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Battle of the barnacle newcomers: niche compression in invading species in Kaneohe Bay, Oahu, Hawaii

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ABSTRACT: Multiple invasions by ecologically similar species can be viewed as 'natural' addition experiments in which access to key resources might be reduced. Possible outcomes might include: (1) the extirpation of a species already present in the ecosystem, (2) the exclusion of a new invader, or (3) niche compression, with each species using less of the shared resource. *Chthamalus proteus,* a barnacle that arrived in the Hawaiian Islands ~30 yr ago, is now the most abundant and widespread non-native barnacle in the intertidal zone on the island of Oahu. In a series of field experiments, I demonstrate that the abundance of an earlier invader — the larger, faster growing barnacle *Balanus reticulatus* — is reduced via substrate pre-emption in the zone of overlap between the 2 barnacle species. A third barnacle, *Balanus amphitrite,* which invaded Hawaii earlier than the other two, is now virtually absent from locations where it was once abundant and where *C. proteus* is now the numerical dominant. *B. amphitrite* did not settle on plates from which *C. proteus* was removed, suggesting that the presence of *C. proteus* is not the proximal cause of its decline. *B. amphitrite* is still present on Oahu, particularly in lower salinity settings. While successively invading barnacles have reportedly replaced each other in other locations around the world, it appears that invasive barnacles on Oahu are undergoing niche compression rather than complete replacement.

KEY WORDS: Competition · Barnacle recruitment · *Chthamalus proteus* · Biological invasions · *Balanus*

INTRODUCTION

Most organisms are prohibited by biotic interactions from having access to all the resources they could potentially use, and are said to be living within their realized rather than their fundamental niches (Hutchinson 1957). This idea is supported by observations of broader resource use by allopatric populations than by populations sympatric with competitors (reviewed in Begon et al. 1996), and by experiments in which the removal of a competitor results in an increase in niche breadth or resource use (reviews in Connell 1980, Schoener 1983).

Biological invasions can be thought of as addition experiments; if ecologically similar species are added to an ecosystem, a reduction in available resources might be expected to occur. Outcomes of invasions could include: (1) the replacement of one (or more) species by the newest invader (e.g. Reitz & Trumble 2002, Abe & Tokumaru 2008); (2) resistance to or exclusion of the newest invader by the established community of species (e.g. Elton 1958, Moulton & Pimm 1983, Robinson & Dickerson 1984, 1987, Case 1990, Drake 1990, Case 1991, Stachowicz et al. 1999); or (3) niche shift or compression, in which species coexist but use less of their fundamental niche than they did prior to the latest invasion (e.g. Duyck et al. 2004, Gray et al. 2005).

Space appears to be a major limiting factor for intertidal barnacles in many locations (Connell 1961a,b, Stanley & Newman 1980, Wethey 1984). Competition

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for space between barnacle species can occur after settlement through overgrowth, undercutting and crushing (Connell 1961b, Wethey 1984). In such interactions, larger, faster growing balanoid barnacles are likely to win over the typically smaller chthamaloid barnacles (Connell 1961b, Stanley & Newman 1980, Wethey 1984). Chthamaloid barnacles as a group tend to have a higher tolerance to air exposure, and where competition with balanoids is strong, may be relegated to the upper intertidal zone, where balanoids either do not settle or do not survive as well.

Competition between barnacles can also occur via pre-emption of space. Some barnacle species tend to settle near conspecifics (Barnett & Crisp 1979, Denley & Underwood 1979, Underwood & Denley 1984), but tend not to settle in already crowded conditions (Crisp 1961, Meadows & Campbell 1972, Gaines & Roughgarden 1985, Minchinton & 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 substratum and few conspecifics (Barnett & Crisp 1979). Patterns of distribution and abundance of barnacle species that display strong conspecific settlement behavior should be governed, at least partly, by priority effects (sensu Paine 1977), and succession involving such barnacles might be expected to follow Connell & Slatyer's (1977) inhibition model.

Four non-native intertidal barnacle species are found in the Hawaiian Islands. *Chthamalus proteus* Dando & Southward is the most recent of these, having arrived sometime after 1973 (Southward et al. 1998). This native of the Caribbean and tropical and subtropical Atlantic co-occurs in the main Hawaiian Islands with 3 balanoid invaders: *Balanus amphitrite* Darwin, *Balanus reticulatus* Utinomi and *Balanus eburneus* Gould. All 3 balanoids range from the lower intertidal zone to the shallow subtidal, with *B. eburneus* being most abundant in brackish water. *C. proteus*, being strictly an intertidal organism, ranges from mean low, low water to the splash zone (Matsuda 1973, Zabin et al. 2007). While Hawaii's native barnacles favor high- to medium-exposure coasts, the non-natives reach highest abundance in protected harbors, lagoons and bays (Matsuda 1973, Zabin 2005).

Balanus amphitrite, a native of the Indian Ocean, has been on the island of Oahu since at least 1902 (Pilsbry 1907). At one time, it was the most abundant non-native barnacle in intertidal locations around the island (Matsuda 1973). In 1973, *B. amphitrite* was found from the high to the low intertidal on numerous hard structures in the southern portion of Kaneohe Bay on the island's windward side, forming nearly 100% cover in many locations (Matsuda 1973). One such location was the cement pier belonging to the Hawaii Institute of Marine Biology (C. Matsuda pers. comm.). A few individuals of *Balanus reticulatus*, a native of the Indo-Pacific first reported from Hawaii in 1929 (J. Carlton & L. Eldredge unpubl.), were also recorded on the pier at that time.

Today, only a few individuals of *Balanus amphitrite* can be found on the pier. *Chthamalus proteus* is the most abundant barnacle on the pier pilings, with *Balanus reticulatus* being found in dense patches in the low intertidal zone (Zabin 2005). *B. amphitrite* is in fact 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 intertidal structures, with occasional individuals of *B. reticulatus* in the low zone or on the undersides of rocks (pers. obs.). This shift is not restricted to Kaneohe Bay. Islandwide, *C. proteus* appears to have replaced *B. amphitrite* as the most widespread and abundant non-native barnacle in the island's intertidal zone (Zabin 2005, Zabin et al. 2007).

Here, I discuss the results of a series of experiments focusing on whether the presence of *Chthamalus proteus* on the pier (1) inhibits *Balanus amphitrite*, (2) restricts the area that could be inhabited by *Balanus reticulatus*, and (3) if so, how the changes in barnacle composition might occur. I asked what species would recruit to the pilings in the absence of the latest barnacle invader, and set up experiments accordingly. The results from this initial work led to the remaining experiments, which focus on the interaction between *B. reticulatus* and *C. proteus.*

METHODS

Study site. Kaneohe Bay is the largest sheltered body of water in the Hawaiian Islands. A barrier reef protects the bay from waves. The bay has an average depth of 8 m, and circulation is slow, particularly in the southern portion, where waters may take up to 10 d to flush out (Smith et al. 1981). The study site is the cement pier (Lilipuna Pier) surveyed by Matsuda in 1973, which is located on a shallow reef flat in the southern portion of the bay (Fig. 1).

Patterns of barnacle abundance by intertidal zone. To quantify the present pattern of barnacle distribution and abundance on the pier, I counted organisms in quadrats placed on randomly selected pier pilings at mean low, low water (MLLW, i.e. 0 cm) and at the 15, 30 and 45 cm tide levels, with 10 replicates at each tidal height. These heights represented nearly the extent of the barnacle zone at this site; below 0 tide, the pier pilings were heavily covered with algae, sponges and tunicates, and no barnacles were seen. I used 10 × 10 cm quadrats made of clear

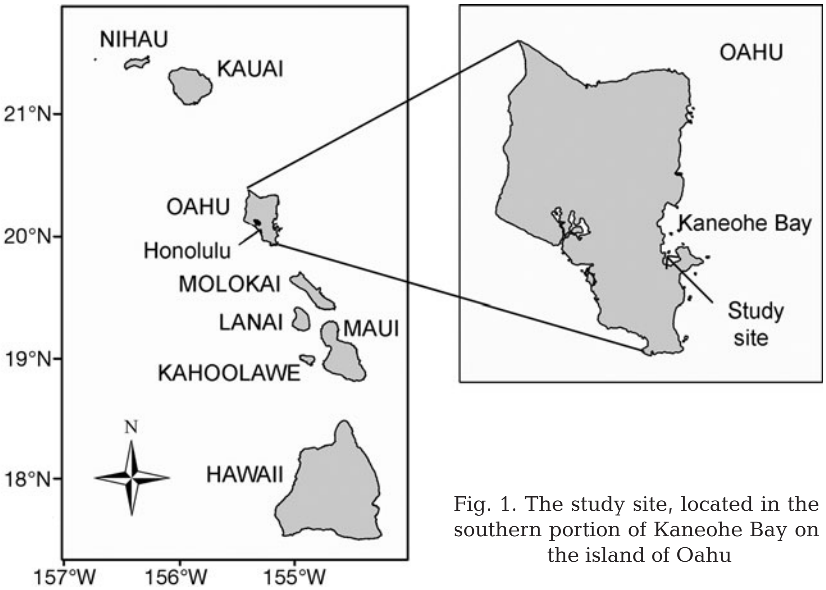

Fig. 1. The study site, located in the southern portion of Kaneohe Bay on the island of Oahu

acetate sheets and counted organisms under points on a 25-point grid. Count data were used to calculate percent cover of barnacle species and other space occupiers by taxonomic group (i.e. sponges, tunicates).

Initial competition experiment. If niche compression is occurring due to space competition between *Chthamalus proteus* and *Balanus* species, it should be most easily detected in the zone of overlap among the different barnacle species, the area to which all species recruit and are able to survive. I set up all of the remaining experiments at the 15 cm tide mark, which the survey indicated was the zone of greatest overlap. While no individuals of *Balanus amphitrite* were encountered in the above survey, this barnacle once had an extensive vertical range on the pilings based on Matsuda's recollection, and should have been able to survive at the 15 cm tide mark.

To determine whether (1) *Balanus amphitrite* would return, or (2) *Balanus reticulatus* would increase in cover with the removal of *Chthamalus proteus,* I attached twenty-four 10 × 10 cm terra cotta settlement plates to the pier pilings. Four plates were placed on each of 6 pilings, with 1 plate on each side. All plates were attached at the same tidal height. On each piling, 2 plates were *C. proteus*-removal treatments and 2 served as controls and were not manipulated. The plates were randomly assigned to different sides of the pilings. Pilings were thus considered as blocks in the experimental design.

Every 2 wk for 1 yr (July 2001 to July 2002) during a spring low tide, I removed the plates from the pilings, placed them in plastic tubs and took them to a laboratory at the Hawaii Institute of Marine Biology. I lightly brushed each plate with a toothbrush and rinsed it with seawater to remove debris for easier identification of 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 6× magnification, which enabled me to distinguish between barnacle species that were at least 1 mm in length. On the plates designated as removal treatments, I used a pin to remove settlers of *Chthamalus proteus* without harming other invertebrate settlers nearby. The control plates were passed under the microscope to mimic handling effects experienced by the barnacles on the removal plates. Plates were returned to the pilings within 2 h.

Every 2 mo, 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. For simplicity, space was considered occupied by a species if its dead test remained on the plate, with one exception: if a point fell over a live barnacle that settled on a dead barnacle, the space was scored as being held by the live barnacle. This method is conservative and favors cover by *Balanus* species, as their tests tend to remain on the substrate longer than those of *Chthamalus proteus,* which does not have a calcified basal plate. Instances of living barnacles settling on top of other living barnacles were extremely rare and were not encountered in the plate point counts. The data were arcsine-square root transformed to meet the assumptions of normality, and analyzed with repeated measures ANOVA. Treatment (removal of *C. proteus* or control) was considered a fixed effect; piling and plate (nested in the treatment × piling interaction) were considered random.

Invasion experiment. As no surveys of intertidal barnacles had been conducted on Oahu between Matsuda's thesis work (1973) and the present study, the distribution and abundance of barnacles at the time when *Chthamalus proteus* first invaded Kaneohe Bay is not known. To determine whether *C. proteus* would have been able to invade areas dominated by *Balanus reticulatus*, I left 12 of the plates (6 *C. proteus*-removal treatments and 6 controls) 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 every 2 mo.

Percent cover was determined and data were transformed as above. I used ANOVA to determine whether there was a difference in the cover of *Balanus reticulatus* on former *Chthamalus proteus*-removal plates between the first and second years and whether the former *C. proteus*-removal plates still had higher cover of *B. reticulatus* than the control plates after a year.

Recruitment and survival of *Balanus reticulatus*. To determine whether lack of recruitment of *Balanus reticulatus* or its lower post settlement survival might be the cause of the greater cover of space by *Chthamalus proteus* on the control plates, I examined the 12 plates used in the invasion study (above) for four 2 wk periods from Nov 11, 2002 to Jan 7, 2003. An ANOVA indicated that there was no difference in empty space between the 2 treatments (former *C. proteus*-removal and control plates) at the beginning of the study period. Every 2 wk, I recorded new recruits of *B. reticulatus* (defined as individuals between 1 and 2 mm in rostrocarinal length) on each plate. After the first time period, I also counted small barnacles in the 3–5 mm size class 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 microalgae). The number of barnacles in this category correlated well with 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. Survival 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 transformation of the recruit counts to improve normality, I used ANOVA to determine whether recruitment and survival differed between the treatment types.

RESULTS

Patterns of barnacle abundance by intertidal zone

At the MLLW (0 cm tide level), algae (*Gracilaria salicornia*) and several sponge species dominated, together making up 62 ± 30% (SD) cover. However, barnacles were also present, with *Balanus reticulatus* attaining a mean cover of 28 ± 23%, and *Chthamalus proteus* comprising 2 ± 4% cover (Fig. 2).

At the 15 cm mark, the cover of *Chthamalus proteus* was 40 ± 10%, while that of *Balanus reticulatus* was 23 ± 18%; oysters (*Dendrostrea hawaiensis*) were also a major space occupier with 23 ± 13% cover. At the 30 cm mark, the cover of *B. reticulatus* dropped to 5 ± 7%, while that of *C. proteus* increased to 58 ± 24%, with oysters covering 27 ± 8%. At the 45 cm mark, *C. proteus* comprised 77 ± 12%, oysters 10 ± 12%, and *B. reticulatus* was absent. While a few individuals of *Balanus amphitrite* were seen during this survey, none were found in the quadrats.

Initial competition experiment

Balanus reticulatus and *Chthamalus proteus* were the only barnacles that recruited to the experimental plates. While both barnacles recruited throughout the year, recruitment of *C. proteus* was an order of magnitude higher than that of *B. reticulatus*.

The cover of *Balanus reticulatus* was clearly higher on the *Chthamalus proteus*-removal plates compared to control plates within 4 mo of the experiment, reaching between 50 and 90% (Fig. 3). The cover of *B. reticulatus* on the removal plates continued to rise and remained higher than on the control plates throughout the course of this 12 mo experiment ($F = 96.79$, df = 1, $p < 0.0005$). The time period, treatment × time period interaction, and plate factors were also highly significant ($F = 58.64$, df = 5; $F = 18.52$, df = 5; $F = 10.43$, df = 12, respectively, all with $p < 0.0005$).

Invasion experiment

The mean percent cover of *Balanus reticulatus* on former *Chthamalus proteus*-removal plates dropped from 87% at the beginning to 44% by the end of the experiment, with a concurrent rise in *C. proteus* cover from nearly 0 to a mean of 33% (second year, Fig. 3). The cover of *C. proteus* on control plates also

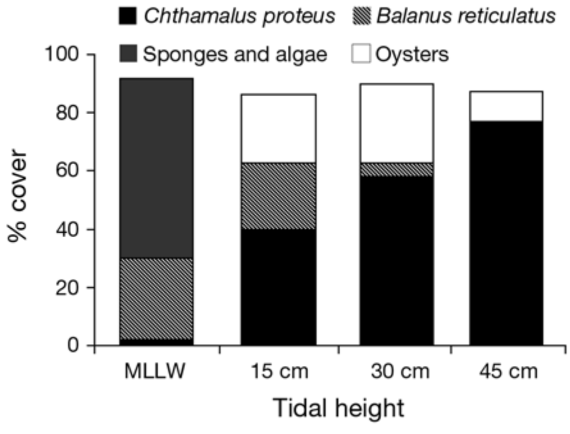

Fig. 2. Percent cover of sessile organisms at 4 tidal heights on the pier pilings at the study site. MLLW: mean low, low water

increased while that of *B. reticulatus* dropped. In some cases, death of *B. reticulatus* was caused by overgrowth by oysters. In other cases, the cause of death was unclear. Recruitment of *C. proteus* occurred on dead tests of *B. reticulatus*, on both live and dead oysters, and on open space created by dead barnacles or oysters falling off the plates. Although the cover of *B. reticulatus* was still higher on formerly manipulated plates than on controls (*F* = 19.15, df = 1, p = 0.048), its cover on *C. proteus*-removal plates was significantly higher in the first than in the second year of the experiment (*F* = 35.07, df = 1, p = 0.002).

Settlement and survival of *Balanus reticulatus*

The mean number of *Balanus reticulatus* settlers for the 2 mo time period was 18.2 ± 9.8 (SD) for *B. reticulatus*-dominated plates (=*Chthamalus proteus*-removal plates), and 4.3 ± 4.4 for *C. proteus*-dominated plates (=control plates). This difference was statistically significant (*F* = 18.72, df = 1, p = 0.049). There was no difference in the percentage of *B. reticulatus* settlers surviving until the end of the observation period between the 2 types of plates (*F* = 0.09, df = 1, p = 0.795).

DISCUSSION

Niche compression of *Balanus reticulatus*

Balanus reticulatus attained higher cover on plates from which *Chthamalus proteus* was removed than it did on control plates. Barnacles of either species rarely settled on other living barnacles. After manipulation ceased, the cover of *C. proteus* increased opportunistically as the balanoid died and space became available. The cover of *B. reticulatus* on control plates also decreased over the course of this experiment, while the cover of *C. proteus* on these plates increased. Juveniles of *B. reticulatus* recruited in higher numbers on plates dominated by conspecifics than on those dominated by *C. proteus,* but survival of settlers was not different between the 2 types of plates. These results suggest that while *C. proteus* does not outcompete the larger *B. reticulatus* via overgrowth or undercutting, it does reduce the abundance of *B. reticulatus* in the zone of overlap via space pre-emption, mediated at least partly by the gregarious settlement tendencies of *B. reticulatus*. The effect of this is a compression of the vertical extent of the balanoid.

Observations during the course of this study and data collected at this site for a longer-term recruitment study (Zabin 2005) suggest that *Chthamalus proteus* is

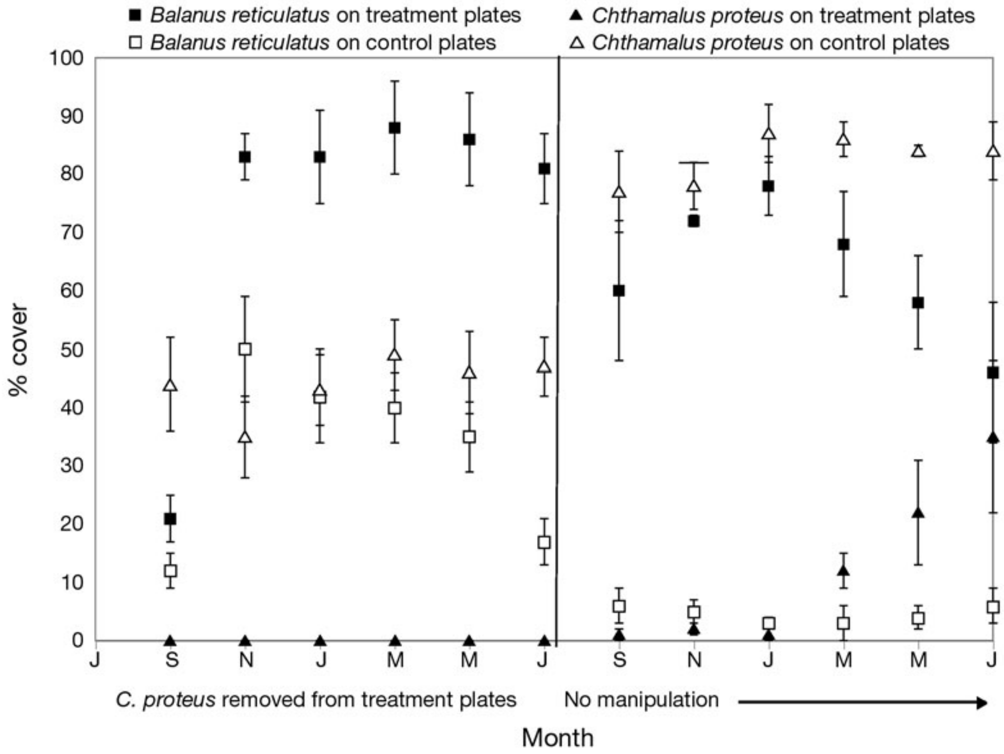

Fig. 3. *Balanus reticulatus* and *Chthamalus proteus*. Mean percent cover (±SD) on the experimental plates every 2 mo over the course of 2 yr beginning in July 2001. Manipulation ceased after 12 mo

able to dominate space by recruiting year round at levels consistently an order of magnitude higher than those of *Balanus reticulatus.* If *B. reticulatus* recruits less frequently and settles gregariously, its early decline on control plates and later decline on removal plates (in the invasion experiment) could be explained by numbers of adults dropping faster than numbers of recruits arriving, and/or by adult numbers falling below some threshold level needed for the attraction of new recruits. While other factors may have contributed to higher recruitment by *B. reticulatus* to control plates in Year 1 vs. Year 2, the overall trend remained: when plates were not manipulated, *C. proteus* eventually increased in abundance while *B. reticulatus* declined. This result concurs with the predictions of Barnett & Crisp (1979), who suggested that one of the ecological consequences of gregarious settlement behavior is competitor dominance via substrate pre-emption.

A strong preference for settling with conspecifics has been reported for *Balanus amphitrite* (Crisp 1990) and *Balanus balanoides* L. (Knight-Jones & Moyse 1961, Larman & Gabbott 1975, Barnett & Crisp 1979, Barnett et al. 1979). To my knowledge, similar studies have not been conducted on *Balanus reticulatus,* but the observations herein suggest a preference for settlement with conspecifics. In the recruitment study mentioned above (Zabin 2005), recruits of both *B. reticulatus* and *Chthamalus proteus* settled preferentially on plates painted with adult cues of *B. reticulatus* vs. those with adult cues of *C. proteus.*

When *Chthamalus proteus* first invaded the bay, presumably in small numbers, its ability to pre-empt space would have been much lower. Indeed, Barnett & Crisp (1979) hypothesized that given a preference for gregarious settlement, only a habitat change that favors a second species could lead to a change in dominance via substrate pre-emption. However, some barnacle species may be less dependent on conspecific cues than others, which theoretically should allow the former to settle more widely. There is some indication that *Elminius modestus* Darwin, an invasive barnacle in Europe, is also less influenced by conspecifics than its native counterpart *Balanus balanoides* (Larman & 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 & Gabbott 1975).

Although this experiment was conducted at only one tidal height, it is likely that *Chthamalus proteus,* like most chthamaloids, can tolerate emersion better than *Balanus reticulatus,* giving it a distinct advantage in the mid- to high intertidal zone. In contrast, *B. reticulatus* may have an advantage in the low intertidal or could settle in higher numbers in this zone (e.g. Grosberg 1982). In a pilot study of recruitment plates at the 0 and 15 cm tide marks (unpubl. data), more settlers of *B. reticulatus* were seen on the lower plates, while more *C. proteus* were recorded at 15 cm. At this tidal height at the Lilipuna Pier, barnacles are overgrown by sponges, tunicates and algae, many of which are non-native. Thus, multiple invasive species potentially limit the vertical distribution of *B. reticulatus* at this location.

Shift from *Balanus amphitrite* to *Chthamalus proteus*

The absence of the once-abundant *Balanus amphitrite* from the experimental plates suggests that the presence of *Chthamalus proteus* is not the proximal cause of the near-absence of this once abundant species on Lilipuna Pier.

Which barnacle species was numerically dominant when *Chthamalus proteus* arrived in Kaneohe Bay remains unknown. It is possible that *Balanus reticulatus* could have replaced *Balanus amphitrite* in the years following Matsuda's study. In the absence of data between that study and the present one, it is impossible to know what might have occurred; however, 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, *Balanus glandula* Darwin, *B. amphitrite* disappeared (Vallarino & Elias 1997). It was hypothesized that *B. glandula* was able to pre-empt settlement space in the harbors by settling in 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 space to settle on, and where it did, it could be easily crushed by the already large and fast-growing *B. glandula.* However, just as in the present study, researchers did not find any *B. amphitrite* even on plots that were cleared monthly, 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 be still the dominant barnacle subtidally in some full-salinity settings (Utinomi 1967).

Invasive barnacles in Hawaii

As barnacle populations around the islands are likely linked via dispersal, changes in the abundance of adults, and thus larval output occurring in one location, have the potential to affect populations elsewhere. However, all 4 invasive barnacles seem likely to persist in Hawaii. *Balanus amphitrite* and *Balanus eburneus* appear to be more tolerant of long-term lowered salinity than are *Balanus reticulatus* (Utinomi 1967, Thiyagarajan et al. 1997) and *Chthamalus proteus* (pers. obs.). In addition, all *Balanus* species can live in the shallow subtidal zone as well as in the intertidal, while *C. proteus* is restricted to the intertidal zone. Thus, *B. amphitrite* is still present in certain locations on Oahu, while *B. reticulatus* is numerous in others, particularly in subtidal fouling situations. *C. proteus,* on the other hand, has attained a wider distribution around the island than any of the *Balanus* species, being found in bays, harbors, open-coast settings where wave exposure is moderate, and even in protected microhabitats in some high wave-exposure sites.

The invasion of *Chthamalus proteus* offers an opportunity to observe competitive interactions between barnacle species. It also demonstrates that despite the fact that the larger, faster-growing balanoid barnacles nearly always win in interference competition for space, smaller chthamaloid barnacles may sometimes outcompete larger ones via substrate pre-emption, resulting in niche compression, if not in replacement. In this case, the result is a pair of invasive species from 2 different oceans assembling themselves into a classic zonation pattern in a new environment.

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