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Using shell middens to assess effects of fishing on queen conch (*Strombus gigas*) populations in Los Roques Archipelago National Park, Venezuela

Diego Schapira · Irene A. Montaño · Andrzej Antczak · Juan M. Posada

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Abstract Queen conch, *Strombus gigas*, is a commercially important gastropod that has been exploited throughout the Caribbean islands for thousands of years. Shell middens in the region are the physical record of a long-term fishery and their study can provide valuable information on selectivity patterns followed by fishermen and on resulting morphological shifts reflected by shells. In this study, we surveyed 27 middens located at Los Roques, Venezuela, to assess pre-Columbian and modern fisheries and measure their impact on local populations of queen conch. Pre-Columbian middens, covering a period of approximately 350 years of exploitation (1160–1540 A.D.), were mostly composed of adult shells (89%) and mean length of catch was estimated at 22.4 ± 0.2 cm (mean ± SE). A decrease in mean length of catch was observed throughout the modern fishery regime, estimated at 22.2 ± 0.3 cm in 1950–1971 and 20.0 ± 0.3 cm in 1990–1995. Higher proportions of immature individuals ranging from 48 to 67% were found in modern middens. Additionally, a decrease in mean length of mature individuals was detected throughout the modern fishery regime. The appearance of younger and smaller specimens is considered as a sign of heavy exploitation of local populations of queen conch during modern fisheries. Pre-Columbian middens in contrast, permitted to establish a relative baseline from which to compare values registered throughout modern times.

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D. Schapira · I. A. Montaño · J. M. Posada
Departamento de Biología de Organismos, Universidad Simón Bolívar, Sartenejas 89000, Venezuela

A. Antczak
Departamento de Diseño, Arquitectura y Artes Plásticas, Universidad Simón Bolívar, Sartenejas 89000, Venezuela

A. Antczak
Unidad de Estudios Arqueológicos (IERU), Universidad Simón Bolívar, Sartenejas 89000, Venezuela

D. Schapira (✉)
2e King Street, Newcastle Upon Tyne NE1 3UQ, UK
e-mail: diego.schapira@gmail.com;
diego.schapira@newcastle.ac.uk

Introduction

Marine species have been subject to exploitation by human populations throughout the Caribbean islands for millennia, as has been shown by an abundance of archaeological evidence within the region (Erlandson 2001; Newsom and Wing 2004; Fitzpatrick and Keegan 2007). Archaeological studies show that humans first settled the Caribbean islands ca. 6,000–7,000 years ago, and evidence suggests these archaic fishermen/foragers were already having an impact on marine and coastal environments as early as ca. 6000–3000 B.P., with reported changes in landscape and species composition as a result of resource exploitation (Jackson et al. 2001; Wing and Wing 2001; Keegan et al. 2003; Fitzpatrick and Keegan 2007). However, it has been recognized that although pre-Columbian settlers were affecting marine environments, it was not until Europeans arrived to the region that major impacts to marine resources occurred, primarily associated with an increase in human population and technological development (Jackson et al. 2001; Holm 2003; Pandolfi et al. 2003; Fitzpatrick and Keegan 2007).

Queen conch, *Strombus gigas* Linnaeus, 1758, is a commercially important gastropod that has been exploited throughout the Caribbean islands for centuries (Stoner and Ray 1996; Chakalall and Cochrane 1997; Torres and Sullivan-Sealey 2002; Keegan et al. 2003). Conch middens located at Los Roques archipelago, Venezuela, provide the physical record of a fishery that has been occurring for hundreds of years (Fig. 1). Archaeological research in these islands demonstrated that Amerindian populations began visiting the archipelago to exploit *S. gigas* by at least 1200–1300 A.D. for a period of approximately 200–300 years (Antczak and Antczak 2006). Although faunal remains of turtles, sea birds, fish and other shellfish have been found in archaeological excavations on Los Roques, the magnitude of middens associated with pre-Columbian exploitation suggests the harvesting of *S. gigas* constituted the principal motivation for these early fishermen to visit the archipelago (Antczak and Antczak 2006). Modern middens are also found in Los Roques and have been accumulating since the early 1950s (Rodríguez and Posada 1994). Their study in conjunction with pre-Columbian ones can provide useful information, not only to characterize these two distinct fishery regimes, but also to establish the potential impacts these regimes had on *S. gigas* populations.

The life history of queen conch is characterized by many traits that simplify the study and interpretation of shell middens. Queen conch ceases its longitudinal growth just after reaching sexual maturity at approximately 3–3.5 years of age (i.e., determinate growth), when the shell edge forms a broadly flared lip (Randall 1964). Body size at maturity can therefore be estimated. Additionally, the deposition of shell material continues on the inside of the developed lip after maturity, therefore its thickness can be used as a proxy for post-maturation age (Appeldoorn 1988; Stoner and Sandt 1992).

In this study, we conducted surveys on 27 shell middens that were formed under different fishery regimes (pre-Columbian and modern), to assess the effects of fishing on local populations of *S. gigas*, and specifically addressed the following questions: (1) did mean size and age of collected specimens change over time? (2) did mean size of matured individuals change over time? (3) were changes observed in middens reflecting changes in *S. gigas* local populations? The study also emphasizes the relevance of historical reconstruction of fisheries to understand vulnerability of shellfish resources.

Materials and methods

Study site

Los Roques Archipelago is a federal dependency of Venezuela located 135 km north of the coast of the South American mainland (11(44(45″N–11°58′36″N, 66°32′42″ W–66°5227″W) with a total extension of extension of 225,153 ha. Geologically, the islands are part of an atoll consisting of ca. 50 islands and more than 300 sand bars around a central lagoon (Fig. 2). Because of the rich diversity of marine life and seabirds, the islands were declared a National Park in 1972 by the Venezuelan government (Rodríguez and Posada 1994).

In this study, shell midden surveys were conducted on Isla Fernando (IF), Dos Mosquises (DM), La Pelona (LP) and Punta de Cayo Sal (PCS) where most of shells extracted throughout the conch fisheries in Los Roques had accumulated. Preliminary surveys characterized La Pelona and Punta de Cayo Sal sites as having the largest pre-Columbian middens in the archipelago, whereas most of shells extracted during modern times were deposited in Isla Fernando. Both pre-Columbian and modern middens were exclusively composed by *S. gigas* shells. Middens varied in shape, but usually formed well defined mounts with heights ranging from 1 to 4 m. Pre-Columbian middens tended to be located inland and arranged as if following ancient

Fig. 1 Representative pre-Columbian (*left*) and modern (*right*) conch middens located in Los Roques, Venezuela

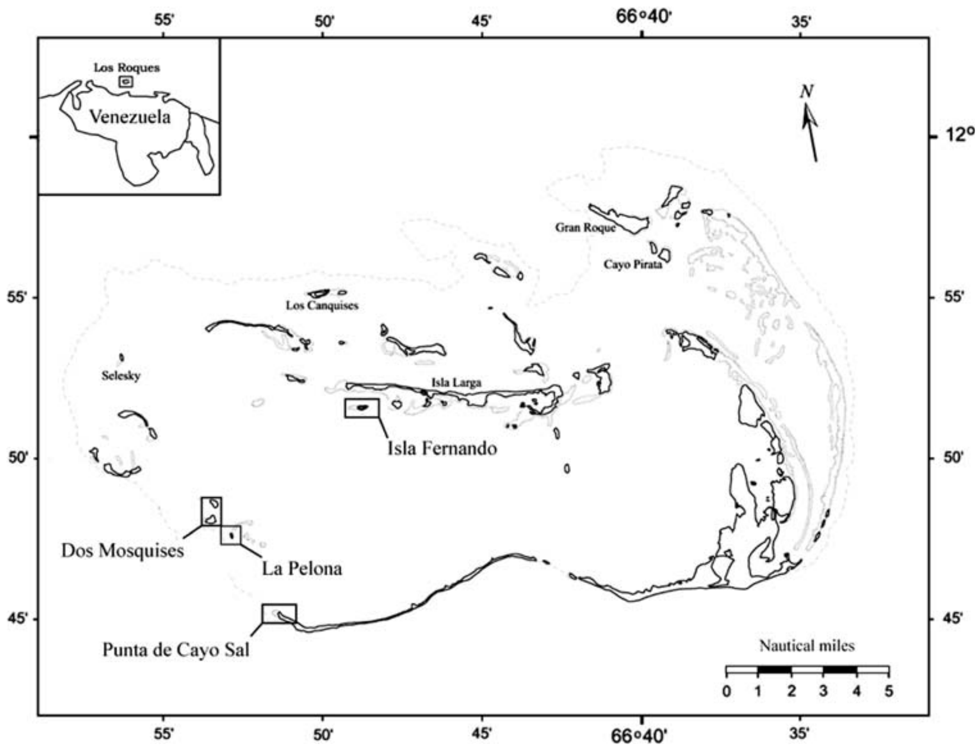

Fig. 2 Studied locations in Los Roques, Venezuela

coastlines, whereas modern ones were all located over the active coast of islands. A total of eleven pre-Columbian middens located at La Pelona (3) and Cayo Sal (8), and 16 modern middens located at Isla Fernando (9), Dos Mosquises (1), La Pelona (4) and Punta de Cayo Sal (2) were selected to be sampled as they could be dated with relatively high accuracy and showed very low levels of disturbance.

Shell midden dating

A preliminary visual assessment of middens was performed to differentiate pre-Columbian from modern middens. Shells deposited in pre-Columbian middens showed a rounded hole in the spire caused by the strike of the apex of another shell used by Amerindian fishermen, whereas those processed by modern fishermen had a narrow slit opening made by a hatchet (Antczak and Antczak 2005). An additional criterion for considering middens as pre-Columbian was the presence of Amerindian potsherds inside and/or scattered on their tops. Five out of eleven pre-Columbian middens were selected for radiocarbon analysis to confirm age. A shell from the bottom of each of the five selected middens was sampled and a fragment per shell was extracted and sent to Beta Analytic Inc. (Miami, USA) for radiocarbon analysis. Radiocarbon age calibration was performed using data provided by Stuiver et al. (1998), and using the cubic spline fit mathematics by Talma and Vogel (1993).

Dating of modern middens was performed through analysis of aerial photographs from 1940 (Source: National Archives and Record Administration, USA), 1971 (Source: Instituto Geográfico Simón Bolívar, Venezuela), 1989 and 2003 (Source: private collections). Comparisons between photographs enabled establishing time of modern middens deposition. Local fishermen and authorities corroborated these estimates, and gave additional information allowing assigning more specific age estimations for each modern midden.

Shell measurements

Shells were sampled from a single 1 × 1 m pit started at the highest top of each selected midden. Overall, shells showed low levels of damage or erosion, apart from those deposited in the outer layer of very old middens. Damaged shells were scarce and when encountered were not considered for measurements. Excavation was finished when the pit reached sterile sand coinciding with an absence of shells.

To determine the composition of excavated middens in terms of age-classes relative abundance, lip thickness was measured in the area of greatest thickness. After being measured, each shell was assigned to a specific age-class (Appeldoorn 1988): juvenile (absence of shell lip, lip thickness = 0), subadult (lip thickness between 0.1 and 0.5 cm), and adult (>0.5 cm of lip thickness). Shell length was also measured from the tip of the spire to the end of the siphonal canal. Due to the high number of shells excavated from each pit (i.e., up to 4,000), a subsample of shells was selected to be measured by randomly selecting two shells out of every ten excavated. Mean length of catch, mean length of mature individuals and the percentage of immature individuals were calculated for each excavated midden, as these measurements have been suggested as useful indicators in fishery management (Link 2005).

Statistical analyses

After dating and grouping middens into defined fishery periods, three-one-way ANOVAs were used to compare mean length of catch, mean length of mature individuals, and the percentage of immature individuals among identified fishery periods. Post hoc Tukey's tests were used to discriminate differences between all combinations of periods examined for each ANOVA. Normality and homocedasticity of data for each indicator was checked prior to analysis using a Kolmogorov–Smirnov's and a Levene's test, respectively (Sokal and Rohlf 1995). All analyses were undertaken using SPSS (v. 15.0).

Results

Tables 1 and 2 show estimated periods of formation for each pre-Columbian and contemporary excavated midden. Pre-Columbian fisheries occurred between 1160 and 1540 A.D.; however, no sub-periods were identified within the pre-Columbian fishery regime due to the limited amount of radiocarbon samples submitted for analysis. Pre-Columbian data was therefore used as a baseline from which to compare changes observed during contemporary fisheries. Modern surveyed middens were deposited between 1950 and 1995, and three sub-periods could effectively be discriminated: 1950–1971 (IFC1, IFC2 and IFC3), 1972–1989 (IFC4, IFC5, IFC6, LPC1, LPC2, LPC3 and DMC1), and 1990–1995 (IFC7, IFC8, IFC9 and LPC4). Evidence suggesting the formation of shell middens during colonial times has not been reported in the archipelago.

Mean length of catch was significantly different among identified fishery periods ($F_{3,27} = 19.85$, $P < 0.001$) (Fig. 3). From multiple comparison tests, mean length of catch was not significantly different between pre-Columbian and 1950–1971 fisheries, estimated at 22.4 ± 0.2 and 22.2 ± 0.3 cm (mean ± SE), respectively (for P values see Table 3). However, a significant decrease in mean length of catch was observed between 1950–1971 and 1990–1995, from 22.2 ± 0.3 to 20.0 ± 0.3 cm. The same pattern was observed for mean length of mature individuals ($F_{3,27} = 26.54$, $P < 0.001$) (Table 2; Fig. 4). In terms of age-class distribution, a significant difference was also observed in the percentage of immature individuals present in middens among fishery periods ($F_{3,27} = 21.87$, $P < 0.001$) (Fig. 5). Pre-Columbian fishermen collected mostly mature individuals, with an average of 11 ± 3% of immature individuals present in middens (i.e., juvenile and subadult shells). During modern fisheries, the percentages of immature individuals collected were all significantly higher compared with pre-Columbian fisheries (Table 2), ranging from 46 ± 7% in 1950–1972 to 67 ± 3% in 1990–1995. However, values observed among modern periods were not significantly different from each other (Table 3).

Discussion and conclusions

The present study showed changes in the composition of shell middens over time in the Archipelago Los Roques. Pre-Columbian middens were comprised of large shells of mostly adult specimens whereas throughout modern fisheries an increase of immature individuals present in middens was recorded, together with a decrease in the size of mature ones. Even though this trend might suggest a change in selectivity patterns of fishermen from pre-Columbian to modern times, we argue that selectivity patterns remained unchanged and that the differences observed were most likely reflecting the condition of *S. gigas* stocks as a result of fishing.

Zoological models of consumer choice (i.e., optimal foraging theory) have been used in the archaeological literature to predict selective behaviour of human shellfish gatherers (Anderson 1981; Thomas 2002, 2007; Nagaoka 2003). Human foragers are expected to collect the most valuable specimens in terms of the maximum quantity of meat obtained per unit effort (MacArthur and Pianka

Table 1 Radiocarbon analysis results for pre-Columbian shell samples extracted form selected middens

Sample	Laboratory number	C13/C12 ratio (‰)	Conventional age (B.P.)	Calibrated age (A.D.)	2 sigma calibrated age (A.D.)
LPP1	Beta-178239	2.6	1150 ± 60	1270	1160–1330
LPP2	Beta-176600	3.3	1070 ± 60	1310	1230–1420
LPP3	Beta-176601	3.4	870 ± 60	1450	1390–1540
PSCP6	Beta-209967	3.3	1130 ± 70	1280	1160–1390
PSCP11	Beta-209968	1.8	1030 ± 60	1330	1270–1440

Table 2 Location, date of deposition and fishery indicators values for each excavated midden

Midden	Location	Date (A.D.)	% immature individuals	Mean length of catch (cm)	Mean length of adults (cm)
Pre-Columbian					
LPP1	11.78610N, 66.88195W	1160–1330	15	22.1	22.4
LPP2	11.78687N, 66.88162W	1230–1420	19	21.6	22.0
LPP3	11.78670N, 66.88095W	1390–1540	10	22.7	23.0
PCSP1	11.74530N, 66.85622W	–	36	21.7	22.6
PCSP2	11.74530N, 66.85621W	–	9	22.4	22.7
PCSP3	11.74531N, 66.85621W	–	13	22.0	22.4
PCSP4	11.74531N, 66.85704W	–	1	23.0	23.0
PCSP6	11.74632N, 66.85705W	1160–1390	4	22.7	22.7
PCSP7	11.74632N, 66.85700W	–	2	23.2	23.2
PCSP8	11.74632N, 66.85698W	–	9	22.2	22.5
PCSP11	11.73993N, 66.84587W	1270–1440	6	23.1	23.3
		Total average (±SE)	11 ± 3	22.4 ± 0.2	22.7 ± 0.1
Modern					
IFC1	11.86510N, 66.80445W	1950–1971	31	22.8	22.4
IFC2	11.86498N, 66.80448W		50	22.1	22.1
IFC3	11.86392N, 66.80440W		56	21.7	21.9
IFC4	11.86127N, 66.80390W	1972–1989	43	20.9	20.9
IFC5	11.86133N, 66.80380W		55	21.2	21.2
IFC6	11.86235N, 66.80320W		79	21.1	22.0
LPC1	11.79808N, 66.86903W		45	22.1	22.3
LPC2	11.79800N, 66.86910W		26	20.7	20.8
LPC3	11.78218N, 66.88158W		61	20.9	21.0
PCSC1	11.74707N, 66.85605W		49	20.4	20.5
PCSC2	11.74557N, 66.85525W		84	19.5	20.5
DMC1	11.80208N, 66.88662W		29	21.1	21.2
IFC7	11.86267N, 66.80300W	1990–1995	58	19.2	19.6
IFC8	11.86272N, 66.80300W		66	20.2	20.0
IFC9	11.86363N, 66.80277W		71	20.4	21.2
LPC4	11.78277N, 66.86552W		73	20.7	20.6
		Total average (±SE)	55 ± 4	20.9 ± 0.2	21.1 ± 0.2

1966). However, this approach on human behaviour has generated debate among archaeologists, centred primarily on whether selective exploitation patterns can be explained considering exclusively non-cultural criteria (Anderson 1981; Bailey 1983; Claassen 1998; Bird and Bliege 1997) (reviewed by Maninno and Thomas 2002).

Assuming all fishermen (whether pre-Columbian or modern) selected their prey using an optimal foraging strategy, shells encountered in middens would represent samples of the most valuable specimens available at the time they were collected. It is also expected that the largest specimens available were regarded by both pre-Columbian and modern fishermen as the most valuable ones, as is the case for other commercially important fishing resources (e.g., oysters, lobsters, groupers, snappers). Additionally, in this particular fishery where gatherers directly controlled selectivity, a personal decision was made on every single item collected, making optimal foraging behaviour more likely to occur.

Fishery methods have fundamentally remained unchanged since pre-Columbian times, as conchs in Los Roques have always been collected by free-divers. However, the use of motorized boats and fins and masks allowed modern fishermen to exploit a broader range of fishing grounds and particularly to have access to deeper areas where spawning aggregations are known to occur (Stoner and Sandt 1992; Stoner and Schwarte 1994). Therefore, a higher fishing intensity is expected to have characterized modern fisheries, as is evident by the higher abundance and larger size of modern middens compared to pre-Columbian ones (Fig. 1).

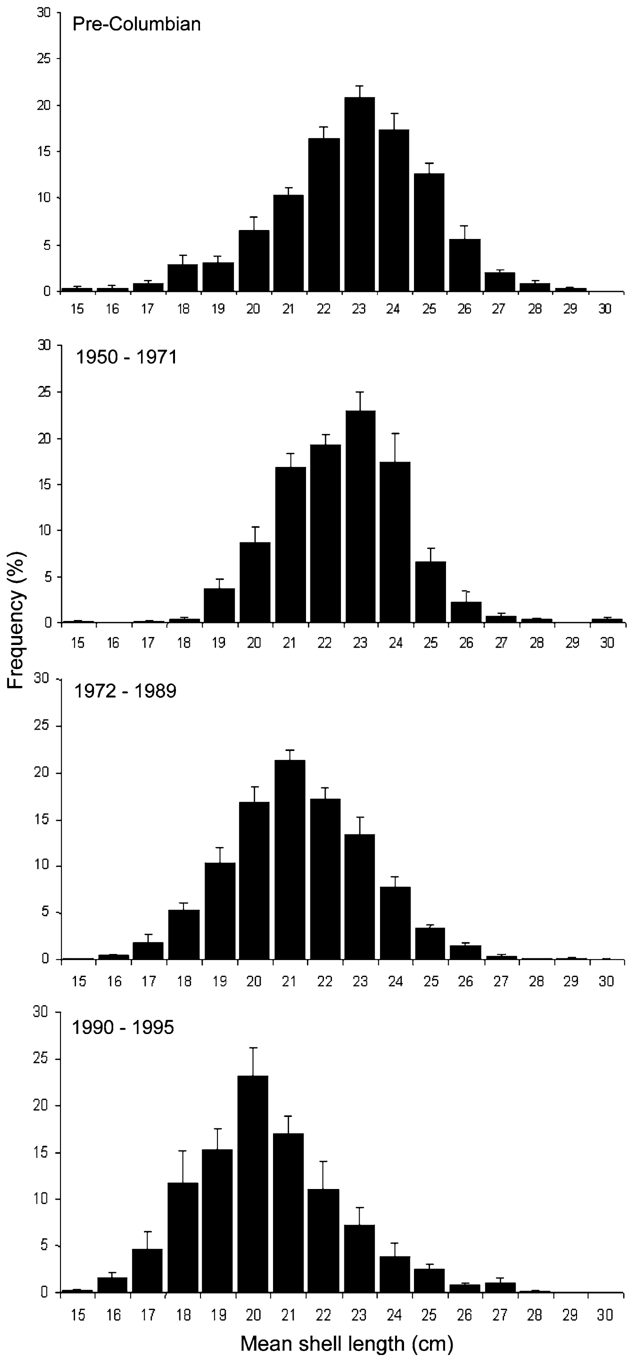

Fig. 3 Frequency distributions of mean shell length for pre-Columbian and modern surveyed periods. Error bars represent plus and minus one standard error

The trend of decrease in average size and age observed in modern middens is thus interpreted as a depletion of the most valuable individuals through time (Figs. 3 and 5). A sustained and intensive foraging strategy as the one expected to have occurred resulted in a progressive decrease in the frequency of larger individuals, as relative abundance of smaller conchs increased in middens. This depletion effect is reflected not only in an increased abundance of younger individuals but also in a decreased size of mature specimens (Figs. 4, 5).

Observed changes in shell length of matured individuals of *S. gigas* can be converted to biomass (meat weight) using the following regression (Appeldoorn 1992):

$$\text{Log}_{10}(\text{Meat weight}) = -2.187 + 3.181\ \text{Log}_{10}(\text{Length})$$

Based on this equation the mean meat weight of a mature conch in 1950–1971 was approximately 123 g (22.1 cm) while in 1990–1995 its mean weight was 94 g (20.3 cm). This represents a 24% reduction in biomass, a difference that would continue into adulthood (i.e., determinate growth). Such a reduction in individual biomass would accompany a reduction in abundance as fishing pressure increased. Thus, even greater rates of mortality would be needed to maintain the level of fishery yield, or more realistically, the decline in overall yield of the fishery would be positively reinforced. Additionally, a reduction in the mean biomass of mature individuals would reduce the overall reproductive potential of the population, as predicted by life-history theory (Stearns 1992; Roff 2001). Even though density-dependent mechanisms could be involved in regulating total biomass of the population, the magnitude of human impact could outweigh the ability of exploited populations to compensate biologically, particularly for species such as *S. gigas*, exhibiting internal fertilization (i.e., the Allee effect) (Stoner and Ray-Culp 2000).

Since the 1980s, the critical status of the species throughout its geographic range has prompted many governments to establish management strategies (e.g., closed seasons and areas, minimum shell length, prohibition of SCUBA gear use), and even total closure of fisheries (Appeldoorn 1997; Chakalall and Cochrane 1997). In Florida, the fishery collapsed and a moratorium was established in 1985. Ever since, populations of conch in the region have maintained low levels of densities compared to the ones reported in the 1970s (Glazer and Berg 1994). Although many initiatives have been developed to enhance stocks (e.g., transplant of spawn, release of hatchery-reared juveniles), no significant recovery has been observed (Stoner and Glazer 1998). Overfishing has also been reported in Colombia (Mora 1994), Mexico (Aldana and Brulé 1994), Puerto Rico (Mateo 1997) and the US Virgin Islands (Friedlander et al. 1994).

In the Archipelago Los Roques, low densities of conch were reported in heavily exploited areas (0.08 ind m^{-2}), compared with densities in areas with low levels of exploitation (0.46 ind m^{-2}) (Weil and Laughlin 1984). This study triggered a series of regulations until in 1991 a moratorium on conch fisheries was nationally established, which is still presently in place (Rodríguez and Posada 1994). A stock assessment of queen conch performed in Los Roques in 1999 (Schweizer and Posada 2006)

Table 3 *P* values of post hoc multiple comparison Tukey's test for analysis of variance of mean length of catch, length of mature individuals and percentage of immature individuals among fishery periods

	Mean length of catch			Length of mature individuals			% of immature individuals		
	1950–1971	1972–1989	1990–1995	1950–1971	1972–1989	1990–1995	1950–1971	1972–1989	1990–1995
Pre-Columbian	0.942	0.001*	0.001*	0.346	0.001*	0.001*	0.006*	0.001*	0.001*
1950–1971		0.019*	0.001*		0.044*	0.001*		0.894	0.229
1972–1989			0.209			0.074*			0.337

* Significant difference between treatments

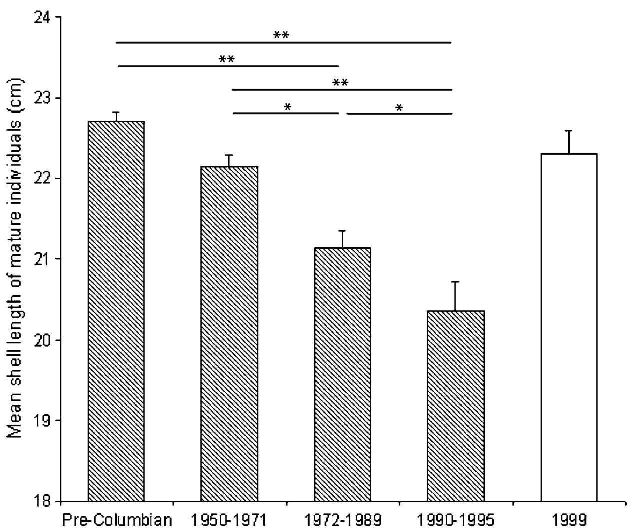

Fig. 4 Mean shell length of mature individuals for pre-Columbian and modern surveyed periods. Data for 1999 extracted from a stock assessment by Schweizer and Posada (2006). *Error bars* represent plus and minus one standard error. *Horizontal lines* represent significant differences between treatments at the beginning and end of the line (Tukey's test). $*P < 0.05$; $**P = 0.001$

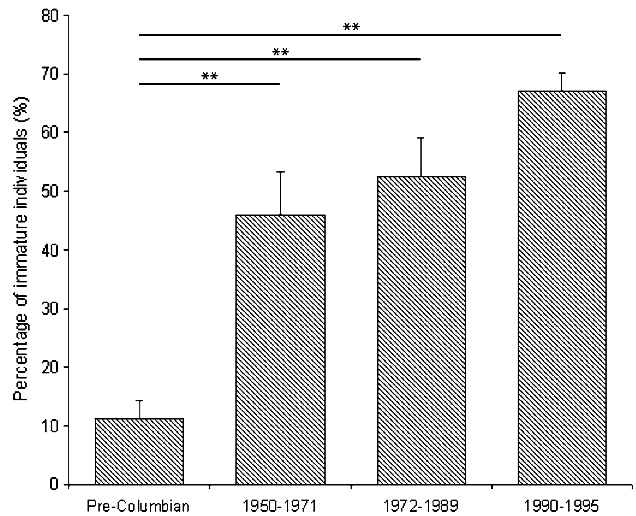

Fig. 5 Mean percentage of immature individuals found in middens for pre-Columbian and modern surveyed periods. *Error bars* represent plus and minus one standard error. *Horizontal lines* represent significant differences between treatments at the beginning and end of the line (Tukey's test). $*P < 0.05$; $**P = 0.001$

estimated a mean size of mature individuals at 22.3 cm, suggesting the moratorium on conch fishery has been effective in reducing fishing pressure, increasing the occurrence of larger individuals (Fig. 4).

A systematic study of middens was never carried out, and only recently a detailed historical reconstruction of the fishery is allowing a better understanding of conch vulnerability in a wider temporal perspective. The appearance of less valuable specimens in the catches (i.e., younger and smaller) is considered as a sign of heavy exploitation of local modern populations of queen conch. Additionally, the detected decrease in mean size of matured individuals suggests heavy exploitation could have acted as a selective force favouring the survival of individuals maturing at smaller sizes had the moratorium not been established, potentially having long-term implications to the overall productivity of the stock.

Pre-Columbian middens in contrast, permitted establishing a relative baseline from which to compare trends registered in modern times. Given that no sub-periods could be established within pre-Columbian exploitation regime, it is difficult to clearly assess whether Amerindians were also significantly impacting *S. gigas* populations. However, the low occurrence of immature specimens and the large size of matured ones throughout the pre-Columbian fishery regime suggest that: (1) fishing intensity was low enough to allow a long-term fishery characterized by large adult specimens, and/or (2) the harvesting of mostly mature individuals allowed effective replenishment of the stock and thus sustainability to the fishing resource.

Queen conch has been shown to be highly vulnerable to intensive fishing throughout the Caribbean islands in modern times and even though regulations have been introduced in several countries, populations have not always recovered. The recovery in the mean size of mature specimens reported in Los Roques suggests this location might be important for replenishing populations in other parts of the country or even at a regional level, justifying even more the status of protected species given to *S. gigas* under current national legislation.

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