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THE FISHERY AND ECOLOGY OF CITTARIUM PICA
IN THE WEST INDIES

BY

REUBEN JAMES-ALLEN MACFARLAN

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

IN

BIOLOGICAL AND ENVIRONMENTAL SCIENCES

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2016

DOCTOR OF PHILOSOPHY
OF
REUBEN JAMES-ALLEN MACFARLAN

APPROVED:

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DEAN OF THE GRADUATE SCHOOL

ABSTRACT

Cittarium pica, the West Indian Top Shell or “whelk,” is an understudied but culturally and ecologically important intertidal gastropod in the Caribbean. The species faces overexploitation and possible extirpation in much of its range due to a confluence of factors including life-history traits, a diffuse artisanal fishery, and lack of basic scientific knowledge. The undocumented, unregulated, and unreported nature of artisanal and small-scale commercial harvesting of this species renders its study quite different from that of other more recognizable species such as conch or spiny lobster. Here I have compiled four manuscripts that address specific questions related to the ecology and fishery of whelks in contemporary, historic, and pre-historic time periods. The first chapter addresses whether there is variation in shell shape and attachment strength related to sea conditions. The second and third chapters are sequential and in chapter 3 I first decouple the contributions of harvesting and wave exposure as drivers of size and abundance of whelks. The second part of that study expands the number of sites, introduces land development as a factor and tests the confounding roles of harvesting, waves, or and development in structuring size and abundance of whelks. In the final manuscript I describe how whelks have been impacted by exploitation pressure during three different occupations of coastal people in the past 1500 years. Based on shell materials excavated from pre-Columbian and colonial era middens I rebuild present a simple time series of body size and abundance metrics to contrast with contemporary size distributions from manuscripts two and three. This collection of projects has been multidisciplinary and involved fisheries science, marine ecology, and zooarchaeological techniques. Field research was

conducted in the British Virgin Islands and Puerto Rico where intertidal surveys and experiments were performed on live whelk along with the processing of archaeological faunal remains. I found that whelks on wave-exposed shores have greater attachment strength and shorter more compact shells than on sheltered shores. I determined that access by fishers to sites was by far the most potent selective factor in structuring the size and abundance of whelks in the region and likely contributing to the general perception that the species is in decline. And in the final chapter I infer, based on the body size and abundance of whelk specimens from middens, that exploitation histories vary substantially through space and time in the archaeological record.

ACKNOWLEDGMENTS

It has been an honor and privilege to conduct a body of work and to have been guided through the process by my major Professor Dr. Graham Forrester. His patience, insight, and good humor have been exemplary. He has shaped me into a better scientist, teacher, and mentor while leading by example. My core and program committee Dr. Carlos Garcia Quijano, Dr. Peter August, Dr. Lianna Jarecki, and Dr. Tom Good have all been rather patient as I have progressed and offered me great encouragement as well as fun and challenging questions through this process. As a group my committee clearly exercised restraint and understanding. They were obviously motivated to help me find a pathway through the dissertation development phase and the overall PhD process in a positive manner. My wife is the only reason that I have been able to proceed for several years of low/no pay and at times long hours, her ability to anchor the ship and support me in this endeavor has, as a matter course, been life-changing. I would also like to thank the Forrester Lab-lab mates first and foremost Elizabeth Mclean who was invariably a couple of steps ahead of me, offering guidance and commiseration while always there to help. As well a host of undergrads need to be thanked that conducted field survey work and aided me with projects that did and did not make it into the dissertation need to be thanked. In particular Russell Dauksis and Allison Holevoet who were integral in regards to getting field and lab work done while also having a great time. My friends inside and outside academia have been nothing short of fantastic in their encouragement of my pursuit of a terminal degree, in particular Dr. Jon Lariviere who counseled me at length when I vacillated about further graduate school work before starting at URI. I

need to also acknowledge URI, the Guana Island Trust, and University of Puerto Rico Sea Grant for their support as funders and encouragers of whelk studies.

DEDICATION

I dedicate this dissertation to my family. I get to acknowledge my wife again in this section by dedicating this dissertation to her first. She inspired me by example to look beyond what I thought I could achieve and to put my head down to just “get it done”. I especially dedicate these pages and the last few years of work to my parents for whom I owe for my earliest childhood exposure to the rocky intertidal zones in New England. Importantly, because of their ability to cut the dock-lines and travel I spent several formative years floating through various marine environments around the world with my sister exploring, learning, and falling in love with plant and animal natural history field guides. Those experiences left their mark and angled the trajectory of my personal and professional lives toward salt water. Without their work ethic, encouragement, support, and open mindedness I would not be involved in the environmental and marine sciences. I also dedicate this work to my sister as a successful marine scientist and a better human being than I could ever be. Her encouragement and especially hand written notes have always motivated, and as well her love and care for the sea is particularly inspiring. My in laws, the Swongers, have also been there to listen and encourage, when I needed an ear or a positive word. As well their bottomless patience and ability to step-in to help with child-care has made the latter part of my PhD possible. And finally I dedicate this to Cyrus, Lorelei and whomever comes next in our family, I hope my work inside and outside academia has some small positive effect on the world that we eventually leave you. I promise to *dedicate* the time to inspire and encourage you to think and ask questions, and to learn

about the nature of things- whether your feet get wet or not is immaterial. So, let's go find some shells together.

PREFACE

This dissertation is in the Manuscript Format. All chapters are either published, in review, or will be submitted to peer reviewed journals.

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CHAPTER 1

Isolating The Effect of Artisanal Fishing on an Intertidal Gastropod in the Caribbean

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ABSTRACT

Small-scale fisheries in the Caribbean are important to coastal communities, but their effects on exploited populations are notoriously hard to quantify. We evaluated the effect of artisanal and recreational fishing on populations of a large tropical intertidal gastropod, *Cittarium pica* or “whelk”, in the British Virgin Islands. Whelks are argued to be the third most important marine invertebrate landed in the Caribbean following spiny lobster and queen conch. It is widely held that whelk populations are in decline from overfishing, but fishers also believe that coastal development has impacted populations. The rarity and small size of whelk on sheltered shore provides circumstantial evidence for overfishing, because sheltered shores are easy for fishers to access. It is, however, unclear whether whelk are more common and larger on exposed shores because of reduced fishing pressure in these areas, or because whelk is simply responding to a natural gradient in wave forces. By surveying sites that spanned gradients in both access by fishers and exposure to prevailing sea conditions, we found that fishing access is at least partly responsible for declines in abundance and body size on shores that are sheltered and/or easy to access on foot. Despite size-regulations and a closed season, chronic over-harvesting of whelk is occurring at some sites, and we consider possible alternative management strategies for whelk to ensure sustainable long-term exploitation.

INTRODUCTION

The fishery for *Cittarium pica* is typical of many of “S” fisheries in that it is small in scale, spatially structured, and targets a nearly sedentary organism (Orensanz et al. 2005). For many such fisheries, there are little data on the fishers themselves, landings, fishing effort, and income generated. Conventional theory developed for industrialized fisheries that are characterized by high capital investment, and harvest of mobile species over large spatial scales, may also not be applicable to their management (Orensanz et al. 2005). “S” fisheries are viewed as particularly vulnerable to overfishing, especially those concentrated on a single species in the narrow habitat space of the intertidal zone. Fishing impacts have been documented in some historical and contemporary fisheries (Kingsford et al. 1991) but, although there are many reports that whelk is being overfished, these claims are generally not substantiated (Randall 1964, Boulon et al. 1986, Toller and Gordon 2005, Arango and Merlano 2006, Jimenez 2006).

Isolating the impact of fishing is challenging because marine population may decline due to any combination of harvest pressure, human direct and indirect effects, or environmental forces (Salomon et al. 2007). For whelk, there is contrasting information in the literature on how population size structure and abundance varies across gradients of wave exposure. It has been our experience, also corroborated in the literature, that larger whelk are more abundant at sites that are hard to reach and dangerous to access, while smaller individuals dominate populations at wave-protected sites that are easier to access and near population centers (Randall 1964, Nelson and Oxenford 2012). Similar patterns have been reported for other harvested

intertidal gastropods in Australia, Africa, and the United States (Hockey et al. 1988, Keough and Quinn 1998, Shalack et al. 2011).

In Costa Rica, whelks were larger in size on an island where collecting was prohibited than at two mainland shores open to fishing (Schmidt et al. 2002 et al. 2002). In the US Virgin Islands, over-harvesting was inferred at shores based on the size structure, estimates of fishing pressure, and on previous growth studies (Randall 1964, Boulon et al. 1986). Separating the effects of fishing versus the effects of exposure to wave action was postulated by Boulon et al to be “extremely difficult” and would take repeated monitoring (Boulon et al. 1986). In the Bahamas, Debrot studied the growth, size at maturity, and population structure of whelk at exposed and protected sites and, because all of the sites were located within a marine protected area, he argued that any differences were attributable to wave exposure (Debrot 1990b). Sheltered shores typically had lower densities of larger individuals, while higher densities of smaller individuals were found on exposed shores. Assuming that there was little poaching in the reserve, Debrot postulated that predation and physical forcing were structuring populations at exposed sites, while low recruitment and low mortality shifted the population size-structure toward larger whelk at sheltered sites. These findings are similar to those of Toller and Gordon in the US Virgin Islands, but are in contrast to those of Jimenez in Puerto Rico, who found low densities of small snails on exposed shores (Debrot 1990b, Toller and Gordon 2005, Jimenez 2006). Furthermore, Jimenez found that there were high densities of small whelk at sheltered shores on Puerto Rico, which she attributed to an effect of overfishing (Debrot 1990a, Jimenez 2006).

It thus remains difficult to separate the influence of exposure to sea conditions and harvest pressure on whelk. We attempted to isolate their effects by surveying populations that span a range of exposures and a range of accessibility to fishers. We predicted that because harvesting is typically size selective, both the population density and the mean body size of whelk would be reduced at sites frequently visited by fishers.

METHODS

We chose a total of 32 sites that varied in both access and exposure in the British Virgin Islands (BVI). At each site, a transect tape was placed along the splash zone, and a combination of walking, wading, and snorkeling was used to collect all whelk across the breadth of the intertidal. Following previously established methods, we measured all shell widths using calipers and then released the snails back to the intertidal (Debrot 1990a, Randall 1964, Jimenez 2006). We chose sites that contained long stretches of continuous rocky intertidal habitat, that local experts suggested as appropriate to target whelk for harvesting and that varied in wave-exposure from sheltered bays to exposed sea cliffs. Each site was then classified based on wave exposure:

- i) Low,
 - ii) Medium, or
 - iii) High,
- and accessibility to fishers:
- i) Easy,
 - ii) Moderate, and

iii) Difficult (Figure 1).

Local fisher and non-fisher input was critical in establishing levels of fishing pressure and exposure to sea conditions during the periods that we were not actively sampling in the region. Additionally, we examined fetch length, the dominant wind direction, and speed from a NOAA data buoy, and local bathymetry, all of which contribute to the variations in relative exposure between sites. Ancillary field notes related to sea conditions, signs of fishing activity, and ease of access to a given site were recorded *in situ*.

ANALYSIS

Sites were replicated in our analyses to test the effect of fishing and wave exposure. We used four metrics to measure fishing effects on the population size structure:

- i) Mean shell width,
- ii) Maximum shell width,
- iii) The fraction of individuals that were adults, and
- iv) The fraction of individuals that were at or above legal harvestable size.

Whelk were considered adults if they were greater than 34 mm in shell width. This estimate was based on analysis of gonad structure performed in the USVI and represents the smallest sexually mature whelk found in that study (Randall 1964). Legally harvestable whelk were those with a shell width of 63.5 mm or above, because 63.5 mm is the size limit in the British Virgin Islands. To assess the effect of harvesting on population density, mean densities were calculated for all whelk above 15 mm shell width, all adults, and all those above the size limit for harvesting.

If we had been able to locate sites that represented all nine possible combinations of fishing access and wave exposure (Figure 1), we would have tested their effects using a simple two-factor analysis of variance ANOVA. We were, however, not able to sample a shoreline that was both medium exposure and difficult for fishers to access (Figure 1). To separate the effects of fishing access, we thus made a series of contrasts using one-way ANOVAs in which we held exposure constant while comparing levels of accessibility to fishers. Likewise, to separate the effects of wave exposure, we made a series of contrasts using one-way ANOVAs in which we compared levels of exposure while holding fishing access constant.

RESULTS

When wave exposure was held constant, both mean ($F_{2,23} = 13.304, p < 0.001$) and maximum ($F_{2,23} = 4.577, p = 0.021$) shell width generally increased with increasing difficulty of access to fishers (Figure 2). Similarly, at a given level of wave exposure, sites that were difficult for fishers to access contained a greater proportion of adult whelk, ($F_{2,23} = 7.002, p = 0.004$) and of legal-sized ($F_{2,23} = 13.383, p < 0.001$) whelk than sites that were easy for fishers to visit (Figure 3).

Unlike the clear effects on size structure, the effects of access on population density were more complex. There was no significant effect of access on the overall mean density of whelk ($F_{2,23} = 0.750, p = 0.483$) (Figure 4). In contrast, the density of adults increased with increasing difficulty of access to fishers ($F_{2,32} = 4.364, p = 0.025$) (Figure 4). There was a significant interaction between access and exposure on the mean density of legal sized whelk indicating interdependence ($F_{3,23} = 6.991, p = 0.002$) (Figure 4).

DISCUSSION

We were successful in decoupling the effects of fishing effort from the effects of exposure to sea conditions. Fishing access to a site had a strong effect on population size structure while both fishing access and exposure appear to influence population density. The current regulations in the BVI do not appear to be preventing overharvesting at sites that are easy to access and there was an obvious loss of large whelk to the extent that legal-sized individuals were rare or absent at accessible sites. Our results are consistent with previous work on whelk along the mainland Central American coastline (Schmidt et al. 2002 et al. 2002), but our findings expand upon that study by effectively holding wave exposure constant and examining various levels of fishing access. Our results are also consistent with the results of previous studies nearby in USVI, and Puerto Rico, where whelks tended to be smaller at sites which were wave-exposed and so also difficult for fishers to access (Toller and Gordon 2005, Jimenez 2006).

Our results clearly differed from Debrot's findings in the Bahamas, where whelk tended to be smaller on exposed shores. Because Debrot's study was conducted inside a no-take reserve, effects of predation and physical stress should account for the size structure rather than fishing pressure (Debrot 1990a). In our study, however, we found no evidence that wave exposure influenced the size-distributions of whelk.

Our communications with resource managers suggest that in different Caribbean countries whelk is managed primarily by 'input control' methods, such as size limits, closed seasons, and fishing licenses. Legal frameworks exist to regulate the fishery in several countries, but like many "S" fisheries, successfully implementing input

controls is often challenging because effort is distributed across many shorelines, there is limited institutional capacity for surveillance and enforcement, legal management instruments are sometimes unclear, and involvement of fishers in the management process is often limited. Fisheries dependent data related to the amount and size of whelk gathered by fishers, plus where and when it is caught would be invaluable but, at this time there are no known records of whelk landings from the study area. In the absence of this information, our results strongly imply that harvesting is focused in sheltered shores that are accessible on foot. A corollary is that wave-exposed, difficult to access, shorelines experience lower fishing pressure and so appear to act as de-facto reserves for whelk.

Because whelk produces planktonic larvae (Bell 1992), a key ecological question is, therefore, whether the sites that represent de-facto reserves are exporting planktonic larvae and so are replenishing more heavily fished sites (Christie et al. 2010, Harrison et al. 2012). If so, management action could involve the implementation of periodic closures of susceptible “easy” to access areas of the intertidal to allow localized recovery of stocks. This “mosaic” approach to management accounts the patchy nature of whelk’s intertidal habitat, and was suggested by Toller and Gordon (2005) for the USVI to work as a series of marine protected areas (MPAs). Despite this study’s focus on BVI, the patterns described here are likely to be repeated throughout the species range. Future research life history traits, monitoring of additional fished and un-fished sites, coupled with localized management schemes that fit within the frame-work of “S” fisheries could protect future harvest potential for whelk throughout its range.

Figures

Figure 1-1- Survey design matrix. Numbers represent a total of 32 sites that were sampled which spanned gradients in relative access by fishers and exposure to sea conditions.

<u>Fishing Access</u>	Difficult	1	No Data	8
	Moderate	8	5	4
	Easy	3	1	2
		Low	Medium	High
		<u>Exposure</u>		

Figure 1-2. Mean of average and maximum shell widths.

Figure 1-3. Mean fraction of adults and legal per m².

Figure 1-4. Mean overall whelk density, the density of legal-sized whelks, and the density of adult-sized whelks, all densities are numbers per m².

LITERATURE CITED

- Arango, A.O. and J.M.D. Merlano. 2006. Explotación, usos y estado actual de la Cigua o Burgao *Cittarium pica* (Mollusca: Gastropoda: Trochidae) en la Costa continental del Caribe colombiano. Bol. Investig. Mar. Costeras 35.
- Bell, Lori J. (1992). Reproduction and larval development of the West Indian topshell, *Cittarium pica* (Trochidae), in the Bahamas. Bulletin of Marine Science 51. 2: 250-266.
- Boulon, R.J., J. Beets, and E.S. Zullo. 1986. Long-term monitoring of fisheries in the Virgin Islands Biosphere Reserve-Research Report #13.
- Christie, M.R., B.N. Tissot, M.A. Albins, et al. 2010. Larval connectivity in an effective network of marine protected areas. PLoS ONE 5:e15715.
- Debrot, A.O. 1990a. Temporal aspects of population dynamics and dispersal behavior of the West Indian topshell, *Cittarium pica* (L.), at selected sites in the Exuma Cays, Bahamas. Bulletin of Marine Science 47:431-447.
- Debrot, A.O. (1990b). Survival, growth, and fecundity of the West Indian Topshell, *Cittarium pica* (Linnaeus), in various rocky intertidal habitats of the Exuma Cays, Bahamas.
- Harrison, H.B., D.L. Williamson, R.D. Evans, et al. 2012. Larval export from marine reserves and the recruitment benefit for fish and fisheries. Current Biology 22:1023–1028.
- Hockey, P.A.R., A.L. Bosman, and W.R. Siegfried. 1988. Patterns and correlates of shellfish exploitation by coastal people in Transkei: an enigma of protein production. Journal of Applied Ecology 25:353–363.
- Jimenez, N. (2006). Caribbean/NMFS Cooperative SEAMAP Program Whelk and Finfish Assessment.
- Keough, M.J. and G.P. Quinn. 1998. Effects of periodic disturbances from trampling on rocky intertidal algal beds. Ecological Applications 8:141–161.

Kingsford, M.J., A.J. Underwood, and S.J. Kennelly. 1991. Humans as predators on rocky reefs in New South Wales, Australia. *Marine Ecology Progress Series* 72:1-14.

Nelson, T. and H.A. Oxenford. 2012. The whelk (*Cittarium pica*) fishery of Saint Lucia: description and contribution to the fisheries sector. *Proceedings of the Gulf Caribbean Fisheries Institute* 65:61-68.

Orensanz, J.M., A.M. Parma, G. Jerez, et al. 2005. What are the key elements for the sustainability of “S-fisheries”? Insights from South America. *Bulletin of Marine Science* 76:527-556.

Randall, H.A. 1964. A study of the growth and other aspects of the biology of the West Indian topshell, *Cittarium pica* (Linnaeus). *Bulletin of Marine Science* 14:424-443.

Salomon, A.K., N.M. Tanape, Sr., and H.P. Huntington. 2007. Serial depletion of marine invertebrates leads to the decline of a strongly interacting grazer. *Ecological Applications* 17:1752-1770.

Schmidt et al. 2002, S., M. Wolff, and J.A. Vargas. 2002. Population ecology and fishery of *Cittarium pica* (Gastropoda: Trochidae) on the Caribbean coast of Costa Rica. *Revista Biologica Tropical* 50:1079-1090.

Shalack, J.D., A.J. Power, and R.L. Walker. 2011. Hand Harvesting Quickly Depletes Intertidal Whelk Populations. *American Malacological Bulletin* 29:37-50.

Toller, W. and S. Gordon. 2005. A population survey of the West Indian topshell or whelk (*Cittarium pica*) in the US Virgin Islands. SEAMAP-C: USVI Whelk Survey Final Report. Department of Planning and Natural Resources, Division of Fish and Wildlife, St. Thomas, US Virgin Islands. 55 pp.

CHAPTER 2

Dislodgement force and shell morphology vary according to wave exposure in a tropical gastropod (*Cittarium pica*)

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Running head: wave exposure and snail morphology

Abstract

Wave exposure has strong influences on population density, morphology and behaviour of intertidal species in temperate zones, but little is known about how intertidal organisms in tropical regions respond to gradients in wave exposure. We tested whether dislodgement force and shell shape of a tropical gastropod, *Cittarium pica* (Linnaeus 1758), differs among shores that vary in wave exposure. After adjusting for body size, we found that whelk from exposed shores required greater force to dislodge from the shore, had slightly larger opercula (the closure to the shell aperture), and were slightly squatter in shape (reduced in shell height relative to shell width) than whelk from sheltered shores. These morphological adjustments are consistent with those observed in temperate gastropods, which may represent adaptive responses to the risk of mortality associated with dislodgement.

Introduction

Rocky shores have been an excellent venue for testing hypotheses about organismal responses to gradients in physical conditions. Differences between shores in wave exposure influence the distribution and abundance of intertidal species, and also induce changes in their morphology and behaviour (Denny 2006, Menge and Sutherland 1976, Menge and Sutherland 1987). These adjustments may be either direct responses to the risk of dislodgement by waves, or indirect responses to other factors that covary with wave exposure, such as predation (Boulding 1990, Boulding et al. 1999).

Research on temperate gastropods provides some of the best evidence for morphological changes across gradients of wave exposure. In several species, gastropods from exposed shores have shells that are squatter (reduced height for a given length) than those on sheltered shores, which is postulated to be a direct response to wave forces because it reduces the projected surface area perpendicular to the shore (Trussell et al. 1993) and so reduces the drag forces experienced when waves wash across the shore (Hollander and Butlin 2010, Trussell and Etter 2001).

Populations on exposed shores also have a larger foot muscle and a larger aperture (the opening in the shell through which the foot protrudes) for a given body size than those on sheltered shores (Hollander and Butlin 2010, Trussell and Etter 2001). A larger foot muscle is also argued to be a direct response to wave exposure because it is one of the factors that increases the wave force required to dislodge the snail from the shore (Trussell 1997a). Indirect responses include morphological adjustments to the risk of predation for example crab predation has been found to covary with wave

exposure (Palmer 1990, Seeley 1986). Crabs typically consume snails by using their claws to crush or break the snail's shell, so snails on sheltered shores often have shells that are thicker and differ in shape from those on exposed shores (Boulding, Holst and Pilon 1999, Good 2004, Hollander and Butlin 2010, Kitching and Lockwood 1974, Trussell and Etter 2001, Trussell, Johnson, Rudolph and Gilfillan 1993).

Most studies testing how intertidal organisms respond to gradients in physical conditions have been done in temperate locations (Bertness 1981, Good 2004). Early work on wave exposure on tropical shorelines was influenced by the assumption that these are physically benign environments (Brosnan 1992, Menge and Lubchenco 1981) and, perhaps for that reason, little is known about how intertidal organisms in tropical regions respond to gradients in wave exposure (Vermeij 1973). We tested effects of wave exposure on a large herbivorous intertidal gastropod, *Cittarium pica* (Linnaeus 1758), the West Indian topshell. *Cittarium pica* occurs on rocky shores throughout the Caribbean (Clench and Abbott 1943, Robertson 2003), and populations differ in density, size-distribution, growth and survival across wave exposure gradients (Debrot 1990a, Debrot 1990b). There are thus potentially direct effects of wave exposure on shell morphology, plus indirect responses to a suite of human and natural predators (Debrot 1990a). *Cittarium pica* is collected extensively by humans for food, and fishing pressure covaries with wave exposure because of the increased difficulty and danger of collecting on wave-exposed shores.

The potential effect of differing selective pressures on exposed and protected shores depends in part on the extent of migration and genetic exchange between populations. Potential effects should be greatest for those gastropods with direct development and

lowest for those species with a long pelagic larval stage that increases the potential for the intermixing of offspring among geographically separated populations. *Cittarium pica* produces larvae that are pelagic for only a few days (Bell 1992), so although larval exchange among sites occurs and DNA sequence variation indicates some connectivity among populations a few hundred kilometres apart (Díaz-Ferguson et al. 2010), the potential for local adaption in *C. pica* is perhaps greater than for species with a long pelagic stage.

We tested the general hypothesis that dislodgement force and shell shape of *C. pica* differs among shores that vary in wave exposure. If wave exposure in the tropics has effects on snail morphology similar to those reported on temperate shores, we expect snails on exposed shores to have features likely to reduce drag and increase the force required to dislodge them. We therefore predicted that, after adjusting for body size, *C. pica* from exposed shores would have: (1) greater dislodgement force, (2) larger opercula (the closure to the shell aperture, a proxy for foot size), and (3) reduced shell height relative to *C. pica* from sheltered shores.

Methods

Study sites

We studied *Cittarium pica* on nine shores around Guana Island, British Virgin Islands (BVI), plus two other BVI sites (Carval Rock and Brandywine Bay). These sites were selected because they provide a strong gradient in wave exposure while being relatively inaccessible to fishing (Table 2-I, Fig. 2-1). We combined several pieces of information to classify shores in terms of relative wave exposure (Ballantine 1961).

We assumed that exposure to waves was a function of fetch, prevailing wind direction, and nearshore topographical features that affect wave forces (shoreline curvature, water depth and slope of the seabed) (Denny 1995, Helmuth and Denny 2003a). Our classification was based on prevailing conditions, including the winter period of elevated wave heights, but does not account for intermittent summer hurricanes whose directional pattern of impacts is little known. The four exposed shores are all steep rocky walls, adjacent to deep water, with high fetch length and face the prevailing winds. The two intermediate shores also have high fetch length and are exposed to prevailing winds, but are shallower in slope and adjacent to shallow reefs that dissipate wave energy. The three sheltered shores are shallow in slope, adjacent to shallow water and are in leeward-facing bays.

On five shores, we also installed maximum wave force dynamometers ($n = 4$ per shore) for 30 days in each of July 2000 and July 2004 (Carrington Bell and Denny 1994). Because the expected range of applied wave force was unknown, the dynamometers at each site were fitted with two types of spring that required differing amounts of force to maximally extend the spring (2 low-force, and 2 high-force dynamometers per site). We found that the wave forces measured were in accord with our exposure classification (Table 2-I), and with wave forces measured at some of the same sites by Good (2004).

Measuring dislodgement force and shell shape

To measure the force required to dislodge *Cittarium pica* from the shore, we sampled individuals greater than 20 mm in shell width that were encountered during daytime low tides, and were positioned on bare rock above water (Table 2-I). Suitable *C. pica*

were approached carefully and first tapped on the shell, because this caused them to visibly withdraw their mantle and move their shell towards the substratum, so presumably standardizing their attachment (Etter 1988, Prowse and Pile 2005, Trussell 1997a, Trussell, Johnson, Rudolph and Gilfillan 1993). We used spring scales to measure dislodgement force to the nearest 1 N (Arbor Scientific, 10N, 20N or 50N Push-Pull Spring Scales). The spring was attached to a line (3 mm diam.) with a sliding loop at its end, so that the loop tightened when pulled. The loop was placed over the shell and pulled snug around the base of the shell where it met the substratum. The scale was then pulled upward in a direction roughly 45° to the shore, and we recorded the scale reading (N) when the *C. pica* became detached (Miller 1974, Prowse and Pile 2005).

To assess differences in shell shape among shores, we measured three shell dimensions using callipers: shell length, shell height (sensu Trussell, Johnson, Rudolph and Gilfillan 1993), and operculum length (sensu Chiu et al. 2002). Operculum length was measured as a rough proxy for foot area (Supplementary material: Fig. 2-SI). We originally intended to measure foot area directly, but *C. pica* are slow to extend their foot when picked up for measurement, making it too time-consuming to obtain a large sample of foot size measurements in the field (Fig. 2-SI). Shell length, shell height, and operculum length were measured using *C. pica* that were removed to measure dislodgment force, and by making additional collections. Additional collections were made on foot at low tide and on snorkel at high tide, during both day and night, to obtain samples of *C. pica* spanning the size-range present (Table 2-I).

Analysis

We used ANCOVA to test whether dislodgement force and shell shape varied among sites, after confirming that data met the assumptions of normality and homoscedasticity. Our analysis focused on how dislodgement force, shell height and operculum length changed relative to shell length (a measure of absolute body size). The full ANCOVA model included terms for the effect of (1) wave exposure - a fixed categorical factor with 3 levels (protected, intermediate, and exposed), (2) site - a random categorical factor nested within wave exposure, (3) shell length - a covariate in order to control for the effect of overall body size, and (4) the interaction between wave exposure and shell length. When differences between sites, and the interaction between exposure and shell length, were non-significant ($p > 0.1$) they were removed from the model to allow more powerful tests for the main effect of exposure (Quinn and Keough 2002).

Results

Dislodgement force changes with wave exposure

The ANCOVA revealed a significant exposure by shell length interaction (ANCOVA, $F(2,103) = 5.20$, $P = 0.0007$; Table 2-SI). Inspection of the data suggests that the interaction arose because the relationship between body size and dislodgement force was steepest on exposed shores, shallowest on protected shores, and intermediate on shores that were intermediate in wave exposure (Fig. 2-2a). The magnitude of difference in dislodgement force between sheltered and exposed shores thus increased

with increasing body size and, for larger *Cittarium pica*, was substantial (e.g. at 60 mm in shell length, whelks from exposed shores took more than twice as much force to dislodge as those from sheltered shores; Fig. 2-2a)

Operculum length changes with wave exposure

The slope of the relationship between shell length and operculum length was unaffected by wave exposure (ANCOVA, $F(2,214) = 1.04$, $P = 0.964$), and did not differ among sites (ANCOVA, $F(4,214) = 3.53$, $P = 0.181$) (Table SII). With these non-significant terms removed, the ANCOVA indicated that operculum length varied according to wave exposure (ANCOVA, $F(2,220) = 6.84$, $P = 0.001$). *Cittarium pica* from exposed shores had larger opercula than those from both other types of shore (marginal mean $\pm$ 95%CI: exposed = 24.1 ± 0.4 mm; intermediate = 23.0 ± 0.5 mm; sheltered = 23.2 ± 0.3 mm; Fig. 2-2b). The difference in operculum length between sheltered and exposed shores was, however, slight (mean operculum length differed by a factor of 1.1; Fig. 2-2b).

Shell height changes with wave exposure

After removing the non-significant interaction term (ANCOVA, $F(2,426) = 1.58$, $P = 0.149$), the ANCOVA revealed that *Cittarium pica* varied in shell height depending on wave exposure (ANCOVA, $F(2,426) = 7.85$, $P < 0.0004$; Fig. 2-2c; Table 2-SIII).

Within each wave exposure category, shell height also differed among individual shores (ANCOVA, $F(5,428) = 5.83$, $P < 0.001$; Table 2-S3). Comparison of marginal mean shell heights showed that average shell height progressively increased with decreasing exposure (marginal mean $\pm$ 95%CI: exposed = 30.2 ± 0.6 mm; intermediate = 31.9 ± 0.7 mm; sheltered = 33.2 ± 0.4 mm), but the difference in shell

height between sheltered and exposed shores was slight (mean shell height differed by a factor of 0.96; Fig. 2-2c).

Discussion

Our results suggest that *Cittarium pica* displays a combination of features that are correlated with wave exposure in a manner qualitatively similar to correlations previously described for several temperate species. For example, like *C. pica*, *Littorina obtusata* (Linnaeus, 1758) and *Nucella lapillus* (Linnaeus, 1758) from exposed shores were harder to dislodge than those from sheltered shores (Etter 1988, Kitching et al. 1966, Trussell 1997a), which may reduce the probability of being ripped from the shore by the high water velocities and acceleration experienced on wave-exposed shores (Trussell 1997b). However, for *C. pica*, the magnitude of difference in dislodgement force between sheltered and exposed shores increased with increasing body size. Larger *C. pica* are thus disproportionately affected by wave forces which is in contrast to studies of *N. lapillus* or *L. obtusata* which have shown isometric scaling of body-size and dislodgement forces (Etter 1988, Kitching, Muntz and Ebling 1966, Trussell 1997a).

Like *C. pica*, several temperate gastropods have squatter shells on exposed shores than on protected shores, which can reduce drag (Branch and Marsh 1978, Grenon and Walker 1981, Kitching and Lockwood 1974, Trussell 1997b, Trussell, Johnson, Rudolph and Gilfillan 1993, Warburton 1976). Increased operculum length on exposed shores is also a possible response to wave forces because the size of the operculum, and the aperture it covers (Chiu et al. 2002), are both proxies for foot size

(Atkinson and Newbury 1984, Etter 1988, Heller 1976, Kitching 1976) and relative foot size is one of the factors controlling dislodgement force in temperate gastropods (Trussell 1997a). Future analyses should thus test directly whether the changes in dislodgement force and shell shape we documented actually reduce the magnitude of drag forces experienced and lower *C. pica*'s probability of dislodgement in nature.

Greater dislodgement force of *C. pica* on wave exposed shores is plausibly a direct response to the higher wave forces experienced at those sites, but is also a potential adaptation to reduce the risk of capture by two of its many predators - humans and octopuses. In some temperate systems, predatory crabs are excluded from wave exposed shores and so prey morphology is influenced by the combination of high wave forces on exposed shores and high predation risk on sheltered shores (Palmer 1990, Seeley 1986). Humans have been preying on *C. pica* for at least 1,000 years, and fishing activity is concentrated on sheltered shores because of the difficulty and danger associated with collecting amidst breaking waves. Although *C. pica* are much more likely to encounter human predators on sheltered shores, the difficulty of fishing amidst crashing waves means that large *C. pica* are more likely to survive attempts to pull them free of the shore at wave exposed sites (based on our own experience, and interviews with over 100 *C. pica* collectors). Octopuses must also pull *C. pica* from the rock surface to consume them, but how wave exposure affects the density, size-distribution, and foraging activity of octopuses is largely unknown. Human predation is thus a possible agent of selection for increased dislodgement force on wave exposed shores, but the effect of octopus predation remains to be determined.

Whether the impacts of *C. pica*'s other predators covary with wave exposure is largely unstudied. *Cittarium pica* is consumed by a diverse group of predators, including dogwhelks, octopuses, oystercatchers, lobsters and various fishes (Robertson 2003). The density of predatory dogwhelks was not associated with wave exposure on Guana Island (Good 2004), but in the Bahamas was highest on exposed shores (Debrot 1990a, Debrot 1990b), so generalizations about their distribution require further study. We know little about how the distribution and foraging of other *C. pica* predators, such as oystercatchers, lobsters and fishes, varies with wave exposure on tropical shores. It would thus be valuable to test whether the combined densities of *C. pica*'s predators follows gradients in wave exposure in a predictable fashion and might exert selective pressures on shell shape. We can then test whether the influence of predators has a different pattern of covariation with wave exposure to that reported on temperate shores.

Although preliminary, our work casts doubt on early assumptions that tropical intertidal habitats are physically benign, and suggests further analysis of tropical gastropods is warranted. In order to develop a better understanding of differences between temperate and tropical shores, future analyses should aim towards replicated phylogenetically controlled comparisons (e.g. Vermeij and Williams 2007) of the magnitude of wave forces, and associated morphological changes, experienced by tropical and temperate species.

Figures

Figure. 2- 1. Map of study sites. See Table 2-1 for site names that correspond to each site number.

Fig. 2-2. Relationships between whelk body size (shell length mm) and (a) force needed to dislodge individuals from the shore (N), (b) operculum length (mm) and (c) shell height (mm). whelks are grouped by wave exposure at their site of origin and regression lines were fit to each group using ANCOVA.

Table 2-1. List of study sites grouped by relative wave exposure. Site numbers correspond to the map of study sites (Fig. 1). Also shown are mean dynamometer readings for four sites (with standard errors) and the sample size by site for each of the response variables (dislodgement force, shell height and operculum length).

Wave exposure		Dynamometer force (N)		Dislodgement force (N)	Shell height (mm)	Operculum length (mm)
Site # and name						
		Mean	(SE)		Sample sizes (n)	
Exposed						
1	Long Point*	-	-	5	26	23
2	Grand Central	-	-	-	51	43
3	Carval Rock	-	-	-	63	-
4	Grand Ghut	-	-	10	-	-
Intermediate						
5	North Beach East	8	(1.5)	31	30	12
6	North Beach West	4.6	(0.9)	28	58	24
Sheltered						
7	Harris Ghut	3.9	(0.3)	14	33	12
8	White Bay	3.8	(0.2)	24	136	70
9	Brandywine Bay	-	-	-	40	40

* At Long Point, four dynamometers were installed but all disappeared. We suspect this occurred because the wave forces were too great for the dynamometer design used.

Table 2-S1. Final ANCOVA table testing treatment effects on dislodgement force.
Model $r^2 = 0.69$.

i) Full Model

Source	SS	df	MS	F	P
Shell length	3309	1	1092	96.7	<0.001
Wave exposure	111.6	2	55.8	1.6	0.201
Wave exposure x Shell length	357.2	2	178.6	5.2	0.007
Site (Wave exposure)	207.9	3	69.3	2.0	0.115
Error	478.6	214	2.24		

ii) Final model, after removal of NS site(wave exposure) term.

Source	SS	df	MS	F	P
Shell length	3485	1	3485	6.2	<0.001
Wave exposure	153.2	2	76.6	2.2	0.119
Wave exposure x Shell length	434.3	2	217.1	6.2	0.003
Error	3732	106	35.2		

Table 2-S2. ANCOVA table testing treatment effects on operculum length. Model $r^2 = 0.98$.

i) Full model

Source	SS	df	MS	F	P
Shell length	3.73	2	1.87	0.83	0.436
Wave exposure	3611	1	3611	1614	<0.001
Wave exposure x Shell length	0.17	2	0.08	0.04	0.964
Site (Wave exposure)	14.13	4	3.53	1.58	0.181
Error	478.6	214	2.24		

ii) Final model, with non-significant effects of Site (Wave exposure) and Wave exposure x Shell length removed

Source	SS	df	MS	F	P
Shell length	14901.2	1	14901	6641.6	<0.001
Wave exposure	30.71	2	15.35	6.84	0.001
Error	493.5	220	2.24		

Table 2-S3. ANCOVA table testing treatment effects on shell height. Model $r^2 = 0.97$

i) Full model

Source	SS	df	MS	F	P
Shell length	18720	1	18720	3223	<0.001
Wave exposure	91.2	2	45.6	7.85	<0.001
Site (Wave exposure)	22.2	2	11.1	1.91	<0.001
Wave exposure x Shell length	386.9	5	77.3	13.3	0.149
Error	2474.1	426	5.808		

ii) Final model, with non-significant effects of Wave exposure x Shell length removed

Source	SS	df	MS	F	P
Shell length	287566	1	28756	4930.2	<0.001
Wave exposure	810.2	2	405.1	69.4	<0.001
Site (Wave exposure)	376.2	5	75.2	12.9	<0.001
Error	2496.3	428	5.83		

Figure 2-S1. Relationship between foot surface area (mm²) and operculum length (mm).

Measurements were made using whelks collected from two sites, North Beach East (n = 12) and White Bay Dock (n = 15). Operculum length was measured using calipers, as described in the Methods section. Whelks were then placed in a clear Plexiglass aquarium that was half full with running seawater. Foot surface area was measured once the whelk extended its foot and was attached to the aquarium wall, above the water line. The whelk was tapped lightly on its shell, which caused it to withdraw its mantle and move the shell towards the substratum, and presumably standardized its attachment (Etter 1988, Prowse and Pile 2005, Trussell 1997a). We then photographed the foot through the clear aquarium wall, with a ruler in the image for scale, and calculated foot surface area from the scaled image (using ImageJ). The plotted regression function is $y = 8x^{1.8}$ ($r^2 = 0.96$).

Bibliography: [PA1]

Atkinson WD, Newbury SF. 1984. The adaptations of the rough winkle, *Littorina rudis*, to desiccation and to dislodgement by wind and waves. *Journal of Animal Ecology* 53:93-105.

Ballantine WJ. 1961. A biologically-defined exposure scale for the comparative description of rocky shores. *Field Studies Journal*, Vol. 1.3: 1-19.

Bell LJ. 1992. Reproduction and larval development of the West Indian topshell, *Cittarium pica* (Trochidae), in the Bahamas. *Bulletin of Marine Science* 51:250-266.

Bertness MD. 1981. Predation, physical stress, and the organization of a tropical rocky inter-tidal hermit crab community. *Ecology* 62:411-425.

Boulding EG. 1990. Are the opposing selection pressures on exposed and protected shores sufficient to maintain genetic differentiation between gastropod populations with high intermigration rates? In: *Progress in Littorinid and Muricid Biology*. Netherlands: Springer, p 41-52.

Boulding EG, Holst M, Pilon V. 1999. Changes in selection on gastropod shell size and thickness with wave-exposure on northeastern pacific shores. *Journal of Experimental Marine Biology and Ecology* 232:217-239.

Branch GM, Marsh AC. 1978. Tenacity and shell shape in six *Patella* species: Adaptive features. *Journal of Experimental Marine Biology and Ecology* 34:111-130.

Brosnan DM. 1992. Ecology of tropical rocky shores: plant-animal interactions in tropical and temperate latitudes. In: D M John, S J Hawkins, and J H Price, ed's *Plant Animal interactions in the marine benthos*. Clarendon Press, Oxford, p Pages-101–131.

Carrington Bell E, Denny MW. 1994. Quantifying “wave exposure”: a simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology* 181:9-29.

Chiu Y-W, Chen H-C, Lee S-C, Chen CA. 2002. Morphometric analysis of shell and operculum variations in the viviparid snail, *Cipangopaludina chinensis* (Mollusca: Gastropoda), in Taiwan. *Zoological Studies-Taipei* 41:321-331.

Clench WJ, Abbott RT. 1943. The genera *Gaza* and *Livona* in the western Atlantic. *Johnsonia: Monographs of the marine mollusks of the Western Atlantic* 1.

Debrot AO. 1990a. Survival, growth, and fecundity of the West Indian topshell, *Cittarium pica* (Linnaeus), in various rocky intertidal habitats of the Exuma Cays, Bahamas. *The Veliger* 33:363-371.

- Debrot AO. 1990b. Temporal aspects of population dynamics and dispersal behavior of the West Indian topshell, *Cittarium pica* (L.), at selected sites in the Exuma Cays, Bahamas. *Bulletin of Marine Science* 47:431-447.
- Denny M. 1995. Predicting Physical Disturbance: Mechanistic Approaches to the Study of Survivorship on Wave-Swept Shores. *Ecological Monographs* 65:371-418.
- Denny MW. 2006. Ocean waves, nearshore ecology, and natural selection. *Aquatic Ecology* 40:439-461.
- Díaz-Ferguson E, Haney R, Wares J, Silliman B. 2010. Population Genetics of a Trochid Gastropod Broadens Picture of Caribbean Sea Connectivity. *PLoS ONE* 5:e12675.
- Etter RJ. 1988. Asymmetrical developmental plasticity in an intertidal snail. *Evolution*:322-334.
- Good TP. 2004. Distribution and Abundance Patterns in Caribbean Rocky Intertidal Zones. *Bulletin of Marine Science* 74:459-468.
- Grenon JF, Walker G. 1981. The tenacity of the limpet, *Patella vulgata* L.: An experimental approach. *Journal of Experimental Marine Biology and Ecology* 54:277-308.
- Heller J. 1976. The effects of exposure and predation on the shell of two British winkles. *Journal of Zoology* 179:201-213.
- Helmuth B, Denny MW. 2003. Predicting wave exposure in the rocky intertidal zone: Do bigger waves always lead to larger forces-9. *Limnology and Oceanography* 48:1338-1345.
- Hollander J, Butlin RK. 2010. The adaptive value of phenotypic plasticity in two ecotypes of a marine gastropod. *Bmc Evolutionary Biology* 10:333.
- Kitching JA. 1976. Distribution and changes in shell form of *Thais* spp.(Gastropoda) near Bamfield, BC. *Journal of Experimental Marine Biology and Ecology* 23:109-126.
- Kitching JA, Lockwood J. 1974. Observations on shell form and its ecological significance in thaisid gastropods of the genus *Lepsiella* in New Zealand. *Marine Biology* 28:131-144.
- Kitching JA, Muntz L, Ebling FJ. 1966. The Ecology of Lough Ine. XV. The Ecological Significance of Shell and Body Forms in *Nucella*. *The Journal of Animal Ecology* 35:113.
- Linnaeus C. 1758. *Systema Naturae*, Ed. 10, Vol. 1. 824 pp. Salvii, Holmiae.

Menge BA, Lubchenco J. 1981. Community Organization in Temperate and Tropical Rocky Intertidal Habitats: Prey Refuges in Relation to Consumer Pressure Gradients. *Ecological Monographs* 51:429-450.

Menge BA, Sutherland JP. 1976. Species Diversity Gradients: Synthesis of the Roles of Predation, Competition, and Temporal Heterogeneity. *The American Naturalist* 110:351-369.

Menge BA, Sutherland JP. 1987. Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment. *The American Naturalist* 130:730-757.

Miller SL. 1974. Adaptive design of locomotion and foot form in prosobranch gastropods. *Journal of Experimental Marine Biology and Ecology* 14:99-156.

Palmer AR. 1990. Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). In: *Progress in Littorinid and Muricid Biology*. Netherlands: Springer, p 155-182.

Prowse TAA, Pile AJ. 2005. Phenotypic homogeneity of two intertidal snails across a wave exposure gradient in South Australia. *Marine Biology Research* 1:176-185.

Robertson R. 2003. The edible West Indian “whelk” *Cittarium pica* (Gastropoda: Trochidae): Natural history with new observations. *Proceedings of the Academy of Natural Sciences of Philadelphia* 153:27-47.

Seeley RH. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. *Proceedings of the National Academy of Sciences* 83:6897-6901.

Trussell GC. 1997a. Phenotypic plasticity in the foot size of an intertidal snail. *Ecology* 78:1033-1048.

Trussell GC. 1997b. Phenotypic selection in an intertidal snail: effects of a catastrophic storm. *Marine Ecology Progress Series* 151:73-79.

Trussell GC, Etter RJ. 2001. Integrating genetic and environmental forces that shape the evolution of geographic variation in a marine snail. *Genetica* 112:321-337.

Trussell GC, Johnson AS, Rudolph SG, Gilfillan ES. 1993. Resistance to dislodgment-Habitat and size-specific differences in morphology and tenacity in an intertidal snail. *Marine Ecology-Progress Series* 100:135-144.

Vermeij G. 1973. Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. *Marine Biology* 20:319-346.

Vermeij GJ, Williams ST. 2007. Predation and the geography of opercular thickness in turbinid gastropods. *Journal of Molluscan Studies* 73:67-73.

Warburton K. 1976. Shell form, behaviour, and tolerance to water movement in the limpet *Patina pellucida* (L.) (Gastropoda: Prosobranchia). Journal of Experimental Marine Biology and Ecology 23:307-325.

CHAPTER 3

Testing the relative effects of coastal development, fishing and wave exposure on the population structure of an intertidal snail

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Abstract

Harvested marine species can vary in size and abundance for several reasons, which makes isolating the impact of fishing a difficult problem. These difficulties are increased for small-scale fisheries that are subject to little formal scientific study. Here we link artisanal fishing and the variation in size distribution and abundance of a Caribbean rocky intertidal gastropod, *Cittarium pica* –West Indian Top Shell or “whelk.” The species is a nearly sedentary intertidal grazing gastropod that has been fished in the region for thousands of years. Although the species is believed to vary in size and abundance based on exposure to sea conditions, declines in the fishery are typically blamed on a long history of overharvesting. Fishers, however, point to pollution and coastal development as negatively affecting whelk populations, and some ecological surveys suggest that whelk populations are influenced by wave exposure. Wave exposure, fishing pressure, and anthropogenic development of coastal lands often covary across sites, therefore we surveyed 75 shoreline sites chosen so that we could isolate the relative effects of these factors. Our results substantiate the often inferred, but unconfirmed, belief that there is a significant effect of fishing pressure that shifts the size-distribution towards smaller individuals and reduces the density of large individuals. We did not, however, detect an effect of either exposure or development on the size distribution of whelks, and none of the factors had a consistent effect on overall whelk densities.

Introduction:

Background

Small-scale fisheries (SS fisheries) (*sensu* Allison and Ellis 2001) are an important, though poorly quantified, component of the world's fisheries, especially in developing countries where coastal communities rely on fishing for food security as well as income (Andrew et al. 2007, Béné 2003, Berkes et al. 2001). Small-scale fisheries are also considered highly vulnerable to overfishing because most are concentrated in near-shore easily accessible habitats (Orensanz et al. 2005). Compounding the difficulty of sustaining these fisheries is that resources to assess and manage them are often limited or absent. For scientists, simply measuring the effect of fishing can be difficult because basic data on the harvested population, or levels of catch and effort are often unavailable (Johannes 1998).

With the aim of improving SS fisheries, there is a growing advocacy to study and manage them using an ecosystem-based approach (Andrew et al 2007, Béné, Hall, Allison, Heck and Ratner 2007). This further complicates the diagnosis of SS fisheries because it places the harvested population in a broader context and acknowledges likely influences of other human activities and natural forces (Andrew and Evans 2009). Isolating the impact of fishing thus becomes more difficult because marine populations may decline due to any combination of harvest pressure, other human-derived impacts, and natural environmental forces (Salomon et al. 2007). Although challenging, there is substantial ecological evidence for the cumulative and interactive effects of multiple stressors on marine populations (Claudet and Fraschetti 2010, Crain et al. 2008, Piggott et al 2015), making it important to test the impacts of fishing relative to those of other factors.

Study system

Here we address the challenging issue of testing the effect of SS fishing in a little-studied system, while at the same time isolating the influence of other human activities and natural factors. As a test case, we studied the fishery for *Cittarium pica* (Linnaeus 1758), a large (maximum size ~130mm) herbivorous gastropod found in the rocky intertidal and shallow subtidal zones from mainland coastlines in northern South America, Central America, and the wider Caribbean (Clench and Abbott 1943,

Robertson 2003). *Cittarium pica* has many common names in different parts of its range; we will use “whelk,” one of the widely used English names. Whelk fishing is a typical “s fishery” (Orensanz et al 2005) because, alongside the usual features of a small-scale fishery, it targets a species whose adults are sedentary and form spatially-structured populations that are connected by a dispersing larval stage (Defeo and Castilla 2005).

Whelks are reported to be harvested widely and intensively for sale and for personal consumption throughout their range (Bell 1992, Debrot 1990, Jimenez 2006, Osorno Arango et al 2006, Randall 1964) but the nature and amount of harvesting has been little studied. Like many species targeted by small-scale fisheries, none of the countries occupied by whelks collects systematic landings data and the status of whelk populations is not well documented. There are published surveys of whelk abundance and size-distributions from the Bahamas (Debrot 1990a,b), U.S. Virgin Islands (USVI) (Randall 1964), Costa Rica (Schmidt et al. 2002 et al. 2002), and Colombia (Osorno et al. 2006, Rosique et al. 2010), plus unpublished surveys from USVI (Toller and Gordon), Puerto Rico (PR) (Jimenez 2006), and British Virgin Islands (BVI) (Forrester unpubl.). The rarity or absence of larger individuals from many sites has long been interpreted as the effect of over-harvesting (Arango and Merlano 2006, Clench and Abbott 1943, Randall 1964, Robertson 2003, Rosique et al 2010), as is the complete disappearance of whelks from Bermuda and Florida (Rhyne et al. 2009, Robertson 2003, Walker 1994). Putative unharvested populations used as “benchmarks” for this interpretation come from surveys of whelks in a remote, little-populated, area in the Bahamas (Debrot 1990a,b), and from surveys inside a Costa Rican reserve (Schmidt et al. 2002). It is, however, important to note that neither study provided direct evidence that “benchmark” sites were unfished and, more generally, there is no direct evidence linking harvesting rates to the status of whelk populations.

In addition to fishing, whelks are potentially impacted by several other human activities and natural factors. In the intertidal zone, reviews have documented impacts of invasive species, trampling, episodic pollution from events like oil spills, plus chronic pollution and sedimentation usually associated with urbanization or

agriculture (Crowe et al. 2000). These impacts are virtually unstudied in the region occupied by whelks (but see Nagelkerken and Debrot 1995, Strand et al. 2009), but we investigated the impact of coastal development because it was identified as the key cause of whelk declines by fishers themselves (Forrester unpubl., Nelson 2012). Of the environmental influences on intertidal communities, we focused on wave exposure because it creates a strong stress gradient among shores with pervasive effects on intertidal communities (Connell 1972, Menge and Sutherland 1976). Like many intertidal species, whelks display striking shifts in size-distribution and population density across wave exposure gradients (Debrot 1990b, Jimenez 2006, Toller and Gordon 2005)

Objective

We tested the relative effects of fishing, coastal development and wave exposure on whelk populations. Separating the combined effect of multiple stressors is problematic, particularly in cases like this where experimental manipulations are impractical or unrealistic. Because adult whelks are sedentary, we used a spatial survey for which shoreline sites were replicates. Perhaps the biggest challenge in adopting this approach arises from covariation of wave exposure, urbanization, and fishing pressure in nature. For example, heavy wave action directly impacts intertidal species by increasing the risk of dislodgement, but similar risks apply to fishers attempting to collect amidst crashing waves, and so we also expect reduced fishing pressure at wave-exposed sites. Furthermore, where land development is concentrated there are usually also more people, so coastal urbanization often increases both pollution and local fishing pressure. We attempted to solve this problem by seeking out sites that were subject to differing combinations of these three stressors.

Methods

Surveying whelk populations

We surveyed whelk populations at 75 rocky intertidal sites in the USVI, BVI, and PR (Figure 3-1). Each site comprised > 120 m of continuous rocky shoreline habitat suitable for whelks, and was separated from other sites by > 500 m of coastline that was unsuitable habitat (sand or gravel). Following established methods, we

sampled transects ($n \geq 3$ per shore) than were 30 m long horizontally and extended vertically from the upper intertidal zone to ≈ 2 m subtidal (Debrot 1990a, Jimenez 2006, Macfarlan et al. 2014, Randall 1964, Toller and Gordon 2005). Depending on shoreline topography, we combined walking, wading, climbing, and snorkeling to collect whelks. We used calipers to measure shell width (in mm) as an index of body-size and age, and then released all whelks immediately (Boulon et al. 1986, Debrot 1990b, Randall 1964). Because small whelks are cryptic and cannot be accurately sampled using large transects, we excluded whelks ≤ 15 mm shell width (age-0). Though whelks ≤ 15 mm were excluded, we still sampled most of the population because whelks typically mature at age-2 (≈ 32 mm), cannot be legal harvested until 63 mm ($\approx$ age 5), and can reach 130 mm (Randall 1964, Jimenez 2006). Sites were replicates in all analyses and the dependent variables were: (i) mean shell width, (ii) maximum shell width and (iii) whelk population density (no. m^{-1} of shoreline).

Whelk surveys were conducted from 2000-2013, and our objective was to test the chronic effects of fishing, coastal development and wave exposure on whelk populations integrated over this time-period. Most sites ($n = 56$) were visited only once, but a subset was revisited to assess changes within the study period. Ten sites in PR were visited twice, roughly a decade apart (initial visit 2000-2003, second visit 2012-2013), and 7 BVI sites were visited annually from 2000-2013. For these 17 sites, mean whelk density ($t_{16} = 1.18$, $p = 0.08$) and mean shell width ($t_{16} = 2.73$, $p = 0.42$) did not differ between the initial and final visits, but maximum shell width increased by 11.9 mm (± 5.1 mm SE) ($t_{16} = -2.23$, $p = 0.033$). This change in maximum size over time was, however, much smaller than the differences detected among sites (see Results below) so we argue that integrating over time for our cross-site comparison is justifiable.

Assessing fishing, coastal development and wave exposure

Each site was classified using simple indices of fishing pressure, coastal development, and wave exposure as follows:

i) Fishing pressure over the study period was ranked as low, medium or high.

Rankings were based partly on structured interviews with local whelk fishers ($n = 76$), vendors and distributors ($n = 8$), plus informal interviews with knowledgeable key

informants such as fisheries staff, scientists and managers (n = 11). Interview responses indicated that fishing is episodic and weather-dependent, so intermittent site visits might not capture long-term fishing effort. Nonetheless, we also incorporated evidence from *in situ* assessments of each site (mean no. visits per site = 3.5, range = 1-22) such as the presence of fishers, shell piles and other signs of recent whelk collecting, legality of access, and the practical difficulty of travelling to and sampling the site. The relative ease of fishing access was also assessed by examining satellite imagery for the proximity to roads, footpaths, relative remoteness from shoreline access points, or if a boat and subsequent shore landing was necessary to reach the intertidal zone.

ii) Wave exposure at each site was ranked as low, medium, or high in terms of prevailing conditions, including the winter period of elevated wave heights. However, our ranking does not reliably capture intermittent summer hurricanes whose directional pattern of impact is unpredictable. We used a set of physical parameters known to determine the force of waves impacting a shoreline: fetch length, shoreline curvature, bathymetry adjacent to the shore, and the dominant wind and swell direction (Ballantine 1961, Denny 1995, Helmuth and Denny 2003b). These classifications were corroborated by informal interviews with local key informants (n = 11) and, for a subset of the BVI sites (n = 5 shores) by the deployment of maximum wave force dynamometers for 30 days in June 2000 and July 2004 (Bell 1992, Good 2004).

iii) Coastal development was ranked as low, medium or high using a land-use and land-cover (LULC) GIS map of the region based partly on Landsat ETM+ image mosaics (Kennaway et al. 2008). Land-use and land-cover data were available for 68 of the 75 sites. For these sites, we quantified the fraction of the landscape covered by urbanized or agriculture landforms within 500 m of the shore. We selected a 500 m “buffer” as a plausible estimate of distance over which point and non-point source pollution might affect intertidal organisms for two reasons. First, whelks are sedentary and tagged individuals are typically recaptured < 100 m from the point of initial capture (Bell 1992, Debrot 1990b, Randall 1964). Second, prior research at higher latitudes suggests a 500m buffer conservatively captures LULC classes

adjacent to the shore, in both the longshore and inland directions, that have produced nutrient, hydrocarbon, and sediment pollution in sufficient quantities to impact intertidal invertebrates (Bilkovic and Roggero 2008, Espinosa et al. 2007, Littler and Murray 1975, Nelson 1982, Raffaelli and Hawkins 2012, Southward et al. 1982). Low (0-0.05% developed), medium (0.05-5% developed) and high (5-100% developed) categories were based on natural breaks in a histogram of LULC data from the 68 sites. The remaining seven sites were on two islands near PR outside the bounds of the LULC map, but were classified as “low” development based on site visits and satellite imagery. LULC map data were collected in 2000, but our site visits confirmed the lack of marked change over the study period.

Analysis

We used analysis of variance (ANOVA) to test the effects of fishing pressure, coastal development and wave exposure (tested as fixed effects). Ideally, we would sample equal numbers of sites for each possible combination of fishing pressure, coastal development and wave exposure survey (a 3-way factorial design). Despite our best efforts, not all combinations were located in the study area (Table 3-1) so it was not possible to estimate a model including the 3-way interaction. Nonetheless, we were able to find sites that permitted testing of the three possible two-way interactions between the factors (Table 3-1). Our starting model thus included the main effects of (i) fishing pressure, (ii) exposure, and (iii) coastal development, plus the two-way interactions between (iv) fishing x exposure, (v) fishing x development and (vi) exposure x development. If interaction terms were non-significant they were removed and the reduced model retested. Models were fitted separately for the three dependent variables mean shell width, maximum shell width, and mean population density. Prior to analyses, we first checked the assumptions that the data were normally distributed and variances homogeneous.

Results

Fishing selectively removes larger whelks

There was no evidence for interactive effects of fishing pressure, wave exposure and coastal development on the two measures of body size (Tables 3-2 and

Table 3-3). Tests for the separate effect of each factor showed that whelk body sizes were reduced at higher levels of fishing pressure (Figs 3-4 and 3-5), but we did not detect effects of wave exposure or coastal development (Tables 3-4 and 3-5). At sites with high fishing pressure, the average whelk (marginal mean $\pm$ 95%CI = 30.4 mm $\pm$ 3.3mm) was slightly below the size-at-maturity (32 mm) and the biggest whelks (marginal mean $\pm$ 95%CI = 64.4 $\pm$ 4.5 mm) were close to the minimum size-limit for harvesting (63 mm). In contrast, where fishing pressure was lower, the size of the average whelk increased by a factor of 1.6 (marginal mean $\pm$ 95%CI = 49.2 mm $\pm$ 3.2 mm) and the largest whelks by a factor of 1.4 (marginal mean $\pm$ 95%CI = 92.1 mm $\pm$ 4.4 mm).

Fishing caused striking shifts in the size-composition of the sampled whelk populations. Adult whelks (> 32 mm) made up 81.0% (95% CI $\pm$ 7.5%) of the population at low-fishing sites, but only 37.5% (95% CI $\pm$ 7.3%) at heavily fished sites. Whelks above the size-limit for harvesting (> 63 mm) were effectively absent from sites with high and medium fishing pressure, making up only 0.7% and 5.9% of the population respectively (95% CI $\pm$ 5.9% and $\pm$ 6.0% respectively), whereas they comprised 43.9% (95% CI $\pm$ 6.1%) of the population at rarely fished sites.

None of the factors strongly affect whelk population density

Although fishing had strong effects on the size of whelks, there was no detectable impact on population density overall (Fig. 3-4). There was no evidence for interactive effects of fishing pressure, wave exposure and coastal development on whelk population density (Table 3-6), nor did we detect any independent effects of these factors on whelk density (Table 3-7).

Discussion:^[GF2]

Here we have addressed the challenging issue of assessing the effects of SS fishing on an important widely exploited marine invertebrate that is representative of ss fisheries around the world. SS fisheries are vulnerable to overfishing and a critical component of livelihood strategies for coastal people (Allison and Ellis 2001, Berkes 2001, Bene 2006, Andrew 2007, Orensanz et al. 2005), and data poor (Johannes 1998). We show that using a straightforward metric for describing fishing,

development, and exposure we have advanced a means for evaluating the population status of a SS intertidal fishery (Johannes 1998, Crain 2008, Claudet 2010, Piggott 2015). In general, as fishing pressure increased in difficulty along a given shore; the average size, maximum size, overall density and fraction of legally harvestable, and fraction of adults increased. These findings extend and build upon the whelk size and abundance patterns that have been noted since the 1940s, however not quantitatively shown (Clench and Abbott 1943, Boulon et al. 1986, Jimenez 2006, Randall 1964, Toller and Gordon 2005). We also tested for interactive effects of those stressors (Crain 2008, Claudet 2010, Piggott 2015) in an effort to understand them in the context of a larger system of SS fisheries (Andrew 2007). Our results are consistent with findings from higher latitudes on intertidal fisheries for species such as limpet and whelk in Chile (Moreno 2001, Moreno et al. 1986) and California (Harley and Rogers-Bennett 2004). Importantly our results are broadly applicable beyond the Caribbean to other ss-fisheries and we have shown the effects of exploitation on size and abundance associated with fishing effort (Crowe et al. 2000). Until now no previous studies on whelks adequately quantified or controlled for fishing, wave exposure, or coastal development as factors exerting influence on abundance and size distributions of whelks. We clearly met the minimum requirements of having two lines of evidence for determining if there are fishing effects, in that i) we showed a gradient of fishing activity at sites that ii) were reflected in smaller size distributions and densities of whelks (Keough and Quinn 1991, Keough et al. 1993, Underwood and Peterson 1988). By linking harvest rates to population size distribution and abundance we show that fishing pressure is likely driving patterns of size, abundance of a sedentary marine snail [JAM3].

Surprisingly we did not find evidence to support the assertion that coastal anthropogenic development and pollution were impacting whelk size distribution or abundance. This contrasts claims documented in structured interviews from fishers in PR, BVI, and St. Lucia that pollution and development were major factors effecting whelks (unpublished Forrester data (Jimenez 2006, Nelson and Oxenford 2012). Whelks naturally occur on shores with surface waters that are generally highly mixed which could dilute the effects of development and pollution (Raffaelli and Hawkins

2012). However, development should not be ignored as a potent factor, chronic anthropogenic hydrocarbon and nutrient pollution has been shown in higher latitudes to cause declines in grazer abundance and shifts in species assemblages (Littler and Murray 1975, Southward, White, Vader, Gray and Crisp 1982).

Unexpectedly our baseline comparisons over the course of the survey period showed an increase in the maximum size of whelks. Though inconsistent with the other results, which show a lack of change in body size and density through time, the weight of evidence rests with fishing as the dominant effect driving population demographics for the species.

The Caribbean whelk fishery is an example of a species of economic and cultural importance that has not been a focus of resource managers and for which we know little about. As we have shown the species appears to be overexploited in portions of its range despite management actions and restrictions on harvest. Given that we can show a strong spatial component to a ss fishery, it would appear that better spatial control of fishing effort is necessary for a sustainable future for whelks and other ss fisheries.

Bibliography:

Atkinson WD, Newbury SF. 1984. The adaptations of the rough winkle, *Littorina rudis*, to desiccation and to dislodgement by wind and waves. *Journal of Animal Ecology* 53:93-105.

Ballantine WJ. 1961. A biologically-defined exposure scale for the comparative description of rocky shores. *Field Studies Journal*, Vol. 1.3: 1-19.

Bell LJ. 1992. Reproduction and larval development of the West Indian topshell, *Cittarium pica* (Trochidae), in the Bahamas. *Bulletin of Marine Science* 51:250-266.

Bertness MD. 1981. Predation, physical stress, and the organization of a tropical rocky inter-tidal hermit crab community. *Ecology* 62:411-425.

Bertness MD, Gaines SD, Hay ME. 2001. *Marine community ecology*: Sinauer Associates Sunderland, Massachusetts, USA.

Bilkovic D, Roggero M. 2008. Effects of coastal development on nearshore estuarine nekton communities. *Marine Ecology-Progress Series*- 358:27.

Blick JP. 2007. Pre-Columbian impact on terrestrial, intertidal, and marine resources, San Salvador, Bahamas (A.D. 950–1500). *Journal for Nature Conservation* 15:174-183.

Boulding EG. 1990. Are the opposing selection pressures on exposed and protected shores sufficient to maintain genetic differentiation between gastropod populations with high intermigration rates? In: *Progress in Littorinid and Muricid Biology*. Netherlands: Springer, p 41-52.

Boulding EG, Holst M, Pilon V. 1999. Changes in selection on gastropod shell size and thickness with wave-exposure on northeastern pacific shores. *Journal of Experimental Marine Biology and Ecology* 232:217-239.

Boulon R, Jr., Beets J, Zullo ES. 1986. Long Term Monitoring of Fisheries in the Virgin Islands Biosphere Reserve-Research Report #13.

Braje TJ, Rick TC, Erlandson JM. 2012. A trans-Holocene historical ecological record of shellfish harvesting on California's Northern Channel Islands. *Quaternary International* 264:109-120.

Braje TJDJKJME, Brendan JC. 2007. Human impacts on nearshore shellfish taxa: A 7,000 year record from Santa Rosa Island, California. *American Antiquity*:735-756.

Branch GM, Marsh AC. 1978. Tenacity and shell shape in six *Patella* species: Adaptive features. *Journal of Experimental Marine Biology and Ecology* 34:111-130.

Brosnan DM. 1992. Ecology of tropical rocky shores: plant-animal interactions in tropical and temperate latitudes. In: D M John, S J Hawkins, and J H Price, ed's *Plant Animal interactions in the marine benthos*. Clarendon Press, Oxford, p Pages-101–131.

Campbell G. 2008. Beyond means to meaning: using distributions of shell shapes to reconstruct past collecting strategies. *Environmental Archaeology* 13:111-121.

Campbell G. 2015. “What do I do with all these shells?” Basic guidance for the recovery, processing and retention of archaeological marine shells. *Quaternary International*.

Carrington Bell E, Denny MW. 1994. Quantifying “wave exposure”: a simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology* 181:9-29.

Chiu Y-W, Chen H-C, Lee S-C, Chen CA. 2002. Morphometric analysis of shell and operculum variations in the viviparid snail, *Cipangopaludina chinensis* (Mollusca: Gastropoda), in Taiwan. *Zoological Studies-Taipei* 41:321-331.

Claudet J, Fraschetti S. 2010. Human-driven impacts on marine habitats: a regional meta-analysis in the Mediterranean Sea. *Biological Conservation* 143:2195-2206.

Clench WJ, Abbott RT. 1943. The genera *Gaza* and *Livona* in the western Atlantic. *Johnsonia: Monographs of the marine mollusks of the Western Atlantic* 1.

Coates K, Jantzen-Marson C, Madeiros J, Meyer E. West Indian topshell, *Cittarium pica*, reintroduction project in Bermuda: Current status. *Proceedings of the Integrative and Comparative Biology*; 2003: Society for Integrative Comparative Biology, 1313 Dolley Madison Blvd, No 402, McLean, VA 22101 USA.

Crain CM, Halpern BS, Beck MW, Kappel CV. 2009. Understanding and managing human threats to the coastal marine environment. *Annals of the New York Academy of Sciences* 1162:39-62.

Crain CM, Kroeker K, Halpern BS. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11:1304-1315.

Crowe TP, Thompson RC, Bray S, Hawkins SJ. 2000. Impacts of anthropogenic stress on rocky intertidal communities. *Journal of Aquatic Ecosystem Stress and Recovery* 7:273-297.

Davis D. 2013. Guana Archaeology-Prehistory Project Report for the October 2012 Field Season.

Davis DD. 2011. Out of the Shadows: A review of the archaeological evidence for the isolation, interaction, and abandonment of the British Virgin Islands in the pre-Columbian Caribbean.

Debrot AO. 1990a. Survival, growth, and fecundity of the West Indian topshell, *Cittarium pica* (Linnaeus), in various rocky intertidal habitats of the Exuma Cays, Bahamas. *The Veliger* 33:363-371.

Debrot AO. 1990b. Temporal aspects of population dynamics and dispersal behavior of the West Indian topshell, *Cittarium pica* (L.), at selected sites in the Exuma Cays, Bahamas. *Bulletin of Marine Science* 47:431-447.

Denny M. 1995. Predicting Physical Disturbance: Mechanistic Approaches to the Study of Survivorship on Wave-Swept Shores. *Ecological Monographs* 65:371-418.

Denny MW. 2006. Ocean waves, nearshore ecology, and natural selection. *Aquatic Ecology* 40:439-461.

Díaz-Ferguson E, Haney R, Wares J, Silliman B. 2010. Population Genetics of a Trochid Gastropod Broadens Picture of Caribbean Sea Connectivity. *PLoS ONE* 5:e12675.

Erlandson JM, Braje TJ, Rick TC, Jew NP, Kennett DJ, Dwyer N, Ainis AF, Vellanoweth RL, Watts J. 2011. 10,000 years of human predation and size changes in the owl limpet (*Lottia gigantea*) on San Miguel Island, California. *Journal of Archaeological Science* 38:1127-1134.

Espinosa F, Guerra-García J, García-Gómez J. 2007. Sewage pollution and extinction risk: an endangered limpet as a bioindicator? *Biodiversity and Conservation* 16:377-397.

Etter RJ. 1988. Asymmetrical developmental plasticity in an intertidal snail. *Evolution*:322-334.

- Faulkner P. 2010. Morphometric and taphonomic analysis of granular ark (*Anadara granosa*) dominated shell deposits of Blue Mud Bay, northern Australia. *Journal of Archaeological Science* 37:1942-1952.
- Fitzpatrick SM, Kappers M, Kaye Q, Giovas CM, LeFebvre MJ, Harris MH, Burnett S, Pavia JA, Marsaglia K, Feathers J. 2009. Precolumbian Settlements on Carriacou, West Indies. *Journal of Field Archaeology* 34:247-266.
- Giovas CM, Clark M, Fitzpatrick SM, Stone J. 2013. Intensifying collection and size increase of the tessellated nerite snail (*Nerita tessellata*) at the Coconut Walk site, Nevis, northern Lesser Antilles, AD 890–1440. *Journal of Archaeological Science* 40:4024-4038.
- Good TP. 2004. Distribution and Abundance Patterns in Caribbean Rocky Intertidal Zones. *Bulletin of Marine Science* 74:459-468.
- Grenon JF, Walker G. 1981. The tenacity of the limpet, *Patella vulgata* L.: An experimental approach. *Journal of Experimental Marine Biology and Ecology* 54:277-308.
- Griffiths C, Branch G. 1997. The exploitation of coastal invertebrates and seaweeds in South Africa: historical trends, ecological impacts and implications for management. *Transactions of the Royal Society of South Africa* 52:121-148.
- Harley CD, Rogers-Bennett L. 2004. The potential synergistic effects of climate change and fishing pressure on exploited invertebrates on rocky intertidal shores. *California Cooperative Oceanic Fisheries Investigations Report* 45:98.
- Heller J. 1976. The effects of exposure and predation on the shell of two British winkles. *Journal of Zoology* 179:201-213.
- Helmuth B, Denny MW. 2003a. Predicting wave exposure in the rocky intertidal zone: Do bigger waves always lead to larger forces-9. *Limnology and Oceanography* 48:1338-1345.
- Helmuth B, Denny MW. 2003b. Predicting wave exposure in the rocky intertidal zone: Do bigger waves always lead to larger forces? *Limnology and Oceanography* 48:1338-1345.
- Hockey PAR, Bosman AL, Siegfried WR. 1988. Patterns and Correlates of Shellfish Exploitation by Coastal People in Transkei: An Enigma of Protein Production. *Journal of Applied Ecology* 25:353-363.

- Hollander J, Butlin RK. 2010. The adaptive value of phenotypic plasticity in two ecotypes of a marine gastropod. *Bmc Evolutionary Biology* 10:333.
- Jerardino A, Navarro R. 2008. Shell morphometry of seven limpet species from coastal shell middens in southern Africa. *Journal of Archaeological Science* 35:1023-1029.
- Jimenez N. 2006. Caribbean/NMFS Cooperative SEAMAP Program Whelk and Finfish Assessment.
- Jones AR. Animal food and human population at Indian Creek, Antigua. *Proceedings of the Proceedings of the Eighth International Congress for the Study of Pre-Columbian Cultures of the The Lesser Antilles*, Arizona State University Anthropological Research Papers; 1980.
- Jones AR. 1985. Dietary Change and Human Population at Indian Creek, Antigua. *American Antiquity* 50:518-536.
- Keegan WF, Fitzpatrick SM, Sealey KS, LeFebvre MJ, Sinelli PT. 2008. The Role of Small Islands in Marine Subsistence Strategies: Case Studies from the Caribbean. *Human Ecology* 36:635-654.
- Kennaway TA, Helmer EH, Lefsky MA, Brandeis TA, Sherrill KR. 2008. Mapping land cover and estimating forest structure using satellite imagery and coarse resolution lidar in the Virgin Islands. *Journal of Applied Remote Sensing* 2:023551-023551-023527.
- Keough M, Quinn G. 1991. Causality and the choice of measurements for detecting human impacts in marine environments. *Marine and Freshwater Research* 42:539-554.
- Keough MJ, Quinn GP, King A. 1993. Correlations between human collecting and intertidal mollusc populations on rocky shores. *Conservation Biology* 7:378-390.
- Kitching JA. 1976. Distribution and changes in shell form of *Thais* spp.(Gastropoda) near Bamfield, BC. *Journal of Experimental Marine Biology and Ecology* 23:109-126.
- Kitching JA, Lockwood J. 1974. Observations on shell form and its ecological significance in thaisid gastropods of the genus *Lepsiella* in New Zealand. *Marine Biology* 28:131-144.
- Kitching JA, Muntz L, Ebling FJ. 1966. The Ecology of Lough Ine. XV. The Ecological Significance of Shell and Body Forms in *Nucella*. *The Journal of Animal Ecology* 35:113.

- Kostro M. 2007. Guana Island Archaeological Project, 2004-2006: An Interim Report.
- Linnaeus C. 1758. *Systema Naturae*, Ed. 10, Vol. 1. 824 pp. Salvii, Holmiae.
- Littler MM, Murray SN. 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Marine Biology* 30:277-291.
- Macfarlan R, Forrester GE, McLean E. 2015. Isolating The Effect of Artisanal Fishing on an Intertidal Gastropod in the Caribbean. In L Creswell, editor. *Proceedings of the 67th Gulf Caribbean Fisheries Institute. Proceedings of the Gulf Caribbean Fisheries Institute, 67th Annual Conference; 2014 November 3-7, 2014: Omnipress.*
- Mannino MA, Thomas KD. 2002. Depletion of a resource? The impact of prehistoric human foraging on intertidal mollusc communities and its significance for human settlement, mobility and dispersal. *World Archaeology* 33:452-474.
- Menge BA, Lubchenco J. 1981. Community Organization in Temperate and Tropical Rocky Intertidal Habitats: Prey Refuges in Relation to Consumer Pressure Gradients. *Ecological Monographs* 51:429-450.
- Menge BA, Sutherland JP. 1976. Species Diversity Gradients: Synthesis of the Roles of Predation, Competition, and Temporal Heterogeneity. *The American Naturalist* 110:351-369.
- Menge BA, Sutherland JP. 1987. Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment. *The American Naturalist* 130:730-757.
- Miller SL. 1974. Adaptive design of locomotion and foot form in prosobranch gastropods. *Journal of Experimental Marine Biology and Ecology* 14:99-156.
- Moreno CA. 2001. Community patterns generated by human harvesting on Chilean shores: a review. *Aquatic Conservation: Marine and Freshwater Ecosystems* 11:19-30.
- Moreno CA, Lunecke KM, xe, pez MI. 1986. The Response of an Intertidal *Concholepas concholepas* (Gastropoda) Population to Protection from Man in Southern Chile and the Effects on Benthic Sessile Assemblages. *Oikos* 46:359-364.
- Murray SN, Denis TG, Kido JS, Smith JR. 1999. Human visitation and the frequency and potential effects of collecting on rocky intertidal populations in southern

California marine reserves. Reports of California Cooperative Oceanic Fisheries Investigations 40:100-106.

Nelson T, Oxenford HA. 2012. The whelk (*Cittarium pica*) fishery of Saint Lucia: description and contribution to the fisheries sector. Proceedings of the Gulf and CaribFisheries Institute 65: .

Nelson WG. 1982. Experimental studies of oil pollution on the rocky intertidal community of a Norwegian fjord. Journal of Experimental Marine Biology and Ecology 65:121-138.

O'Dea A, Shaffer ML, Doughty DR, Wake TA, Rodriguez FA. 2014. Evidence of size-selective evolution in the fighting conch from prehistoric subsistence harvesting. Proceedings of the Royal Society of London B: Biological Sciences 281:20140159.

Orensanz JM, Parma AM, Jerez G, Barahona N, Montecinos M, Elias I. 2005. What are the key elements for the sustainability of " S-fisheries"? Insights from South America. Bulletin of Marine Science 76:527-556.

Palmer AR. 1990. Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). In: Progress in Littorinid and Muricid Biology. Netherlands: Springer, p 155-182.

Poteate AS, Fitzpatrick SM, Clark M, Stone JH. 2014. Intensified mollusk exploitation on Nevis (West Indies) reveals ~six centuries of sustainable exploitation. Archaeological and Anthropological Sciences:1-14.

Prowse TAA, Pile AJ. 2005. Phenotypic homogeneity of two intertidal snails across a wave exposure gradient in South Australia. Marine Biology Research 1:176-185.

Raffaelli D, Hawkins SJ. 2012. Intertidal ecology: Springer Science & Business Media.

Randall HA. 1964. A study of the growth and other aspects of the biology of the West Indian topshell, *Cittarium pica* (Linnaeus). Bulletin of Marine Science 14:424-443.

Reitz EJ, Wing ES. 1999. Zooarchaeology: Cambridge University Press.

Richter C, Roa-Quiaoit H, Jantzen C, Al-Zibdah M, Kochzius M. 2008. Collapse of a new living species of giant clam in the Red Sea. Curr Biol 18:1349-1354.

Rick TC, Erlandson JM. 2008. Human impacts on ancient marine ecosystems: a global perspective: University of California Press.

Robertson R. 2003. The edible West Indian “whelk” *Cittarium pica* (Gastropoda: Trochidae): Natural history with new observations. *Proceedings of the Academy of Natural Sciences of Philadelphia* 153:27-47.

Salas S, Chuenpagdee R, Seijo JC, Charles A. 2007. Challenges in the assessment and management of small-scale fisheries in Latin America and the Caribbean. *Fisheries Research* 87:5-16.

Salomon AK, Tanape Sr NM, Huntington HP. 2007. Serial depletion of marine invertebrates leads to the decline of a strongly interacting grazer. *Ecological Applications* 17:1752-1770.

Schmidt et al. 2002 S, Wolff M, Vargas JA. 2002. Population ecology and fishery of *Cittarium pica* (Gastropoda: Trochidae) on the Caribbean coast of Costa Rica. *Revista de Biología Tropical* 50:1079-1090.

Seeley RH. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. *Proceedings of the National Academy of Sciences* 83:6897-6901.

Serrand N. 2008. The Use of Molluscs in the Precolumbian Amerindian Lesser Antilles: Human, Animal, and Environmental Parameters (with an emphasis on metrics). *Archaeofauna* 17:21-34.

Siegfried WR. 2013. Rocky shores: exploitation in Chile and South Africa: Springer Science & Business Media.

Singh GG, McKechnie I. 2015. Making the most of fragments: a method for estimating shell length from fragmentary mussels (*Mytilus californianus* and *Mytilus trossulus*) on the Pacific Coast of North America. *Journal of Archaeological Science* 58:175-183.

Southward A, White B, Vader S, Gray J, Crisp D. 1982. An Ecologist's View of the Implications of the Observed Physiological and Biochemical Effects of Petroleum Compounds on Marine Organisms and Ecosystems (and Discussion). *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 297:241-255.

Simple linear regression using SPSS Statistics. Available from <https://statistics.laerd.com/>

Strand J, Jørgensen A, Tairova Z. 2009. TBT pollution and effects in molluscs at US Virgin Islands, Caribbean Sea. *Environment international* 35:707-711.

Toller W, Gordon S. 2005. A population survey of the West Indian topshell or whelk (*Cittarium pica*) in the US Virgin Islands. Department of Planning and Natural Resources Division of Fish and Wildlife St Thomas, Virgin Islands < <http://bcrb.bio.umass.edu/vifishandwildlife>.

Torres RE, Sullivan-Sealey KM. Shell Midden Surveys as Source of Information about Fished Queen Conch (*Strombus gigas*) Populations: A Case Study in Parque Nacional Del Este, Dominican Republic. *Proceedings of the Proceedings of the Gulf and Caribbean Fisheries Institute*; 2002.

Trussell GC. 1997a. Phenotypic plasticity in the foot size of an intertidal snail. *Ecology* 78:1033-1048.

Trussell GC. 1997b. Phenotypic selection in an intertidal snail: effects of a catastrophic storm. *Marine Ecology Progress Series* 151:73-79.

Trussell GC, Etter RJ. 2001. Integrating genetic and environmental forces that shape the evolution of geographic variation in a marine snail. *Genetica* 112:321-337.

Trussell GC, Johnson AS, Rudolph SG, Gilfillan ES. 1993. Resistance to dislodgment-Habitat and size-specific differences in morphology and tenacity in an intertidal snail. *Marine Ecology-Progress Series* 100:135-144.

Underwood A, Peterson C. 1988. Towards an ecological framework for investigating pollution. *Marine Ecology Progress Series* 46:227-234.

Underwood AJ. 1999. Physical disturbances and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. *Journal of Experimental Marine Biology and Ecology* 232:125-140.

Vermeij G. 1973. Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. *Marine Biology* 20:319-346.

Vermeij GJ, Williams ST. 2007. Predation and the geography of opercular thickness in turbinid gastropods. *Journal of Molluscan Studies* 73:67-73.

Warburton K. 1976. Shell form, behaviour, and tolerance to water movement in the limpet *Patina pellucida* (L.) (Gastropoda: Prosobranchia). *Journal of Experimental Marine Biology and Ecology* 23:307-325.

Weaver PL, Ramirez JL, Jorge L, Rivera C, International Institute of Tropical F. 1999. Las Cabezas de San Juan Nature Reserve (El Faro): US Department of Agriculture, Forest Service, International Institute of Tropical Forestry.
[http://www.fs.fed.us/global/iitf/pubs/gtr_iitf005_\(62\).pdf](http://www.fs.fed.us/global/iitf/pubs/gtr_iitf005_(62).pdf).

Wing ES. 2001. The sustainability of resources used by Native Americans on four Caribbean islands. *International Journal of Osteoarchaeology* 11:112-126.

Figures:

Figure 3-1. Map of Sites in the U.S. Virgin Islands, Puerto Rico and the British Virgin Islands.

Figure 3-2_[GF4]. Estimated marginal means _[PA5] for mean shell width, standard error bars shown.

Figure 3-3. Estimated marginal means for the mean of maximum shell width for each level of fishing access across sites, standard error bars shown[PA6].

Figure 3-4 Estimated marginal means of whelk density by fishing access, standard error bars are shown.

Table 3-1. Number of sites and whelks measured per combination of independent variables for each two way ANOVA model: i-fishing x exposure, ii-exposure x development, iii-fishing x development.

		<u>Exposure</u>		
		Low	Medium	High
Fishing	i)			
	Low	1(40)	7(1036)	25(5171)
	Medium	5(1260)	5(2619)	10(1351)
	High	9(3696)	6(164)	7(1084)
		<u>Development</u>		
		Low	Medium	High
Exposure	ii)			
	Low	.	9(2207)	6(2789)
	Medium	4(434)	10(3149)	4(236)
	High	16(3964)	17(2203)	9(1439)
		<u>Development</u>		
		Low	Medium	High
Fishing	iii)			
	Low	18(4347)	13(1660)	2(240)
	Medium	.	15(4275)	5(955)
	High	2(51)	8(1624)	12(3269)

Table 3-2. ANOVA table testing the interactive effects of fishing pressure, wave exposure, and coastal development on mean whelk width.

Source	SS	df	MS	<i>F</i>	<i>P</i>
Exposure x Fishing	635.69	4	158.923	0.915	0.462
Fishing x Development	209.086	3	69.695	0.401	0.753
Exposure x Development	592.926	3	197.642	1.137	0.342
Access	3007.475	2	1503.737	8.654	0.001
Exposure	1018.495	2	509.247	2.931	0.061
Development	89.976	2	44.988	0.259	0.773
Error	10077.769	58	173.755		
R Squared = .461 (Adjusted R Squared = .312)					

Table 3-3. ANOVA table testing the interactive effects of fishing pressure, wave exposure, and coastal development on maximum whelk width.

Source	SS	df	MS	<i>F</i>	<i>P</i>
Exposure x Fishing	364.287	4	91.072	0.227	0.922
Fishing x Development	737.32	3	245.773	0.612	0.61
Exposure x Development	1463.457	3	487.819	1.215	0.312
Access	2830.664	2	1415.332	3.525	0.036
Exposure	1032.948	2	516.474	1.286	0.284
Development	510.87	2	255.435	0.636	0.533
Error	23290.296	58	401.557		
R Squared = .389 (Adjusted R Squared = .221)					

Table 3-4. Tests for the separate effects of fishing, exposure and development on whelk_[PA7] width.

Source	SS	df	MS	<i>F</i>	<i>P</i>
Fishing	3438.075	2	1719.038	8.554	0
Exposure	955.683	2	477.841	2.378	0.1
Development	481.02	2	240.51	1.197	0.308
Error	13665.228	68	200.959		
R Squared = .268 (Adjusted R Squared = .204)					

Table 3-5. Tests for the separate effects of fishing, exposure and development on maximum width.

Source	SS	df	MS	<i>F</i>	<i>P</i>
Fishing	6354.757	2	3177.379	8.466	0.001
Exposure	1617.07	2	808.535	2.154	0.124
Development	12.177	2	6.089	0.016	0.984
Error	25522.11	68	375.325		

R Squared = .331 (Adjusted R Squared = .272)

Table 3-6. ANOVA table testing the interactive effects of fishing pressure, wave exposure, and coastal development on whelk density.

Source	SS	df	MS	<i>F</i>	<i>P</i>
Exposure x Fishing	22.291	4	5.573	1.475	0.222
Fishing x Development	17.552	3	5.851	1.549	0.212
Exposure x Development	32.371	3	10.79	2.857	0.045
Fishing	3.745	2	1.872	0.496	0.612
Exposure	4.163	2	2.082	0.551	0.579
Development	6.111	2	3.056	0.809	0.45
Error	215.298	57	3.777		
R Squared = .220 (Adjusted R Squared = .002)					

Table 3-7. Tests for the separate effect of fishing, exposure and development on whelk density.

Source	SS	df	MS	<i>F</i>	<i>P</i>
Fishing	6354.757	2	3177.379	8.466	0.001
Exposure	1617.07	2	808.535	2.154	0.124
Development	12.177	2	6.089	0.016	0.984
Error	25522.11	68	375.325		

R Squared = .331 (Adjusted R Squared = .272)

CHAPTER 4

Pre and Post-Columbian era exploitation histories of an intertidal gastropod differ across time scales and islands in the West Indies

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Abstract

Examining the archaeological record of food remains found in pre-historic shell piles known as “middens” can yield inferences on the past exploitation histories of marine fauna. Prior studies of middens for various marine taxa have claimed to detect fishing effects on hard shelled marine invertebrates based on changes in their size and abundance. Here we examine exploitation histories of a Caribbean intertidal gastropod found in three shell middens that were formed by three distinct human occupations prior to and following the European migration to the West Indies.

Cittarium pica, the West Indian Top Shell, “whelk,” is currently thought to be in decline throughout its range due to overfishing but was once the third most important invertebrate fished in the region. Whelks were a reliable intertidal food source to the early colonizers of the Caribbean and their shells are ubiquitous in middens.

However, the taphonomic and depositional processes that shape middens have resulted in significant portions of whelks that are fragmented which can bias estimates of both size and abundance. Recently midden analysis of whelk size and abundance at several islands has shown contrasting exploitation histories-but those studies used crude metrics to infer fishing pressure. In contrast we analyzed intact shells and fragmented shells previously underutilized in midden studies of whelks to arrive at more precise estimates of size distributions. We conducted a simple linear regression analysis of several shell characters to predict shell width. We compared three middens two of which were formed prior to the Columbian exchange and the third during the middle 18th century. Sites in British Virgin Islands and Puerto Rico were excavated in 2004, 2006, and 2012. We contrast the results of measurements of body size and abundance within middens with contemporary intertidal field surveys and discarded fisher shell measurements collected between 2000-2013. We found that within all middens the amount of shell material decreased through time, but that only within the pre-Taino midden on Puerto Rico was there significant changes in body size.

Introduction

Pre-historic exploitations of marine invertebrates for subsistence have been well documented throughout the world (Rick and Erlandson 2008) and in the Caribbean for pre-Columbian, and colonial times (Jerardino and Navarro 2008, Keegan et al. 2008, Serrand 2008, Wing 2001). The contribution of shellfish to human diets was typically underestimated in past studies and harvest pressures on marine resources considered fairly benign when compared to modern levels of commercial exploitation. This view has been challenged in the contemporary literature with the expanding analysis of shell deposits housed in “middens.” Middens, which can be large in total area and volume are typically subsampled and systematically excavated by the removal of layers of material known as “context”. It is assumed that these layers contain the dietary remains of the human inhabitants from the surrounding area. These layers may be of fixed arbitrary thickness or based on depositional cues found whilst excavating, and contain both faunal remains and artifacts. Prior midden excavations on several continents have revealed significant changes in the size distribution and abundance of species through time that have been linked to over-exploitation of marine resources (Braje and Brendan 2007, O'Dea et al. 2014, Richter et al. 2008). Additional evidence from the Caribbean, has supported the notion of changes in size distributions of species and prehistoric exploitation patterns of intertidal mollusks have been inferred (Giovas et al. 2013, Poteate et al. 2014). In the Caribbean *Cittarium pica* (Linnaeus 1758), also known as “whelk,” is a large generalist intertidal grazer has been found in middens throughout the region. It is assumed to have been an important protein source (Davis 2013, Davis 2011, Fitzpatrick et al. 2009, Jones 1985, Poteate et al. 2014) and has been shown to vary widely in abundance within different middens and through layers of context.

Analyses of midden remains for whelks have mostly relied upon weight or counts of shells and shell fragments to estimate both the size and abundance. Rough approximations of the size and age structure of whelks are rarely accomplished and whelks are typically only weighed and counted. This has yielded little ecologically appropriate data to infer exploitative effects other than gross simplifications of fishing effort or the amount of whelk fragments in a given layer of context. For instance,

overexploitation of whelk resources was inferred following the excavation of a Bahamian midden by summing weights per layer of context, however that author did not measure the size of those snails (Blick 2007). In another midden analysis conducted on Antigua, another researcher states that whelk of ~35mm in height were common and even small specimens were found throughout layers of context, but goes no further with an analysis of those shells (Jones 1985). In Jamaica, it was found that there were more Queen Conch (*Strombus gigas*) and whelk in older layers of context than more recent layers (Keegan et al. 2003). In contrast Poteate et al. (2014) found the opposite that there were increases in size of three taxa within middens including whelks that showed “sustainable” exploitation. Those inferences were made based on higher total shell weight and shell fragment abundance in the upper layers of context compared to lower older layers.

These inferences about the relative amounts and sizes of marine organisms within the middens themselves should be viewed with caution. Variation in shell breakage based on differing taphonomic histories and post-depositional processes likely influence the amount and type of measureable shell fragments (Faulkner 2010, Jerardino and Navarro 2008). Whelks are not rare in Caribbean middens and even when shells appear severely broken their fragments can yield proxy measures for estimating body sizes. We examine [PA8] with more precision than prior studies of the species that whelk exploitation histories can be carefully rebuilt with whole shells and fragment analysis. It is expected that over-exploitation of whelks would result in a sequential decline in size, age, and abundance through layers of context within a midden (Mannino and Thomas 2002). We examine the whelk remains from three time periods, on two different island groups which yielded three inferences: 1) pre-Taino inhabitants had significant effects on whelk size in North East of Puerto Rico, 2) Amerindian and a subsequent colonial exploitation on Guana Island, British Virgin Islands (BVI) showed no change in size, and 3) within all three middens there were was a significant decrease in whelk abundance through time.

The study species

Whelks are particularly susceptible to human over-exploitation, are well represented in Caribbean shell middens, and are an ideal case study for exploring

exploitation histories. Recently the species has come under threat of overfishing throughout its range, and may have been fished to extinction in Bermuda during the late 19th century (Coates et al. 2003, Robertson 2003). A large whelk can consist of ~3/4 shell weight by total mass [PA9] and grow in excess of 120 mm in shell width (Jones 1985, Robertson 2003). Their heavy shells are fairly robust to breakage and those that are broken tend to have regularly shaped measureable fragments. They do not migrate, they are likely recruitment limited once localized depletion occurs (Bell 1992, Randall 1964, Debrot 1990b, Robertson 2003). Like many intertidal invertebrates, large amounts of them are needed to create even a small amount of protein. Which results in large piles of shell remains and potentially reductions in population abundance in nearby rocky intertidal habitats (Campbell 2015). The contemporary fishery of the species is widespread in the region and was at one point thought to be the 3rd most important invertebrate fished after queen conch (*Strombus gigas*) and spiny lobster (*Panulirus argus*) (Robertson 2003). There is clear evidence that overfishing is occurring along heavily exploited shores where large whelks are absent, and there is reason to assume that similar trends could have prevailed in the past (Macfarlan et al unpublished). The species is slow growing, taking upwards of 5 years to reach a size of 35-40 mm diameter (Debrot 1990a, Randall 1964). Nearly sedentary, whelks are thought to move ~ 50m alongshore in a lifetime and because of the patchy nature of the rocky intertidal they are also less likely to immigrate into areas where they have been over-exploited (Debrot 1990a, Randall 1964). Whelks broadcast spawn and their planktonic larvae settle in ~3 days which is thought to impact the dispersal of recruits (Bell 1992).

We complement the analysis of midden-derived metrics of size and abundance with findings from contemporary field surveys at sites near the middens. We carefully examine the criteria for evaluating whether the archaeological samples meet the requirements for inferring exploitation as defined by prey choice theory. It is assumed that the largest individual whelk would be exploited first (deepest layers of context) and declines in size and abundance would follow (see Claassen 1986 in Mannino and Thomas 2002, Poteate et al. 2014). We address potential bias from taphonomic and depositional processes by examining fragmentation of shell material within each

excavation, and discuss how post depositional processes could influence our results. Different from other studies, we did not use weight as a proxy for shell size because we were able to measure and accurately approximate shell widths and determine size distributions based on whole and fragmented shells (Keegan et al. 2003, Poteate et al. 2014). Specifically we ask whether there are differences in exploitation histories for pre-Columbian and 18th century periods at two sites across three middens in Puerto Rico (PR) and the British Virgin Islands (BVI). Furthermore we explore how those archaeological size distributions compare to contemporary fisher harvests and intertidal surveys of whelks within relatively close proximity to the middens.

Methods

Archaeological Excavations: British Virgin Islands: 2004 and 2006

In the British Virgin Islands, Guana Island (Figure 4-1) lies just off the northern coast of the island of Tortola. The island has been settled discontinuously in the last 1400 years by Amerindians, Quakers, emancipated slaves, and since the 1930s by two American families (Richter in Davis 2011, 2013). In 2004 and 2006 a single excavation unit adjacent to the foundation of a late 18th century structure revealed a mid-1700s midden consisting of various species of shells and artifacts superimposed above a pre-Columbian “Amerindian” midden (Kostro 2007). The contents of the two middens were dominated in volume by whelks. All materials were systematically removed, screened, their contents sorted by taxa, and curated. The excavation of the Amerindian midden was 1m³ and excavated by removing 14 layers of ~3cm thick context. The age of the lowest context has been estimated at ~600 CE [PA10] and the most recent ~1500 CE, these estimates are based on the presence and technological stage of pottery shards. The Amerindian midden held 956 whelks, there were 289 complete shells, 146 measureable fragments, and 532 fragments that were identified as being parts of whelk shells but too broken to yield useable measurements. The 18th century “Colonial” midden was estimated by C₁₄ dating to be between 1725-75 CE and represents approximately 40-50 years of human occupation on that site. Little is known about the inhabitants that created the Colonial era midden. Each of the 30 layers of context in that midden was ~2cm in thickness, and the resulting sample

consisted of 835 whelk, of which there were 435 complete shells, and 53 measurable fragments, and 347 fragments that could not be measured. The Amerindian midden is representative of the late-Saledoid culture based on the presence of ceramics within excavated layers. Additional archaeological research conducted on Guana Island has found evidence the Amerindian settlement was permanent and abandoned prior to the arrival of Columbus (Richter in (Davis 2011,13).

Archaeological Excavations: Puerto Rico: 2012

The Reserve de Naturales Cabezas de San Juan is located on the northeastern tip of Puerto Rico, the excavation site is located on the north east facing shore (see Figure 4-1). The site is thought to have been a settlement of “pre-Taino” early Saledoid peoples from ca. 600-800 CE based on analysis of pottery shards and stone tools found within the context of the midden. The evidence for early Saledoid occupation is consistent with other archaeological sites in Puerto Rico that are associated with a horticultural sedentary culture (personal communication with Dr. Carlos Perez, Weaver et al. 1999). The pre-Taino midden excavation is located behind the fore-dune at Jayuya Beach, and was 2m² in surface area and 1.4 m [PA11] in depth and consisted of seven layers of 20 cm thick context. As on Guana Island, each layer was carefully screened, sorted for various faunal and anthropogenic remains, and curated. 1576 fragments and whole shells were identified as whelks, of which there were 114 complete shells, 406 measurable fragments, and 1056 non-measurable fragments.

Contemporary Whelk Surveys: 2000-2013

Shell measurement data were obtained from several sources to compare the size distributions of modern whelks to those found in midden excavations. As contemporary comparisons and based on several optimal foraging theory (OFT) assumptions we chose intertidal survey sites that were geographically close in proximity to the middens and we examined shell piles left by artisanal fishermen. Broadly speaking OFT assumes that humans will exploit local environments to maximize yield and energy harvested while minimizing the time invested and risk to the forager (Reitz and Wing 1999, [PA12]Rivera-Collazo 2010, Giovas et al. 2013). We further assumed that 1) because whelks are heavy, transporting large amounts of them

long distances was impractical, 2) the rocky intertidal areas are extensive near the middens, and 3) the three human occupations examined had access to seaworthy small vessels. Based on OFT and whelk-specific assumptions it is logical that whelks found in middens were from local (<10km) intertidal areas and could become overexploited through time and chronic fishing pressure. In the area near to the midden in Fajardo, PR we chose 4 sites where intertidal surveys had been conducted in 2003 (Jimenez 2006). On Guana Island seven sites were chosen from around the island where intertidal survey data had been collected from 2000-2013 (Macfarlan in Review). Modern shell piles were found on Guana Island in the course of intertidal field-work, and fisher-landed whelks were obtained for Puerto Rico from artisanal collectors in a community nearby the midden.

Shell Size: Whole Shell and Fragments

Shell width is an accepted measure of body size for whelks, and is a robust measure for detecting exploitation effects on age structure and distribution (Debrot 1990a, Randall 1964). Body width is a commonly sampled for character and used to infer exploitation effects on other marine gastropods (Campbell 2015, Randall 1964, Robertson). [PA13]Here we examined trends through layers of context (a proxy for time) in both overall mean shell width (see Figure 4-4 pictures i), as well as the fraction of adults ($\geq 33\text{mm}$ size at sexual maturity).

Measurement bias

To avoid bias created by selectively measuring intact shells found within the middens we chose two commonly found but unique shell fragments that yielded measurements that were proxies for body size. The use of unique parts of hard shelled marine organism as proxy measures to estimate body size for analysis have increased in popularity for exploring exploitation histories (Faulkner 2010, Jerardino and Navarro 2008). Fishermen in the past and in present tend to break whelks to extract meat, these fragments of shell typically outnumber the whole shells by mass in middens and are of a consistent pattern with regards to fragmentation. We found that shell breakage patterns at both sites were similar in all three middens and to contemporary discarded broken shells (author's unpublished data), and were similar to published descriptions of shell fragments from Antigua (Jones 1980). First

measurements were needed of intact shells body width and other shell characters that vary isometrically. Second, commonly found fragments that are unique and measureable were needed to estimate simple linear regression models. These regression models were then used to predict body widths from measurements of fragments.

Based on contemporary observations of fished whelk shells we are confident [PA14] that the presence of recognizable fragments indicated that the shells within the middens were deposited there after being consumed by humans. There are other possible ways that shells can arrive within the context of middens. The land hermit crab *Coenobita clypeatus* is a known archaeological and fossil scavenger (Walker 1994) [JAM15] of whelk shells. This species could be a possible vector of both delivering and removing whelks from a midden. However they are not known to break shells and are assumed not to have had a significant effect on the shell measurement data from the three middens in this study. [JAM16]. We introduce two metrics for measuring common fragments of whelk for estimating overall body widths.

Linear Regression Models to Predict Shell [PA17] Width

Following the basic methodology of previous studies on estimating shell parameters via linear regression models, an analysis was conducted to model the relationship of “aperture” and “Um-An” shell metrics to width (Figure 4-4) (Jerardino and Navarro 2008, Singh and McKechnie 2015). The “Um-An” character employs the distance measured between the umbilicus and the terminal end of the aperture (see Figure 4-4 picture ii). The second metric for measuring shell fragments was the “aperture,” and defined as the distance from the center of the collumella across the operculum to the inside edge of the lower whirl (see figure 4-4). To estimate the regression models we first measured whole shells for width, aperture, and Um-An to the nearest 0.1mm as the reference group. Those whole shell measures were then pooled to estimate the regression models (Faulkner 2010). The regression equations were then applied to all Um-An [PA18] and aperture shell fragment measurements from each excavations. Both regression models were developed in SPSS v.22, using the simple linear regression procedure. Although the aperture measure was smaller in

sample size it yielded a highly significant result for whelk width and as a predictor variable surpasses >85% limit for coefficient of determination (r^2) used in a similar study (Faulkner 2010, Statistics 2015). The prediction equation for shell width = $1.228 + 1.528 \times \text{aperture}$, the aperture measurement was highly significant $r^2=.995$, $F_{(1,87)}=2.560$, $p < 0.0004$. The prediction equation for shell width = $3.302 + 2.80 \times \text{Um-An}$, where the Um-An measurement was also highly significant, $r^2=0.957$, $F_{(1,809)} = 5.545$ $p < 0.0004$. [PA19]

Abundance:

Overall abundance of whelk material in each layer of an archaeological unit was determined by summing the counts of whole shells and fragments. Fragments for this study fell into two classes 1) those that were unique belonging to one whelk shell and therefore were counted as a single whelk, and yielded a proxy measure for shell width and 2) shell fragments that were too small or broken to be measured and could be from any number of whelks. We define measurable non-repetitive elements (MNRE) as the sum of all whole shell and measureable shell fragments that are unique and unable to be counted more than once (1). The number of individual specimens present (NISP) was a summation of all fragments (1+2) and whole shells found regardless of whether they could be measured or if they were from the same whelk. Counts of measurable non-repetitive shell elements (MNRE) yielded the amount of useable material per layer of context. Limiting counts to those whole whelk and easily distinguishable fragments likely results in a conservative estimate of the number of individual whelks within each layer. To assess potential bias in measuring fragments based on layers of context we divided the MNRE by NISP (Poteate et al. 2014) the result of which is a ratio. The higher the resulting number indicated more non-measurable elements which a source of measurement bias, while values close to one indicate that most of what was recovered was measurable.

Analysis:

We examined the exploitation history of whelks in three midden excavations at two islands and over three disjoint time periods. We examined summaries and plots of descriptive statistics and due to non-normally distributed data conducted non-parametric analyses [PA20] to explore variation in the size distribution and abundance of

whelks across layers of context. Four metrics were used to assess if there were changes over time from exploitation: maximum and mean shell width, the proportion of adults ($\geq 33\text{mm}$), and abundance of whelks in the middens. We also explored possible biases created by shell fragmentation through plots of the number of individual specimens present (NISP), the abundance of measurable non-repetitive elements (MNRE), and examined the variation in the amount of fragmented and whole shells through layers of context. Detecting a change in time at each excavation site based on shell width and abundance of shell materials within each layer was accomplished via a non-parametric test of ranks. To determine if there was a monotonic change in the average size, maximum size, and fraction of adult, MNRE, fragmentation, and NISP of whelks across layers of context we performed a Kendall's tau-b analysis (SPSS 22.0). The Kendall's tau-b measured the direction of the relationship between layers of context (+/- value) and the whelk size or abundance metrics, via a two tailed test of the null hypothesis of no trend ($\alpha=.05$).

Results:

There were differences between the two sites and among middens for measures of body size and fragmentation of shell material. Across all middens the amount of whelk shell material decreased through time.

MNRE and fragmentation

The results of the Kendall's τ_b show that within the pre-Taino midden shell fragmentation was significantly higher in older layers of context (4-1). Fragmentation in those older layers of context could be due to trampling or compaction over time. In contrast the overall fragmentation within the Amerindian and Colonial [PA21] middens on Guana Island were not significantly different across layers of context (Table 4-1). The pattern holds for the MNRE (minimum number of repetitive elements) for the Guana Island middens in that there was no significant trend through layers of context. However within the pre-Taino midden there was a decrease in the amount of MNRE in the recent layers of context (Table 4-).

Abundance and size

The abundance of whelk materials declined from the oldest to most recent layers in all middens. The Kendall's τ_b test showed significant ($p < .05$) declines from oldest to most recent layers of context in the amount of NISP (Table 4-1).

The mean shell width, fraction of adults, and maximum shell width differed between the two island groups. The two Guana Island middens showed no trend in the mean size of whelks, the maximum size, nor the fraction of adults through layers of context. However within the pre-Taino midden there was a significant decrease in the mean width, maximum width, and fraction of adults from oldest to most recent layers of context (Table 4-1).

Comparison with contemporary whelk surveys and discarded shells

There were differences in the size distributions between the discarded shells collected by fishers, the intertidal field surveys, and the archaeological middens. In the Fajardo region of Puerto Rico at the pre-Taino midden the older layers of context had more numerous and larger whelk shells. The contemporary field surveys are similar in overall distribution to the middle layers of that midden context. In stark contrast is the relatively large average size of the discarded fisher-collected shells from the same area (Figure 4-2). Additionally the present day average whelk body size from around Guana Island is lower than at any point in the Amerindian midden layers of context. While the present day average size is similar to layers 3 and 23 of context within the colonial midden it is smaller than the majority of layers in that deposit.

Discussion:

Shell midden analysis must address the facts that each excavation is different and needs to be viewed as unique glimpse into the past. Inferring fishing patterns or overexploitation based on shell widths and abundances should be done with caution. Middens can reflect the preferences and biases of the people within the locality that created them as well as the biases of the archaeologists performing the excavations (Campbell 2008, Mannino and Thomas 2002). Analyzing shell size and abundance within middens is by definition not the same as looking at similar parameters in the intertidal zone. In his study of the Indian Creek midden site in Antigua Jones (1985)

postulates that there can be many reasons for a culture or population to shift in focus from one resource to another and that assuming that what is in a midden is a reflection of the natural world at the time could lead to erroneous inference. We found that a single species displayed contrasting rates of fragmentation, abundance, and body size across several middens. Prehistoric subsistence collectors as well as taphonomic, depositional, and curating processes can affect both the amount and size of fauna analyzed within layers of excavated context. Post depositional processes such as trampling, sedimentation, and soil compaction can have differential effects on shells based on the depth at which a specimen is buried. It follows that variation in fragmentation can be a source of bias when establishing counts of individual whelks and their shell sizes. We did not find evidence in the amounts of non-repetitive measurable elements, rate of fragmentation, or number of individual specimens collected to indicate that our results were biased due to the condition of the shell material. However we found that our results for the pre-Taino midden are consistent with established theory related to the hand collection of food and “optimal foraging”. Meeting three fundamental assumptions related to optimal foraging theory has been postulated as enough evidence to infer overexploitation of taxa found within middens.

- 1) Large whelk are preferentially chosen by fishers due to better shell to meat ratio and their visibility to fishers in the intertidal wash zone
- 2) As localized depletion progresses large individuals become rare and the maximum size represented in the midden decreases.
- 3) Over exploitation can depress the average size and age structure of populations (Bell 1992, Campbell 2008, Mannino and Thomas 2002, Randall 1964).

The pre-Taino midden met the three criteria while the Colonial and Amerindian middens showed only significant decreases in shell material over time. Based on studies of the contemporary effects of hand harvesting whelks (Macfarlan et al. 2016 in progress) a likely driver of shifts in size distributions and abundance of whelks in the West Indies is exploitation. Prior archaeological research has also shown that high levels of exploitation can have detectable effects on the body size and abundance of invertebrates, while low intensity harvesting is likely to be as significant as other naturally occurring factors in the absence of collecting (Campbell 2008). The two Guana Island middens could be representative of lower harvest pressures or

smaller overall human populations contributing to the midden which resulted in fewer whelks deposited over time or be representative of a shift away from reliance on hunting and gathering food.

Large and small gastropods exploited in the Caribbean have been shown in the archaeological record to vary substantially in prevalence amongst sites and middens. The West Indian Fighting Conch, after intensive harvest pressure over the course of ~1000 years to the present day has shifted to smaller size at maturity in Caribbean coast of Panama (O'Dea et al. 2014). Nerites and whelks have been shown to exhibit both no changes in size and increase in abundance at excavations on the island of Nevis, leading researchers to conclude that harvest levels of invertebrates in the vicinity of the middens was sustainable (Poteate et al. 2014). Worldwide there is ample evidence of non-sustainable over-exploitation of mollusks. The earliest of which was a species of giant clam postulated to have been fished to near extinction in the upper Red Sea ~125,000 years ago (Richter et al. 2008). A temporally more recent study of 10,000 years of shellfish harvesting in the Northern Channel Islands of California revealed size decreases in shellfish taxa that were easy to access from the shore (Braje et al. 2012, Erlandson et al. 2011).

The decline in size and abundance within the pre-Taino midden could result from any of a number of reasons other than overexploitation. A non-human agent of change in shell middens is the Caribbean Soldier Crab or land hermit crab, *Coenobita clypeatus*, a known thief and depositor of shells from middens and naturally occurring shell deposits (author's personal observations, Walker 1994). Cultural uses for shell materials can result in a biased midden sample where the largest of organisms might be used for tool making, traded, or kept as a curio instead of being discarded. Further investigation on all marine taxa within the three excavations could answer questions related to whether there is variation in exploitation patterns across species. Although middens should not be interpreted as entirely representative of wild faunal assemblages at the time of their formation-they do allow insight and inference as to how humans interacted with their environments. In the case of whelks we detected change over time in the body size and abundance of important food item. We found differences between average body sizes within middens and contemporary field and

fisher surveys. Given these preliminary results there is compelling evidence that whelks were over-exploited at various times in the past.

Figures

Figure 4-1. Map of the region and the locations of the three excavations.

Figure 4-2. Puerto Rico, mPre[PA22]-Taino mean whelk shell [PA23]widths for the pre-Taino midden, , modern surveys, and contemporary surveys, and discarded shells. sBars indicate one standard error.

Figure 4-3. Guana Island, BVI mean whelk shell width for , Amerindian, Colonial, and contemporary whelks mean shell widths. B, bars indicate one1 standard error.

Figures

Figure 4-4. Shell measurements: (i) Um-An, (ii) width, and (iii) aperture measurement indicated by orange line.

i)

ii)

iii)

Table

Table 4-1. [PA24]Results[PA25] of the Kendall's Tau-beta test of monotonic change over time for whelk shell width, abundance metrics, and shell fragmentation rate(p-value of <.05 indicates a significant [JAM26]trend[PA27][JAM28]. [JAM29]

	Mean shell width	Fraction of adults (>33mm)	Maximum shell width	Number of Individual Specimens Present	Measureable Non-Repetitive Elements	Fragmentation	Layers of Context
Guana I. Amerindian	$\tau_b=.011$, $p=.956$	$\tau_b=-.022$, $p=.913$	$\tau_b=-.341$, $p=.090$	$\tau_b=-.398$, $p=.048$	$\tau_b=-.380$, $p=.062$	$\tau_b=.099$, $p=.622$	14
Guana I. Colonial	$\tau_b=-.200$, $p=.121$	$\tau_b=-.179$, $p=.173$	$\tau_b=.030$, $p=.817$	$\tau_b=.275$, $p=.034$	$\tau_b=.178$, $p=.174$	$\tau_b=.182$, $p=.163$	30
Puerto Rico pre-Taino	$\tau_b=.810$, $p=.011$	$\tau_b=.810$, $p=.011$	$\tau_b=.905$, $p=.004$	$\tau_b=1.0$, $p=.000$	$\tau_b=.951$, $p=.003$	$\tau_b=.810$, $p=.011$	7

Bibliography [PA30]

Allison EH, Ellis F. 2001. The livelihoods approach and management of small-scale fisheries. *Marine policy*. 2001;25:377-388.

Andrew N, Evans L. 2009. *Approaches and Frameworks for Management and Research in Small-scale Fisheries in the Developing World*. . Penang, Malaysia.: TW Center.

Andrew NL, Béné C, Hall SJ, Allison EH, Heck S, Ratner BD. 2007. Diagnosis and management of small-scale fisheries in developing countries. *Fish and Fisheries*. 2007;8:227-240.

Arango AO, Merlano JMD. 2006. Explotación, usos y estado actual de la Cigua o Burgao *Cittarium pica* (Mollusca: Gastropoda: Trochidae) en la Costa continental del Caribe colombiano. *Boletín de investigaciones marinas y costeras*. 2006;35.

Atkinson WD, Newbury SF. 1984. The adaptations of the rough winkle, *Littorina rudis*, to desiccation and to dislodgement by wind and waves. *Journal of Animal Ecology*. 1984;53:93-105.

Ballantine WJ. 1961. A biologically-defined exposure scale for the comparative description of rocky shores. *Field Studies Journal*. 1961;1:1-19.

Bell LJ. 1992. Reproduction and larval development of the West Indian topshell, *Cittarium pica* (Trochidae), in the Bahamas. *Bulletin of marine science*. 1992;51:250-266.

Béné C. 2003. When Fishery Rhymes with Poverty: A First Step Beyond the Old Paradigm on Poverty in Small-Scale Fisheries. *World Development*. 2003/06//;31:949-975.

Berkes F, Mahon R, McConney P. 2001. *Managing small-scale fisheries: alternative directions and methods*: International Development Research Centre.

Bertness MD. 1981. Predation, physical stress, and the organization of a tropical rocky inter-tidal hermit crab community. *Ecology*. 1981;62:411-425.

Bilkovic D, Roggero M. 2008. Effects of coastal development on nearshore estuarine nekton communities. *Marine Ecology-Progress Series*-.358:27.

Blick JP. 2007. Pre-Columbian impact on terrestrial, intertidal, and marine resources, San Salvador, Bahamas (A.D. 950–1500). *Journal for Nature Conservation*. 2007/10//;15:174-183.

Boulding EG. 1990. Are the opposing selection pressures on exposed and protected shores sufficient to maintain genetic differentiation between gastropod populations with high intermigration rates? In: *Progress in Littorinid and Muricid Biology*. Springer: Netherlands. p 41-52.

Boulding EG, Holst M, Pilon V. 1999. Changes in selection on gastropod shell size and thickness with wave-exposure on northeastern pacific shores. *Journal of Experimental Marine Biology and Ecology*. 1999;232:217-239.

Boulon R, Jr., Beets J, Zullo ES. 1986. Long Term Monitoring of Fisheries in the Virgin Islands Biosphere Reserve-Research Report #13.

Braje TJ, Rick TC, Erlandson JM. 2012. A trans-Holocene historical ecological record of shellfish harvesting on California's Northern Channel Islands. *Quaternary International*.264:109-120.

Braje TJDJKJME, Brendan JC. 2007. Human impacts on nearshore shellfish taxa: A 7,000 year record from Santa Rosa Island, California. *American Antiquity*. 2007:735-756.

Branch GM, Marsh AC. 1978. Tenacity and shell shape in six *Patella* species: Adaptive features. *Journal of Experimental Marine Biology and Ecology*. 1978;34:111-130.

Brosnan DM. 1992. Ecology of tropical rocky shores: plant-animal interactions in tropical and temperate latitudes. In: D M John, S J Hawkins, and J H Price, ed's *Plant Animal interactions in the marine benthos*. Clarendon Press, Oxford101–131.

Campbell G. 2008. Beyond means to meaning: using distributions of shell shapes to reconstruct past collecting strategies. *Environmental Archaeology*.13:111-121.

Campbell G. 2015. "What do I do with all these shells?" Basic guidance for the recovery, processing and retention of archaeological marine shells. *Quaternary International*.

Carrington Bell E, Denny MW. 1994. Quantifying "wave exposure": a simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology*. 1994;181:9-29.

Chiu Y-W, Chen H-C, Lee S-C, Chen CA. 2002. Morphometric analysis of shell and operculum variations in the viviparid snail, *Cipangopaludina chinensis* (Mollusca: Gastropoda), in Taiwan. *Zoological Studies-Taipei*. 2002;41:321-331.

Claudet J, Fraschetti S. 2010. Human-driven impacts on marine habitats: a regional meta-analysis in the Mediterranean Sea. *Biological Conservation*.143:2195-2206.

Claassen, Cheryl. "Temporal patterns in marine shellfish-Species use along the Atlantic coast in the Southeastern United States." *Southeastern Archaeology* 5.2 (1986): 120-37. Web.

Clench WJ, Abbott RT. 1943. The genera *Gaza* and *Livona* in the western Atlantic. *Johnsonia: Monographs of the marine mollusks of the Western Atlantic*. 1943;1:1-12.

Coates K, Jantzen-Marson C, Madeiros J, Meyer E. West Indian topshell, *Cittarium pica*, reintroduction project in Bermuda: Current status. *Proceedings of the Integrative and Comparative Biology*; 2003: Society of Integrative and Comparative Biology 1313 Dolley Madison Blvd, No 402, McLean, VA 22101 USA.

Connell JH. 1972. Community Interactions on Marine Rocky Intertidal Shores. *Annual Review of Ecology and Systematics*. 1972;3:169-192.

Crain CM, Kroeker K, Halpern BS. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology letters*.11:1304-1315.

Crowe TP, Thompson RC, Bray S, Hawkins SJ. 2000. Impacts of anthropogenic stress on rocky intertidal communities. *Journal of Aquatic Ecosystem Stress and Recovery*. 2000/10/01;7:273-297.

Davis D. 2013. Guana Archaeology-Prehistory Project Report for the October 2012 Field Season. (Report; no.).

Davis DD. 2011. Out of the Shadows: A review of the archaeological evidence for the isolation, interaction, and abandonment of the British Virgin Islands in the pre-Columbian Caribbean. 2011.

Debrot AO. 1990a. Survival, growth, and fecundity of the West Indian topshell, *Cittarium pica* (Linnaeus), in various rocky intertidal habitats of the Exuma Cays, Bahamas. *The Veliger*.33:363-371.

Debrot AO. 1990b. Temporal aspects of population dynamics and dispersal behavior of the West Indian topshell, *Cittarium pica* (L.), at selected sites in the Exuma Cays, Bahamas. *Bulletin of marine science*. 1990a;47:431-447.

- Defeo O, Castilla JC. 2005. More than one bag for the world fishery crisis and keys for co-management successes in selected artisanal Latin American shellfisheries. *Reviews in Fish Biology and Fisheries*. Aug;15:265-283.
- Denny M. 1995. Predicting Physical Disturbance: Mechanistic Approaches to the Study of Survivorship on Wave-Swept Shores. *Ecological Monographs*. 1995/11/01/;65:371-418.
- Denny MW. 2006. Ocean waves, nearshore ecology, and natural selection. *Aquatic Ecology*. 2006/12//undefined;40:439-461.
- Díaz-Ferguson E, Haney R, Wares J, Silliman B. 2010. Population Genetics of a Trochid Gastropod Broadens Picture of Caribbean Sea Connectivity. *PLoS ONE*. 2010/09/10/;5:e12675.
- Erlandson JM, Braje TJ, Rick TC, Jew NP, Kennett DJ, Dwyer N, Ainis AF, Vellanoweth RL, Watts J. 2011. 10,000 years of human predation and size changes in the owl limpet (*Lottia gigantea*) on San Miguel Island, California. *Journal of Archaeological Science*. 2011/05//;38:1127-1134.
- Espinosa F, Guerra-García J, García-Gómez J. 2007. Sewage pollution and extinction risk: an endangered limpet as a bioindicator? *Biodiversity and Conservation*. 16:377-397.
- Etter RJ. 1988. Asymmetrical developmental plasticity in an intertidal snail. *Evolution*. 1988:322-334.
- Faulkner P. 2010. Morphometric and taphonomic analysis of granular ark (*Anadara granosa*) dominated shell deposits of Blue Mud Bay, northern Australia. *Journal of Archaeological Science*. 37:1942-1952.
- Fitzpatrick SM, Kappers M, Kaye Q, Giovas CM, LeFebvre MJ, Harris MH, Burnett S, Pavia JA, Marsaglia K, Feathers J. 2009. Precolumbian Settlements on Carriacou, West Indies. *Journal of Field Archaeology*. 2009;34:247-266.
- Giovas CM, Clark M, Fitzpatrick SM, Stone J. 2013. Intensifying collection and size increase of the tessellated nerite snail (*Nerita tessellata*) at the Coconut Walk site, Nevis, northern Lesser Antilles, AD 890–1440. *Journal of Archaeological Science*. 40:4024-4038.
- Good TP. 2004. Distribution and Abundance Patterns in Caribbean Rocky Intertidal Zones. *Bulletin of Marine Science*. 2004/03/01/T00:00:00;74:459-468.

- Grenon JF, Walker G. 1981. The tenacity of the limpet, *Patella vulgata* L.: An experimental approach. *Journal of Experimental Marine Biology and Ecology*. 1981;54:277-308.
- Harley CD, Rogers-Bennett L. 2004. The potential synergistic effects of climate change and fishing pressure on exploited invertebrates on rocky intertidal shores. *California Cooperative Oceanic Fisheries Investigations Report*. 2004;45:98.
- Heller J. 1976. The effects of exposure and predation on the shell of two British winkles. *Journal of Zoology*. 1976;179:201-213.
- Helmuth B, Denny MW. 2003a. Predicting wave exposure in the rocky intertidal zone: Do bigger waves always lead to larger forces-9. *Limnology and Oceanography*. 2003/05//undefined;48:1338-1345.
- Helmuth B, Denny MW. 2003b. Predicting wave exposure in the rocky intertidal zone: Do bigger waves always lead to larger forces? *Limnology and Oceanography*. 2003;48:1338-1345.
- Hollander J, Butlin RK. 2010. The adaptive value of phenotypic plasticity in two ecotypes of a marine gastropod. *BMC Evolutionary Biology*. 2010/10//undefined;10:333.
- Jerardino A, Navarro R. 2008. Shell morphometry of seven limpet species from coastal shell middens in southern Africa. *Journal of Archaeological Science*. 2008/04//;35:1023-1029.
- Jimenez N. 2006. Caribbean/NMFS Cooperative SEAMAP Program Whelk and Finfish Assessment. 2006.
- Johannes RE. 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. *TREE*.13:243-246.
- Jones AR. Animal food and human population at Indian Creek, Antigua. *Proceedings of the Proceedings of the Eighth International Congress for the Study of Pre-Columbian Cultures of the The Lesser Antilles*, Arizona State University Anthropological Research Papers; 1980.
- Jones AR. 1985. Dietary Change and Human Population at Indian Creek, Antigua. *American Antiquity*. 1985/07/01//;50:518-536.

- Keegan WF, Fitzpatrick SM, Sealey KS, LeFebvre MJ, Sinelli PT. 2008. The Role of Small Islands in Marine Subsistence Strategies: Case Studies from the Caribbean. *Hum Ecol.* 2008/10/01/;36:635-654.
- Keegan WF, Portell RW, Slapcinsky J. 2003. Changes in invertebrate taxa at two pre-Columbian sites in southwestern Jamaica, AD 800–1500. *Journal of Archaeological Science.* 2003/12//;30:1607-1617.
- Kennaway TA, Helmer EH, Lefsky MA, Brandeis TA, Sherrill KR. 2008. Mapping land cover and estimating forest structure using satellite imagery and coarse resolution lidar in the Virgin Islands. *Journal of Applied Remote Sensing.* 2:023551-023551-023527.
- Keough M, Quinn G. 1991. Causality and the choice of measurements for detecting human impacts in marine environments. *Marine and Freshwater Research.* 42:539-554.
- Keough MJ, Quinn GP, King A. 1993. Correlations between human collecting and intertidal mollusc populations on rocky shores. *Conservation Biology.* 7:378-390.
- Kitching JA. 1976. Distribution and changes in shell form of *Thais* spp. (Gastropoda) near Bamfield, BC. *Journal of Experimental Marine Biology and Ecology.* 1976;23:109-126.
- Kitching JA, Lockwood J. 1974. Observations on shell form and its ecological significance in thaisid gastropods of the genus *Lepsiella* in New Zealand. *Marine Biology.* 1974;28:131-144.
- Kitching JA, Muntz L, Ebling FJ. 1966. The Ecology of Lough Ine. XV. The Ecological Significance of Shell and Body Forms in *Nucella*. *The Journal of Animal Ecology.* 1966/02//;35:113.
- Kostro M. 2007. Guana Island Archaeological Project, 2004-2006: An Interim Report.
- Linnaeus C. 1758. *Systema Naturae*, Ed. 10, Vol. 1. 824 pp. Salvii, Holmiae. 1758.
- Littler MM, Murray SN. 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Marine Biology.* 30:277-291.
- Macfarlan R, Forrester GE, McLean E. 2015. Isolating The Effect of Artisanal Fishing on an Intertidal Gastropod in the Caribbean. In L Creswell, editor. *Proceedings of the*

67th Gulf Caribbean Fisheries Institute. Proceedings of the Gulf Caribbean Fisheries Institute, 67th Annual Conference; 2014 November 3-7, 2014: Omnipress.

Mannino MA, Thomas KD. 2002. Depletion of a resource? The impact of prehistoric human foraging on intertidal mollusc communities and its significance for human settlement, mobility and dispersal. *World archaeology*.33:452-474.

Menge BA, Lubchenco J. 1981. Community Organization in Temperate and Tropical Rocky Intertidal Habitats: Prey Refuges in Relation to Consumer Pressure Gradients. *Ecological Monographs*. 1981/12/01/;51:429-450.

Menge BA, Sutherland JP. 1976. Species Diversity Gradients: Synthesis of the Roles of Predation, Competition, and Temporal Heterogeneity. *The American Naturalist*. 1976/05/01/;110:351-369.

Menge BA, Sutherland JP. 1987. Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment. *The American Naturalist*. 1987/11//;130:730-757.

Miller SL. 1974. Adaptive design of locomotion and foot form in prosobranch gastropods. *Journal of Experimental Marine Biology and Ecology*. 1974;14:99-156.

Moreno CA. 2001. Community patterns generated by human harvesting on Chilean shores: a review. *Aquatic Conservation: Marine and Freshwater Ecosystems*. 2001;11:19-30.

Moreno CA, Lunecke KM, xe, pez MI. 1986. The Response of an Intertidal *Concholepas concholepas* (Gastropoda) Population to Protection from Man in Southern Chile and the Effects on Benthic Sessile Assemblages. *Oikos*.46:359-364.

Nagelkerken IA, Debrot AO. 1995. Mollusc communities of tropical rubble shores of Curaçao: long-term (7+ years) impacts of oil pollution. *Marine Pollution Bulletin*.30:592-598.

Nelson T, Oxenford HA. 2012. The whelk (*Cittarium pica*) fishery of Saint Lucia: description and contribution to the fisheries sector. sector Proceedings of the Gulf and CaribFisheries Institute 65:.. 2012.

Nelson WG. 1982. Experimental studies of oil pollution on the rocky intertidal community of a Norwegian fjord. *Journal of Experimental Marine Biology and Ecology*.65:121-138.

O'Dea A, Shaffer ML, Doughty DR, Wake TA, Rodriguez FA. 2014. Evidence of size-selective evolution in the fighting conch from prehistoric subsistence harvesting. *Proceedings of the Royal Society of London B: Biological Sciences*.281:20140159.

Orensanz JM, Parma AM, Jerez G, Barahona N, Montecinos M, Elias I. 2005. What are the key elements for the sustainability of "S-fisheries"? Insights from South America. *Bulletin of Marine Science*. 2005;76:527-556.

Osorno Arango A, Díaz Merlano JM. 2006. Explotación, usos y estado actual de la Cigua o Burgao *Cittarium pica* (Mollusca: Gastropoda: Trochidae) en la Costa continental del Caribe colombiano. 2006.

Osorno Arango A, Gil Agudelo DL, Gómez Lemos LA. 2009. Plan de Investigación para la Conservación de *Cittarium pica* (Linnaeus, 1758).. INVEMAR, Serie de Publicaciones Especiales.

Palmer AR. 1990. Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). In: *Progress in Littorinid and Muricid Biology*. Springer: Netherlands. p 155-182.

Piggott JJ, Townsend CR, Matthaei CD. 2015. Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution*. Apr;5:1538-1547.

Poteate AS, Fitzpatrick SM, Clark M, Stone JH. 2014. Intensified mollusk exploitation on Nevis (West Indies) reveals ~six centuries of sustainable exploitation. *Archaeol Anthropol Sci*. 2014/06/03/:1-14.

Prowse TAA, Pile AJ. 2005. Phenotypic homogeneity of two intertidal snails across a wave exposure gradient in South Australia. *Marine Biology Research*. 2005/07//undefined;1:176-185.

Quinn GP, Keough MJ. 2002. *Experimental design and data analysis for biologists*: Cambridge University Press.

Raffaelli D, Hawkins SJ. 2012. *Intertidal ecology*: Springer Science & Business Media.

Randall HA. 1964. A study of the growth and other aspects of the biology of the West Indian topshell, *Cittarium pica* (Linnaeus). *Bulletin of Marine Science*. 1964;14:424-443.

Rhyne A, Rotjan R, Bruckner A, Thlusty M. 2009. Crawling to Collapse: Ecologically Unsound Ornamental Invertebrate Fisheries. *PLoS ONE*. 2009/12/22/;4:e8413.

Richter C, Roa-Quiaoit H, Jantzen C, Al-Zibdah M, Kochzius M. 2008. Collapse of a new living species of giant clam in the Red Sea. *Curr Biol.* Sep 9;18:1349-1354.

Rick TC, Erlandson JM. 2008. Human impacts on ancient marine ecosystems: a global perspective: University of California Press.

Robertson R. 2003. The edible West Indian “whelk” *Cittarium pica* (Gastropoda: Trochidae): Natural history with new observations. *Proceedings of the Academy of Natural Sciences of Philadelphia.* 2003;153:27-47.

Rosique J, Toro B, Marín JG, Galeano N, Correa T. 2010. Algunos lineamientos para la conservación de *Cittarium pica* en la costa Caribe del Darién colombiano. *Boletín de Antropología.* 2010;22.

Salomon AK, Tanape Sr NM, Huntington HP. 2007. Serial depletion of marine invertebrates leads to the decline of a strongly interacting grazer. *Ecological Applications.* 2007;17:1752-1770.

Schmidt et al. 2002 S, Wolff M, Vargas JA. 2002. Population ecology and fishery of *Cittarium pica* (Gastropoda: Trochidae) on the Caribbean coast of Costa Rica. *Revista de biología tropical.* 2002;50:1079-1090.

Seeley RH. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. *Proceedings of the National Academy of Sciences.* 83:6897-6901.

Serrand N. 2008. The Use of Molluscs in the Precolumbian Amerindian Lesser Antilles: Human, Animal, and Environmental Parameters (with an emphasis on metrics). *Archaeofauna.* 2008/10//;17:21-34.

Singh GG, McKechnie I. 2015. Making the most of fragments: a method for estimating shell length from fragmentary mussels (*Mytilus californianus* and *Mytilus trossulus*) on the Pacific Coast of North America. *Journal of Archaeological Science.* 58:175-183.

Southward A, White B, Vader S, Gray J, Crisp D. 1982. An Ecologist's View of the Implications of the Observed Physiological and Biochemical Effects of Petroleum Compounds on Marine Organisms and Ecosystems [and Discussion]. *Philosophical Transactions of the Royal Society of London B: Biological Sciences.* 297:241-255.

Simple linear regression using SPSS Statistics. Available from <https://statistics.laerd.com/>

Strand J, Jørgensen A, Tairova Z. 2009. TBT pollution and effects in molluscs at US Virgin Islands, Caribbean Sea. *Environment international*.35:707-711.

Toller W, Gordon S. 2005. A population survey of the West Indian topshell or whelk (*Cittarium pica*) in the US Virgin Islands. Department of Planning and Natural Resources Division of Fish and Wildlife St Thomas, Virgin Islands< <http://bcrc/bio.umass.edu/vifishandwildlife>. 2005.

Trussell GC. 1997a. Phenotypic plasticity in the foot size of an intertidal snail. *Ecology*. 1997;78:1033-1048.

Trussell GC. 1997b. Phenotypic selection in an intertidal snail: effects of a catastrophic storm. *Marine Ecology Progress Series*. 1997;151:73-79.

Trussell GC, Etter RJ. 2001. Integrating genetic and environmental forces that shape the evolution of geographic variation in a marine snail. *Genetica*. 2001;112:321-337.

Trussell GC, Johnson AS, Rudolph SG, Gilfillan ES. 1993. Resistance to dislodgment-Habitat and size-specific differences in morphology and tenacity in an intertidal snail. *Marine Ecology-Progress Series*. 1993/10//undefined;100:135-144.

Underwood A, Peterson C. 1988. Towards an ecological framework for investigating pollution. *Mar Ecol Prog Ser*.46:227-234.

Vermeij G. 1973. Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. *Marine Biology*.20:319-346.

Vermeij GJ, Williams ST. 2007. Predation and the geography of opercular thickness in turbinid gastropods. *Journal of Molluscan Studies*.73:67-73.

Walker SE. 1994. Biological remanics: gastropod fossils used by the living terrestrial hermit crab, *Coenobita clypeatus*, on Bermuda. *Palaios*. 1994:403-412.

Warburton K. 1976. Shell form, behaviour, and tolerance to water movement in the limpet *Patina pellucida* (L.) (Gastropoda: Prosobranchia). *Journal of Experimental Marine Biology and Ecology*. 1976/09//;23:307-325.

Weaver PL, Ramirez JL, Jorge L, Rivera C, International Institute of Tropical F. 1999. Las Cabezas de San Juan Nature Reserve (El Faro): US Department of Agriculture, Forest Service, International Institute of Tropical Forestry. [http://www.fs.fed.us/global/iitf/pubs/gtr_iitf005_\(62\).pdf](http://www.fs.fed.us/global/iitf/pubs/gtr_iitf005_(62).pdf).

Wing ES. 2001. The sustainability of resources used by Native Americans on four Caribbean islands. *International Journal of Osteoarchaeology*. 2001;11:112-12.