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Sandrine Grouard *Muséum national d'Histoire naturelle*, grouard@mnhn.fr

Sophia Perdikaris University of Nebraska-Lincoln, sperdikaris2@unl.edu

Nídia Cristina Espíndola Rodrigues Muséum national d'Histoire naturelle

Irvy R. Quitmyer Florida Museum of Natural History

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Special Issue Paper

Size Estimation of Pre-Columbian Caribbean Fish

Sandrine Grouard, Sophia Perdikaris, Nídia Cristina Espíndola Rodrigues, Irvy R. Quitmyer

Abstract

In this contribution, we present a methodological approach to the identification of pre-Columbian Caribbean fisheries and examine the interrelationships of exploitation according to size for eight fish families, in a diachronic perspective for the Lesser Antilles. Based on the principles of size and growth allometries, biometric repositories have been reconstructed for modern families that represent different ecological environments: Holocentridae, Serranidae, Carangidae, Lutjanidae, Haemulidae, Scaridae, Acanthuridae, and Scombridae. The measured fish bone elements were selected based on their robustness and potential for recovery at archaeological sites. This resulted in a sample size totaling 563 modern osteological specimens, which provided reconstructed standard, fork, total lengths (SL, FL, TL), and body mass (BM) of fish. The calculations were based on 21,437 measurements and 5,889 log-linear and exponential equations. These formed the comparative baseline for the archaeoichthyofaunal bone samples. The zooarchaeological ichthyofauna studied by Funding information the authors derive from 142 assemblages and 11 major islands following the eastern Fondation Fyssen; ATM Biodiversité of MNHN and western arcs of the Lesser Antilles: Saint-Martin, Barbuda, Antigua (including Long Island), Guadeloupe (Grande-Terre, Basse-Terre, Les Saintes, Islets from Cul-de-Sac-Marin, la Désirade, Petite Terre, and Marie-Galante), and Martinique. Previous zooarchaeological analyses by the same authors identified 1,050,649 specimens of which 397,803 were fish. Among them, the skeletal remains of Holocentridae, Serranidae, Carangidae, Lutjanidae, Haemulidae, Scaridae, Acanthuridae, and Scombridae bones were measured, and biometric constants were applied. During the pre-Columbian period in the Caribbean, the length distribution curves possibly represent anthropogenic selections that follow statistical normal, Poisson, or bimodal distributions. Coral reef fish became increasingly important in subsistence, but fish sizes from all ecosystems decreased over time. From the estimates of zooarchaeological fish size and the ethnoarchaeological, historical, ethnographical, and biological sources, it was possible to infer the various strategies and equipment used by the Amerindian fishermen. It is likely that the same triad of practices (hooks/lines, nets, and traps) survived the passage of time and emerged to be among the most popular fishing techniques used by modern fishermen in the Lesser Antilles.

Keywords

Biometrics, Lesser Antilles, Pre-Columbian, Fish size, Palaeofishery, Zooarchaeology, Archaeoichthyology

Introduction

The subsistence quest of pre-Columbian Antillean populations is fundamentally linked to island environmental biodiversity and marine resources (Wing and Wing, 1995, 2001). Each settlement features unique choices that are a result of local availability and biodiversity. In other words, the archaeofauna recovered provides a baseline (Pauly, 1995) of specific patterns for marine species targeted in each time period of settlement (Grouard, 2010). Thus, the analysis of subsistence behaviors, food econo-

Grouard, Espindola Rodrigues: Muséum national d'Histoire naturelle, Paris, France

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Perdikaris: University of Nebraska-Lincoln, Lincoln, Nebraska, USA **Quitmyer**: Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA

Correspondence to Grouard, grouard@mnhn.fr (ORCID 00000002-2101-0879)

mics, fishing, hunting, and gathering are powerful indicators of the region-specific evolution of social structures and cultural relationships. Mauss (1923-1924) defined food as a social construct. Fishing practices contribute to this cultural definition as they are linked to nautical proficiency, fisheries expertise, knowledge of the sea and fish behavior, spatial organization of the sea bottom, and vernacular taxonomy of the selected species. They are also linked to economic choices of risk-taking versus working time and to age and gender group task sharing organization in a specific society (Grouard, 2001a). These parameters are often evaluated through the analysis of material culture, but only a few fishing artefacts (e.g. hooks and net weights) have been recovered from archaeological sites in the West Indies. The reconstruction of zooarchaeological fish size from bone measurements provides another indicator of technology as it directly correlates with standard length (SL) and body mass (BM) parameters of the fish and the environment to which they live in. Each habitat requires different forms of exploitation techniques. Many tropical fish spend time as juveniles in a mangrove environment before migrating during adulthood to another ecosystem such as a coral reef. The fishing technology (e.g. nets, traps, hook/line, spear, bow, and harpoons) used in each of these environments is therefore very distinct and hence size selective. Due to size, behavior, or abundance, some fish cohorts may be present in the environment but not accessible via some fishing techniques.

In this research, we apply the concepts of allometry to calculate fish body size (Reitz et al., 1987), SL (mm) and BM (g) of pre-Columbian zooarchaeological assemblages spanning 5,000 years in the Lesser Antilles. In so doing, we examine technological changes, procurement strategies and the habitats targeted by these people. The data also address the need to understand changing fish SL and BM baselines (Pauly, 1995; Pauly, Christensen, Dalsgaard, Froese, and Torres, 1998) that have been reported in previous research from island communities (Grouard et al., 2017; Perdikaris, 1999; Quitmyer et al., 2013; Wing and Wing, 1995, 2001). Zooarchaeological fish body size. SL and BM, were estimated through the use of log-linear regression constants (Peters, 1983). Allometry has the advantage of being biologically based and facilitates estimation of the biometrics of an organism through ontogeny (Peters, 1983; Reitz et al., 1987; Schmidt-Nielsen, 1984). A large comparative osteological collection of modern fish taxa of known size and weight representing each of the eight families, Holocentridae, Serranidae, Carangidae, Lutjanidae, Haemulidae, Scaridae, Acanthuridae, and Scombridae, was measured and allometrically correlated with zooarchaeological specimens to estimate SL and BM (Gould, 1966: 587; Gould, 1971; Huxley, 1932; Peters, 1983; Reitz et al., 1987). These data help in interpreting past harvest techniques and occasionally even the season of capture. Modern reference collections and environmental setting

Calculating fish body size is key to understanding the ecology and ecosystems of where the fish originated.

Many coral reef fish exhibit habitat partitioning throughout ontogeny. For example, schools of juvenile grunts (Haemulidae) early in their life cycles grow in the mangroves and seagrass beds, whereas the adults are found on coral reefs (Kimirei et al., 2013; Nagelkerken et al., 2000). Thus, the sizes of many tropical fish taxa are highly correlated with ontogenetic age and growth maturity and thus, their ecosystemic location.

Zooarchaeological studies in the West Indies (Bain et al., 2017; Giovas, 2016; Grouard, 2001a, 2010; Mac-Arthur and Wilson, 1967; Perdikaris et al., 2017; Serrand, 2007; Wing and Wing, 2001) have demonstrated the long-term productivity of the island ecosystems, identifying a high diversity of marine taxa, which is still present today.

The Lesser Antilles form a double arch of Cenozoic islands over almost 850 km (Figure S1): the external one was formed during the Miocene and is characterized by calcareous islands and islets, and the inner (western) arc is made up of still active volcanic islands. These two arcs present two very different environments. The volcanic islands are mountainous with rainforests and rivers, surrounded by deep sea waters, and rocky reefs. On the other hand, the calcareous Miocene islands are covered by xerophytic forests with rolling hills, mangroves, lagoons, and extended coral reefs.

Four main ecosystems characterize the Lesser Antilles: coral reefs, mangroves, seagrasses, and deep offshore waters (Bouchon, Bouchon-Navarro, and Louis, 2002). Coral reefs, which protect the coastline from swells, represent an extremely rich and intricate ecosystem, harboring a great diversity of animal species and enabling the development of mangroves and seagrasses in bays and lagoons. Marine phanerogam meadows (seagrasses) are at the interface between coral reefs and mangroves. The deep offshore waters have poor productivity of phytoplankton and zooplankton; thus, this oligotrophic zone contains only few pelagic fish taxa. Extant pelagic fish, such as tuna, are only opportunistically harvested by local fishermen, but the zone supports a modern recreational fishery (Blanchet et al., 2002, p. 17).

Recent studies of marine biodiversity in the French West Indies have recorded 14 species of marine mammals, five species of sea turtles, more than 40 species of decapod crustaceans, 360 species of marine mollusks, and 40 species of echinoderms. Among the fishes, more than 300 species have been recorded along the coasts of the French West Indies. Within this region, about 220 species inhabit coral reefs, 87 species are in mangrove habitats, and 65 over seagrass bed bottoms (Bouchon et al., 2002; Pointier and Lamy, 1998).

Regarding the availability of fish families present on the Caribbean coasts, the most important ones for human consumption are, in terms of the number of species: Serranidae (34 spp.), Haemulidae (19 spp.), Carangidae (15 spp.), Scaridae (14 spp.), Lutjanidae (14 spp.), Labridae (10 spp.), Scombridae (10 spp.), Pomacentridae (9 spp.), and Holocentridae (7 spp.; see Page et al., 2013 for common and scientific names of fishes). These families correspond to more than half of the modern inventories (Blanchet et al., 2002; Bouchon et al., 2002; Carpenter, 2002; Froese and Pauly, 2018; Nagelkerken et al., 2000; Rousseau, 2010). The Acanthuridae have a small number of species (n = 3) but are numerically abundant. The Labridae and Pomacentridae specimens were not statistically viable in the modern osteological collections, so these two taxa were excluded. The eight families selected in this study represent 563 modern osteological specimens (Table 1).

Archaeological collections and historical setting

The Lesser Antilles have yielded many well-preserved and well-stratified archaeological sites that have been extensively excavated. The first recorded human settlement dates to around 3,500 years BCE on the Mesoindian (Archaic Age) site of Etang Rouge on Saint-Martin (Bonnissent et al., 2018). By 500 BCE, new migrations of farmer-potters from the Orinoco Basin in Venezuela (Keegan, 2000) had colonized the entire archipelago of the Lesser Antilles (Early Neoindian, Early Ceramic Age, Saladoid Cultures). Around AD 900, new cultures emerged and settled in various areas of the region (Late Neoindian, Late Ceramic Age, and Troumassoid Cultures) (Hofman and Hoogland, 2004). These people were hunter-gatherer-fishers and horticulturalists. Since 1492, European Plantation economies dominated the region and changed both nature and culture on the islands.

The zooarchaeological materials forming the core of this analysis are listed in Table 2 with the locations shown on the map in Figure S1. They represent 142 assemblages, mostly village refuse middens and, to a lesser extent, natural cave deposits and shell middens. The sampling methods were the same on each site (all the features and square meters divided by stratigraphic cultural layer were water sieved through a 2-mm screen). The number of archaeological specimens recovered (1,050,649) and the number of different assemblages (142) circumvent preservation bias. The samples were excavated from 11 islands: Saint-Martin, Barbuda, Antigua, Long Island, Guadeloupe (Grande-Terre, Basse-Terre, Les Saintes, Islets from Grand and Petit-Cul-de-Sac-Marin and Petite-Terre, La Désirade, Marie-Galante), and La Martinique. The earliest faunal assemblages were recovered from 12 pre-Amerindian Holocene deposits, eight Archaic, 11 Early Ceramic A, 13 Early Ceramic B, 31 Late Ceramic A, 18 Late Ceramic B, along with 49 Colonial period assemblages (17th-19th centuries AD). All the archaeological collections are new datasets, and the analyses were all carried out by the authors of the study.

Methods

The identification and analysis of the modern and zooarchaeological assemblages were made by one of us (SG) using the reference collections of the Muséum national d'Histoire naturelle Zooarchaeology Laboratory (MNHN-AASPE) in Paris, France, the University of Nebraska-Lincoln Zooarchaeology Laboratory (UNL) in Lincoln, Nebraska, USA (previously at Brooklyn College, CUNY), and the Environmental Archaeology Laboratory, Florida Museum of Natural History (FLMNH), University of Florida in Gainesville, Florida, USA.

The MNHN-AASPE Laboratory houses a large vertebrate and invertebrate osteological and zooarchaeological collection from the Caribbean (758 specimens and 346 taxa), providing a solid comparative collection for the identification of the zooarchaeological specimens. The UNL Zooarchaeology Laboratory curates 650 specimens representing 325 taxa. Some of the rarer zooarchaeological remains were identified at the FLMNH. The FLMNH osteological comparative collection is among the largest in the world, covering the individual variability known to exist in various taxa: nearly 12,000 individual vertebrate and invertebrate specimens accompanied by weights and measures are housed there. The identification of fish remains to species can often prove difficult, especially with closely related tropical taxa. The identifications were facilitated by the use of these extensive comparative collections, along with illustrations of skeletal elements of 100 common fish in the Lesser Antilles and a table key with the criteria for morphological recognition of skeletal parts of 44 fish taxa (Grouard, 2001a, Vol. II Annexes 8 and 9).

The zooarchaeological remains were recovered from water-sieved soil samples using 1- and 2.7-mm screens from all sealed contexts, allowing for the recovery of small body faunal remains (e.g. fish, amphibians, squamates, birds, and small mammals). Samples from the middens were collected volumetrically: A minimum of 1 m^2 per unit for each cultural layer, plus 100% of the features and structures. The screen residue from each sample was sorted using a binocular microscope, either in the field laboratory or in the MNHN or CUNY laboratories. The use of this screening protocol enables all zooarchaeological remains, large and small, an equal chance of being recovered (Brinkhuizen and Clason, 1986; Casteel, 1974, 1976; Clason and Prummel, 1977; Payne, 1975; Quitmyer, 2004).

The sizes of the zooarchaeological fishes illustrate both the different ecosystems where the animals were probably caught, as well as the techniques used to catch them. It also provides information on age, trophic level, and can also identify possible anthropogenic or environmentally caused shifts in the population dynamics of reef, riverine, or mangrove taxa (Grouard, 2001b; Reitz and Wing, 1999; Schmidt-Nielsen, 1984; Wheeler and Jones, 1989; Wing and Wing, 2001).

As dimensions of fish bones correlate well with live body size and weight (allometric size and growth are close to isometric distribution), there are many ways of estimating body size, live BM (grams) or SL (mm), based upon different measurements of fresh fish skeletal parts (Casteel, 1974, 1976; Desse et al., 1987, 1989; Leach and Boocock, 1993; Leach et al., 1996a; Leach et al., 1996b; Wheeler and Jones, 1989). For some Caribbean

Family	MNI	Number of measurements	Number of equations (SL, TL, and mass)
Holocentridae	44	1,729	525
Holocentrus	29	1,174	
Holocentrus adscensionis	10	398	
Holocentrus rufus	19	776	
Myripristis	9	314	
Plectrypops	1	40	
Neoniphon	1	40	
Sargocentron	4	161	
Serranidae	135	4.656	1.056
Serraninae	54	1.799	-,
Serranus	3	73	
Centropristis	12	401	
Diploctrum	25	927	
Diplectrum formosum	20	657	
Hypoplactrus	20 8	262	
Danalahaan	6	102	
Commission (Densilians)	0	192	
Grammistinae (<i>Rypticus</i>)	3	105	
Epinephelinae	/8	2,754	
Alphestes afer	1	117	
Epinephelus	36	1,241	
Epinephelus guttatus	15	536	
Mycteroperca	10	362	
Cephalopholis	31	1,115	
Cephalopholis fulva	20	732	
Carangidae	93	3,133	825
Alectis ciliaris	1	32	
Carangoides	8	256	
Caranx	30	1,065	
Caranx hippos	17	640	
Caranx ruber	8	256	
Chloroscombrus	8	266	
Decanterus	3	96	
Hemicarany	2	62	
Oligonlites	5	149	
Salana	17	580	
Seriela	6	103	
Seriola Tua akin atua	0	195	
Trachinolus Tracshuma	0	422	
	15	425	152
Lutjandae	/0	2,105	455
Lutjanus	61	1,837	
Lutjanus apodus	1	209	
Lutjanus buccanella	13	421	
Lutjanus campechanus	17	499	
Etelis	62	453	
Ocyurus	6	158	
Pristipomoides	1	4	
Rhomboplites	6	122	
Haemulidae	95	3,305	717
Anisotremus	8	278	
Conodon	7	241	
Haemulon	66	2,306	
Haemulon plumieri	30	1,044	
Haemulon flavolineatum	8	281	
Orthopristis	7	421	
Pomadasys	1	35	
Xenichthys	3	101	
Isacia	3	103	
Scaridae	50	2 121	666
Sparisoma	46	1 984	
Sparisona chrysoptarum	16	694	
Sparisoma curysopierum	2 Q	338	
Sparisoma ruoripinne	0	721	
Sparisoma viride	1/	127	
Scarus	4	137	

Table 1. MNI, Number of Measurements, and Number of Equations by Family

(Continues)

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Family	MNI	Number of measurements	Number of equations (SL, TL, and mass)
Acanthuridae	30	2,688	1,173
Acanthurus	30	2,688	
Acanthurus bahianus	13	1,167	
Acanthurus chirurgus	6	502	
Acanthurus coeruleus	11	1,019	
Scombridae	40	1,622	474
Acanthocybium	1	39	
Auxis	2	80	
Euthynnus	15	635	
Katsuwonus	1	42	
Scomber	5	195	
Scomberomorus	10	402	
Thunnus	6	229	
Total	563	21,437	5,889

Table 1. (Continued)

taxa, body weights are estimated using the first vertebrae width or otolith length (Ouitmver et al., 1985: Reitz et al., 1987; Reitz and Cordier, 1983; Reitz and Wing, 1999). Correlations between the body weight or length and otolith length (mm) or vertebral width (mm) did not provide accurate estimates of weight for some taxa in this study (correlation coefficients $[r^2]$ were too weak). As a result, various regression constants were calculated for each skeletal part (cranial bones and vertebrae) of the most common taxa from the zooarchaeological samples. Grouard and colleagues (Espindola Rodrigues and Grouard, 2014; Grouard, 2001b; Grouard et al., 2017) have previously established regression relationships using modern specimens for the most common fish species, genera, and families in the Lesser Antilles (Holocentridae, Serranidae, Carangidae, Lutjanidae, Haemulidae, Scaridae, Acanthuridae, and Scombridae). The comparative specimens used in calculating the allometric constants associated with fish taxa living in the Greater and Lesser Antilles, and Florida are from the osteological collections of the "Antilles in ASSPE laboratory" and FLMNH.

Allometry (scaling) best describes the consequences of changes in body metrics through ontogeny and is characterized by a mathematical function: $y = ax^b$ (Huxley, 1932; Krebs, 1989; Peters, 1983; Schmidt-Nielsen, 1984).

The allometric formula is transformed using the common logarithm to produce a straight line-regression because ontogenetic growth is nonlinear (Peters, 1983).

The transformed formula is

$$\log y = a + b (\log x)$$
, where

- *y* the dependent variable, the predicted standard length or body mass
- a empirically derived y-intercept
- b empirically derived slope of the line
- *x* the independent variable (skeletal measurement of the zooarchaeological bone).

However, the standard error, the determination coefficient (R^2) and the coefficient correlation (r) of the exponential and the linear functions are similar in most cases. Consequently, the linear equations were chosen to be presented in the length estimates of the archaeozoological specimens (Tables S1 to S8).

Because the identification of fragmented archaeological bones is often difficult to differentiate at the species level, for the most common taxa of each family mentioned above, allometric constants were calculated at the level of species, genus, subfamily, and family, including measurements of the vertebrae and cranial bones (Figure 1). We only use those constants when the correlation is excellent (when the correlation coefficient [r] is between .9 and 1 and the probability is less than .0001) as recommended by Desse and Desse-Berset (1996b); Grouard, 2001b; examples at the level of genus in Figure 2). Fish sizes for all zooarchaeological taxa were calculated using

Islands	Sites	Holecene	Ar- chaic	Early Ceramic A	Early Ceramic B	Late Ceramic A	Late Ceramic B	XVII– XIX	NISP Total
Saint-Martin	Baie Orientale Etang Rouge 04 Lot 73 Baie Longue Hope Estate BK76–Grand Case BK77–Route l'espérance BK78–rue de la petite plage Pointe du Canonnier Baie aux Prunes Habitation Mont Vernon		X X X	x		X X X X	X	X X X X	86,023
Barbuda	Barbuda Cave I Barbuda Cave II Barbuda Cave III Barbuda Cave IV Barbuda Cave V Rat Poket Two Foot Bay 1 Burton's Field 2012 Cattle Field 2012 River site 2011 Strombus line Seaview Sufferers Indian Town Trail Welches Castle Bay Cave Castle Hill Cave 2008 Nicey Cave 2009 Overview Cave Two Foot Bay 2 Two Foot Bay 3	X X X X X X X X	X X X X	Х	Х	х	X X	X X X X X X X X X	7,965
Antigua	Burma Quarry Blackman's Indian Creek Muddy Bay Mill Reef Marmora Bay Jumpy Bay Sugar Mill	X				X X X X X	X X	х	16,978
Basse Terre	Cathédrale de Basse Terre Gare Maritime 24, rue Schoelcher Place Saint François Embouchure Rivière de Bailiff Sainte Rose La Ramée Pointe de Grande–Anse Trois Rivières Roseau Capesterre Couvent des Capucins–EHPAD Habitation Berg Habitation Berg Habitation teveillard–Diavet Habitation La Mahaudière La Diotte			X X X X	X X X	X X	X X	591 X X X X X X X X X X X	88,188
Grande Terre	Anse à l'Eau Morel Petites Salines Anse à la Gourde Grotte Papin CHU Belle Plaine			X X	X X	X X	X X	X X (Con	232,835 ntinues)

Table 2. Sites by Island, Number of Assemblages, Cultural Time Period, and NISP

Islands	Sites	Holocene	Archaic	Early Ceramic A	Early Ceramic B	Late Ceramic A	Late Ceramic B	XVII –XIX	NISP Total
	Pointe du Helleux Grotte de l'Anse à la Gourde Grotte de l'Anse à l'Ecu Habitation Laprade, Barbès Habitation Macaille Trou Lolo						Х	X X X X X X	
Cul-de-Sac-Marin	Ilet Colas Ilet Chasse							X X	198
La Désirade	Les Sables Pointe Gros Rempart Puits 6 Petite Rivière Aéroport Grand Abaque 1 Voûte à Pin A l'Escalier Mome Cythèle				X X	X X X X	X	X X X	53,393
Ilets de Petite Terre	Baleine du Sud Caille à Bélasse Est de Mouton de Bas Name Unknown Pointe Sablé					X X X X X X	Λ	X X	1,677
Marie-Galante	Abri Cadet 3 Grotte Cadet 2 Grotte Blanchard Grotte Blanchard 2 Grotte Blanchard 2 Grotte du Morne Rita Folle Anse Stade José Bade Tourlourous Taliseronde Fossé Petite Anse Anse du Coq Bavire	X X X X	х	X X	X X X X	X X X X X X X	X	X X X X X X X X	473,188
Les Saintes	Grande Anse Terre de Bas						Х	X	49,704
La Martinique	Etmoarcheologie Clavius Marius Salines Dizac Macabou Paquemar Anse Trabaud Habitation Crève Cœur Moulin Val d'Or			х	X X X	х	X X X X X	X X X X X X X	40,500
Total NISP Total N sites		103,592	2,636	109,701	69,053	333,414	141,216	40,981	1,050,649
Total IN sites		12	ō	11	13	51	18	49	142

Table 2. (Continued)

identifiable elements complete enough for precise measurement. Before choosing measurements for analysis, the random nature of the processes of destruction indicated by the distribution of body parts was verified for each sample, as suggested by Leach and Boocock (1995: 27). All linear measurements are in millimeters, and all weights are in grams. The total length (TL) or the BM could have been used to illustrate the archaeological estimations of fish sizes. However, in this study, we applied the SL because it seems to better correspond with the mesh size of the casts and nets.



Figure 1. Osteometry of Haemulidae, Serrandiae, Acanthuridae, and Scaridae

Results

Modern comparative specimens: Fish size estimation equations

The 563 osteological specimens (*n*) resulted in 21,437 measurements (m) and 5,889 equations for size estimations at the level of family (including different genera and several species), at the level of genera and at the level of species (Table 1; see also Table S1 Holocentridae, Table S2 Serranidae, Table S3 Carangidae, Table S4 Lutjanidae, Table S5 Haemulidae, Table S6 Scaridae, Table S7 Acanthuridae, and Table S8 Scombridae) of the SL (mm), TL (mm), and BM (g). We note that BM represents soft and supportive tissue.

We found that not all the measurements have a good correlation with body metrics, when the r coefficient is < .9, and probabilities .02 > p > .01, according to the df. In this case, our hypothesis Ho, which advocates the absence of correlation between the variables X (measurement of the skeletal part analyzed) and Y (SL), was rejected, but the equations were used with caution because the probability was slightly less significant. Only 25 of 5,889 equations (.42%) had to be rejected because the correlation was not significant (p > .2), and the size estimation of the zooarchaeological individuals cannot be used (see Tables S1–S8).

As highlighted elsewhere (Cooke and Jiménez, 2004; Jiménez-Cano and Masson, 2016; Lidour, Vorenger, and Béarez, 2018), working at the species level allows the finest application of ecological studies to document ancient fishing; however, the identification of fragmented archaeological bones is often difficult to differentiate at the species level. Consequently, allometric constants were calculated at the level of family, subfamily, genera, and species. Number is important for statistical significance, but body size ranges resulted in highly accurate data. The metrics could be a powerful specific identification tool. Indeed, the species or genera within a family can be determined using the measurements (e.g. the grunts, Haemulidae: *Anisotremus* spp. and *Conodon* spp., or jacks, Carangidae: *Trachurus* spp. and *Trachinotus* spp.).

Finally, > 97% of the size estimation equations (5,731/5,889) have a high correlation coefficient and a highly significant probability (p < .01) at the level of species, genus, subfamily, and family. Consequently, these series of predictive equations are statistically useful to reconstruct the size of the zooarchaeological specimens but require staying within the range indicated by the two extreme size margins noted in the equation. Indeed, if a zooarchaeological fish were bigger or smaller than the sizes covered in the reference collection, size estimation would be hypothetical because of the lack of direct correlates.



Figure 2. Examples of regression of the standard length based on the Measure 2 of premaxillary of Serranidae, Epinephelinae, *Diplectrum* sp., *Centropristis* sp., *Cephalopholis* sp., *Epinephelus* sp., *Mycteroperca* sp., *Cephalopholis* fulva, *Diplectrum* formosum, and *Epinephelus* guttatus [Color figure can be viewed at https://onlinelibrary.wiley.com]

Zooarchaeological applications

Zooarchaeological analysis of the 142 archaeological assemblages resulted in the identification of 1,050,649 specimens, of which 397,803 were fish (ray-finned fishes, Teleostei, and sharks/skates/ rays, Chondrichthyes), and 379,634 were terrestrial vertebrates (Lissamphibians—frogs, Squamates—lizards and snakes, Testudines—tortoises and turtles, Aves—birds, and Mammalia—mammals). This resulted in a total of 46 fish families and 212 fish species within the vertebrate specimens (Table 3), with differences among the time periods: pre-Amerindian

Holocene (8/9), Archaic (6/17), Early Ceramic A (30/114), Early Ceramic B (35/119), Late Ceramic A (42/166), Late Ceramic B (35/118), and Colonial (32/84).

The sample sizes of the Archaic and pre-Amerindian Holocene assemblages are small, thus contributing to less taxonomic diversity (Figure 3), and cannot be confidently used to represent zooarchaeological diversity during those periods. Greater numbers of fish taxa were identified in the Late Ceramic Age A (S = 166), where there are also a greater number of sites (n = 42). The highest percentage of fish remains was found within the Late Ceramic Age B (86%) deposits.

Table 3. NISP of Vertebrata, NISP of Fish, Number of Fish Families, and Number of Fish Taxa (S), Margaleff index dI = (S-1)/Logn(N)

					-	-		
	Holocene	Archaic	Early	Early	Late	Late	XVII-	Total assemblages
			Coromic A	Coromic B	Caramic A	Coromic B	VIV	e
			Ceranne A	Ceranne B	Ceranne A	Ceranne B	ΛΙΛ	
Number of sites	12	8	11	13	31	18	49	142
NISP total Vertebrata	103,592	2,636	109,701	69,053	333,414	141,216	40,981	1,050,649
NISP fish	210	148	38,498	52,233	182,832	121,649	2,233	397,803
S fish families	8	6	30	35	42	35	32	46
S fish taxa	9	17	114	119	166	118	84	212
% Fish	0%	6%	35%	76%	55%	86%	5%	38%
Dl Fish	1.5	3.2	10.7	10.9	13.6	10.0	10.8	16.4



Figure 3. Identified fish families by archaeological period ordered by contribution to assemblage (NISP) [Color figure can be viewed at https://onlinelibrary.wiley.com]

Estimation of fish size

For the entire assemblage (21,265 measured fish), the estimations of the fish populations have a mean SL of 293.1 mm (Figure 4 and Table 4) and range between 22.8 mm SL and 3041.1 mm SL.

Figure 4 shows the size histogram for the eight families during all periods. We can see at least a bimodal curve. The distribution is a double curve with a large distribution weighted to the left of the mean, suggesting that many of the fish are smaller than the median (between 100 and 300 mm), but a second distribution is present, with large specimens between 450 and 800 mm. The smaller fish include mostly juvenile Lutjanidae, Haemulidae, Acanthuridae, Holocentridae, and Scaridae. The larger individuals are mostly Scombridae, Carangidae, Serranidae, Scaridae, and Lutjanidae and likely represent pelagic schools or solitary adult carnivorous fish feeding on the reef and inshore fish.

According to the Agostino test (Chenorkian, 1996), none of the size class distributions of any family but Scombridae follow a normal distribution (Figure 5 and Table 4). Indeed, each fish family has their its [*sic*], but three kinds of distributions appear: The Acanthuridae, Haemulidae, and Holocentridae are very close to each other; the Lutjanidae and Scaridae have the same kind of distribution; and the Scombridae, Serranidae, and Carangidae have bimodal curves.

Within the Holocentridae (min 89 mm, max 403 mm, mean 189 mm), the Acanthuridae (min 60 mm, max 456 mm, mean 161 mm), and the Haemulidae (min 44 mm, max 611 mm, mean 193 mm), most individuals are between 100 and 300 mm in length with many smaller individuals giving a slight skew towards the smaller size classes.

The Scaridae (min 42 mm, max 944 mm, mean 260 mm) and Lutjanidae (min 23 mm, max 981 mm, mean 256 mm) do not have a normal distribution, although they resemble normal curves with a few large individuals giving the curve a slight skew towards the larger size.

The Serranidae (min 35 mm, max 1217 mm, mean 350 mm), Scombridae (min 63 mm, max 3041 mm, mean 551 mm), and Carangidae (min 62 mm, max 1412 mm, mean 269 mm) present bimodal distributions with two

population sizes, each corresponding to different species living in different environments.

In order to establish a baseline for discussion of the fishing techniques and gear used by the Amerindian populations studied, a biometric reference has been developed (Froese and Pauly, 2018; http://specifyportal.flmnh.ufl.edu/fishes/), including TL at the juvenile phase, maturity, as well as the mean and maximum size during the adult phase (Table 5).

The Carangidae, Haemulidae, and Lutjanidae were harvested undersize at maturity, but none of the other families were fished under the mature size. However, the high diversity of species in these families requires caution regarding interpretation.

The mean fish sizes from all ecosystems decreased over time (Figure 6), especially from the Early Ceramic Age through the Late Ceramic Age and the Colonial period: Archaic 244.6 mm, ECA 303.8 mm, ECB 403.3 mm, LCA 249.8 mm, LCB 249.8 mm, Colonial 203.3 mm. This result supports the findings of previous research about decreasing coral fish size from the Early to Late Ceramic Age (Quitmyer, 2003; Wing and Wing, 2001, p. 3) and from the 17th to late 19th century AD (Quitmyer et al., 2013; Wallman and Grouard, 2017). This appears to be associated with human agency. Indeed, rising human populations and demand for food increased the pressure on marine ecosystems with long-term costs in terms of available biomass (Burgess et al., 2013; Jackson et al., 2001). However, the distributions are different through time: Bimodal distributions are clearly seen in the Archaic and Early Ceramic Age suggesting the simultaneous use of diverse fishing techniques in different environments, whereas the Late Ceramic Age and Colonial appeared as normal distributions with a few large individuals giving the curve a slight skew towards the larger sizes, suggesting a selection over the natural range of the smaller species. Thus, the subsistence economy was highly influenced by cultural and/or environmental choices.

Techniques, Strategies, and Fishing Gears

The main purpose of the development of this set of biometric parameters was to better interpret where species were caught (and how), according to their modes and





	Ν	Mean	Max	Min
Family				
Holocentridae	176	188.9	403.1	89.0
Serranidae	1,740	350.2	1,1216.6	35.3
Carangidae	2,663	268.7	1,412.3	62.4
Lutjanidae	3,261	256.4	980.5	22.8
Haemulidae	3,742	193.4	610.9	43.7
Scaridae	3,983	259.7	943.7	41.9
Acanthuridae	2,184	161.2	455.8	59.9
Scombridae	3,516	550.6	3,041.1	63.1
Total	21,265	293.1	3,041.1	22.8
Period				
Archaic	109	244.6	483.0	150.6
ECA	2,533	303.8	1,035.6	102.8
ECB	5,439	40.3	1,555.2	22.8
LCA	2,438	249.8	1,725.5	43.7
LCB	9,713	249.8	3,041.1	35.3
Colonial	1,033	203.3	943.7	59.9
Total	21,265	293.1	3,041.1	22.8

Table 4. Basic statistics of the archaeological fish size estimations (standard length in mm)

and place of life during their growth cycle, because we can observe specimens that are born in one ecosystem and mature in another (Nagelkerken et al., 2000). So, the elaboration of hypotheses about Amerindian fishery strategies have generally been based on the ethology of the species from bibliographical sources and from ethnographic and ethnohistorical data (Archambault, 1972; Aubin-Roy, 1968; Benoist, 1959; Blanchet et al., 2002; Bonniol, 1980; Bouchon et al., 2002; Carpenter, 2002; Froese and Pauly, 2018; Handler, 1970). The Amerindians from the Lesser Antilles are close in genetics, language, space, and time with the last Amerindians from North America. Consequently, the ethnohistorical data provide very strong inferences for interpreting palaeofisheries' techniques.

With respect to the sizes of the fish captured by these populations, our reconstruction work has revealed definite trends. The trends from our study are those revealed by the SL distribution curves. They have given us a glimpse of the possible anthropogenic selections that follow a normal, Poisson, or bimodal distribution (statistical test). Of course, some species or specimens' sizes are available in nature but not available for the fishery method at that time and are not present in the archaeological samples. As a result, the aggregation and dispersal elements have guided us in interpreting the fishing techniques used by these Amerindian peoples. Finally, from the fish size estimates and the consulted sources (archaeological, ethnohistorical, ethnographic, and biological), it was possible to infer various strategies and gear used by the Amerindian fishermen.

The zooarchaeological fishing techniques vary according to the targeted species, specimen size and age, and its environment (bottom cover, depth, distance from shore, and seasonality):

- The pelagic channel fish zooarchaeological populations (Figure 5) were large fishes, normally distributed, such as mackerels/tunas/ bonitos, and jacks with a bimodal distribution, which translates to several capture techniques: bow and arrow, harpoon, large nets, and longlines. The deployment of these various fishing technologies in such habitats suggests that pre-Columbian people would have most likely used watercraft.
- The rocky bottom zooarchaeological fish populations, the groupers, follow a normal distribution, but with several large individuals,



Figure 5. Fish size (standard length) of the Holocentridae (n = 176), Serranidae (n = 1,740), Carangidae (n = 2,663), Lutjanidae (n = 3,261), Haemulidae (n = 3,742), Scaridae (n = 3,983), Acanthuridae (n = 2,184), Scombridae (n = 3,516). The blue arrow symbolizes the mean and the line symbolizes the size at maturity (see Table 5) [Color figure can be viewed at https://onlinelibrary.wiley.com]

Family	Species	Juvenile phase LT LS (mm)	Maturity LT/LS (mm)	Adult phase Mean LT/LS (mm)	Maximum size LT max (mm)
Holocentridae	Holocentrus adscencionis	< 135	135	250	350
	Holocentrus rufus	< 145	145	250	610
Serranidae	Cephalopholis cruentata	< 160	160	200	426
	Epinephelus guttutus	< 250	250	400	760
	Epinephelus itajara	< 1,280	1,280	1,500	2,500
	Epinephelus adscendionis	?	?	350	610
	Cephalopholis fulva	< 160	160	?	410
	Mycteroperca acutrirostris	?	?	?	800
	Mycteroperca tigris	< 460	460	400	1,010
Carangidae	Seriola rivoliana Caranx ruber Caranx latus Carangoides bartholomaei Trachinotus carolinus Trachinotus goodei Trachinotus falcatus Seriola dumerili Decapterus punctatus Decapterus macarellus Selar ceumenophthalmus	? < 310 < 370 < 450 < 250 ? < 547 < 1,090 > 110 ?	? 310 370 450 250 ? 547 1,090 110 ?	900 500 600 500 400 350 1,220 1,000 180 300 2	1,600 590 ♀ 690 ♂ 1,010 1,000 640 500 486 ♀ 547 ♂ 1,900 300 460 700
Lutjanidae	Lutjanus vivanus	< 500	500	450	830
	Lutjanus apodus	< 250	250	350	672
	Etelis oculatus	?	?	640	1,000
	Lutjanus bucanella	< 310	310	500	750
Haemulidae	Anisotremus surinamensis Anisotremus virginicus Conodon nobilis Haemulon album Haemulon aurolineatum Haemulon flavolineatum Haemulon melanurum Haemulon plumierii Haemulon sciurus	< 200 < 406 < 180 < 305 < 140 \bigcirc 180 \bigcirc < 160 < 190 < 167 \bigcirc 186 \bigcirc < 185 \bigcirc 250 \bigcirc	$\begin{array}{c} 200 \ \bigcirc \ 200 \ \Diamond \\ 406 \ \bigcirc \ 500 \ \Diamond \\ 180 \ \bigcirc \ 180 \ \Diamond \\ 305 \ \bigcirc \ 500 \ \Diamond \\ 140 \\ 160 \ \bigcirc \ 170 \ \Diamond \\ 190 \ \bigcirc \ 200 \ \Diamond \\ 190 \\ 300 \ \oslash \ 350 \ \Diamond \end{array}$	450 250 250 500 180 170 250 300 250	830 406 336 790 250 300 330 530 460
Scaridae	Sparisoma viride	< 163	163	380	640
	Sparisoma chrysopterum	?	?	250	460
	Scarus coeruleus	?	?	350	1,200
Acanthuridae	Acanthurus bahianus	< 150	151	250	380
	Acanthurus chirurgus	?	?	250	390
	Acanthurus coeruleus	?	?	350	390
Scombridae	Thunnus albacares	< 1,033	1,033	1,050 FL	2,930 FL
	Thunnus atlanticus	?	?	720 FL	1,080 FL
	Auxis thazard	< 300	300	600	650 FL
	Katsuwonus pelamis	< 400	400	800 FL	110 FL
	Euthynus alletteratus	< 418	418	800	1,220
	Scomberomorus brasiliensis	< 419	419	650	1,250 FL
	Scomberomorus cavalla	< 500	500	700 FL	1,840
	Scomberomorus maculatus	< 425	425	?	910 FL
	Scomberomorus regalis	< 405	405	?	1,830

Table 5. Biometric table of taxa studied in archaeoichthyological assemblages (data extracted from fishbase.org and flmnh.ufl.edu)

which probably hides a multimodal curve, reflecting the use of three or four capture techniques: Nets, traps, hook/line, and bow and arrow.

- The size classes of parrotfishes follow a natural distribution, called a Poisson law distribution, with many individuals of small sizes, which indicates the use of traps, seine nets, and fine mesh nets.
- The mangrove and sandy bottom fish zooarchaeological populations, such as the juveniles of grunts and snappers (Table 5), show a statistically Poisson law distribution that results from the nonselective nature of techniques that causes the mortality of fish of all ages, especially young individuals. For example, fish poison was widely used, as described by early Europ-



Figure 6. Size of the height fish families through time: Archaic (n = 109), Early Ceramic A (n = 2,533), Early Ceramic B (n = 5,439), Late Ceramic A (n = 2,438), Late Ceramic B (n = 9,713), Colonial (n = 1,033) [Color figure can be viewed at https://onlinelibrary.wiley.com]

ean chroniclers in the West Indies. The use of fish poisons is found cross-culturally and is widely practiced by modern Amazonian Amerindians, Barbuda fisher folk, and even fisheries biologists.

It is likely that these Amerindian societies were able to employ fishing strategies adapted to specific underwater environments, as is the case for the capture of fish from rocky habitats using longlines. The same is true for the development of traps placed on reefs or coral reefs to catch the fish specific to these ecosystems. Finally, if we look at migratory pelagic species that do not approach the coast (such as yellowfin tuna, Thunnus albacares, blackfin tuna, Thunnus atlanticus, and skipjack tuna, Katsuwonus *pelamis*), it is reasonable to think that the use of a boat was necessary for their capture. These fish appear along the Atlantic coast during the first months of the year, in very fast schools hunting off the continental slope. From April-May, they get closer to the coast to hunt around the coral reefs and bays of the Caribbean Sea. At the beginning of autumn these fish are less abundant and even seem to disappear from the coast (Sacchi et al., 1981).

Moreover, many coral reef fish exhibit habitat partitioning throughout their lifetimes as ontogenetic shifters: juveniles of Haemulidae, Labridae, Pomacentridae, Lutjanidae, and Scaridae schools grow in the mangroves and seagrass beds (during the dry season from April to June), but coral reefs are dominated by adult fish (Nagelkerken et al., 2000). Because fish size is highly correlated with age and growth maturity and hence their ecosystemic location, seasonality can be estimated (Grouard et al., 2017).

The fishing methods varied over time, as illustrated by the size curves (Figure 6): the bimodal curves (with angling and spearing) are more prevalent during the Early Ceramic Age, and they tend to give way to Poisson's law curves during Late Ceramic Age: the Amerindians refocused on smaller fish using nets and traps. So, the seasonality of the fisheries during the Early Ceramic Age is strongly marked by the presence of these pelagic fish. However, only a sclerochronological study will make it possible to discern the seasonality of the other species (Grouard et al., 2017).

Conclusions

One of the immediate objectives of this work was the reconstruction of fish sizes from archaeological fish remains recovered from Amerindian midden environments. Amerindian peoples thrived in the Lesser Antilles for 1,500 years before the arrival of European colonial forces. The colonial settlers of the Caribbean initially employed techniques and approaches to hunting, fishing, and gathering native to their homelands. As the waves of South American settlers became familiar with the possibilities and limitations of their new homelands, there was a culturally driven adaptation to these environments that resulted in the artisanal, traditional practices of Antillean subsistence fishing that survive today.

Our osteometric approach, focusing on the eight fish families most consumed by the Amerindian populations of the Lesser Antilles, has sought to bring a deeper understanding of the interrelationships between fishery culture, environmental parameters, and long-term exploitation profiles. Going beyond the species of fish caught, we looked at the sizes of fish to try and identify the techniques used by fishermen to capture these resources along with the environments exploited. Even when considering the limitations of the zooarchaeological fish remains due to taphonomic and sampling strategies, the wealth, breadth, and volume of the ichthyofauna from the assemblages studied is indeed a good representation of the Amerindian fishery as discussed through this osteometric work. In terms of the fishing technology applied in the various time periods, as noted by the anthropologist J. Benoist (1959), lines, nets, and traps are the three main gear of Martinique fishermen. It is likely that the same triad of practices survived the passage of time and emerged to be among the most popular set of fishing techniques used by local fishermen. This gear was adapted towards the capture of desired species and would reflect good knowledge of the natural environment and the logic that governed the social relations of these groups, because, according to R. Cresswell (2003, p. 4), "the concept of techniques 'nested in the social' means that technical decisions are made for social reasons and vice versa."

Although there are no "perfect" models and all models are subject to the data and techniques available at the time of their construction, this work resulted from 6,000 measurements, and thus provides unique insights into aspects of the *chaîne opératoire* of the Amerindian fishery of the Lesser Antilles. Interaction between nature and culture placed unique markers in the landscape, seascape, and its resources but more importantly provided a cultural template for many of the Indigenous peoples that followed.

These activities, carried out individually or collectively, show a depth of knowledge about the local environment and all the species, migratory or not. It alludes to navigation techniques, the construction of boats, the making of tailor-made equipment for the targeted fish species and, in the terrestrial domain, the exploitation of plant species for the manufacture of fishing gear and boats.

This *chaîne opératoire* is a web of cognitive and practical tools necessary for the world of subsistence fishing. It includes multiples stages of acquisition and preparation (cooking, drying, smoking, etc.) and social signatures, such as indicators of the existence of collaborative networks of exchange between villages or islands. This approach provides a rather encouraging opportunity to expand this work to other species exploited in the region and extend this osteometric work to archaeoichthyological assemblages uncovered in the greater Caribbean region (Florida, Mexico, Nicaragua, Panama, Colombia, and Venezuela) and in the Brazilian island of Marajó. Whereas in the short term we will work on additional species and consider increasing the reference collections for Centropomidae, Labridae, Carangidae, and Scombridae, in the longer term, we will work towards building larger regional profiles of Amerindian fishing.

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Zooarchaeological Curation

The zooarchaeological remains will be curated at Direction Régionale de l'Archéologie de la Guadeloupe, Direction Régionale de l'Archéologie de la Martinique, Barbuda Research Complex and MNHN-AASPE laboratory. The modern fish osteological collections will be curated at FLMNH, University of Nebraska-Lincoln and MNHN-AASPE laboratories. The details of the basic statistics of the formulas and equations are available from the corresponding author (Grouard) on request.

Supporting Information

Additional supporting information may be found online at https://onlinelibrary.wiley.com/journal/10991212.

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