REPORT

S.R. Wing · E.S. Wing

Prehistoric fisheries in the Caribbean

Received: 1 October 1999 / Accepted: 19 September 2000 / Published online: 19 May 2001 © Springer-Verlag 2001

Abstract We studied faunal remains from archaeological sites on five Caribbean islands, each with an early (1,850-1,280 years B.P.) and late (1,415-560 years B.P.)occupation. On each of these islands (Puerto Rico, St. Thomas, St. Martin, Saba, and Nevis), the mean size of reef fishes in the faunal remains declined from the early to the late occupation. The large samples from sites on St. Thomas and Nevis allowed examination of the size distribution of individual taxa. Samples of obligate reef fishes (Scaridae, Acanthuridae, Lutjanidae, and Serranidae) showed large reductions in size between the early and late occupations. Samples of facultative reef fishes (Carangidae and Clupeidae) showed little change in size frequency distribution. The percentage of estimated reef fish biomass in the total aquatic faunal record sharply declined in the samples from four of the islands, while on Nevis there was a slight increase. The mean trophic level of reef fishes declined from the early to the late occupations on each island. Together these patterns suggest that populations of reef fishes adjacent to occupation sites on these islands were heavily exploited in prehistoric times. Such exploitation resulted in shifts in size structure and species composition among the reef fish fauna. On some islands the decline in reef fish resources corresponded with a shift towards greater exploitation of pelagic species.

Keywords Caribbean · Prehistoric fisheries · Species shift · Trophic level analysis

S.R. Wing (\boxtimes)

Department of Marine Science, P.O. Box 56, University of Otago, Dunedin, New Zealand E-mail: steve.wing@stonebow.otago.ac.nz

Tel.: +11-64-34799038 Fax: +11-64-34798336

E.S. Wing

Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611-7800, USA

Introduction

Efforts to understand modern patterns in reef fish populations in the Caribbean and other tropical reef systems are hampered by a lack of understanding of historical patterns of exploitation (Jackson 1997). People have fished coral reefs for at least 2,000 years in the Caribbean. However, few fisheries have an historical record dating back more than 50 years (Pauly et al. 1998). As a consequence, very little is known about how great the effects of human exploitation have been on marine systems in the Caribbean or in other areas. To what extent have the ghosts of past exploitation influenced modern patterns of distribution and abundance? Historical records suggest that profound changes have occurred since European contact, but what state were Caribbean marine systems in before contact? Tangible evidence for the history and pattern of exploitation of these resources can be examined in the form of faunal remains excavated from archaeological sites. These fragmentary remains include vertebrate skeletal specimens, molluscan shells, and crab exoskeletons.

Fish and shellfish were the most important animal protein sources in the subsistence of the human colonists of the Caribbean islands. These colonists were horticulturists, they produced pottery, and began their migration into the West Indian islands from northwestern South America about 200 years B.C. They moved up the Lesser Antillean island archipelago and ultimately throughout the Greater Antilles and the Bahamas by the time of European expansion in 1492 (Rouse 1992). The first colonists found both volcanic and limestone islands populated by relatively few land vertebrates and those that they found were small. Among the most abundant land animals used by people colonizing the Lesser Antilles were rice rats, several species of pigeons, landnesting sea birds, and land crabs. The sea, however, was a source of diverse animal species which provided most of the protein in the diets of the people living along the island coasts during prehistoric times.

Cultural development during the Ceramic Age can be divided into two periods: the Saladoid and the Post-Saladoid (Rouse 1992). The Saladoid lasted from about 200 years B.C. to A.D. 600 in the Lesser Antilles and eastern Greater Antilles and is characterized by cultivation of crops and fruit trees, feasting on land crabs, and fishing focused on species associated with coral reefs. This culture was followed by two Post-Saladoid cultures, the Ostionoid in the Greater Antilles and the Virgin Islands and the Troumasoid in the Lesser Antilles. Archaeologists have documented an increase in the numbers and sizes of sites during the Post-Saladoid. The Ostionoid culture of the Greater Antilles is associated with major landscape changes, including terraced agricultural fields and constructed ball courts or plazas. The spread of sites into western Greater Antilles and the Bahamas also occurred during this time period. These changes indicate more and larger permanent settlements and dispersal of people spurred by population growth. Accompanying these population changes is evidence of stress on animal resources. The Native American population of the West Indies did not survive long after their encounter with Europeans.

Archaeological material rarely allows close, year-by-year tracking of the catch as is possible in the analysis of present-day fisheries (Pauly et al. 1998). Furthermore, archaeological deposits are not a completely faithful representation of the whole spectrum of animals used. Despite these unavoidable drawbacks of archaeological deposits, patterns observed in size and species composition, as well as trophic level analysis provide a method for gaining a better understanding of prehistoric fisheries.

This paper focuses on the prehistoric fisheries during the Ceramic Age and the evidence of stress on these resources as seen in the animal remains excavated from archaeological sites. We analyzed changes in body size and species composition, and we applied mean trophic level analysis to the identified remains from archaeological deposits. This analysis takes into account the numbers and sizes of represented species in the catch and their position in the food web (Pauly et al. 1998). It

Table 1 Archaeological sites upon which this paper is based, their location, approximate dates of deposits, archaeologists, and reference to faunal studies

Island	Site name/context	Date в.р.	Archaeologist	Reference
Puerto Rico	Maisabel			
	32°N 32°E, level 20-40	1350	P. Siegel	deFrance (1990)
	96°N 13°W, level 0–150	1850	P. Siegel	deFrance (1990)
St. Thomas	Tutu		C	` '
	2,036°N 1,842°E, middle and base	560	E. Righter	
	2,044°N 1,837°E, zone I	1,380	E. Righter	
St. Martin	Hope Estate		· ·	
	Units A3 and A5, levels 3 and 4	1415	J. Haviser	Wing (unpublished data)
	Unit 16, zone 18	1760	C. Henocq	Wing (unpublished data)
Saba	Kelbey's Ridge			<i>,</i>
	KR IÍ	600	M. Hoogland	Wing (1996)
	KR I	1280	M. Hoogland	Wing (1996)
Nevis	Indian Castle (GE-1)			
	95, -2, level 20-40	1280	S. Wilson	
	55, -15, level 20-40, 50-60	1660	S. Wilson	

allows an assessment of the ecological structure of the catch; fishing technology of the targeted species; over-exploitation of local territorial species in successive pairs of deposits; and compensation for decline in some resources by shift in the focus of the fishery.

Methods

This study is based on identification and analysis of samples of animal remains excavated from five pairs of archaeological deposits from Caribbean islands (Table 1). Some of these samples are successive deposits in a single cultural period, such as the sites of Maisabel on Puerto Rico and Hope Estate on St. Martin, which were occupied during the Saladoid period, while Kelbey's Ridge on Saba is entirely a Post-Saladoid occupation. The other sites, Tutu on St. Thomas, the neighboring sites of Hichman's and Indian Castle on Nevis, represent successive deposits by people with Saladoid culture followed by Post-Saladoid culture. The two sites on Nevis are located side-by-side facing the same bay and presumably fishing on the same reef. All of the samples are refuse deposits or middens of a household.

The archaeological sites from which the faunal samples are derived were excavated by different archaeologists using basically the same excavation procedures. Usually, though not always, a grid is superimposed on an archaeological site and units that measure 1×1 m, or similar increments, are excavated in either arbitrary levels or by zones, defined by changes in the color of the soil. The entire deposit is rarely sieved with fine-gauge screen. More often a sub-sample is taken from a square measuring 0.5×0.5 m within each $1-\text{m}^2$ unit. This sub-sample is recovered with fine-gauge screen expressly for faunal analysis.

Critical features of these samples which made them adequate for this research were their size and the strategy used to recover them from the archaeological deposit. Recovery of samples with fine-gauge screen sieves (at least 1/8th-inch gauge) is important for unbiased representation of the full range of sizes of species and individuals preserved in the deposit. Fragmentary vertebrate remains were sorted from the archaeological matrix, which included soil, charcoal, and cultural artifacts.

Identification and quantification of the animal remains followed accepted zooarchaeological procedures (Reitz and Wing 1999). Identifications of the remains were made by comparison with modern reference material at the Florida Museum of Natural History. Efforts were made to identify all skeletal elements. Quantification of the identified remains included a count and weight of identified specimens and calculation of the minimum numbers of individuals (MNI). MNI is the smallest number of individuals that is necessary to account for all of the skeletal ele-

ments of a particular taxon found in the sample (Reitz and Wing 1999). MNI reduces biases resulting from the inclusion of species in the sample with different numbers of identifiable elements, for example a snail and a fish.

Measurements of skeletal dimensions were taken to estimate the sizes of the fishes in the deposits. Widths of unbroken vertebral centra correlate well with body weight and can be used as a proxy for sizes of the individuals in the prehistoric catch. Size distributions of vertebral measurements of scarids, acanthurids, serranids, lutjanids, carangids, and clupeids from early and late deposits were compared. To facilitate comparisons of the size distributions, we normalized the data by dividing the frequency distribution by the sample size. Each frequency was scaled to total sample size which makes it possible to compare distributions with different sample sizes.

Measurements (in millimeters) of modern reference skeletons that correlate allometrically with body weights (in grams) were taken to generate allometric constants (Table 2). These allometric constants were then applied to measurements of the archaeological bone to estimate live body weight of species represented in the faunal samples. We used estimates of average body weight multiplied by the calculated MNI of each taxon to estimate biomass contribution of each family or group of families to the prehistoric catch.

Estimates of biomass were used in a modification of the mean trophic level analysis proposed by Pauly et al. (1998). Mean trophic level analysis includes the position in the food web of each taxon and its biomass contribution to the catch on a regional or global basis (Pauly et al. 1998). Pauly et al. established a scale of trophic levels from 1 for primary producers to 4.6 for top predators, such as tunas and snappers. The trophic level values for each taxon are published on the Internet (www.fishbase.org) and the procedures for using them are described by Pauly et al. (1998).

We modified these procedures for application to archaeological data. The vast majority of aquatic vertebrates were fishes. The estimated biomass was multiplied by the trophic level value for the taxon using the values published on the Internet. The taxa were grouped according to the habitat in which the animals are typically found. The mean trophic level was calculated by dividing the sum of the trophic levels for all taxa in a group by their total biomass.

An exception to this procedure was followed in the calculation of biomass of the two large aquatic vertebrates, Caribbean monk seal and sea turtle. They are represented in the sites by small fragments: a tooth, a phalanx, and a shell fragment. It is not possible to estimate total weight from such fragmentary remains. Furthermore, there is reason to believe that these large animals were shared throughout the community. The fragments found in the sample are probably only the remains of the discarded portion allotted to one group in the community. If the entire carcass was discarded in the studied deposit one would expect more of its remains to be preserved and represented in the sample. The possibility exists that the large animals were butchered at the shore and only meat was taken back to the home site. This alternative cannot be tested easily. Rather than attempting to estimate the entire body weight for each of these large marine vertebrates, we estimated the amount of meat that would have adhered to the recovered remains. This estimated weight was then multiplied by the trophic level following the same procedure described above.

Table 2 Allometric constants used in estimating body weight (Reitz and Wing 1999). These use the formula $\log Y = \log a + b(\log X)$, where X is the measurement or weight of the skeletal

In addition to calculating the mean trophic levels for the entire aquatic fauna, we subdivided the vertebrate assemblages into two groups: reef fishes and inshore and pelagic vertebrates. We then examined the changes in mean trophic level in successive deposits for each component of the aquatic fauna. Details of these data can be found in Wing (2001). Reef fishes are those listed by Sale (1991) as typically associated with coral reefs. Inshore and pelagic vertebrates include all aquatic species other than obligate reef fishes. This component includes sea turtles, monk seals, herrings, needlefishes, snook, mullets, and tunas. In this paper, aquatic fauna includes only aquatic vertebrates even though marine mollusks played an important role in the prehistoric economies of the Caribbean.

Results

Consistent differences are evident between the faunal samples from the early and late deposits excavated from the study sites. The estimated average weight of reef fishes (Fig. 1) and the size distribution of individual obligate reef taxa decreased through time at the sites on all five islands (Figs. 2 and 3). However, no change was observed in the size distribution of facultative reef fishes (Fig. 4). Other differences between the early and late deposits were decreased contribution of reef fishes to the total estimated aquatic vertebrate biomass (Table 3; Fig. 5) except in the two deposits from Nevis. The mean trophic level of reef fishes (Table 4; Fig. 6) declined through time and was accompanied by a change in the taxa that dominated the fish fauna (Table 5).

Decrease in average weight of reef fishes

Data from pairs of deposits allow observations on trends of change. One fundamental change that was found in all samples was a decrease in the estimated average weight of reef fishes through time at each location (Fig. 1). Common reef fishes in the early deposits at Tutu had vertebral measurements with means between 5 and 7 mm that were predicted to weigh between 437 and 1,024 g. These same fish families in the later deposits had mean vertebral widths of 3 mm that were estimated to weigh 120 g. Large serranids and lutjanids from the early deposit at Tutu had vertebral widths up to 22 mm that were estimated to weigh as much as 18.5 kg. Deposits from islands were used as replicates for the paired time-period comparisons. A t-test of these comparisons indicates that this change is significant (t = 2.99, df = 4, P = 0.04).

element or shell and Y is the estimated body weight derived from using the appropriate allometric constants. Length in mm, weight in g, unless indicated otherwise

Measurement	n	Slope b	Y intercept a	r^2
X = skeletal weight of mammals in kg: Y = total weight of mammals in kg	97	0.90	1.12	0.94
X = skeletal weight of turtles in kg: $Y =$ total weight of turtles in kg	26	0.68	0.51	0.55
X = width of teleost atlas: $Y =$ total weight of fishes	43	2.53	0.872	0.87
X = aperture height of marine snails: $Y =$ total weight of marine snails	59	1.93	-1.64	0.96
X = shell weight of marine snails: $Y =$ total weight of marine snails	59	1.01	0.164	0.99
X = shell weight of marine bivalves: $Y = $ soft tissue weight of marine bivalves ^a	80	0.68	0.018	0.83

^a Estimated soft tissue weight and shell weight need to be added to obtain total weight

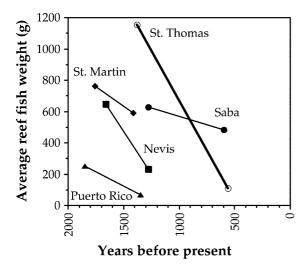


Fig. 1 Decline through time in mean reef fish estimated weight (g) in archaeological deposits on five Caribbean islands

Size frequency of individual taxa

We examined the size distribution of six common taxa from the large samples from the Tutu site and the neighboring sites on Nevis. We observed a shift to smaller sizes in the size frequency distribution of Scaridae (Fig. 2a), Acanthuridae (Fig. 2b), Serranidae (Fig. 3a), and Lutjanidae (Fig. 3b). Mean vertebral width measurements were smaller and the large-size classes were underrepresented in the later deposits. No such changes were seen in the vertebral measurements for Carangidae and Clupeidae (Fig. 4a, b).

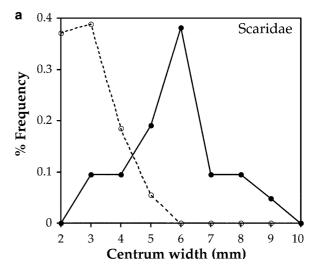
The behaviors of these six families of fishes differ. Scarids, acanthurids, lutjanids, and serranids are obligate reef taxa and tend to be territorial. Scarids and acanthurids are either herbivores or omnivores. Lutjanids and serranids include large predatory species. Both carangids and clupeids are facultative reef taxa. Some carangid species are top predators, while others, such as *Selar* and *Decapterus*, feed on plankton and other small organisms.

Decrease in percent reef fish biomass

The percent of estimated reef fish biomass in the total aquatic vertebrate biomass decreased in the later deposits of all sites except the pair from the coast of Nevis (Table 3; Fig. 5). This decrease is statistically significant (chi square, P < 0.05) for all pairs except those from Nevis and the site of Hope Estate. As a corollary to this result, we saw a trend for an increase in the estimated biomass of inshore and pelagic fishes as a percentage of the total estimated aquatic vertebrate biomass in all pairs of deposits, except the pair of sites on Nevis.

Decrease in mean trophic level of reef fishes

The decreases in the size of reef fishes and changes in the species composition affected the mean trophic level of



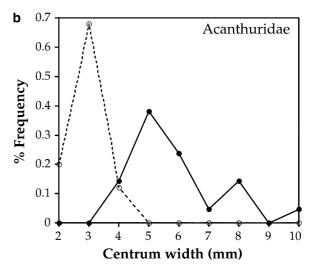


Fig. 2 Normalized size frequency of vertebral centra for a Scaridae from the early (1380 years B.P., n=21) and late (560 years B.P., n=53) St. Thomas deposits and **b** Acanthuridae from the early (1660 years B.P., n=21) and late (1280 years B.P., n=25) Nevis deposits. Solid line is the size frequency of fishes in early deposits and dashed line is the size frequency of fishes in late deposits. Values near each line are means and ranges for each time period

this component of the aquatic fauna. Omnivores, such as scarids, acanthurids, and balistids, have trophic level values between 3 and 3.5, while carnivores, such as serranids and lutjanids, have trophic levels between 3.8 and 4.6. The mean trophic level of the reef fish component in each site declined in the later deposits (Table 4; Fig. 6). A t-test of paired comparisons indicates that these changes are significant (t = 5.49, t = 4, t = 0.006).

Taxa that dominate the mean trophic level

While vertebrate assemblages in most coastal West Indian sites were similar, they differed in the dominant taxa, where dominance is defined as those taxa whose trophic level was 10% or more of the total mean trophic

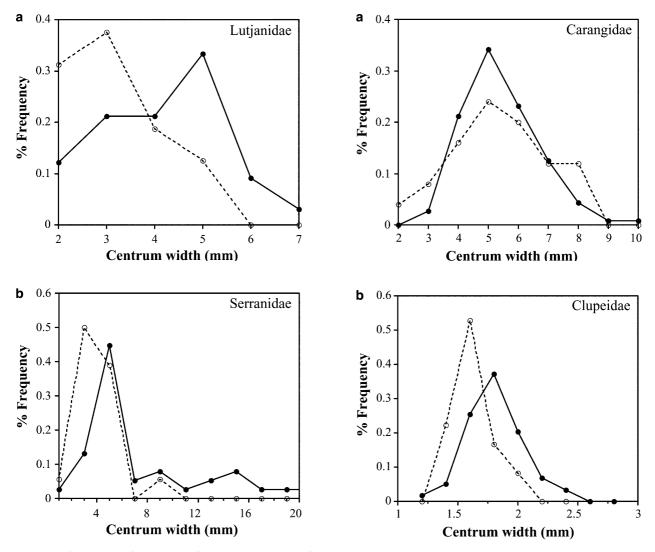


Fig. 3 Normalized size frequency of vertebral centra for **a** Lutjanidae from the early (1380 years B.P., n=35) and late (560 years B.P., n=18) St. Thomas deposits and **b** Serranidae from the early (1380 years B.P., n=37) and late (560 years B.P., n=16) St. Thomas deposits. Solid line is the size frequency of fishes in early deposits and dashed line is the size frequency of fishes in late deposits. Values near each line are means and ranges for each time period

Fig. 4 Normalized size frequency of vertebral centra for a Carangidae from the early (1380 years B.P., n = 254) and late (560 years B.P., n = 25) St. Thomas deposits and **b** Clupeidae from the early (1380 years B.P., n = 59) and late (560 years B.P., n = 38) St. Thomas deposits. Solid line is the size frequency of fishes in late deposits and dashed line is the size frequency of fishes in early deposits. Values near each line are means and ranges for each time period

level (Table 5). In the later deposits at Maisabel no reef fish taxon represented as much as 10% of the total trophic level for vertebrates. At Tutu and Kelbey's Ridge, serranids that dominated the early samples were less dominant or absent in the later samples. Scombrids and other offshore pelagic species predominate in most of the later deposits.

Discussion

Differences exist between the data available from modern and archaeological fisheries. Modern fisheries can rely on actual annual catch statistics, but archaeological

samples do not lend themselves to such detail. The scale of the data is also quite different. Modern catch data are expressed in tons per year while archaeological data are estimated in kilograms of the refuse from catches made over much longer time periods. Though the prehistoric colonists of the West Indies were accomplished mariners, they probably caught and gathered resources close to the home site. Simple energy expenditures, before boats were powered by wind or fossil fuel, is expected to have precluded regular fishing far from the home site. This supposition is supported by the absence of deep-sea fishes in archaeological deposits. The value of archaeological materials is that they provide a glimpse into the past and the conditions that prevailed before factory

Table 3 Summary of estimated biomass (in g) for vertebrates typically found among coral reefs and in inshore/pelagic waters. The percent of estimated biomass for each component of the total aquatic vertebrate fauna is presented

Site/period	Reef biomass	(%)	Inshore/pelagic biomass	(%)	Total
Maisabel, Puerto Rico					
Late	1,296	14	7,953	86	9,249
Early	8,333	61	5,297	39	13,630
Tutu, St. Thomas					
Late	6,274	31	14,049	69	20,323
Early	65,831	85	11,645	15	77,476
Hope Estate, St. Martin					
Late	15,939	65	8,590	35	24,529
Early	17,502	70	7,449	30	24,951
Kelbey's Ridge, Saba			,		
Late	58,985	73	21,372	27	80,357
Early	129,592	92	10,627	8	140,219
Indian Castle, Nevis	,		,		,
Late	24,956	74	8,662	26	33,621
Hichman's, Nevis	,		,		,
Early	24,230	70	10,301	30	34,531

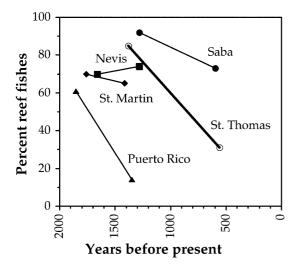


Fig. 5 Change through time in percent biomass of reef fish in total biomass of aquatic vertebrates for each of the sites on the five Caribbean islands

ships combed the oceans and extracted animals in masses from all water depths. Archaeological data represent catches by subsistence or artisanal fishermen who aimed at providing fish for the family or the community. Archaeological deposits provide data on a fishing enterprise that was focused and small scale. Animal remains from successive deposits can show the effects of changes in technology and the impact of human predation on local animal populations.

Cultural and ecological differences and similarities existed between the study sites, which influenced the resources used and refuse recovered. The length of time of continuous occupation and the size of the population deriving food resources from the coastal waters are factors in the degree of exploitation of resources. The Tutu site is the only one that was occupied continuously over 800 years, encompassing cultural change from Saladoid to Post-Saladoid. The neighboring sites on the southeastern coast of Nevis had approximately 400 years of

Table 4 Summary of the mean trophic level for early and late components of each site. The mean trophic level values are for vertebrates only

Site/period	Mean trophic level			
	Reef fishes	Inshore/ pelagic	Aquatic vertebrates	
Maisabel, Puerto Rico				
Late	3.59	3.50	3.51	
Early	3.68	3.29	3.53	
Tutu, St. Thomas				
Late	3.59	3.40	3.46	
Early	3.76	3.83	3.77	
Hope Estate, St. Martin				
Late	3.52	3.59	3.54	
Early	3.58	3.25	3.48	
Kelbey's Ridge, Saba				
Late	3.50	3.93	3.61	
Early	3.59	3.28	3.57	
Indian Castle, Nevis				
Late	3.44	3.70	3.51	
Hichman's, Nevis				
Early	3.59	3.74	3.64	

occupation. The two sites on Nevis were preceded by an earlier Archaic occupation that was not as big a site as the subsequent ones and consequently may not have impacted the resources as intensively. The other three study sites were occupied during a single cultural period that lasted approximately 300–700 years. The data show that the impact on resources may be greater where exploitation was more sustained and intensive.

The sizes of the islands and ecological conditions around the site can also influence the availability of resources. One site is on the large island of Puerto Rico, which is 8,900 km² in area, while at the other extreme is the one on the tiny island of Saba, which is only 13 km² in area. These differences affect the size of the island shelf, the amount of fresh-water runoff, size of estuaries, and the abundance of land animals that were available for capture or management, and, therefore, reduce some of the pressure on marine resources. The other islands

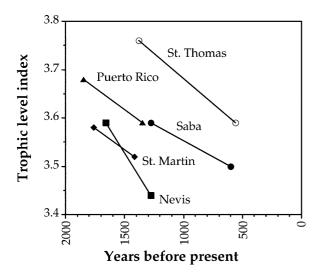


Fig. 6 Change through time in mean trophic level of reef fishes from each of the sites from the five Caribbean islands. The decline is significant (t = 5.43, df = 4, P = 0.006)

are intermediate in size. St. Thomas (70 km² in area) is located in the relatively shallow waters around the Virgin Islands. St. Martin and Nevis are 88 and 130 km² in area, respectively and are surrounded by deep ocean waters. Two sites, Tutu (St. Thomas) and Hope Estate (St. Martin), are located approximately 2 km inland. The other sites are situated directly on the coast.

Despite the differences between the islands and the locations of the archaeological sites, similar patterns of exploitation and change between the early and late deposits are evident. Preliminary information from other sites supports this information. By all measures, reef fishes contributed most to the aquatic vertebrates in the early deposits and were clearly the focus of the fishing enterprise. However, the reef fish component of these sites changed through time at each site. Decreased mean trophic levels in the later deposits encompass other measures of change such as decrease in the size of fishes and decline in the relative abundance of predatory species high

in the food web. These changes have all the characteristics of overfishing observed in modern-day examples (e.g., Russ 1991; Sale 1991; Roberts 1995). Comparisons of fished and unfished reefs show declines in fish biomass and a disproportional decline in predatory fishes such as serranids, lutjanids, and haemulids, relative to omnivores and herbivores, such as scarids and acanthurids. A study of trap fishing on two reefs in Haiti showed that the "modal sizes of scarids and chaetodontids (the most abundant groups in the catch) were significantly lower in the more heavily exploited reef" (Russ 1991). The changes we observed among obligate reef taxa are consistent with "growth overfishing" that occurs when "fish are caught before they have time to grow" (Russ 1991).

To understand the causes of these changes, we must weigh all of the variables including intensity of exploitation by growing human populations, fishing technology and its development, and the resource base of the different islands. For example, the reef fishes from the later deposits at Tutu show a particularly great decline in size. This is accompanied by a profound decline in the mean trophic level of reef fishes during the occupation. Herrings rather than tuna appear to have supplemented the decreased reef fish resources in the later time period at Tutu, reducing the mean trophic level for aquatic vertebrates at that site. The people living at the other sites (Maisabel, Hope Estate, and Kelbey's Ridge) initially overexploited their nearby reef resources but apparently made the transition to catching off-shore, large-fish resources with the result of maintaining a productive but changed fishing economy. The neighboring sites on Nevis appear to have overfished their reef fish resources but maintained a stable tuna fishery throughout the occupation. Easier access to tuna may have been the local conditions that bring them closer to shore on Nevis than on other islands.

While our observations suggest direct evidence for heavy exploitation of reef fish resource by Native Americans in the Caribbean, several alternative explanations should be discussed. Changes in size and species composition may reflect a change in fishing technology.

Table 5 The dominant taxa in each faunal sample are considered to be those that make up < 10% of the total vertebrate mean trophic level. They are listed in order of decreasing dominance

Site/period	Dominant reef taxa	Dominant inshore/pelagic taxa
Maisabel, Puerto Rico		
Late	_	Scombridae; Belonidae
Early	Lutjanidae; Balistidae; Haemulidae	Scombridae; Centropomidae
Tutu, St. Thomas		
Late	Lutjanidae	Carangidae; Scombridae; Rajiformes
Early	Epinephelus sp.; Labridae	_
Hope Estate, St. Martin		
Late	Scaridae; Labridae; Haemulon sp.; Epinephelus sp.	Scombridae
Early	Scaridae; Serranidae; <i>Lutjanus</i> sp.	Belonidae
Kelbey's Ridge, Saba		
Late	Scaridae; Acanthurus sp.; Balistidae; Serranidae	Chondrichthyes
Early	Serranidae; Scaridae; Balistidae; Labridae	_
Indian Castle, Nevis		
Late	Serranidae; Balistidae; Scaridae	Scombridae
Hichman's, Nevis		
Early	Serranidae; Scaridae	Scombridae

While this is a possibility, it is likely that shifts in fishing technology that target smaller and lower-trophic-level fishes would be a response to a decline in the abundance of large predatory fishes. The observed size changes could be caused if preservation of remains was biased towards remains of smaller-sized organisms in the later deposits. However, we would have expected a similar bias between obligate and facultative reef fishes, but we did not observe such change in the facultative group. Technology has implications for what animals were targeted and changes in exploitation through time, both of which will affect the mean trophic level. Each deposit examined in this study includes both carnivores and herbivores which indicates that a variety of catch techniques were probably used, such as hook and line, nets, and traps. No actual remains of fishing equipment have been found. Therefore interpretation of what techniques may have been used is based on fish behavior and traditional catch methods. Traps, typically used today to catch reef fishes, attract fishes seeking a place to hide and fish hunting the trapped prey items. One characteristic of fishes caught in traps is their uniform size. A typical curve of vertebral measurements of unidentified fishes (probably a cross section of the identified species) has a peak around 1-2 mm, a second peak between 5 and 7 mm, and a few records from 9-13 mm and occasionally larger. The smallest fishes include clupeids and exocoetids. Those fishes intermediate in size represent the bulk of the reef fishes, and the largest fishes are primarily predators. The really small fishes were probably caught with nets. Those within the second peak are primarily reef fishes and may have been caught in traps. The large fishes, usually serranids, lutjanids, carangids, and scombrids, were probably caught with hook and line. Large predatory fishes represented in the later deposits were typically tuna and may have been caught with hook and line.

Shifts in size and species composition could be a response to a large-scale environmental change. If environmental factors were responsible for the observed changes, we would expect those changes to have occurred at approximately the same time in the northeastern Caribbean. Instead of a change affecting the reefs at one time period, the evidence indicates change after a period of exploitation at different times. The magnitude of the change in reef fishes appears to relate to the length of time of human occupation and the intensity of the exploitation of the fishing resources. Shifts in size could be attributed to evolutionary responses to exploitation. Trophic level analysis may be insensitive to changes in sizes of exploited fishes (Caddy et al. 1998, but see Pauly et al. 1998). However, we observed both a decrease in size and trophic level, suggesting that the two are not confounded.

This study showed that people fishing at a subsistence level can have a large effect on the composition of the fishery resources they exploit. In marine systems such as the Caribbean, this exploitation had a long history that began before the time of European contact. Patterns in the aquatic faunal remains suggest that as reef resources became stressed offshore fisheries became more important to subsistence. The mean trophic levels of aquatic vertebrates sampled from study sites were much higher than the values published by Pauly et al. for modern fisheries (1998). Though we saw declines that suggest population and ecosystem response to heavy exploitation of reef fishes, these were generally compensated for by a change in the fishing focus. Therefore the mean trophic level values fall between extremes of 3.46 and 3.77, depending on the apparent success of the offshore fishing enterprise. These data offer a glimpse into the history of exploitation of reef fish resources in the Caribbean and a baseline for fisheries exploitation in this region.

Acknowledgments This research was supported by National Science Foundation grant BNS 8903377, Virgin Islands Division of Archaeology and Historic Preservation, l'Association Archéologique Saint Martin, and funds from Samuel Wilson. We are also grateful to the archaeologists who entrusted faunal samples to us for study. This work could not have been accomplished without the help with identifications from Susan deFrance, Laura Kozuch, Sylvia Scudder, and focusing ideas through discussions with Elizabeth Reitz. They are all gratefully acknowledged. We are also grateful to the reviewers and editors for their advice and assistance in improving this manuscript.

References

Caddy JF, Csirke J, Garcia SM, Grainger RJR (1998) How pervasive is "Fishing down marine food webs"? Science 282:1383–1387

deFrance SD (1990) Zooarchaeological investigations of an early ceramic age frontier community in the Caribbean, the Maisabel site, Puerto Rico. Antropológica 73–74:3–180

Jackson JBC (1997) Reefs since Columbus. Coral Reefs 16:523–532
Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr (1998)
Fishing down marine food webs. Science 279:860–863

Reitz E J, Wing E S (1999) Zooarchaeology. Cambridge University Press, Cambridge

Roberts CM (1995) Rapid build-up of fish biomass in a Caribbean marine reserve. Cons Biol 9(4):815–826

Rouse I (1992) The Tainos: rise and decline of the people who greeted Columbus. Yale University Press, New Haven

Russ GR (1991) Coral reef fisheries: effects and yields. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp 601–635

Sale PF (1991) Ecology of coral reef fishes. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp 3–15

Wing ES (1996) Vertebrate remains excavated from the sites of Spring Bay and Kelbey's Ridge, Saba, Netherlands West Indies. In: Hoogland MLP (ed) In search of the native population of pre-Columbian Saba (400–1,450 A.D.). PhD Thesis, University of Leiden, pp 261–279

Wing ES (2001) The sustainability of resources used by Native Americans on four Caribbean islands. In: Anderson A, Leach F (eds) Symposium on Archaeozoology of Oceanic Islands. Int J Osteoarchaeol (in press)