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

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Abstract Predictive models in invasion biology rely on knowledge of the life history and ecological role of invading species. However, species may change in key traits as they invade a new region, making prediction difficult. For marine invertebrate invaders there have been too few comparative studies to determine whether change in key traits is the exception or the rule. Here we examined populations of the intertidal barnacle *Chthamalus proteus* in three locations in its native range in the Caribbean and Atlantic, and in the Hawaiian Islands, where it has recently invaded, as a model system for such comparative studies. We measured body size, fecundity, population density and vertical distribution, compared habitat use and investigated aspects of the barnacle's ecological role in Curaçao, Panama and Brazil and the main Hawaiian Islands. In terms of these measures, the barnacle has undergone little change in its invasion of Hawaii. Thus, if this barnacle had been studied in its native range, predictions about its spread in Hawaii could have been made. As little was known about this barnacle in either its native range or Hawaii, we also carried out studies of its larval life history, fecundity, growth, and mortality. Based on this work, we predict that this barnacle will continue to spread, aided by vessel traffic, throughout the Hawaiian Islands and elsewhere in the Pacific.

Keywords Barnacles · Body size · Brazil · Caribbean · Changes in invaders · *Chthamalus* · Hawaii · Hull-fouling · Life history of invaders · Native-invaded habitat comparison

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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 (i.e., Grosholz and Ruiz 2003, who looked at body size in 19 species of decapod crustaceans, molluscs and a sea star; 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 *Amphibalanus* (formerly *Balanus*, Pitombo 2004) *amphitrite*, *A. eburneus*, and *A. reticulatus* (J.T. Carlton and L.G. Eldredge, in preparation). 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 1928; 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 2 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 et al. 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 (Dando and Southward 1980) and throughout the Caribbean. Molecular work indicates that Hawaii populations came from the Caribbean and Brazil (Zardus and Hadfield 2005). *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 (S. 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 2002–2003 and 2003–2004. 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 μg/ml penicillin and 50 μg/ml streptomycin) and cultures were adjusted to a density of 1,000 larvae/l. In 2002–2003, 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 2003–2004, larvae were fed either *I. galbana* at 250,000 cells/ml or a combination of *I. galbana* and the diatom *Skeletonema costatum* (Bacillariophyta) 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. 1, *arrows*). Fifty individuals from each site were haphazardly selected each collecting period and removed from the rocks using a thin blade. The rostro-carinal 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, yellowish 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 1-year periods in Hawaii at a site in Waikiki (Kuhio Beach) and over one 13-month and one 9-month period at Kualoa Beach Park on Oahu's windward side (Fig. 1, sites 39 and 62). Twenty permanent 12 cm × 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 rostro-carinal length of the mapped barnacles was recorded every 2 months from October 1999 to October 2000 and December 2000 to December 2001 at Waikiki and from June 2000 to July 2001 and July 2001 to March 2002 at Kualoa. Measurements were made using Vernier calipers; measurement error was

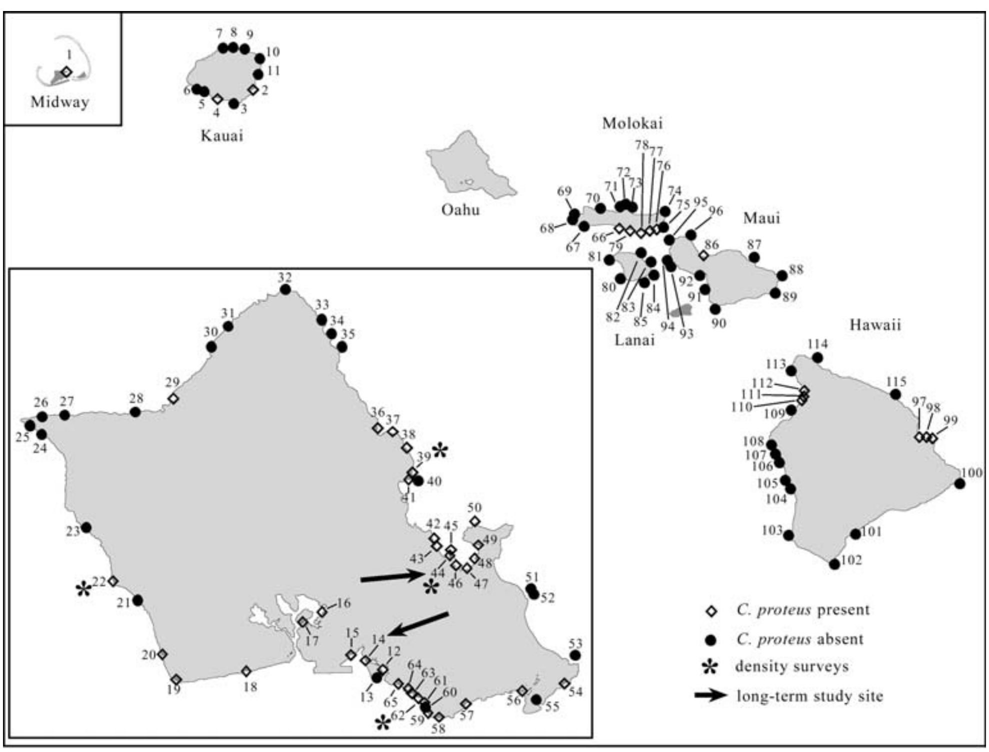

Fig. 1 Map of main Hawaiian Islands, showing survey and study sites. Sites are numbered for reference in Appendix

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 5 months of the first year, and 10 of these survived for the entire first time period. Growth was calculated for the first 5 months using the 25 barnacles, and for the 13-month period using the remaining 10. In the second time period, 9 out of 23 barnacles survived and were used for growth measurements.

Additional data on growth of *C. proteus* were gathered from a site in Kaneohe Bay (Lilipuna Pier, Fig. 1, site 44). Here, growth was determined by tracking individuals that had settled onto 10 cm × 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 2-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. Since 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 (7 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 2 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 (rostro-carinal 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. 1 and Appendix). 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 h during each survey. The islands of Molokai, Maui, Lanai, Kauai and Hawaii were also surveyed, although less intensively (Fig 1 and Appendix). Searches on these islands focused on harbors and boat ramps, with additional sites along the open coast. Sites were surveyed for about 1 h, 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). These sites included a range of habitat types from open-coast rocky intertidal areas to harbors and canals. 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.

Reproduction, body size and spatial variation

In addition to the studies at Keehi Lagoon and the Kaneohe Bay site, data on reproduction were also collected once from an additional five sites on Oahu from December 2001 to February 2002 (Fig. 1, sites 22, 41, 44, 58 and 62). At three of these sites, Waikiki (Kuhio Beach), Kaneohe Bay (Lilipuna Pier pilings) and Kualoa Beach Park, where *C. proteus* was abundant, we used a 10 m transect line and randomly placed 12.5 cm × 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.

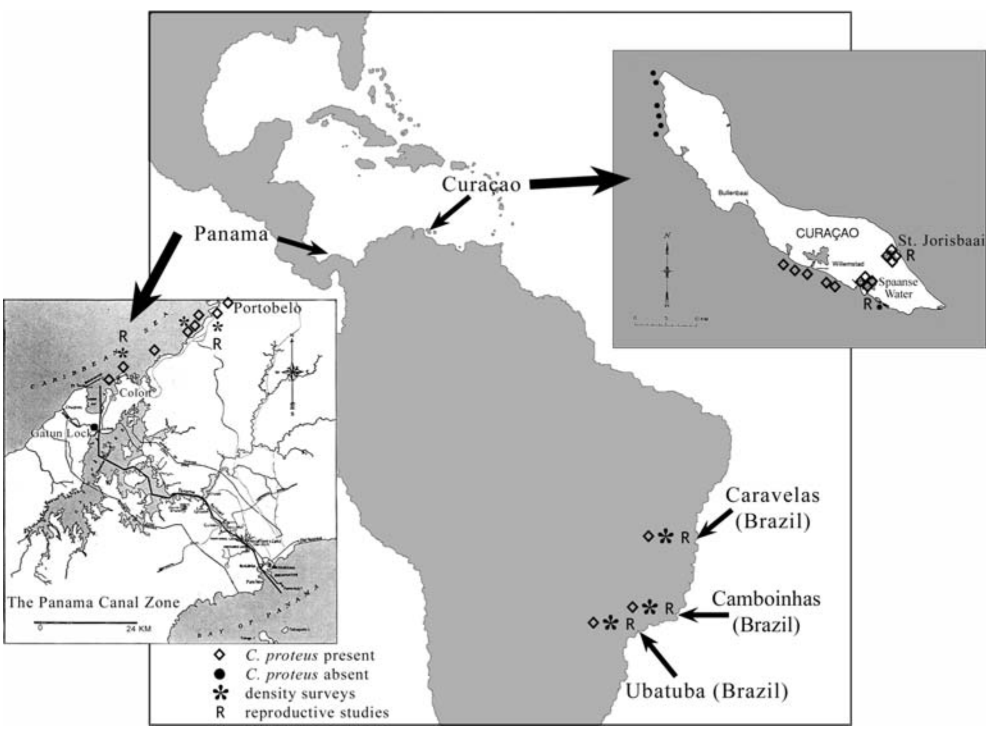

Fig. 2 Map of Caribbean and Atlantic, showing areas surveyed and study sites

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, 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. 1, *asterisks*), using a transect line placed in the middle of the barnacle zone. The number of 25 randomly placed points in 15–20 12.5 cm × 15 cm quadrats which were directly over a barnacle was used 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%, 10–25%, 26–50%, 51–75%, and >75%.

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 at high food concentration 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. 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 2001/2002 followed by peaks in the spring and fall of both 2002 and 2003. A less distinct peak in the winter of 2002/2003 was observed at Keehi Lagoon and was equivocally present at the Kaneohe Bay site. On average, 46% of the animals carried propagules during peaks of production.

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, SD = 1.12, respectively). Since 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.

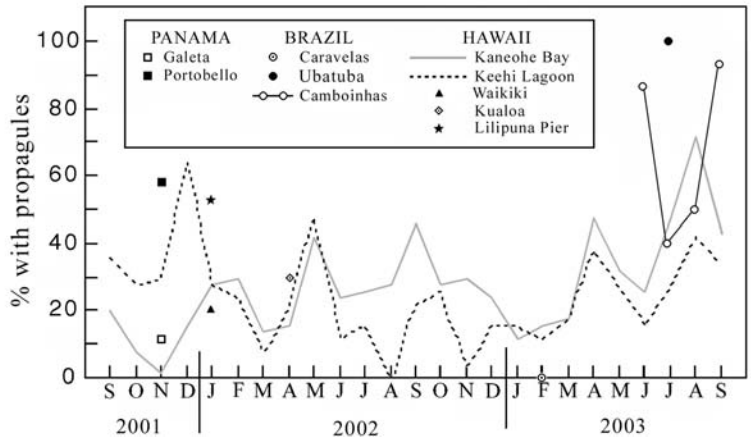

Fig. 3 Monthly proportion of individuals of *C. proteus* with eggs or unhatched larvae across two annual cycles at two localities in Hawaii. Also included are data for single time-point surveys elsewhere in Hawaii, Panama, Brazil, and a multi-time-point survey in Brazil. Not shown are values taken during September 2000 in Curaçao, Netherlands Antilles: St. Jorisbaai (40%) and Spaanse Water (64%)

$r^2 = 0.31, P < 0.000001$ ($N = 207$). 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.

Growth

Plots of the ratio of initial to final size versus 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 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 very small barnacles were not included in calculations of overall mean growth.

Mortality

Mortality rates, summarized in Table 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

Table 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	0.07 (.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

classes between 8.0 and 12.9 mm to die in lower percentages than other size classes (Table 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 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 2C, D).

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. 1, Appendix). 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. 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 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

Table 2 Waikiki and Kualoa year 1 and year 2 mortality by size class

Size class (mm)	# alive/expected	# dead/expected	Total
(A) Waikiki year 1 mortality by size class			
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
$\chi^2 = 12.449$, $df = 6$, $P = 0.053$			
(B) Waikiki year 2 mortality by size class			
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
$\chi^2 = 4.203$, $df = 7$, $P = 0.756$			
(C) Kualoa year 1 mortality by size class			
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
$\chi^2 = 1.632$, $df = 2$, $P = 0.442$			
(D) Kualoa year 2 mortality by size class			
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
$\chi^2 = 0.684$, $df = 2$, $P = 0.684$			

Table 3 Habitat use and population measures of selected sites in Hawaii, the Caribbean and Brazil

Location	*C. proteus* habitat comparisons				*C. proteus* 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
Maili Point, Oahu, Hawaii	BR/B	S-P to E	C	1 m	60 cm	<1%	N/A	N/A	*Ni* 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	*Ar*, *Ae*, *Aa*, *C* sp.
Kaneohe Bay, Oahu, Hawaii	BR/B	E	C	1 m	1 m	<10%	~4	N/A	*Ni*
Kualoa, Oahu, Hawaii	CSW	S-P	C	1 m	60 cm	38%	5 ± 1.4	319 ± 282	*Ni* 4% cover
Diamond Head, Oahu, Hawaii	LB	S-P	C	1 m	~30 cm	0.04%	N/A	0	*Ni* 5% cover
Waikiki, Oahu, Hawaii	CSW	S-P	C	1 m	1 m	2%	5.75	350	*Ni* 39%, few *Eh*
Galeta Marine Lab, Colon, Panama	OCS	S-P	C	59 cm	88 cm	32%	4.9 ± 0.99	209 ± 117	None
Galeta Marine Lab, Colon, Panama	*Rm*	P	C	59 cm	~30 cm	N/A	6.6 ± 1.33	600 ± 200	Unid *A*
Galeta Marine Lab, Colon, Panama	CSW	P	C	59 cm	20 cm	58%	5 ± 0.92	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, Curaçao	*Rm*	S-P	C	30 cm	30 cm	HDP	8 ± 1.44	507 ± 457	*Ca*
Spaanse Water, Curaçao	BH, R/P, OCS, W	P	T	30 cm	30 cm	HDP	N/A	N/A	*Ca*
Spaanse Water, Curaçao	VR	S-P	C	30 cm	30 cm	S	N/A	N/A	A sp., *Ca*
St. Jorisbaai, Curaçao	VR	P	C	30 cm	30 cm	HDP	4.9 ± .72	108 ± 40	None
mouth of Piscadero Bay, Curaçao	BH, OCS, CR, MS	P	T	30 cm	30 cm	S	N/A	N/A	*Aa*
Barbara Beach, Curaçao	VR, OCS, MS	S-P	C	30 cm	30 cm	S	N/A	N/A	None

Table 3 continued

Location	*C. proteus* habitat comparisons				*C. proteus* 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
Willemstad, Curaçao	CSW	P	T	30 cm	30 cm	HDP	N/A	N/A	*Aa*
Spaanse Water, Curaçao	*Rm,* A sp., OCS, MS, VR, BH	P	T	30 cm	30 cm	HDP	N/A	N/A	*Ca*
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	*Cb, Aa, Ts*
Multiple dates						10–25%	5.3 mm ± 1.1	417 ± 142	*Cb, Aa, Ts*
						10–25%	6.3 mm ± 1.6	815 ± 426	*Cb, Aa, Ts*
Caravelas, BA, Brazil	*Rm,* OCS, O	P	T	2.5 m	80 cm	>75%	6.3 mm ± 1.6	N/A	*Er*
Ubatuba, SP, Brazil	GR,	P	C	1.2 m	20 cm	10–25%	4 mm ± 0.5	245 ± 56	*Cb, Ts*

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: *Amphibalanus* sp., A; *A. amphitrite*, *Aa*; *A. eburneus*, Ae; *A. reticulatus*, *Ar*; *Chelonibia* sp., *C* sp.; *Chthamalus angustitergum, Ca*; *Chthamalus bisinuatus*, *Cb*; *Euraphia hemblei*, *Eh*; *Euraphia rhizophorae*, *Er*; *Nesochthamalus intertextus*, *Ni*; *Tetraclita stalactifera*, *Ts*.

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 rostro-carinal 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 8 of 12 sites where *C. proteus* was found at >40% 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 (a pier in Kaneohe Bay, site 44). *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 *Amphibalanus* 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*.

Reproduction 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. 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. 4). However, an ANCOVA examining fecundity with shell length as a covariate showed that fecundity per body size does vary with region (Fig. 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 ($F = 18.644$, $P < 0.00005$).

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% to >75% (Table 3).

In Panama, cover ranged from 32 to >75%. In Brazil, most sites had 10–25% cover, with one at 50–75%. In Curaçao, *C. proteus* was typically patchy, but there were dense clusters, with cover within a patch in the 50–75% 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. Possible explanations include a 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, faster larval development in areas of higher food concentration and warmer water, or some other 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.

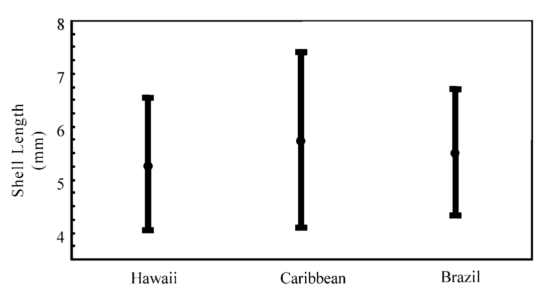

Fig. 4 Mean rostro-carinal length of barnacles sampled in Hawaii ($N = 1896$), the Caribbean ($N = 291$) and Brazil ($N = 129$)

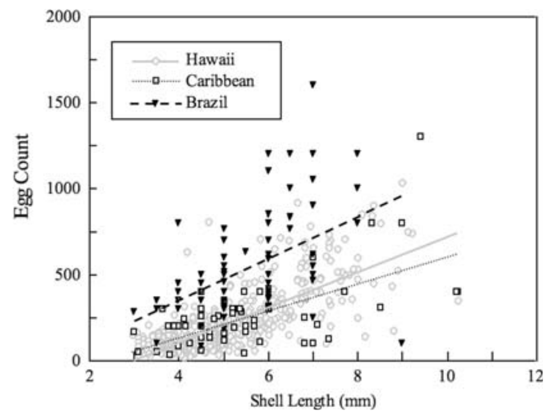

Fig. 5 Mean number of eggs/individual with eggs for barnacles samples in Hawaii, the Caribbean and Brazil

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 2 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 man-made 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 *Amphibalanus* spp. appear to be able to overgrow *C. proteus*.

Observations of overgrowth by oysters, sponges, tunicates and algae 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 (J.T. Carlton and L.G. Eldredge, in preparation). 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. Interestingly, another barnacle has been reported as first appearing in the 1960–1970s: *Balanus glandula* in Mar del Plata, Argentina (Vallarino and Elias 1997) and Japan (Kado 2003). Of course, it is always possible that *C. proteus* arrived in Hawaii earlier than 1973, but remained in very low abundance for some time.

At this point, the conditions under which this invader can successfully be transported long distance are not known. Due to the lack of data between 1973 and the present study, we only know that it took some 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.

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 2–3 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*.

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. Since 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.

Spread to subtropical mainland US and Mexico

Individuals of *C. proteus* have been found on commercial vessels about to leave Hawaii for the US 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 2005). 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 mangers in different parts of the world.

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Appendix 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)	*C. proteus* present	Habitat characteristics: Wave exposure (L = low; M = medium; H = high)	Substratum (C = concrete; R = rock)	Water clarity (C = clear; T = turbid)	Boat traffic (C = commercial; M = military; 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	Kolaeloa – Barbers Point Beach County Park (shoreline)	X	M	R	C	R/F
Oahu	20	Kolaeloa "Barbers Point" Harbor (shore & seawall)	X	L	R, C	C	C, R/F
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

Appendix continued

Island	Site No.	Place name (area searched)	*C. proteus* present	Habitat characteristics			
				Wave exposure (L = low; M = medium; H = high)	Substratum (C = concrete; R = rock)	Water clarity (C = clear; T = turbid)	Boat traffic (C = commercial; M = military; R/F = recr./fishing; S = scientific)
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	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
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 – Kuau ‘‘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

Appendix continued

Island	Site No.	Place name (area searched)	*C. proteus* present	Habitat characteristics			
				Wave exposure (L = low; M = medium; H = high)	Substratum (C = concrete; R = rock)	Water clarity (C = clear; T = turbid)	Boat traffic (C = commercial; M = military; R/F = recr./fishing; S = scientific)
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
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

Appendix continued

Island	Site No.	Place name (area searched)	*C. proteus* present	Habitat characteristics			
				Wave exposure (L = low; M = medium; H = high)	Substratum (C = concrete; R = rock)	Water clarity (C = clear; T = turbid)	Boat traffic (C = commercial; M = military; R/F = recr./fishing; S = scientific)
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

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