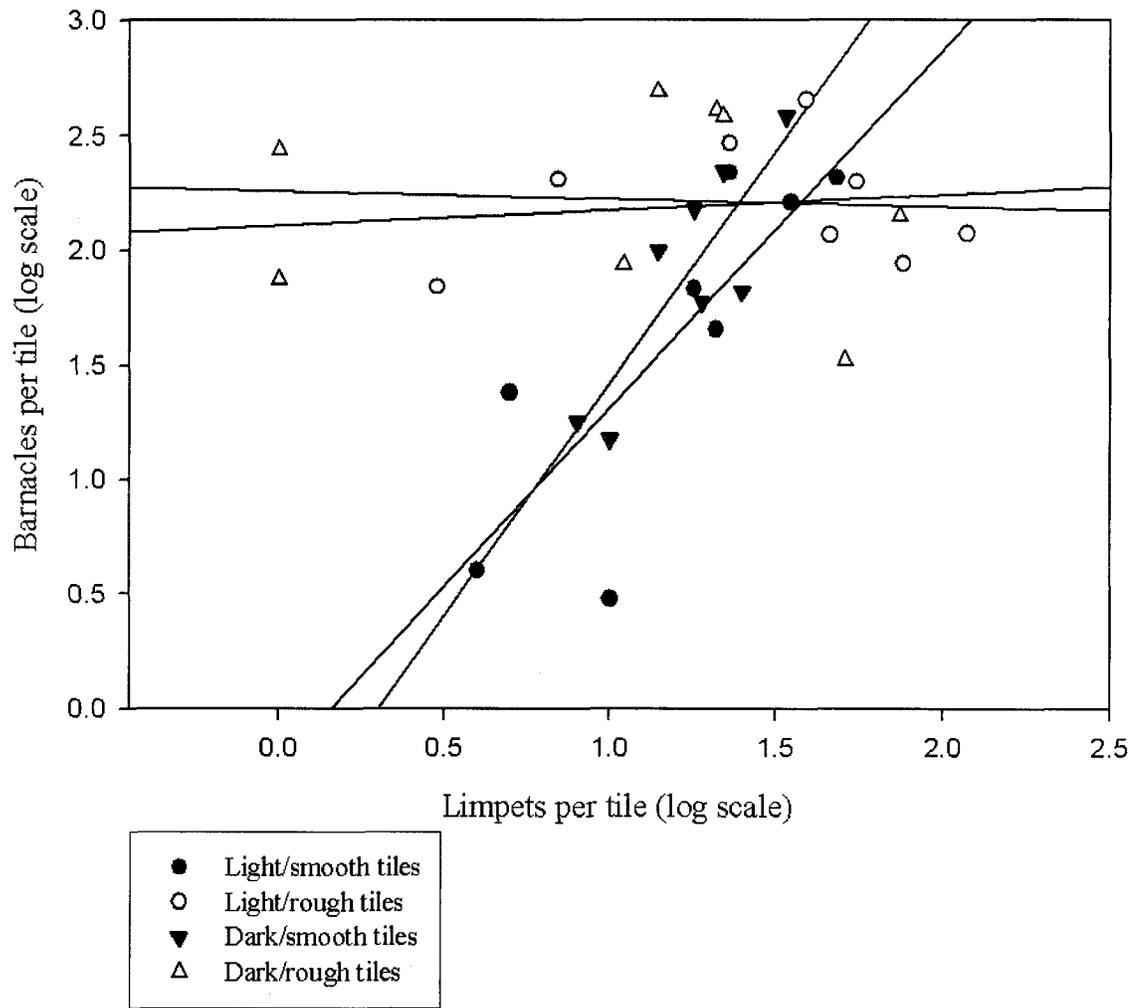


Figure 5.4. A plot of limpets vs. barnacles across each of the four tile types in the cage experiment.

Effects of *C. proteus* on recruitment of *S. normalis*.

All of the blocks gained limpets over the period of the experiment, but greater gains were seen on the treatments cleared once and those that were kept cleared of barnacles (Fig. 5.5). Differences between the unmanipulated plots and two types of experimental plots (control and cleared) were statistically significant within four weeks. By 6 weeks there were more limpets on the maintained treatment than the one-time cleared treatment; this difference became statistically significant in 10 weeks (Table 5.5).

Table 5.5. ANOVA table for limpet recruitment/abundance on barnacle-removal plots.

Source	DF	Adj SS	Adj MS	F	P
Block	6	174.67	29.11	2.42	0.091
Treatment	2	667.81	333.90	27.79	<0.0005
Error	12	144.19	12.02		
Total	20	986.67			

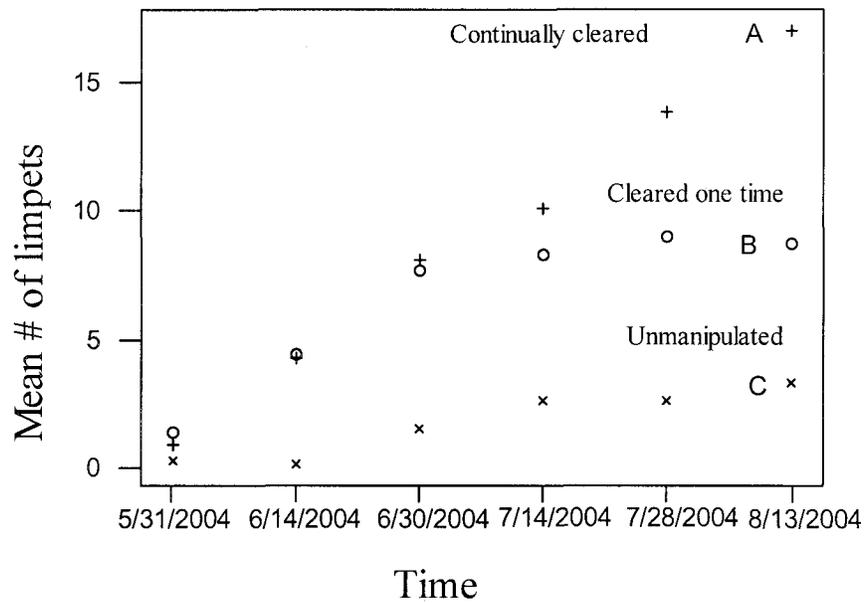


Figure 5.5. Mean number of limpets on the three barnacle-removal treatment types across 6 2-week periods. The letters indicate that the three treatments were significantly different from each other during the last two time periods.

Discussion

Abundance of *C. proteus*

The different outcomes of the above experiments indicate that a number of factors likely contribute to patterns in the small-scale distribution of *Chthamalus proteus*. For example, *Siphonaria normalis* positively affected the abundance of *C. proteus* in the caged and barrier experiments. This was most likely the result of grazing activities of *S. normalis*: the caged plates with lower numbers of limpets were visibly different from the plates with higher numbers. There were more filamentous (mostly *Enteromorpha* sp.) and encrusting algae (mostly *Ralfsia* sp. and unidentified coralline crusts) on the plates with few limpets, and the algae trapped sediment, making the underlying tile inaccessible or unattractive to barnacle settlers. Inclusion plates were mostly free from algae and sediment. Cover of encrusting algae was greatest on the smooth plates; on the rough plates, low-lying areas had higher algal cover than higher ridges. This may explain the trend toward greater positive effects of *S. normalis* on *C. proteus* on the smooth plates. The amount of algal growth may have been in part an artifact of the cages. In the barrier experiment, where there was less shade, the effects of limpet grazing were more subtle. In the limpet inclusion areas the seawall had a greenish cast; in the limpet exclusion areas it was brown. The green color was due to the presence of a cyanobacterial mat; the brown color was due to the presence of diatoms. While I did not quantify this difference in flora, other studies have noted higher abundances of diatoms in limpet-exclusion plots (Geller

1991, Kim 1997). It is not known what effects, if any, these differences in substrate flora made to the recruitment of *C. proteus*.

Siphonariid limpets (which are in the subclass Pulmonata) have weaker radulae than those in the subclass Prosobranchia (families Patellidae and Fissurellidae) and tend to crop rather than completely remove the algae on which they graze (Hodgson 1999). As a result, in some intertidal locations, their feeding activities appear to have little impact on algae (Underwood and Jernakoff 1981, Black et al. 1988). Similarly, while prosobranch limpets have been reported to “bulldoze” barnacle settlers or otherwise loosen barnacles from substrate, this behavior has not been reported in siphonariids. Nonetheless, grazing by siphonariids has been shown to be important in structuring algal communities in some locations (Jara and Moreno 1984, Levings and Garrity 1984, Iwasaki 1993a, b), and thus might affect other organisms that interact with algae. The impact of siphonariid grazing on barnacle recruitment and survival has been demonstrated to be negative in at least one case (Levings and Garrity 1984) and positive in several others (Bastida et al. 1971, Iwasaki 1993b, Iwasaki 1993d).

Grazing or other positive effects of limpets in this study were, however, negligible in the recruitment preference experiment, and barnacles were negatively correlated with limpets in the seawall survey. These differing outcomes may be due to differences in the number of limpets: the mean number of limpets in the recruitment preference experiment was low ($9/100 \text{ cm}^2$, with a range of 0-28) and higher in the caged and barrier experiments (means and ranges of $25/100 \text{ cm}^2$, 0-107 and $40/100 \text{ cm}^2$, 0-106, respectively). The difference in outcomes between the exclusion experiments and the

seawall survey cannot be explained by the number of limpets, however, as these numbers were similar (mean 31/100 cm², range 0-112).

Other factors also varied in importance for barnacle recruitment. Rugosity did not appear to be important in barnacle abundance on the survey of the seawall, but barnacles recruited preferentially to rough tiles in the recruitment experiments, and there was a trend toward higher recruitment on rough tiles in the caged experiment. The lack of an effect of rugosity in the seawall survey may have been an artifact of the qualitative nature of the category “rugose.” Because the materials varied along the wall, there was really a continuum of rugosity: separating areas into smooth or rough categories was a qualitative decision. The smooth tiles I created were smoother than any of the seawall components, and the rough tiles may not have been comparable to the “rough” portions of the wall.

Likewise, substrate color was an inconsistent factor in barnacle abundance. It was important in the seawall survey, with barnacles found in higher numbers on dark-colored wall materials. There was a trend toward higher recruitment of barnacles on dark rough tiles in the recruitment experiment and in the limpet inclusion cages, although the trend was toward higher recruitment on the light rough tiles in the limpet exclusion cages. This reversal was likely due to the positive effects on barnacle settlement of limpet grazing; higher numbers of limpets recruited to the light rough tiles in what were meant to be exclusion cages, and these were visually freer of algae and sediment than the other “exclusion” tile types.

Other barnacle species have been observed to settle preferentially on dark substrate (Edmondson and Ingram 1939, Pomerat and Reiner 1942, McDougall 1943, Smith 1948, but see Barnes et al. 1951, Luckens 1970) and the absence of tropical barnacles from

coral rock, which is generally light-colored, has been noted in the literature (Southward and Newman 1977). Coral rock is highly porous and it has been suggested that barnacles, especially those with non-calcified bases would be more subject to desiccation (Southward and Newman 1977). Many other light colored substrates, such as sandstone, weather easily and may not be good settlement sites for this reason.

Abundance of *S. normalis*

The effect of *C. proteus* on the abundance of *S. normalis* appeared to vary with barnacle densities in the different experiments. *Chthamalus proteus* was negatively correlated with *S. normalis* in the seawall survey (mean 54 barnacles/100 cm², range 0-476) and had negative impacts on *S. normalis* in the barnacle-removal experiment (unmanipulated plots, mean 1054/100 cm², range 733-1258). Barnacles did not impact limpets in the recruitment experiment (mean 34, range 0-273).

Barnacles have been shown to have negative impacts on siphonariid abundance at other locations. In Florida, *Siphonaria* species were found to be most abundant both above and below the highest densities of three barnacle species (Voss 1959); this spatial arrangement was thought to be the result of competition for space, although the author did not confirm this experimentally. *Siphonaria gigas* was less abundant following a heavy recruitment of *Chthamalus fissus* in Costa Rica (Sutherland and Ortega 1986).

Other factors varied in importance for *S. normalis* in the present study. Rugosity was not important on the seawall, but there was a trend toward higher recruitment to rough substrate in the recruitment experiment, and higher numbers of limpets were found on the rough tiles in the caged experiments. This was a factor of both retention and recruitment.

I always needed to add more limpets to the smooth tiles to maintain a mean of 32 limpets per tile; I also had to remove limpets from rough tiles in the “exclusion” treatments. As mentioned above, differences in how rugosity was defined may have been to blame for the different outcomes between the seawall survey and the recruitment experiment.

Limpets recruited in highest numbers to both types of light-colored tiles in the recruitment experiment and recruited primarily to the light rough tiles in the “exclusion” cages. In fact, limpets were found in higher numbers on the light-colored portions of the seawall, but barnacles were found in lower numbers on light-colored substrate and were a better explanatory factor than color in analysis of variance.

Observations of substrate preferences have not been made previously for *S. normalis*. Vermeij (1971b) found that body temperatures of *S. normalis* were generally higher than substrate temperatures and were higher on basalt vs. limestone substrate (1971b), but whether these differences are enough to result in differential survival on the two types of substrate is unknown. The light-colored tiles remained 0.5 to 1° C cooler than the dark tiles during a spring afternoon at Coconut Island and cooled more quickly (unpublished data); higher temperatures might be expected in the summer. It is possible that the limpets, particularly juveniles, which might be more susceptible to heat stress and desiccation, survive better on light-colored substrate. In fact, small limpets are particularly numerous on the light substrate of the wall and were proportionately more abundant on light-colored tiles in the experiments.

Generality of the pattern

The best explanation of the changing nature of the interactions between *S. normalis* and *C. proteus* may be that at some threshold level of abundance, the grazing activities of *S. normalis* positively affect recruitment of *C. proteus* by reducing algal cover and associated sediment accumulation; below this level its effects are negligible. However, the barnacles negatively impact the limpets when their abundance is above some threshold level, perhaps by creating suboptimal grazing conditions, and limpets, if they can, move to patches with lower numbers of barnacles. Additionally, on heterogeneous surfaces, substrate preferences may add to small-scale spatial segregation of the two species.

Other studies have found an initially positive association between a limpet and a barnacle shifting to a negative one as densities of barnacles increased. Settlement of the barnacle *Chthamalus anisopoma* was facilitated by the grazing activities of the limpet *Collisella strongiana*, but the limpet subsequently disappeared when high numbers of the barnacle recruited (Dungan 1986). Benedetti-Cecchi (2000) reported positive effects of limpet grazing (*Patella* spp.) on recruitment of *Chthamalus* spp. and subsequent negative effects on *Patella* of *Chthamalus* after the barnacles had settled in high numbers. Hawkins and Hartnoll (1982) found highest numbers of recruits of *Patella vulgata* at intermediate levels of abundance of the barnacle *Semibalanus balanoides* (50 percent cover as opposed to 100 percent or 2 percent) and highest limpet mortality where barnacle cover was 100 percent.

Surveys conducted at three additional intertidal sites on Oahu in the summer of 2002 in which barnacles and limpets were counted in 10 cm by 10 cm quadrats (Andrew Altieri, unpublished data) appear to generally support the idea of positive interactions between barnacles and limpets at intermediate densities and negative interactions at high densities (Fig. 5.6). Barnacles at these sites included *C. proteus* and the native *Nesochthamalus intertextus*; *S. normalis* was the only limpet present. At sites where the means of barnacles and limpets were lowest and the range of densities smallest (Diamond Head and Kualoa) there was no correlation between barnacle and limpet abundance. At Waikiki, which had a higher mean and greater range of densities of both species, a positive correlation was found. At Coconut Island, where a negative correlation was found, there was a much greater range in both barnacle and limpet densities than any of the other three sites, and much higher mean number of limpets.

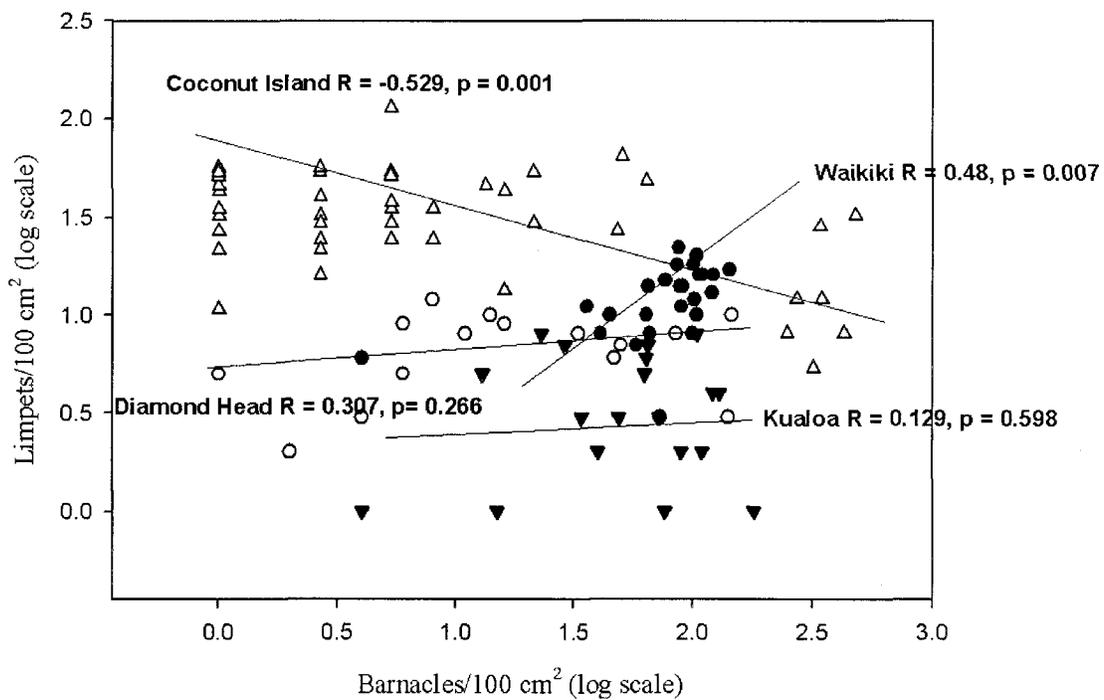


Figure 5.6. Correlations between barnacles and limpets at four sites. Barnacles and limpets were counted in 51 quadrats at Coconut Island; 50 at Waikiki, 15 at Diamond Head and 20 at Kualoa.

While differences in substrate preferences may have contributed to the patches of substrate dominated by *C. proteus* and patches dominated by *S. normalis* seen on the Coconut Island seawall, the substrate was homogeneous at the other three locations surveyed, so comparisons of substrate use across locations could not be made.

Other factors not measured in this set of experiments might be expected to increase or decrease the potential impacts each species might have on each other. For example, in a location where algae recruit in high abundance, *S. normalis* might not be able to effectively reduce algal cover. Factors not related to interactions between these two species, including water flow, substrate type, differences in small-scale hydrodynamics and in micro-climates at a site, weather, larval supply, predators and space competitors are likely to affect the abundance and distribution of barnacles and limpets. While correlations between barnacle and limpet abundance were statistically significant at Waikiki and Coconut Island, the correlation coefficient was approximately 0.50 at these sites, indicating that factors other than interactions between these two species are likely contributors to patterns of barnacle and limpet abundance.

Earlier in the history of this invasion, the impacts of *C. proteus* on native species were predicted to be minimal, as the intertidal zone in Hawaii is generally characterized as being “barren,” precluding competition between invertebrate species via space limitation (Southward et al. 1998, Coles and Eldredge 2002). Other studies of tropical intertidal organisms have suggested that competition plays a lesser role in structuring these communities than it does in more temperate systems (*e.g.*, Sutherland 1987, Menge 1991); the negative impacts of the barnacle on *S. normalis* might not necessarily have been predicted from previous studies.

As dense patches of barnacles are rare in most intertidal locations in Hawaii, the invasion of *C. proteus* represents a novel situation for the native pulmonate limpet. In the barnacle-removal experiment, the absence of barnacles increased the numbers of both new limpet recruits and large limpet adults. The implication of this is *S. normalis* prefers cleared patches, suggesting that barnacle-covered substrate is not optimal. Limpets have been demonstrated to grow more slowly in the presence of barnacles, probably due at least in part of limited grazing space, but this did not measurably increase mortality (Lewis and Bowman 1975, Branch 1976, Choat 1977, Hawkins and Hartnoll 1982, Sutherland and Ortega 1986, Crisp et al. 1990). Size depression also likely leads to lowered fecundity in limpets, particularly at extremely high levels of barnacle cover (Branch 1976). If the pulmonate limpet does produce crawl-away juveniles that do not disperse very far, we might, over time, expect to see fewer individuals of *S. normalis* in locations with high densities of *C. proteus* such as Kaneohe Bay, assuming other factors, such as disturbance and predation, do not eventually lower barnacle cover.

This study, along with other research cited here, indicates that the nature of interactions between barnacles and limpets is complex. Whether interactions will be positive negative for any given pair of barnacle and limpet species may depend on size, life history stage, the nature of grazing activities by the limpets, the intensity of predation, variations in recruitment intensity and in density of adults, and a host of abiotic factors (*e.g.*, Branch 1979, Hawkins and Hartnoll 1982, Underwood et al. 1983, Dungan 1986, Wootton 1993). Thus, the results of experimental work carried out at a single site or time or at single density of barnacles or limpets may not be applicable in another situation. Additionally, patterns of abundance and distribution may also be at least partially the result of

settlement/recruitment preferences or higher survival on different substrate types; these need to be taken into account along with biotic factors in the evaluation of community structure.

CHAPTER 6.

Invasibility of intertidal communities is not linked to native species diversity in a field microcosm experiment

Introduction

In his seminal work on biological invasions, Elton (1958) suggested that ecological communities rich in native species were less vulnerable than species-poor communities to invasion by non-natives. Subsequent support for Elton's idea has come from correlational studies examining native and non-native species (*e.g.*, Moulton and Pimm 1983, Fox and Fox 1986, Moyle 1986), and from mathematical models (MacArthur 1970, 1972, Robinson and Valentine 1979, Post and Pimm 1983, Case 1990, Drake 1990b, Case 1991) and assembled microcosm communities (Robinson and Dickerson 1984, Drake et al. 1993) which have examined the success of new (but not necessarily non-native) species in invading established communities. More recent evidence has been mixed, with some studies supporting the hypothesis that species richness results in lowered vulnerability to invasion (*e.g.*, McGrady-Steed et al. 1997, Tilman 1997, Stachowicz et al. 1999, Naeem et al. 2000), but numerous other studies finding a positive relationship between the richness of established species and degree of invasion (Robinson et al. 1995, Planty-Tabacchi et al. 1996, Wiser et al. 1998, for review and re-examination of some earlier studies, see Levine and D'Antonio 1999, Lonsdale 1999, Stohlgren et al. 1999, Law et al. 2000, Meiners et al. 2004).

In one of the few studies to test Elton's hypothesis in the marine environment, Stachowicz et al. (1999) assembled communities of sessile marine invertebrates settled on tiles into treatments of 0, 1, 2, 3 and 4 species and then seeded these with a non-native tunicate. The ability of the tunicate to invade (defined as increasing in area and becoming reproductive) was clearly negatively correlated with increasing diversity in the assembled communities, which were composed of both native and non-native species. The authors hypothesized that the mechanism was more complete utilization of the limiting resource, which was primary substrate, as species diversity increased. These results are similar to experiments that have demonstrated increased invasion resistance via shading effects with increasing diversity in plots of terrestrial plants (*e.g.*, Tilman 1997, Levine 2000, Naeem et al. 2000).

While these results make intuitive sense, it's not clear how often this mechanism operates in real communities. Where disturbance opens up resources or where invaders may rely on resources such as microhabitats or prey that are enhanced rather than limited by resident species, invasion may be unrelated or positively associated with species diversity. For example, in the marine environment, numerous organisms are able to make use of (or even require) secondary substrate, settling on top of other organisms that have colonized bare space. Additionally, in many marine communities, complete occupation of primary substrate in space and time is likely to be rare due to disturbance, predation, seasonal mortality and recruitment limitation. This is certainly true in the intertidal zone in Hawaii, where cover of algae and animals is low relative to many temperate locations and competition for resources may be less of a factor than it is elsewhere (Chapter 4).

I used communities of native species assembled on settlement tiles to test whether the diversity of native species affects invasion success — defined as the ability of organisms to colonize and grow on the tiles — in the intertidal zone in Hawaii.

Methods

I created communities of two diversity levels using four native bivalve species: the oyster *Dendostrea sandvicensis*, and the mussels *Isognomon californicum*, *I. perna* and *Brachidontes crebristriatus*. These species were chosen because they are abundant in the intertidal zone in Hawaii and can form dense aggregations like the ones I planned to assemble. Four different types of single-species communities were created on 10 by 10 cm terra cotta tiles; four different types of three-species communities were created using the bivalve species in all possible combinations. These diversity levels are realistic for sessile organisms on primary substrate for plots 100 cm² in Hawaii's intertidal zone (personal observations). Four replicates of each community type were created, for a total of 16 single-species tiles and 16 three-species tiles.

Communities were assembled in the following manner: adult bivalves were collected during low tide in July 2001 from two sites where they were abundant by cutting byssal threads for the mussels and by carefully chiseling the oysters from rocks. Z Spar Splash Zone marine epoxy was used to cement bivalves to the tiles in a natural orientation. Mussels were attached by cementing byssal threads to the Z Spar; oysters were attached by a valve. Bivalves on the three-species tiles were placed in three horizontal rows of

equal size; cover was nearly 100 percent on both types of tiles. The tiles were placed in outdoor seawater tables overnight and checked the next day to determine how well the animals survived transplant. Nearly all individuals were filter-feeding in the tables and responded to touch by closing their valves. Stainless steel mesh cages (3 mm gage, 10 openings per 2.5 cm²) were placed over each tile to exclude predators. To reduce sedimentation, the tiles were placed upside down inside of a cinderblock, two tiles to a block. In this setup, conditions are probably most similar to shaded or under-rock microhabitats. Four replicates of the eight community types plus a bare (and caged) plate, were arranged in a randomized block layout at the 0 tide mark along a sandy bottom reef flat at the Hawaii Institute of Marine Biology (Coconut Island, Fig. 6.1). After one month, the tiles were checked, dead animals were replaced, and individuals that had come loose were reattached. Mortality was low and animals opened their valves when placed back in the seawater tables. After August, I did not replace dead animals, as I wanted primary space to open up as it would under natural conditions. The epoxy occasionally held empty mussel shells on the tiles; I removed these with a brush.

Once a month from August to November 2001, and bimonthly from January to July 2002, the tiles were removed from the cinderblocks during a low tide and photographed on land using a Nikonos V camera with a 2:1 macro set up. Percent cover was calculated for each tile at each time point by projecting a grid with 45 uniform points over the photographs and recording what was under each point. For many organisms, identifications could only be made to morphospecies without destructive sampling. In July 2002, the tiles were removed from the field. Each tile was placed into a separate container of seawater to which MgCl had been added. After 24 hours, when most

organisms appeared to be relaxed, the tiles were fixed in 10 percent buffered formalin for 48 hours, rinsed, and then preserved in 70 percent ethanol. Barnacles, bryozoans, tunicates, polychaetes, hydroids and molluscs were identified to the lowest taxonomic level possible. Because the Hawaiian sponge fauna is not well defined (deFelice, personal communication), sponges were recorded as morphospecies.

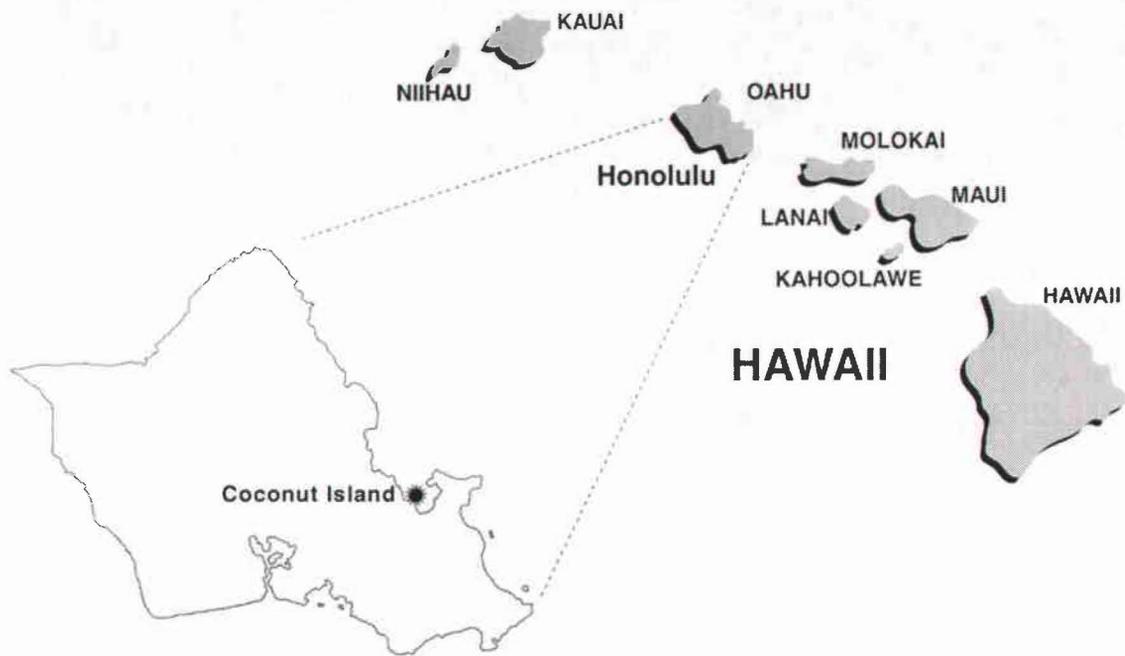


Figure 6.1 Map of Oahu, showing site of experiment.

I relied on the relevant literature (Kay 1979, Coles 1997, Southward et al. 1998, Carlton and Eldredge in prep) to determine the biogeographic status (native, introduced, cryptogenic) for each species or genus. However, many of the organisms that recruited to the tiles could not be confidently designated as native or nonnative because of uncertainty about their identification or because of insufficient information about their historical presence in Hawaii. Because of this, I first tested the broader question of whether there were differences in the communities of all sessile organisms that had invaded the tiles and then asked which organisms were contributing the most to these differences. In addition, I tested whether the invasion success of the known non-native species varied among tiles.

I used DISTLM (McArdle and Anderson, 2001 and Anderson, 2001a) to calculate multivariate multifactorial ANOVAs based on 1) the ecological distances among communities of all sessile organisms and 2) among the assemblage of the eight non-native species. Organisms that were recorded only once were eliminated from the analyses. Diversity level (1 or 3 species), time, and their interaction were analyzed as fixed factors; community type (initial species composition) nested in diversity level, block, all two-way interactions involving these factors and the three-way interaction of diversity level, block and time were random factors. To make these results more comparable to other studies, differences in total cover of invading species at the final time period were also analyzed using the above ANOVA model without the time factor.

For analysis, I used only bimonthly data (eliminating October and December) so that each time point was two months apart. Percent cover data were square-root transformed to improve normality. In an examination of invasibility, the shared absence of a species

between pairs of communities is important information. Thus, Euclidean distance measures, which consider the joint absence of species between two communities to be an indication of similarity, were chosen to generate the distance matrix.

Because their inclusion would have led to an unbalanced design, the tiles that were initially bare were not included in statistical analyses. Instead, total cover of invading organisms, empty space (primary substrate) and hard foulers (calcareous tube worms, bryozoans, barnacles and bivalves) and soft foulers (tunicates and sponges) were visually compared over time using simple scatterplots. Differences between the communities on the single-species, three-species tiles and the initially empty tiles over all time periods and for the final time period were also examined using non-metric multi-dimensional scaling plots using Primer v5 statistical software. Non-metric multi-dimensional scaling (nMDS) plots place community samples into 2 or 3 dimensions based on distance measures, such that those that are most similar cluster together.

Redundancy analysis (RDA; Legendre & Legendre, 1998) was used to constrain the ordinations of the eight community types, and to relate these axes to individual species. Because the DISTLM analysis had shown significant effects of community type (the four types of single-species tiles and the four types of three-species tiles) within a level of diversity, but no effect of diversity, the RDA was conducted using community types (8 levels) as the independent variable. Only data from the last sample date were used, and block effects were ignored. The analysis was conducted using the "vegan" package, version 1.6-4 (<http://cc.oulu.fi/~jarioksa/>), in the R statistical language, version 1.9.1 (<http://www.r-project.org>). RDA results were visualized in a 2-dimensional biplot with the strongest species vectors, calculated as the sum of the absolute values of species

loadings from both RDA axes, plotted in relation to sample scores and centroids for community types. Sample scores in biplots were weighted sums of species scores, using RDA scaling 1 (site scores scaled proportional to axis eigenvalues and species unscaled), which preserves distances among samples.

Results

Even with the precaution of the mesh cages, stomatopods (*Gonodactylaceus* spp.) were able to gain access to the tiles and preferentially ate individuals of *Isognomon californicum*. Despite this, the amount of empty space calculated over all time periods was similar on single-species tiles with *I. californicum* (community type 3, 27.2 percent, SD 22.5) and single-species tiles with *B. crebristriatus* or *D. sandvicensis* (community type 2, 19.6, SD 20.9, and community type 1, 24.4, SD 19.3, respectively). There was no pattern based on presence or absence of *I. californicum* on the three-species tiles.

Thirty-three sessile species or morphospecies were enumerated using the percent cover estimates, nine were singletons and eliminated from the analysis. Of the 24 used for analysis, 21 were identified to species or genus (Table 6.1). Eight are considered non-native, 3 are native, and biogeographic status is unknown for the rest. The most abundant species was the cryptogenic hydroid *Dynamena* sp., which was present on nearly all tiles at a mean of 26 percent cover (across all time points); other species were much less abundant, with the second most abundant species, the non-native tube worm *Hydroides*

elegans, appearing on only about ¼ of the tiles across all time points and on these at a mean of 5 percent cover.

Table 6.1. List of species on experimental tiles used in the analysis.

Porifera	Biogeographic status
<i>Sigmadocia</i> sp.	Uncertain
Sponge 1	Uncertain
Sponge 2	Uncertain
Sponge 3	Uncertain
Sponge 4	Uncertain
Sponge 5	Uncertain
Sponge 6	Uncertain
Cnidaria	Uncertain
<i>Dynamena</i> sp.	Uncertain
Annelida	
<i>Pomatoleios kraussii</i>	Introduced ¹
<i>Hydroides elegans</i>	Introduced ¹
Spirorbids	Uncertain
<i>Chaetopterus</i> sp.	Uncertain
Mollusca	
<i>Dendrostrea sandvicensis</i>	Native ²
<i>Isognomon legumen</i>	Native ²
<i>Ostrea hanleyana</i>	Native ²
Crustacea	
<i>Chthamalus proteus</i>	Introduced ³
<i>Balanus reticulatus</i>	Introduced ¹
Bryozoa	
<i>Watersipora edmondsoni</i>	Introduced ¹
Chordata	
<i>Botryllus</i> sp.	Uncertain
<i>Ascidia</i> sp. "B"	Introduced ⁴
<i>Herdmania momus</i>	Introduced ⁴
<i>Cnemidocarpa areolata</i>	Uncertain (some taxonomic dispute about name)
<i>Ascidia sydeiensis</i>	Introduced ⁴
Rhodophyta	
Coralline algae	Uncertain

References: 1 = Carlton & Eldredge, in prep; 2 = Kay, 1979; 3 = Southward et al., 1998; 4 = Coles et al., 1997.

Total cover of invading organisms, empty space and the abundance of different taxa varied with time and in some cases by diversity level when initially empty tiles were considered. For example, across all time periods the highest cover of invading organisms was on the empty tiles (Fig.6.2). Bare space was initially higher on the empty tiles, but soon became indistinguishable from the other tiles (Fig. 6.3.) Total cover of hard foulers was also highest on the empty tiles (Fig. 6.4), while some of the highest cover of soft foulers (tunicates and sponges) was found on the single-species tiles (Fig. 6.5).

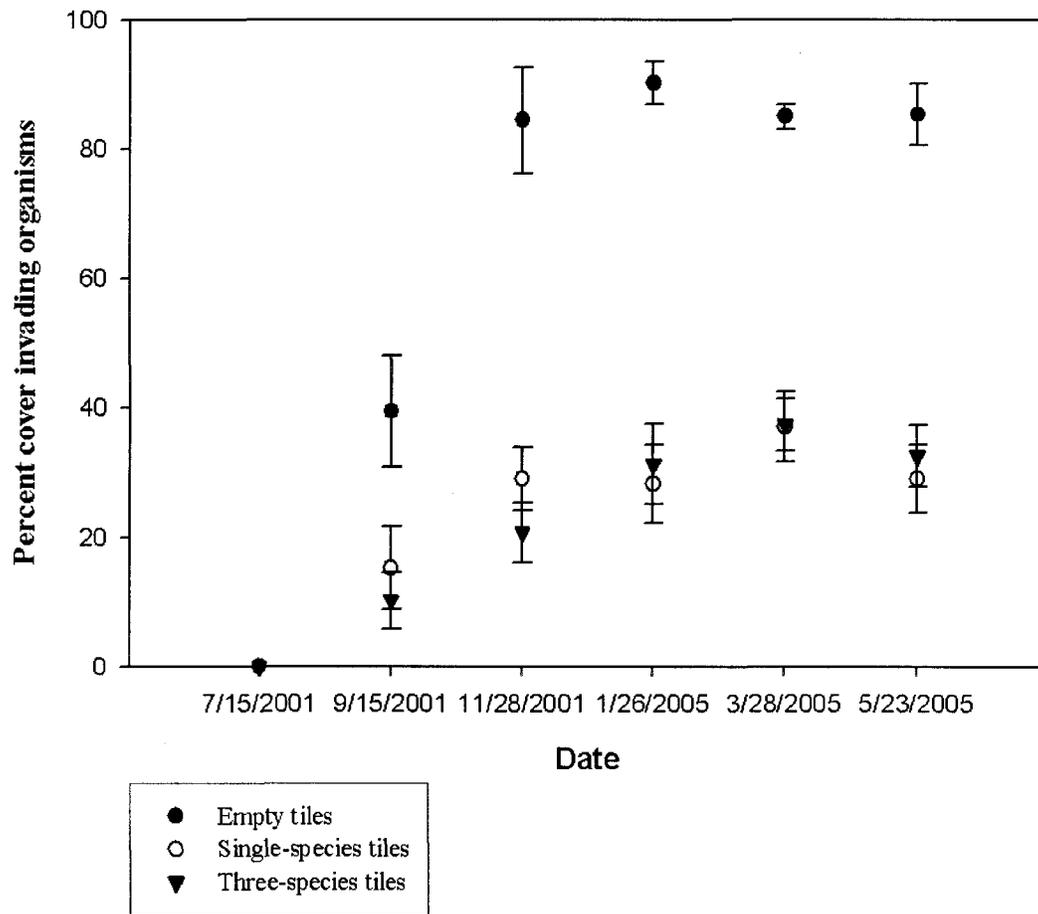


Figure 6.2. Mean cover of all invading organisms over time.

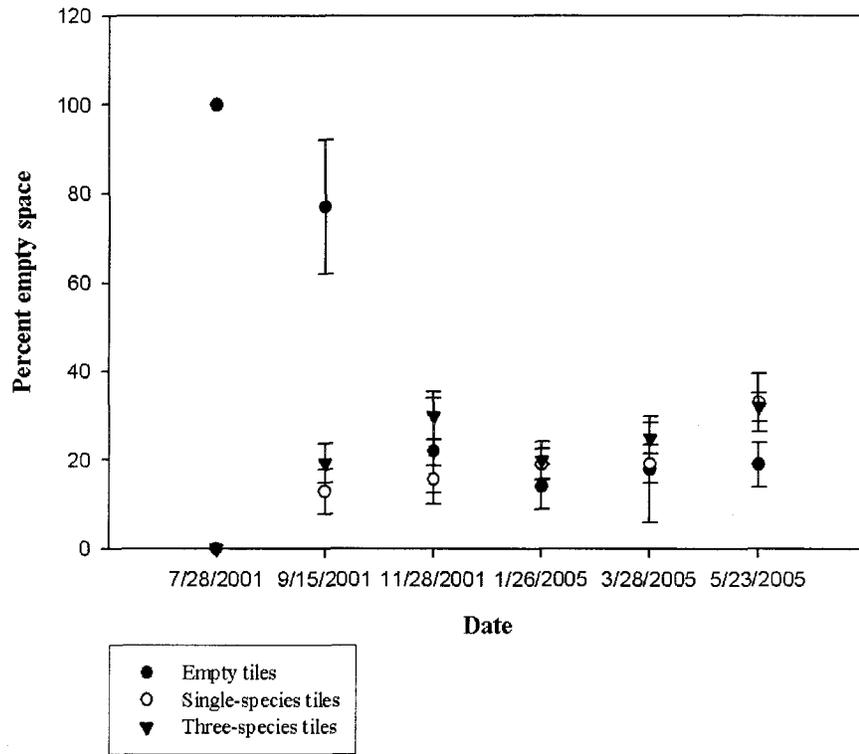


Figure 6.3. Empty space (primary substrate) over time.

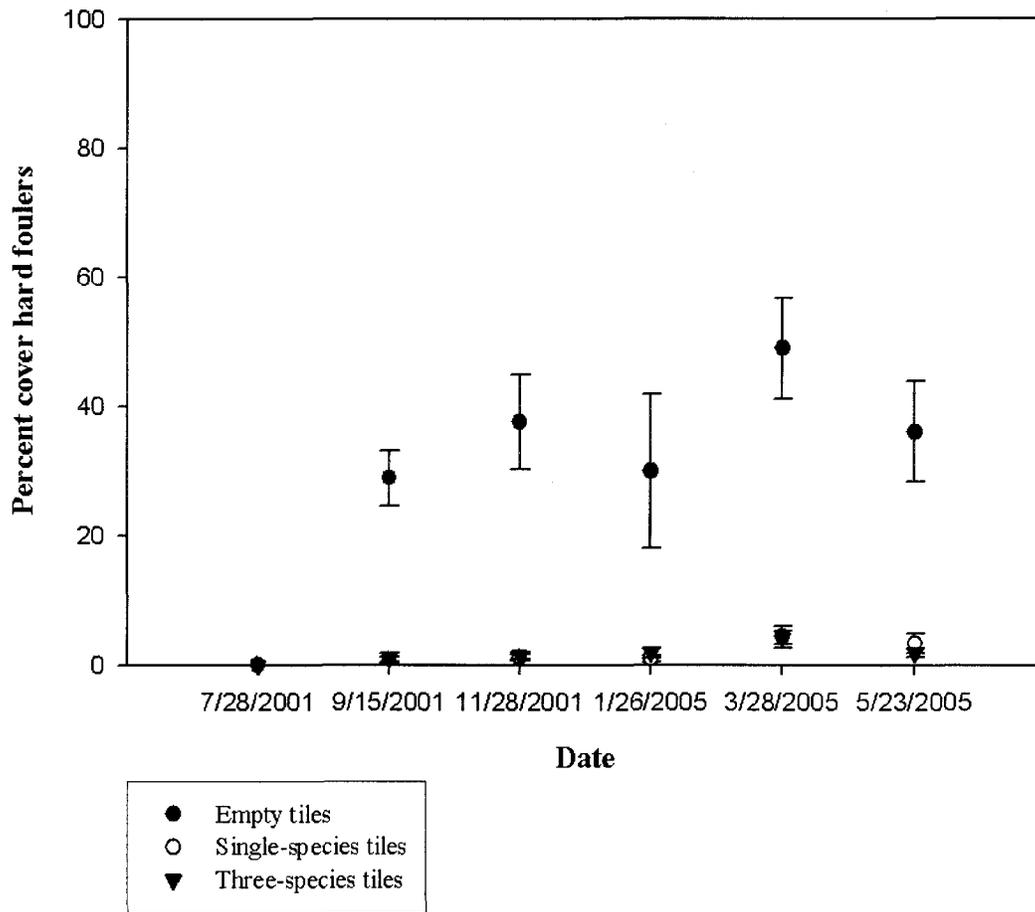


Figure 6.4. Total cover of hard foulers (calcareous tube worms, bryozoans, barnacles, bivalves) over time.

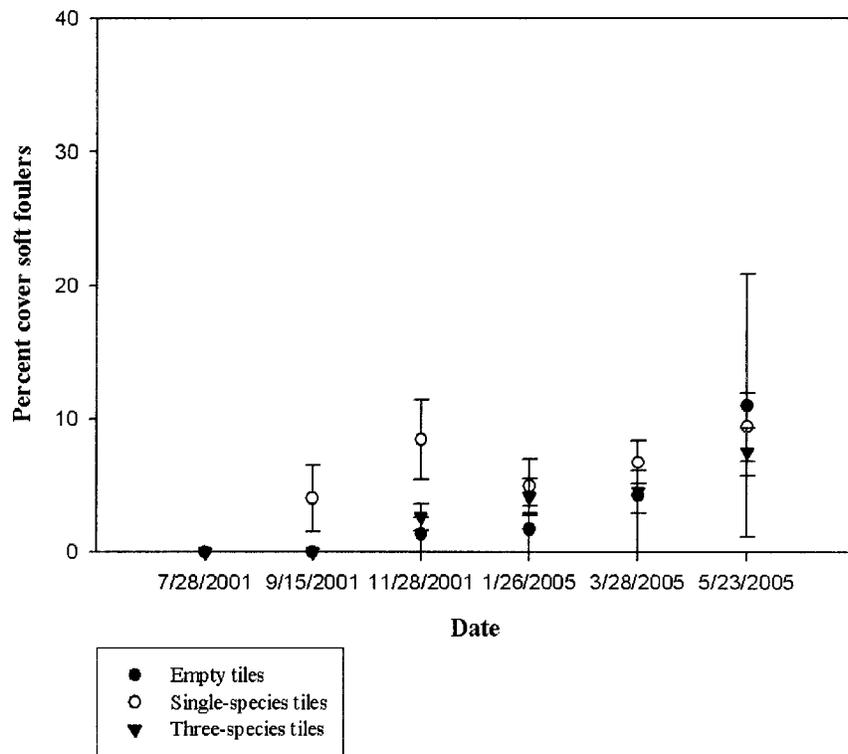


Figure 6.5. Total cover of soft foulers (tunicates and sponges) over time.

Diversity level (one vs. three species) was not a statistically significant factor in the communities that recruited to the tiles, but time, community type and the block by community type interaction were significant (Table 6.2). The results were the same for analysis of the assemblage of the eight known non-natives.

Table 6.2. ANOVA table for the effect on invading sessile species of initial diversity level (1- or 3 species), community type (the original community composition) and time. Significant factors are in bold.

Factor	DF	SS	MS	F	P	Denominator MS
Diversity level	1	8.698	8.698	0.175	0.996	49.808
Community type	6	283.909	47.318	2.411	0.006	19.629
Time	4	187.623	46.906	7.630	0.002	6.148
Block	3	69.964	23.321	1.029	0.556	22.664
Block x time	12	73.770	6.148	0.825	0.664	7.454
Diversity x block	3	66.356	22.119	1.111	0.394	19.907
Diversity x time	4	33.609	8.402	1.127	0.280	7.454
Block x community type	18	353.319	19.629	2.735	0.002	7.176
Diversity x block x time	12	89.451	7.454	1.039	0.382	7.176
Error	96	688.88	7.176			
Total	159	1855.58				

Diversity (one vs. three species) was not an important factor in total cover for the last time period, but community type was statistically significant (Table 6.3).

Table 6.3. ANOVA table for the effect of diversity level and community type on total cover of colonizing species.

Factor	DF	SS	MS	F	P
Diversity level	1	19.2	19.2	0.03	0.884
Community type	6	8732.7	1455.4	3.42	0.020
Block	3	802.4	267.5	0.35	0.793
Block*Diversity	3	2283.6	761.2	1.79	0.185
Error	18	7661.9	425.7		
Total	31	19499.7			

The nMDS plot of communities at the final time point showed no clustering by diversity level (Fig. 6.6); this was also the case when all time points were included.

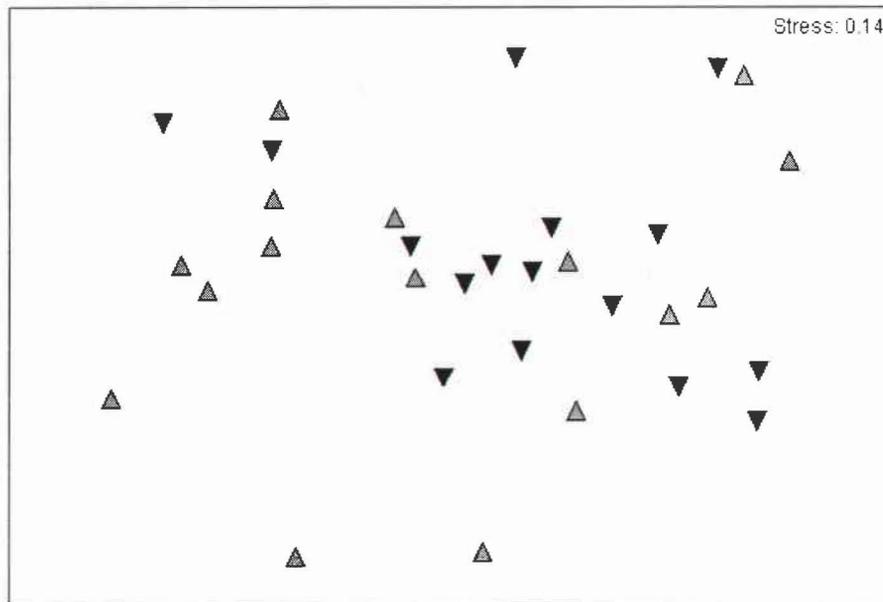


Figure 6.6. Nonmetric multidimensional scaling plot showing the distances between the communities that developed on single-species tiles (gray triangles) and on three-species tiles (black triangles).

The tiles that had no species on them at the start of the experiment are clearly distinct in nMDS plots for all time points and for the final time point, although there are some outliers (Fig.6.7).

A plot of community type at the final time point shows tiles of community type 3 (single-species tiles *Isognomon californicum*) and type 6 (the three-species community without *I. californicum*) each clustering closer together than other plate types (Fig.6.8). While these don't form a separate cluster when all time points are included in the plot (Fig. 6.9), they remain closer together than do other tiles.

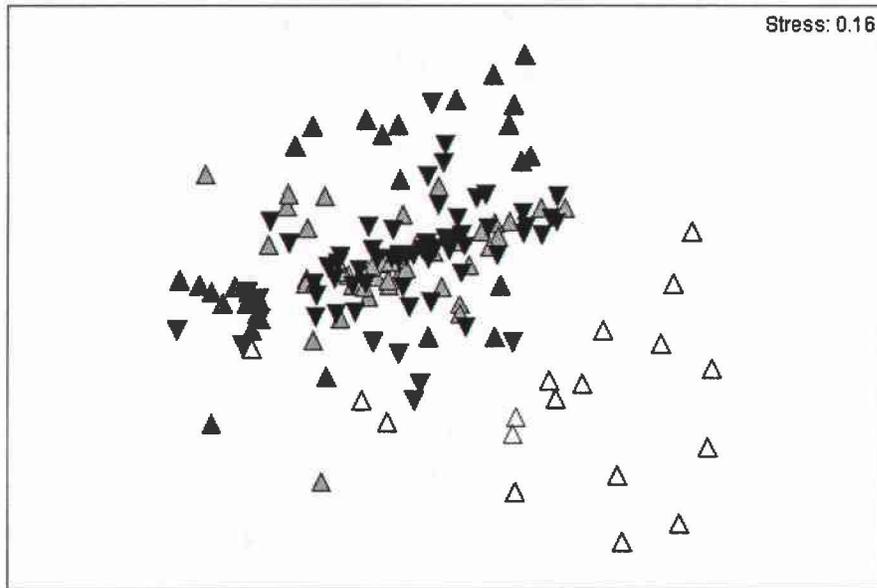


Fig. 6.7. Nonmetric multidimensional scaling plot of showing distances between the communities of invading organisms on tiles of the three initial diversity levels. White triangles = empty tiles; gray triangles = 1 species; black upside down triangles = 3 species.

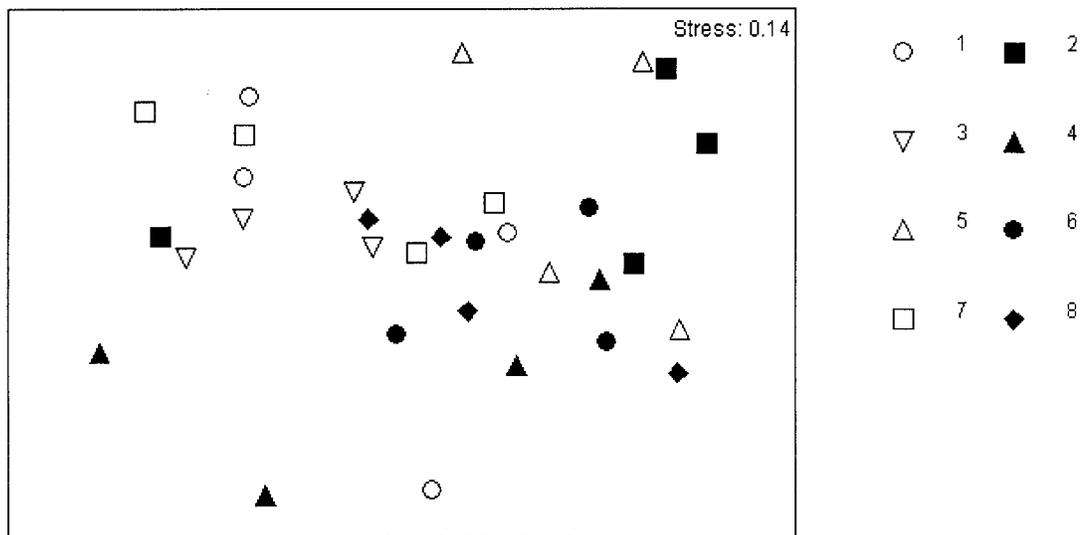


Figure 6.8. Nonmetric multidimensional scaling plot showing distances between the invading communities by initial community type, final time point: 1-4 single-species tiles 1. *Dendostrea sandvicensis* (*Ds*), 2. *Brachidontes crebristriatus* (*Bc*), 3. *Isognomon californicum* (*Ic*) 4. *I. perna* (*Ip*) ; 5-8 three-species tiles, 5. *Ds-Bc-Ic*, 6. *Ds-Bc-Ip*, 7. *Ds-Ic-Ip*, 8. *Bc-Ic-Ip*.

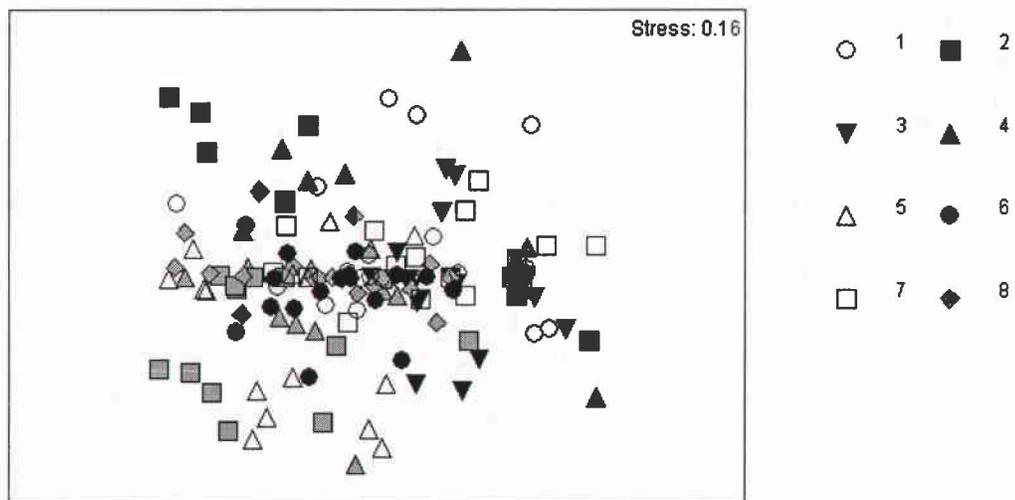


Figure 6.9. Nonmetric multidimensional scaling plot showing distances between the invading communities by initial community type, all time points included. 1-4 single-species tiles 1. *Dendostrea sandvicensis* (*Ds*), 2. *Brachidontes crebristriatus* (*Bc*), 3. *Isognomon californicum* (*Ic*) 4. *I. perna* (*Ip*) ; 5-8 three-species tiles, 5. *Ds-Bc-Ic*, 6. *Ds-Bc-Ip*, 7. *Ds-Ic-Ip*, 8. *Bc-Ic-Ip*.

Community type accounted for about 32% of the total variation among tiles in the RDA; the first RDA axis alone accounted for over half of this (18% of total variation). The RDA ordination of samples, like the nMDS, shows community types 3 and 6 forming fairly tight clusters with little overlap with other types (Fig. 6.10). Types 4 and 5 form larger, somewhat overlapping clusters to the upper and left sides of the plot. Three of the type 2 tiles form a tight cluster to the bottom left, but the fourth plate of this type is at the far right, near types 1 and 3.

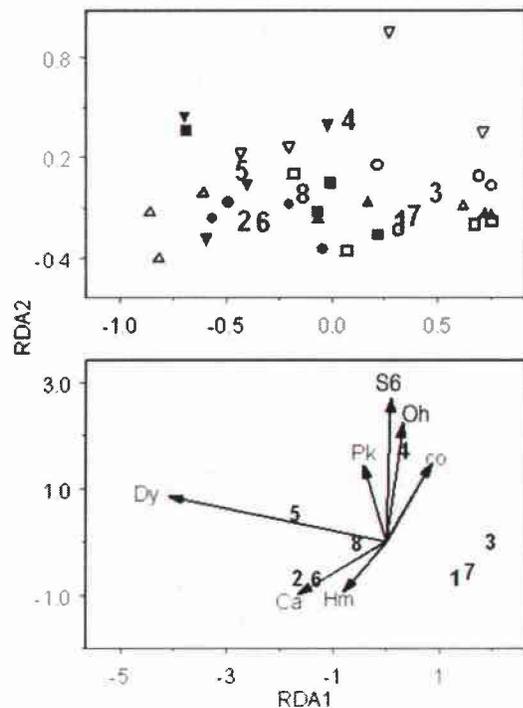


Figure 6.10. Biplot of RDA results for final time point.

Top panel: Ordination of samples. Numbers show means for the community types (numbered as in Figs. 7-9). Symbols show samples, by community type. Empty symbols are single-species tiles (types 1-4), filled symbols are three-species tiles (types 5-8). Squares are tiles with/without *D. sandvicensis* (types 1 & 8); up-pointing triangles are tiles with/without *B. crebristriatus* (types 2 & 7); circles are tiles with/without *I. californicum* (types 3 & 6); down-pointing triangles are tiles with/without *I. perna* (types 4 & 5).

Bottom panel: Ordination of important species: Dy = *Dynamena* sp.; Pk = *Pomatoleios kraussii*; S6 = sponge#6; Oh = *Ostrea hanleyana*; co = coralline algae; Hm = *Herdmania momus*; Ca = *Cnemidocarpa areolata*. Lengths and angles of the vectors show the importance of species in the two RDA dimensions. Numbers show rescaled means for the community types, as in the top panel; projecting from a mean perpendicularly to a species vector gives the relative abundance of that species in that community type.

When species scores are plotted on the RDA axes, axis 1 is dominated by the hydroid *Dynamena* sp. (negatively associated), the tunicate *Cnemidocarpa areolata* has moderate negative loadings on both axes, and the other important species are associated primarily with axis 2. Relating community types to species, types 1, 3 and 7 were characterized by low abundances of *Dynamena* sp. and high abundances of sponge #3. Community type 2 had high abundances of *Dynamena* sp. and the tunicates *Cnemidocarpa areolata* and *Herdmania momus* and low abundances of most other species. Tiles of type 4 had nearly the opposite communities of type 2, with high abundances of the tube worms *Pomatoleios kraussii* and coralline algae, sponge #6 and the oyster, *Ostrea hanleyana* and low abundances of the tunicates *Cnemidocarpa areolata* and *Herdmania momus*. Community type 5 was typified by high abundances of *Dynamena* sp., and also was somewhat associated with the tube worm *Pomatoleios kraussii*. Type 6 had similar communities to type 2, though with a somewhat smaller loading on the *Dynamena* sp. vector. Community type 8 had small loadings on all species vectors, the largest being with *Dynamena* sp. and the tunicate *Cnemidocarpa areolata*.

In terms of the bivalve species placed on the tiles, abundance of *Dynamena* sp. was strongly positively associated with the presence of *B. crebristriatus* (types 2, 5, 6 and 8), and had little apparent relationship to the presence or identity of other bivalves. The tube worm *Pomatoleios kraussii*, coralline algae, and sponge #6 were found primarily on tiles with only *I. perna* (type 4); many of these taxa were at particularly low abundances on tiles with only *B. crebristriatus* (type 2) and also on tiles with *I. perna* together with *B. crebristriatus* and *D. sandvicensis* (type 6). In contrast, the two tunicates were negatively

associated with the *I. perna*-only tiles (type 4) and positively associated with most types containing *B. crebristriatus* (types 2, 5 and 6).

Discussion

Although the communities of organisms recruiting to the experimental tiles varied over time and by initial community type, diversity (one vs. three species) did not result in statistically significant differences. The data suggest that the differences in community types are the result of the inclusion or exclusion of a specific native species in the initial community. At this time, it is not clear why certain invading organisms were negatively or positively associated with the various native bivalves. The bivalve species differ from each other in size, rugosity, orientation to the substrate, three-dimensional structure and mortality levels due to differential predation by the stomatopods. Any of these factors might have encouraged or discouraged settlement by other organisms.

While more of the hard foulers such as barnacles, bivalves and tube worms were found on the tiles that started out empty, few tunicates or sponges were found on these tiles. This pattern is not surprising based on observations of succession in fouling communities in Hawaii (Ingram 1937, Edmondson and Ingram 1939, Hurlbut 1991b). Disturbance on the tiles that initially contained bivalves might have been expected to result in tiles that more closely resembled those that started out bare. But the patches that opened up apparently were not big enough to result in changes in the types of organisms settling on the tiles, and nearly all of the hard foulers will also settle, at least to some degree, on secondary substrate (personal observation).

The results of this experiment need to be interpreted with caution because the assembled communities differ from natural ones in several ways. First, although all four species are found in the intertidal zone, they inhabit distinctive zones and would rarely co-occur within 100 cm² plots. Second, the tiles were shaded due to their position under the blocks, which encouraged the settlement of sponges, tunicates and bryozoans.

Although *Dendostrea sandvicensis* is frequently part of the fouling community, growing in shade on pier pilings, and *Isognomon perna* generally inhabits the underside of rocks, where it is frequently overgrown with soft foulers such as tunicates and sponges, the other mussels exist higher in the intertidal zone are rarely found with soft foulers. Finally, the presence of the wire cages, although meant to discourage predation, probably created a structure that encouraged the predatory activities of the stomatopods, which usually occupy dead coral heads.

The finding of no relationship between resident species diversity and degree of invasion contrasts with the results of Stachowicz et al. (1999), the experiment which this one most closely resembles. This is not because Stachowicz et al. used a higher number of species in assembling their communities; they would have still found a strong negative correlation between species richness and invasibility if they had used three initial species as their maximum (see their Fig. 2). While this experiment differs from theirs in that they allowed organisms to settle naturally and then “gardened” tiles to achieve the desired community types and started each set of tiles with the non-native tunicate already present, the most likely explanation for the difference in outcomes is that the invading tunicate they measured requires primary substrate (Whitlatch, personal communication). Higher

species diversity led to less available primary substrate and thus to the greater invasion of this tunicate.

If I had only measured the invasion success of the non-native bryozoan, tube worms and barnacles, I might have concluded that the empty tiles are more easily invaded than tiles with organisms already on them (but that there was no difference between the single- and the three-species tiles). On the other hand, if I had tracked the success of the three non-native tunicate species, I would have found greater invasion success on the plates with organisms already on them than on the empty tiles, at least for some of the time points. This suggests that the effects of residents on invaders may be inhibitory or facilitative, depending on species identities.

Despite its limitations, this experiment can be taken as a reminder that many factors other than competition control the success of invading species in ecological communities. In fact, competition should only be expected to result in invasion resistance when an invader is competing with resident species for a necessary resource in short supply that resident species are better at controlling. Disturbance, low recruitment, differential predation on resident species or invaders that are superior competitors may make this a rather rare occurrence. On the other hand, rather than using up resources, resident species may create resources for invading species, through forming a prey or host base, providing habitat structure, or otherwise facilitating settlement and growth of invaders. Finally, competition between resident and invading species may mostly be important on small or neighborhood scales, while larger-scale factors such as recruitment supply, disturbance regimes or abiotic factors may be more important to invasion success on larger scales (Levine 2000).

CHAPTER 7.

Conclusions

The objectives at the beginning of this study were essentially three-fold: 1) to determine whether *Chthamalus proteus* had changed in life history and ecological role between the native and invaded range; 2) to examine the interactions of *C. proteus* with other intertidal organisms; 3) to examine, using assembled microcosm communities set out in the intertidal zone, whether low-diversity native communities are more easily invaded than high-diversity communities. The results of these investigations are discussed in detail in the conclusions at the end of each chapter. Here, I briefly summarize the results of the dissertation research and provide an overall synthesis.

- Unlike the numerous examples of invasive species that have been successful due to ecological release, *C. proteus* appears to have undergone little change in its biology or ecology, at least for the traits measured. Although some differences in fecundity and habitat use were found between regions, measures in Hawaii fall within the variation seen in the native region. If the basic biology and ecology of this barnacle had been studied in its native range, accurate predictions could have been made about the types of habitats it would be able to occupy in Hawaii.

- Contrary to the idea proposed by Stanley and Newman (1980) that *Balanus* species are always superior competitors in *Balanus-Chthamalus* interactions, *C. proteus* was demonstrated to outcompete *Balanus reticulatus* for space in Kaneohe Bay. While the

larger and faster-growing *B. reticulatus* might be expected to have an advantage in interference competition, *C. proteus* dominates via substrate pre-emption, rapidly colonizing open substrate and making it unattractive to the settlers of *B. reticulatus*. *Balanus amphitrite*, also invasive in Hawaii and the dominant barnacle species at least as late as the early 1970s (Matsuda, 1973), is now nearly gone from Kaneohe Bay. It is not known what caused its decline. Fauna inhabiting the tests of live and dead barnacles did not differ between plates dominated by *C. proteus* and those dominated by *B. reticulatus*. This suggests that a change in the identity of the dominant barnacle, at least when both barnacles are non-native, does not have cascading effects into the epifaunal community.

- The native pulmonate limpet *Siphonaria normalis* may, by its grazing activities, facilitate settlement of *C. proteus* under certain conditions, but dense settlement of the barnacle negatively impacts the limpet. Whether these organisms will have a neutral, positive or negative association with each other appears to vary with densities of each.

- Chthamalus proteus* does not appear to be competing for space with the native barnacle *Nesochthamalus intertextus*, at least at the densities at which the two species now co-occur. Differences in recruitment to different sites around Oahu may be the best explanation for patterns of abundance of barnacle species and may determine whether competition will occur between co-occurring barnacle species. Differences in current patterns, water circulation and the origin of water masses bathing coastal sites may be the driver behind recruitment differences.

•The ease with which the microcosm communities were invaded does not vary with native bivalve species diversity, at least over the levels tested (1-3 species). Differences between community types, *i.e.*, the presence or absence of a given native bivalve species does, however, appear to affect later settlers. Organisms that invaded plates with and without bivalves were distinctly different, suggesting that native bivalve species facilitate settlement by some species, notably soft foulers such as tunicates and sponges, while inhibiting the settlement of hard foulers such as barnacles, calcareous tube worms and oysters.

Taken as whole, these results suggest that the interactions of *C. proteus* with other organisms are by in large subtle, and vary over time and space and with densities of organisms. At high densities, the barnacle appears to negatively impact the limpet *S. normalis*.

Of the native species included in this research, the limpet is the only native organism that seems to be negatively impacted by *C. proteus*. In fact, the presence of *C. proteus* might create habitat for some native species, such as the bivalve *Lasaea hawaiiensis* and provide an additional food source for others, such as the whelk *Morula granulata*. This should not be taken to demonstrate that this is a benign invasion; only a handful of native species were included in this research. Additionally, I only studied interactions occurring at adult stages. The larvae of *C. proteus* are likely interacting with an entirely different suite of species, particularly in Kaneohe Bay and other sheltered bodies of water in which they may be abundant.

From a management perspective, the replacement of *B. reticulatus* by *C. proteus* may be of little consequence. However, the mechanism by which this is occurring demonstrates that assumptions should not be made about relative competitive abilities of pairs of organisms. At this time, it appears that *Nesochthamalus intertextus* and *C. proteus* are limited by recruitment, not by competitive interactions. It is possible that increases in the number of larvae arriving at a given site (*i.e.*, due to changes in current patterns or a build up of down-current source populations) or increases in adult densities due to low mortality could lead to competition between these species in the future. It is not possible at this point to predict which barnacle would be the winner.

Observations in its native range and in Hawaii indicate that *C. proteus* is an opportunistic species able to survive in artificial and anthropogenically altered habitats, and as such is likely to continue to thrive and spread around the Hawaiian Islands. The presence of large, fecund individuals in semi-exposed locations suggests that this species is not limited to ports and harbors. The current high abundance of *C. proteus* in ports is likely due to number of factors, including the effectiveness of ship traffic in spreading the invader. Efforts to reduce hull fouling may prevent or slow the spread of this barnacle to new regions.

Several questions remain about the invasion of the Hawaiian Islands by *C. proteus*. Among these, the timing of the invasion remains puzzling. A number of Caribbean fauna have invaded Hawaii (Carlton and Eldredge in prep) but these have by all accounts been in the islands for many decades. As far as I have been able to determine from conversations with people involved in shipping, there are no obvious changes in routes or shipping traffic that would have increased the likelihood of an invasion from the

Caribbean. Further, genetic research indicates multiple invasions of this barnacle (Zardus and Hadfield, in press). It is difficult to imagine what sort of barrier might have existed until the 1970s that prevented this barnacle from invading Hawaii and then disappeared, allowing for entry from multiple locations.

Additionally, the cause of the virtual disappearance of *Balanus amphitrite* from Kaneohe Bay remains a mystery. That there has been a shift in the identity of the dominant barnacle there is clear based on Matsuda's 1973 surveys. Whether this barnacle was first replaced by *B. reticulatus*, which was in turn replaced by *C. proteus*, whether it was directly replaced by *C. proteus*, or whether its decline was due to another factor will probably never be known.

The results of the microcosm experiment, coupled with those from the other investigations, indicate that competition generally does not play a major structuring role in the distribution and abundance of the organisms tested. Physical factors, such as wave exposure and substrate type, facilitation and recruitment seem equally or more important. Predation was not explicitly tested, and cannot be ruled out as an important structuring factor for either larval or adult stages.

For most of the organisms examined resources do not appear to be limiting, at least in the life phase included in this study. This was the conclusion reached by Whipple (Whipple 1966) in her studies of intertidal littorines. She concluded that recruitment limitations, not predation or lack of food or space resources were responsible for the abundance of littorines at her study sites. Parnell (2000) also found strong correlations between adult densities of several taxa and the abundance of their larvae in waters just offshore. In my study, relative abundances of barnacle recruits paralleled relative

abundances of adults at the various study sites and the dominant species recruited in highest numbers at each site. Percent cover of barnacles at the study sites has not appreciably changed during the course of this study and sites were remarkably consistent in terms of recruitment over the time periods studied.

Why is recruitment so different between sites? In his study of Malama Bay, Parnell (2000) observed that the bay water was not well mixed. Rather, parcels of water of either coastal or oceanic origin appeared to fairly consistently bathe certain areas of the coastline, depositing different amounts of larvae in his traps. While Parnell's study was limited to Malama Bay, such a mechanism might explain the consistent differences in abundance and identity of barnacle larvae arriving at my study sites. In addition, a long water-retention time in the southern portion of Kaneohe Bay is likely the cause of high larval accumulation and recruitment at the Lilipuna Pier site. A greater understanding of what happens to larvae in the plankton and the combination of physical factors and larval behavior that returns them to shore is needed to fully understand the dynamics of this invasion and of the intertidal community in general.

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