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Integrating Ecology, Natural History, and Regional Management for Conservation of Tropical Intertidal Gastropod Fisheries

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Integrating Ecology, Natural History, and Regional Management for Conservation of Tropical Intertidal Gastropod Fisheries

By

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ABSTRACT

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Doctor of Philosophy in Integrative Biology

University of California, Berkeley

Dr. Carole S. Hickman, Chair

Overexploitation and habitat alteration are pushing individual species toward extinction and may precipitate the collapse of entire ecosystems. Fishing pressure is continuing to increase in response to rising global demand and more efficient fishing technologies. To address anthropogenic impacts on marine ecosystems, management and conservation actions must be direct, strictly enforced, and adaptable. Priority should be allotted to those species that are highly visible and easily accessible, as these will likely experience extinction first. Invertebrates, in general, suffer from a lack of awareness and knowledge, which is exacerbated by the lack funding for basic research. The status of most invertebrate fisheries is unknown, and often the basic information required to develop management plans is lacking. Efforts and funding for marine conservation should thus be concentrated on invertebrate fisheries.

Molluscs account for nearly half of the reported, marine invertebrate catch worldwide. Although gastropods do not account for a large percentage of the catch, they play an important role in structuring rocky intertidal communities and are potentially important indicators of climate change. *Cittarium pica* (Linnaeaus, 1758) is a large gastropod with a disjunct distribution in the Tropical Northwestern Atlantic. It is an important artisanal fishery throughout its range and is commercially harvested in only the U.S. Virgin Islands and Colombia. In the mid-1800s, *C. pica* was fished to extinction in Bermuda due to overharvesting. It was reintroduced to Bermuda in 1982, where it is currently fully-protected. Following analysis of population growth and expansion, along with documentation of the reintroduction protocol and subsequent monitoring, this reintroduction was determined to be a success (Chapter 4). The current level of fishing pressure on *C. pica* is explained by a combination of socioeconomic factors and marine conservation status, including human population density, level of affluence, management rank, and coverage of marine protected areas (MPAs) (Chapter 1). Countries with a higher management rank do have lower fishing pressure, which suggests that management regulations have a positive affect on the population of *C. pica*, as expected. In contrast, countries with high coverage of MPAs have higher fishing pressure on *C. pica*. This is most likely because the majority of MPAs

within the territories and countries included in this study do not extend into the rocky intertidal habitat. Thus, understanding the interactions between socioeconomic motivations for fishing and marine conservation metrics is an important step in evaluating fishing pressure on and developing management plans for *C. pica*.

Understanding the socioeconomic motivation for harvesting the species and whether current management is adequate are not alone sufficient. To improve current regulations, predict population growth or decline, and to target locations for MPAs, knowledge and maps of the distribution of preferred habitat are needed. *Cittarium pica* inhabits the rocky intertidal mostly on windward shores. The distribution of rocky intertidal and other coastal habitats in Bermuda, where it was reintroduced, had not been assessed prior to this project. High-resolution imagery was used to generate maps of the intertidal habitats of Bermuda, which indicate that most of the coastline of Bermuda consists of rocky intertidal (Chapter 2). The population of *C. pica* in Bermuda is projected to expand because much of the windward rocky shores are currently unoccupied. The distribution of *C. pica* on a local scale (within sites) is affected by the unique biological diversity and geomorphological complexity of the rocky intertidal (Chapter 3). Although extensive research has addressed community structuring in the rocky intertidal, visualization of distribution patterns on geomorphological structures is largely ignored or oversimplified. Geomorphological and topographic complexity influence local scale distributions of species and thus the broad-scale patterns. Intertidal zonation of *C. pica* is habitat-specific, illustrating weak zonation by size only within sites with low wave action and medium vertical relief. Classifying the rocky intertidal into habitat categories contributes to a new understanding of the observed zonation patterns. Because range boundaries of rocky intertidal species at high latitudes have reacted quickly to environmental conditions, species in the rocky intertidal may be useful as indicators of climate change and its impacts. Thus, documenting and interpreting the current distribution of rocky intertidal organisms is increasingly important.

Cittarium pica is a non-commercial, artisanal fishery throughout the Tropical Northwestern Atlantic, except in a few locations. It is managed in six territories and countries in the region, even though management is needed throughout. The species has also recently entered the aquarium trade, so exploitation rates are only going to continue to increase. To combat the high (and growing) demand for *C. pica*, I recommend developing a multi-faceted management plan, including maximum harvest size (1-gallon per day, per person), minimum landing size (62 mm), seasonal closure of the fishery (variable by location), and establishment of marine protected areas targeting the rocky intertidal habitat. Enforcement is of extreme concern, so involvement of the local fishers, community, and other stakeholders is vital throughout the process of development and implementation of management plans.

Dedicated to my parents,
who always believed I could do anything;
and to Michael,
who has been there for me and with me through it all.

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Do not let your fire go out, spark by irreplaceable spark,
in the hopeless swamps of the approximate,
the not-quite, the not-yet, the not-at-all.
Do not let the hero in your soul perish,
in lonely frustration for the life you deserved,
but have never been able to reach.
Check your road and the nature of your battle.
The world you desired can be won.
It exists, it is real, it is possible, it is yours.

- Ayn Rand

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Because of all of you, I am now a doctor, off to save the world, one snail at a time.

Introduction

Adventures in fisheries conservation: a snail's tale

> *'Just a snail' is the sum total of the conscious thought given by most of us to these creatures. Even when we become enthusiastic over the delicacy of form and color of a collection of shells, we think of them rather as an assemblage of inorganic crystals than as the homes of living individual animals, which have sought food and a mate, have travelled perhaps many miles in their lifetime, and experienced adventures as momentous to them as a shipwreck or a creeping barrage to us.*
>
> -- William Beebe (1932), "Snail Folk" in Nonsuch: Land of Water

Globally, fisheries are crashing, which is attributed mainly to overexploitation and habitat alteration (Lotze 2006; Robbins et al. 2006; Stobutzki et al. 2006; Worm et al. 2006). Overexploitation not only pushes individual species toward extinction (Martin 1984; Myers & Ottensmeyer 2005; Norse 1993) and negatively affects the world economy, but also may precipitate the collapse of entire ecosystems (Jackson 2001; Pandolfi et al. 2005; Scheffer et al. 2005). The term "fisheries" includes all aquatic species that serve as resources, including vertebrates (e.g., fishes, turtles, whales), invertebrates (e.g., crabs, shrimps, clams, snails), and algae (e.g., kelps). Fishing pressure is continually increasing in response to rising global demand due to rapid human population growth and rising international seafood markets (Jacquet et al. 2009; Lotze 2006; Pomeroy et al. 2006) along with more efficient fishing technologies (Lotze 2006; Pauly 2006; Pinnegar & Engelhard 2008). Increased demand for the crustacean resources of Alaska – king crabs (*Paralithodes* spp. and *Lithodes aequispina*), Tanner and snow crab s(*Chionoecetes* spp.), Dungeness crab (*Cancer magister*), and pandalid shrimps (*Pandalus* spp. and *Pandalopsis dispar*) – resulted in an expansion of the area fished and drove the development of more efficient extraction technologies (Orensanz et al. 1998). After twenty years of fishing at this higher intensity, most of these fisheries collapsed. A similar increase in demand for the hard clam or "quahog" (*Mercenaria mercenaria*) resulted in a five-fold increase in the harvest, made possible by the implementation of a mechanical harvesting technique that is significantly more efficient than hand-harvesting (Peterson 2002).

As species go commercially extinct, fishing pressure shifts to species lower on the food chain. This unique trend is called "fishing down the food chain," which results in the loss of top trophic levels (Pauly 1998; Scheffer et al. 2005). This loss causes a trophic cascade that affects all species in the focal ecosystem, directly through interactions between trophic levels and indirectly as fishing pressure shifts to the next largest species. For example, overfishing of the apex predators in the Gulf of Maine resulted in a 70% decline in the diversity of fishery landings, and led to the development of a "monoculture" fishery in which 80% of the current economic value is from American lobsters (Steneck et al. 2011). Within populations, many species are subject to "size-selective harvesting," which negatively affects population biology (Fenberg & Roy 2007) and results in a net loss of young because reproductive output in marine organisms is often scaled with size (Heino & Godø 2002; Sadovy 2001). Despite the many commercial extinctions (e.g., Peruvian anchovy, North Atlantic cod), demand for seafood products has resulted in an increase in exploitation (see Pauly et al. 2002). The combination of climate change and anthropogenic impacts will likely increase extinction rates and ecosystem collapse (Harley et al. 2006; Jackson 2001). To address anthropogenic impacts on marine ecosystems, including climate change, management and conservation actions must be direct, strictly enforced, and adaptable. The once common perception that the ocean is completely resilient against any impact of human exploitation is now widely acknowledged as a misconception (see Lotze 2006; Pauly 2006).

Habitat fragmentation and complete habitat loss are both common in marine ecosystems (Myers & Ottensmeyer 2005), although largely undocumented. This puts an increasing amount of pressure on the reproductive ouput of the remaining reproductive adults to disperse distances required to maintain genetic diversity. Overexploitation and habitat alteration typically result in reduction of population size, and these reduced populations are more likely to collapse. However, loss of subpopulations is often overlooked because the population as a whole may not appear overexploited (Mullon et al. 2005). Even with all of these alarming trends, the biggest threat to fisheries is likely inadequate knowledge of their basic biology, without which sustainable management and conservation plans cannot be implemented. Priority should be allotted to those species that are highly visible and easily accessible, as these will likely experience extinction first. Invertebrates, in general, suffer from a lack of awareness and knowledge, which is exacerbated by the lack funding for basic research (Cardoso et al. 2011). Over the past 60 years, invertebrate catch rates, mainly crustaceans and molluscs, have increased six-fold (Anderson et al. 2011), and the ornamental invertebrate trade (e.g., aquaria, curio) has grown into a major (unsustainable) industry (Rhyne et al. 2009). The status of most invertebrate fisheries is unknown, and often the basic information required to development management plans is lacking. Efforts and funding for marine conservation should thus be concentrated on invertebrate fisheries.

Cittarium pica as a Model System

Molluscs account for 48.2% of the reported, marine invertebrate catch worldwide (FAO 2011), 7.3% of which is gastropods. Although they do not account for a large percentage of the invertebrate catch, gastropods play an important role in structuring rocky intertidal communities (Underwood et al. 1983) and may serve as important indicators of climate change (see Helmuth et al. 2006 and references therein). *Cittarium pica* (Linnaeus, 1758) is a large, intertidal gastropod that has a disjunct distribution in the Tropical Northwestern Atlantic ecoregion (Spalding et al. 2007). It is an important artisanal fishery throughout the Tropical Northwestern Atlantic, and is commercially harvested (and managed) in a few territories and countries (see Chapter 1). Humans have harvested the species since they first arrived in the Caribbean 6,000-7,000 years ago (Crosby 2003; Fitzpatrick & Keegan 2007), eating the meat, and using the shells to make tools (O'Day & Keegan 2001), caulk for ships (Verrill 1902a, b), and as ornamentation (Fig. 1a-d). Today, the minimum size at which humans harvest *C. pica* in Costa Rica is 40 mm (Schmidt *et al.* 2002), but is ~25 mm in the Bahamas, Jamaica, Puerto Rico, and Turks and Caicos Islands (J. Cedeño, H. Nixon, & B. Riggs, personal communication; E.M., personal observation; see Chapter 1). Because of this, in most localities for which minimum take size is known, *C. pica* is fished before it reaches sexual maturity, an unsustainable practice. The species was fished to extinction in Bermuda in the mid-1800s, and successfully reintroduced in 1982 (see Chapter 4). There is no evidence that it was extirpated due to overexploitation elsewhere. By 2003, 21 Caribbean nations had established 55 no-take marine reserves, distributed across a diversity of habitats, including coral reefs, seagrass beds and mangroves (Appeldoorn & Lindeman 2003). However, these reserves do not extend into the rocky intertidal, which is the preferred habitat of *C. pica*, and there are no management plans for the species in most of its range even though they are desperately needed (see Chapter 1).

Evolutionary history and relationships

Cittarium pica is known since the Pleistocene (Clench & Abbott 1943), but has a scattered and mysterious fossil record (Fig. 1e-f). The genus *Cittarium* can be traced to the Upper Oligocene of Europe (Lozouet 2002). Despite how widespread it is today, *C. pica* is not present in Neogene deposits of two intensively studied locations, the Dominican Republic (Nehm & Budd 2008; Saunders et al. 1986) and Panama (Collins et al. 1996; Jackson et al. 1996). Fossils of other species in the intertidal (an erosional environment) are represented in these deposits. Specimens of *C. pica* are found in Pleistocene and Holocene deposits throughout the Caribbean, and are often associated with *Strombus gigas* (Berry 1939; Crosby 2003; de Waal 2006; Fitzpatrick & Keegan 2007; Jones 1985; Keegan 2003), which is commonly found in Neogene deposits in the Caribbean. The current distribution of *C. pica* must be linked to its historic range, so either it was uncommon in the Neogene or not present. The large, robust shells of *C. pica* have the potential for a long fossil record, but they are heavily biofouled, which damages the external structure and affects preservation probability (Best & Kidwell 2000).

Turbo pica Linnaeus, 1758 is the type species of *Cittarium* Philippi, 1847. *Livona* Gray, 1847 is an objective synonym of *Cittarium*. The common name for *C. pica* is officially West Indian topsnail (Turgeon et al. 1998), but the vernacular varies by location. Bermuda is the only location known to refer to *C. pica* as "magpie shell." "Wilke," "wilk," and "topshell" are common in Bermuda, Bahamas (Fig. 1a), and Turks and Caicos Islands. "Wilek" is the variation used in Jamaica. It is erroneously called "whelk" in the U.S. Virgin Islands and Barbados, which presents confusion with snails in the Family Buccinidae, which are the "true" whelks. "Burgau," "burgaux," and "burgos" are all common names used in the French Antilles. Territories and countries where Spanish is the dominant language (i.e., Costa Rica, Panamá, Puerto Rico), refer to *C. pica* as "burgao", "bwigo," or "cigua." Aruba, and presumably the whole of the Netherlands Antilles, refer to *C. pica* as "kiwa." It even has a unique common name in the aquarium trade, "Zebra Turbo."

AREA DE RESERVA DE NATUREZA

A pesca é permitida mas a colecção de caracóis marinhos e de outros animals da linha de costa é proibida.

O búzio (Alto Indian Ocidental - CITTARIUM PICA) é uma espécie inteiramente protegida sob as provisões do decreto lei de 1972 do departamento de pesca.

A colecção ilegal é punível por uma multa de $5,000 e por uma prisão até 1 ano.

Esta área é patrulhada pelo pessoal do departamento de pesca e dos parques e pela polícia marinha.

Telefone: 236-4201 para informar as autoridades da colecta ilegal.

Pela ordem do Ministro do Ambiente.

Figure 1: Photographs of (a) "wilke" for sale sign posted in a driveway of a private residence on New Providence Island, Bahamas, (b) *Cittarium pica* management sign posted on Cooper's Island, Bermuda, (c) small *C. pica* midden south of Whalehouse Bay on Salt Cay, Turks and Caicos Islands, (d) large *C. pica* midden near Sandy Ground, Anguilla, (e) *C. pica* fossils embedded in a coastal, limestone outcrop near Priory, Jamaica, and (f) *C. pica* fossils embedded in a coastal, limestone outcrop near Bathsheba, Barbados.

The family group allocation of *C. pica* is contentious. Although it tends to fall within the Superfamily Trochoidea, *C. pica* shifts between two trochoidean families, Trochidae and Turbinidae. Ultimately, its classification depends on which characters are used in the phylogenetic analysis. Based on an analysis of 43 morphological characters, *C. pica* is classified within the Family Trochidae (Hickman 1996). Based on three molecular characters (i.e., 18S, 28S, COI), *C. pica* has an affinity with the Family Turbinidae and shifts from the Tribe Monodontinae to Tegulinae (Williams et al. 2008). Aktipis and Giribet (2010) do not evaluate the family or tribe affinities, but in their analysis of seven molecular characters (i.e., 16S, 18S, 28S, COI, EF-1α, H3, MYO) the Superfamily Trochoidea is not monophyletic. The most recent phylogenetic analysis of Trochoidea, which included four molecular characters (i.e., 12S, 16S, 18S, COI), propose a clade consisting of *Cittarium* and *Tectus* (Williams *in-press*). In a previous analysis (Williams et al. 2008), *C. pica* was sister to a clade of *Tectus* species, so their close relationship is not novel. Whether the new clade, holds within phylogenetic analyses with additional taxa and characters remains to be tested.

General description and ecology

The external surface of the shell often has jagged black and white markings. However, there are several variations on the shell coloration, including stripe thickness, shape, and color, along with overall shell color (Fig. 2a-i). The shell patterning is often obscured by encrusting epibionts (Fig. 3a-i), such as calcareous (*Goniolithon* spp.) and filamentous algae, and shell-penetrating cyanobacteria, such as *Plectonema terebrans* (Randall 1964). Cyanobacteria may differentially erode the white areas of the shell (Robertson 2003), resulting in the black areas of the shell appearing raised in comparison to the white areas. Encrusting animals are also found on *C. pica* shells, including vermetid gastropods (e.g., *Dendropoma corrodens*), at least two species of barnacles, polychaete worms (e.g., *Spirorbis* sp.), and a foraminiferan (e.g., *Homotrema* sp.). In addition to the encrusting organisms, at least four species of patellogastropods (*Acmaea* spp.*,* *Lottia* spp.) and two species of juvenile polyplacophorans (*Acanthopleura* spp.) occur on *C. pica* shells (Fig. 4a-e). The limpets and chitons often occur on the ventral surface of the shell near the umbilicus. All other species occur almost exclusively on the dorsal surface of the shell. Neritid gastropod egg cases also occur on the dorsal surface of *C. pica* shells (Fig. 4f). Along with external symbionts, the pea crab, *Pinnotheres barbatus* (Desbonne, 1867), lives in the mantle cavity of *C. pica*, and adults of the large, land hermit crab, *Coenobita clypeatus* (Herbst, 1791), depend on *C. pica* shells because it is the only shell available with an aperture large enough for adult hermit crabs (Fig. 5a-b).

Cittarium pica inhabits the rocky intertidal, mostly on windward shores (see Chapters 2 and 3) throughout the Tropical Northwestern Atlantic. Its range extends north to Bermuda, east to Barbados, south to the Caribbean coast of Panamá, and west to the Yucatán Peninsula in Mexíco. Previously published reports (Debrot 1990; Hess et al. 1994; Hoffman 1980; Randall 1964; Robertson 2003 and references therein; Toller & Gordon 2005) suggest that *C. pica* exhibits size-specific zonation. However, their distribution is habitat-specific, illustrating weak zonation by size only within sites with low wave action and medium vertical relief (see Chapter 3). The species

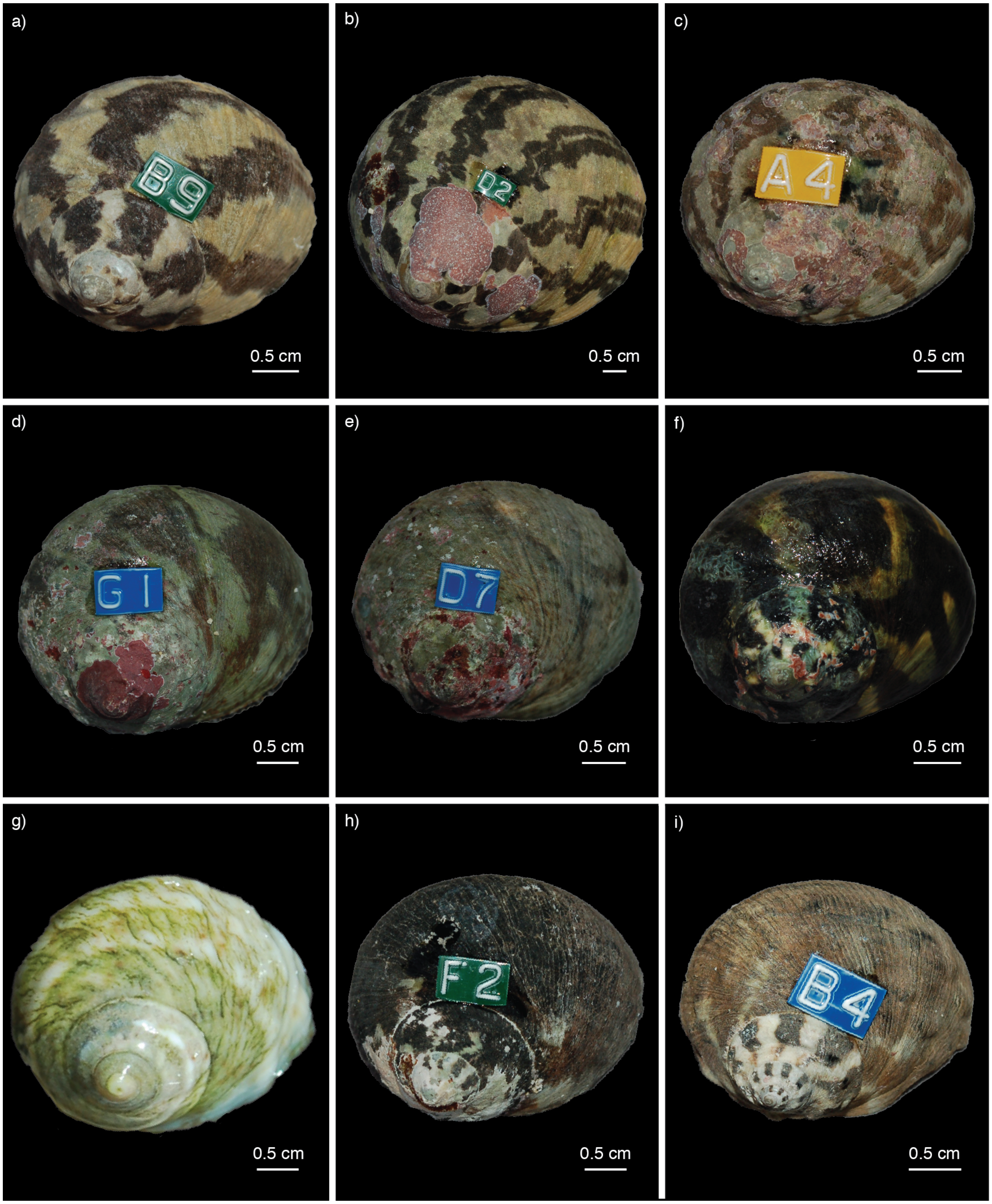

Figure 2: Photographs of variations in shell patterning; (a) thick black stripes, from Sherrick's Bay, Anguilla, (b) black strips with white vein through the center, from Sherrick's Bay, Anguilla, (c) brown stripes, from Bathsheba, Barbados, (d) splotchy, from California Dunes, Aruba, (e) no stripes, from California Dunes, Aruba, (f) patchy turquoise, from Playa Bonita, Costa Rica, (g) white with green algae staining, from California Dunes, Aruba, (h) nearly black, from Long Pond Bay, Anguilla, and (i) nearly brown, from Plage de l'Anse, Basse-Terre, Guadeloupe.

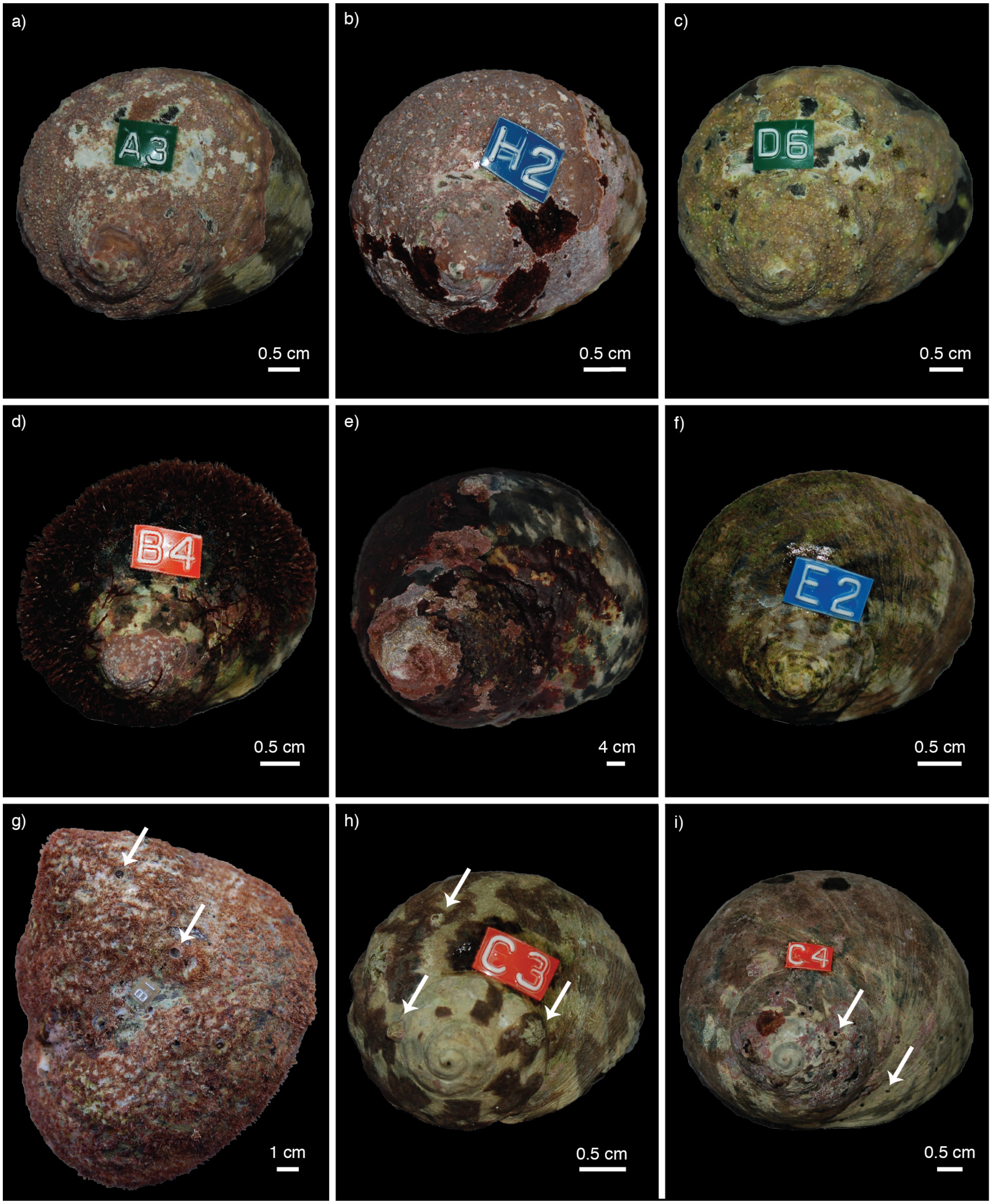

Figure 3: Photographs of encrusting organisms found on *Cittarium pica* shells, including (a) pink coralline alga, from Half Moon Bay, Mexíco, (b) purple coralline alga, from Plage de la Chapelle, Grand Terre, Guadeloupe, (c) orange alga, from Isla Mujeres, Mexíco, (d) filamentous red alga, from Pigeon Beach, Antigua, (e) filamentous red alga, from Playa Bonita, Costa Rica, (f) filamentous green alga, from l'Anse Noir, Trinidad, (g) *Dendropoma corrodens*, from Rocky Hole, Bermuda, (h) barnacles, from Pigeon Point, Antigua, and (i) *Spirorbis* sp., from Pigeon Point, Antigua.

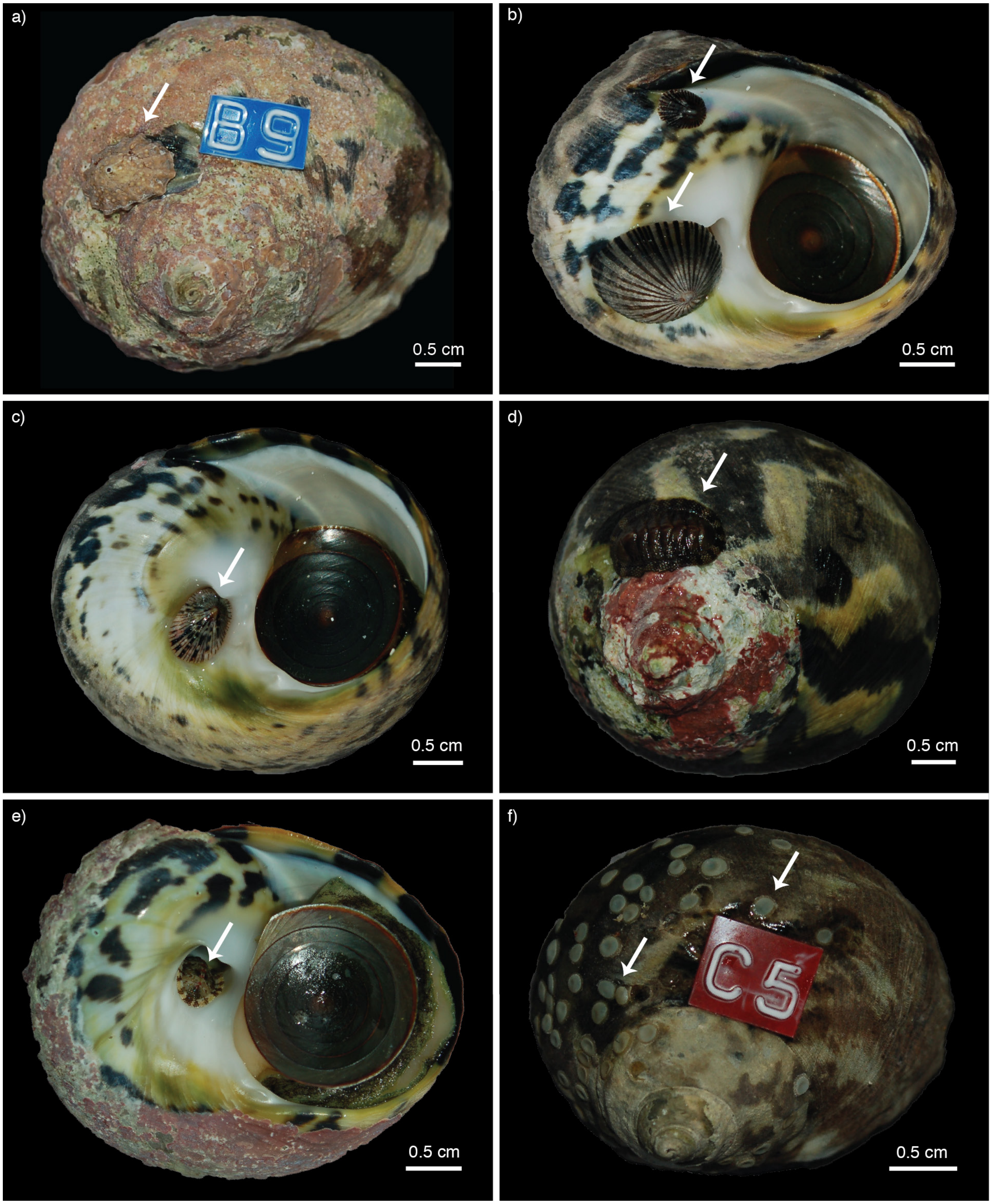

Figure 4: Photographs of epibionts found on *Cittarium pica* shells. Arrows point to featured epibiont(s) in each photograph; (a) one species of limpet and its home scar, from Andicuri Beach, Aruba, (b) two species of limpets, from Long Pond Bay, Anguilla, (c) *Acmaea antillarum*, from Long Pond Bay, Anguilla, (d) *Acanthopleura* sp., from Playa Bonita, Costa Rica, (e) *Acanthopleura* sp., from Isla Mujeres, Mexíco, and (f) nerite egg cases, from Playa Manzanillo, Costa Rica.

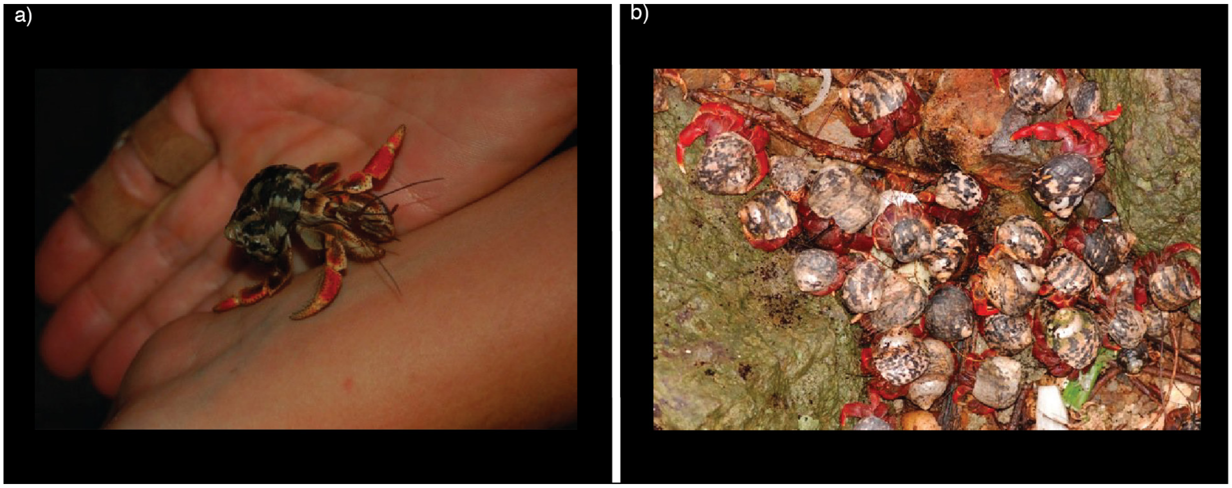

Figure 5: Photographs of *Coenobita clypeatus* in *Cittarium pica* shells; (a) *C. clypeatus* from Cabo Rojo, Puerto Rico, and (b) *C. clypeatus* foraging on coffee grounds from St. John, U.S. Virgin Islands.

is most active at night (Debrot 1990), and reacts to shading by dropping from the rocks, which is especially common to populations in Jamaica (E.M., personal observations) and Colombia (Bandel 1974). This behavior is likely an adaptation to aerial predators, such as Oyster Catchers, *Haemotopus ostralegus* (Randall 1964). *Cittarium pica* is sexually mature at approximately 32-34 mm (Robertson 2003). Growth rate data gathered through tag-recovery work done from 2003-2007 in Bermuda indicates that growth rate is inversely related to size (see Chapter 4). These data suggest that *C. pica* is approximately 2.5 years old at sexual maturity. *Cittarium pica* has lecithotrophic, planktonic larvae, with a planktonic larval duration (PLD) of 3-7 days (Bell 1992). At some locations within its range (e.g., Bahamas, U.S. Virgin Islands), *C. pica* spawns in the late fall to early winter (Bell 1992; Randall 1964), but in Bermuda it spawns continuously throughout the year (Meyer & Coates 2005). The species sometimes releases a white exudate upon disturbance. This fluid was first suggested to cause alarm in nearby gastropods (Bandel 1974) and later re-interpreted as a cloud of sperm (Robertson 2003). Hickman et al. (*in-prep*) examine the fluid and confirm that it is not sperm; the chemical composition of the white exudate remains unknown.

Chapter Summaries

Fishing pressure on a snail caught in a matrix of culture, economics, and geography

Successful management of exploited species is complicated by the interactions between socioeconomic and conservation status. Socioeconomic status impacts the level of subsistence harvesting, but conservation of selected species or habitats impacts those that are not protected. These interactions are especially apparent in small-scale fisheries targeting easily accessible species, such as those in the rocky intertidal. In this study, I question whether the level of fishing pressure on *C. pica* varies across Bermuda and the Wider Caribbean, and whether this variation can be attributed to socioeconomic and marine conservation status. I also address whether current management practices are sufficient for sustaining adequate populations of this vital resource. I compiled fishery background information, socioeconomic statistics, and marine conservation data from multiple sources for this investigation, and conducted surveys of *C. pica* population structure in Bermuda and 13 territories and countries throughout the Wider Caribbean. The species is fully-protected by-law in Bermuda, and managed in three other territories (i.e., Guadeloupe, Puerto Rico, U.S. Virgin Islands). The level of fishing pressure is not constant across the region; it is lowest in Bermuda, the Turks and Caicos Islands, and the Bahamas. Of the three territories where the fishery is regulated, only the population in the U.S. Virgin Islands is comparable to that of Bermuda, indicating that the management plan in place is successful. The level of fishing pressure is neither explained by socioeconomics nor marine conservation status, but rather a combination of the two, suggesting that understanding the interactions between these metrics is an important step in predicting fishing pressure and managing the species. To combat the high fishing pressure on *C. pica*, I recommend developing a multi-faceted management plan, including maximum harvest size, minimum landing size, seasonal closure of the fishery, and establishment of marine protected areas targeting the rocky intertidal habitat. Enforcement is of extreme concern, so involvement of the local fishers, community, and other stakeholders is vital throughout the process of development and implementation of management plans.

Scale-dependent assessment of intertidal habitat projects population expansion of West Indian topsnail (Cittarium pica) *in Bermuda*

Habitat assessments are essential components of biological conservation planning. Mapping the geographic distribution of preferred habitat is as important as mapping species distribution for establishing management plans and targeting locations for protected areas. The distribution of coastal habitats in Bermuda was not assessed prior to this study, although it could provide data essential to the conservation and management of coastal fisheries and ecosystems. *Cittarium pica* is an important fishery resource throughout the Tropical Northwestern Atlantic and is found along rocky intertidal shores. The species was recently reintroduced to Bermuda, following an extirpation event in the mid-1800s. Here, we investigated the effect of image resolution on the extent of inferred intertidal habitat and generate an intertidal habitat map for Bermuda. We combined the distribution of rocky shores with population survey data to project future population size of *C. pica*. We mapped the distribution of coastal habitats in Bermuda using a high-resolution image and manual classification. The coastline length was calculated at different resolutions using the *R* package *rgeos*. To confirm that moderate-resolution imagery has comparatively little capability for mapping intertidal habitats, the classified pixels were overlaid onto a Landsat image and were used in supervised classifications. To test whether the distribution of *C. pica* correlates with its preferred habitat (i.e., windward rocky shores), we overlaid the distribution of *C. pica* onto the intertidal habitat map. The population size was predicted using the length of preferred habitat and population density. Of the four habitat classes mapped, the Bermuda coastline is dominated by rocky shores. Our results suggest that overall coastline length depends on image resolution. Using low resolution imagery results in a drastically low estimate of coastline length. Unsurprisingly, supervised classifications of the Landsat image were not highly successful. The classifiers often overfit the data and could not discern between rock, sand, soft sediment, and seawall. The distribution of *C. pica* closely matches the distribution of rocky shores, but much of this habitat is unoccupied. We project that the *C. pica* population in Bermuda will expand because much of the windward rocky shores are currently unoccupied. This prediction, however, depends on the accuracy of intertidal habitat mapping, which is directly linked to image resolution. The sensitivity of linear features to image resolution is not only pertinent to intertidal habitat mapping, but also to other dynamic habitats and transition zones. As global climate continues to change, we must be able to accurately map the extents of these sensitive habitats before we can understand and predict how changes will affect them.

Habitat preferences and intertidal zonation of Cittarium pica*: what rocks their world*

The rocky intertidal is characterized by unique biological diversity and geomorphological complexity. A variety of forces shape the coastal rock features found in this globally distributed habitat. Although extensive research has addressed community structuring in the rocky intertidal, visualization of distribution patterns on geomorphological structures is largely ignored or oversimplified. For example, intertidal zonation is typically treated as a linear, continuous habitat, but rocky intertidal ecosystems are often not this neatly organized because of the variation in rock features and environmental gradients. This study re-emphasizes the importance of observational data and proposes a new illustrative method for visualizing rocky intertidal shores. The Tropical Northwestern Atlantic is a unique geographic region with abundant rocky intertidal habitat. *Cittarium pica*, which occupies the rocky intertidal, is an important gastropod fishery in the region. This location and species are an ideal case study for investigating fine-scale distribution within rocky intertidal systems and the results will provide important information to resource managers throughout the region. This study includes 48 field sites from 17 territories or countries across the Tropical Northwestern Atlantic. To document intertidal zonation and habitat preferences of *C. pica*, I completed detailed field observations and quantitative assessments. These data were used to delineate rocky intertidal habitat categories and to create cross-sections of the rock features that characterize each category. To determine intertidal zonation patterns of *C. pica*, I mapped size and location of individual snails onto these cross-sections. Unlike previous studies, the data reported here suggest that size-specific zonation of *C. pica* does not follow a simple linear relationship with vertical position. Regardless of the habitat category or the size of the snail, *C. pica* is most common at or near mean low water (MLW). Individuals <10 mm are most common below mean high water (MHW) for all habitats. The largest snails are rarely found above MHW; they are most common at MLW. Dividing the rocky intertidal into habitat categories can lead to a better understanding of the observed zonation patterns. Because range boundaries of rocky intertidal species at high latitudes have reacted quickly to environmental conditions, species in the rocky intertidal may be useful as indicators of climate change and its impacts. Thus, documenting and interpreting the current distribution of rocky intertidal organisms is increasingly important. The method developed herein provides the foundation for illustrating and understanding species distributions at multiple spatial and temporal scales.

Post-extinction recovery of Cittarium pica *in Bermuda*

Translocation of species is a useful and increasingly applied tool in conservation biology and species management. Reintroductions, one type of translocation, can be used in combination with mitigation of anthropogenic impacts to restore species diversity and the corresponding ecosystem functions. The goal of any reintroduction program is to re-establish the target species in a specific location where it does not exist. Determining when reintroductions are "successful" is often complicated. The simplest documentation of success is when the population is self-sustaining. Marine reintroductions are rare, perhaps because documentation of marine extinctions is problematic, which is mainly due to the difficulty with determining when there are no individuals remaining. One marine extinction, that of *Cittarium pica* in Bermuda, has not been well-documented in the scientific literature, nor have the reintroduction attempts. The third reintroduction attempt occurred in 1982. Although the Bermuda Department of Conservation Services has been monitoring the species since this last reintroduction, the last survey was conducted in 2003 and no formal analysis or evaluation has been published. The objectives of this study are to (1) assess population expansion, (2) evaluate whether the reintroduction was successful, and (3) provide management recommendations for *C. pica* in Bermuda. To assess the status of the recovery of *C. pica*, population surveys were conducted in 1989, 2000, 2003/2004, and 2007. Data are reported from 48 sites from the 2000 surveys, and six sites from the follow-up surveys. To determine the status of local populations, I compared population structures for four sites over two to three survey years. I also generated a map of the 2000 field sites, with size histograms plotted by location to evaluate the population expansion. The population of *C. pica* in Bermuda has recovered successfully and expanded from Nonsuch Island, where it was released, to as far west as Sea Swept Farm and as far east as Red Hole Cove. By 2000, the population had grown to nearly 4,000 individuals. Successful reproduction is evident across the island. Overall, the reintroduction of *C. pica* to Bermuda is an ongoing success story. Even though the details of the reintroduction were not determined a priori, most of the criteria for success were fulfilled. No re-stocking, or release of additional individuals, is needed because the population is self-sustaining. This study highlights the need for greater allocation of resources for continued monitoring and additional enforcement of current regulations, which have been violated.

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Chapter One

Fishing pressure on a snail caught in a matrix of culture, economics, and geography

> *At root, fisheries management involves managing people. It is a process in which humans develop rules and institutions to constrain exploitative effort on marine resources in the common good... If fisheries management rules are to be effective, they must be supported by resource users.*
>
> -- James M. Acheson (2005),
> "Developing Rules to Manage Fisheries: A Cross-Cultural Perspective"

INTRODUCTION

The conservation of a species, especially one that is exploited for human use, is often confounded by a complicated matrix of cultural history, economic status, and political geography. Overexploitation must be addressed by not only understanding the biological influences on population size and catch rates, but also the "non-biological components," such as the socioeconomic characteristics of the surrounding communities (Balmford & Cowling 2006; Clausen & York 2008). Biological and environmental characteristics may control the potential geographic distribution of an exploited species, but the socioeconomic motivations for harvesting the species and its political geography govern its management. Consideration of local traditions and economic status is vital to conservation planning (Leslie 2005; Lundquist & Granek 2005). In most cases, management plans cannot be successfully implemented without the cooperation of the local community, so understanding economic viability on a local scale (Andrew et al. 2007; Kronen et al. 2010) and socioeconomic factors on a national scale are important components of species management. Further, small-scale fisheries are an important economic component of fisheries around the world, and they should not be ignored because they too have a discernible impact on populations (Pinnegar & Engelhard 2007).

Detailed quantitative data, such as landing size or catch per unit effort (CPUE), are often missing and irretrievable for small-scale fisheries (Andrew et al. 2007). One method for obtaining such data involves interviewing local fishermen (Weeks et al. 2010) to gather data on their catch sizes. This can be a very rewarding task, but can also be labor intensive for species with a locally dispersed or geographically disjunct distribution, especially if the species is already overexploited. In the absence of such data, size structure can be used as a proxy for fishing pressure (e.g., Foster & Hodgson 2000; Haedrich & Barnes 1997; Moreno et al. 1986). If there is a size above which non-human predation does not occur, high fishing pressure can be diagnosed when a decrease in, or absence of, individuals above this threshold size is observed. Fishing pressure is often linked to economic development, as fishing technologies, such as more efficient gear and faster boats, become more accessible and thus more widely used (Pinnegar & Engelhard 2007).

To evaluate the economic development in a country, gross domestic product (GDP) per capita, urbanization, and population density are useful metrics and can be compared with biodiversity (see Clausen & York 2008) or measures of fishing pressure. In four major regions of the world – Africa, Asia, Europe, and the Middle East – fish consumption is positively correlated with GDP per capita but not affected by urbanization (York & Gossard 2004). However, Czech et al. (2000) identified urbanization as the most common factor contributing to the decline of species listed as threatened or endangered by the U.S. Department of Fish and Wildlife; urbanization is implicated for 31% of the listed species. They further suggest that economic growth in general is directly linked to species endangerment. Urbanization depletes habitat and increases the intensity of resource extraction (Czech et al. 2000). Even though this occurs mainly on land, marine habitats are indirectly affected through increased sedimentation associated with deforestation and altered erosion patterns associated with coastal development (e.g., beach replenishment, shoreline hardening structures). With 39% of the world's population living within 100 kilometers of a coastline (World Resources Institute 2001), the effects of human modification and increased pressure on marine resources are apparent. This is especially evident on islands, as high population density can quickly lead to overexploitation of marine fisheries, especially those that are easily accessible (see Thomas 2001), likely because access to alternative sources of protein is limited.

Political geography directly affects management of a species and establishment of marine reserves because these are often governed by territorial boundaries of human populations, rather than population connectivity of the target species (Cumming et al. 2006). As such, species or populations of species that are contained within few political boundaries are easier to protect than those that cross many international borders. Species or populations that extend across political boundaries demand international cooperation when developing conservation and management plans, which is inherently more difficult as the number of countries involved increases. The "Wider Caribbean" region, for example, is densely packed with individual political entities, including 22 countries and 12 overseas departments and territories (Barker 2002). Because of this, management of fisheries that are regionally distributed in the Wider Caribbean could involve up to 34 individual political entities, encompassing a wide array of cultural and economic diversity.

Within the Wider Caribbean, most economies are based on tourism, encompassing 17% of GDP (Dulal et al. 2009), with the exception of the five nations whose economies are based on oil and gas exploration – Mexíco, Republic of Trinidad and Tobago, United States, and Venezuela (Barker 2002). In either case, high GDP indicates a shift from subsistence to industry-based living, which is reflected in fishing pressure within artisanal fisheries. The expected trend is an initial decrease in fishing pressure on a local scale, with the potential to increase over time if the resource maintains cultural value or if demand escalates due to tourism. There are over 150 managed fisheries in the Caribbean, nine of these species are currently listed as overfished and three entire families are listed as at-risk, but the condition of nearly all of these stocks is unknown (Appeldoorn 2008). The West Indian topsnail, *Cittarium pica* (Linnaeus, 1758), is an important artisanal and commercial fishery throughout the Wider Caribbean, ranking as the second most important gastropod fishery (Flores & Talarico 1981; Randall 1964; Schmidt et al. 2002) and the third overall invertebrate fishery in the region (1st=*S. gigas*, 2nd=*Panulirus argus*, Caribbean Spiny Lobster). This species is currently not officially listed as either overfished or at-risk, but is considered overexploited or "imperiled" in many locations throughout the West Indies (Flores & Talarico 1981; Randall 1964; Rodríguez 2000).

Focusing on a single fishery, this study explores the relationship between population structure of *C. pica* and metrics of socioeconomic and marine conservation status, addressing the following four questions: (1) How is fishing pressure on *C. pica* regionally distributed? (2) Does socioeconomic status drive the fishery? (3) Does marine conservation status affect fishing pressure? This research also evaluates the status of the *C. pica* fishery in 14 territories and countries, determines whether current management strategies are sufficient, and provides a foundation for establishing local and regional management plans for *C. pica*.

METHODS

Compilation of Fishery Background Information

Cittarium pica is a large, rocky intertidal gastropod with a disjunct distribution in the Wider Caribbean region and Bermuda. Humans have exploited *C. pica* for food, bait, tools, and decoration since their first arrival in the Caribbean 6,000–7,000 years ago (Crosby 2003; Fitzpatrick & Keegan 2007; O'Day & Keegan 2001). However, fishing pressure on *C. pica* has increased in recent years due to overexploitation of another gastropod fishery, *Strombus gigas* (J. Cedeño & B. Riggs, personal communication). The shift in fishing pressure to *C. pica* has prompted some territories to begin monitoring and managing the species (e.g., Bermuda, Cayman Islands, Guadeloupe, Puerto Rico, U.S. Virgin Islands). The species experienced a local extinction in Bermuda in the 1820s, but was reintroduced in 1982. Following a near-devastating fishing event in 1989 (Wingate 1989), the species was fully-protected in 1989 under the Fisheries (Protected Species) Order of 1978, which is part of the Bermuda Fisheries Act of 1972 (Wingate 2006). Bermuda is currently the only location where harvesting *C. pica* is prohibited. Across most of its range, *C. pica* is actively fished and not included in fisheries management plans. Today, it is a non-commercial, artisanal fishery, except in the U.S. Virgin Islands (Sjoken & Uwate 2005; Toller & Gordon 2005) and Colombia (Arango & Merlano 2006). It is well-established in the Wider Caribbean as a local delicacy. Considering that *C. pica* is conspicuous, highly accessible, and has an unrestricted harvest that is increasing throughout most of its geographic range, it is at risk of additional local extinctions due to overexploitation.

Cittarium pica is sexually mature at approximately 32-34 mm (Robertson 2003). After compiling cohort-based growth rate data from the literature (Bell 1992; Debrot 1990; C. Jantzen-Marson, unpublished data; Randall 1964) with direct growth rate data collected in Bermuda (E.M., unpublished data), I calculated that *C. pica* grows to approximately 25 mm after two years and 32 mm after 2.5 years. In the Bahamas (Bell 1992) and U.S. Virgin Islands (Randall 1964), recruitment is greatest in January, but in Bermuda, there is no evidence for a peak recruitment period (Meyer & Coates 2005). This temporal and geographic fluctuation in spawning behavior complicates the interpretation of size structure data from a single collection event. The minimum size at which humans harvest the species in Costa Rica is 40 mm (Schmidt et al. 2002), but is ~25 mm in the Bahamas, Turks and Caicos Islands, Jamaica and Puerto Rico (J. Cedeño, H. Nixon, & B. Riggs, personal communication; E.M., unpublished data). The latter is an unsustainable practice because *C. pica* is being fished before it reaches sexual maturity (Thomas 2001). Non-human predators of the species, which include other molluscs (Randall 1964; Wodinsky 1969), lobsters (Herrnkind et al. 1975), fishes (Warmke & Erdman 1963), and birds (Randall 1964), eat individuals that are 45 mm in width or less (E.M., unpublished data), thus humans are the only predator who harvests the species above 45 mm.

Study Sites

To collect data on population size structure of *C. pica*, I conducted field research over four summers, in 2007-2010. Data were compiled on geographic distribution and size structure of *C. pica* throughout the West Indies. I used these data as a proxy to assess *C. pica* fishing pressure and population status within each territory and country visited. Additionally, I compiled information for each territory and country on fishery management of *C. pica*, socioeconomic status, and the marine protected areas (MPAs) present.

The study area included Bermuda and 13 territories and countries in the Wider Caribbean (Fig. 1). The territories and countries, other than Bermuda, include (from east to west and north to south): The Bahamas, Turks and Caicos Islands (United Kingdom), Jamaica, Puerto Rico (United States), U.S. Virgin Islands, Anguilla (United Kingdom), Antigua and Barbuda, Guadeloupe (France), Martinique (France), St. Vincent and the Grenadines, Barbados, Republic of Trinidad and Tobago, and Aruba (Kingdom of the Netherlands). Territories and countries were chosen to maximize both the geographic coverage of *C. pica* populations and the variability in socioeconomic status, while maintaining feasibility.

Assessment of Fishery

To identify the location(s) of the largest populations, I documented the island-wide distribution of *C. pica* before choosing 1-4 sites per island. The number of sites chosen depended on the size of the island and the distribution of *C. pica* on the island. To determine the level of fishing pressure, I conducted population surveys at each site. These two-hour surveys consisted of recording the length – defined by the longest distance across the dorsal surface of the shell that transects the aperture (Fig. 2) – for up to 350 (or all) of the snails present. Due to the high variation in habitat complexity between sites (i.e., beach rock, boulders, carbonate platform, coral rubble, rip-rap), accurately documenting population density was not possible.

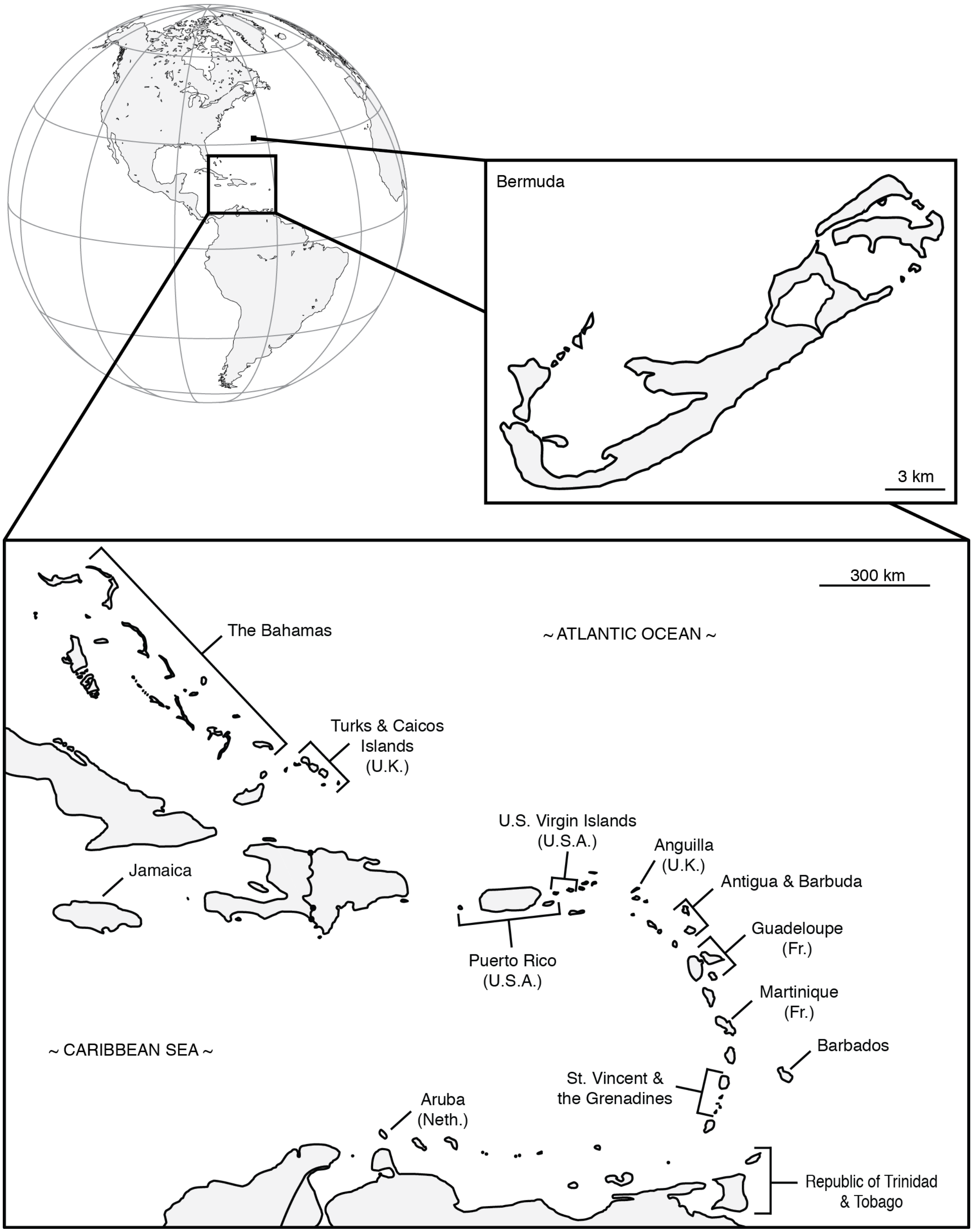

Figure 1: Islands within the West Indies where sampling was conducted are marked with stars. Bermuda is provided as an inset map because it is not part of the Wider Caribbean; it is located approximately 1,080 kilometers southeast of Cape Hatteras, North Carolina and about 1,700 kilometers northeast of Miami, Florida.

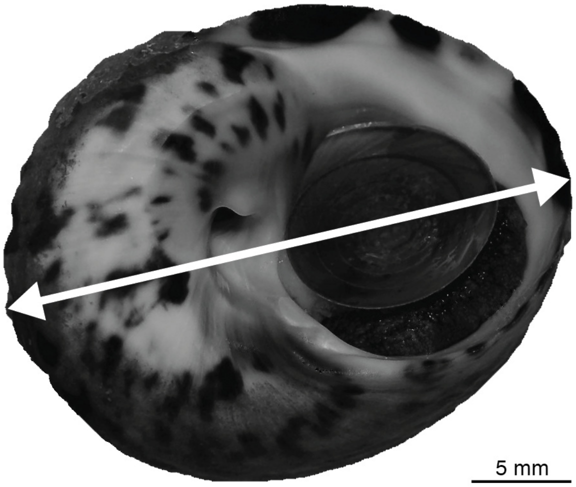

Figure 2: Photograph of *Cittarium pica*. The arrow identifies its width (28.2 mm), which is defined as the maximum distance across the dorsal surface of the shell that transects the aperture.

Compilation of Socioeconomic Statistics and Marine Conservation Data

To identify the socioeconomic motivations for harvesting *C. pica*, I compiled economic development statistics, including human population density (individuals/km^2), GDP per capita (current US$), unemployment rate (%), and urbanization rate (%). These data were acquired from UNData (http://data.un.org), World Development Indicators (World Bank 2010), World Factbook (CIA 2009), and Tableaux Économiques Régionaux (INSEE 2009). The "national" statistics were used for all islands within a given territory or country, because GDP per capita, unemployment rate, and urbanization rate were not available by island or by site. These island and regional socioeconomic data are sufficient for this study because the focus is on fishing pressure and motivations for harvest motivations on a national level.

To determine the marine conservation status within each territory or country, I compiled data on four conservation factors: (1) size of MPAs, (2) International Union for Conservation of Nature (IUCN) designation of the MPAs, (3) total marine area within the Exclusive Economic Zone (EEZ) of each territory and country, and (4) management status. Data on the first three factors were acquired from the World Database on Protected Areas (IUCN & UNEP 2010) and Spalding et al. (2001). I compiled management status of *C. pica* within each territory or country from the literature or by directly contacting fisheries managers (see Appendix 1, Table A1.1). These four factors were used to create two marine conservation metrics: (1) coverage of MPAs (i.e., total area protected divided by total marine area) and (2) management rank. A "management rank" was assigned to each territory or country (see Appendix 2) and calculated based on the following criteria: fully-protected (+15), seasonal closures of the fishery (+4), minimum take size enforced (+2), number of MPAs that are not designated by IUCN (+1 if 10-19, +2 if 20-29, +3 if ≥30), number of MPAs present in IUCN category Ia, Ib, II, or III (+2 if only 1, +3 if >1), and number of MPAs present in IUCN category V or VI (+1 if only 1, +2 if >1). Localities where the species is fully-protected received a score of 15 regardless of the other criteria, whereas localities where the species is not protected through legislation could not receive a score higher than 14. The score for all criteria were summed for each territory and country to determine the management rank value.

Data Analysis

To test for differences between the size structures of populations in each territory and country, I conducted a one-way analysis of variance (ANOVA) in JMP v8.0 (SAS Institute 1998). Because when the species spawns or if it spawns at the same time throughout its range is uncertain, I excluded all individuals that were less than 25.0 mm in width. This removed recently settled individuals and sub-adults. Within this subset, only the individuals in the top 15% by size within each territory and country were maintained because *C. pica* is subject to size-selective harvesting (Fenberg & Roy 2007) in which fishers concentrate their efforts on the largest individuals within a population (e.g., Ceccherelli et al. 2011; Foale & Day 1997; Foster & Hodgson 2000). Focusing the analyses in this way should reflect recent fishing pressure by including only the largest individuals and a sample size that is proportional to the population size, which itself is another indicator of fishing pressure. This percentage also allows for each population to have a minimum of five size points maintained, which is required for both the ANOVA and the models described below. The sample sizes among territories/countries are uneven, so Tukey's HSD test with the Tukey-Kramer modification was conducted, which uses the harmonic mean to determine which populations have significantly different-sized snails (Quinn & Keough 2002). Specifically, this test addressed whether the population on Bermuda, where the species is fully-protected, contains significantly larger-sized individuals than all other locations. Histograms bins were produced in *R* (2009) and histogram figures were generated in Microsoft Excel v.12.3.0 (Microsoft Corporation, 2007) to illustrate size distributions in each territory and country.

To test whether minimum landing size (MLS) regulations are well-enforced, I compared the distribution of size below the size restrictions set in the territory to the same distribution in Bermuda, where *C. pica* is fully-protected. This is the only test for which data were used from the initial subset of the data (i.e., individuals greater than 25.0 mm), rather than the final subset of the data as described above (i.e., only the top 15%). Boxplots were generated in *R* (2009) using the *boxplot* function, and a Mann-Whitney U-test was conducted using the *wilcox.test* function.

To test for inter-parameter correlation, I calculated Spearman's correlation coefficients (r) for the socioeconomic and marine conservation metrics using the *cor.test* function in R (2009). In linear models, it is difficult to determine whether correlated variables have an independent contribution to explaining variation in the dependent variable. Because of this, if the correlation analysis revealed any metrics to be highly correlated, I collapsed the variables into a single metric using a principle components analysis (PCA) in JMP v8.0 (SAS Institute 1998). Principle components (PCs) were retained if eigenvalues were greater than one (Norman & Steiner 1998; Quinn & Keough 2002). To establish whether there is a linear relationship between each parameter and the dependent variable, I produced scatterplots for all of the parameters and conducted basic linear regressions. These tests are important because linearity is an assumption of the models described below, and they establish whether the relationship between each parameter and the dependent variable is positive or negative, which is important for model selection. Parameters were transformed prior to any analyses to achieve normality and to remove any affect of unit-choice on the results. Size and human population density were natural-log-transformed, and

GDP per capita (US$, current) was log-transformed. Unemployment rate, urbanization rate, and coverage of MPAs were arcsin-square-root-transformed. I chose these transformations based on the standard transformations recommended for similar parameters.

To determine which variables have a significant effect on snail size, I generated linear regression models (LMs) for each set of variables independently (e.g., socioeconomic metrics, marine conservation metrics) and in combination. I generated LMs using the *lm* function in *R* (2009). Models that produced inaccurate relationships between the parameters and the dependent variable were removed from consideration. I identified the strongest models by comparing corrected Akaike's Information Criterion (AIC_C). Prior to model selection, I conducted the non-constant variance score test (Breusch & Pagan 1979; Cook & Weisberg 1983) with the *ncvTest* function in the *car* package (Fox 1997) in *R* (2009). Significant p-values for this test indicate that the data are heteroscedastic, so robust standard errors should be generated for the LMs. To do this, a heteroscedasticity consistent covariance matrix (HCCM) was generated using the *hccm* function in the *car* package. The HCCM was generated using the HC3 modification, which is recommended by Long and Ervin (2000) for small sample sizes. Robust standard errors were then generated with the HCCM using the *robust.se* function in the *car* package. Using robust standard errors improves the p-values produced without altering the coefficient estimators.

RESULTS

Assessment of the Fishery, Socioeconomic Status, and Marine Conservation Status

Management plans exist in only four of the territories and countries visited: Bermuda (Wingate 2006), Guadeloupe (L. Le Mesnager, personal communication), Puerto Rico (Jiménez 2006; Schmidt et al. 2002), and U.S. Virgin Islands (Schmidt et al. 2002; Sjoken & Uwate 2005; Toller & Gordon 2005). I contacted the managers in all of the territories and countries visited, and no others reported *C. pica* as a managed species (see Appendix 2, Table A2.1). *C. pica* is still fully-protected in Bermuda and violating the Fisheries (Protected Species) Order is subject to a US$5,000 fine and/or a six-month jail sentence. In spite of these strict penalties, illegal harvesting still occurs. Wingate (2006) suggests that this is partly due to a rising immigrant population who are unaware of the regulations. However, local fishermen were responsible for the two illegal harvesting events documented by the Bermuda government (K. Coates, personal communication). There are MLS regulations in Guadeloupe of 40 mm (L. Le Mesnager, personal communication) and Puerto Rico of 63 mm (Schmidt et al. 2002), although enforcement of the regulation in Puerto Rico is weak (J. Cedeño, personal communication). The U.S. Virgin Islands established no-take reserves specifically targeting the species, MLS restriction of 62 mm, a six-month seasonal closure of the fishery from 1 April to 30 September, and a maximum harvest size (MHS) of one gallon (in shell) per person, per day (Sjoken & Uwate 2005; Toller & Gordon 2005). This is the only territory or country included in this study where the species is commercially harvested, and thus the only location for which there exists landing data. The price per pound (in the shell) for *C. pica* in the U.S. Virgin Islands rose steadily from $2.25 in 1974 to an average of $9 in 1998; it later fell to $2.00 in 2003 (Holt & Uwate 2004). In the conservation plan of 2005 for this territory (Sjoken & Uwate 2005), *C. pica* was included on a list of "species of greatest concern". In The Bahamas, artisanal fishermen sell *C. pica* as whole animals for US$20 per dozen, and the shells are often sold in street markets (E.M., personal observation). International trade of the meat occurs between only two territories, when fishermen from Anguilla bring snails to St. Maarten to sell to the fish markets (S. Wynne, personal communication). The shells, however, are sold online and in markets all around the world, from the Caribbean to Italy (E.M., personal observation), and the live animal has recently entered the aquarium trade, where it is often called the "Zebra Turbo."

Within the 14 territories and countries included in this study, I surveyed *C. pica* populations at 38 field sites on 22 islands (see Appendix 3, Table A3.1). When individuals less than 25.0 mm in width are removed from the data, as described in the methods, the total number of data points is 3,386. Since I included only the largest 15% of the individuals in the analyses, the number of data points included is 509. However, St. Vincent and the Grenadines was excluded from all analyses because the sample size was reduced to two when including only the top 15% from the >25.0 mm subset. The size structures of the populations on each island (Fig. 3) are significantly different (one-way ANOVA, p<0.0001). Two territories (i.e., Bermuda, Turks

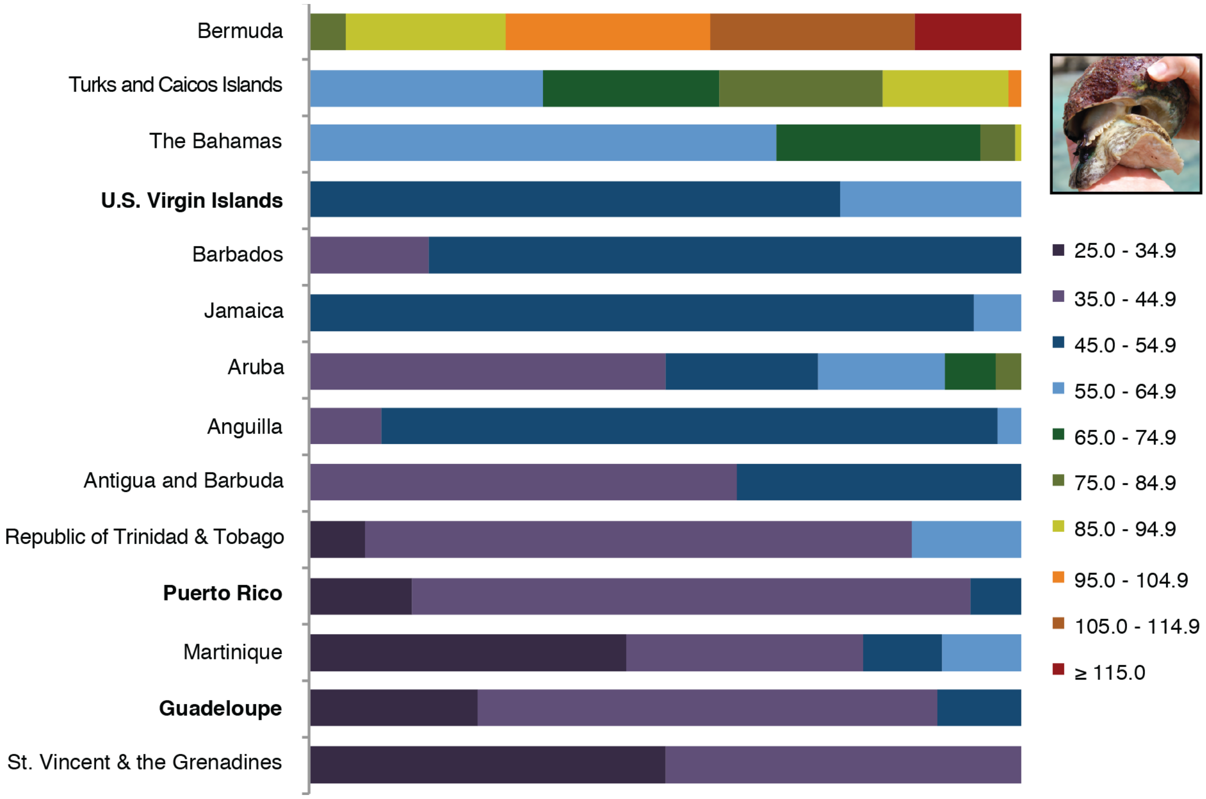

Figure 3: Size structure histograms of *Cittarium pica* populations, by territory or country, in order by largest mean size (highest at the top). Only the top 15% within individuals greater than 25.0 mm are include for each territory or country. The four territories where the species is managed are in bold (e.g., Bermuda, U.S. Virgin Islands, Puerto Rico, Guadeloupe). Bermuda has a significantly different size structure from all of the other populations (one-way ANOVA, p<0.0001). Non-human predation occurs below 45.0 mm. The maximum take size limits in Guadeloupe, Puerto Rico, and U.S. Virgin Islands are 40.0 mm, 63.0 mm, and 62.0 mm, respectively.

and Caicos Islands) and one country (i.e., Bahamas) have significantly different size structures (Tukey's HSD tests, α=0.05, p<0.0001). If these territories and country are removed from the analysis, the size structures remain significantly different (one-way ANOVA, p<0.0001), but no population is significantly different from any of the others. Within the greater dataset (25.0 mm+), snails greater than or equal to 45.0 mm in shell width account for more than 15% of the total population in Bermuda (58.7%), Turks and Caicos Islands (30.0%), Bahamas (24.1%), and U.S. Virgin Islands (19.5%) (Fig. 3), compared to the average across all territories and countries of 13.9%. Only two territories and one country had individuals greater than 90.0 mm, Bermuda, Turks and Caicos Islands, and Bahamas, accounting for 12.4%, 1.5%, and 0.1% of the populations respectively.

The three territories with MLS regulations in place are Guadeloupe (MLS=40.0 mm), Puerto Rico (MLS=63.0 mm), and U.S. Virgin Islands (MLS=62.0 mm). In Guadeloupe, only 3.6% of the population is over 40.0 mm, and the maximum size is 47.0 mm. The size distribution below 40.0 mm is significantly different from the same subset in Bermuda (p<0.0001, Mann-Whitney U-test). These distributions have little overlap, and the population in Guadeloupe has a smaller spread than Bermuda, with interquartile ranges of 3.6 and 6.7, respectively (Fig. 4a). In Puerto Rico, there are no snails over 63.0 mm, only 1% of the snails are greater than 45.0 mm, and the maximum size is 46.5 mm. The size distribution below 63.0 mm is significantly different from the same subset in Bermuda (p<0.0001, Mann-Whitney U-test). These distributions overlap slightly, and the population in Puerto Rico has a much smaller spread than Bermuda, with interquartile ranges of 4.8 and 21.6, respectively (Fig. 4b). In the U.S. Virgin Islands, 2.7% of the snails are greater than 62 mm, and the maximum size is 63.0 mm. The size distribution below 62.0 mm is significantly different from the same subset in Bermuda (p<0.0001, Mann-Whitney U-test). The U.S. Virgin Islands distribution overlaps

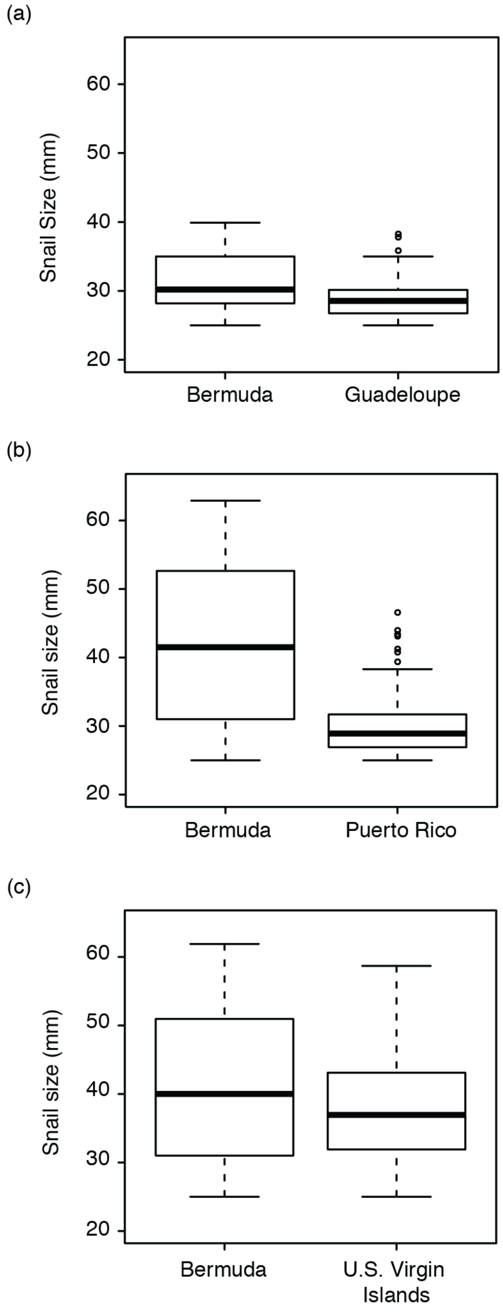

Figure 4: Boxplots of *Cittarium pica* size (mm) within the four territories where the fishery is managed. The species is fully-protected in Bermuda, and minimum landing size (MLS) is regulated in the other three territories. a) Boxplots for individuals that are ≤ 40.0 mm, which is the MLS for Guadeloupe; b) Boxplots for individuals that are ≤ 63.0 mm, which is the MLS for Puerto Rico; c) Boxplots for individuals that are ≤ 62.0 mm, which is the MLS for the U.S. Virgin Islands.

completely with that of Bermuda, but has a smaller spread than Bermuda, with interquartile ranges of 11.2 and 19.95, respectively (Fig. 4c).

Impact of Socioeconomic and Marine Conservation Status on Fishing Pressure

The 14 territories and countries included in this study span a wide range of socioeconomic and marine conservation status (Table 1). Population density varies from 31 people/km^2 in the Bahamas to 1,272 people/km^2 in Bermuda. Bermuda also has the highest GDP per capita (US$, current) at $29,842, whereas Jamaica has the lowest GDP per capita at $2,004. Guadeloupe has the highest unemployment rate (31.3%), with Martinique (27.5%) less than 4% lower; both of these island groups are overseas departments (i.e., Département d'Outre Mer) of France. Antigua and Barbuda, and Bermuda are tied for the lowest unemployment rate (6.0%), followed closely by the U.S. Virgin Islands (6.3%) and Aruba (6.9%). Urbanization rate is very high in many territories and countries, including 100% in Anguilla and Bermuda, with Guadeloupe (98.3%), Martinique (98.0%), Puerto Rico (97.6%), and the U.S. Virgin Islands (94.2%) not far behind. The Republic of Trinidad and Tobago has by far the lowest urbanization rate at 12.2%. Coverage of MPAs within the EEZ of each territory and country ranges from 0.03% to 3.72%, with an average of 0.79%. The global coverage of MPAs within EEZs is only 1.6% (Wood et al. 2008), so most of these territories and countries have less than the average marine area protected. Aruba has the highest area protected (3.72%), followed by the U.S. Virgin Islands (2.0%). Barbados and Bermuda have the lowest area protected, with only 0.03%. The management rank ranges from a low of 0 in Aruba, with Anguilla (1) and St. Vincent and the Grenadines (2) not far ahead, to 15 in Bermuda, with the U.S. Virgin Islands a distant second (10).

Most of the socioeconomic and marine conservation metrics are very, weakly correlated with each other ($r<|0.3|$). There is only one pair of metrics that is strongly correlated, GDP per capita (US$, current) and urbanization rate ($r=0.722$, $p<0.01$). Urbanization rate and management rank are weakly correlated ($r=0.311$), but this correlation is not significant ($p=0.3016$). GDP per capita and urbanization rate were collapsed into one metric using a PCA (eigenvalue 1.7221, 86.1%). For the remainder of this study, GDP per capita and urbanization rate are considered factors that contribute to a new metric called "level of affluence." Human population density and snail size have a quadratic relationship, such that increasing human population density initially has a negative correlation with size, followed by a positive correlation after some threshold population density is reached ($R^2=0.5896$, $p=<0.0001$). Unemployment rate ($R^2=0.3056$, $p<0.001$) and coverage of MPAs ($R^2=0.2592$, $p<0.0001$) are negatively correlated with size. Snail size is positively correlated with the PC of GDP per capita and urbanization rate ($R^2=0.2102$, $p<0.0001$) and management rank ($R^2=0.4622$, $p<0.0001$).

In the simple model of socioeconomic status, the strongest LM ($AIC_C=-425$, $R^2=0.75$, $p<0.0001$) contains three metrics and one interaction term (Table 2, Model 1): human population density with unemployment rate. This model excludes level of affluence; including this metric in the model (Table 2, Model 2) only decreases AIC_C by one ($AIC_C= -426$), so the better model is the one with fewer parameters. The actual versus predicted plot for this model reveals that none of the points

Table 1: Socioeconomic factors and marine conservation metrics by territory/country.

Country / Territory	Population Density (people per km^2)	GDP per Capita (current US$)	Unemployment (%)	Urbanization (% of total popn)	Total Marine Area[e] (km^2)	Marine Area Protected[5] (km^2)	Mangement Rank (0-15)
Anguilla	166[a]	12,200[a]	8.0[a]	100.0[a]	110,000	123	7
Antigua and Barbuda	199[a]	7,059[c]	6.0[c]	30.7[c]	6,000	223	0
Aruba	590[a]	14,851[c]	6.9[a]	46.6[c]	90,000	69	1
The Bahamas	31[a]	11,414[c]	12.1[c]	83.1[c]	652,000	2970	6
Barbados	667[a]	6,323[c]	17.1[c]	38.4[c]	186,000	52	3
Bermuda	1,272[a]	29,842[c]	6.0[c]	100.0[c]	450,000	146	15
Guadeloupe	247[b]	17,300[b]	31.3[b]	98.3[d]	90,000	217	4
Jamaica	265[a]	2,004[c]	15.7[c]	52.7[c]	251,000	2408	5
Martinique	346[b]	19,150[b]	27.5[b]	98.0[d]	45,000	664	4
Puerto Rico	450[a]	10,212[c]	16.8[c]	97.6[c]	205,000	2288	5
Republic of Trinidad and Tobago	239[a]	3,677[c]	18.5[c]	12.2[c]	74,000	326	5
St. Vincent and the Grenadines	267[a]	2,210[c]	19.8[c]	45.9[c]	38,000	38	2
Turks and Caicos Islands	47[a]	11,048[d]	7.9[c]	89.7[c]	153,000	571	7
U.S. Virgin Islands	317[a]	18,728[c]	6.2[a]	94.2[c]	6,000	120	10

[a] CIA WF (2009)

[b] INSEE (2009)

[c] World Bank (2010)

[d] UNData (http://data.un.org)

[e] Spalding et al. (2001)

Table 2: Coefficients and significance for the parameters within the strongest models, including the simple socioeconomic models.

Parameter		Model Coefficient	p-value
Model 1:	Human population density	-2.5129	< 0.0001
	Human population density (squared)	0.2027	< 0.0001
	Unemployment rate	-8.9410	< 0.0001
	Human population density * Unemployment rate	1.3783	< 0.0001
Model 2:	Human population density	-2.5469	< 0.0001
	Human population density (squared)	0.2047	< 0.0001
	Unemployment rate	-9.2125	< 0.0001
	Level of affluence	0.0149	< 0.0500
	Human population density * Unemployment rate	1.4174	< 0.0001

Table 3: Coefficients and significance for the parameters within the strongest models, including the simple marine conservation models.

Parameter		Model Coefficient	p-value
Model 1:	Coverage of marine protected areas (MPAs)	-1.8600	< 0.0001
	Management rank	0.0432	< 0.0001
Model 2:	Coverage of MPAs	-0.0665	8.19E-01
	Management rank	0.0601	< 0.0001
	Coverage of MPAs * Management rank	-0.3236	< 0.0001

for two territories (i.e., Guadeloupe, Puerto Rico) and two countries (i.e., Barbados, Jamaica) overlap with the regression line, but most of the points fall within the 95% confidence curves (see Appendix 4, Fig. A4.1a). The larger sizes for three territories (i.e., Bermuda, Martinique, Turks and Caicos Islands) and two countries (i.e., the Bahamas, Republic of Trinidad and Tobago), and the smaller sizes for one territory (i.e., Aruba) and one country (i.e., Barbados) fall outside the confidence curves.

In the simple models of marine conservation metrics, if both metrics and the interaction between them are included in the LM (AIC_C =-191, R^2=0.60, p<0.0001), then coverage of MPAs is not significant (Table 3, Model 2). If the interaction term is removed, AIC_C increases by 81

Table 4: Coefficients and significance for the parameters within the strongest models, including the combined models.

Parameter		Model Coefficient	p-value
Model 1:	Human population density	-1.7963	< 0.0001
	Human population density (squared)	0.1410	< 0.0001
	Unemployment rate	-6.9941	< 0.0001
	Coverage of MPAs	-1.0658	< 0.0001
	Management rank	0.0204	< 0.0001
	Human population density * Unemployment rate	1.0388	< 0.0001
Model 2:	Human population density	-0.9057	< 0.0001
	Human population density (squared)	0.0985	< 0.0001
	Unemployment rate	-1.2186	< 0.0001
	Level of affluence	0.1282	< 0.0010
	Coverage of MPAs	-2.0741	< 0.0001
	Management rank	0.1226	< 0.0001
	Human population density * Level of affluence	-0.0302	< 0.0010
	Human population density * Management rank	-0.0160	< 0.0100

(AIC_C=-110, R^2=0.52, p<0.0001), but coverage of MPAs is significant (Table 3, Model 1). Thus, even though the AIC_C is greater for the model without the interaction term, it better reflects the pattern seen in the data, which indicates that there is a relationship between size and coverage of MPAs. None of the points from three territories (i.e., Aruba, Guadeloupe, Puerto Rico) and two countries (i.e., Antigua and Barbuda, Barbados) overlap with the regression line for the actual versus predicted plot. The points for two of these countries fall completely within the boundaries of the 95% confidence curves, but many points for the other three countries do not (Appendix 4, Fig. A4.1b). The largest individuals for two territories (i.e., Aruba, Turks and Caicos Islands) and one country (i.e., Bahamas) and the smallest individuals for one territory (i.e., Guadeloupe) and one country (i.e., Antigua and Barbuda) fall outside the 95% confidence curves.

The strongest linear regression model overall (AIC_C=-575, R^2=0.81, p<0.0001) maintained two socioeconomic (i.e., excluding level of affluence), both marine conservation metrics, and includes one interaction term: human population density with unemployment rate. All six metrics are significant in the model (Table 4, Model 1), hereafter called "C-model 1". When the interaction term is removed from C-model 1, the AIC_C value increases by 47. If level of affluence is added to the model, the AIC_C decreases by 14 (AIC_C=-589), but has an inaccurate relationship – negative instead of positive. The best linear regression model (AIC_C=-561, R^2=0.81, p<0.0001) that includes level of affluence maintains all five basic metrics and adds two interaction terms: human population density with level of affluence, and human population density with management rank. All eight metrics are significant in this model (Table 4, Model 2), hereafter called "C-model 2". For the two simpler models, a total of six territories or countries do not overlap with the regression line of the actual versus predicted plots. In C-model 1, one territory (i.e., Anguilla) and three countries (i.e., Antigua and Barbuda, Barbados, Jamaica) do not overlap with the regression line, but all of the data points fall within the 95% confidence curves (Appendix 4, Fig. 4.1c). The values for the smallest individuals fall below the 95% confidence curves for one territory (i.e., Bermuda) and one country (i.e., Antigua and Barbuda). C-model 2 has only one territory (i.e., Antigua and Barbuda) and one country (i.e., Barbados) that do not overlap with the regression line (Appendix 4, Fig. A4.1d). The values for Barbados fall within the 95% confidence curves, whereas the values for Antigua and Barbuda do not. The values for the smallest individuals in only one territory (i.e., Bermuda) fall below the 95% confidence curves. Within both combined models, the values for the largest individuals fall outside of the 95% confidence curves for six of the 13 territories or countries, the same six as in the simpler models: Martinique, Republic of Trinidad and Tobago, Aruba, The Bahamas, Turks and Caicos Islands, and Bermuda.

Overall, C-Model 1, a model with both socioeconomic and marine conservation metrics, is the strongest model, explaining more of the variation in size than either of the two simpler models. For the largest individuals in a population, the model predicts individuals to be smaller than their actual size. Thus, the model predicts the low and middle sizes with the most confidence, but it should not be used to predict the sizes of the largest individuals present. The model predicts smaller individuals within the Guadeloupe population than are present, but larger individuals than actually present within the Puerto Rico population. All sizes of individuals within the Bermuda and U.S. Virgin Island populations are well predicted by the model, except for the extreme sizes (i.e., both the smallest and the largest) in Bermuda.

DISCUSSION

Assessment of Fishery and Management Status

Fishing pressure on *C. pica* is clearly not consistent across its range, with the highest fishing pressure in Guadeloupe, St. Vincent and the Grenadines, and Martinique, and the lowest fishing pressure in Bermuda, Turks and Caicos Islands, and the Bahamas. Bermuda is the only territory where *C. pica* is managed that has low fishing pressure, whereas Guadeloupe, another territory where it is managed, has the highest fishing pressure. For most fisheries, fishing pressure is highest on the largest individuals within a population, which ultimately leads to a decrease in average size (Martins et al. 2010). However, *C. pica* is harvested for bait, regardless of size, in several territories and countries, including Barbados and Bermuda (E.M., personal observations), and is harvested as small as 20 mm in territories and countries where large individuals are absent. Non-size-selective harvesting is common in other invertebrate fisheries too (e.g., Martins et al. 2008). Because *C. pica* does not reach sexual maturity until it is 32-34 mm (Robertson 2003), harvesting individuals smaller than this removes them from the population before they reproduce. For these fisheries, the establishment of MLS regulations is vital to the conservation of the integrity of a viable breeding population.

In Bermuda, where *C. pica* is fully-protected, the population structure is significantly different than all other populations, with a size distribution that is centered at a larger size. The species has continued to recover steadily since 1982, when the species was reintroduced to Bermuda, spreading from the isolated locality where it was released (i.e., Nonsuch Island) to all along the southshore of the island (see Chapter 4). However, illegal harvesting is a recurring problem in Bermuda (Wingate 2006), due at least in-part to insufficient infrastructure to adequately enforce the no-take regulation (K. Coates, personal communication). Bilingual signs were posted at two sites where illegal harvesting was documented, but education of the general public should be made a priority, perhaps starting with bilingual pamphlets and community awareness presentations outlining the fishing regulations in place in Bermuda. A major violation of the no fishing regulation in 2011 resulted in enforcement of the $5,000 fine, and prompted the Bermuda Government to consider increasing the fine (K. Coates, personal communication). In spite of illegal fishing, more than half of the individuals in the Bermuda population are greater than 45 mm, which is above the size refuge for non-human predators.

Using size structure as a proxy of fishing pressure is a common practice (e.g., Foster & Hodgson 2000; Haedrich & Barnes 1997; Moreno et al. 1986), and it can be used to evaluate both the level of fishing pressure and enforcement of MLS regulations. In Guadeloupe, MLS is set to 40 mm, and only four individuals measured in this population were greater than or equal to this limit. Although this may suggest that the MLS regulation is enforced, the number of individuals and the population structure below this size do not reflect that of a protected population (e.g., Bermuda). These data suggest that the population is at-risk of over-exploitation, either due to illegal fishing of individuals smaller than the MLS or to depressed reproduction. Another potential explanation for this pattern is that non-human predators, which prey on snails that are 45 mm in width or less, exist in higher density in Guadeloupe, when compared to Bermuda, resulting in higher non-human predation rates. However, higher non-human predation is unlikely to affect the snail population dramatically unless the population size of all non-human predators is significantly higher, thus impacting individuals throughout its habitat. Schmidt et al. (2002) suggest a MLS of 40 mm for *C. pica* based on their calculations of sustainable relative yield per recruit, but the authors acknowledge that their growth curve may not be based on the most accurate model for *C. pica*. Based on a simple logistic growth curve fitted to growth data from both cohort analyses (Bell 1992; Debrot 1990; C. Jantzen-Marson, unpublished data; Randall 1964; Wingate 1989) and direct growth rates from individuals (see Chapter 4, Appendix 2), an MLS of 40 mm allows for only four months of spawning. In lieu of establishing stock-specific MLS regulations, MLS should be set high enough to buffer populations to potential environmental stochasticity and increasing fishing pressure.

When fishery management regulations were first developed for gastropods, they were based on strategies used for bivalves. As Jamieson (1993) asserts, the two groups of organisms differ in several, major biological characteristics (e.g., planktonic larval duration, reproductive strategies, reproductive output), and there is a huge variation within gastropods among these and other traits (e.g., determinate/indeterminate growth, growth rate, size at maturity, lifespan). New strategies have been and must continue to be developed to specifically target gastropods. Broadcast spawning gastropods, like *C. pica*, often require a spawning aggregation to achieve a high enough density of eggs and sperm for successful fertilization to occur (Hobday et al. 2000; Levitan & Sewell 1998; Tegner et al. 1996). Additionally, larger individuals produce more gametes (Espinosa et al. 2009; Harding et al. 2008; Sundelöf et al. 2009), thus size and reproductive success are tightly linked. Thus establishing the MLS with the target of allowing individuals to spawn only once or twice is likely not sufficient for gastropods (Jamieson 1993). Furthermore, MLS regulations alone are insufficient for management of intertidal gastropods because their accessibility makes them easily susceptible to over-harvesting. For conspicuous intertidal species, all or most individuals above the MLS can be collected at a site within a matter of weeks (Shalack et al. 2011) or as quickly as a few hours (Jamieson 1993), which rapidly suppresses the maximum size and subsequently decreases the reproductive output. Based on the recommendation of Jamieson (1993) and the simple logistic growth curve, managers in all territories should consider increasing the MLS regulation to 62 mm, allowing individuals to reproduce for two years prior to being harvested.

The MLS regulations in Puerto Rico and the U.S. Virgin Islands are established at nearly this size, 63 mm and 62 mm, respectively. However, the regulation is not well-enforced in Puerto Rico, as evidenced by the depressed size structure of this population and that the maximum sized individual found was 16.5 mm less than the regulated size. A territory-wide survey conducted in 2003-2004 by Jimenez (2006) revealed large individuals (>63 mm) present at twenty offshore sites and seven mainland sites. Off-shore sites are not easily accessible by fisherman because of both travel time and adverse ocean conditions, and one of the mainland sites is also characterized as having “life-threatening” conditions (Jiménez 2006). These offshore sites are likely vital to maintaining a population on the mainland, but an investigation of population connectivity is required to determine the metapopulation dynamics. Of the other mainland sites with large individuals, three were adjacent to fished sites, but not identified as fished sites themselves. Two of the three were in fact the same site, Punta Aguila and Cabo Rojo. The site was resurveyed within two weeks of first visit, so likely the same individuals were counted twice. I conducted a population survey at this site in 2008, and the largest individual found was 46.5 mm. Enforcement of the MLS is critical to the future of this fishery in Puerto Rico, especially in the absence of targeted protected areas.

The MLS regulation in the U.S. Virgin Islands is combined with a MHS or bag limit (per day) of 1-gallon (in the shell) and a six-month seasonal closure of the fishery. Violations of these regulations result in fines of up to $500, or up to $5,000 if the violation occurs within a MPA. The combination of these regulations, likely coupled with better enforcement, has resulted in successful management of the species in this territory, maintaining a size structure comparable to that of Bermuda. However, fishing pressure is very high in the U.S. Virgin Islands, as evidenced by the presence of so few individuals above the MLS and a maximum size only 1 mm greater than the MLS. To address this high fishing pressure and buffer against further population declines, I suggest re-evaluating the six-month seasonal closure of the fishery. A study conducted by Randall (1964) on St. John, U.S. Virgin Islands revealed that recruitment occurs throughout the year, but peaks in January. The current closure of the fishery seems to be based on data collected by Debrot (1990) in the Exuma Cays, Bahamas, where there is seasonal recruitment in the summer. Because the recruitment patterns of *C. pica* are geographically variable, any seasonal closure regulations need to be based on data collected on and observations of local populations.

Factors Influencing Fishing Pressure

Both socioeconomic status and marine conservation status affect fishing pressure on *C. pica*. More variation in size is explained by the combination of socioeconomic and marine conservation metrics than either set alone. Thus, human population density, unemployment rate, level of affluence (GDP per capita and urbanization rate), management rank, and coverage of MPAs are all important predictors of fishing pressure (Fig. 5). Socioeconomic status explains the level of fishing pressure better than marine conservation status in two locations: the territory of Aruba and the island nation of Antigua and Barbuda. For Aruba, the marine conservation model predicts that it should have smaller-sized snails, indicating that even though it does not have strong fishing regulations and does have relatively high coverage of MPAs, people do not harvest the species as often as expected. Instead, the fishing pressure on *C. pica* is better predicted by *high* level of affluence. For Antigua and Barbuda, the marine conservation model predicts that it should have larger-sized snails. This indicates that even though the country has low coverage of MPAs, people harvest *C. pica* quite heavily, which is better explained by the *low* level of affluence. The coverage of MPAs and management rank better explain the level of fishing pressure only in Jamaica, where the socioeconomic model predicts larger-sized individuals than are present. Jamaica may not have the highest overall human population density, but it does have the lowest GDP per capita. Even when fishing regulations are in place, the variation in snail size will not necessarily be best explained by marine conservation metrics. For example, in Guadeloupe and Puerto Rico, fishing pressure is not well-predicted by either simple model; only the combination of socioeconomic and marine conservation metrics explains fishing pressure in these territories.

Relative to socioeconomic status, fishing pressure is lower in countries with higher GDP per capita, lower unemployment, and higher urbanization (Fig. 5). For example, the Turks and Caicos Islands and the Bahamas, which have the second and third largest-sized *C. pica*, respectively, also have low human population density, relatively low unemployment rate, and high GDP per capita. For territories and countries with high unemployment rate and human population density, these two factors have a combined effect that results in even higher fishing pressure. This suggests that not only do impoverished people drive the fishery, but also if there are more people overall, there are more people who are unemployed who depend on harvesting wild resources. However, fishing pressure is not linearly related to human population density. It is highest in places with both very low and very high human population density. Other studies have found a strong negative linear relationship between human population density and catch rates (Clausen & York 2008; Kronen et al. 2010). In Venezuela, Rodriguez (2000) found that fishing

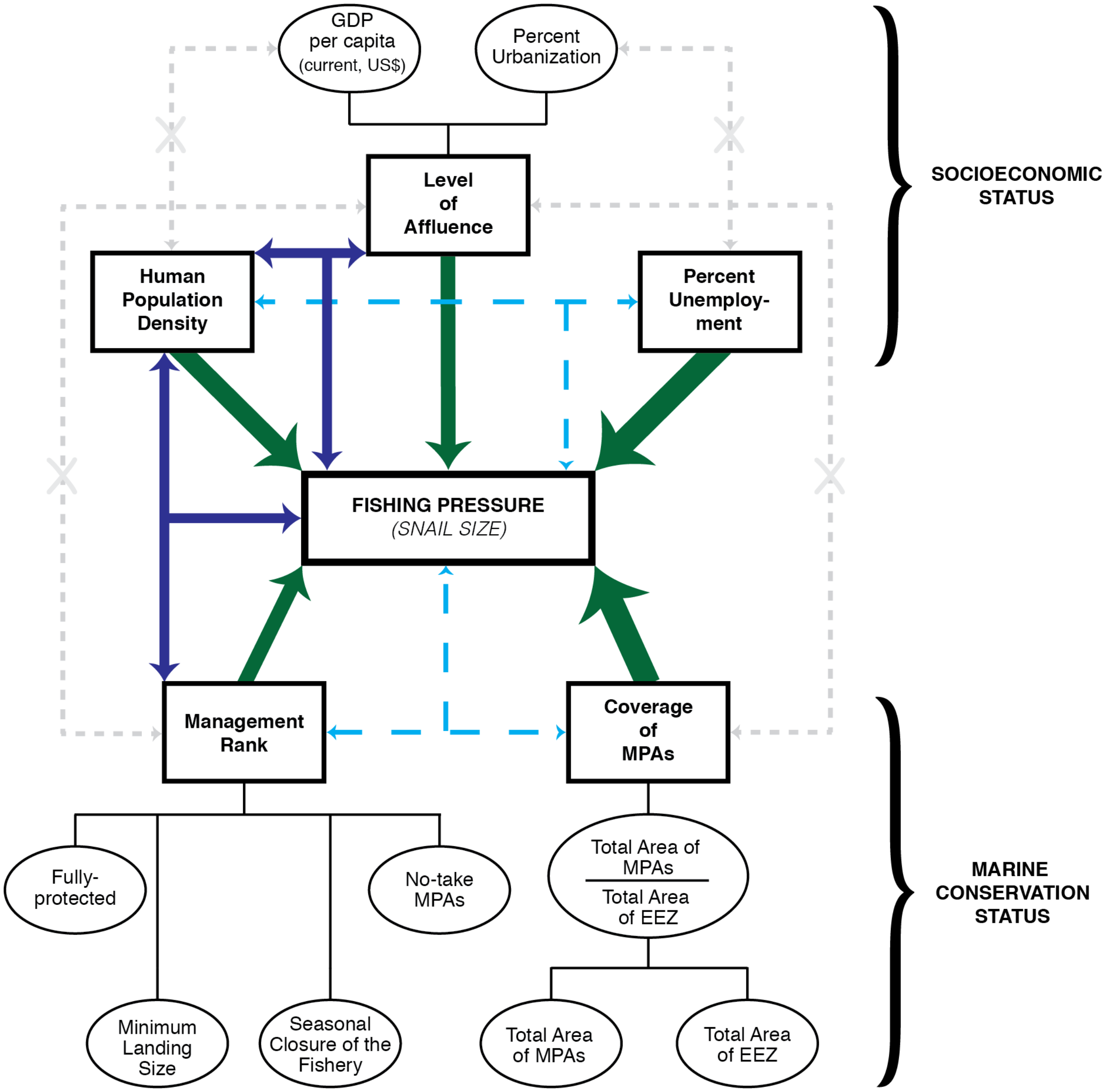

Figure 5: Flowchart of the factors that are used to assess the socioeconomic and marine conservation status and how they affect the level of fishing pressure. The factors within circles are components of factors in rectangles (e.g., GDP per capita and percent urbanization are components of level of affluence). The factors within rectangles are metrics used within the models. The green arrows indicate metrics that influence level of fishing pressure; their thickness represents the degree of effect. The blue arrows indicate metrics that are interacting in the models; the combined effect on level of fishing pressure is represented by arrow thickness. The dashed light blue arrows indicate metrics that interact in simple models that contain only socioeconomic or marine conservation metrics. The dashed and crossed-out light gray lines indicate expected correlations that were absent.

pressure increased at a greater rate than human population growth and instead suggests that an increase in unemployment resulted in an increase in subsistence harvesting of fishery resources, including *C. pica*.

Incorporating additional socioeconomic and fine-scale population parameters could help enhance the interpretation of how socioeconomic status affects the *C. pica* fishery. However, gathering socioeconomic information on the local scale is time-intensive and expensive for species that cross several national boundaries, and conducting an assessment of an at-risk species, like *C. pica*, needs to be completed quickly so that management plans can be established before the fishery collapses. Using national-level statistics can enable this quick, broad assessment of fishing pressure, revealing whether a fine-scale assessment is necessary and where. Even though the results of this study suggests that increased socioeconomic development has a positive affect on fishing pressure of *C. pica*, it is linked to increased marine pollution and coastline modification (Clausen & York 2008), both of which directly affect populations in the rocky intertidal.

Interestingly, fishing pressure is not positively correlated with both of the marine conservation metrics (Fig. 5). Countries with a higher management rank do have lower fishing pressure, which suggests that management regulations have a positive affect on the population of *C. pica*, as expected. In contrast, if coverage of MPAs within a territory or country is higher, then there is *higher* fishing pressure on *C. pica*. This is most likely because the majority of MPAs within the territories and countries included in this study do not extend into the rocky intertidal. If a country has MPAs covering reef, seagrass, and other sub-tidal habitats where fishing is restricted, fishers must shift their efforts to areas outside of those that are protected and to species that are not regulated. Although MPAs often result in spillover effects to areas outside their boundaries (Roberts 2001), this is not applicable between sub-tidal and intertidal habitats for species that are restricted to the intertidal.

Conclusions

The level of fishing pressure on *C. pica* varies throughout the West Indies, depending on the level of affluence, human population density, and management practices for the species and for the other marine resources present. Current management practices are insufficient in most locations to ensure the future of this important fishery. However, the level of fishing pressure in most territories and countries is linked to low socioeconomic status, suggesting that those who harvest the species likely depend on it as a free food resource. As a result, fine-scale surveys of localized fishing pressure, especially in Antigua and Barbuda, and Aruba, should be conducted on each island to ensure that fishing regulations and new MPAs are established in such a way that local fishers are not completely restricted from accessing their fishing grounds. Fine-scale protection that is distributed around the island is preferred to eliminating access completely because fishing pressure is mainly for subsistence. Completely closing the fishery is not feasible. Establishing MPAs in this way is previously recognized to encourage local fishers to acknowledge the potential benefits of MPAs to their livelihoods (Weeks et al. 2010). Further, management that is established on a local scale that incorporates the combined input and enforcement from fishers and with local and regional agencies is more likely to be successful (Aldon et al. 2011; McClanahan et al. 2008).

These conclusions provide strong support for implementing the following policies:

Multi-faceted Management Plan: Management plans are more likely to be successful if they incorporate multiple management strategies (Hilborn & Walters 1992), including targeted harvest reduction (e.g., maximum harvest limit), controlling species size when harvested (e.g., minimum and maximum landing size), and full protection temporally or locally (e.g., seasonal fishery closure, targeted MPAs). Conspicuous intertidal species are easily accessible and often experience heavy fishing pressure, as such these species are highly susceptible to over-exploitation, and multi-faceted management plans are especially vital to their conservation.

> *Maximum Harvest Size (MHS) or Bag Limit:* To control the number of *C. pica* removed and effectively alleviate the possibility of decimating entire populations in one harvest event, the MHS should be set no higher than 1-gallon (in the shell) per day, per person (preferably per site). However, the MHS must be determined based on the local abundance and density of *C. pica*.
>
> *Minimum Landing Size (MLS)*: To allow *C. pica* to reproduce for at least two years prior to harvest, the MLS should be set at 62 mm.
>
> *Seasonal Closure of the Fishery*: To simultaneously allow *C. pica* to recover from past overfishing and to remain an open fishery, a seasonal closure of the fishery should be established, based on timing of local reproduction and recruitment.
>
> *Marine Protected Areas*: To provide a buffer to future population fluctuations and potential increases in exploitation as human population density continues to rise, targeted MPAs should be created.

Enforcement of Regulations: As in all cases where regulations are established but not comprehensively enforced, successful recovery is minimal. A lack of enforcement not only undermines the success of targeted harvest reductions and MLS regulations, but also indirectly enables illegal harvesting. This could affect the integrity of seasonal closures (e.g., Martins et al. 2010) and MPAs. As such, adequate resources must be allocated to ensure comprehensive enforcement and publication of all regulations, including involvement of local fishers, community education, and posting multilingual notification signs at both protected and fished locations.

More rigorous understanding of the complex network of interactions between socioeconomics and management practices is an important step toward developing successful conservation strategies, not only for extracted resources, but also whole ecosystems. The rocky intertidal is a conspicuous and highly productive ecosystem that supports thousands of species around the world and from which hundreds of species are harvested. Inclusion of rocky intertidal habitats in MPAs is long overdue. A qualitative as well as theoretical understanding of these interactions is needed to provide the foundation for conserving these resources and protecting this vital habitat.

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Appendix 1, Table A1.1: The names, titles, and contact information for the fisheries managers and other government workers contacted for this study. When applicable, information on where the species is managed and the level of management is also included.

Territory/Country	Contact Name	Organization	Email Address
Anguilla (United Kingdom)	Mr. Larry Franklin	Dept of Fisheries and Marine Resources (DFMR)	Larry.Franklin@gov.ai
	Mr. James Gumbs, Director	Dept of Fisheries and Marine Resources (DFMR)	james.gumbs@gov.ai
	Mr. Merwyn Rogers	Dept of Fisheries and Marine Resources (DFMR)	Merwyn.Rogers@gov.ai
	Mr. Stuart Wynne, Marine Biologist	Dept of Fisheries and Marine Resources (DFMR)	Stuart.Wynne@gov.ai
Antigua and Barbuda	Mrs. Cheryl Appleton, Chief Fisheries Officer	Fisheries Division - Ministry of Agriculture, Lands, Housing, and the Environment	fisheries.antigua.gov.ag
Aruba (Kingdom of the Netherlands)	Ms. Ayesha Engelbrecht, Adjunct / Operational Director	Dept di Integracion for, Maneho y Admision di Stra Hero	Ayesha.Engelbrecht@aruba.gov.aw
The Bahamas	Mr. Roland Albury, Director	Dept of Marine Resources	Unknown
Barbados	Ms. Joyce Leslie, Deputy Chief Fisheries Officer	Fisheries Division, Ministry of Agriculture and Rural Development	fishbarbados.dcfo@caribsurf.com
Bermuda (United Kingdom)	Mr. Jeremy Madeiros, Terrestrial Conservation Officer	Dept of Conservation Services	jlmadeiros@gov.bm
	Dr. Tammy Trott, Sr. Marine Resources Officer	Dept of Conservation Services	ttrott@gov.bm
Guadeloupe (France)	Mr. Frederic Blau, Director of Maritime Affairs	Ministère de L'Écologie, du Développement Durable, des Transports et du Logement	Frederic.Blau@developpement-durable.gouv.fr
	Mr. Fabrice Le Mesnager, Deputy Regional Director of Maritime Affairs	Ministère de L'Écologie, du Développement Durable, des Transports et du Logement	Fabrice.Lemesnager@developpement-durable.gouv.fr
Jamaica	Ms. Yvette Strong	Resources Conservation Authority, National Environmental Planning Agency	ystrong@nepa.gov.jm
Martinique (France)	Mr. Faben Vedie, Head of Marine Environments Mission	Direction régionale de l'environnement	Fabien.vedie@developpement-durable.gouv.fr

Appendix 1, Table A1.1 continued

Territory/Country	Contact Name	Organization	Email Address
Puerto Rico (United States)	Mrs. Myrna Abreu	Dept de Recursos Naturales y Ambientales	mabreu@drna.gobierno.pr
	Mr. Ernesto Díaz Velázquez, Director / Administrator	Dept de Recursos Naturales y Ambientales	ediaz@drna.gobierno.pr
Republic of Trinidad and Tobago	Ms. Candidace DaBreo, Fisheries Biologist	Fisheries Division, Ministry of Agriculture	dabreo.c@gmail.com
	Mr. Garth Ottley, Fisheries Officer	Fisheries Division, Ministry of Agriculture	gaottley@hotmail.com
St. Vincent and the Grenadines	None	Ministry of Agriculture, Forestry, and Fish	office.agriculture@mail.gov.vc
	None	Fisheries Division, Ministry of Agriculture, Forestry, and Fish	fishdiv@caribsurf.com
Turks and Caicos Islands (United Kingdom)	Mr. Brian Riggs, Manager and Curator	Dept of Environment and Coastal Resources, National Environmental Centre	bmr@tciway.tc
U.S. Virgin Islands (United States)	Dr. Rafe Boulon, Chief Resources Manager	National Parks Service, U.S. Virgin Islands National Park	Rafe_Boulon@nps.gov
	Dr. William Coles, Chief of Environmental Education	Dept of Planning and Natural Resources, Division of Fish and Wildlife	william.coles@dpnr.gov.vi
	Ms. Ruth M. Gomez, Fisheries Coordinator, Educational Officer	Dept of Planning and Natural Resources, Division of Fish and Wildlife	olewife@hotmail.com
	Dr. David Olsen, Director	Dept of Planning and Natural Resources, Division of Fish and Wildlife	olsen41@aol.com
	Ms. Judy Pierce, Acting Director, Chief of Wildlife	Dept of Planning and Natural Resources, Division of Fish and Wildlife	judy.pierce@dpnr.gov.vi

Appendix 2, Table A2.1: Designation of the management rank for each of the 14 territories and countries included in this study.

Territory / Country	Fully Protected (+ 8)	Seasonal Closures (+ 4)	Min Take Size (+ 2)	Non-IUCN Reserves[a] (+ 1 if 10 - 19, + 2 if 20 - 29, + 3 if 30 +)	IUCN 1a, 1b, II, or III[a] (+ 2 if only 1, + 3 if > 1)	IUCN V & Vi[a] (+ 1 if only 1, + 2 if > 1)	Mangement Rank (0 - 15)
Anguilla	0	0	0	1	0	0	1
Antigua and Barbuda	0	0	0	2	3	2	7
(The) Bahamas	0	0	0	3	3	0	6
Barbados	0	0	0	0	3	0	3
Bermuda	8	0	0	3	3	1	15
Guadeloupe	0	0	2	1	2	1	6
Jamaica	0	0	0	1	2	2	5
Martinique	0	0	0	1	2	1	4
Netherlands Antilles	0	0	0	0	0	0	0
Puerto Rico	0	0	2	3	0	0	5
Republic of Trinidad and Tobago	0	0	0	1	3	1	5
St. Vincent and the Grenadines	0	0	0	2	0	0	2
Turks and Caicos Islands	0	0	0	2	3	2	7
U.S. Virgin Islands	0	4	2	1	2	1	10

[a] IUCN & UNEP (2010)

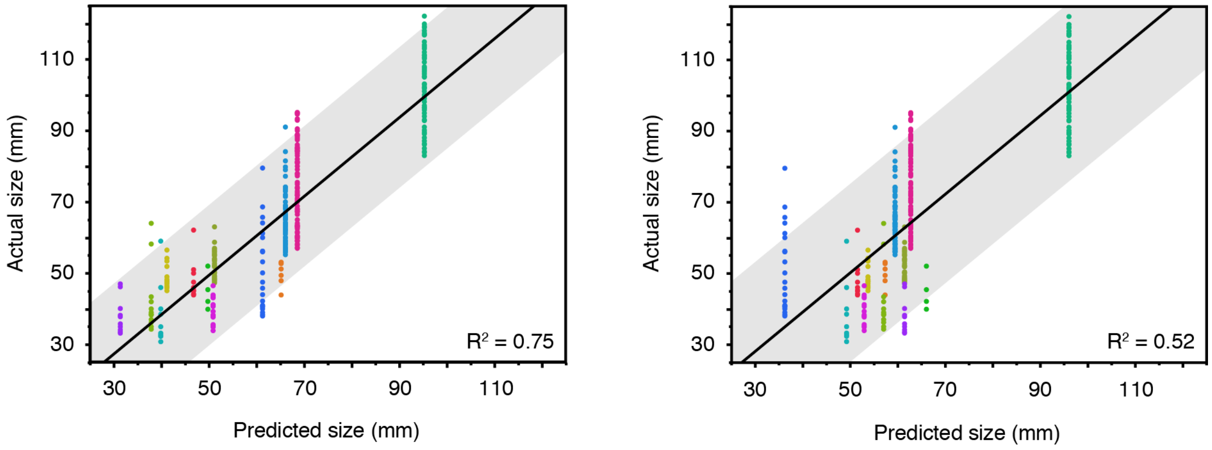
Appendix 3, Table A3.1: Geographic information for the sites included in this study.

Island Group (Country/Territory, if applicable)	Date	Site	Latitude (decimal degrees)	Longitude (decimal degrees)
Aruba (Kingdom of the Netherlands)	July 23, 2010	Andicuri Beach, Aruba	12.5378	-69.9551
	July 24-25, 2010	California Dunes, Aruba	12.6198	-70.0471
	July 23, 2010	North of Natural Bridge, Aruba	12.5409	-69.9587
Anguilla (United Kingdom)	July 24, 2009	Long Pond Bay, Anguilla	18.2156	-63.0136
	July 22-23, 2009	Sherrick's Bay, Anguilla	18.1626	-63.1648
Antigua and Barbuda	July 28, 2009	North Pigeon Beach, Antigua	17.0109	-61.7755
Barbados	August 13, 2009	Bathsheba, Barbados	13.2127	-59.5166
	August 14, 2009	Hastings Rocks, Barbados	13.0726	-59.5871
Bermuda (United Kingdom)	August 10 & 15, 2007	Rocky Hole, St. David's Island	32.3530	-64.6565
	August 14, 2007	Spittal Pond, Main / Bermuda Island	32.3120	-64.7237
	August 10, 2007	Turtle Bay, Main / Bermuda Island	32.3530	-64.6565
Guadeloupe (France)	August 1, 2009	Plage de l'Anse, Basse-Terre	16.1489	-61.7752
	August 2, 2009	Anse Tabarin, Grand-Terre	16.2057	-61.4978
	August 3, 2009	Plage de la Chapelle, Grand-Terre	16.4721	-61.5112
Jamaica	July 26, 2008	Portland Point, Jamaica	17.7486	-77.1370
	July 24-25, 2008	Priory, Jamaica	18.4457	-77.2262
Martinique (France)	August 8, 2009	Pointe Burgos, Martinique	14.4914	-61.0844
	August 6, 2009	Pointe d'Enfer, Martinique	14.3973	-60.8566
Puerto Rico (United States)	August 4, 2008	Cabo Rojo, Puerto Rico	17.9339	-67.1878
	July 31, 2008	Piñones, Puerto Rico	18.4581	-65.9770
	August 3, 2008	Poncé Playa, Puerto Rico	17.9629	-66.6138

Appendix 3, Table A3.1 continued

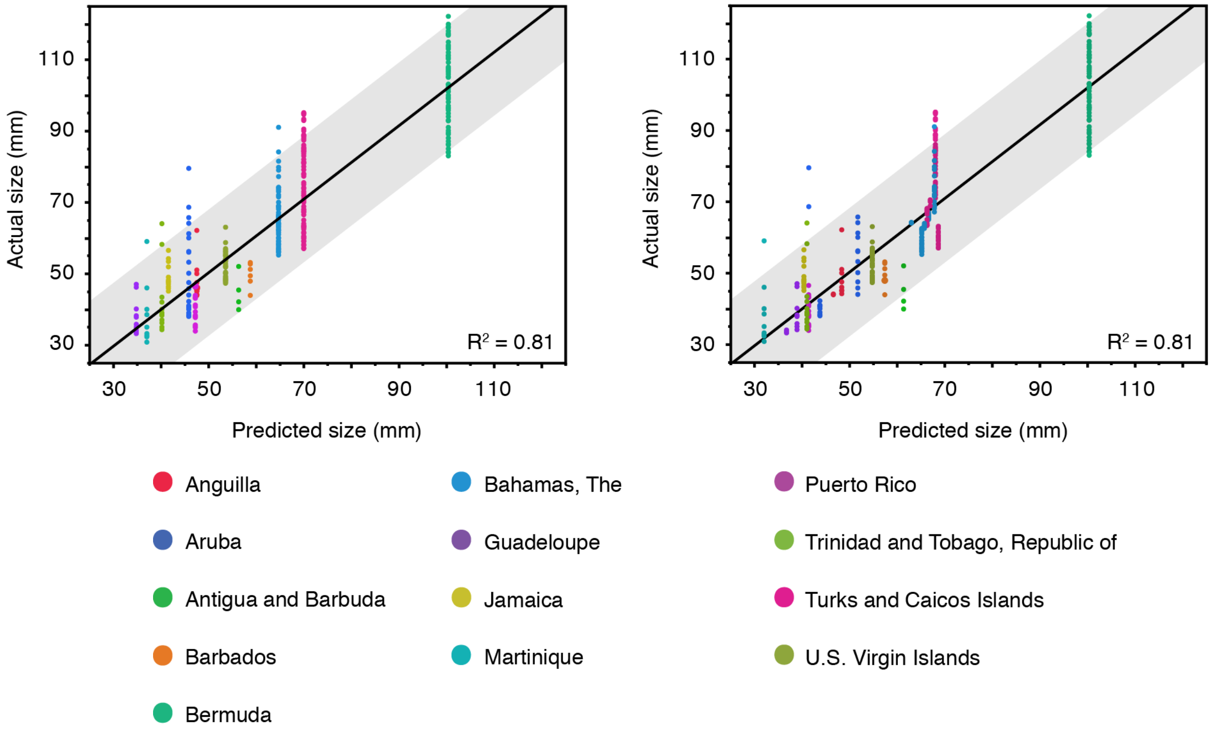
Island Group (Country/Territory, if applicable)	Date	Site	Latitude (decimal degrees)	Longitude (decimal degrees)
Republic of Trinidad and Tobago	August 21, 2009	Mount Irvine Bay, Tobago	11.1886	-60.7961
	August 29, 2009	L'Anse Noir, Trinidad	10.8360	-60.9841
St. Vincent and the Grenadines	August 17, 2009	East Calliaqua, St. Vincent	13.1243	-61.1901
The Bahamas	June 29, 2008	Bootle Bay, Grand Bahama Island	26.6484	-78.9395
	June 28 & 30, 2008	Running Man Jetty, Grand Bahama Island	26.4947	-78.6597
	July 8-9, 2008	Northwest Point, Great Inagua Island	21.1103	-73.6677
	July 2 & 4, 2008	Delaporte Point, New Providence Island	25.0775	-77.4353
	July 3, 2008	Turtle Pen, New Providence Island	25.0073	-77.5482
Turks and Caicos Islands (United Kingdom)	July 13014, 2008	Mudjin Harbor, Middle Caicos Island	21.8317	-71.8102
	July 21, 2008	North of Whale House Bay, Salt Cay	21.3376	-71.1852
	July 22, 2008	South of Northwest Point, Salt Cay	21.3371	-71.2131
	July 16, 2008	Coast Guard Station, South Caicos Island	21.5733	-71.4948
	July 18, 2008	High Point, South Caicos Island	21.5255	-71.4970
U.S. Virgin Islands (United States)	August 13, 2008	Lameshire Bay, St. John	18.3188	-64.7207
	August 14, 2008	West America Point, St. John	18.3563	-64.7523
	August 11, 2008	Mandahl Bay, St. Thomas	18.3606	-64.8966
	August 10, 2008	Secret Harbor, St. Thomas	18.3187	-64.8533

Appendix 4, Figures A4.1a-d: Scatterplots and regression lines for actual size vs. size predicted by the strongest linear regression models. (a) linear regression (AIC$_C$=-425, p<0.0001) with three socioeconomic parameters (i.e., human population density, unemployment rate, PC of GDP per capita, urbanization rate) and one interaction term (i.e., human population density x unemployment rate); (b) linear regression (AIC$_C$=-191, p<0.0001) with both marine conservation parameters (i.e., coverage of marine protected areas, management rank); (c) combined linear regression model 1 (AIC$_C$=-575, p<0.0001) with two socioeconomic (i.e., human population density, unemployment rate) and both marine conservation parameters, along with one interaction term (i.e., human population density x unemployment rate); (d) combined linear regression model 2 (AIC$_C$=-561, p<0.0001) with all three socioeconomic and both marine conservation parameters, along with two interactions terms (i.e., human population density x level of affluence, human population density x management rank).



(a) Socioeconomics Model

(b) Marine Conservation Model



(c) Combined Model 1

(d) Combined Model 2

Chapter Two

High-resolution mapping and scale-dependent assessment of intertidal habitat projects population expansion of *Cittarium pica* in Bermuda

Erin Meyer, Nicholas Matzke, and Simon Williams

INTRODUCTION

Habitat assessments are essential components of biological conservation planning. Mapping the geographic distribution of preferred habitat is as important as mapping species distribution for establishing management plans and targeting locations for protected areas (Margules & Pressey 2000). Remote sensing and GIS have become valuable assessment tools for mapping habitat distribution in the absence of extensive ground surveys. These tools provide not only precise mapping capabilities but also information on elevation, substrate, and vegetation. The ability to map remotely is especially important for habitats that are difficult to access and those that are distributed over broad areas (De Wulf et al. 1988), such as seabed habitat for oysters (Smith et al. 2001), the distribution of mangroves and seagrass beds (Green et al. 1998; Howari et al. 2009), and the habitats used by salmon (Garono et al. 2004). For terrestrial environments, climate variables, such as air temperature and precipitation are often combined with remote sensing to predict the distribution of habitats (e.g., Buermann et al. 2008; Wang et al. 2010). For marine environments, climate variables are good predictors of habitat distribution at a global scale (Mellin et al. 2012; Spalding et al. 2007; Tyberghein et al. 2012), but they are poor predictors on a local scale. On a local scale, physical characteristics and processes such as substrate, upwelling/downwelling, and wave action are more relevant. Because intertidal habitats (e.g., beaches, estuaries, mangroves, mudflats, rocky shores) are the boundary or transition zone between terrestrial and marine habitats, a combination of these variables should be useful for predicting distributions. Temperature and tidal flux, for example, have a strong influence on intertidal zonation. However, for tropical intertidal habitats, sea-surface temperature varies by only 1-2ºC annually (Schneider & Helmuth 2007), air temperature varies typically by less than 10ºC annually, and tidal flux is relatively low and constant throughout the year. Thus tropical latitudes have less seasonal variation in habitat because these variables are nearly constant. Furthermore, on islands, these variables are likely consistent along entire coastlines. Because of the unique attributes of the intertidal zone, there is a need for new predictive tools directed toward this habitat.

Intertidal habitats result from their unique hydrologic and geologic history, controlled by a completely different set of processes than subtidal and terrestrial habitats. According to Fairbridge (2004), coastal habitats are classified by their composition or "material" (i.e., rock/sediment type and associated characteristics), "agencies" (e.g., latitude, wave energy, weathering), and historic factors (e.g., tectonics, eustatic changes of sea level). According to Short and Woodriffe (2009) ocean waves, which are defined by their "wave climate" (i.e., energy, direction, length, period) and tidal system, are the dominant processes that affect coastal habitats. The magnitude of the effects of these processes depends on historic factors and the material. For example, the distribution of coastal wetlands is well-documented (Belluco et al. 2006; e.g., Guan & Chamberlain 1999; Nezlin et al. 2007; Thomson et al. 2003), and the habitat is mainly defined by the amount (i.e., precipitation, tidal system, sea level) and duration of water inundation. Duration is in turn determined by the material (e.g., sand, silt, pebbles), wave energy, and coastal slope. Remote sensing can be used to map the distribution of these habitats by providing information on coastal slope, and the distribution of sediment and vegetation type (e.g., Thomson et al. 2003), in combination with data on precipitation and wave climate. Unlike coastal wetlands, other intertidal habitats, such as rocky shores and beaches, are less well mapped, likely because they are more difficult to define and distinguish using remote sensing data, especially at tropical latitudes.

Rock formations along coastlines result from a combination of plate tectonics, geologic history, weathering (e.g., wind, waves, precipitation), and in recent years, human activity (Griggs 2007a). Coastal rock on tropical islands is often dominated by sedimentary and volcanic rocks (Fairbridge 2004), and beaches are typically found adjacent to rocky outcrops. Because terrestrial sources of sediment are often lacking on tropical islands, beaches are dominated by broken shells, coral fragments (Griggs 2007b), and eroded rock. Many studies have focused on developing remote sensing techniques for intertidal habitats (Green et al. 1998; Howari et al. 2009; Larsen et al. 2004; Thomson et al. 1998), but few have focused on mapping rocky shores (Banks & Skilleter 2002; Chust et al. 2008) and mostly at a local scale (Guichard et al. 2000; Murphy et al. 2008). Techniques for mapping rocky shores over large geographic areas involve the use of light detection and ranging (LIDAR), multi-spectral imagery, and/or aerial photography (Banks & Skilleter 2002; Chust et al. 2008). These types of imagery are typically not available for small island nations and are expensive to obtain. Development of alternative, affordable methods for habitat assessment is crucial for exploited species because conservation planning cannot be delayed by lack of funding.

Bermuda is an ideal model system for testing remote sensing techniques for mapping intertidal habitats because it has only one exposed rock type and only three intertidal habitat types. Currently, no detailed information on the distribution of rocky shores, or any other intertidal habitat type in Bermuda, is available. One of the species that occupies the rocky shores of Bermuda, West Indian topsnail, *Cittarium pica* (Linnaeus, 1758), was fished to extinction in Bermuda by the mid-1800s

(Verrill 1902a, b) and was reintroduced in 1982 (Bickley & Rand 1982). This conspicuous and edible snail inhabits the rocky shores throughout the Tropical Northwestern Atlantic (as defined by Spalding et al. 2007), but information on the distribution of *C. pica* habitat is currently not available. Mapping intertidal habitat types in Bermuda will not only provide managers with information on the distribution of the preferred habitat of *C. pica*, but will also provide the foundation for testing the agreement of habitat distribution generated by remote sensing with the actual distribution of a species.

The objectives of this research are to (1) generate a map with the distribution of coastal habitat types in Bermuda using a high-resolution image (digital aerial image, 20-cm ground sampling distance) and manual classification, (2) investigate whether mapping resolution impacts the extent of inferred intertidal habitat or the proportions of each habitat type, (3) quantitatively confirm that moderate-resolution imagery (Landsat ETM+, 30-m spatial resolution) has comparatively little capability for mapping intertidal habitats, (4) overlay *C. pica* population distribution onto the map of habitat distribution, and (5) project future *C. pica* population size. The map generated is compared to the distribution of *C. pica* to verify its accuracy, and also to predict future population size of *C. pica* based on the population density from the survey and the amount of rocky shores present in Bermuda.

METHODS

Case Study

Bermuda is located in the western, North Atlantic at 32º20'N and 64º45'W (Fig. 1). The territory is composed of more than 150 islands (James & Schenk 1983) and has a total land area of 54 square kilometers. The islands are composed almost entirely of calcium carbonate that formed during Pleistocene sea level fluctuations, and which rests on top of a volcanic base (Bretz 1960; James & Schenk 1983). The platform is composed mainly of eolianites, with small proportions of marine limestone and paleosols (Land et al. 1967; Vacher & Hearty 1989). Water temperature at shallow, nearshore sites ranges from 14.4ºC to 31.6ºC, varying by up to 17.1ºC (S. Manuel, personal communication, 2012). Only three, natural coastal habitat categories are on Bermuda: rocky shores, mangroves and/or soft sediment, and beaches. Artificial coastal habitats, include seawalls, riprap, and docks.

Cittarium pica inhabits only the rocky shores. This snail is an important fishery resource that is harvested throughout its range and has been since pre-Columbian times (Crosby 2003; Fitzpatrick & Keegan 2007; O'Day & Keegan 2001). Fishing pressure on *C. pica* increased recently, resulting in the establishment of management plans in six island territories (see Chapter 1 for a detailed review). In Bermuda, *C. pica* was harvested from the time of the first human settlement in 1609, until it became locally extinct in the mid-1800s (Wingate 1995). The species was reintroduced to Bermuda in 1982 (Bickley & Rand 1982), and fully-protected in 1989 under the Fisheries (Protected Species) Order of 1978 (see Chapter 4).

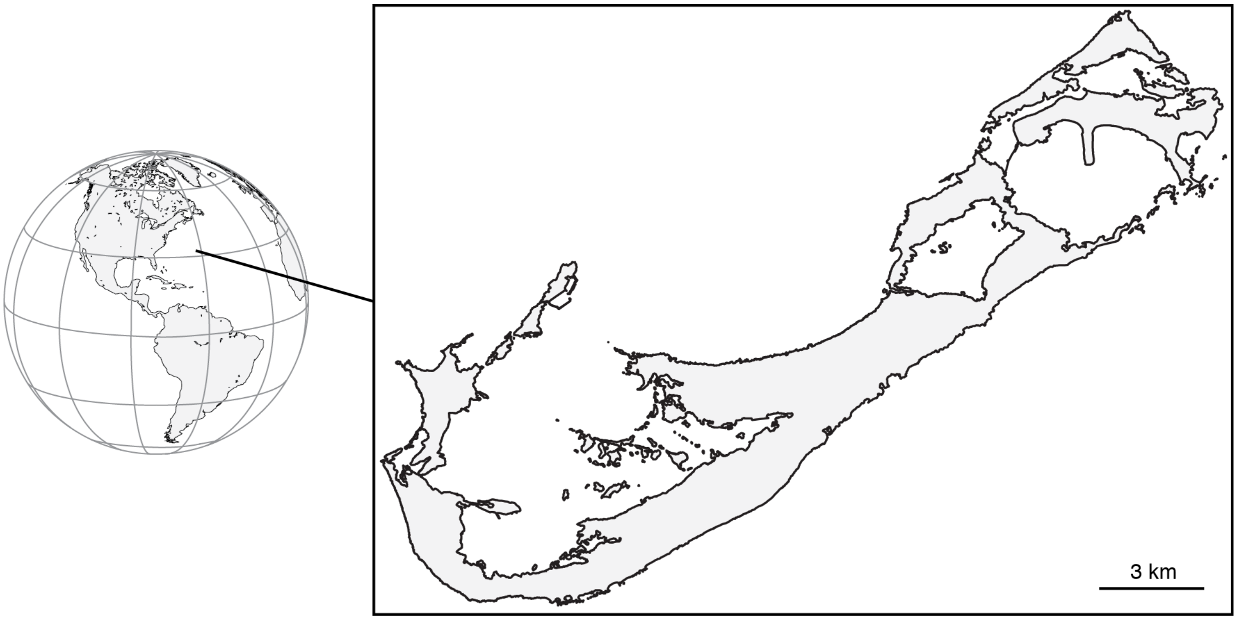


Figure 1: Bermuda is located in the western, North Atlantic at 32º20'N and 64º45'W. The territory is composed of more than 150 islands (James & Schenk 1983) and has a total land area of 54 square kilometers.

Remote Sensing

To assess the viability of available remote sensing approaches for mapping the intertidal habitat of *C. pica*, two approaches were compared: manual classification of a high-resolution image (digital aerial image, 20-cm ground sampling distance), and automated classification of a moderate-resolution image (Landsat ETM+, 30-m spatial resolution).

High-resolution manual mapping of the Bermuda coastline

The high-resolution image used was a 20-cm resolution (ground sampling distance) digital aerial image provided by the Bermuda government and taken by BKS of Northern Island (now part of Fugro-BKS group). This image was taken using a Beechcraft King Air BE-90 survey aircraft, fitted with a Leica RC30 Forward Motion Compensation (FMC) aerial camera, which has a gyro-stabilized mount and a 153 mm wide-angle lens. The image was taken in good weather conditions on February 20, 2003. This image contains three color channels (red, green, blue). Automated classification of this image was not attempted because of the limited spectral resolution of the image and the large diversity of features identifiable by eye (e.g., individual boulders, trees). Instead, visual interpretations of the image, combined with field observation of many locations on the Bermuda coast, were used to produce a manual classification of the coastline.

Intertidal habitat was mapped as a linear feature at 1:500 map scale (Tobler 1988) in ArcGIS v.10.0 (ESRI, Redlands, CA, USA). The minimum size of a mapped section of coastline was approximately 2.5 meters; habitat sections smaller than this could not be reliably identified. Choice of the map scale is important because statistics such as coastline length are heavily scale-dependent; mapping a coastline at high-resolution will produce a coastline length much higher than a low-resolution mapping (Gregory et al. 2009). This map scale was an appropriate choice, because it is feasible given the image resolution, and because meaningful extensions of the intertidal zone, which is 1-10 meters wide in Bermuda (E.M., personal observation) could be mapped. For example, if a small headland extends the length of the coastline, thus providing more habitat for *C. pica*, this would be mapped, but very small features (such as individual rocks) would not be. The coastline was classified into four categories: rocky shores, mangroves/soft sediment, beaches, and seawalls/docks. Habitat classifications were confirmed via extensive ground-truthing (E.M., personal observations). The rocky shores class included riprap because it serves as habitat for *C. pica*. The seawalls/docks class included all other forms of anthropogenic coastal armoring, including seawalls, miscellaneous concrete, and docks. Once the coastline was mapped, it was divided into relevant geographic regions (i.e., windward and leeward sides of the major islands) so that the proportion of each habitat type in each region could be estimated. Shores of bays and inlets were defined as windward. The shores within Castle Harbour and St. George's Harbour, which connect with the ocean to the southeast, were classified as windward. The shores within Ferry Reach and Harrington Sound, which connect with the ocean to the northwest, were classified as leeward. The exact delimitation of the borders of these regions was subjective but based on ground observations. For each main island, polygons were drawn over the island outline to define the windward and leeward regions (see Appendix 1, Fig. A1.1). For each polygon, a GIS overlay union function was performed in *R*, resulting in a line feature representing only the shoreline within that polygon. Windward and leeward coastline lengths were then directly determined for each island.

Assessment of the effect of smoothing the coastline on estimates of habitat

The finished coastline map was extracted as an ArcGIS shapefile and analyzed using *R* 2.14.1 (Ihaka & Gentleman 1996; R Development Core Team 2009). The length of the coastline was calculated at different resolutions using the *gSimplify* function in the *R* package *rgeos* 0.2-1 (Bivand & Rundel 2012; R Development Core Team 2009). *gSimplify* uses the Douglas-Peuker algorithm (Heckbert & Garland 1997) to smooth a piecewise linear feature into a coarser feature coded by more widely-spaced points. The degree of coarsening is determined by a tolerance limit, in this case specified in meters. For any line feature, a straight line is drawn between the start- and end-points. The vertex on the curved line feature that is farthest from the straight line is then checked to determine if it is within the tolerance; if it is, the vertex is eliminated from the curved line feature, if not, it is retained. Thus, increasing the tolerance limit will result in line features specified by fewer and fewer vertices. These will inevitably be shorter than the original line features, and different coastline types may experience more smoothing and shortening than others, depending on their roughness as originally mapped.

Assessment of supervised classification of intertidal habitats using Landsat ETM+

The availability of high-accuracy data on the location of rocky shores in the form of field observations and a "true" manual classification of the coastline with 20-cm imagery makes possible rigorous assessment of the utility of Landsat imagery in the case of Bermuda. Knowing in advance that coastline habitat mapping would be a difficult problem for Landsat data, we endeavored to maximize each classifier's chances by providing a massive training dataset – either 100% of pixels overlapping with the completely manually mapped coastline, or a randomly-selected 50% of the coastline pixels. In the latter case, the other 50% of the pixels were used as test data.

A 30-m orthorectified Landsat ETM+ image was downloaded from the Global Land Cover Facility (GLCF) Earth Science Data Interface (ESDI). The image was path 006 and row 038, acquired by the sensor on August 14, 1999, and the small section of the image covering Bermuda was almost entirely cloud-free. This image was cropped to the extent of Bermuda, resulting in an image 996 rows and 666 columns (29.88 km by 19.98 km). The coastline shapefile was projected onto this image in *R* using the *rgdal*, *sp*, and image libraries. All pixels touching the coastline feature were considered coastline and were extracted for statistical analysis. This resulted in 10,775 pixels, each with six brightness values for the six bands of the Landsat image (channels 1, 2, 3, 4, 5, and 7). Training and test pixels were input into twelve different automated supervised classification routines available in *R* (see Appendix 2 for a list and description of these routines). Accuracy was measured with the standard methods of a confusion matrix giving mapping accuracy, and the mean and variance of the kappa statistic (Congalton 1991; Congalton & Green 2009; Powell et al. 2004; Stehman 1997).

Cittarium pica Population and Distribution Projection

To test whether the distribution of *C. pica* correlates with its preferred habitat, as defined herein, we overlaid the distribution of *C. pica* from surveys conducted in 2000 (Cattell 2000; Madeiros 2000) onto the map of preferred habitat. These surveys, which included 48 unique field sites, were conducted by the Bermuda Department of Conservation Services, and the data are used in this study with permission. More recent *C. pica* population surveys conducted in Bermuda have not included all of the sites from the 2000 survey, but the densities on the different islands have remained fairly constant. The species almost exclusively inhabits rocky shores on the windward sides of the islands (i.e., coastlines with high wave action). Because of this, the map of preferred habitat was restricted to windward rocky shores

To project future population size of *C. pica* in Bermuda, the length of windward rocky shores was multiplied by the population density observed in the 2000 survey. Both the length of windward rocky shores and the population density vary across the Bermuda Islands, so the island-specific lengths and densities were used. This population projection assumes that all available habitat will be occupied. This provides important information for managers as they continue to monitor the recovery of this reintroduced species.

RESULTS

High-resolution Manual Mapping of the Bermuda Coastline and Intertidal Habitats

The total length of coastline determined via high-resolution manual mapping is 296.38 km, more than double what is typically quoted as the length of Bermuda's coastline (i.e., 103 km). Three of the habitat classes are found more commonly on the leeward side of the island and within its bays: rocky shores, mangroves/soft sediment, and seawalls/docks (Fig. 2, Appendix 1). Beaches, however, are more common on the windward side of the islands. Rocky shores are the dominant class on the Main Island, Cooper's Island, and the Castle Harbour Islands. St. David's Island and St. George's Island have about equal proportions of rocky shores and mangrove/soft sediment.

Overall, the dominant intertidal habitat in Bermuda is rocky shore, comprising approximately half of the coastline (50.38%). Rocky shores have an irregular distribution along the coastline, bordering on both windward and leeward sides of the larger islands and dominating the coastlines of the small, offshore islands (Fig. 2). Over 66% of rocky shores are along the leeward coast of Bermuda. Mangroves/soft sediment is the second most common habitat class, found along 26% of the coastline, with nearly 77% found along the leeward coast. Beaches are the least common of the natural habitat classes, existing along only 8% of the coastline. Finally, seawalls, docks, and other shoreline armoring structures are present along 15% of Bermuda's coast, primarily along the leeward side of the islands and within Hamilton Harbour.

Assessment of the Effect of Smoothing the Coastline on Estimates of Habitat

As coastline resolution decreases and becomes coarser, the apparent coastline of Bermuda shifts dramatically. Jagged coastal features are smoothed into straight lines, and small or narrow offshore islands disappear altogether (Fig. 3). These simplifications change the coastline length from 296.38 km (Fig. 3a) to 181.06 km (Fig. 3b), a decrease in coastline length of 115.32 km. Coastline length reaches a plateau at 184 km, a corresponding tolerance level of 300 (Fig. 4). In absolute terms, the length of rocky shores declined by 6.45% (69.78 km), mangroves/soft sediment by 3.62% (23.84 km), beaches by 4.11% (1.77 km), and seawalls/docks by 1.28% (20.03 km). Coarsening the mapping resolution had a unique effect on each habitat type, differentially affecting their relative proportions of the coastline. Mapping resolution had the least effect on the relative proportion of seawalls/docks, which declined by only 7% from highest to lowest resolution. Rocky shores and mangroves/soft sediment illustrated very similar declines along the same gradient, 14% and 13%, respectively. Coarsening the mapping resolution had the biggest effect on the percentage of beaches, which increased by 33%.

Assessment of Supervised Classification of Intertidal Habitats Using Landsat ETM+

Supervised classification of all four habitat classes using Landsat ETM+ did not produce highly accurate results (see summary tables, Appendix 2, Tables A2.1 & A2.2). Four out of twelve classification methods (i.e., *mars*, *mars.glm*, *tree* and *supportVector*), produced kappas less than

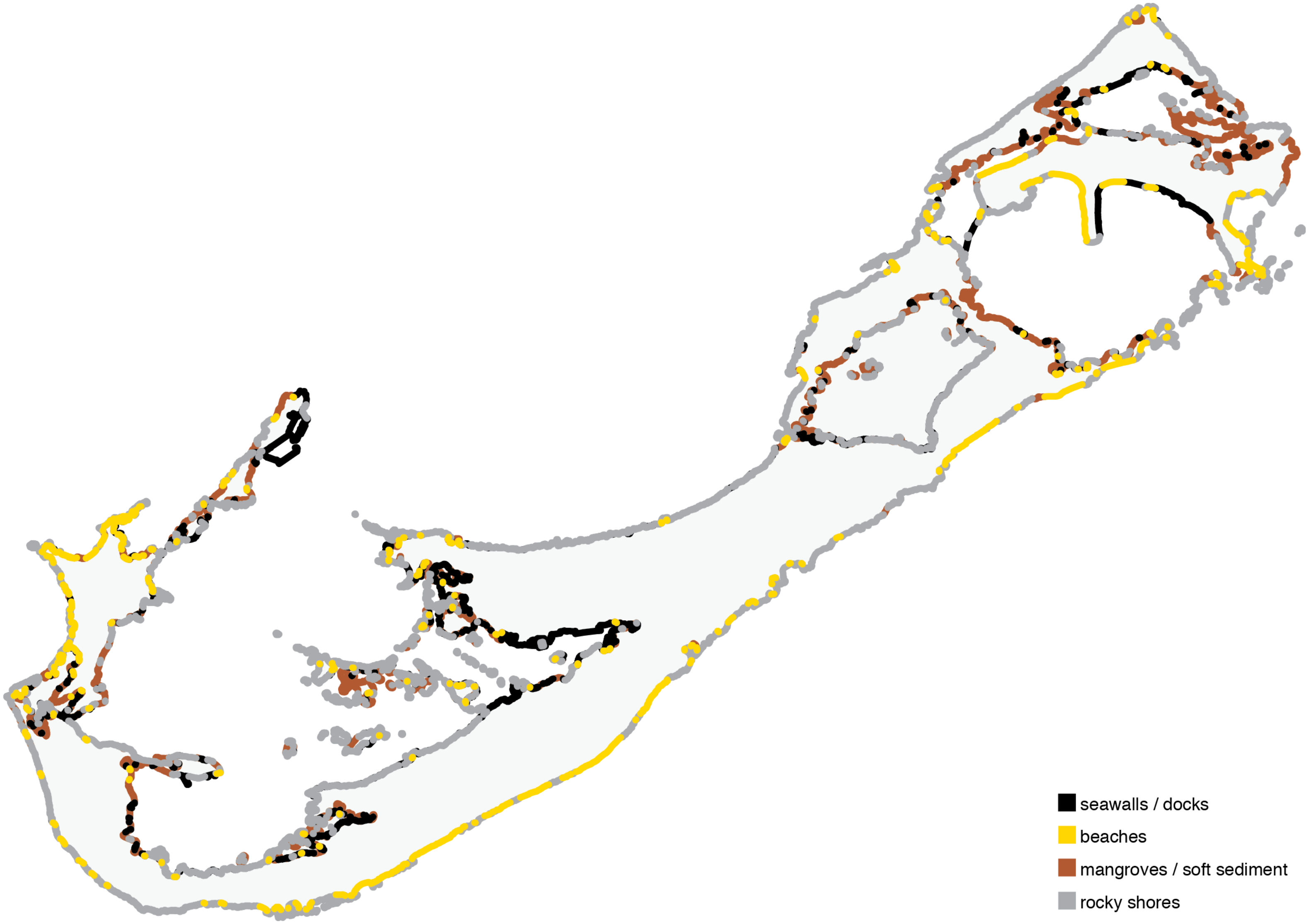


Figure 2: Manually classified intertidal habitats along the coast of Bermuda, including three natural habitat classes (e.g., rocky shores, mangroves/soft sediment, beaches) and one artificial habitat class (e.g., seawalls/docks). The rocky shores class included riprap because it serves as habitat for C. pica. The seawalls/docks class included all other forms of anthropogenic coastline armoring, including seawalls, miscellaneous concrete, and docks.

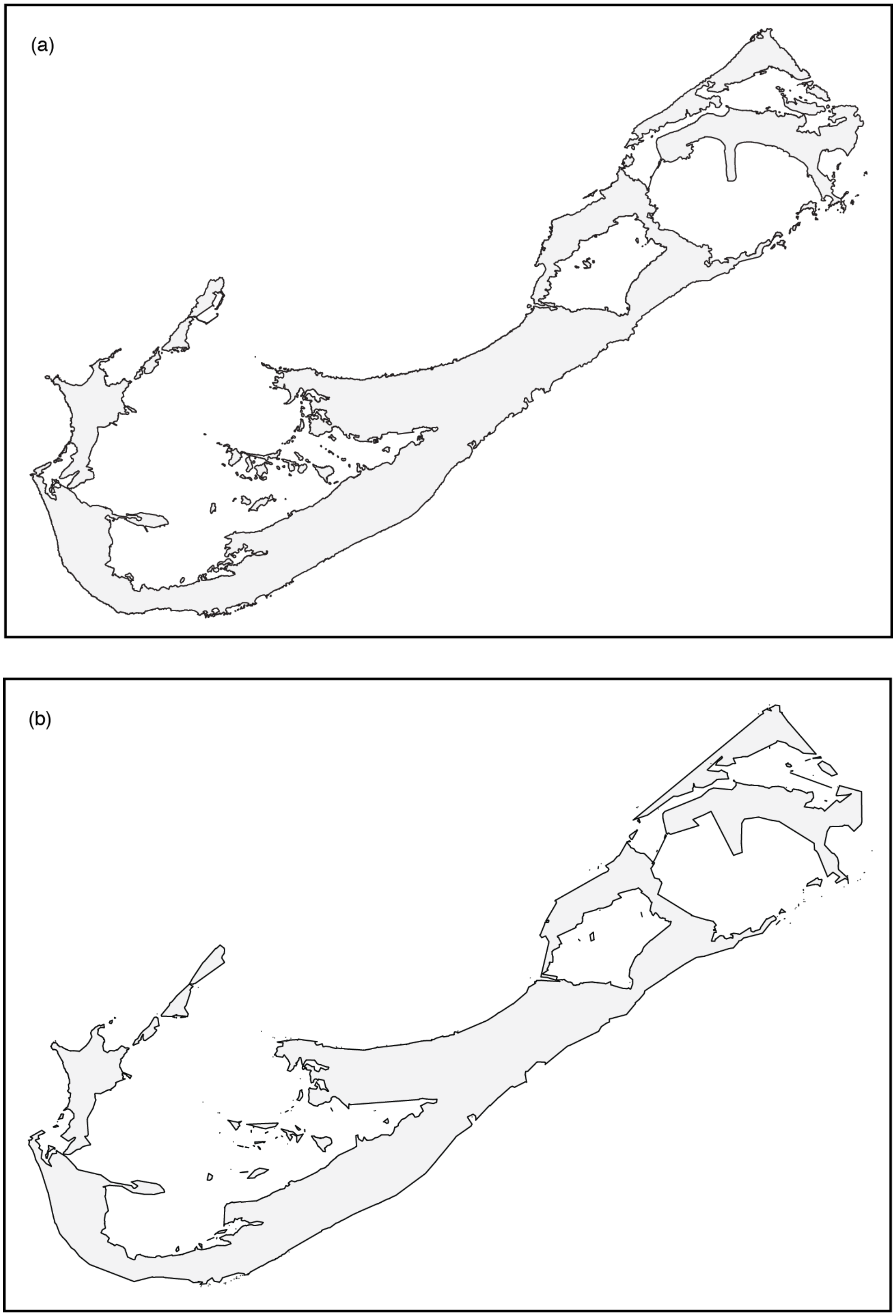


Figure 3: Assessment of the effect of smoothing the Bermuda coastline on estimates of the coastline length and thus total intertidal habitat. a) Coastline was generated via manual classification of a 20-cm resolution digital aerial photograph provided by the Bermuda government. The coastline length is 296.38 km.; b) Coastline was generated at a tolerance level of 700 – the coarsest resolution used – using the *gSimplify* function in the R package *rgeos* 0.2-1 (Bivand & Rundel 2012; R Development Core Team 2009). The coastline length is 181.06 km.

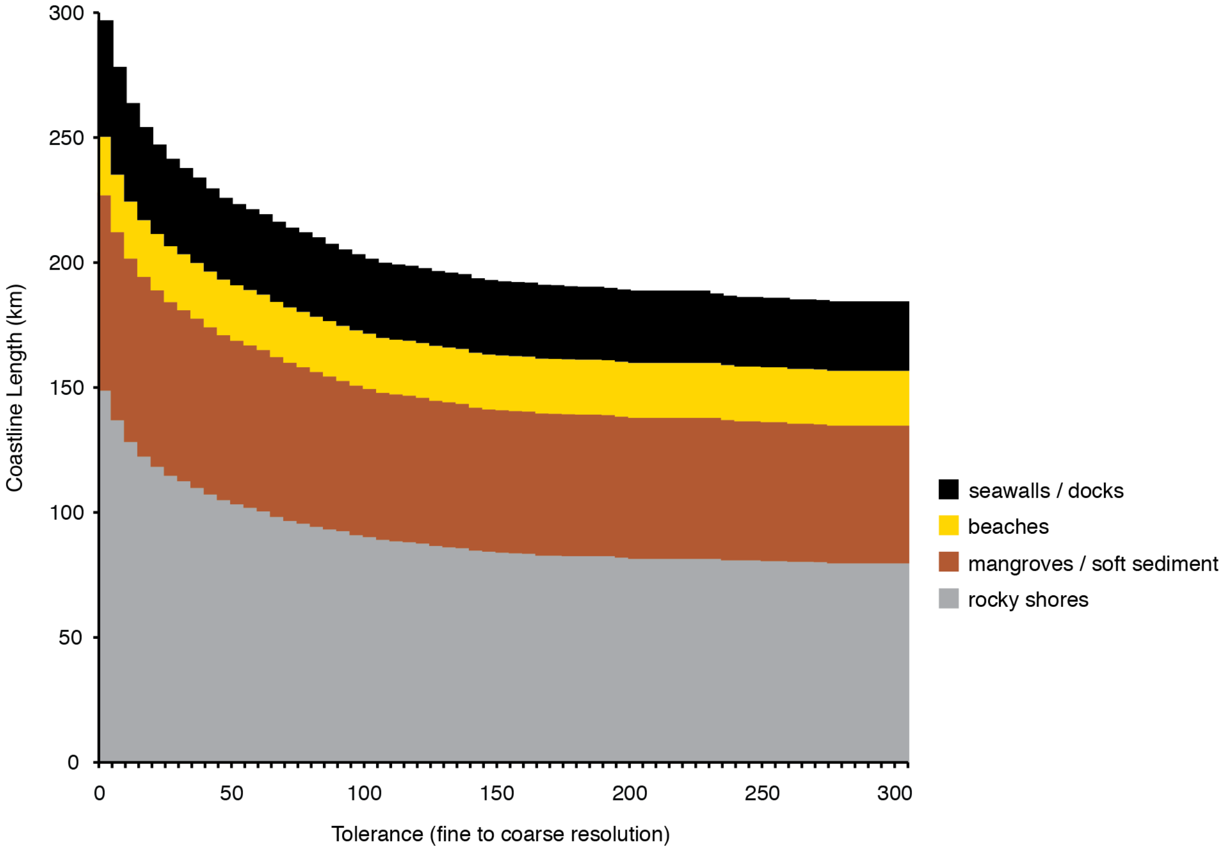


Figure 4: Assessment of the effect of smoothing the coastline on estimates of the length of coastline and the proportions of each habitat type, ranging from a tolerance of 0 to 300. This range of tolerance values is illustrated because coastline length plateaus at a tolerance level of 300, corresponding to a coastline length of 184 km. The maximum coastline length is 296.38 km. The relative proportions of three habitat classes decreases with decreasing resolution (increasing tolerance): rocky shores, mangroves/soft sediment, and seawalls/docks. The proportion of beaches increases with decreasing resolution.

0.2. While determining cut-offs for kappa statistics is a somewhat arbitrary process (Fleiss 1981; Landis & Koch 1977), this kappa result is rated as either “slight” or “poor”. Nine out of ten of the remaining methods produced “fair” agreements, with kappas between 0.21-0.40, with only one producing “substantial” to “perfect” agreements (i.e., *randomForest*). The two most successful classifiers overall were *randomForest* and *knncat*. For most of the classification methods, pixels are less likely to be misclassified as beaches than any other habitat (i.e., lowest percent commission). This means that the classifiers are good at identifying pixels that *are not* beach (see confusion matrices, Appendix 2, Tables A2.3-A2.5), but not necessarily good at identifying pixels that *are* beach. For all of the classification methods, rocky shores pixels are less likely to be misclassified than any other habitat (i.e., lowest percent omission). Therefore the classifiers are good at identifying pixels that *are* rocky shores, but not necessarily good at identifying pixels that *are not* rocky shores.

Even when 100% of the classified pixels are used in the classifier, no classification method produces highly accurate results. The *tree* and *supportVector* classifiers generated slight or

Table 1: *Cittarium pica* population projection, based on the distribution of windward rocky shores and island-specific densities from an island-wide population survey conducted in 2000.

Island / Island Group	Windward Rock (km)	Percent of Windward Rock Surveyed	Population Density (inds/km)	Population Projection
Castle Harbor Islands	6.89	41%	63	486
Cooper's Island	6.09	55%	928	8,005
Main Island	27.34	14%	499	18,972
St. David's Island	5.82	46%	252	3,431
St. George's Island	5.14	15%	6	150
Total Windward Rock: 51.28 km / Projected Population Size: 31,045 individuals				

poor agreements (kappa <0.2), nine methods generated fair agreement (kappa 0.21-0.40), and one produced perfect agreement. The *randomForest* classifier produced perfect agreement, but was less accurate for the test data than the training data. The *knncat* classification method yielded the second highest kappa (0.3163) and a mapping accuracy of 59.35%. A kappa value of this magnitude suggests that the results are significantly higher than a randomly guessing classifier, indicating some signal in the data. However, merely doing better than random is not by itself a satisfactory result for a classification. The results produced from a second round of supervised classifications, which merged the rocky shores and seawalls/docks classes, were not much different (see confusion matrices, Appendix 2, Tables A2.6-A2.8). The most successful classification methods were *randomForest*, *knncat*, *maximumLikelihood*, producing fair to perfect kappas.

Cittarium pica Population and Distribution Projection

The island-wide survey of *C. pica* conducted in 2000 indicates a population size of 3,704 individuals. These individuals are distributed along the windward coasts of the Bermuda islands (Fig. 5), but do not extend along the entirety of the rocky shores. The population density of *C. pica* in Bermuda varies across the islands (Table 1). Cooper's Island has the highest density, with 928 individuals per kilometer of coastline (ind/km). The Castle Harbour Islands have a density of only 63 ind/km, but St. George's Island has the lowest density, only 6 ind/km.

The length of rocky shores along the windward coasts of the Bermuda islands is 51.28 km (Table 1), which is the extent of preferred habitat of *C. pica*. When the distribution of *C. pica* is overlain onto the distribution of windward rocky shores, the two distributions overlap almost perfectly (Fig. 5). However, since 50% of the coastline is rocky shore, this is not surprising. Using population densities from the 2000 survey to predict the population size if all rocky shores of Bermuda are inhabited, the projected population size is 31,045 individuals. This is

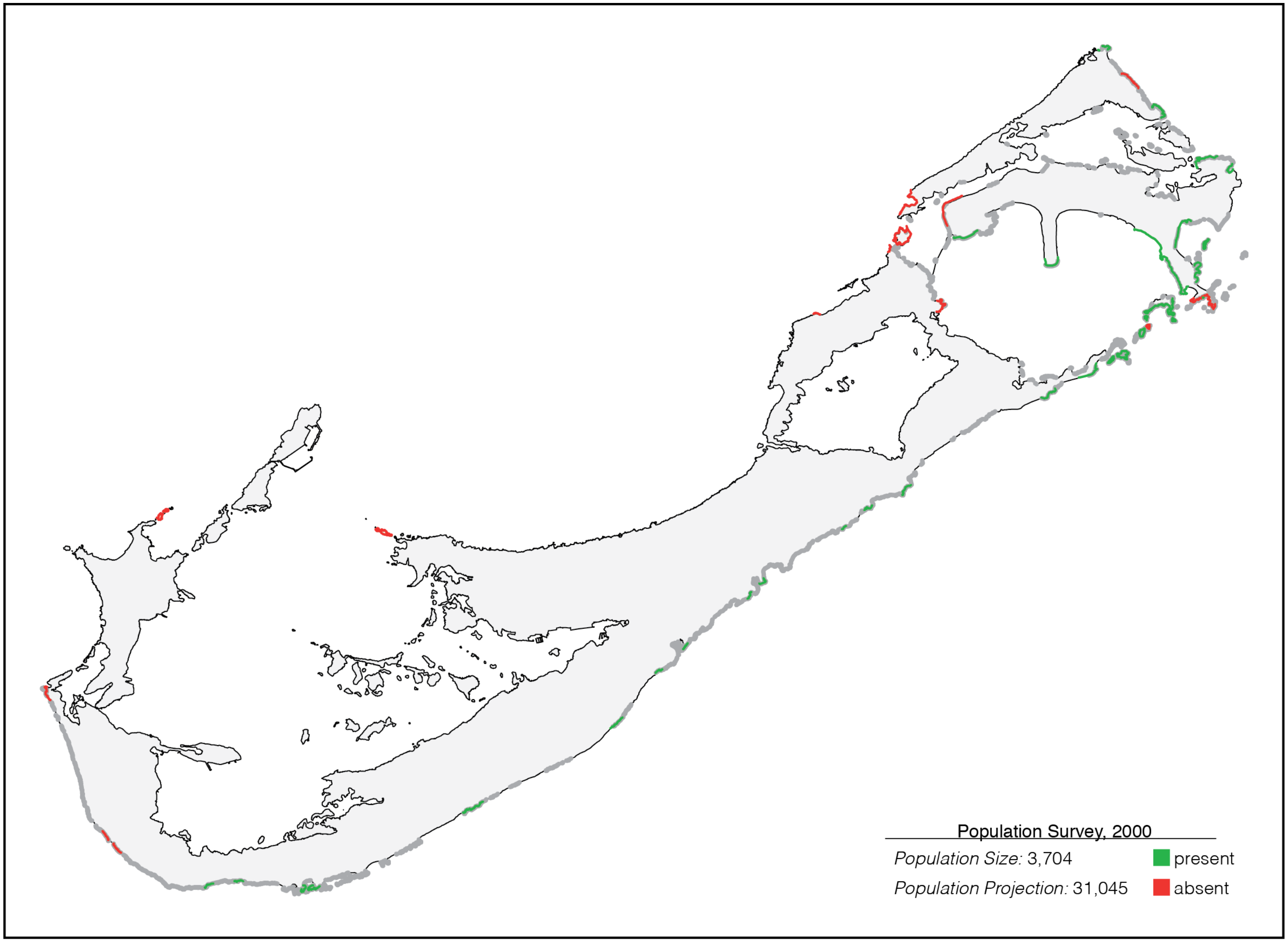


Figure 5: The distribution of windward rocky shores (gray), overlaid with the distribution of Cittarium pica from a population survey completed in 2000. The population size from the 2000 survey is 3,704 individuals. Using the island-specific population densities observed in the 2000 survey, we projected the future population size of the species in Bermuda, assuming that all available, windward rocky shores will be occupied.

an overestimation of expansion potential, though, because most likely not all rocky shores are equally suitable habitat for *C. pica* (see Chapter 3).

DISCUSSION

This study is the first detailed measurement of intertidal habitats conducted in Bermuda, and the associated distribution of *C. pica* habitat. Assessments of intertidal habitats typically require high-resolution imagery and extensive ground truth data to provide robust results. This research not only confirms that classification of intertidal habitat requires high-resolution imagery, but it also suggests that high-resolution imagery is required even for determining the linear extent of intertidal habitat.

Coastline and Intertidal Habitat Mapping of Bermuda

Manual classification of high-resolution aerial images can generate fine-scale maps of the extent and distribution of intertidal habitats (Chopra et al. 2001; Gang & Agatsiva 1992; Lathrop et al. 2006), especially when supported by ground truth data. After generating such a map for Bermuda, this study suggests that the extent of intertidal habitat is nearly twice the generally recognized length of coastline for Bermuda. This is at least partially because all small islands and large offshore boulders were mapped, which are not included in general outlines of Bermuda that are primarily concerned with land area large enough for development. The same phenomenon is common for delineation of coastline length across the world. In Australia, for example, the coastline length experiences a similar doubling in length when fine-scale coastal features are carefully mapped (see Harvey & Woodroffe 2008 and references therein). Small islands and boulders, however, provide a large surface area for settlement and inhabitation by marine organisms (Le Hir & Hily 2005; McGuinness 1984). Decreasing the coastline mapping resolution directly affects the amount of inferred coastline length, as well as the proportion of each intertidal habitat type that occupies that coastline. Thus, coarse resolution coastline mapping will result in underestimating the amount of habitat, which not only affects our knowledge of habitat distribution but also limits our ability to predict species distribution and population size. For Bermuda, the relative proportions of rocky shores and mangroves/soft sediment decreased, whereas the proportion of beaches increased. This is likely due to the loss of offshore islands as resolution decreased – offshore islands consist mainly of rocky shores and mangroves/soft sediment. However, the proportion of seawalls/docks remained nearly constant. Seawalls are restricted to the mainland and when constructed, they effectively straighten the coastline, making these stretches of coastline less susceptible to change in length with changing resolution.

The dominant intertidal habitat in Bermuda is rocky shores, followed by mangroves/soft sediment, and finally beaches. Seawalls and docks are actually a more common coastal feature in Bermuda than beaches, 15% and 8% respectively. This is comparable to the amount of armored coastline of California, where seawalls are found along 17.7% of the coastline (Hanak & Moreno 2011) and considerably less than the proportion of shoreline armored along the coast of the Emilia Romagna region of Italy, where 60% of the 130-km coastline is armored (Bacchiocchi &

Airoldi 2003). Differentiating between the four habitat classes, even by eye, is difficult because the substrates (except mangroves) are all drawn from the same source material. The Bermuda beaches are composed of coarse shell fragments and sand that is produced through weathering of limestone rocks or shells (James & Schenk 1983), which results in similar spectral signatures for both rocky shores and beaches. The soft sediment adjacent to mangroves makes even the mangrove regions difficult to differentiate from beaches and rock. Finally, seawalls and other shore-hardening structures are typically made from cement, which is simply ground limestone. When viewed from an airplane or satellite, seawalls are very narrow bands of cement, so they compose an even smaller fragment of a single coastal pixel than do the other habitat classes. Because all of these habitat classes have similar spectral signatures, manual classification of high-resolution imagery, coupled with ground-truthing, will always be preferred to automated classification of moderate-resolution imagery when the imagery and personnel resources are available.

We fully expected that mapping the narrow coastline feature with the relatively coarse (30-m) Landsat pixels would be very difficult and do not recommend it as an estimation procedure. The coastline pixels of such images are as wide or wider than the intertidal zone, which is just a thin linear feature when view from a plane or satellite. In addition, the habitat classes of interest (i.e., rocky shores, mangroves/soft sediment, beaches, seawalls/docks) are interdigitated at a scale finer than the pixel resolution, resulting in mixed pixels that give mixed spectral signatures. Coastline pixels also contain portions of ocean and wave crests on the seaward side, and buildings and other irrelevant land-cover on the landward side, resulting in further mixing of the signal in some pixels. Finally, because the rocks, beaches, and seawalls are derived from the same parent material, the spectral differences between these habitat classes are minimal and thus lack fundamental differences in spectral signatures. Shadows produced by rocks and seawalls provide unique signatures that may help distinguish them from beaches, and encrusting red algae and cyanobacteria cover much of the rock surfaces (Thomas & Logan 1992) that may help distinguish rocky shores from beaches. However, the encrusting organisms effectively darken rocks, which causes them to look spectrally similar to soft sediment. Despite these limitations, quantifying the accuracy of Landsat-based classification is nevertheless of scientific interest. For example, it could be used as a preliminary assessment of whether existing Landsat imagery is sufficient or not, which would establish whether acquisition of higher resolution multi- or hyperspectral imagery is required. Also, if high-resolution imagery (e.g., 5-m or 1-m resolution) is available for only a portion of an island's coastline, coarser (but multispectral) imagery could be used to target field sampling on the rest of the island.

Population Projection and Recovery of *Cittarium pica* in Bermuda

The current study generated a map of intertidal habitat in Bermuda by manual classification of a 20-cm resolution digital aerial image and assessed the distribution of habitat classes. By the time of the 2000 island-wide survey, 18 years after it was reintroduced, *C. pica* had dispersed all along the windward rocky shores of Bermuda, spreading as far as Red Hole Cove to the east and Sea Swept Farm to the west (see Chapter 4). However, a significant amount of available habitat is unoccupied. Because rocky shores have a patchy distribution, *C. pica* cannot simply spread across the island by direct movement of adults. Dispersal of *C. pica* is also controlled by the local current patterns because its planktonic larvae must be transported to new habitat patches for it to disperse. The distribution of rocky shores suggests that the population of *C. pica* could continue to expand in Bermuda to nearly eight-times its current population, based on current densities by region. *Cittarium pica* has few natural predators in Bermuda and because the fishery is currently closed, the population size should continue to rise steadily in the coming years. However, the population projection should be revised after more detailed habitat maps are generated for Bermuda because rocky shores can consist of cobble, coral rubble, individual boulders, carbonate platforms, erosional rocky cliffs (see Chapter 3), or a combination of these. *Cittarium pica* prefers more stable rocky shores, such as boulders, platforms and cliffs, but can be found in low density on coral rubble and is rarely found associated with cobble or small rock fragments (E.M., personal observation). Higher resolution imagery (<5 m), such as retrieved via CASI, MIVIS, ROSIS (e.g., Banks & Skilleter 2002; Belluco et al. 2006), or WorldView-2 can be used effectively in Bermuda not only to help distinguish between habitats, but also within habitats. Differentiating among the alternative rocky shores habitat types will provide stronger predictive power for species distribution mapping. The results of this study are particularly useful to resource managers in Bermuda, not only for providing maps of intertidal habitats, which they do not currently have, but also for documenting the continued recovery of a reintroduced species.

Conclusions

When digital aerial imagery is freely accessible for localized regions or small islands, manual classification of coastal habitats is likely more cost-effective than commissioning high-resolution, multi-spectral and/or hyperspectral imagery for automated classification. For broader regions or inclusion of coastal zones from multiple islands, however, manual classification is likely too time-consuming to be cost-effective. Although Landsat imagery has been successful for mapping coastal habitats at high latitudes (e.g., Larsen et al. 2004), high-resolution imagery of at least 10-m resolution is required for these habitats in the tropics and other locations where tidal flux is low because the intertidal is often restricted to a narrow coastal zone. As this research suggests, classification of 30-m resolution spectrally mixed pixels, when the target habitat is only 1-10 m wide, will likely produce a map with only ~50% accuracy. For terrestrial habitat mapping, researchers are often classifying large, continuous sets of pixels, often entire regions or continents (Buermann et al. 2008; De Wulf et al. 1988), which are much easier to classify than a line of single pixels. More sophisticated remote sensing techniques could be applied to improve mapping accuracy, such as spectral mixture models (e.g., Roberts et al. 1998). However, using these methods for automated classification of a thin linear feature would still be difficult for the case of Bermuda because there is high variation within habitat classes (e.g., rocky shores, mangroves/soft sediment) and low variation between classes (e.g., rocky shores, beaches, seawalls).

When high-resolution aerial images are not available, multi-spectral satellite imagery from IKONOS (1-4 meter resolution), QuickBird (0.61 meter resolution), or WorldView-2 (0.5 meter resolution) can be requested and purchased. However, *eurimage*, a company that specializes in multi-mission satellite data, charges \$17/km^2 for QuickBird imagery. At this price, commissioning imagery for the Bermuda coastline would cost ~\$5,000 for a 1-m wide image of the 297 km coastline, or ~\$42,000 for a 10-m wide image. Funding can be sought from local governments (e.g., Banks & Skilleter 2002; Chust et al. 2008; Larsen et al. 2004; Thomson et al. 2003) to cover the costs of such imagery, but not all petitions for funding can or will be met. Further, the imagery that already exists is scattered across several databases and webpages, with no central repository that documents what is already available, let alone how to gain permission for use of the imagery.

The intertidal habitat maps generated by this research provide a valuable asset to the Bermuda government as they continue to pursue the conservation and management of marine resources. *Cittarium pica* is a fully-protected species in Bermuda that was once extirpated due to over-exploitation; this study produced a map of the distribution of its preferred habitat (i.e., windward rocky shores). This map allows managers to more precisely focus population monitoring of this reintroduced species. Other threatened species also live in Bermuda intertidal habitats, such as the giant land crab (*Cardisoma guanhumi*), which burrows into the substratum within mangrove swamps (James & Schenk 1983). Also, other protected species require resources from intertidal habitats. The terrestrial hermit crab *Coenobita clypeatus* requires shells from a variety of gastropod species during their lifecycle, all of which occupy rocky shores, including *C. pica*, *Nerita versicolor*, *N. peloronta*, *N. tessellata*, and *Batillaria minima* (=*Lampanella minima*) (Lewis & Rotjan 2009). The Nassau grouper (*Epinephelus striatus*) eats crabs (Randall & Bishop 1967) that live within mangrove swamps (James & Schenk 1983). Having knowledge of the habitat distribution of protected species and their prey affords resource managers the information required to enforce present laws and identify ideal locations for marine reserves targeting these protected species.

Coverage of existing coastal habitat assessments is limited and patchy, especially in the tropics. Generation of high-resolution imagery of these habitats is critical for conservation research and resource management, as is making existing imagery easily accessible. The sensitivity of linear features to image resolution is particularly pertinent to intertidal habitat mapping throughout the world because these habitats are dynamic on both ecologic (i.e., due to tidal fluctuations and coastal construction) and geologic timescales (i.e., due to weathering, eustatic changes of sea level, and tectonics). It is also applicable to other dynamic habitats and transition zones, such as riparian habitats, altitudinal transitions in habitat, and ecotones between forests and grasslands and along the edges of glaciers or oceanic ice sheets. As global climate continues to change, we must first be able to accurately map the extents of these sensitive habitats before we can understand and predict how changes in climate (e.g., rising temperature, rising sea level, increased storm frequency) will affect them.

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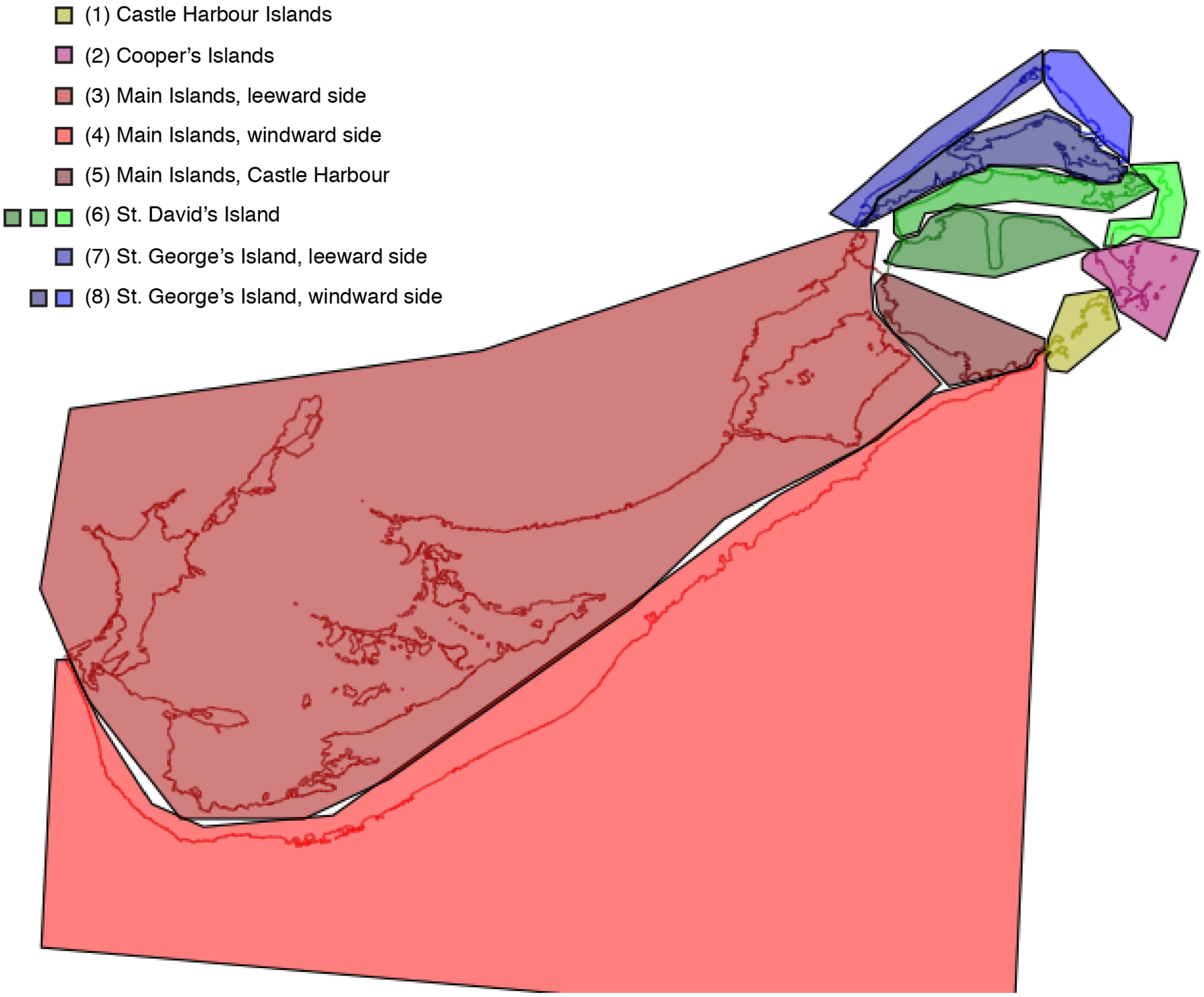
Appendix 1, Figure A1.1: Coastal outline of Bermuda broken into seven geographic regions: 1) Castle Harbour Islands (yellow); 2) Cooper's Islands (pink); 3) Main Islands, leeward side (dark red); 4) Main Islands, windward side (red); 5) Main Islands, Castle Harbour coast (brown); 6) St. David's Island (light, medium, and dark greens); 7) St. George's Island, leeward side (medium blue); and 8) St. George's Island, windward side (lightest and darkest blues).



Appendix 2, Tables A2.1-8: Methods for and results from each of the 12 classification methods for supervised classification of the Bermuda coastline. Summary tables of results (Tables A2.1-2.2) and confusion matrices for each classification run (Tables A2.3-A2.8) are provided.

Because measurement of the difficulty of using Landsat for mapping a linear coastline was peripheral to the main project, a variety of easily accessible R packages were used to classify the training and test data. All classifiers were run using default settings. Use of spatial information in the classification in a specialized GIS or remote-sensing package might improve the results, but are unlikely to overcome the main difficulty of mixed pixels and indistinct spectral signatures. The twelve different classification methods used are as follows (each is followed by the name of the pertinent R function): Quadratic Discriminant Analysis (*qda*), Linear Discriminant Analysis (*lda*), classification tree (*tree*), Multivariate Discrimination Analysis (*mda*), Multivariate Adaptive Regression Splines (*mars*), Multivariate Adaptive Regression Splines plus Generalized Linear Model (*mars.glm*), nearest-neighbor classification with categorical variables (*knncat*; Buttrey 1998), and classifiers available in the raster classification package *rasclass*, including Maximum Likelihood (*maximumLikelihood*), Multinomial Logistic Regression (*logit*), Neural Networks (*neuralNetwork*), Random Forests (*randomForest*), and Support Vector Machines (*supportVector*). The classifications were repeated after merging the rocky shores and seawalls/docks classes to test the possibility that confusion between these two similar classes was unduly influencing the accuracy assessment. All analyses were performed via R scripts and Excel.

To assess the maximum accuracy of Landsat-based classification of coastline, we presented the supervised classification algorithms with massive amounts of training data – either 100% of the coastline pixels (~10,000 observations) or 50% of the coastline pixels randomly selected (~5,000 observations). In the cases in which only 50% of the coastline pixels were used as training data, the other 50% were used as a test dataset. Confusion matrices and accuracy statistics were calculated for both the training and test datasets. The "ground truth" for each Landsat pixel was derived from the shapefile produced by manual classification of the coastline using high-resolution digital imagery (see Methods, main text). For each 30-meter Landsat pixel touched by the shapefile, the "true" class was the most-dominant class in the intersecting portion of the shapefile. The analysis was conducted for the original four-class dataset, and repeated after rocky shores and seawalls/docks were merged into one class.

As expected, low mapping accuracy and kappa statistics confirm that Landsat is unlikely to be useful for mapping coastline features. However, kappa statistics do indicate that some classifiers do significantly better than random, even on the test data. This indicates that there may be some spectral signal that can be exploited by a higher-resolution sensor. Furthermore, some insight is given into the relative performance of supervised classification algorithms. For example, classification trees do very poorly, whereas a Random Forest algorithm performs the best. The latter is definitely overfitting the data, given the near-100% accuracy of the method in classifying the training datasets, and the lower accuracy on test datasets. However, the Random Forest classification still retains 83% accuracy on test data. This is likely made possible by the huge training dataset (50% of the completely "known" coastline), which will closely share statistical features with the test dataset (the other 50% of the coastline pixels). Such large amounts of training data are only available through manual mapping of high-resolution imagery, which produces a more accurate map when the imagery and personnel resources are available. If high-resolution imagery was available for only a portion of an island, however, a technique such as this might allow extrapolation to portions of the island where only lower-resolution imagery is available.

Appendix 2, Tables A2.1a-c: Summary tables for classification of three sets of pixels: (a) 100% training pixels, (b) 50% training pixels, and (c) 50% test pixels. Results from all twelve supervised classification methods, and four habitat classes (rocky shores, mangroves/soft sediment, beaches, and seawalls/docks).

a) 100% training pixels (i.e., all data used for training and test)

Classification Method	Mapping Accuracy	Kappa	Kappa Variance	Signal to Noise (kappa/stddev)	Significantly different from 0?
randomForest	100	1	0	N/A	yes
supportVector	68.1206	0.1821	0.0040	2.8687	yes
neuralNetwork	67.9165	0.2654	0.0025	5.3584	yes
logit	67.7494	0.2070	0.0034	3.5582	yes
knncat	59.3503	0.3163	0.0022	6.8097	yes
maximumLikelihood	58.4130	0.2584	0.0011	7.6502	yes
mars.glm	55.2297	0.2315	0.0026	4.5111	yes
qda	54.8677	0.2559	0.0022	5.5004	yes
mars	54.6172	0.2153	0.0027	4.1107	yes
lda	54.5615	0.2230	0.0026	4.3965	yes
mda	53.5220	0.2217	0.0024	4.5363	yes
tree	50.9884	0.0667	0.0047	0.9770	no

b) 50% training pixels (i.e., 50% of data used for training and test)

Classification Method	Mapping Accuracy	Kappa	Kappa Variance	Signal to Noise (kappa/stddev)	Significantly different from 0?
randomForest	100	1	0	N/A	yes
neuralNetwork	68.6154	0.2234	0.0068	2.7030	yes
supportVector	68.0030	0.1646	0.0088	1.7560	no
logit	67.8545	0.2037	0.0070	2.4332	yes
maximumLikelihood	60.4677	0.2715	0.0025	5.4392	yes
knncat	59.2056	0.3164	0.0043	4.8353	yes
qda	53.3036	0.2386	0.0042	3.6681	yes
lda	53.2108	0.2019	0.0053	2.7744	yes
mda	52.4684	0.2106	0.0047	3.0644	yes
tree	46.9606	-0.0010	0.0046	-0.0151	no
mars.glm	34.7624	-0.0297	0.0027	-0.5700	no
mars	34.6511	-0.0333	0.0028	-0.6344	no

Appendix 2, Tables A2.1 continued

c) 50% test pixels (i.e., 50% of data used for training, other 50% for test)

Classification Method	Mapping Accuracy	Kappa	Kappa Variance	Signal to Noise (kappa/stddev)	Significantly different from 0?
randomForest	83.6674	0.6552	0.0013	18.2921	yes
neuralNetwork	68.2442	0.2580	0.0053	3.5468	yes
logit	67.8916	0.2037	0.0070	2.4287	yes
supportVector	67.7060	0.1492	0.0093	1.5491	no
qda	55.4669	0.2581	0.0044	3.8820	yes
lda	55.4297	0.2208	0.0056	2.9552	yes
maximumLikelihood	55.3823	0.2357	0.0021	5.1319	yes
mda	54.7986	0.2355	0.0048	3.3911	yes
knncat	49.8608	0.1527	0.0052	2.1181	yes
tree	47.7773	-0.0036	0.0049	-0.0514	no
mars.glm	35.7899	-0.0236	0.0028	-0.4445	no
mars	35.2515	-0.0320	0.0028	-0.6052	no

Appendix 2, Tables A2.2a-c: Summary tables for classification of three sets of pixels: (a) 100% training pixels, (b) 50% training pixels, and (c) 50% test pixels. Results from all twelve supervised classification methods, and three habitat classes (rocky shores/seawalls/docks, mangroves/soft sediment, and beaches).

a) 100% training pixels (i.e., all data used for training and test)

Classification Method	Mapping Accuracy	Kappa	Kappa Variance	Signal to Noise (kappa/stddev)	Significantly different from 0?
randomForest	99.9907	0.9998	0	5479.5062	yes
knncat	70.5522	0.3084	0.0024	6.2373	yes
neuralNetwork	68.1671	0.2258	0.0032	4.0236	yes
supportVector	68.1206	0.1821	0.0040	2.8687	yes
mars.glm	68.0557	0.2162	0.0033	3.7617	yes
mars	67.7494	0.1962	0.0036	3.2872	yes
logit	67.7494	0.2070	0.0034	3.5582	yes
lda	66.9884	0.2175	0.0030	3.9816	yes
mda	66.1624	0.2313	0.0025	4.6007	yes
tree	65.8376	0.0491	0.0063	0.6190	no
qda	65.5592	0.2648	0.0020	5.9632	yes
maximumLikelihood	58.4130	0.2584	0.0011	7.6502	yes

b) 50% training pixels (i.e., 50% of data used for training and test)

Classification Method	Mapping Accuracy	Kappa	Kappa Variance	Signal to Noise (kappa/stddev)	Significantly different from 0?
randomForest	100	1	0	N/A	yes
knncat	70.5457	0.3042	0.0050	4.2807	yes
supportVector	68.0030	0.1646	0.0088	1.7560	no
mars.glm	67.9844	0.2152	0.0067	2.6373	yes
neuralNetwork	67.9659	0.2215	0.0065	2.7570	yes
logit	67.8545	0.2037	0.0070	2.4332	yes
mars	67.7988	0.1948	0.0073	2.2823	yes
lda	66.9079	0.2082	0.0063	2.6255	yes
tree	66.0913	0.0660	0.0120	0.6037	no
mda	65.9614	0.2318	0.0050	3.2757	yes
qda	64.5509	0.2426	0.0041	3.7730	yes
maximumLikelihood	60.4677	0.2715	0.0025	5.4392	yes

Appendix 2, Tables A2.2 continued

c) 50% test pixels (i.e., 50% of data used for training, other 50% for test)

Classification Method	Mapping Accuracy	Kappa	Kappa Variance	Signal to Noise (kappa/stddev)	Significantly different from 0?
randomForest	83.3890	0.6485	0.0013	17.6936	yes
neuralNetwork	67.8545	0.2030	0.0070	2.4330	yes
supportVector	67.8359	0.1576	0.0090	1.6642	no
logit	67.7060	0.2112	0.0066	2.5941	yes
mars	67.6815	0.1826	0.0076	2.0878	yes
mars.glm	67.6443	0.1957	0.0071	2.3224	yes
lda	66.9575	0.1976	0.0067	2.4220	yes
mda	65.8437	0.2111	0.0055	2.8446	yes
knncat	65.6395	0.1747	0.0065	2.1731	yes
tree	65.6209	0.0445	0.0126	0.3972	no
qda	65.3982	0.2501	0.0042	3.8426	yes
maximumLikelihood	59.5954	0.2637	0.0024	5.3402	yes

Appendix 2, Tables A2.3a-l: Confusion matrices for supervised classification using 100% of the pixels as training data, for twelve classification methods for four habitat classes (rocky shores, mangroves/soft sediment, beaches, and seawalls/docks), including (a) Quadratic Discriminant Analysis, (b) Linear Discriminant Analysis, (c) Classification Tree, (d) Multivariate Discriminate Analysis, (e) Multivariate Adaptive Regression Splines, (f) Multivariate Adaptive Regression Splines plus Generalized Linear Model, (g) Nearest-neighbor Classification with Categorical Variables, (h) Maximum Likelihood, (i) Multinomial Logistic Regression, (j) Neural Networks, (k) Random Forests, and (l) Support Vector Machines.

a) Quadratic Discriminant Analysis (*qda*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	4,205	669	174	244	5,292	79.46
Mangroves / Soft Sediment	1,499	899	25	150	2,573	34.94
Beaches	514	187	431	84	1,216	35.44
Seawalls / Docks	1,009	242	66	377	1,694	22.26
Predicted Total	7,227	1,997	696	855	10,775	
Producer's Accuracy (%)	58.18	45.02	61.93	44.09	Kappa = 0.2559	
Errors of comission (%)	41.82	54.98	38.07	55.91	Kappa variance = 0.0022	
Errors of omission (%)	20.54	65.06	64.56	77.74	Overall accuracy (%) = 54.57	

b) Linear Discriminant Analysis (*lda*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	4,522	504	154	112	5,292	85.45
Mangroves / Soft Sediment	1,773	688	41	71	2,573	26.74
Beaches	571	166	433	46	1,216	35.61
Seawalls / Docks	1,188	157	113	236	1,694	13.93
Predicted Total	8,054	1,515	741	465	10,775	
Producer's Accuracy (%)	56.15	45.41	58.43	50.75	Kappa = 0.2230	
Errors of comission (%)	43.85	54.59	41.57	49.25	Kappa variance = 0.0026	
Errors of omission (%)	14.55	73.26	64.39	86.07	Overall accuracy (%) = 54.56	

Appendix 2, Tables A2.3 continued.

c) Classification Tree (*tree*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	5,233	0	59	0	5,292	98.89
Mangroves / Soft Sediment	2,549	0	24	0	2,573	0
Beaches	955	0	261	0	1,216	21.46
Seawalls / Docks	1,574	0	120	0	1,694	0
Predicted Total	10,311	0	464	0	10,775	
Producer's Accuracy (%)	50.75	N/A	56.25	N/A	Kappa = 0.0667	
Errors of comission (%)	49.25	N/A	43.75	N/A	Kappa variance = 0.0047	
Errors of omission (%)	1.11	100	78.54	100	Overall accuracy (%) = 50.99	

d) Multivariate Discrimination Analysis (*mda*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	4,306	508	237	241	5,292	81.37
Mangroves / Soft Sediment	1,690	711	61	111	2,573	27.63
Beaches	554	154	411	97	1,216	33.80
Seawalls / Docks	1,099	183	73	339	1,694	20.01
Predicted Total	7,649	1,556	782	788	10,775	
Producer's Accuracy (%)	56.29	45.69	52.56	43.02	Kappa = 0.2217	
Errors of comission (%)	43.71	54.31	47.44	56.98	Kappa variance = 0.0024	
Errors of omission (%)	18.63	72.37	66.20	79.99	Overall accuracy (%) = 53.52	

Appendix 2, Tables A2.3 continued.

e) Multivariate Adaptive Regression Splines (*mars*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	4,580	491	108	113	5,292	86.55
Mangroves / Soft Sediment	1,807	654	32	80	2,573	25.42
Beaches	629	143	399	45	1,216	32.81
Seawalls / Docks	1,243	153	46	252	1,694	14.88
Predicted Total	8,259	1,441	585	490	10,775	
Producer's Accuracy (%)	55.45	45.39	68.21	51.43	Kappa = 0.2153	
Errors of comission (%)	44.55	54.61	31.79	48.57	Kappa variance = 0.0027	
Errors of omission (%)	13.45	74.58	67.19	85.12	Overall accuracy (%) = 54.62	

f) Multivariate Adaptive Regression Splines plus Generalized Linear Model (*mars.glm*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	4,548	488	132	124	5,292	85.94
Mangroves / Soft Sediment	1,785	668	44	76	2,573	25.96
Beaches	601	123	448	44	1,216	36.84
Seawalls / Docks	1,203	153	51	287	1,694	16.94
Predicted Total	8,137	1,432	675	531	10,775	
Producer's Accuracy (%)	55.89	46.65	66.37	54.05	Kappa = 0.2315	
Errors of comission (%)	44.11	53.35	33.63	45.95	Kappa variance = 0.0026	
Errors of omission (%)	14.06	74.04	63.16	83.06	Overall accuracy (%) = 55.23	

Appendix 2, Tables A2.3 continued.

g) Nearest-neighbor Classification with Categorical Variables (knncat)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	4,588	485	95	124	5,292	86.70
Mangroves / Soft Sediment	1,468	978	37	90	2,573	38.01
Beaches	550	155	459	52	1,216	37.75
Seawalls / Docks	1,046	208	70	370	1,694	21.84
Predicted Total	7,652	1,826	661	636	10,775	
Producer's Accuracy (%)	59.96	53.56	69.44	58.18	Kappa = 0.3163	
Errors of comission (%)	40.04	46.44	30.56	41.82	Kappa variance = 0.0022	
Errors of omission (%)	13.30	61.99	62.25	78.16	Overall accuracy (%) = 59.35	

h) Maximum Likelihood (*maximumLikelihood*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	3,747	1,017	253	275	5,292	70.80
Mangroves / Soft Sediment	1,185	1,176	32	180	2,573	45.71
Beaches	431	227	472	86	1,216	38.82
Seawalls / Docks	833	367	85	409	1,694	24.14
Predicted Total	6,196	2,787	842	950	10,775	
Producer's Accuracy (%)	60.47	42.20	56.06	43.05	Kappa = 0.2713	
Errors of comission (%)	39.53	57.80	43.94	56.95	Kappa variance = 0.0018	
Errors of omission (%)	29.20	54.29	61.18	75.86	Overall accuracy (%) = 53.87	

Appendix 2, Tables A2.3 continued.

i) Multinomial Logistic Regression (*logit*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	*4,599*	*452*	*116*	*125*	*5,292*	86.90
Mangroves / Soft Sediment	*1,860*	*618*	*24*	*71*	*2,573*	24.02
Beaches	*599*	*149*	*416*	*52*	*1,216*	34.21
Seawalls / Docks	*1,225*	*140*	*72*	*257*	*1,694*	15.17
Predicted Total	*8,283*	*1,359*	*628*	*505*	*10,775*	
Producer's Accuracy (%)	55.52	45.47	66.24	50.89	Kappa = 0.2162	
Errors of comission (%)	44.48	54.53	33.76	49.11	Kappa variance = 0.0027	
Errors of omission (%)	13.10	75.98	65.79	84.83	Overall accuracy (%) = 54.66	

j) Neural Networks (*neuralNetwork*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	4,273	600	100	319	5,292	80.74
Mangroves / Soft Sediment	1,589	817	30	137	2,573	31.75
Beaches	634	110	394	78	1,216	32.40
Seawalls / Docks	990	184	45	475	1,694	28.04
Predicted Total	7,486	1,711	569	1,009	10,775	
Producer's Accuracy (%)	57.08	47.75	69.24	47.08	Kappa = 0.2553	
Errors of comission (%)	42.92	52.25	30.76	52.92	Kappa variance = 0.0023	
Errors of omission (%)	19.26	68.25	67.60	71.96	Overall accuracy (%) = 55.30	

Appendix 2, Tables A2.3 continued.

k) Random Forests (*randomForest*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	5,292	0	0	0	5,292	100
Mangroves / Soft Sediment	0	2,573	0	0	2,573	100
Beaches	0	0	1,216	0	1,216	100
Seawalls / Docks	0	0	1	1,693	1,694	99.94
Predicted Total	5,292	2,573	1,217	1,693	10,775	
Producer's Accuracy (%)	100	100	99.92	100	Kappa = 0.9999	
Errors of comission (%)	0	0	0.08	0	Kappa variance = 1.96E-08	
Errors of omission (%)	0	0	0	0.06	Overall accuracy (%) = 99.99	

l) Support Vector Machines (*supportVector*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	4,706	483	51	52	5,292	88.93
Mangroves / Soft Sediment	1,798	743	6	26	2,573	28.88
Beaches	706	136	349	25	1,216	28.70
Seawalls / Docks	1,302	168	18	206	1,694	12.16
Predicted Total	8,512	1,530	424	309	10,775	
Producer's Accuracy (%)	55.29	48.56	82.31	66.67	Kappa = 0.2220	
Errors of comission (%)	44.71	51.44	17.69	33.33	Kappa variance = 0.0029	
Errors of omission (%)	11.07	71.12	71.30	87.84	Overall accuracy (%) = 55.72	

Appendix 2, Tables A2.4a-l: Confusion matrices for supervised classification using 50% of the pixels as training data, for twelve classification methods for four habitat classes (rocky shores, mangroves/soft sediment, beaches, and seawalls/docks), including (a) Quadratic Discriminant Analysis, (b) Linear Discriminant Analysis, (c) Classification Tree, (d) Multivariate Discriminate Analysis, (e) Multivariate Adaptive Regression Splines, (f) Multivariate Adaptive Regression Splines plus Generalized Linear Model, (g) Nearest-neighbor Classification with Categorical Variables, (h) Maximum Likelihood, (i) Multinomial Logistic Regression, (j) Neural Networks, (k) Random Forests, and (l) Support Vector Machines.

a) Quadratic Discriminant Analysis (*qda*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,036	357	105	121	2,619	77.74
Mangroves / Soft Sediment	744	436	21	76	1,277	34.14
Beaches	260	90	238	32	620	38.39
Seawalls / Docks	518	143	49	162	872	18.58
Predicted Total	3,558	1,026	413	391	5,388	
Producer's Accuracy (%)	57.22	42.50	57.63	41.43	Kappa = 0.2386	
Errors of comission (%)	42.78	57.50	42.37	58.57	Kappa variance = 0.0042	
Errors of omission (%)	22.26	65.86	61.61	81.42	Overall accuracy (%) = 53.30	

b) Linear Discriminant Analysis (*lda*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,228	247	82	62	2,619	85.07
Mangroves / Soft Sediment	933	296	23	25	1,277	23.18
Beaches	288	78	232	22	620	37.42
Seawalls / Docks	633	73	55	111	872	12.73
Predicted Total	4,082	694	392	220	5,388	
Producer's Accuracy (%)	54.58	42.65	59.18	50.45	Kappa = 0.2019	
Errors of comission (%)	45.42	57.35	40.82	49.55	Kappa variance = 0.0053	
Errors of omission (%)	*14.93*	*76.82*	*62.58*	*87.27*	Overall accuracy (%) = 53.21	

Appendix 2, Tables A2.4 continued.

c) Classification Tree (*tree*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	5,006	0	232	0	5,238	95.57
Mangroves / Soft Sediment	2,438	0	115	0	2,553	0
Beaches	1,186	0	54	0	1,240	4.35
Seawalls / Docks	1,681	0	63	0	1,744	0
Predicted Total	10,311	0	464	0	10,775	
Producer's Accuracy (%)	48.55	N/A	11.64	N/A	Kappa = -0.0010	
Errors of comission (%)	51.45	N/A	88.36	N/A	Kappa variance = 0.0046	
Errors of omission (%)	4.43	100	95.65	100	Overall accuracy (%) = 46.96	

d) Multivariate Discrimination Analysis (*mda*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,094	271	138	116	2,619	79.95
Mangroves / Soft Sediment	848	351	39	39	1,277	27.49
Beaches	274	81	231	34	620	37.26
Seawalls / Docks	584	100	37	151	872	17.32
Predicted Total	3,800	803	445	340	5,388	
Producer's Accuracy (%)	55.11	43.71	51.91	44.41	Kappa = 0.2106	
Errors of comission (%)	44.89	56.29	48.09	55.59	Kappa variance = 0.0047	
Errors of omission (%)	20.05	72.51	62.74	82.68	Overall accuracy (%) = 52.47	

Appendix 2, Tables A2.4 continued.

e) Multivariate Adaptive Regression Splines (*mars*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	1,721	289	609	0	2,619	65.71
Mangroves / Soft Sediment	1,022	77	178	0	1,277	6.03
Beaches	242	309	69	0	620	11.13
Seawalls / Docks	433	82	357	0	872	0
Predicted Total	3,418	757	1,213	0	5,388	
Producer's Accuracy (%)	50.35	10.17	5.69	N/A	Kappa = -0.0333	
Errors of comission (%)	49.65	89.83	94.31	N/A	Kappa variance = 0.0028	
Errors of omission (%)	34.29	93.97	88.87	100	Overall accuracy (%) = 65.35	

f) Multivariate Adaptive Regression Splines plus Generalized Linear Model (*mars.glm*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	1,727	263	629	0	2,619	65.94
Mangroves / Soft Sediment	1,022	78	177	0	1,277	6.11
Beaches	231	321	68	0	620	10.97
Seawalls / Docks	429	73	370	0	872	0
Predicted Total	3,409	735	1,244	0	5,388	
Producer's Accuracy (%)	50.66	10.61	5.47	N/A	Kappa = -0.0297	
Errors of comission (%)	49.34	89.39	94.53	N/A	Kappa variance = 0.0027	
Errors of omission (%)	34.06	93.89	89.03	100	Overall accuracy (%) = 34.76	

Appendix 2, Tables A2.4 continued.

g) Nearest-neighbor Classification with Categorical Variables (*knncat*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,279	246	39	77	2,641	86.29
Mangroves / Soft Sediment	737	474	16	54	1,281	37.00
Beaches	286	77	233	25	621	37.52
Seawalls / Docks	499	114	28	204	845	24.14
Predicted Total	3,801	911	316	360	5,388	
Producer's Accuracy (%)	59.96	52.03	73.73	56.67	Kappa = 0.3164	
Errors of comission (%)	40.04	47.97	26.27	43.33	Kappa variance = 0.0043	
Errors of omission (%)	13.71	63.00	62.48	75.86	Overall accuracy (%) = 59.21	

h) Maximum Likelihood (*maximumLikelihood*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	1,719	689	119	144	2,671	64.36
Mangroves / Soft Sediment	466	695	15	92	1,268	54.81
Beaches	192	120	248	35	595	41.68
Seawalls / Docks	325	255	42	232	854	27.17
Predicted Total	2,702	1,759	424	503	5,388	
Producer's Accuracy (%)	63.62	39.51	58.49	46.12	Kappa = 0.2891	
Errors of comission (%)	36.38	60.49	41.51	53.88	Kappa variance = 0.0032	
Errors of omission (%)	35.64	45.19	58.32	72.83	Overall accuracy (%) = 53.71	

Appendix 2, Tables A2.4 continued.

i) Multinomial Logistic Regression (*logit*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,319	224	53	75	2,671	86.82
Mangroves / Soft Sediment	910	310	10	38	1,268	24.45
Beaches	293	60	219	23	595	36.81
Seawalls / Docks	597	68	35	154	854	18.03
Predicted Total	4,119	662	317	290	5,388	
Producer's Accuracy (%)	56.30	46.83	69.09	53.10	Kappa = 0.2326	
Errors of comission (%)	43.70	53.17	30.91	46.90	Kappa variance = 0.0054	
Errors of omission (%)	13.18	75.55	63.19	81.97	Overall accuracy (%) = 55.72	

j) Neural Networks (*neuralNetworks*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,335	182	79	75	2,671	87.42
Mangroves / Soft Sediment	932	265	30	41	1,268	20.90
Beaches	313	37	229	16	595	38.49
Seawalls / Docks	581	46	60	167	854	19.56
Predicted Total	4,161	530	398	299	5,388	
Producer's Accuracy (%)	56.12	50.00	57.54	55.85	Kappa = 0.2307	
Errors of comission (%)	43.88	50.00	42.46	44.15	Kappa variance = 0.0055	
Errors of omission (%)	12.58	79.10	61.51	80.44	Overall accuracy (%) = 55.61	

Appendix 2, Tables A2.4 continued.

k) Random Forests (*randomForest*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,671	0	0	0	2,671	100
Mangroves / Soft Sediment	0	1,268	0	0	1,268	100
Beaches	0	0	595	0	595	100
Seawalls / Docks	0	0	0	854	854	100
Predicted Total	2,671	1,268	595	854	5,388	
Producer's Accuracy (%)	100	100	100	100	Kappa = 1	
Errors of comission (%)	0	0	0	0	Kappa variance = 0	
Errors of omission (%)	0	0	0	0	Overall accuracy (%) = 100	

l) Support Vector Machines (*supportVector*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,395	225	21	30	2,671	89.67
Mangroves / Soft Sediment	894	350	2	22	1,268	27.60
Beaches	352	49	177	17	595	29.75
Seawalls / Docks	655	70	10	119	854	13.93
Predicted Total	4,296	694	210	188	5,388	
Producer's Accuracy (%)	55.75	50.43	84.29	63.30	Kappa = 0.2285	
Errors of comission (%)	44.25	49.57	15.71	36.70	Kappa variance = 0.0059	
Errors of omission (%)	10.33	72.40	70.25	86.07	Overall accuracy (%) = 56.44	

Appendix 2, Tables A2.5a-l: Confusion matrices for supervised classification using 50% of the pixels as test data, for twelve classification methods for four habitat classes (rocky shores, mangroves/soft sediment, beaches, and seawalls/docks), including (a) Quadratic Discriminant Analysis, (b) Linear Discriminant Analysis, (c) Classification Tree, (d) Multivariate Discriminate Analysis, (e) Multivariate Adaptive Regression Splines, (f) Multivariate Adaptive Regression Splines plus Generalized Linear Model, (g) Nearest-neighbor Classification with Categorical Variables, (h) Maximum Likelihood, (i) Multinomial Logistic Regression, (j) Neural Networks, (k) Random Forests, and (l) Support Vector Machines.

a) Quadratic Discriminant Analysis (*qda*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,148	333	104	88	2,673	80.36
Mangroves / Soft Sediment	758	464	13	61	1,296	35.80
Beaches	270	93	204	29	596	34.23
Seawalls / Docks	484	123	43	172	822	20.92
Predicted Total	3,660	1,013	364	350	5,387	
Producer's Accuracy (%)	58.69	45.80	56.04	49.14	Kappa = 0.2581	
Errors of comission (%)	41.31	54.20	43.96	50.86	Kappa variance = 0.0044	
Errors of omission (%)	19.64	64.20	65.77	79.08	Overall accuracy (%) = 55.47	

b) Linear Discriminant Analysis (*lda*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,356	204	78	35	2,673	88.14
Mangroves / Soft Sediment	927	321	18	30	1,296	24.77
Beaches	314	64	201	17	596	33.72
Seawalls / Docks	596	65	53	108	822	13.14
Predicted Total	4,193	654	350	190	5,387	
Producer's Accuracy (%)	56.19	49.08	57.43	56.84	Kappa = 0.2208	
Errors of comission (%)	43.81	50.92	42.57	43.16	Kappa variance = 0.0056	
Errors of omission (%)	11.86	75.23	66.28	86.86	Overall accuracy (%) = 55.43	

Appendix 2, Tables A2.5 continued.

c) Classification Tree (*tree*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	5,102	0	245	0	5,347	95.42
Mangroves / Soft Sediment	2,482	0	110	0	2,592	0
Beaches	1,146	0	46	0	1,192	3.86
Seawalls / Docks	1,581	0	63	0	1,644	0
Predicted Total	10,311	0	464	0	10,775	
Producer's Accuracy (%)	49.48	N/A	9.91	N/A	Kappa = -0.0036	
Errors of comission (%)	50.52	N/A	90.09	N/A	Kappa variance = 0.0049	
Errors of omission (%)	4.58	100	96.14	100	Overall accuracy (%) = 47.78	

d) Multivariate Discrimination Analysis (*mda*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,226	221	145	81	2,673	83.28
Mangroves / Soft Sediment	846	354	39	57	1,296	27.31
Beaches	288	65	198	45	596	33.22
Seawalls / Docks	520	90	38	174	822	21.17
Predicted Total	3,880	730	420	357	5,387	
Producer's Accuracy (%)	57.37	48.49	47.14	48.74	Kappa = 0.2355	
Errors of comission (%)	42.63	51.51	52.86	51.26	Kappa variance = 0.0048	
Errors of omission (%)	16.72	72.69	66.78	78.83	Overall accuracy (%) = 54.80	

Appendix 2, Tables A2.5 continued.

e) Multivariate Adaptive Regression Splines (*mars*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	1,758	295	620	0	2,673	65.77
Mangroves / Soft Sediment	1,016	78	202	0	1,296	6.02
Beaches	256	277	63	0	596	10.57
Seawalls / Docks	385	76	361	0	822	0
Predicted Total	3,415	726	1,246	0	5,387	
Producer's Accuracy (%)	51.48	10.74	5.06	N/A	Kappa = -0.0320	
Errors of comission (%)	48.52	89.26	94.94	N/A	Kappa variance = 0.0028	
Errors of omission (%)	34.23	93.98	89.43	100	Overall accuracy (%) = 35.25	

f) Multivariate Adaptive Regression Splines plus Generalized Linear Model (*mars.glm*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	1,779	270	624	0	2,673	66.55
Mangroves / Soft Sediment	1,017	80	199	0	1,296	6.17
Beaches	248	279	69	0	596	11.58
Seawalls / Docks	383	68	371	0	822	0
Predicted Total	3,427	697	1,263	0	5,387	
Producer's Accuracy (%)	51.91	11.48	5.46	N/A	Kappa = -0.0236	
Errors of comission (%)	48.09	88.52	94.54	N/A	Kappa variance = 0.0028	
Errors of omission (%)	33.45	93.83	88.42	100	Overall accuracy (%) = 35.79	

Appendix 2, Tables A2.5 continued.

g) Nearest-neighbor Classification with Categorical Variables (*knncat*)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,076	384	80	111	2,651	78.31
Mangroves / Soft Sediment	875	319	27	71	1,292	24.69
Beaches	319	61	174	41	595	29.24
Seawalls / Docks	594	113	25	117	849	13.78
Predicted Total	3,864	877	306	340	5,387	
Producer's Accuracy (%)	53.73	36.37	56.86	34.41	Kappa = 0.1527	
Errors of comission (%)	46.27	63.63	43.14	65.59	Kappa variance = 0.0052	
Errors of omission (%)	21.69	75.31	70.76	86.22	Overall accuracy (%) = 49.86	

h) Maximum Likelihood (maximumLikelihood)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	1,621	816	102	132	2,671	60.69
Mangroves / Soft Sediment	437	737	11	83	1,268	58.12
Beaches	188	129	243	35	595	40.84
Seawalls / Docks	327	277	40	210	854	24.59
Predicted Total	2,573	1,959	396	460	5,388	
Producer's Accuracy (%)	63.00	37.62	61.36	45.65	Kappa = 0.2710	
Errors of comission (%)	37.00	62.38	38.64	54.35	Kappa variance = 0.0032	
Errors of omission (%)	39.31	41.88	59.16	75.41	Overall accuracy (%) = 52.17	

Appendix 2, Tables A2.5 continued.

i) Multinomial Logistic Regression (logit)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,291	248	59	73	2,671	85.77
Mangroves / Soft Sediment	875	340	15	38	1,268	26.81
Beaches	278	72	225	20	595	37.82
Seawalls / Docks	581	84	38	151	854	17.68
Predicted Total	4,025	744	337	282	5,388	
Producer's Accuracy (%)	56.92	45.70	66.77	53.55	Kappa = 0.2407	
Errors of comission (%)	43.08	54.30	33.23	46.45	Kappa variance = 0.0052	
Errors of omission (%)	14.23	73.19	62.18	82.32	Overall accuracy (%) = 55.81	

j) Neural Networks (neuralNetwork)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,416	155	38	62	2,671	90.45
Mangroves / Soft Sediment	987	249	2	30	1,268	19.64
Beaches	342	28	197	28	595	33.11
Seawalls / Docks	644	39	18	153	854	17.92
Predicted Total	4,389	471	255	273	5,388	
Producer's Accuracy (%)	55.05	52.87	77.25	56.04	Kappa = 0.2168	
Errors of comission (%)	44.95	47.13	22.75	43.96	Kappa variance = 0.0062	
Errors of omission (%)	9.55	80.36	66.89	82.08	Overall accuracy (%) = 55.96	

Appendix 2, Tables A2.5 continued.

k) Random Forests (randomForest)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,375	199	43	54	2,671	88.92
Mangroves / Soft Sediment	311	901	17	39	1,268	71.06
Beaches	119	50	401	25	595	67.39
Seawalls / Docks	246	60	18	530	854	62.06
Predicted Total	3,051	1,210	479	648	5,388	
Producer's Accuracy (%)	77.84	74.46	83.72	81.79	Kappa = 0.6562	
Errors of comission (%)	22.16	25.54	16.28	18.21	Kappa variance = 0.0013	
Errors of omission (%)	11.08	28.94	32.61	37.94	Overall accuracy (%) = 78.08	

l) Support Vector Machines (supportVector)

	Rocky Shores	Mangroves / Soft Sediment	Beaches	Seawalls / Docks	Actual Total	User's Accuracy (%)
Rocky Shores	2,442	189	15	25	2,671	91.43
Mangroves / Soft Sediment	947	298	2	21	1,268	23.50
Beaches	375	37	163	20	595	27.39
Seawalls / Docks	675	52	6	121	854	14.17
Predicted Total	4,439	576	186	187	5,388	
Producer's Accuracy (%)	55.01	51.74	87.63	64.71	Kappa = 0.2125	
Errors of comission (%)	44.99	48.26	12.37	35.29	Kappa variance = 0.0064	
Errors of omission (%)	8.57	76.50	72.61	85.83	Overall accuracy (%) = 56.12	

Appendix 2, Tables A2.6a-l: Confusion matrices for supervised classification using 100% of the pixels as training data, for twelve classification methods for three habitat classes (rocky shores/seawalls/docks, mangroves/soft sediment, and beaches), including (a) Quadratic Discriminant Analysis, (b) Linear Discriminant Analysis, (c) Classification Tree, (d) Multivariate Discriminate Analysis, (e) Multivariate Adaptive Regression Splines, (f) Multivariate Adaptive Regression Splines plus Generalized Linear Model, (g) Nearest-neighbor Classification with Categorical Variables, (h) Maximum Likelihood, (i) Multinomial Logistic Regression, (j) Neural Networks, (k) Random Forests, and (l) Support Vector Machines.

a) Quadratic Discriminant Analysis (*qda*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	5738	853	395	6986	82.14
Mangroves / Soft Sediment	1643	880	50	2573	34.20
Beaches	595	175	446	1216	36.68
Predicted Total	7976	1908	891	10775	
Producer's Accuracy (%)	71.94	46.12	50.06	Kappa = 0.2648	
Errors of comission (%)	28.06	53.88	49.94	Kappa variance = 0.0020	
Errors of omission (%)	17.86	65.80	63.32	Overall accuracy (%) = 65.56	

b) Linear Discriminant Analysis (*lda*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	6343	414	229	6986	90.80
Mangroves / Soft Sediment	2074	470	29	2573	18.27
Beaches	714	97	405	1216	33.31
Predicted Total	9131	981	663	10775	
Producer's Accuracy (%)	69.47	47.91	61.09	Kappa = 0.2175	
Errors of comission (%)	30.53	52.09	38.91	Kappa variance = 0.0030	
Errors of omission (%)	9.20	81.73	66.69	Overall accuracy (%) = 66.99	

Appendix 2, Tables A2.6 continued.

c) Classification Tree (*tree*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	6965	0	21	6986	99.70
Mangroves / Soft Sediment	2570	0	3	2573	0
Beaches	1087	0	129	1216	10.61
Predicted Total	10622	0	153	10775	
Producer's Accuracy (%)	65.57	N/A	84.31	Kappa = 0.0491	
Errors of comission (%)	34.43	N/A	15.69	Kappa variance = 0.0063	
Errors of omission (%)	0.30	100	89.39	Overall accuracy (%) = 65.84	

d) Multivariate Discrimination Analysis (*mda*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	*6095*	*608*	*283*	*6986*	87.25
Mangroves / Soft Sediment	*1903*	*633*	*37*	*2573*	24.60
Beaches	*669*	*146*	*401*	*1216*	32.98
Predicted Total	*8667*	*1387*	*721*	*10775*	
Producer's Accuracy (%)	70.32	45.64	55.62	Kappa = 0.2313	
Errors of comission (%)	29.68	54.36	44.38	Kappa variance = 0.0025	
Errors of omission (%)	12.75	75.40	67.02	Overall accuracy (%) = 66.16	

Appendix 2, Tables A2.6 continued.

e) Multivariate Adaptive Regression Splines (*mars*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	6588	346	52	6986	94.30
Mangroves / Soft Sediment	2149	417	7	2573	16.21
Beaches	843	78	295	1216	24.26
Predicted Total	9580	841	354	10775	
Producer's Accuracy (%)	68.77	49.58	83.33	Kappa = 0.1962	
Errors of comission (%)	31.23	50.42	16.67	Kappa variance = 0.0026	
Errors of omission (%)	5.70	83.79	75.74	Overall accuracy (%) = 67.75	

f) Multivariate Adaptive Regression Splines plus Generalized Linear Model (*mars.glm*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	6538	368	80	6986	93.59
Mangroves / Soft Sediment	2114	446	13	2573	17.33
Beaches	788	79	349	1216	28.70
Predicted Total	9440	893	442	10775	
Producer's Accuracy (%)	69.26	49.94	78.96	Kappa = 0.2162	
Errors of comission (%)	30.74	50.06	21.04	Kappa variance = 0.0033	
Errors of omission (%)	6.41	82.67	71.30	Overall accuracy (%) = 68.06	

Appendix 2, Tables A2.6 continued.

g) Nearest-neighbor Classification with Categorical Variables (*knncat*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	6453	444	89	6986	92.37
Mangroves / Soft Sediment	1774	766	33	2573	29.77
Beaches	752	81	383	1216	31.50
Predicted Total	8979	1291	505	10775	
Producer's Accuracy (%)	71.87	59.33	75.84	Kappa = 0.3084	
Errors of comission (%)	28.13	40.67	24.16	Kappa variance = 0.0024	
Errors of omission (%)	7.63	70.23	68.50	Overall accuracy (%) = 70.55	

h) Maximum Likelihood (*maximumLikelihood*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	4256	2155	575	6986	60.92
Mangroves / Soft Sediment	954	1527	92	2573	59.35
Beaches	426	279	511	1216	42.02
Predicted Total	5636	3961	1178	10775	
Producer's Accuracy (%)	75.51	38.55	43.38	Kappa = 0.2584	
Errors of comission (%)	24.49	61.45	56.62	Kappa variance = 0.0011	
Errors of omission (%)	39.08	40.65	57.98	Overall accuracy (%) = 58.41	

Appendix 2, Tables A2.6 continued.

i) Multinomial Logistic Regression (*logit*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	6535	351	100	6986	93.54
Mangroves / Soft Sediment	2148	413	12	2573	16.05
Beaches	787	77	352	1216	28.95
Predicted Total	9470	841	464	10775	
Producer's Accuracy (%)	69.01	49.11	75.86	Kappa = 0.2070	
Errors of comission (%)	30.99	50.89	24.14	Kappa variance = 0.0034	
Errors of omission (%)	6.46	83.95	71.05	Overall accuracy (%) = 67.75	

j) Neural Networks (*neuralNetwork*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	6482	430	74	6986	92.79
Mangroves / Soft Sediment	2020	541	12	2573	21.03
Beaches	832	62	322	1216	26.48
Predicted Total	9334	1033	408	10775	
Producer's Accuracy (%)	69.45	52.37	78.92	Kappa = 0.2258	
Errors of comission (%)	30.55	47.63	21.08	Kappa variance = 0.0032	
Errors of omission (%)	7.21	78.97	73.52	Overall accuracy (%) = 68.17	

Appendix 2, Tables A2.6 continued.

k) Random Forests (*randomForest*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	6985	0	1	6986	99.99
Mangroves / Soft Sediment	0	2573	0	2573	100
Beaches	0	0	1216	1216	100
Predicted Total	6985	2573	1217	10775	
Producer's Accuracy (%)	100	100	99.92	Kappa = 0.9998	
Errors of comission (%)	0	0	0.08	Kappa variance = 3.33E-08	
Errors of omission (%)	0.01	0	0	Overall accuracy (%) = 99.99	

l) Support Vector Machines (*supportVector*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	6734	216	36	6986	96.39
Mangroves / Soft Sediment	2264	305	4	2573	11.85
Beaches	879	36	301	1216	24.75
Predicted Total	9877	557	341	10775	
Producer's Accuracy (%)	68.18	54.76	88.27	Kappa = 0.1821	
Errors of comission (%)	31.82	45.24	11.73	Kappa variance = 0.0040	
Errors of omission (%)	3.61	88.15	75.25	Overall accuracy (%) = 68.12	

Appendix 2, Tables A2.7a-l: Confusion matrices for supervised classification using 50% of the pixels as training data, for twelve classification methods for three habitat classes (rocky shores/seawalls/docks, mangroves/soft sediment, and beaches), including (a) Quadratic Discriminant Analysis, (b) Linear Discriminant Analysis, (c) Classification Tree, (d) Multivariate Discriminate Analysis, (e) Multivariate Adaptive Regression Splines, (f) Multivariate Adaptive Regression Splines plus Generalized Linear Model, (g) Nearest-neighbor Classification with Categorical Variables, (h) Maximum Likelihood, (i) Multinomial Logistic Regression, (j) Neural Networks, (k) Random Forests, and (l) Support Vector Machines.

a) Quadratic Discriminant Analysis (*qda*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	2,853	410	228	3,491	81.72
Mangroves / Soft Sediment	857	390	30	1,277	30.54
Beaches	304	81	235	620	37.90
Predicted Total	4,014	881	493	5,388	
Producer's Accuracy (%)	71.08	44.27	47.67	Kappa = 0.2426	
Errors of comission (%)	28.92	55.73	52.33	Kappa variance = 0.0041	
Errors of omission (%)	18.28	69.46	62.10	Overall accuracy (%) = 64.55	

b) Linear Discriminant Analysis (*lda*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,195	177	119	3,491	91.52
Mangroves / Soft Sediment	1,068	196	13	1,277	15.35
Beaches	364	42	214	620	34.52
Predicted Total	4,627	415	346	5,388	
Producer's Accuracy (%)	69.05	47.23	61.85	Kappa = 0.2082	
Errors of comission (%)	30.95	52.77	38.15	Kappa variance = 0.0063	
Errors of omission (%)	8.48	84.65	65.48	Overall accuracy (%) = 66.91	

Appendix 2, Tables A2.7 continued.

c) Classification Tree (*tree*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,474	0	17	3,491	99.51
Mangroves / Soft Sediment	1,270	0	7	1,277	0
Beaches	533	0	87	620	14.03
Predicted Total	5,277	0	111	5,388	
Producer's Accuracy (%)	65.83	N/A	78.38	Kappa = 0.0660	
Errors of comission (%)	34.17	N/A	21.62	Kappa variance = 0.0120	
Errors of omission (%)	0.49	100	85.97	Overall accuracy (%) = 66.09	

d) Multivariate Discrimination Analysis (*mda*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,036	287	168	3,491	86.97
Mangroves / Soft Sediment	960	290	27	1,277	22.71
Beaches	324	68	228	620	36.77
Predicted Total	4,320	645	423	5,388	
Producer's Accuracy (%)	70.28	44.96	53.90	Kappa = 0.2318	
Errors of comission (%)	29.72	55.04	46.10	Kappa variance = 0.0050	
Errors of omission (%)	13.03	77.29	63.23	Overall accuracy (%) = 65.96	

Appendix 2, Tables A2.7 continued.

e) Multivariate Adaptive Regression Splines (*mars*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,310	148	33	3,491	94.82
Mangroves / Soft Sediment	1,098	173	6	1,277	13.55
Beaches	415	35	170	620	27.42
Predicted Total	4,823	356	209	5,388	
Producer's Accuracy (%)	68.63	48.60	81.34	Kappa = 0.1948	
Errors of comission (%)	31.37	51.40	18.66	Kappa variance = 0.0073	
Errors of omission (%)	5.18	86.45	72.58	Overall accuracy (%) = 67.80	

f) Multivariate Adaptive Regression Splines plus Generalized Linear Model (*mars.glm*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,271	165	55	3,491	93.70
Mangroves / Soft Sediment	1,070	198	9	1,277	15.51
Beaches	391	35	194	620	31.29
Predicted Total	4,732	398	258	5,388	
Producer's Accuracy (%)	69.13	49.75	75.19	Kappa = 0.2152	
Errors of comission (%)	30.87	50.25	24.81	Kappa variance = 0.0067	
Errors of omission (%)	6.30	84.49	68.71	Overall accuracy (%) = 67.98	

Appendix 2, Tables A2.7 continued.

g) Nearest-neighbor Classification with Categorical Variables (*knncat*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,246	196	44	3,486	93.12
Mangroves / Soft Sediment	916	356	9	1,281	27.79
Beaches	376	46	199	621	32.05
Predicted Total	4,538	598	252	5,388	
Producer's Accuracy (%)	71.53	59.53	78.97	Kappa = 0.3042	
Errors of comission (%)	28.47	40.47	21.03	Kappa variance = 0.0050	
Errors of omission (%)	6.88	72.21	67.95	Overall accuracy (%) = 70.55	

h) Maximum Likelihood (*maximumLikelihood*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	2,301	894	296	3,491	65.91
Mangroves / Soft Sediment	542	686	49	1,277	53.72
Beaches	229	120	271	620	43.71
Predicted Total	3,072	1,700	616	5,388	
Producer's Accuracy (%)	74.90	40.35	43.99	Kappa = 0.2715	
Errors of comission (%)	25.10	59.65	56.01	Kappa variance = 0.0025	
Errors of omission (%)	34.09	46.28	56.29	Overall accuracy (%) = 60.47	

Appendix 2, Tables A2.7 continued.

i) Multinomial Logistic Regression (*logit*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,294	149	48	3,491	94.36
Mangroves / Soft Sediment	1,097	173	7	1,277	13.55
Beaches	393	38	189	620	30.48
Predicted Total	4,784	360	244	5,388	
Producer's Accuracy (%)	68.85	48.06	77.46	Kappa = 0.2037	
Errors of comission (%)	31.15	51.94	22.54	Kappa variance = 0.0070	
Errors of omission (%)	5.64	86.45	69.52	Overall accuracy (%) = 67.85	

j) Neural Networks (*neuralNetwork*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,245	177	69	3,491	92.95
Mangroves / Soft Sediment	1,062	207	8	1,277	16.21
Beaches	387	23	210	620	33.87
Predicted Total	4,694	407	287	5,388	
Producer's Accuracy (%)	69.13	50.86	73.17	Kappa = 0.2215	
Errors of comission (%)	30.87	49.14	26.83	Kappa variance = 0.0065	
Errors of omission (%)	7.05	83.79	66.13	Overall accuracy (%) = 67.97	

Appendix 2, Tables A2.7 continued.

k) Random Forests (*randomForest*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,491	0	0	3,491	100
Mangroves / Soft Sediment	0	1,277	0	1,277	100
Beaches	0	0	620	620	100
Predicted Total	3,491	1,277	620	5,388	
Producer's Accuracy (%)	100	100	100	Kappa = 1	
Errors of comission (%)	0	0	0	Kappa variance = 0	
Errors of omission (%)	0	0	0	Overall accuracy (%) = 100	

l) Support Vector Machines (*supportVector*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,409	67	15	3,491	97.65
Mangroves / Soft Sediment	1,171	104	2	1,277	8.14
Beaches	452	17	151	620	24.35
Predicted Total	5,032	188	168	5,388	
Producer's Accuracy (%)	67.75	55.32	89.88	Kappa = 0.1646	
Errors of comission (%)	32.25	44.68	10.12	Kappa variance = 0.0088	
Errors of omission (%)	2.35	91.86	75.65	Overall accuracy (%) = 68.00	

Appendix 2, Tables A2.8a-l: Confusion matrices for supervised classification using 50% of the pixels as test data, for twelve classification methods for three habitat classes (rocky shores/seawalls/docks, mangroves/soft sediment, and beaches), including (a) Quadratic Discriminant Analysis, (b) Linear Discriminant Analysis, (c) Classification Tree, (d) Multivariate Discriminate Analysis, (e) Multivariate Adaptive Regression Splines, (f) Multivariate Adaptive Regression Splines plus Generalized Linear Model, (g) Nearest-neighbor Classification with Categorical Variables, (h) Maximum Likelihood, (i) Multinomial Logistic Regression, (j) Neural Networks, (k) Random Forests, and (l) Support Vector Machines.

a) Quadratic Discriminant Analysis (*qda*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	2,907	371	217	3,495	83.18
Mangroves / Soft Sediment	863	408	25	1,296	31.48
Beaches	306	82	208	596	34.90
Predicted Total	4,076	861	450	5,387	
Producer's Accuracy (%)	71.32	47.39	46.22	Kappa = 0.2501	
Errors of comission (%)	28.68	52.61	53.78	Kappa variance = 0.0042	
Errors of omission (%)	16.82	68.52	65.10	Overall accuracy (%) = 65.40	

b) Linear Discriminant Analysis (*lda*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,223	164	108	3,495	92.22
Mangroves / Soft Sediment	1,084	199	13	1,296	15.35
Beaches	378	33	185	596	31.04
Predicted Total	4,685	396	306	5,387	
Producer's Accuracy (%)	68.79	50.25	60.46	Kappa = 0.1976	
Errors of comission (%)	31.21	49.75	39.54	Kappa variance = 0.0067	
Errors of omission (%)	7.78	84.65	68.96	Overall accuracy (%) = 66.96	

Appendix 2, Tables A2.8 continued.

c) Classification Tree (*tree*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,474	0	21	3,495	99.40
Mangroves / Soft Sediment	1,292	0	4	1,296	0
Beaches	535	0	61	596	10.23
Predicted Total	5,301	0	86	5,387	
Producer's Accuracy (%)	65.53	N/A	70.93	Kappa = 0.0445	
Errors of comission (%)	34.47	N/A	29.07	Kappa variance = 0.0126	
Errors of omission (%)	0.60	100	89.77	Overall accuracy (%) = 65.62	

d) Multivariate Discrimination Analysis (*mda*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,085	251	159	3,495	88.27
Mangroves / Soft Sediment	984	282	30	1,296	21.76
Beaches	357	59	180	596	30.20
Predicted Total	4,426	592	369	5,387	
Producer's Accuracy (%)	69.70	47.64	48.78	Kappa = 0.2111	
Errors of comission (%)	30.30	52.36	51.22	Kappa variance = 0.0055	
Errors of omission (%)	11.73	78.24	69.80	Overall accuracy (%) = 65.84	

Appendix 2, Tables A2.8 continued.

e) Multivariate Adaptive Regression Splines (*mars*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,323	143	29	3,495	95.08
Mangroves / Soft Sediment	1,108	181	7	1,296	13.97
Beaches	430	24	142	596	23.83
Predicted Total	4,861	348	178	5,387	
Producer's Accuracy (%)	68.36	52.01	79.78	Kappa = 0.1826	
Errors of comission (%)	31.64	47.99	20.22	Kappa variance = 0.0076	
Errors of omission (%)	4.92	86.03	76.17	Overall accuracy (%) = 67.68	

f) Multivariate Adaptive Regression Splines plus Generalized Linear Model (*mars.glm*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,284	165	46	3,495	93.96
Mangroves / Soft Sediment	1,081	207	8	1,296	15.97
Beaches	414	29	153	596	25.67
Predicted Total	4,779	401	207	5,387	
Producer's Accuracy (%)	68.72	51.62	73.91	Kappa = 0.1957	
Errors of comission (%)	31.28	48.38	26.09	Kappa variance = 0.0071	
Errors of omission (%)	6.04	84.03	74.33	Overall accuracy (%) = 67.64	

Appendix 2, Tables A2.8 continued.

g) Nearest-neighbor Classification with Categorical Variables (*knncat*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,148	299	53	3,500	89.94
Mangroves / Soft Sediment	1,034	242	16	1,292	18.73
Beaches	405	44	146	595	24.54
Predicted Total	4,587	585	215	5,387	
Producer's Accuracy (%)	68.63	41.37	67.91	Kappa = 0.1747	
Errors of comission (%)	31.37	58.63	32.09	Kappa variance = 0.0065	
Errors of omission (%)	10.06	81.27	75.46	Overall accuracy (%) = 65.64	

h) Maximum Likelihood (*maximumLikelihood*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	2,235	971	285	3,491	64.02
Mangroves / Soft Sediment	519	705	53	1,277	55.21
Beaches	236	113	271	620	43.71
Predicted Total	2,990	1,789	609	5,388	
Producer's Accuracy (%)	74.75	39.41	44.50	Kappa = 0.2637	
Errors of comission (%)	25.25	60.59	55.50	Kappa variance = 0.0024	
Errors of omission (%)	35.98	44.79	56.29	Overall accuracy (%) = 59.60	

Appendix 2, Tables A2.8 continued.

i) Multinomial Logistic Regression (*logit*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,258	168	65	3,491	93.33
Mangroves / Soft Sediment	1,076	194	7	1,277	15.19
Beaches	382	42	196	620	31.61
Predicted Total	4,716	404	268	5,388	
Producer's Accuracy (%)	69.08	48.02	73.13	Kappa = 0.2112	
Errors of comission (%)	30.92	51.98	26.87	Kappa variance = 0.0066	
Errors of omission (%)	6.67	84.81	68.39	Overall accuracy (%) = 67.71	

j) Neural Networks (*neuralNetwork*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,277	189	25	3,491	93.87
Mangroves / Soft Sediment	1,050	224	3	1,277	17.54
Beaches	443	22	155	620	25.00
Predicted Total	4,770	435	183	5,388	
Producer's Accuracy (%)	68.70	51.49	84.70	Kappa = 0.2030	
Errors of comission (%)	31.30	48.51	15.30	Kappa variance = 0.0070	
Errors of omission (%)	6.13	82.46	75.00	Overall accuracy (%) = 67.85	

Appendix 2, Tables A2.8 continued.

k) Random Forests (*randomForest*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,291	153	47	3,491	94.27
Mangroves / Soft Sediment	492	775	10	1,277	60.69
Beaches	169	24	427	620	68.87
Predicted Total	3,952	952	484	5,388	
Producer's Accuracy (%)	83.27	81.41	88.22	Kappa = 0.6485	
Errors of comission (%)	16.73	18.59	11.78	Kappa variance = 0.0013	
Errors of omission (%)	5.73	39.31	31.13	Overall accuracy (%) = 83.39	

l) Support Vector Machines (*supportVector*)

	Rocky Shores / Seawalls / Docks	Mangroves / Soft Sediment	Beaches	Actual Total	User's Accuracy (%)
Rocky Shores / Seawalls / Docks	3,411	63	17	3,491	97.71
Mangroves / Soft Sediment	1,171	103	3	1,277	8.07
Beaches	464	15	141	620	22.74
Predicted Total	5,046	181	161	5,388	
Producer's Accuracy (%)	67.60	56.91	87.58	Kappa = 0.1576	
Errors of comission (%)	32.40	43.09	12.42	Kappa variance = 0.0090	
Errors of omission (%)	2.29	91.93	77.26	Overall accuracy (%) = 67.84	

Chapter Three

Habitat preferences and intertidal zonation of *Cittarium pica*: what rocks their world

> *Once the wave had passed, I realized that I would remain a living and breathing organism upon this earth with just a few minor bleeding gashes that would readily heal. Two thoughts came immediately to mind: I had finally gleaned an inkling of the sheer power of the ocean, and I felt in awe of the hellish existence in which these damnéd creatures live on the rocky shores of the world.*
>
> *- Michael Beetham (2009),*
> *from a journal entry written during fieldwork in the Caribbean*

INTRODUCTION

The rocky intertidal zone is a unique feature of coastlines throughout the world, both in terms of the diversity of biological communities and the variety and complexity of geomorphological habitats. Coastal rock features are shaped by many forces, such as chemical (e.g., precipitation), mechanical (e.g., wave action, dissolution), and biotic (e.g., burrowing, drilling) weathering (Trenhaile 2002). Through chemical and mechanical weathering, uplifted rock features erode into rough-textured cliffs with wave-cut notches and caves, sea stacks, and boulder and slab fields. Biotic and chemical weathering add topographic complexity, resulting in depressions, pits, and holes in the rock surface. On tropical islands, complexity is increased via eustatic-tectonic interactions combined with the growth of hermatypic corals, creating thick carbonate banks and extensive intertidal shoreline platforms and terraces. Patterns of zonation of intertidal organisms have been treated in an immense body of ecological literature, with emphasis on quantifying and establishing relationships between spatial patterns and ecological processes. An historical account of research on vertical zonation on rocky intertidal shores (Benson 2002) confirms a focus on causal explanation of pattern. Visualization of pattern on geological and geomorphological structure is largely ignored. In general, it is not necessary to understand subsurface geology or geologic history of a region or its coastlines to identify recurring or replicated observational features of rocky shore topography. However, it is necessary to use a consistent vocabulary and develop a visual memory of recurring topographic settings. The vocabulary for characterizing the structural topography of the intertidal zone includes terms for bedrock (e.g., cliff, wave-cut notch, channel, platform) and clasts (e.g., boulders, cobbles, pebbles), along with a long list of modifiers (e.g., composition, angularity and other shape descriptors, orientation, packing, elevation, surface texture, fractures, cracks).

Distribution of organisms within the rocky intertidal is typically discussed as vertical zonation, employing environmental stressors (e.g., desiccation, heat, radiation), biological interactions (e.g., competition, predation), and behavior to explain the patterns observed. The boundaries of an organism's distribution are attributed to environmental stressors for the upper limit (Connell 1972; Dayton 1971; Somero 2002) and to biological interactions for the lower limit (Connell 1970, 1972; Dayton 1971; Fawcett 1984; Rochette & Dill 2000). Disturbance is also identified as an important process that affects the distribution and diversity patterns observed in the intertidal (Menge & Sutherland 1976; Sousa 1979). These classic processes may provide well-supported explanations for the distribution of sessile organisms but often fall short when it comes to mobile organisms, which can be variably distributed based on tidal height and size-specific predation and mortality. Bertness et al. (1981) suggest that foraging patterns and refuge-seeking behavior of gastropods vary with tidal height in response to predation pressure. Similarly, Fawcett (1984) suggests that adult gastropods respond to tidal height, but young gastropods respond less, remaining in the mid-intertidal region. Thus, size-specific zonation within a species affects the observed patterns of distribution. Size-specific zonatio results differential post-settlement mortality due to mechanical stress and size-selective predation (Connell 1970; Kitching et al. 1959; McCormack 1982; Vermeij 1972). While developing an understanding of the processes that influence intertidal zonation is an important field of research, this must be *preceded* by thorough documentation of the distribution patterns observed in the field (see Underwood et al. 2000). Without prior documentation of species-specific zonation, field experiments to investigate processes are likely to be conflated by the experimental design, which will aim to investigate only the processes of interest and will likely be ill-suited to address the actual distribution. This can lead to overlooking the "true" pattern or a more interesting one (see Diamond 2001), which may, for example, lie on a different spatial scale. There are certainly methods for developing sound field data collection and experimental protocols (Andrew & Mapstone 1987), but even the most well-planned fieldwork must be based on sound, previously documented observations of distribution patterns. Understanding the distribution of a single species within the rocky intertidal requires considering not only the geomorphology and community assemblage but also the species-specific characteristics that govern its responses to that environment.

In the tropics, a unique set of geomorphological and environmental traits characterize the rocky intertidal, such as shallow rock platforms, low tidal range, relatively high water temperature, and low seasonality. Zonation within the tropical rocky intertidal, especially on islands, is tied to these traits, along with the local tectonic and volcanic history. Although the species richness and diversity are not necessarily different between temperate and tropical rocky intertidal communities (e.g., Coates 1998), the distribution of organisms and habitat use are quite distinctive (e.g., Menge & Lubchenco 1981). The shallow rock platforms provide greater surface area for colonization and foraging in a habitat that is more commonly discontinuous. However, they impart higher thermal stress than vertical surfaces (Helmuth & Hofmann 2001), which restricts distribution, especially at low tide. Also, the platform surface is often at mean low water, where it experiences persistent weathering from both wave action and subaerial processes (Trenhaile 2002). The low and relatively constant tidal range in the tropics results in unabating weathering throughout the year. These platforms and other rock features in tropical rocky intertidal habitats are often composed of sedimentary rock, usually either limestone (e.g., eolianites, oolites, reefal carbonates) or sandstone. The persistent weathering of the sedimentary rock results in distinctive rock features with wavecut notches from wave erosion, dimpled and sharply edged surfaces from wind and water erosion, and fractured rock from a combination of both. These geomorphological and environmental characteristics, coupled with the tectonic and volcanic history, create the unique rocky intertidal habitats that are characteristic of the tropics.

Tropical Northwestern Atlantic

Coastlines throughout the Tropical Northwestern Atlantic (Spalding et al. 2007) are commonly lined with rocky intertidal habitat. For the purposes of this paper, this ecoregion includes Bermuda, the West Indies, and the Caribbean coasts of South and Central Americas. A detailed description of the geologic history of this region is beyond the scope of this paper, but a general overview, with particular focus on the West Indies, is provided. The formation of the Caribbean islands is very complex and was assembled over the course of over 75-100 million years (Robertson 2009). There are two competing models of the origin of the Caribbean plate, the allochthonous model (Pindell et al. 2006; Pindell & Barrett 1990) and the autochthonous model (James 2005; James 2006). The allochthonous model suggests a Pacific origin of the Caribbean plate in the late Mesozoic and subsequent eastward migration. The autochthonous model suggests that the Caribbean plate originated between North and South America. Although the origin of the plate is in contention, both models agree on the Cenozoic history of the plate, and the rocks exposed at the surface, and thus in the rocky intertidal, are the same in either case. The islands of the Caribbean region can be classified as: (1) carbonate buildups, (2) ancient or active volcanic arcs, and (3) fragments of continental crust that include various rock types (e.g., clastic and biogenic sedimentary, metamorphic, both intrusive and extrusive igneous). Both the Caribbean islands and Central America originated as island arc systems, the formation of which began over 70 Ma (Buskirk 1985; Jackson et al. 1996). Many of the coastlines in these regions can be described as emergent (stepped) coastlines resulting from uplift and/or eustatic change (e.g., Greater Antilles). Other islands within the Tropical Northwestern Atlantic, but outside the Caribbean, exhibit submergent coastlines, resulting from subsidence and/or eustatic change (e.g., Bahama carbonate platform and banks). Many processes have been involved in shaping these coastlines and influencing the rocks cropping out at the surface, including oblique convergence and subduction of Atlantic oceanic lithosphere, oblique underthrusting, island arc volcanism, transform faulting, and seafloor spreading. Further, plate convergence has resulted in folding and faulting of these surficial rocks in several locations, and subduction has resulted in arc volcanism and compressional features such as the formation of accretionary wedges of sediment and deformed oceanic complexes. All of these geophysical processes affect the composition and layout of the rock features in the rocky intertidal, often adding broad-scale topographic complexity that would be absent in a tectonically inactive coastal region.

The exposed coastal substrates in the Tropical Northwestern Atlantic are dominated by carbonates and volcanic rocks. The islands of Bermuda are composed mostly of Pleistocene carbonates formed during sea level fluctuations, which rest on top of a volcanic base (Bretz 1960;

James & Schenk 1983). The carbonate platform consists of eolianites, with small proportions of marine limestone and paleosols (Land et al. 1967; Vacher & Hearty 1989). The Bahama Archipelago, which includes the Bahamas and the Turks and Caicos Islands, is characterized as a carbonate province throughout the Cenozoic, with older rocks buried under thousands of meters of limestone; it is currently organized as a series of shallow carbonate banks separated by deep basins (Jansa 1981). These islands have no history of volcanic activity on these islands. The Greater Antilles Archipelago (i.e., Cuba, Jamaica, Hispaniola, Puerto Rico) has a complex Cenozoic history, with alternating periods of uplift and submergence, and periodic emergence due to sea level lowstands (in the absence of uplift). Older igneous rocks (e.g., basalt, granite, diorite, gabbro) and metamorphics (e.g., slate, serpentine, dolomite) were emplaced, and sandstones and significant Cenozoic limestone were deposited during submergence periods (Donovan & Jackson 1994). The Lesser Antilles Archipelago is composed of the Windward and Leeward Islands as part of an oblique subduction zone. The exposed rock on the Leeward Islands includes both limestone (e.g., Anguilla, Antigua) and older Cenozoic volcanics (e.g., Grand Terre) (Harris 1965). In contrast, the Windward Islands (e.g., Basse Terre, Martinique, St. Vincent) are exclusively volcanic from the Eocene to the present (Martin-Kaye 1963). Trinidad and Tobago, which are traditionally included as part of the Windward Islands, are composed of Jurassic and Cretaceous metamorphic rocks; these islands are geologically part of northern South America (Donovan & Jackson 1994). Similar to the West Indies, the rocky coasts of Central America are composed of a mixture of volcanics and carbonates. The coastal exposures along the coasts of Panama and Costa Rica are composed of intrusive volcanic rocks, with volcaniclastic sedimentary rocks in the south and predominantly Quaternary surficial deposits in the north (Donovan & Jackson 1994). Similar to the Bahama archipelago, the Yucatán is purely carbonate, and is geologically part of the North American Plate. Most of the rock types that dominate the coastlines in the Tropical Northwestern Atlantic are highly vulnerable to weathering. The combination of often fierce weather (e.g., tropical storms, hurricanes) with ongoing volcanic and tectonic activities created the topographically and spatially complex rocky intertidal habitats that are present throughout this region today.

Cittarium pica

Gastropods are ubiquitous on rocky shores, and those in the Tropical Northwestern Atlantic are no exception. One gastropod is of particular interest, as not only is it the largest rocky intertidal gastropod in the region but also is at risk of local extinction due to overexploitation (see Chapters 1 and 4). *Cittarium pica* (Linnaeus, 1758), which has at least 12 common names aside from its official name of West Indian topsnail (Turgeon et al. 1998), inhabits the rocky intertidal shores throughout the Tropical Northwestern Atlantic, ranging from Bermuda to the north, Honduras to the west, Trinidad to the south, and Barbados to the east (Robertson 2003). The species ranges in size from ~1 mm when it first settles to a maximum recorded size of 137 mm (Hutsell et al. 2001). Lacking the ability to move along sand or other unconsolidated substrates, it is found exclusively on hard substrates (E.M., personal observations). Qualitative descriptions of the distribution of *C. pica* on a local scale abound (Hess et al. 1994; Hoffman 1980; Randall 1964; Robertson 2003 and references therein; Toller & Gordon 2005), but few studies attempt to quantify this distribution

(Debrot 1990). In addition, few previous studies attempt to describe the complex topography of the rocky shores with which they are associated or detail the different substrates on which they are found (Boulon 1987; Schmidt et al. 2002). Many of these studies suggest that *C. pica* exhibits size-specific zonation, although only one collected detailed data on size with respect to tidal height (Debrot 1990). This species is an ideal case study for investigating fine-scale distribution within rocky intertidal systems, and the results will provide important information to resource managers through the region. The results will provide important information for resource managers throughout the region.

Research Objectives

Historically, treatment of rocky intertidal zonation has focused on vertical distribution within a site and has characterized horizontal bands of community assemblages sampled and quantified in terms of linear distances and areas (e.g., transects, quadrats, points). It is depicted in two-dimensional graphs (distance vs. elevation) or translated from the three-dimensional real world onto a flat, two-dimensional map. This research is increasingly based on experimental manipulations, with data collection based on predetermined expectations of how biological (e.g., competitive interactions, predation) and environmental (e.g., disturbance, tidal flux) processes affect the distribution and resulting zonation of species (see Underwood 2000). However, individual species often occur along vertical gradients in the rocky intertidal, not just a single elevation or within a single horizontal band of habitat. Also, the habitat itself is more complex than a simple vertical or sloping slab of continuous habitat, as it is often described and visualized. Instead, the rocky intertidal is characterized by broad and fine scale topographical features, which play an important role in the distribution of the species that inhabit them. If the patterns of distribution observed are not characterized more accurately, the result is an over-simplification of a complex and dynamic ecosystem. Theory and hypothesis testing have been strong determinants of prevailing research directions, and rigorous designs and protocols have become increasingly important. The growing field of landscape ecology, with an emphasis on ecosystem patterning, has intensified the focus on models and theory reinforced by the objectives of quantifying pattern as a mapped categorical representation of the real world. Research objectives, methods and issues in landscape ecology (see Gustafson 1998) are not relevant to this paper and the underlying motivation for visualizing variations in the distribution of intertidal organisms on recurring patterns of geomorphology. Instead, this research reemphasizes the importance of observational and exploratory research to provide a fresh perspective on the distribution of organisms within a heavily studied habitat. I propose a new illustrative method for visualizing rocky intertidal shores that relies on detailed documentation of field observations in combination with quantitative assessments of location and size of individuals within each site. This research includes sites from across the Tropical Northwestern Atlantic and focuses on *C. pica*. Through these field observations and quantitative assessments, the range of intertidal zonation and habitat preferences of *C. pica* are documented, detailing the effects of habitat composition on zonation.

METHODS

Study Sites

Fieldwork was conducted during the summer months (June-August) of 2007-2010. The study area encompasses 17 territories and countries in the Caribbean Sea and Western Atlantic Ocean: Anguilla (United Kingdom), Antigua and Barbuda, Aruba (Netherlands), Barbados, Bermuda (United Kingdom), Bahamas, Guadeloupe (France), Jamaica, Martinique (France), Mexíco, Puerto Rico (United States), Republic of Trinidad and Tobago, República de Costa Rica, República de Panamá, St. Vincent and the Grenadines, Turks and Caicos Islands (United Kingdom), and U.S. Virgin Islands. Locality data from museum collections and Caribbean geology were used to target these territories and countries. A few locations were excluded because of inaccessibility (e.g., Cuba), safety concerns (e.g., Haiti, Venezuela), and excessive permitting costs (e.g., Colombia, Dominica).

Upon arrival at each locality, surveys of the coastal habitats were conducted to document locations of accessible rocky intertidal shores, to determine whether *C. pica* was present, and if present, to estimate the number of individuals. Study sites were chosen based on these surveys, targeting 1-4 sites per island or continental nation at which more than 100 individuals were found. All chosen sites were accessible by public roads or trails, unless advanced permission was received to sample at protected sites (e.g., Bermuda, St. John, St. Thomas) or on private land (e.g., Bermuda). Detailed population and ecological surveys were conducted at each site. All surveys began at low tide and continued for two hours or until all *C. pica* individuals were documented. Location was recorded only once for each individual for two reasons: (1) individuals were not previously tagged, so documentation of individual movements was not possible and (2) data collection was constrained by field-time allotted to each locality (i.e., sites could be visited only once for population surveys). Each survey consisted of documenting total number of individuals, measuring maximum shell width (Fig. 1) with calipers, and recording vertical and horizontal position of individuals relative to mean low water (MLW). Position was documented relative to the rock feature on which the individual rested. For example, if a snail was on a large boulder, vertical distance from MLW was recorded as such, and horizontal distance from MLW was recorded from the edge of the boulder (0-m) inward. If the rock feature had angular surfaces, horizontal distance was estimated as a horizontal line from the surface of the rock outward until vertically above MLW. The substrate types present were also recorded. To document topographic complexity, site photographs were taken with a Nikon D50, digital single lens reflex camera,

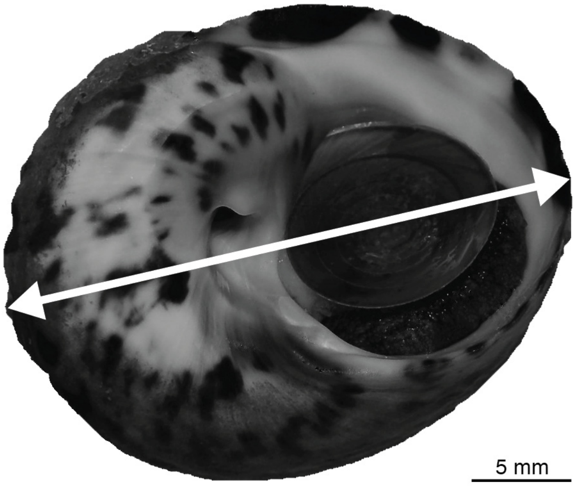


Figure 1: Photograph of *Cittarium pica*. The arrow identifies its width (28.2 mm), which is defined as the maximum distance across the dorsal surface of the shell that transects the aperture.

using an AF Nikkor 70-300 mm lens, and individual rock features were photographed with an AF Nikkor 28-80 mm lens.

Delineation of Rocky Intertidal Habitat Categories

Sites were divided into rocky intertidal habitat categories using a visual classification system, based on field observations and photographic documentation of topographic complexity and site layout. The visual classification system considered characteristics of rock features and overall site layout. After habitat categories were determined and sites were classified, typical rock features from each category were sketched. These sketches were scanned into Adobe Photoshop v12.1 (Adobe Systems, Inc.) and traced in Adobe Illustrator v15.1 (Adobe Systems, Inc.). Rock features from each habitat category were uniformly scaled and arranged to depict typical cross-sectional views of each habitat category. MLW and mean high water (MHW) were standardized across all habitat types because tidal range is nearly constant across all sites. The height of the splash zone was averaged across all sites within each habitat category.

Determination of Intertidal Zonation

To test whether *C. pica* exhibits size-specific zonation, snail position on rock features was plotted versus size in two ways. First, classic scatterplots of snail size (width) versus vertical position (height) and snail size versus horizontal position were plotted using data from all of the sites combined, and linear regression analyses were conducted. These plots and analyses did not consider rock-feature-specific position. To test whether a zonation pattern is specific to any of the habitat categories, similar scatterplots and analyses were conducted for the subset of data within each habitat category. All scatterplots and linear regression analyses were conducted in JMP v.8.0 (SAS Institute, Inc.).

The second method for testing for size-specific zonation addresses the presence of rock features and topographic complexity that are unique to specific habitat categories. These unique features could have a differential effect on whether size-specific zonation is observed because the height, orientation, and topographica complexity of a feature may influence zonation. The cross-sections of each habitat category were used as the plotting space. A vertical axis was added to each cross-section, as were MLW, MHW, and splash zone. To make the plot easier to read, size data were binned to reduce the number of points because thousands of data points on a single graph makes viewing individual points difficult when many of them overlap. The bounds of the size bins were chosen based on life history characteristics of *C. pica*, such that recent recruits (0.0-10.0 mm), juveniles (10.1-30.0 mm), size at sexual maturity (30.1-40.0 mm), adults (40.1-60.0 mm), and rare large snails (60.1+ mm) were grouped together. The bins of size data were then binned by unique position (rounded to the nearest 0.05 m). Points representing each bin were variably colored to allow for visual interpretation of zonation based on biological factors other than size. Point size was scaled based on abundance within a size category at a particular position.

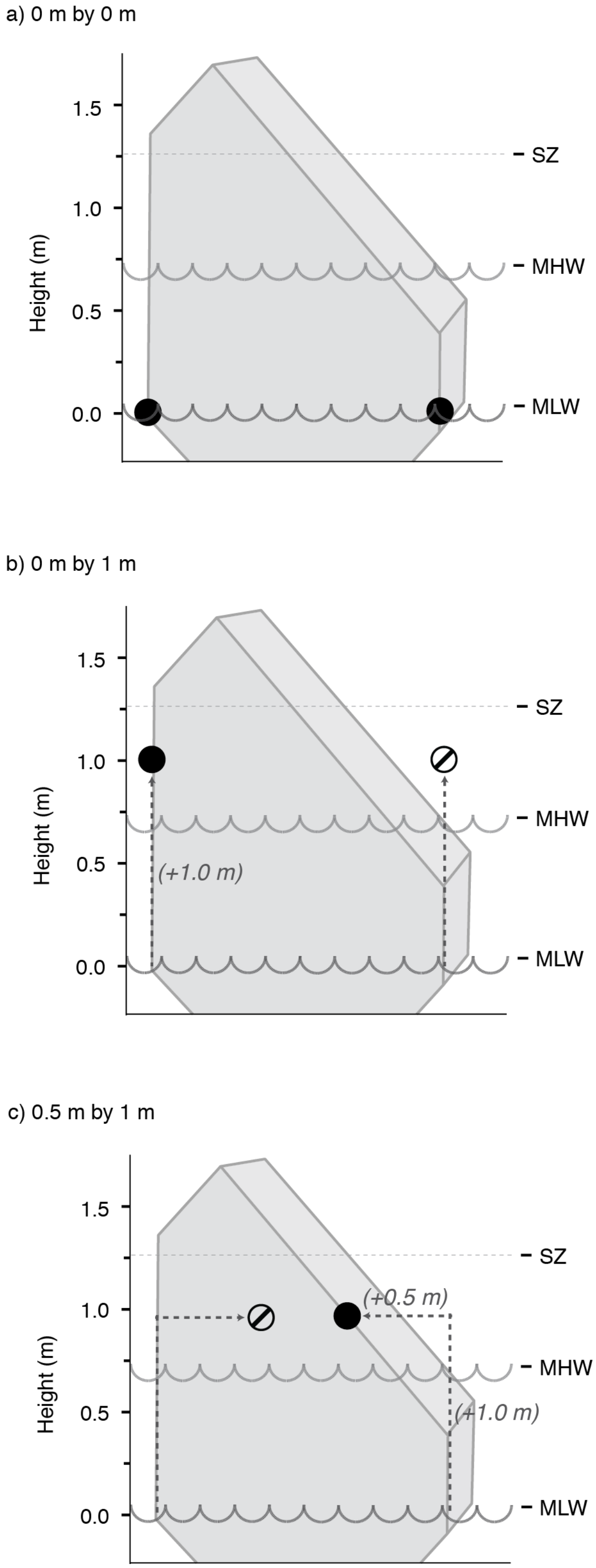


Figure 2: Example intertidal zonation plots: a) position coordinates 0.0 m by 0.0 m; b) position coordinates 0.0 m by 1.0 m; c) 0.5 m by 1.0 m

After data were binned by size and unique position, dots were plotted by hand onto individual rock features within each habitat category. All plotting and illustrations for this method were conducted in Adobe Illustrator. Because position was recorded relative to MLW in the field, the MLW lines mark “0-m” on the y-axis. The rock features were treated as cross-sections, so dots were plotted only on the edges. For example, a dot with position 0-m (horizontal) by 0-m (vertical) is plotted onto all rock features on which MLW crosses its edge(s); this could mean plotting the point twice on the same rock feature (Fig. 2a). If a dot has position 0-m by 1-m, then the dot is plotted onto all rock features on which the edge of the feature is vertical and extends 1-m above MLW (Fig. 2b). This point would not be plotted on features with angular edges because the horizontal distance from MLW would not be 0-m. If a dot has position 0.5-m by 1-m, then plotting the dot is a little more complex. To satisfy the horizontal position, the edge of the feature must either extend horizontally >0.5 m or diagonally inward from the point on the rock feature where it first meets MLW. To satisfy the vertical position, the edge must also extend vertically 1 m above MLW (Fig. 2c). Dots were not plotted if the position landed mid-rock, mid-water, or mid-air.

RESULTS

Delineation of Rocky Intertidal Habitat Categories

This study includes habitat and ecological survey data from 48 field sites across 28 islands and continental nations (Fig. 3). Habitat data, which consists of rock type and intertidal position, were collected for 6,642 individual snails. The visual classification system delineated these sites into four different habitat categories (see

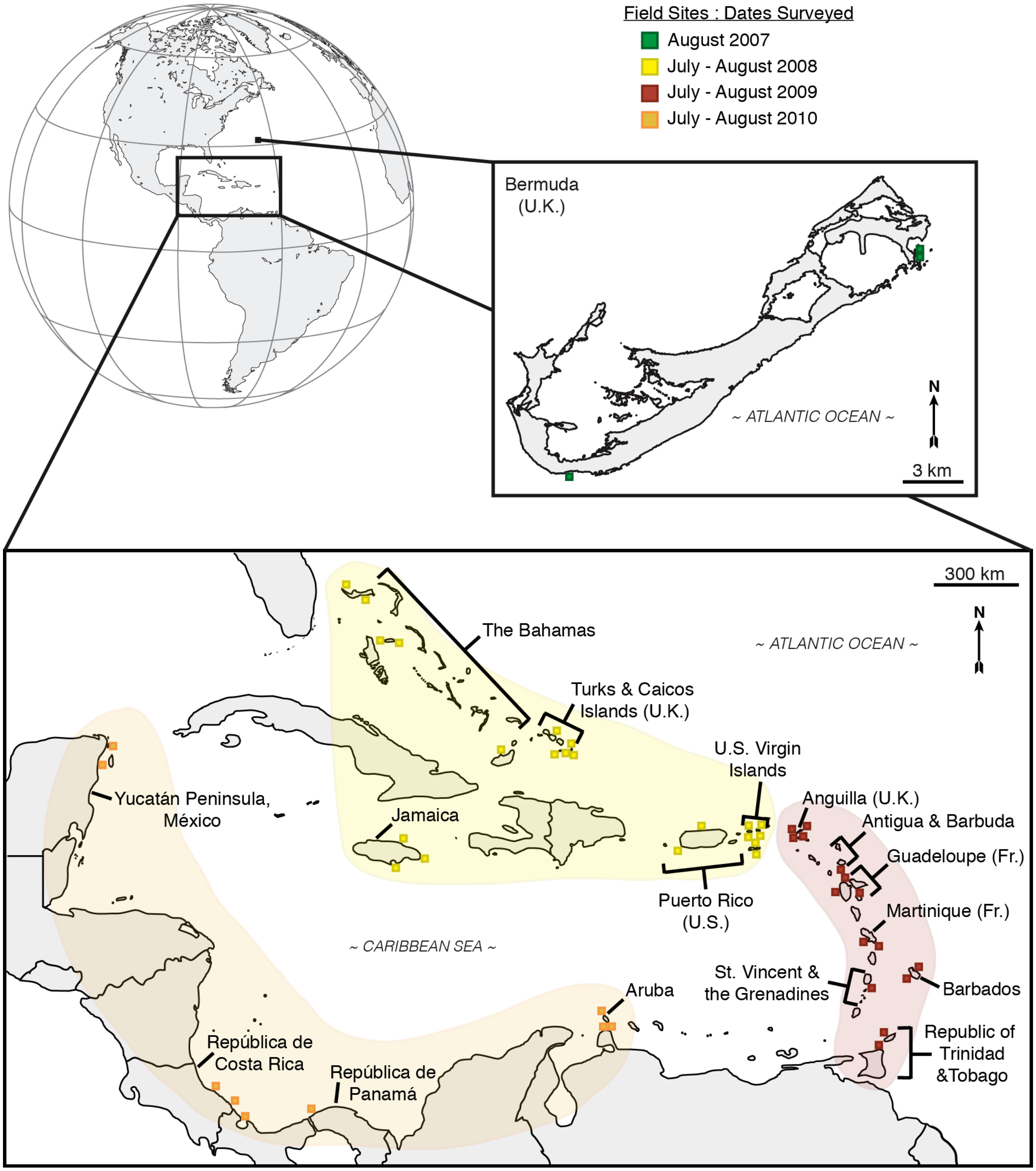


Figure 3: Fieldwork was conducted in July-August 2007-2010. The study area encompassed 17 territories/countries in the Greater Caribbean marine province, including 48 field sites across 28 islands and continental nations.

Appendix 1, Figs. A1.1-1.4) based on the following characteristics: presence of a vertical rock feature along the shore, presence of specific rock features (e.g., boulders, slabs), evidence of mechanical weathering, overall site length and height, and rock types present (Table 1). The four habitat categories into which field sites were classified (Table 2) include "angled habitat" (5 sites, 571 individuals), "boulder habitat" (7 sites, 1,617 individuals), "platform habitat" (13 sites, 1,864 individuals), and "cliff habitat" (15 sites, 2,590 individuals). Eight sites were not categorized either because of incomplete habitat data for the site or because it did not fit into any of the habitat categories. Incomplete data were collected for sites at which dangerous weather conditions were encountered, preventing photography and restricting data collection.

The angled habitat consists of angular coastal features, often with adjacent rock slabs (Appendix 1, Fig. A1.1). It has the shortest average length of all of the habitat categories. At many sites in this category, rock slabs lean against each other in such a way that a vault or shelter is created, which generates shaded areas in otherwise very exposed sites. This is the only habitat category that is dominated by extrusive igneous rock and rarely by sedimentary rock. Sites classified as angled habitat have moderate to high wave exposure, with an average splash zone of 1 m above MLW. Andesite and basalt, the two most common igneous rocks at these sites, have smooth and often relatively flat surfaces, resulting from angular fracturing and slow, subaerial weathering. This is in stark contrast to the topographical complexity that results from mechanical and chemical weathering of sedimentary rocks, which is a common rock type in all other habitat categories.

The boulder habitat consists of boulder fields, sometimes adjacent to a mechanically weathered, vertical coastal feature with under-cut notches near the base (Appendix 1, Fig. A1.2). The piles of boulders extend up to two meters above MLW and are usually highest toward the shore and grade downward to and below MLW seaward. Both extrusive igneous rock (e.g., andesite, basalt, diabase-schist-tuff) and sedimentary rock (e.g., conglomerate, sandstone, shale) are equally common in this habitat. The sites categorized into the boulder habitat category have low to moderate wave action, and an average splash zone of 0.5 m above MLW. When boulder piles extend above the splash zone, they are dry, and rock surfaces external to the pile are exposed to high radiation.

The platform habitat is unique - it has no vertically oriented coastal feature (Appendix 1, Fig. A1.3). It is characterized by a horizontal, limestone platform. Platforms covered in unconsolidated material (e.g., sand, shell fragments) and beach rock (i.e., cemented beach sand that forms platforms at mid-intertidal levels on beaches) were not judged as appropriate habitat for *C. pica*. As such, they are not considered in this study. The shoreward edge of the platform extends below MLW and exhibits prominent chemical, mechanical, and biological weathering, as does the surface of the platform and any rock features present on the platform itself. This habitat has the longest average length of all of the habitat categories. The only kind of rock found within platform habitats is sedimentary rock (e.g., limestone). Similar to the boulder habitat, sites classified as platform habitat also have low to moderate wave action, with an average splash zone of 0.75 m. Some rock features, other than the platform extend above MLW. The limestone surfaces of these features are topographically complex due to weathering, which generates

Table 1: Descriptors for each of the four rocky intertidal habitat categories.

Habitat Category	Vertical Coastline?	Boulders, Slabs, or Neither?	Mechanical Weathering?	Average Height / Length (m)	Rock Type
(a) Angled Habitat	never	slabs	never	1.50 / 12.00	Igneous - extrusive (e.g., andesite, basalt) Sedimentary - limestone or clastic (e.g., conglomerate, sandstone, shale)
(b) Boulder Habitat	sometimes	boulders	sometimes	2.00 / 15.00	Sedimentary - limestone or clastic (e.g., conglomerate, sandstone, shale) Igneous - extrusive (e.g., andesite, basalt, diabase-schist-tuff)
(c) Platform Habitat	never	neither	always	1.25 / 20.00	Sedimentary - limestone
(d) Cliff Habitat	always	boulders or slabs	always	3.00 / 19.75	Sedimentary - limestone Igneous - extrusive (e.g., basalt)

Table 2: Survey sites sorted by rocky intertidal habitat category: (a) angled habitat, (b) boulder habitat, (c) platform habitat, (d) cliff habitat, and (e) not categorized

(a) Angled Habitat

Island Group (Country/Territory)	Island	Date	Site Name	Latitude (decimal degrees)	Longitude (decimal degrees)
Antigua and Barbuda	Antigua	July 28, 2009	N. Pigeon Point	17.0109	-61.7755
Martinique (France)	Martinique	August 8, 2009	Pointe Burgos	14.4914	-61.0844
Puerto Rico (USA)	Puerto Rico	July 31, 2008	Piñones	18.4581	-65.9770
U.S. Virgin Islands (USA)	St. Croix	August 7, 2008	Cramer Park	17.7619	64.5831
	St. John	August 14, 2008	W. America Point	18.3563	-64.7523

(b) Boulder Habitat

Island Group (Country/Territory)	Island	Date	Site Name	Latitude (decimal degrees)	Longitude (decimal degrees)
Aruba (Netherlands)	Aruba	July 24-25, 2010	California Dunes	12.6198	-70.0471
		July 23, 2010	N. of Natural Bridge	12.5409	-69.9587
Bahamas, The	Grand Bahama	June 28 & 30, 2008	Running Man Jetty	26.4947	-78.6597
Guadeloupe (France)	Basse-Terre	August 1, 2009	Plage de l'Anse	16.1489	-61.7752
Jamaica	Jamaica	July 26, 2008	Portland Point	17.7486	-77.1370
Trinidad and Tobago, Republic of	Tobago	August 21, 2009	Mount Irvine Bay	11.1886	-60.7961
U.S. Virgin Islands (USA)	St. John	August 13, 2009	Little Lameshur Bay	18.3188	-64.7207

Table 2 continued.

(c) Platform Habitat

Island Group (Country/Territory)	Island	Date	Site Name	Latitude (decimal degrees)	Longitude (decimal degrees)
Anguilla (U.K.)	Anguilla	July 22, 2009	Forest Point	18.1973	63.0398
		July 24, 2009	Long Pond Bay	18.2156	-63.0136
Bahamas, The	Grand Bahama	June 29, 2008	Bootle Bay	26.6484	-78.9395
	New Providence	July 2 & 4, 2008	Delaporte Point	25.0775	-77.4353
	Great Inagua	July 8-9, 2008	Northwest Point	21.1103	-73.6677
Costa Rica, República de	---	August 6, 2010	Playa Manzanillo	9.6391	82.6498
	---	August 7, 2010	W. Playa Bonita	10.0088	83.0618
Jamaica	Jamaica	July 24-25, 2008	Priory	18.4457	-77.2262
Mexico	---	August 12, 2010	Half Moon Bay	20.4007	87.3077
Panamá, República de	---	July 27, 2010	Punta Galeta	9.4050	79.8643
Turks and Caicos Islands	Salt Cay	July 21, 2008	N. of Whale House Bay	21.3376	-71.1852
		July 22, 2008	S. of NW. Point	21.3371	-71.2131
U.S. Virgin Islands (USA)	St. Thomas	August 11, 2008	Mandahl Bay	18.3606	-64.8966

Table 2 continued.

(d) Cliff Habitat

Island Group (Country/Territory)	Island	Date	Site Name	Latitude (decimal degrees)	Longitude (decimal degrees)
Aruba (Netherlands)	Aruba	July 23, 2010	Andicuri Beach	12.5378	-69.9551
Anguilla (U.K.)	Anguilla	July 22, 2009	Blolly Ham Bay	18.1675	63.1647
		July 22-23, 2009	Sherrick's Bay	18.1626	-63.1648
Bahamas, The	New Providence	July 3, 2008	Turtle Pen	25.0073	-77.5482
Barbados	Barbados	August 13, 2009	Bathsheba	13.2127	-59.5166
Bermuda (U.K.)	St. David's	August 10 & 15, 2007	Rocky Hole	32.3530	-64.6565
		August 10, 2007	Turtle Bay	32.3530	-64.6565
Bocas del Toro Archipelago (Rep. de Panamá)	Isla Carenera	August 2, 2010	NE. Point of Isla Carenera	9.3540	82.2296
Guadeloupe (France)	Grand-Terre	August 2, 2009	Anse Tabarin	16.2057	-61.4978
		August 3, 2009	Plage de la Chapelle	16.4721	-61.5112
Mexíco	Isla Mujeres	August 16, 2010	Isla Mujeres	21.2612	86.7473
Turks and Caicos Islands (U.K.)	Middle Caicos	July 13-14, 2008	Mudjin Harbor	21.8317	-71.8102
	South Caicos	July 16, 2008	Coast Guard Station	21.5733	-71.4948
		July 18, 2008	High Point	21.5255	-71.4970
U.S. Virgin Islands (USA)	St. Thomas	August 8, 2008	Long Point	17.6827	64.8340

Table 2 continued.

(e) Not Categorized

Island Group (Country/Territory)	Island	Date	Site Name	Latitude (decimal degrees)	Longitude (decimal degrees)
Barbados	Barbados	August 14, 2009	Hastings Rocks *	13.0726	59.5871
Bermuda (U.K.)	Main / Bermuda	August 12, 2007	Church Bay *	32.2492	64.8476
Jamaica	Jamaica	July 25, 2008	Folly Point, Port Antonio †	18.1881	76.4417
Martinique (France)	Martinique	August 6, 2009	Pointe d'Enfer †	14.3973	-60.8566
Puerto Rico (USA)	Puerto Rico	August 4, 2009	Cabo Rojo *	17.9339	-67.1878
St. Vincent and the Grenadines	St. Vincent	August 17, 2009	East Calliaqua *	13.1243	-61.1901
Trinidad and Tobago, Republic of	Trinidad	August 29, 2009	L'Anse Noir *	10.8360	-60.9841
U.S. Virgin Islands (USA)	St. Thomas	August 10, 2008	Secret Harbor †	18.3187	64.8533

* Not categorized because of incomplete habitat data for the site

† Not categorized because site does not fit into any of the four categories

elaborate angling, thin edges, and small tidepools. The sharply angled and twisted features lead to shaded rock surfaces below; these shaded surfaces and tidepools provide refuge from radiation and desiccation stresses, respectively.

Finally, vertical rock features dominate the cliff habitat, including a vertical coastline and the presence of large, offshore rock features (Appendix 1, Fig. A1.4). Boulders or slabs are commonly present at this site, but never both. The coastline and offshore rock features always display evidence of mechanical weathering, such as under-cut notches. This habitat has the tallest average height and the highest splash zone (2.75 m) due to high wave action. Cliff habitats are dominated by sedimentary rock (e.g., limestone), but sometimes contain extrusive igneous rock (e.g., basalt). This category is the most discontinuous habitat, such that rock features are arranged far away from each other resulting in large areas of water without rock features. The cliff habitat is the most common type of rocky intertidal habitat occupied by *C. pica*.

Evaluation of Intertidal Zonation of *Cittarium pica*

When the data for all habitat categories are combined, the dominant size class is 10.1-30.0 mm (Table 3a), with an overall size range of 1.0-119.1 mm. Only 11.1% of the individuals are ≥40.1 mm. Overall snail height (vertical position) relative to MLW ranges from -0.60 m to 1.80 m, and snail horizontal position within rock features relative to MLW ranges from 0.00 m to 4.00 m. There is a very weak, slightly negative relationship between snail size and height (R^2=0.0481, p<0.0001), such that larger snails are sometimes found at lower heights. The smallest size class (≤ 10.0 mm) has the largest variance in height, and the sexually mature size class (30.1-40.0 mm) has the largest range in height (2.40 m). There is also a very weak, positive relationship between snail size and horizontal position (R^2=0.0016, p<0.01), meaning that large snails are found farther inward on rock features. The second smallest size class (10.1-30.0 mm) has the highest variance and largest range in horizontal position (4.00 m).

Angled habitat

The overall size range for the angled habitat is the lowest among all the habitat categories; this category is dominated by snails that are ≤30.0 mm (Table 3b). When compared to the other habitat categories, the angled habitat has the lowest maximum size, smallest size range, and smallest range in snail position, both in height and horizontal position. The smallest two size classes (e.g., ≤10.0 mm, 10.1-30.0 mm) illustrate the largest variances in position, and ranges in horizontal position and height, respectively (Fig. 4a, Table 3b). The linear regression analysis suggests that a weak, negative relationship exists between snail size and height (R^2=0.1146, p<0.001), illustrated in the standard scatterplot (Fig. 4e). Snail size and horizontal position exhibit no significant relationship (R^2=0.0064; p=0.0554). However, when rock features extend above MLW, small snails (≤30.0 mm) do occupy the edges of such features (Figs. 4a & 5a), a pattern that is evident only on the cross-section scatterplot. All snails >30 mm are found at the edge of rock features (horizontal position= 0 m), and all snails in the largest size class present (40.1-60.0 mm) are found below MLW. In general, snails are most abundant at MLW (Fig. 4a)

Table 3: Data and statistics of individuals within each size bin overall and in each habitat category. The bold values identify the maximum value for each statistic within each subset of the data: (a) all habitats, (b) angled habitat, (c) boulder habitat, (d) platform habitat, and (e) cliff habitat.

(a) All Habitat Categories
n=6,642

Size Bins	Count	Percent	Height (m)				Horizontal Position (m)			
			Minimum	Maximum	Standard Deviation	Variance	Minimum	Maximum	Standard Deviation	Variance
0.0 - 10.0	1,779	26.78%	-0.10	1.22	0.2031	0.0412	0.00	3.05	0.2342	0.0548
10.1 - 30.0	3,519	52.98%	-0.60	1.22	0.1598	0.0255	0.00	4.00	0.4316	0.1863
30.1 - 40.0	609	9.17%	-0.60	1.80	0.1430	0.0204	0.00	2.40	0.2183	0.0476
40.1 - 60.0	536	8.07%	-0.20	0.60	0.0892	0.0080	0.00	1.52	0.1166	0.0136
60.1 +	199	3.00%	-0.40	0.90	0.1509	0.0228	0.00	0.60	0.0716	0.0051

(b) Angled Habitat
n=571

Size Bins	Count	Percent	Height (m)				Horizontal Position (m)			
			Minimum	Maximum	Standard Deviation	Variance	Minimum	Maximum	Standard Deviation	Variance
0.0 - 10.0	289	50.61%	-0.08	0.15	0.0380	0.0014	0.00	0.30	0.0310	0.0010
10.1 - 30.0	243	42.56%	-0.15	0.61	0.0767	0.0059	0.00	0.28	0.0213	0.0005
30.1 - 40.0	15	2.63%	-0.15	0.03	0.0636	0.0040	0.00	0.00	0.0000	0.0000
40.1 - 60.0	24	4.20%	-0.15	-0.15	0.0000	0.0000	0.00	0.00	0.0000	0.0000
60.1 +	0	0.00%	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

Table 3 continued.

(c) Boulder Habitat
n=1,617

Size Bins	Count	Percent	Height (m)				Horizontal Position (m)			
			Minimum	Maximum	Standard Deviation	Variance	Minimum	Maximum	Standard Deviation	Variance
0.0 - 10.0	311	19.23%	0.00	0.76	0.1805	0.0326	0.00	0.61	0.1099	0.0121
10.1 - 30.0	1,127	69.70%	-0.30	**1.22**	0.1304	0.0170	0.00	1.52	0.1260	0.0159
30.1 - 40.0	104	6.43%	-0.10	0.61	0.1115	0.0124	0.00	0.38	0.0949	0.0090
40.1 - 60.0	75	4.64%	-0.10	0.30	0.0424	0.0018	0.00	0.30	0.0655	0.0043
60.1 +	0	0.00%	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

(d) Platform Habitat
n=1,864

Size Bins	Count	Percent	Height (m)				Horizontal Position (m)			
			Minimum	Maximum	Standard Deviation	Variance	Minimum	Maximum	Standard Deviation	Variance
0.0 - 10.0	469	25.16%	0.00	**1.22**	0.2847	**0.0810**	0.00	3.05	0.4073	**0.1659**
10.1 - 30.0	1,004	53.86%	-0.05	0.91	0.2192	**0.0481**	0.00	3.05	0.5708	**0.3258**
30.1 - 40.0	216	11.59%	-0.05	0.61	0.1196	0.0143	0.00	1.83	0.2883	**0.0831**
40.1 - 60.0	125	6.71%	-0.10	0.30	0.0751	0.0056	0.00	1.52	0.1539	**0.0237**
60.1 +	50	2.68%	0.00	0.25	0.0711	0.0051	0.00	0.15	0.0464	0.0021

Table 3 continued.

(e) Cliff Habitat
n=2,590

Size Bins	Count	Percent	Height (m)				Horizontal Position (m)			
			Minimum	Maximum	Standard Deviation	Variance	Minimum	Maximum	Standard Deviation	Variance
0.0 - 10.0	710	27.41%	**-0.10**	0.90	0.1418	0.0201	0.00	1.80	0.1375	0.0189
10.1 - 30.0	1,145	44.21%	**-0.60**	1.20	0.1279	0.0164	0.00	4.00	0.5050	0.2550
30.1 - 40.0	274	10.58%	**-0.60**	**1.80**	0.1701	**0.0289**	0.00	2.40	0.1882	0.0354
40.1 - 60.0	312	12.05%	**-0.20**	**0.60**	0.0932	**0.0087**	0.00	1.50	0.1131	0.0128
60.1 +	149	5.75%	**-0.40**	**0.90**	0.1697	**0.0288**	0.00	0.60	0.0783	**0.0061**

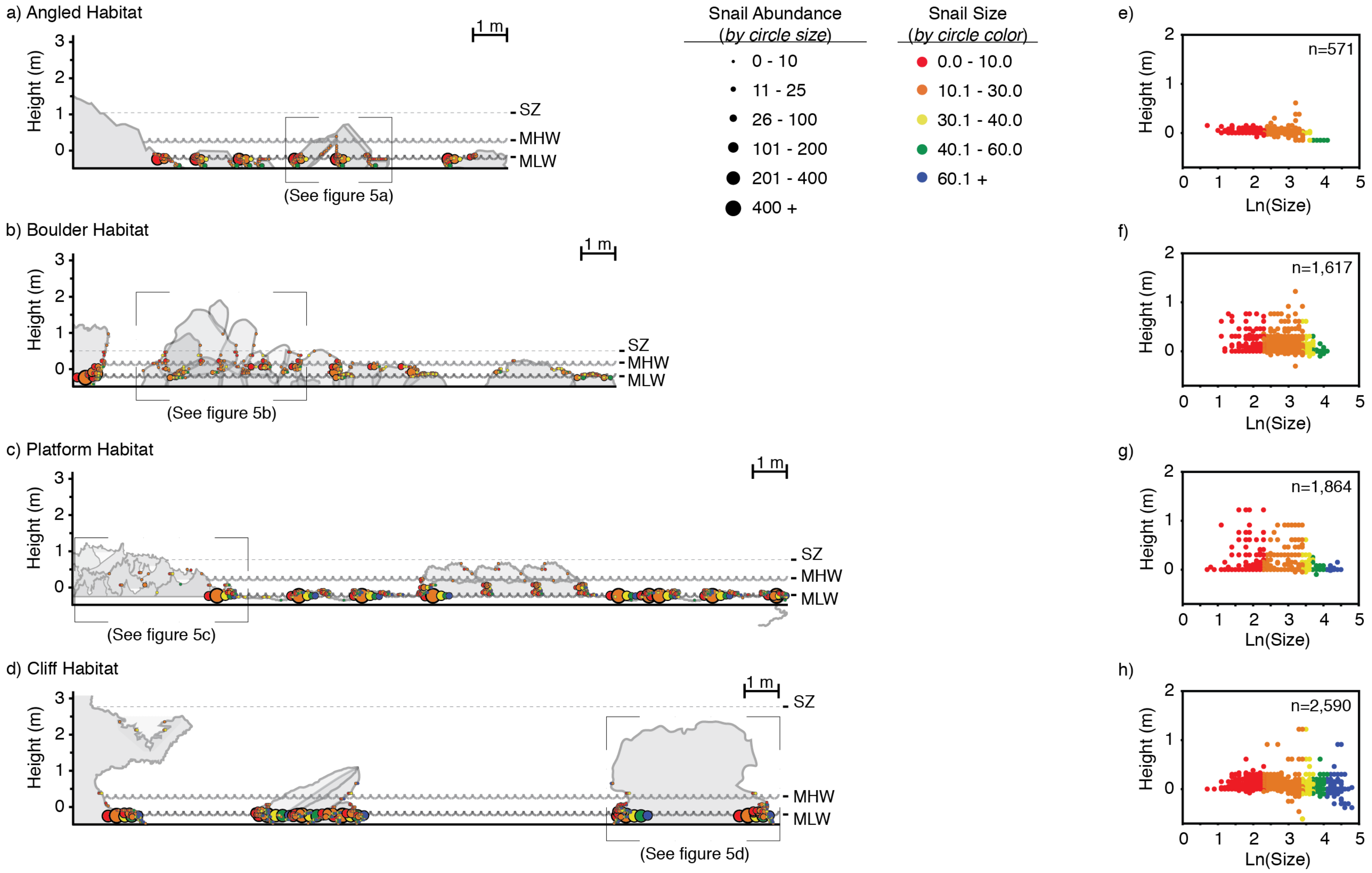


Figure 4: Intertidal zonation of *Cittarium pica* within each of the four rocky intertidal habitat categories: (a)/(e) Angled, (b)/(f) Boulder, (c)/(g) Platform, (d)/(h) Cliff. The left panel of figures includes hand-plotted scatterplots, with dots representing different sized snails (by dot color) and different snail abundance (by dot size). Dots were plotted individually onto each rock feature within each habitat category. Mean low water (MLW), mean high water (MHW), and splash zone (SZ) are marked on all plots. The brackets denote rock features for which close-ups are provided in Figure 3. The right panel of figures includes scatterplots of snail size (shell width) versus height. Dot color corresponds to the same snail size categories plotted on the figures at left. Dot size does not correspond to abundance – coordinates for each of the 6,642 snails were plotted individually.

and along the vertical edges of rock features, rather than along the flatter or angled surfaces of slabs (Fig. 5a). The flat and angled surfaces are occupied mostly by snails ≤30.0 mm, but some snails in the 30.1-40.0 mm size class are also present on these surfaces. Very few snails are distributed above MHW (<1%), and no snails are above the splash zone. The angled habitat has the lowest overall variance in position, with 57.3% of snails found at 0-m in height.

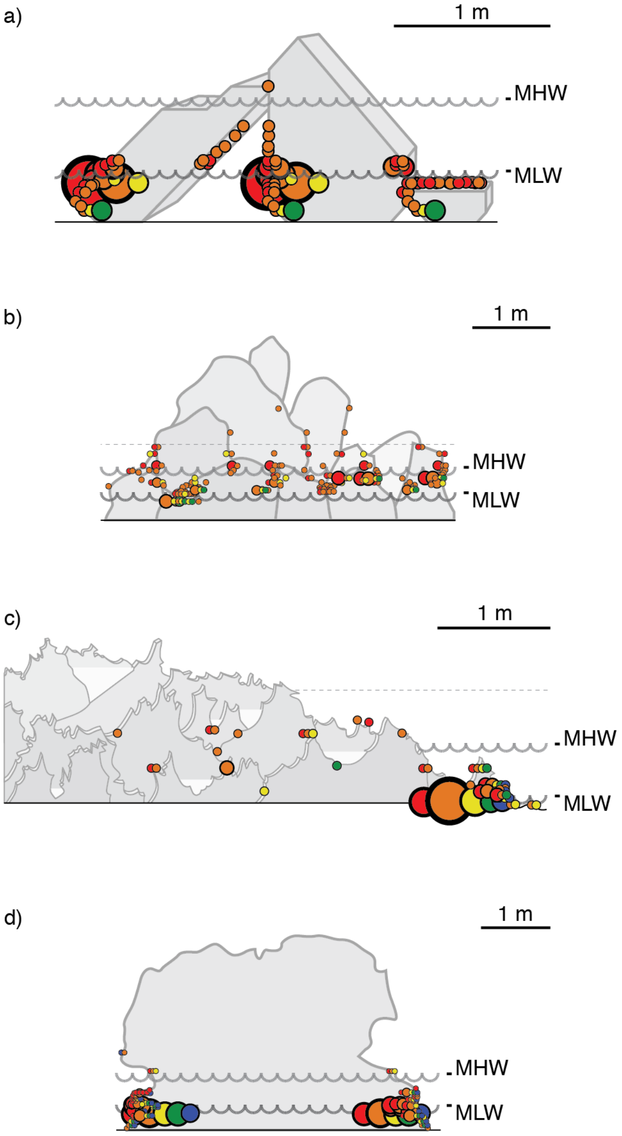


Figure 5: Close-ups of rock features illustrated in Figure 2 with snail size and abundance plotted onto each individual feature. Mean low water (MLW) and mean high water (MHW) are marked on all features. (a) Angled Habitat – slab rock feature; (b) Boulder Habitat – boulder pile rock feature; (c) Platform Habitat – heavily weathered limestone rock feature; (d) Cliff Habitat – large, offshore rock feature with undercutting from exposure to heavy wave action.

Boulder habitat

The boulder habitat has the second smallest size range among the four habitat categories and is dominated by snails that are 10.1-30.0 mm (Table 3c). This habitat category has the second largest range in overall snail height (vertical position), but the second smallest range in snail horizontal position. The smallest size class illustrates the largest variance in height, but none were found below MLW (Fig. 4b). The second smallest size class illustrates the largest range in height (1.52 m) and horizontal position (1.52 m), as well as the largest variance in horizontal position (Fig. 5b). Snails of this size category were found at their highest recorded height in the boulder habitat (1.22 m). According to the linear regression analyses, a very weak, negative relationship occurs between size and height (R^2=0.0632, p<0.0001) and no significant relationship exists between size and horizontal position (R^2=0.0002, p=0.5372). Neither the standard scatterplot (Fig. 4f) nor the cross-section scatterplot (Fig. 4b) convey these trends. The snails in the boulder habitat have the second greatest variance in height among the four habitat types and a greater variance in horizontal position than snails in the angled habitat. This is illustrated by the distribution of all snail sizes in the cracks among the boulders (Fig. 5b). Unlike the angled habitat, 61.7% of snails in the boulder habitat are found above MLW, with 12.9% above MHW, and even a few snails above the splash zone (2.2%).

Platform habitat

The range of snail size is the second largest in the platform habitat, but is dominated by snails that are 10.1-30.0 mm (Table 3d). This habitat has the lowest range in height, but the second longest range in horizontal position (3.05 m). Because the platform habitat is characterized by horizontal limestone platforms with topographically complex rocks, it has the greatest variance in both snail height and horizontal position (Fig. 4c). There is a very weak, negative relationship between snail size and height ($R^2=0.0703$, $p<0.0001$), which is illustrated in the standard scatterplot (Fig. 4g). Snail size and horizontal position ($R^2=0.0016$, $p=0.0852$) show no significant relationship, although most snails ≥40.1 mm are found along the edges of rock features (Fig. 4c). Snails ≤40.1 mm can be found up to 3.05 m away from the waterline on complex topographical rock features (Fig. 5c). The smallest size class has the highest range (1.22 m) and the largest variance in height (Fig. 4c). It ties for the highest range in horizontal position (3.05 m) with the second smallest size category, which has the highest variance. None of the smallest (≤10.0 mm) or largest (>60.0 mm) snails were found below MLW – less than 1% of all snails in this habitat were found below MLW. Nearly one-quarter of the snails (21.6%) were found above MHW, but <1% of the snails were found above the splash zone. The smallest snails were found at their highest recorded height in the platform habitat (1.22 m).

Cliff habitat

With the largest rock features (Fig. 4d), the cliff habitat illustrates the largest overall range both in snail height (vertical position) and horizontal position (Table 3e). The linear regression analyses suggest a very weak, negative relationship between snail size and height ($R^2=0.060$, $p<0.0001$), and no relationship between snail size and horizontal position ($R^2=0.0006$, $p=0.2157$). The standard scatterplot does not illustrate a clear trend in snail size versus height (Fig. 4h), but the cross-section scatterplot illustrates that snails are most abundant (56.0%) at MLW (Fig. 4d), nestled in wave-cut notches (Fig. 5d). A small percentage (7.1%) of snails are found above MHW, and no snails are found above the splash zone. The cliff habitat also has the largest range in snail size (117.6 mm). The dominant size class is 10.1-30.0 mm, which has the largest range (4.00 m) and variance in snail horizontal position for the cliff habitat (Table 3e). This is the only habitat for which the middle size class (30.1-40.0 mm) has the largest range (2.40 m) and variance in snail height. It is also the only habitat in which snails >40.0 mm are found above MHW. The cliff habitat contains the lowest recorded height for all five size classes, and the highest recorded height for the largest three size classes (i.e., snails ≥30.1 mm).

DISCUSSION

Determination of *Cittarium pica* Habitat Preferences

The habitat preferences of *C. pica* encompass a complex array of characteristics that result from the unique geologic history, topographic complexity, and environmental characteristics of the Tropical Northwestern Atlantic. *Cittarium pica* is most often associated with a broad range of biogenic and clastic carbonate rocks (not including beach rock), where it is found in relatively high abundance. Beach rock was not judged an appropriate habitat for *C. pica* and was not considered in this study, although it is an important tropical intertidal habitat for some motile gastropods and is especially prominent in the Caribbean (Stoddart & Cann 1965). On both biogenic and clastic carbonates, *C. pica* is often found on the undersides of rocks or in cracks, crevices, and holes, which result from either the arrangement of rock features (e.g., boulder fields, slab "piles") or weathering (i.e., chemical, mechanical, biological). Presumably, *C. pica* seeks these locations because they provide some form of refuge, either from predators (Bertness et al. 1981; Menge & Lubchenco 1981) or environmental stresses, such as high wave energy, desiccation, or radiation (Kohn & Leviten 1976).

Figure 6: *Cymatium* sp. with its proboscis between the operculum and shell of a *Cittarium pica*.

The microhabitats are likely to deter some predators of *C. pica*, such as birds (Randall 1964), fishes (Warmke & Erdman 1963), and lobsters (Herrnkind et al. 1975). However, gastropod predators, such as *Purpura patula* (Randall 1964), *Cymatium* sp., *Thais deltoidea* (E.M. personal observations), *Thais rustica*, and *Thais haemastoma floridana* (Hoffman & Weldon 1978) can likely gain access, unless the hole is too small for both predator and prey. If *C. pica* is in a narrow microhabitat, these predators may be unable to feed on *C. pica* because they need to wedge their proboscis between the operculum and the shell (Fig. 6). If the prey snail is in a space that is only slightly larger than its shell, then predators may be unable to flip the shell over to gain access to the operculum. *Octopos vulgaris*, another common predator on *C. pica* (E.M. personal observation; Randall 1964) could likely extract the snail from a refuge or drill through the shell in place.

Vertical position of *C. pica* ranges from 0.60 m below to 1.80 m above MLW, sometimes found above MHW and even above the splash zone. Other researchers report finding *C. pica* up to 1 m below MLW (Boulon 1987; Debrot 1990; Robertson 2003) and up to 0.61 m above MLW (Randall 1964). However, this range in vertical position is related to site-specific topographic features and environmental characteristics. As such, generalizations for *C. pica* zonation, though providing broad guidelines for where *C. pica* is distributed within the rocky intertidal, are oversimplifications of complex patterns of distribution. The range in vertical position varies among the four rocky intertidal habitat categories (i.e., angled, boulder, platform, cliff), but *C. pica* is found above MLW and MHW within all categories. The splash zone is a site-specific characteristic, determined by wave exposure, offshore slope, and rock features within the site. The boulder and platform habitats consist of low to moderately exposed sites, with either rock features that have lower relief seaward or low relief overall. These rock features dissipate wave energy, resulting in a low splash zone. Within both boulder and platform habitats, the vertical position of *C. pica* extends above the splash zone.

The distribution of the smallest snails (≤10.0 mm) is the most restricted in the angled habitat, where it is only found below MHW. In all three of the other habitats, these snails are commonly found above MHW, or even above the splash zone (e.g., boulder and cliff habitats), but they are less common above MLW than they are at or below it. The middle two size classes (10.0-40.0 mm) are the most common size classes found above MHW. For the boulder habitat, these snails are actually found more commonly above MLW than at or below it. In the other three habitats, they are equally common above and below MLW. The largest two size classes (>40.0 mm) are most common in cliff habitats and least common in angled habitats. Because cliff habitats are the least accessible to humans due to dangerous conditions, this likely contributes to the larger snails present at these sites. Individuals >60.0 mm are found only in the platform and cliff habitats. In the platform habitat, these individuals are most common at MLW and are never found above MHW. In the cliff habitat, however, they extend above MLW, but not above the splash zone. Angled habitats have the most vertically restricted distribution of snails among all habitat categories. This may result from the combination of smoother rock surfaces and moderate to high wave action, which may allow the snails to get easily dislodged from the rock surface.

Regardless of the habitat category or the size of the snail, *C. pica* is most common at or slightly above or below MLW. Size-specific zonation is evident within all habitat categories, but varies depending on the site-specific geomorphological and environmental characteristics. Unlike previous studies, the data reported here suggest that size-specific zonation of *C. pica* does not follow a simple linear relationship with vertical position. The largest snails at a site are not always found at or below the water level, and the mid-sized individuals are common throughout. The smallest individuals (<10 mm) are often not at the highest vertical position, as previously suggested (Debrot 1990; Hoffman & Weldon 1978; Randall 1964). Instead, these individuals are most common below MHW for all habitats. They are, however, only slightly less common above MHW in platform habitats, where there is high topographic complexity and tidepools. The largest snails (>40.0 mm) are rarely found above MHW; they are most common at MLW, not below it, contrary to data previously reported (Debrot 1990). No direct experiments were conducted during this study to explain the distribution of *C. pica*. However, Debrot (1990) suggests that the size-specific zonation of *C. pica* is driven by differential predation. Predators of *C. pica*, other than humans, include other molluscs (Randall 1964; Wodinsky 1969), lobsters (Herrnkind et al. 1975), fishes (Warmke & Erdman 1963), and birds (Randall 1964). These predators eat individuals that are 45 mm in width or less (E.M., unpublished data), so *C. pica* >45 mm obtain a size refuge from predation. As suggested by Debrot (1990), this can explain the distribution of the largest size classes (>40 mm) and the intermediate individuals (10-40 mm), but not the distribution of the smallest size class. Further data documenting the activity patterns of *C. pica* predators (e.g., high versus low tide, day versus night) and the range tolerance of environmental stressors (e.g., temperature, desiccation, radiation) is needed before a causal explanation for *C. pica* zonation can be confidently interpreted.

Evaluation of New Method for Visualizing Rocky Intertidal Zonation

Intertidal zonation is typically treated as a linear, continuous habitat with horizontal bands of organisms zoned vertically with tidal height. When illustrated, these bands are depicted on smooth vertical or angular surfaces with little to no topographical complexity. At sites with low spatial and temporal variation in processes, this treatment may be supported with field data and observations. However, not all rocky intertidal ecosystems are so neatly organized because geomorphological and environmental variation between sites confounds the observations. In most locations, even those where past research suggested banding patterns, the simple models of intertidal zonation fail when tested with quantitative data (Underwood 2000). The processes that affect zonation are neither constant nor widespread, but rather localized. Most recent studies fail to produce a visual representation of the pattern, providing only descriptive and statistical interpretation of data (e.g., Sibaja-Cordero & Cortés 2008). Also, research on rocky intertidal zonation still focuses on ecological and environmental processes affecting zonation (e.g., Rochette & Dill 2000; Somero 2002), with little regard to how geomorphological variation affects the effects of these processes. Visualization of these complex patterns is desperately needed, and must focus on patterns within rock features and then scale up to view larger patterns. For example, Beck (2000) suggests that habitat complexity and structural components of habitat differentially affect zonation patterns, but does not provide a visual representation of his findings. Along tropical coastlines topographic complexity abounds, often due to the prominence of limestone, which is easily weathered, chemically, mechanically, and biologically. Here, the distribution of organisms cannot be easily illustrated by looking at a single surface along a single rock feature. In such habitats, a more detailed documentation of distribution that is feature-oriented will provide a more accurate view of the patterns present.

The method described and used here allowed for a more comprehensive view of the overall and size-specific zonation for a single species. Classifying the rocky intertidal into habitat categories can provide insight into the reasons why species are distributed where they are because it allows for comparisons between categories with different geomorphological and environmental characteristics. Categories could be chosen to minimize differences in wave exposure and maximize differences in geomorphological characteristics (e.g., boulder, platform) to facilitate understanding how rock features drive distribution. In this study, sites were chosen to encompass the overall variation in sites where *C. pica* occurs. The structured visualization provided a basis for rigorous analysis that led to a thorough comprehension of the zonation and habitat preferences of this conspicuous intertidal gastropod. These methods can be applied to rocky intertidal ecosystems throughout the world to gain a more precise understanding of intertidal zonation and of the fine-scale distribution of individual organisms.

Climate change is pushing organisms in tropical latitudes to or beyond their thermal maxima (Cheung et al. 2009; Walther et al. 2002) and sea-level rise is altering the size and distribution of intertidal habitats (Barange & Perry 2009; Fish et al. 2005; Thompson et al. 2002). The higher latitude range boundaries of rocky intertidal species have changed faster than most terrestrial species, indicating that rocky intertidal organisms are quick to react to environmental change and

"…may serve as early warning systems for the impact of climate change" (Helmuth et al. 2006 and references therein). Predicting how organisms will respond to these changes depends on the availability of extensive data on how distribution relates to geomorphological and environmental characteristics on multiple spatial scales. The method developed herein provides the foundation for illustrating and understanding these multi-scale species distributions, along with a platform for including large quantities of data. Detailed observational data can be transformed into generalized cross-sections of rocky intertidal habitats, and changes in environmental variables (e.g., MLW, MHW, rates of weathering) can be simulated onto individual rock features. Future research could expand the method developed herein to integrate across not only additional spatial scales but also multiple temporal scales.

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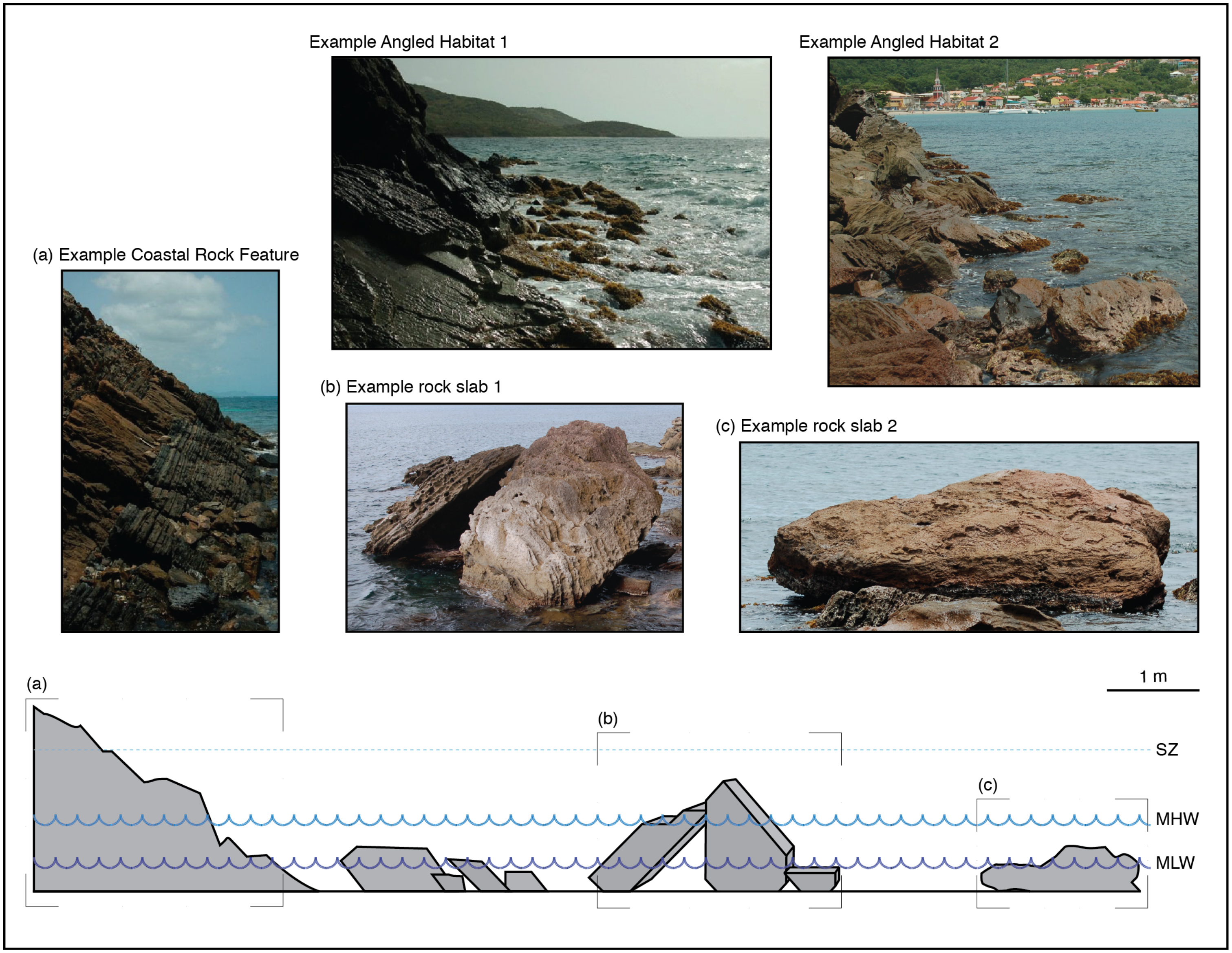
Appendix 1: The West Indian Top Snail, *Cittarium pica*, is a conspicuous gastropod that inhabits a wide variety of rocky intertidal habitats throughout the Neotropical Western Atlantic. Fieldwork was conducted at 48 sites, across 28 islands or continental localities, within 17 territories or countries. The sites were classified based on the geomorphological and environmental characteristics of each site, gleaned from field notes and photographs. These photographs were taken in the field with a Nikon D50 digital single lens reflex (SLR) camera, using a Nikon AF Nikkor 70-300 mm lens or a Nikon AF Nikkor 28-80 mm lens. These characteristics include (i) presence of a vertical coastline, (ii) presence of boulders or slabs, (iii) prominent mechanical weathering, (iv) average height and length of the site, and (v) what major rock types were present. Following the development of this system, 40 of the 48 sites were classified into four different habitat categories. Eight sites were left unclassified, either because of incomplete habitat data for the site or because the site did not fit into any of the four categories. Incomplete data was the result of dangerous weather conditions, often due to tropical storms and offshore hurricanes.

The four habitat categories are illustrated in the following figures: (A1.1) Angled Habitat, (A1.2) Boulder Habitat, (A1.3) Platform Habitat, and (A1.4) Cliff Habitat. These figures include hand-drawn cross-sections that represent the rock features of the average site within each of the categories. The cross-sections were scanned into Adobe Photoshop v12.1 (Adobe Systems, Inc.) and traced in Adobe Illustrator v15.1 (Adobe Systems, Inc.). Rock features from each habitat category were uniformly scaled and arranged to depict typical cross-sectional views of each habitat category. MLW and mean high water (MHW) were standardized across all habitat types because tidal range is nearly constant across all sites. The height of the splash zone (SZ) was averaged across all sites within each habitat category. Mean low water (MLW), mean high water (MHW), and splash zone (SZ) are indicated on each of the figures. Above the cross-sections, photographs of example rock features from sites within the categories are provided, along with a photograph of a "typical" site.

Appendix 1, Figure A1.1: Angled Habitat



(a) Example Coastal Rock Feature

Example Angled Habitat 1

(b) Example rock slab 1

Example Angled Habitat 2

(c) Example rock slab 2

Appendix 1, Figure A1.2: Boulder Habitat

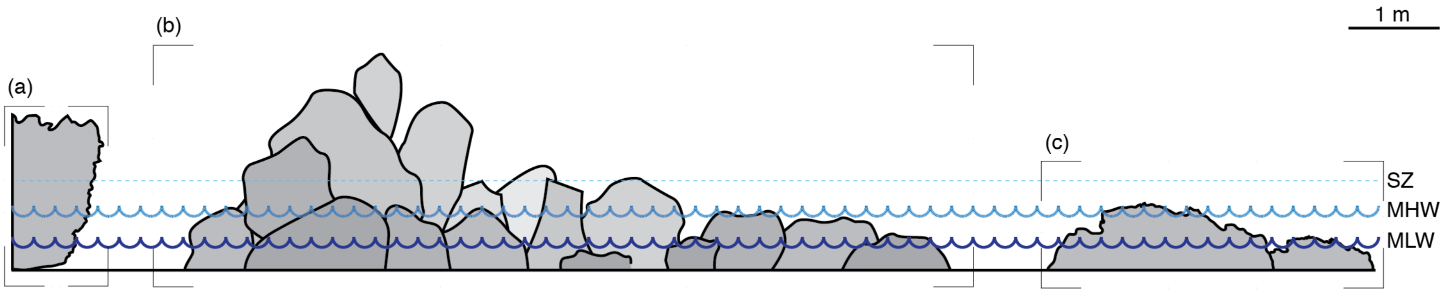

Example Boulder Habitat 1


Example Boulder Habitat 2


(a) Example Coastal Rock Feature


(b) Example Boulder Pile


(c) Example Rock Feature



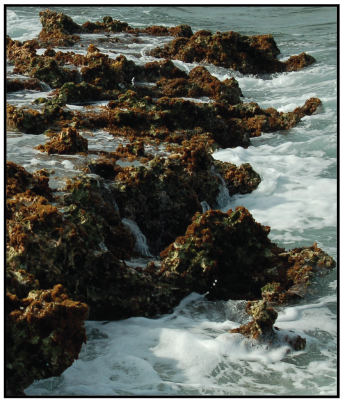
Appendix 1, Figure A1.3: Platform Habitat

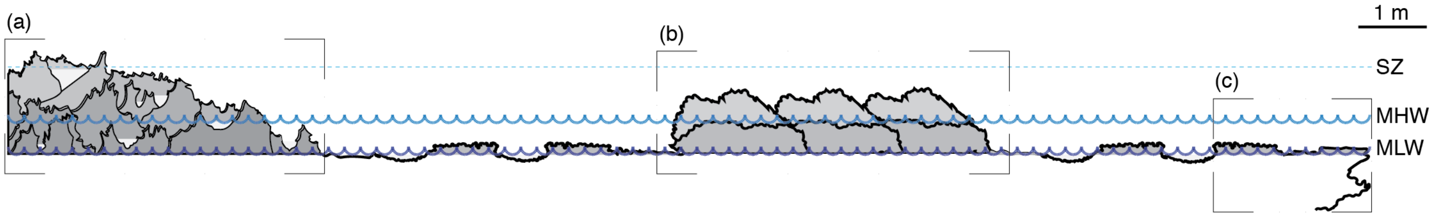

Example Platform Habitat 1


Example Platform Habitat 2

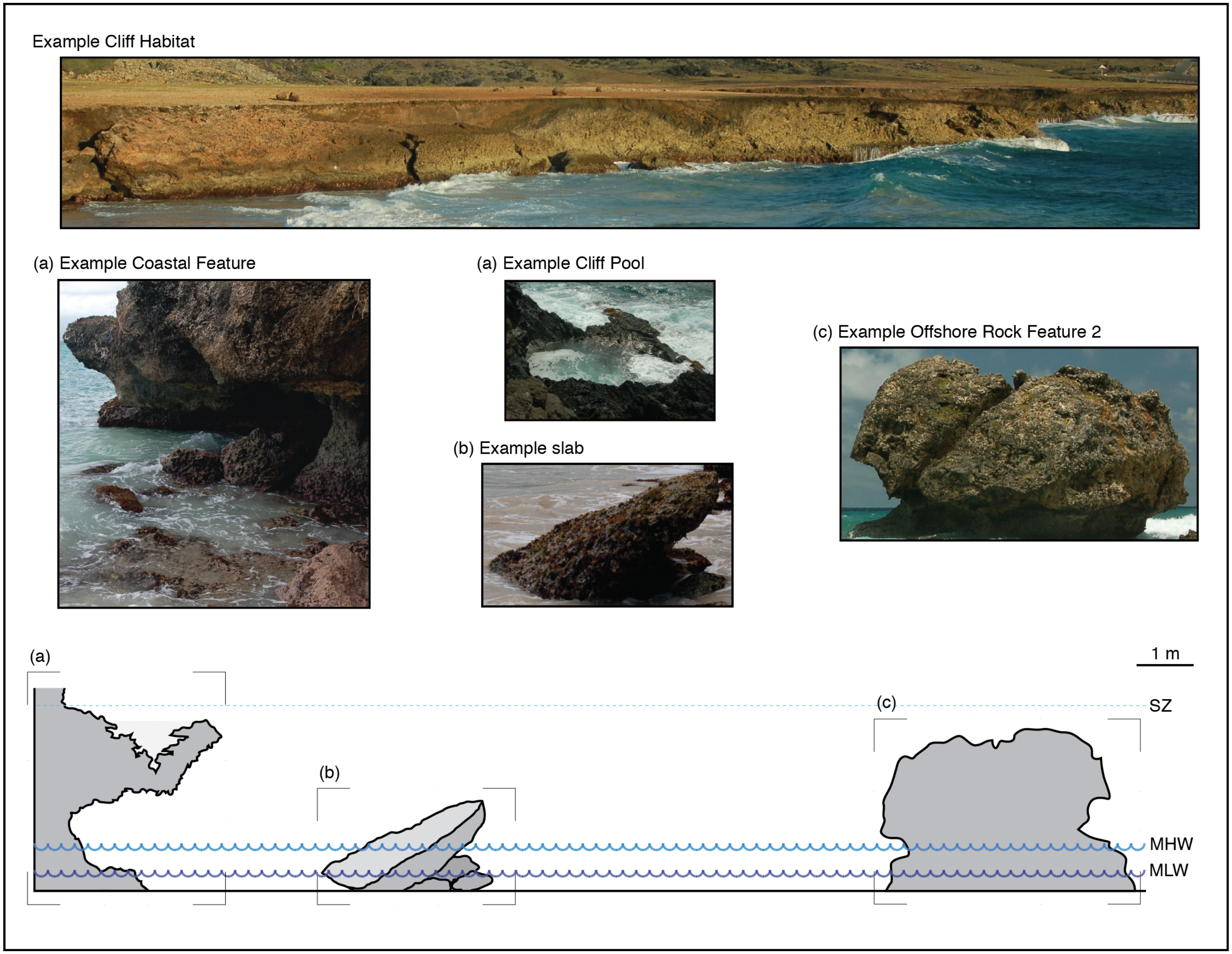

(a) Example Rock Feature 1


(b) Example Rock Feature 2


(c) Example Rock Feature 3



Appendix 1, Figure A1.4: Cliff Habitat



Example Cliff Habitat

(a) Example Coastal Feature

(a) Example Cliff Pool

(b) Example slab

(c) Example Offshore Rock Feature 2

Chapter Four

Post-extinction recovery of *Cittarium pica* in Bermuda

One amongst the rest hid himself in the woods, and lived only on Wilkes and Land Crabs, fat and lusty, many moneths.

-- Captain John Smith,
on surviving during the Bermuda famine of 1614-1615

INTRODUCTION

Translocation of species is a useful and increasingly applied tool in conservation biology and species management. There are three different kinds of translocations, including introduction, restocking, and reintroduction (Armstrong & Seddon 2008), the latter of which is a common tool used to address local extinctions, often focusing on those that resulted from human activity. Reintroduction is defined by the International Union for Conservation of Nature and Natural Resources (IUCN) as releasing individuals of a species to a region where it went extinct in historic times (IUCN 1998), with no implication that the extinction must be caused by anthropogenic factors (Jørgensen 2011). The goal of any reintroduction program is to re-establish the target species in a specific location where it does not exist. According to a review of all published reintroductions from 1979 to 1998 (Fischer & Lindenmayer 2000), there are approximately equal numbers of "successful" and unsuccessful reintroductions, but nearly half are unclassifiable, mostly because monitoring programs are insufficient. Over half of these cases involve captive-bred source populations, and over 90% are reintroductions of mammals and birds. A review of 62 recent reintroductions includes only three marine cases and only four invertebrate cases, two of which were marine (Soorae 2008). Overall, reintroductions are an important conservation tool that can be used in combination with mitigation of anthropogenic impacts to restore species diversity and the corresponding ecosystem functions.

Determining when reintroductions are "successful" is often complicated. Reintroduction success is typically declared when monitoring reveals that the population is self-sustaining (Fischer & Lindenmayer 2000; Sarrazin & Barbault 1996). This success depends on habitat quality and release location within the species' range, number released, characteristics of the release event itself, ecological and demographic characteristics of the species, whether the cause of the local extinction was mitigated or removed, and the long-term management and community involvement with the reintroduction process (Beck et al. 1994; Fischer & Lindenmayer 2000; Griffith et al. 1989; Kleiman et al. 1994). Reintroductions of species to interior sites within the species' range tend to be more successful than those to the periphery. Species that breed earlier in their life history and produce more offspring are more amenable to reintroductions (Griffith et al. 1989), and typically do not require multiple releases to be successful, similar to species that are wild-caught rather than captive-bred. However, in the absence of long-term monitoring or follow-up studies, as in many reintroduction cases, success can never be declared.

Because reintroduction success depends on the removal of threats to the species' reproductive success, an understanding of the causes of the local extinction is vital, but these are often very difficult to determine. Documentation of marine extinctions, let alone defining the causes, is problematic, mainly because it is nearly impossible to be positive that there are no individuals remaining; surveying in all possible habitats and localities in the ocean is an unachievable task. However, many neo-extinctions of marine organisms have been documented, including several species of corals, fishes (Roberts & Hawkins 1999), gastropods (Carlton 1993; Carlton et al. 1991; Roberts & Hawkins 1999), and vertebrates (Carlton et al. 1999). The term "neo-extinction" is defined as the documented disappearance in the Holocene of all individuals of a species (Carlton 1993). Marine invertebrate neo-extinctions are particularly difficult to document because of an overall lack of data collection, so there may be hundreds of overlooked neo-extinctions of such organisms (Carlton 1993). This lack of data and population monitoring also confounds the process of diagnosing the cause of extinctions. Causes of documented marine extinctions and near extinctions include habitat alteration and destruction, introduced species, natural causes, overexploitation, and combinations of these (Roberts & Hawkins 1999).

The West Indian topsnail, *Cittarium pica* (Linnaeus, 1758) is an important fishery resource throughout the Tropical Northwestern Atlantic (Spalding et al. 2007), where the species has been harvested since humans first migrated to the region 6,000-7,000 years ago (Crosby 2003; Fitzpatrick & Keegan 2007; O'Day & Keegan 2001). The species reportedly went locally extinct in Bermuda sometime in the mid-1800s (Wingate 1995), with no live specimens found well into the next century (Peile 1926). Humans established settlements in Bermuda in 1609, and immediately began harvesting live *C. pica* as food and bait (Wingate 1995), and collecting *C. pica* shells to grind them with limestone to produce caulk for ships (Verrill 1902a, b). Settlers continued to harvest *C. pica* from the early 1600s into the early 1800s (Abbott 1972; Bickley & Rand 1982). The species was listed in two accounts of shell collections in the mid-1800s (Godet 1860; Jones 1859), but no descriptions of or statements about live specimens were provided. There are misconceptions surrounding the date and cause of the extinction of *C. pica* in Bermuda (Verrill 1902a, b; Wingate 1995), but there are no data to support any major environmental change so likely the extinction was caused by overexploitation.

There have been three documented reintroduction attempts of *C. pica* in Bermuda, only one of which was pre-planned and monitored. The first reintroduction attempt occurred in 1901 by 'Mr. Roberts' (Verrill 1902a, b), six years before what is acknowledged as the first reintroduction of any kind, that of the American bison (*Bison bison*) to Oklahoma (Seddon et al. 2007). This first attempt to reintroduce *C. pica* to Bermuda failed, as the population did not become established, likely because the individuals were released in Hamilton Harbour, which does not have high quality *C. pica* habitat (see Chapters 2 and 3). The second reintroduction attempt occurred in 1930 by Vincent Astor, who released individuals in Castle Harbour (Abbott 1972). This attempt also failed. There is habitat available for *C. pica* in Castle Harbour (see Chapters 2 and 3), but there is no documentation for where Astor released the individuals. The Bermuda airport was built ten years after this reintroduction attempt, which likely buried a substantial amount of suitable habitat under dredged fill. Historic photographs taken from the Astor estate reveal many small, rocky islands creating a partial barrier between Ferry Reach and Castle Harbour, which were subsequently destroyed (K. Coates, personal observation). Another potential problem with these first two reintroduction attempts, other than a complete lack of planning, was that no restrictions were put in place to protect the recovering population. Because *C. pica* went locally extinct due to overexploitation, without restricting harvest these reintroductions were doomed to failure.

The most recent attempt at reintroducing the species occurred on June 19, 1982 when 82 individuals collected by Teddy Tucker from either the northern Bahamas or Turks and Caicos Islands (Bickley & Rand 1982; Robertson 2003; Wingate 1989; Wingate 1995) were released on the Nonsuch Island Nature Reserve in Nonsuch Bay (Bickley & Rand 1982). These specimens were tagged prior to their release, and size (i.e., breadth, height, width, weight) was recorded. Tucker released additional individuals off of High Point on the southshore of Bermuda (P. Rouja, pers. communication). Because detailed information about the reproductive traits of *C. pica* were and are not available (e.g., fertilization rate, survival rate of larvae, number of metamorphosed snails per reproduction event, etc.), a population viability analysis (PVA) could not be executed. PVAs are often used to determine a priori predictions of population viability and extinction risk (Seddon et al. 2007) based on different reintroduction characteristics (e.g., number released, location released, age of released individuals) and environmental conditions (e.g., habitat quality, number of release sites). PVAs, however, are mostly designed for vertebrate species in which you can easily observe the required input variables. Invertebrates often have more complex life histories, like *C. pica*, which is a broadcast spawner with lecithotrophic planktonic larvae and has no standard temporal patterns to reproduction. In highly studied taxa, such as abalone (*Haliotis* spp.), some of these and other important data are available, so a PVA could be developed (Tegner et al. 1996), but most of these data are not available for *C. pica*. Tegner et al. (1996) acknowledge that for abalone, a high population density of individuals is needed to overcome allee effects on successful fertilization and that the “zone of effective fertilization” is approximately one meter. Likely similar requirements are important for *C. pica* since abalone are also broadcast spawning vetigastropods.

The objectives of this study are to (1) assess the success of *C. pica* population recovery in Bermuda, (2) evaluate the population expansion, and (3) provide local management recommendations of and for *C. pica* in Bermuda. The Bermuda Department of Conservation Services has been monitoring the recovery of the species in Bermuda since it was reintroduced, but the last survey was conducted in 2003 and no formal analysis or evaluation has been published. A devastating harvest event in 1988 motivated the Bermuda government to fully-protect the species with the Fisheries (Protected Species) Order of 1978, under the provisions of the Bermuda Fisheries Act of 1972 (Wingate 2006). By removing what is thought to be the original threat to population stability, the Bermuda government reaffirmed its commitment to the local recovery and re-establishment of *C. pica*. As the largest rocky intertidal gastropod, *C. pica* is in an important member of that community, although its reintroduction likely had a low-impact on the surrounding ecology because of the simple nature of the community structure in Bermuda. The shells of *C. pica* are also a vital resource to the terrestrial hermit crab, *Coenobita clypeatus*, because *C. pica* provides the only source of shells that are large enough to house the larger individuals of this species (Randall 1964; Robertson 2003; Walker 1994).

METHODS

Study Location and Population Surveys

The islands of Bermuda are located in the North Atlantic, approximately 1,036 kilometers east of Cape Hatteras, North Carolina, and approximately 1,500 kilometers north of San Juan, Puerto Rico, 32°20'N / 64°45'W (Fig. 1). To assess the status of the recovery of *C. pica*, population surveys were conducted in 1989, 2000, 2003/2004, and 2007. The 1989 survey only included 14 sites in and around Castle Harbor and on St. David's Island. The data from this survey consists of only total population size, with no information on individual snail size (Cattell 2000). An island-wide survey conducted in 2000 was reported in two separate government reports. Survey data are reported from 25 (Cattell 2000) and 47 (Madeiros 2000) sites across the island. The data overlap for 24 sites, so the total number of sites surveyed in 2000 is 48 (Appendix 1). However, individuals size measurements were only reported in one report (Cattell 2000), whereas the other (Madeiros 2000) reported binned size data (i.e., <10 mm, 10-50 mm, >50 mm). The data from these surveys were released to me by the Bermuda Department of Conservation Services and are re-analyzed herein. No Global Positioning System (GPS) coordinates were provided for these surveys, so latitude and longitude coordinates for surveys were estimated in GoogleEarth v.6.0.1.2032 based on site descriptions provided within the reports.

Follow-up surveys were conducted at one site in 2003 (i.e., Hungry Bay), three sites in 2004 (i.e., 'Officer's Beach', 'Rocky Hole', 'Unused Runway'), and two sites in 2007 (i.e., 'Rocky Hole', 'Turtle Bay'). Three of these sites are located on Cooper's Island (Fig. 1), which was connected to St. David's Island during construction of the L.F. Wade International Airport during the early 1940s. Officer's Beach is located on the west side of Cooper's Island, at approximately 32.355ºN and 64.663ºW; extending from the center of the beach area is an old jetty, which is now composed of fractured concrete intermixed with discarded metal. Rocky Hole and Turtle Bay are adjacent to each other, on the east side of Cooper's Island, located at approximately 32.353ºN / 64.656ºW and 32.352ºN / 64.667ºW, respectively. Rocky Hole is composed mainly of large, limestone boulders and coral rubble abutting a weathered limestone outcrop. Turtle Bay lacks loose boulders and rubble. This site is composed of a limestone platform and wall to the north and a near-90º angled limestone wall to the south. The Unused Runway is located on St. David's

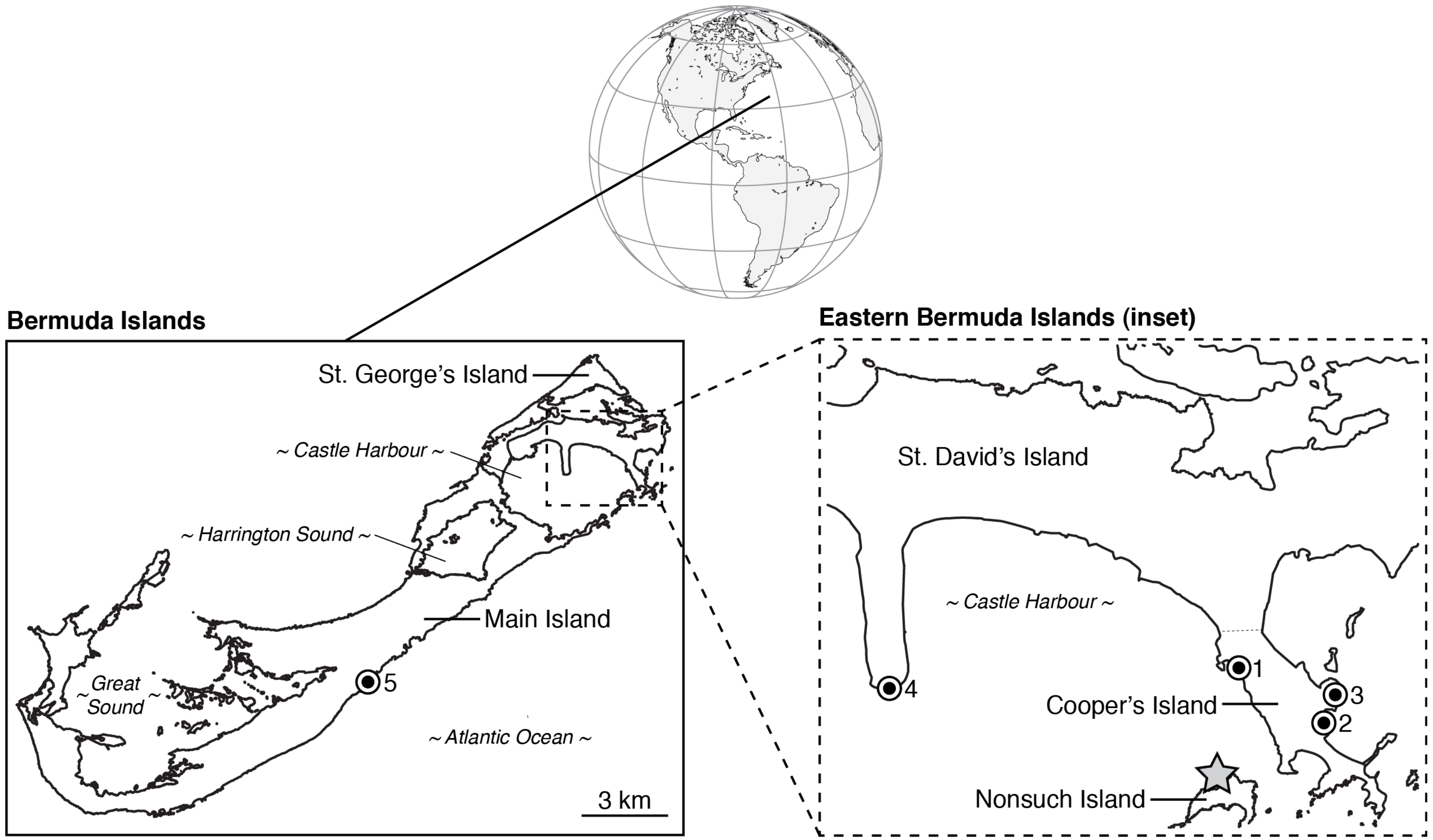


Figure 1: The islands of Bermuda are located in the North Atlantic, approximately 1,036 kilometers east of Cape Hatteras, North Carolina, and approximately 1,500 kilometers north of San Juan, Puerto Rico, 32°20′N / 64°45′W. The site of the 1982 reintroduction is marked with a shaded star. The five survey sites are marked with the dotted circles: (1) Officer's Beach, (2) Rocky Hole, (3) Turtle Bay, (4) Unused Runway, and (5) Hungry Bay.

Island (Fig. 1) at approximately 32.354ºN / 64.687ºW, and surveys focus on the area around the tip of the runway, where it has weathered into large fragments of concrete and now resembles rip-rap. The final site, Hungry Bay, is located on the Main Island (Fig. 1) at approximately 32.290ºN / 64.758ºW. The substrate at this site is a mixture of an eroding limestone platform landward of large boulders and coral rubble.

Population surveys involved measuring the shell width (Fig. 2) of individual snails with calipers for two hours along a two-meter band-transect. Survey length was set by time, rather than distance, because the three-dimensional topography varied by site, making horizontal distance an inaccurate measurement of area covered (see "platform habitat," Chapter 3). Cattell (2000) and Madeiros (2000) did not define shell width in their report, but Madeiros confirms that he and Cattell measured shell width with the same method as I did (J. Madeiros, personal communication).

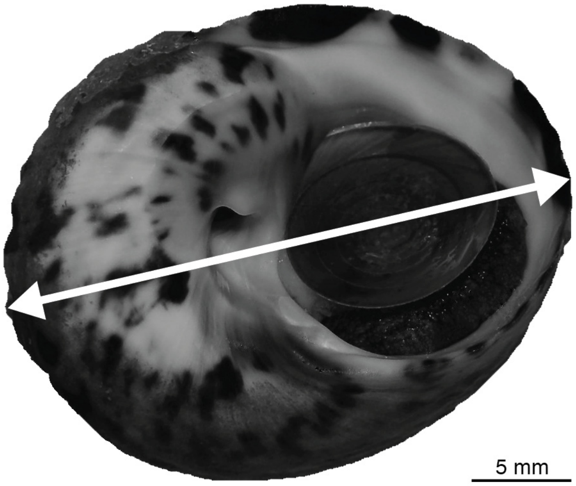


Figure 2: Photograph of *Cittarium pica*. The arrow identifies its width (28.2 mm), which is defined as the maximum distance across the dorsal surface of the shell that transects the aperture.

To determine whether the populations have declined, stabilized, or continued to increase, the population structures for four sites for two to three survey years were compared. The data were divided into histogram bins in *R* (R Development Core Team 2009), and histograms were generated in Microsoft Excel v.12.3.0 (Microsoft Corporation, 2007). A one-way analysis of variance (ANOVA) or *t*-test was calculated in JMP v8.0 (SAS Institute 1998) to compare the means among years. Sample sizes are unequal among survey years, so Tukey's HSD test was conducted with the Tukey-Kramer modification. Snail size was natural-log transformed for these analyses. To evaluate the differences between the spread of the populations from year to year, boxplots were constructed in *R* (R Development Core Team 2009). The data for two of the sites (i.e., Hungry Bay, Unused Runway) are only available as binned data from the survey conducted in 2000, so *t*-tests and boxplots could not be generated for these sites.

Population Expansion and Reintroduction Success

To evaluate population expansion, a map of the 2000 field sites was generated, with size histograms plotted by location. Locations of the 2000 field sites were mapped based on site descriptions, ground-truthing, and habitat characteristics viewed in GoogleEarth. The locations mapped in GoogleEarth were overlaid onto a finescale coastal outline (see Chapter 2). To ascertain the timing of reproduction, the presence of recently settled individuals was documented, and the approximate time since the most recent reproduction event was calculated using a *C. pica* growth curve (see Appendix 2, Figure A2.1). This curve was also used to extrapolate the average age of the population reintroduced in 1982 and to determine the maximum individual age at each site. The average size of the reintroduced individuals is provided by Bickley and Rand (1982). This assessment of population expansion will also help determine whether the individuals released at High Point survived, and serves as the first attempt at predicting local ocean currents and thus population connectivity.

To determine whether the reintroduction was a success, evaluation criteria were compiled from Griffith et al. (1989), Beck et al. (1994), Kleiman et al. (1994), and Fischer and Lindenmayer (2000). Factors to specify prior to the reintroduction include identifying an appropriate source population, how many individuals to release and of what size/age, where to release the individuals based on habitat quality and protection, and whether acclimatization is necessary prior to full release. Most of these factors were not considered prior to the reintroduction, but are still evaluated here. Factors identified as important to success and evaluated after the reintroduction include whether the original threat to the species was successfully alleviated, establishment of long-term monitoring, continued education and scientific research (i.e., community education, local employment, professional training), and adequate habitat protection.

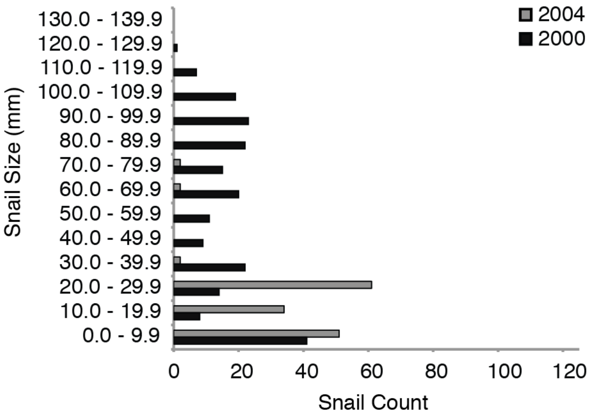
RESULTS

Population Structure Through Time

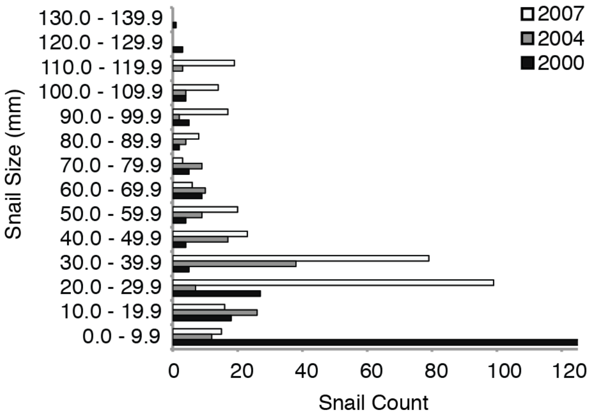
The population structure of *C. pica* in Bermuda varies between survey years at the five long-term survey sites reported here: ‘Officer’s Beach’, ‘Rocky Hole’, ‘Turtle Bay’ (Figs. 3 and 4), ‘Hungry Bay’, and ‘Unused Runway’ (Fig. 5). At Officer’s Beach, the population structure in 2000 is significantly different from the survey conducted in 2004 (Students’ *t*-test, two-tailed, p<0.0001), with population size decreasing from 212 individuals to 152 individuals (Fig. 3a, Table 1). The mean snail size and interquartile range are greater in 2000 than in 2004 (Fig. 4a), with means of 55.4 mm and 16.9 mm, and interquartile ranges of 64.0 and 16.3, respectively. Thus, the population structure at this site not only decreased in spread but is now currently centered around smaller individuals. There is evidence of a recent recruitment event (i.e., individuals <10 mm) in both years (Fig. 3a), with ten more successful recruits in 2004 than in 2000. The maximum size present in 2000 is 46 mm higher than in 2004. The number of individuals in the smaller size classes (<50 mm) actually increased over this period from 94 to 148. However, the larger size classes (≥ 50 mm) almost completely disappeared, with 118 individuals in 2000 and only four found in 2004.

Population structure at Rocky Hole varied significantly between survey years (one-way ANOVA, p<0.0001). The mean size of *C. pica* is significantly greater in 2004 and 2007 than in 2000 (Tukey’s HSD tests, α=0.05, p<0.0001). There is no significant difference between mean sizes for the surveys conducted in 2004 and 2007 (p=0.3491). The population size at this site increased from 2000 to 2007, even though recruitment was much lower in the two later years (Fig. 3b). The interquartile range is comparable between the 2000 and 2007 surveys, but is greater for

a) Officer's Beach



b) Rocky Hole



c) Turtle Bay

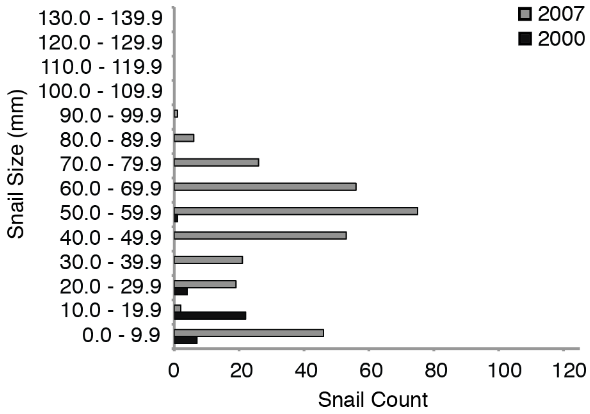
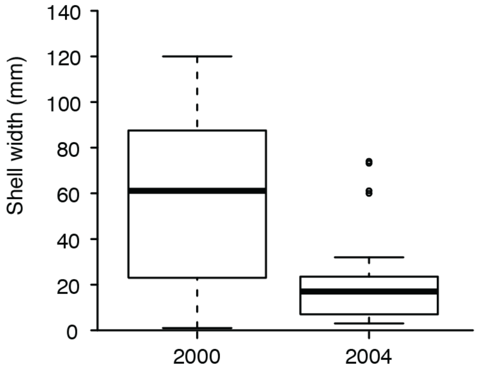
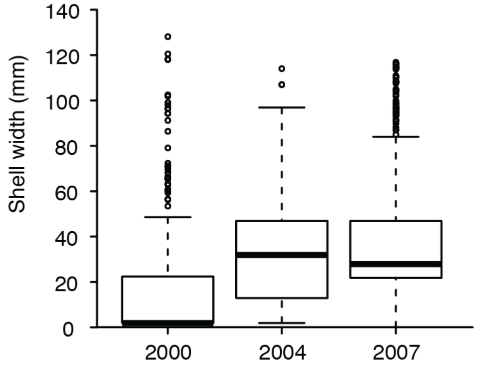


Figure 3: Histograms of snail size (shell width) from 2-3 survey years of *Cittarium pica* in Bermuda at three sites: a) Officer's Beach, b) Rocky Hole, and c) Turtle Bay.

a) Officer's Beach



b) Rocky Hole



c) Turtle Bay

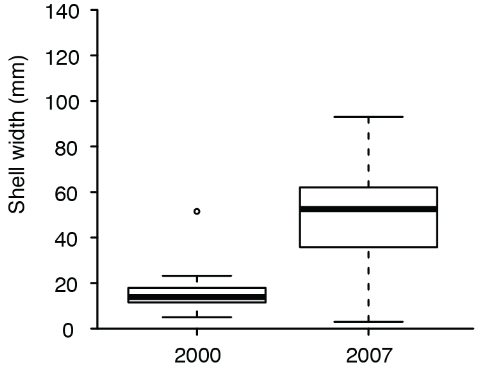
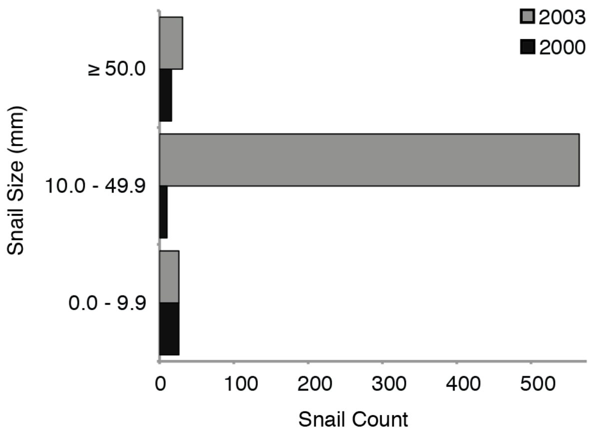


Figure 4: Box and whisker plots of snail sizes from 2-3 survey years of Cittarium pica in Bermuda at three sites: a) Officer's Beach, b) Rocky Hole, and c) Turtle Bay. The boxes are bounded by the first and third quartiles of the data from each survey year. The horizontal line within each box is the median size value. The open circles (if present) mark data points identified as outliers. The whiskers mark the maximum (above boxes) and minimum (below boxes) sized snail for each site, excluding the outliers.

a) Hungry Bay



b) Unused Runway

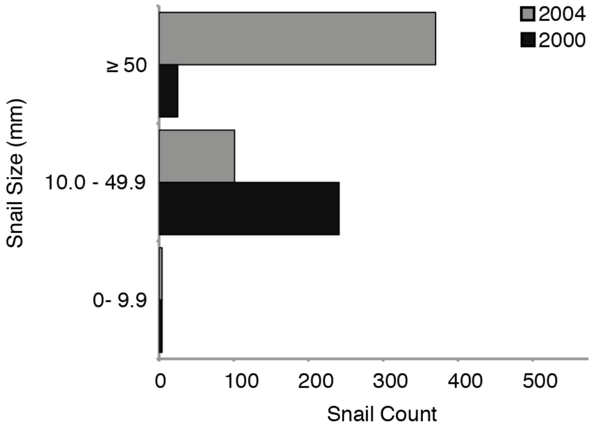


Figure 5: Histograms of snail size (shell width) from two survey years at two sites: (a) Hungry Bay and (b) Unused Runway.

2004 survey (Table 1). This indicates that the spread of the data is similar (Fig. 4b). The maximum size recorded in 2000 is 131.5 mm, which is 11.2 and 14.5 mm greater than the maximum size recorded for 2004 (117.0 mm) and 2007 (119.9 mm), respectively. Only four individuals larger than 117 mm were found in 2000, compared to none in 2004, and eight in 2007. Both the smaller and larger size classes increased from 2000 to 2007, 180 to 232 and 33 to 87, respectively. The spread, size range, and overall structure of the population at this site appears to be fairly constant.

The final site with individual size data, Turtle Bay, also has significantly different population structure between survey years (Students' *t*-test, two-tailed, $p<0.0001$). Both population size and mean snail size increased dramatically from 34 individuals and 14.7 mm in 2000 to 305 individuals and 46.7 mm in 2007 (Table 1). The number of recent recruits also increased, from seven individuals in 2000 to 46 individuals in 2007 (Fig. 3c). The interquartile range of the population at Turtle Bay is greater in 2007 (26.2) than in 2000 (6.2) (Fig. 4c). Population structure has obviously changed in all aspects, shifting to a larger population with a higher size range and more successful recruitment.

At both of the sites from which we have only binned size data for 2000, there were substantial changes in population sizes. The population size at Hungry Bay increased from 52 individuals in 2000 to 622 individuals in 2003 (Table 2). In 2000, there were nearly equal numbers of individuals in all three size categories, but in 2003 the majority of individuals are 10 to 49.9 mm (Fig. 5a). The number of recruits recorded in 2000 cannot explain the large increase in mid-sized individuals. The population size at Unused Runway increased from 270 in 2000 to 475 in 2004 (Table 2). The mid-sized individuals decreased at this site, but an associated increase in individuals greater than 50 mm was observed (Fig. 5b). There was no change in recruitment from 2000 to 2004 at this site.

Table 1: Population parameters for multiple surveys for three sites, along with the results of the Student's T-tests.

	Officer's Beach		Rocky Hole			Turtle Bay	
	2000	2004	2000	2004	2007	2000	2007
Population Size	*212*	*152*	*213*	*141*	*319*	*34*	*305*
0 - 9.9 mm	41	51	126	12	15	7	46
10.0 - 49.9 mm	53	97	54	88	217	26	95
≥ 50 mm	118	4	33	41	87	1	164
Max Size (mm)	*120.0*	*74.0*	*131.1*	*117.0*	*119.9*	*51.4*	*93.0*
Max Age (years)	7.5 - 8.0	3.7 - 4.2	> 8.0	7.4 - 7.9	7.5 - 8.0	2.7 - 3.3	5.2 - 5.7
Median Size (mm)	*61.1*	*17.0*	*5.0*	*35.0*	*31.0*	*13.9*	*52.5*
Median Age (years)	3.2 - 3.7	1.5 - 1.8	0.6	2.2 - 2.7	2.1 - 2.5	1.4 - 1.7	2.7 - 3.3
Mean Size (mm)	*55.4*	*16.9*	*22.0*	*39.2*	*43.6*	*14.7*	*46.7*
Mean Age (years)	3.0 - 3.5	1.5 - 1.8	1.7 - 2.0	2.4 - 2.9	2.5 - 3.0	1.4 - 1.7	2.6 - 3.1
Interquartile Range	*64.0*	*16.3*	*20.5*	*34.0*	*25.1*	*6.2*	*26.2*
Quartile 1	23.5	7.0	5.0	16.0	24.9	11.6	35.8
Quartile 3	87.5	23.3	25.5	50.0	50.0	17.8	62.0
Student's T-test	$p < 0.0001$		$p < 0.0001$			$p < 0.0001$	

Table 2: Population parameters for two surveys for two sites, along with the results of the Student's T-tests.

	Hungry Bay		Unused Runway	
	2000	2003	2000	2004
Population Size	*52*	*622*	*270*	*475*
0 - 9.9 mm	26	26	4	4
10.0 - 49.9 mm	10	565	241	101
≥ 50 mm	16	31	25	370
Student's T-test	$p < 0.0001$		$p < 0.0001$	

Population Expansion

By 2000, *C. pica* had thoroughly settled the rocky intertidal on St. David's Island, from the Civil Air Terminal near Longbird bridge on the southwest coast all around Cooper's Island and Ruth's Point to Red Hole Cove and Little Head Park on the northeast coast (Fig. 6, Appendix 1). The site on St. David's Island that is farthest from Nonsuch Island, the documented release site for *C. pica* in 1982, is the Civil Air Terminal, about 3.2 km to the northwest (Fig. 6). The largest individual at this site was 119.2 mm, which is 7.5-8.0 years old. Thus, the oldest individuals at this site settled in 1992. Because the species also expanded around the northeast coast of St. David's Island, currents and/or wind, which can result in capillary or wind waves, travel in both directions to facilitate bi-directional transport of larvae. The dominant winds in Bermuda are from the southwest, although east winds also occur.

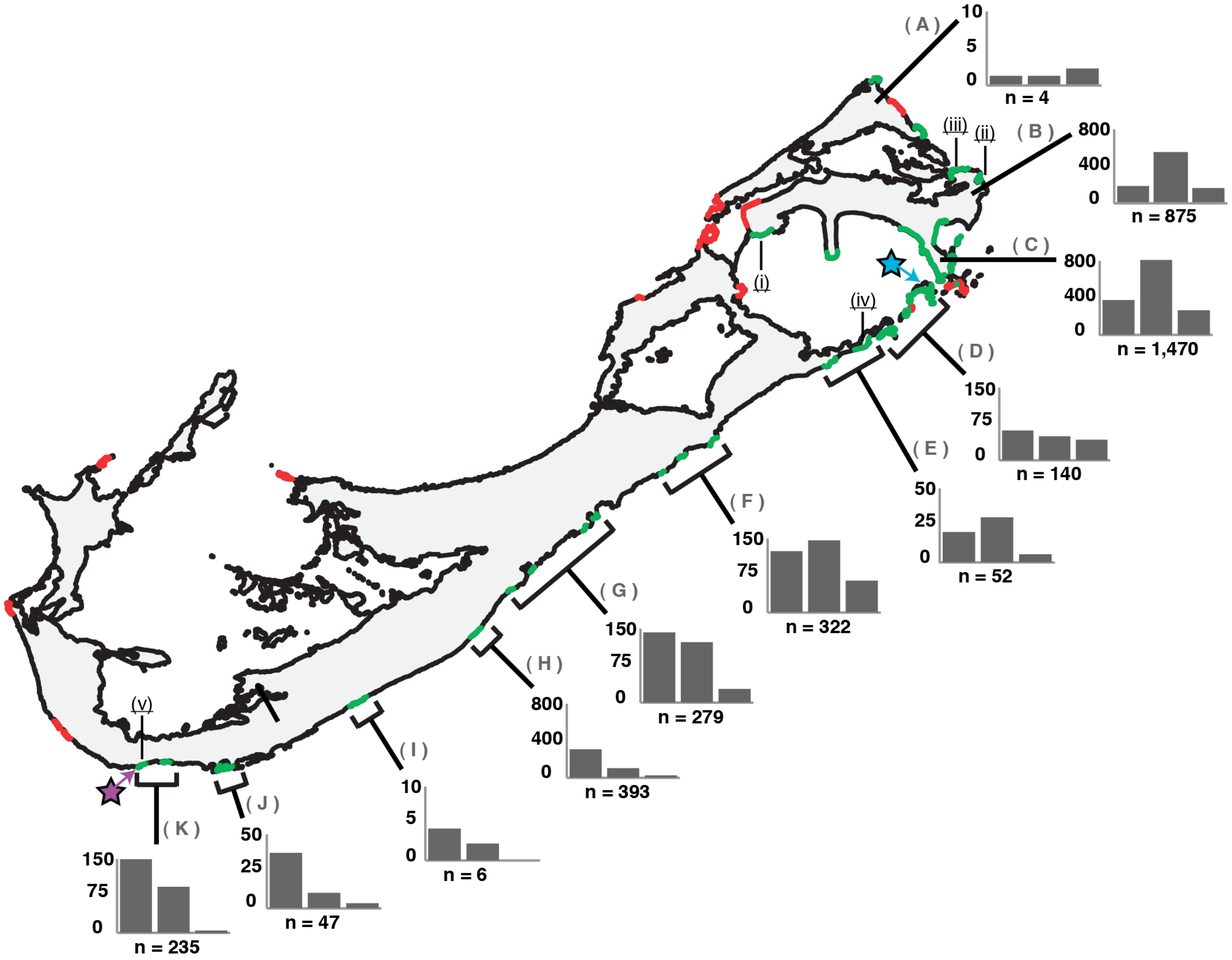


Figure 6: Outline of Bermuda with the 2000 Cittarium pica survey sites mapped. Sites where C. pica is present are marked in green, and sites where it is absent are marked in red. The size structure histograms are provided based on data from Cattell (2000) and Madeiros (2000). The sites included in each histogram are provided in Appendix 1. The blue star marks Nonsuch Island, the 1982 site where 82 individuals were reintroduced. The purple star marks High Point, where additional individuals were released. The following sites are labeled to map the extent of population expansion: (i) Civil Air Terminal, (ii) Red Hole Cove, (iii) Little Head Park, (iv) Howard Bay, and (v) Sea Swept Farm.

The species also expanded across the southern coast of Main Island, occupying most of the rocky intertidal from Howard Bay near Tuckers Town to Sea Swept Farm near High Point (Appendix 1). Without individual size measurements, which are not available for many of the Main Island sites surveyed in 2000 (e.g., Cattell 2000; Madeiros 2000), maximum age can only be estimated. The farthest site from Nonsuch Island is Sea Swept Farm to the west. Individuals greater than 50 mm were documented at this site, along with most of the other sites along the south coast (Fig. 6). According to a growth curve for *C. pica* (Appendix 2), individuals of this size are more than three years old, which suggests that the oldest individuals at these south coast sites settled in 1997, at the latest. This is a conservative estimate since some of these individuals could be much greater than 50 mm.

Table 3: Success criteria for the reintroduction of *Cittarium pica* to Bermuda, modified from Table 14.1 in Kleiman (1994).

Pre-reintroduction Factors	
Reintroduction strategies	
- Acclimatization	no
- Appropriate source colony	yes
- Quarantined prior to release	yes
- No jeopardy to wild population	unknown
Release location assessment	
- Protected habitat	yes
- Unsaturated habitat	yes
Characteristics of the Reintroduction	
- Release location	Nonsuch Is. Nature Reserve[1]
- Release year(s)	1982
- Date of documented recruitment	1986 [3]
- Total number released	82
- Mean size (age) of individuals	80.8 mm[1] (4.0 - 4.6 years[2])
- Total number survived	71 [1]
Post-reintroduction Factors	
Alleviation of the original threat?	
- Fishery regulations	yes
- Habitat protection	yes
Sufficient resources for ongoing program?	
- Community education	yes (initially)
- Local employment	no
- Monitoring	yes
- Negative impact on local people	no
- Professional training	yes

[1] Bickley and Rand (1982)

[2] Appendix 2

[3] Wingate (1995)

Recent recruitment (i.e., within 1.5 years of the date surveyed) is evident at all but two sites (i.e., Civil Air Terminal and Buildings Bay). There are 19 sites surveyed in 2000 that had population sizes greater than 50 individuals. At nine of these sites, individuals less than 10 mm in width, which are 15-17 months old, account for more than 40% of the populations, indicating large recruitment events occurred between 1998 and 2000 (Fig. 6). All of the surveys were conducted between June and September 2000, so these data suggest that *C. pica* spawns from January through June. This is supported by data collected in March 2004 at two of these sites, at which there is no evidence of a recent recruitment event (E.M., unpublished data).

Evaluation of Reintroduction Success

Although the pre-reintroduction criteria were not specifically evaluated, many of the criteria were met (Table 3). The species were not acclimatized in the field prior to full release, but they were quarantined at the Bermuda Aquarium for one-week (Bickley & Rand 1982; Wingate 1989) in tanks filled with local seawater. The choice of source population seems to be roughly based on habitat characteristics that are similar to those in Bermuda, but no extensive evaluation was done. There are no other data available on the source population, so there is no way to evaluate whether taking 89 individuals jeopardized it. The release location on Bermuda was chosen because Nonsuch Island is a nature reserve where the Bermuda Government is attempting to remove all non-native species and restore the habitat and biodiversity to that which existed prior to human settlement. The rocky intertidal in Bermuda, in general, is unsaturated, with regards to species diversity and species abundance, which includes the habitat on Nonsuch Island. The mean size of the 82 individuals released is 80.8 mm, which cooresponds with an approximate age of 4.0-4.6 years (Appendix 2), but only 71 of these survived the reintroduction (Bickley & Rand 1982). Successful recruitment was documented in 1986 (Wingate 1995).

Most post-reintroduction factors were also met (Table 3). Fishery regulations are still in place, and snail habitat is officially protected on Nonsuch and Cooper's Islands. However, illegal harvesting events suggest that the regulations and protected areas are not enforced adequately. The government issued a sign that was posted at Officer's Beach to deter illegal harvesting, and the Bermuda Aquarium, Museum, and Zoo now has a small exhibit on *C. pica*. No other ongoing community education or local employment directly related to *C. pica* has been documented. Active population monitoring began in 1986, although only a few sites are included in population surveys after 2000. In general, there has been no negative impact of the reintroduction on the local human population, and no documented change to the rocky intertidal ecosystem.

DISCUSSION

Population Structure and Expansion

The population of *C. pica* in Bermuda, following the 1982 reintroduction, has recovered successfully and expanded from Nonsuch Island, where it was released, to as far west as Sea Swept Farm and as far east as Red Hole Cove. By 2000, the population had grown from a mere 82 released individuals at one site, to nearly 4,000 individuals. Successful reproduction is evident across the island. Although illegal harvesting has occurred, there are large numbers of breeding adults present within the island-wide population. The largest concentration of individuals occurs on St. David's Island, or more specifically, on Cooper's Island, where approximately one-quarter of the whole population resides.

Officer's Beach

The population size at Officer's Beach dropped by more than half from 2000 to 2004, and the individuals greater than 50 mm almost disappeared completely by 2004. This dramatic loss of the larger individuals cannot be attributed to natural mortality and non-human predation alone. Most likely, this decline is the result of an illegal harvesting event that occurred at the site sometime between 2000 and 2004. Officer's Beach is located on the southwest coast of Cooper's Island and can be accessed fairly easily by a path through coastal scrub, making it more accessible than other sites on Cooper's Island. An illegal harvesting event on Nonsuch Island only six years after the species was reintroduced nearly eradicated the population; this motivated the Bermuda government to add *C. pica* to the local protected species list (Wingate 1995). Additional illegal harvesting events in subsequent years (Wingate 2006), including a recent event in 2011 at Hungry Bay that led to the only documented conviction of a *C. pica* poacher (K. Coates, pers. communication), suggest that this is an ongoing problem (see Chapter 1). A bilingual sign notifying visitors that *C. pica* is a fully-protected species is posted at Officer's Beach, but additional actions, such as increased enforcement, additional signage, and public education, are clearly needed.

Rocky Hole

From 2000 to 2004, the population size increased significantly at Rocky Hole, although the number of recent recruits declined dramatically. This site is located on the northeast shore of Cooper's Island where access was, until recently, difficult (see "Management Recommendations" below). The remoteness of the site could explain why it was unaffected by illegal harvesting, in spite of the large-sized individuals present. The population size was fairly steady from 2004 to 2007. Recruitment was low in 2003 (E.M., unpublished data), 2004, and 2007, which tends to coincide with hurricanes. Hurricane Fabian made landfall in 2003 and was a category three hurricane with category four wind gusts. Surveys conducted before and after this hurricane indicate a nearly complete loss of juveniles (E.M., unpublished data). In 2006, Bermuda experienced another hurricane, Hurricane Florence, but this was only a category one and passed 50-60 miles west of Bermuda. Because Rocky Hole consists mainly of loose boulders, Hurricane Fabian substantially reconfigured the habitat at the site (E.M., pers. observation), so settlement habitat declined significantly. Without additional information about settlement requirements, population connectivity, and larval retention, determining the cause in the decline in recruitment is difficult.

Turtle Bay

Over a seven-year period (2000-2007), the population size at Turtle Bay increased by nearly a factor of ten, with evidence of much higher recruitment and more than half the population represented by individuals greater than 50 mm. Turtle Bay was largely unaltered by the 2003 hurricane because the habitat consists mainly of limestone platforms and eroding limestone cliffs. If larvae indeed have less settlement habitat available at Rocky Hole, which is adjacent to and north of Turtle Bay, then more larvae remain in the water column and thus are available to settle elsewhere. In general, the currents move clockwise around the islands, which is consistent with this hypothesis. However, an investigation of finescale ocean currents around the islands is necessary to determine how larvae are mass transported from site to site.

Hungry Bay & Unused Runway

The population size at Hungry Bay (2000-2003) increased by a factor of 12 over three years, and it more than doubled at Unused Runway over four years (2000-2004). This dramatic increase was likely due to incomplete sampling of the smaller size classes in 2000, especially because the number of individuals in the larger size classes increased more than can be explained by the number of small individuals. These data are still useful to highlight an increase in large individuals at these sites, which results from increasing recruitment and survival rates. There could also be a decline in illegal harvesting, especially at Hungry Bay, which is more accessible than Unused Runway. To visit the Unused Runway site, you must travel by boat and obtain special permission to land from airport and government security. If monitored carefully, this could be useful as another long-term and protected study site, like Rocky Hole and Turtle Bay.

Was the Reintroduction a Success?

Overall, the reintroduction of *C. pica* to Bermuda is an ongoing success story. Even though the details of the reintroduction were not determined a priori, most of the criteria for success were fulfilled. The reintroduced individuals were wild-caught, which are often more successful than captive-bred individuals (Fischer & Lindenmayer 2000; Griffith et al. 1989). Individuals were released in a habitat similar to the source location, after being quarantined in tanks filled with local seawater, so acclimatization was not necessary. For reintroduced mammals, acclimatization and provisioning are important for their survival (Fischer & Lindenmayer 2000), but this trend is not apparent for birds and not evaluated for other groups. In the case of *C. pica*, provisioning is not necessary since it indiscriminately feeds on algae that covers the rocks in its habitat (Randall 1964).

The ecological and demographic characteristics of the original population in Bermuda likely reflected the unique local habitat. Compared to other suitable habitat within the geographic range for *C. pica*, Bermuda is located at the highest latitude and has, on average, cooler sea surface and air temperatures, heavy wave action along nearly all rocky coastal areas, and only carbonate rock as substrate in the rocky intertidal. Carbonate rock is also the only substrate present in the Bahamas and Turks and Caicos Islands, but most other locations have additional rock types present (see Chapter 3). The precise location of the source population is unknown, but care was taken to choose a site that experiences cooler water temperatures, similar to that in Bermuda (Wingate 1995). This careful source population choice coupled with choosing suitable habitat for the point of release, likely contributed to the success of the 1982 reintroduction, unlike the unsuccessful reintroduction attempts of 1901 and 1930. However, because Bermuda is an isolated set of islands that is about 1,300 km from the Bahamas, where the nearest *C. pica* population is located, long-term monitoring of the health of the Bermuda population is important because the probability of natural recruitment from outside of Bermuda is quite low.

No re-stocking, or release of additional individuals (Armstrong & Seddon 2008), is needed because the population is self-sustaining, one of the defining characteristics of a successful reintroduction

(Fischer & Lindenmayer 2000; Sarrazin & Barbault 1996). The population surveys provide evidence that the population reproduced successfully following the 1982 reintroduction, and continues to do so across the island. The successful reproduction of the reintroduced population indicates that there was a suitable male:female ratio and that allee effects were overcome. There is no evidence for survival of individuals that were released prior to and in 1982 off of High Point on the southshore (P. Rouja and T. Tucker, personal communication). This suggests that 71 individuals is an adequately large population size, and that the individuals released on Nonsuch Island remained in close proximity. Since their sex cannot be determined externally, the male:female ratio of the released individuals was pure chance, and luckily sufficient. Species that produce a large number of offspring tend to be more successful in reintroductions (Griffith et al. 1989), so this accidental male:female ratio and apparent high fertilization rate ensured the success of the reintroduction. The overall population size, which was nearly 4,000 individuals in 2000, produces enough gametes not only to overcome allee effects but also to provide enough successful recruits to create a population that is continually increasing.

Although the Bermuda Government did not initiate the reintroduction, it provided vital support by allowing for the release of individuals after they were quarantined and by supplying resources and personnel to conduct population monitoring. Also, the Fisheries Protected Species Order of 1989 continues to protect the species from overfishing, which is the hypothesized cause of the local extinction that occurred in the mid-1800s. However, people are becoming more aware of the presence of *C. pica* in Bermuda, which, when combined with a lack of ongoing public education, contributes to the increase in illegal harvesting (e.g., Wingate 2006; K. Coates personal communcation). This highlights the need for greater allocation of resources to not only continue monitoring recovery but also for additional enforcement and expanding community education to increase public awareness of the regulation, especially at more accessible sites. The future of *C. pica* in Bermuda depends on the continued support from the Bermuda Government.

This research highlights the importance of seeking out and accessing unpublished and governmental reports, which can provide vital information about local species. Prior to this research, there was little documentation in the scientific literature of the Bermuda reintroduction (e.g., Robertson 2003), and no detailed information about yearly fluctuations in population size, rate of population expansion, or illegal harvest events. All of the population survey data prior to 2004 were obtained from reports held by the Bermuda Government, not accessible other than through their library. Details about the timing of the local extinction were compiled from several books describing the natural history of Bermuda and accounts from the journals of early settlers. Descriptions and data on the reintroduction event of 1982 and the subsequent monitoring were documented in newsletters of the Bermuda Department of Agriculture and Fisheries and the Re-introduction Specialist Group of IUCN's Species Survival Commission (SSC). When conducting research on local conservation and fisheries management, establishing a connection with the local community and government is important not only when implementing regulations, but also when investigating the local history of the species or habitat.

Management Recommendations

The reintroduction of *C. pica* to Bermuda was successful, even though it was not planned according to more recent standards (Beck et al. 1994; Fischer & Lindenmayer 2000; Griffith et al. 1989; Kleiman et al. 1994). The species is currently full-protected in Bermuda, so no additional management regulations are needed. However, illegal harvesting is a recurring problem in Bermuda. It must be addressed through both stricter enforcement and by increasing awareness of regulations. Monitoring of the species should continue, including documentation of size, changes in population structure, and careful documentation of illegal harvesting events (Fischer & Lindenmayer 2000). If the Bermuda government plans to open the fishery in the future, a multi-faceted management plan must be implemented to attempt to prevent the species from experiencing another extinction event due to overfishing. In addition to the general *C. pica* management recommendations provided Chapter 1, the following are the recommendations specific to the Bermuda population:

Seasonal closure of the fishery

To ensure that *C. pica* are not disturbed during their spawning season, the fishery should be seasonally closed from December through July. The peak spawning season for *C. pica* in Bermuda is from January through June. The recommended closure period provides a 1-month buffer at the beginning and ending of this spawning period in case it fluctuates from year to year.

Marine protected areas (MPAs)

To protect vital source populations, even outside of the spawning season, MPAs should be established in key locations where large numbers of breeding individuals are currently located. Cooper's Island is a one such location; over 1,000 *C. pica* individuals were recorded in 2000, almost as many as were documented on all of the Main Island (~1,200). In 2008, 77 acres of land and marine habitats up to 100 meters from shore were set aside as part of the Cooper's Island Nature Reserve (Government of Bermuda 2008). Most of the island has been off-limits to the general public since the construction of the NASA base in the 1960s. The current management plan protects the rocky shore on the west side of the island, with *C. pica* targeted as the "flagship animal species" (Government of Bermuda 2008), but fails to protect two key sites on the east side of the island. Rocky Hole and Turtle Bay (on the east side) house the majority of the *C. pica* population on Cooper's Island, so these sites should be designated as protected. The east side of the island is slated for a visitor center and snorkel park, which are not in conflict with designating the coastline as protected rocky shores. Also, because this area is now open to the public – no longer fenced in and thus preventing access – additional resources should be designated to this area to continue monitoring these sensitive populations and to fund fisheries patrols to deter illegal harvesting within the park. Informational placards could also be strategically placed to alert visitors of the protection status of *C. pica* and other species within the reserve boundaries.

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Appendix 1: Site information for two island-wide surveys of *Cittarium pica* in Bermuda.

Appendix 1, Table A1.1: Site group A.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
St. George's Is.	Barry Rd. / St. George's E.	32.3847° N	64.6687° W	0	*n/a*	Madeiros (2000)	September 6, 2000
	Gates Fort / Buildings Bay	32.3789° N	64.6633° W	2	- *unknown* -	Madeiros (2000)	September 6, 2000
	St. Catherine's Pt.	32.3904° N	64.6740° W	2	- *unknown* -	Madeiros (2000)	September 6, 2000
	Whalebone Bay / Ferry Pt. Park	32.3654° N	64.7141° W	0	*n/a*	Cattell (2000); Madeiros (2000)	July 12, 2000

Appendix 1, Table A1.2: Site group B.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
Long Rock Is.	Long Rock	32.3566° N	64.6552° W	156	- *unknown* -	Madeiros (2000)	August 12, 2000
St. David's Is.	Annie's Bay	32.3568° N	64.6608° W	90	72.9	Cattell (2000); Madeiros (2000)	July 3, 2000
	Civil Air Terminal / Longbird Bridge	32.3590° N	64.7055° W	22	119.2	Cattell (2000); Madeiros (2000)	July 12, 2000
	Little Head Park	32.3704° N	64.6565° W	46	- *unknown* -	Madeiros (2000)	August 29, 2000
	Nininger Rd. Landing lights	- *unknown* -	- *unknown* -	94	- *unknown* -	Madeiros (2000)	July 3, 2000
	Perimeter Road	32.3557° N	64.6636° W	177	107.5	Cattell (2000); Madeiros (2000)	July 11, 2000
	Red Hole Cove	32.3698° N	64.6491° W	25	82.3	Cattell (2000); Madeiros (2000)	July 10, 2000
	Stonecrusher Corner	32.3597° N	64.7061° W	0	*n/a*	Cattell (2000); Madeiros (2000)	July 28, 2000
	Unused Runway	32.3544° N	64.6867° W	270	- *unknown* -	Madeiros (2000)	July 19, 2000

Appendix 1, Table A1.3: Site group C.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
Cooper's Is.	Cooper's Is. West / Nat. Res.*	32.3545° N	64.6623° W	266 / 222	115.7	Cattell (2000); Madeiros (2000)	June 20-21, 2000
	Officer's Beach & Jetty*	32.3551° N	64.6631° W	216 / 258	120.0	Cattell (2000); Madeiros (2000)	June 26-27, 2000
	Rocky Hole & Turtle Bay	32.3523° N	64.6568° W	247	131.1	Cattell (2000); Madeiros (2000)	July 5-6, 2000
	Well Bay / NASA W. coastline	32.3497° N	64.6595° W	14	117.7	Cattell (2000); Madeiros (2000)	July 4, 2000
Goat's Is.	Goat's Is. / Promontory*	32.3551° N	64.6634° W	168 / 682	114.2	Cattell (2000); Madeiros (2000)	June 27-28, 2000
Turtle Bay Is.	Turtle Bay Is.	32.3522° N	64.6564° W	3	103.6	Cattell (2000)	July 5, 2000

Appendix 1, Table A1.4: Site group D.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
Castle Harbour Islands	Charles Is.	32.3391° N	64.6703° W	19	- *unknown* -	Madeiros (2000)	September 26, 2000
	Nonsuch Is.	32.3476° N	64.6615° W	60	- *unknown* -	Madeiros (2000)	September 23, 2000
	N. Cock Rock	32.3460° N	64.6661° W	29	- *unknown* -	Madeiros (2000)	September 12, 2000
	Rushy Is.	32.3382° N	64.6729° W	11	- *unknown* -	Madeiros (2000)	September 23, 2000
	Southampton Is.	32.3429° N	64.6674° W	21	- *unknown* -	Madeiros (2000)	September 12, 2000

Appendix 1, Table A1.5: Site group E.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
Main Is.	Howard Bay W.	32.3368° N	64.6768° W	50	- *unknown* -	Madeiros (2000)	September 25, 2000
	Windsor Beach	32.3314° N	64.6886° W	2	- *unknown* -	Madeiros (2000)	September 25, 2000

Appendix 1, Table A1.6: Site group F.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
Main Is.	John Smith's Bay / Winterhaven Nat. Res.	32.3158° N	64.7151° W	55	47.6	Cattell (2000); Madeiros (2000)	June 20, 2000
	Spittal Pond Park E.	32.3126° N	64.7223° W	76	- *unknown* -	Madeiros (2000)	September 18, 2000
	Spittal Pond Park W. / Checkerboard	32.3093° N	64.7268° W	70	- *unknown* -	Cattell (2000); Madeiros (2000)	July 21, 2000

Appendix 1, Table A1.7: Site group G.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
Main Is.	Captain Williams Bay	32.2997° N	64.7440° W	76	- *unknown* -	Cattell (2000); Madeiros (2000)	June 13, 2000
	Devonshire Bay Park	32.2983° N	64.7456° W	5	- *unknown* -	Cattell (2000); Madeiros (2000)	July 13, 2000
	Grape Bay	32.2842° N	64.7654° W	146	- *unknown* -	Cattell (2000); Madeiros (2000)	July 24, 2000
	Hungry Bay	32.2883° N	64.7597° W	52	- *unknown* -	Cattell (2000); Madeiros (2000)	July 17-18, 2000

Appendix 1, Table A1.8: Site group H.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
Main Is.	Stonington / Gilbert Park	32.2753° N	64.7737° W	393	- *unknown* -	Cattell (2000); Madeiros (2000)	July 24, 2000

Appendix 1, Table A1.9: Site group I.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
Main Is.	Astwood Park	32.2608° N	64.8034° W	6	- *unknown* -	Cattell (2000); Madeiros (2000)	July 25, 2000

Appendix 1, Table A1.10: Site group J.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
Main Is.	Sinky Bay / Great Whale Pt.*	32.2485° N	64.8330° W	47 / 43	- *unknown* -	Cattell (2000); Madeiros (2000)	July 25, 2000

Appendix 1, Table A1.11: Site group K.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
Main Is.	Church Bay Park	32.2492° N	64.8476° W	195	- *unknown* -	Madeiros (2000)	September 14, 2000
	Sea Swept Farm	32.2486° N	64.8535° W	40	- *unknown* -	Cattell (2000); Madeiros (2000)	July 25, 2000

Appendix 1, Table A1.12: Site group L.

Island / Island Group	Site Name	Latitude	Longitude	Population Size	Max Size (mm)	Source	Survey Date
Cobblers Is.	Cobblers Is.	32.3079° N	64.8174° W	0	*n/a*	Madeiros (2000)	September 29, 2000
Coney Is.	Coney Is.	32.3594° N	64.7144° W	0	*n/a*	Cattell (2000); Madeiros (2000)	September 28, 2000
King's Point Is.	King's Point Is.	32.3106° N	64.8643° W	0	*n/a*	Madeiros (2000)	September 29, 2000
Main Is.	Bailey's Bay	32.3454° N	64.7317° W	0	*n/a*	Madeiros (2000)	September 28, 2000
	Gibbet's Is.	32.3236° N	64.7440° W	0	*n/a*	Madeiros (2000)	September 28, 2000
	Luke's Pond	32.2553° N	64.8731° W	0	*n/a*	Cattell (2000); Madeiros (2000)	July 25, 2000
	Walsingham Trust / Blue Hole Park	32.3478° N	64.7083° W	0	*n/a*	Madeiros (2000)	July 13, 2000
	West Whale Bay	32.2561° N	64.8741° W	0	*n/a*	Cattell (2000); Madeiros (2000)	July 25, 2000
	Wilkinson Park	32.3571° N	64.7179° W	0	*n/a*	Madeiros (2000)	June 28, 2000
	Wreck Hill	32.2820° N	64.8868° W	0	*n/a*	Madeiros (2000)	September 27, 2000

Appendix 2: Growth curve for *Cittarium pica*, compiled from cohort growth studies in the Bahamas (Bell 1992; Debrot 1990) and the Virgin Islands (Randall 1964), along with direct growth measurements from Bermuda (E. Meyer and K. A. Coates, unpublished data). The growth rates for individuals 0 to 38 mm in width are assembled from data from the literature. All other growth rates were calculated through tag-recovery studies conducted in 2003-2007 in Bermuda. The brackets denote the ages of individuals within the binned size classes used in population surveys, and the age at which the species is sexually mature. The lightest gray brackets indicate that individuals that are 0 – 10 mm in width are 1.2-1.4 years old. The darkest gray brackets indicate that individuals that are 50 mm in width or greater are 2.7-3.2 years old. *Cittarium pica* is sexually mature when it is 32-34 mm in width (Randall 1964), or 2.1-2.6 years old.