



Fishery biology of the Caribbean reef sharks, *Carcharhinus perezii* (Poey, 1876), in a Caribbean insular platform: Los Roques Archipelago National Park, Venezuela

RAFAEL TAVARES^{1,2}

¹Instituto Nacional de Investigaciones Agrícolas (INIA), La Asunción 6311, Isla de Margarita, Estado Nueva Esparta, Venezuela. Telephone/ Fax: +58 (295) 242.22.20. / 242.02.52.

E-mail: rtavares@inia.gob.ve

²Centro para la Investigación de Tiburones (CIT).

Av. Don Bosco, Qta ABC, No. 10, La Florida, Caracas 1050, Venezuela.

Abstract. Catches of *Carcharhinus perezii* by the artisanal shark fishery in the Los Roques Archipelago during 2001 and 2002 were analyzed in terms of spatial distribution, abundance, diet composition, population structure and growth. The species accounted for 37.7% of the total shark catch. The 303 *C. perezii* specimens examined measured between 67 and 270 cm TL. Mean size estimates of mature males and females were 180.8 and 182.6 cm TL, respectively. Neonates and juveniles were caught mainly in shallow waters (< 20 m depth) along coral reefs bordering the islands. Annual mean CPUE were 1.7 and 1.9 sharks 100-hooks⁻¹ in 2001 and 2002, respectively. Stomach contents were mainly teleost fishes (99.5 %IRI), with the most important prey group being Carangidae (10.0 %IRI). Analysis of the length-frequency distribution allowed separation of five age groups (from 0 to 4 years old). The estimated growth rate fell from 31.6 to 17.4 cm year⁻¹ during the first four years of life. The von Bertalanffy growth model predicted similar estimates of the parameter K for males (0.16 year⁻¹) and females (0.15 year⁻¹). Of the *C. perezii* caught by the local shark fishery in Los Roques, 88.6% were immature; hence, a conservation strategy for this species must be included in the management of this national park.

Keywords: conservation, elasmobranchs, fishery, management, nursery area.

Resumen. Biología pesquera del tiburón coralino, *Carcharhinus perezii* (Poey, 1876), en una plataforma insular del Caribe: Parque Nacional Archipiélago Los Roques, Venezuela. Se analizó la distribución espacial, abundancia, composición de dieta, estructura poblacional y crecimiento de la especie *Carcharhinus perezii* en el Archipiélago Los Roques. Durante el periodo de estudio, el 37,7% de la captura total de tiburones estuvo constituida por la especie *C. perezii*. Los 303 ejemplares examinados midieron entre 67 y 270 cm LT y la talla media de los individuos sexualmente maduros fue 180,8 cm LT en los machos y 182,6 cm LT en las hembras. Los recién nacidos y juveniles fueron capturados principalmente en aguas poco profundas (< 20 m) en áreas que bordean las islas. Las medias anuales de la CPUE fueron 1,7 y 1,9 individuos 100-anzuelos⁻¹ en los años 2001 y 2002, respectivamente. La dieta estuvo dominada por peces teleósteos (99,5 %IRI), siendo el ítem Carangidae (10,0 %IRI) el más importante. El análisis de la distribución de frecuencias de talla resultó en la separación de cinco grupos de edad (0-4 años). A su vez, la tasa de crecimiento durante los primeros cuatro años de vida decreció desde 31,6 hasta 17,4 cm año⁻¹. El ajuste del modelo de von Bertalanffy resultó en valores del parámetro K similares en los machos (0,16 año⁻¹) y hembras (0,15 año⁻¹). El 88,6% de las capturas de *C. perezii* estuvieron constituidas por individuos inmaduros, por consiguiente medidas de conservación dirigidas a esta especie deberían ser incluidas en los actuales planes de manejo del parque nacional.

Palabras-Clave: conservación, elasmobranquios, pesquería, planes de manejo, área de criadero.

Introduction

The Caribbean reef shark, *Carcharhinus perez*, is a bottom-dwelling species of continental and insular shelves, and is commonly associated with tropical coral ecosystems. It is distributed along the western Atlantic seaboard, from the southeastern coast of Florida to southern Brazil, including the Gulf of Mexico, the chain of greater and lesser Caribbean islands and the northern coast of South America (Compagno 2002). In the Caribbean Sea, *C. perez* is one of the species most frequently caught by many diverse fisheries targeting sharks (Bonfil 1997, Castro *et al.* 1999). Monitoring of medium-scale longline fleets has indicated that shark catches are largely dominated by *C. perez* off several oceanic islands of the southern Caribbean Sea (Tavares 2005, Ballesteros & Castro 2006). Moreover, this species has acquired economic importance for the diving industry as a living resource in eco-tourism and shark-feeding activities (Compagno 2002). In spite of the economic and ecological value of *C. perez*, the conservation status is unknown throughout its distribution range. The species has been poorly studied in the Caribbean Sea and there is little information concerning its contribution to catches, its abundance and its biology.

Los Roques Archipelago is recognized in the Caribbean Sea for its high diversity and abundance in marine resources, and also by the high standard of conservation of the coral reef ecosystems (Baamonde 2003). Although the archipelago has the status of national park, and commercial exploitation of its marine resources is controlled, the current conservation and management measures do not include regulation of fishing for sharks. Previous studies have shown the importance of Los Roques Archipelago as habitat for several species of sharks, including *C. perez* (Tavares 2001, 2005). Those earlier studies provided information regarding the catch contribution and relative abundance of *C. perez* on the basis of shark fishery data. *Carcharhinus perez* has been studied also by Chapman *et al.* (2005) and Pikitch *et al.* (2005) in the Glover's Reef Atoll (Belize) and by Garla *et al.* (2006a, 2006b) in the Fernando de Noronha Archipelago and Atol

das Rocas (Brazil). Those authors employed a combination of tag-recapture and acoustic telemetry techniques to describe the population structure, movement patterns and habitat use of this species, with particular emphasis on juvenile populations.

In several areas of the world, scientific evidence indicates that sharks are particularly vulnerable to overexploitation (FAO 2005). Two main factors have contributed to the collapse of several shark populations: the large numbers of immature individuals caught by the fisheries, and the degradation of areas inhabited by neonates and juveniles (Camhi *et al.* 1998). Both actions directly interfere with recruitment processes; affecting the rate of population increase. Shark nursery habitats are geographically discrete areas where parturition occurs and neonates spend their first weeks, months, or years (Castro 1993). These areas can be easily identified by the capture of neonates or juveniles, or of females at advanced stages of pregnancy. Because sharks have a low reproductive potential and do not support high levels of fishing mortality (Stevens *et al.* 2000), the identification and protection of shark nurseries could constitute an important conservation measure for heavily exploited species. With the purpose of obtaining basic information required for future management plans in the Los Roques Archipelago, the present study aimed to examine the horizontal and vertical distribution, parturition season, abundance, diet composition, population structure and growth of *C. perez* on the basis of individuals caught by artisanal shark fishing.

Materials and Methods

The Los Roques Archipelago National Park is situated in the southern Caribbean Sea, approximately 160 km directly north of the mainland central coast of Venezuela (11° 43' - 11° 58' N/66° 35' - 6° 57' W; Figure 1). The archipelago consists of one main island (Gran Roque) and about 40 small low keys grouped around a central lagoon. Water temperature varies between 25 °C (February) and 30 °C (August). Mean annual rainfall is ~256 mm, in contrast to the 1841 mm mean annual evaporation (source: Hydrography and

Navigation Dept, Cagigal Naval Observatory). Los Roques contains diverse coral forms, such as dense and diffuse patch reefs, fringing reefs, and two major barrier reefs 24 and 30 km in length that are respectively located along the southern and eastern edges of the archipelago (Baamonde 2003).

The samples analyzed in the present study were obtained from the local shark fishery operating in the Los Roques Archipelago during the years 2001 and 2002. This fishery uses artisanal bottom longlines

of either mono- or multi-filament with 100 to 400 hooks (J-type, size # 3-5). The fishing vessels are mainly small wooden boats between 6 m and 8 m in length and equipped with one or two outboard motors, commonly 40 to 48 hp. Bait is usually composed of grunts (Haemulidae), parrots (Scaridae), porgies (Sparidae), snappers (Lutjanidae) and moray eels (Muraenidae). Fishing zones comprise both internal shallow waters (< 20 m) and bordering deep zones (20-80 m) of the archipelago (Figure 1).

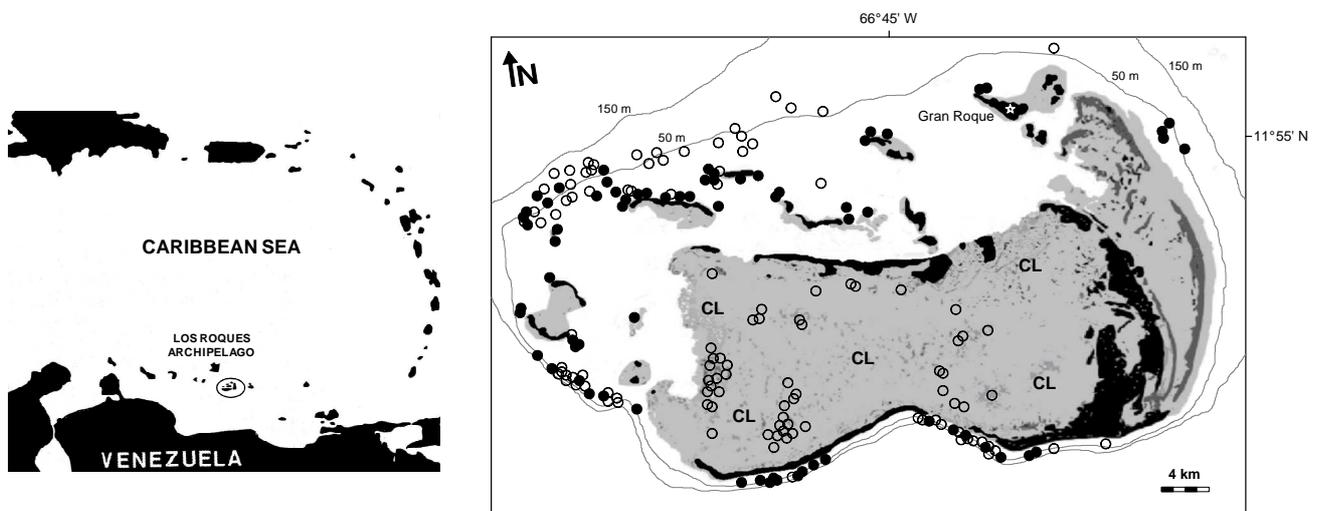


Figure1. . Location of the Los Roques Archipelago National Park, showing the catch distribution of sharks registered during fishing monitoring in 2001 and 2002. Map colors: black = islands or keys, dark gray = eastern coral reef barriers, light gray = shallow-water zones maximum depth 8 m. Symbols: ● = catches positive for *Carcharhinus perezii*, ○ = catches of other shark species, CL = central lagoon.

Carcharhinus perezii specimens were measured, weighed, sexed and examined for reproductive status and stomach contents. The size measures used were the total length (TL) and fork length (FL) in cm, and the total weight (TW) was measured in kg. Sexual maturity was determined on the basis of the general development and characteristics of the reproductive organs in both sexes. Males were considered mature if they had calcified claspers and developed testis; and females when they showed developed ovaries or pregnancy. Neonates were easily identified by the presence of an open or only partially closed umbilical scar. Fishing locations were recorded by using a

manual GPS (Global Positioning System) and fishing depths were obtained with the assistance of the local fishermen.

The population structure of *C. perezii* was characterized in the study area on the basis of the size composition by sex of the artisanal fishing catches. Variation in sex ratios for each year and trimester (years combined) was evaluated by employing a chi-square (χ^2) test. In order to determine if length data (sexes combined) were normally distributed, a quantile-quantile plot of total length was done to compare the observed and normal distributions of this variable. The goodness of fit between the two distributions was measured with a

Kolmogorov-Smirnov statistic. Because length data violated the assumption of normal distribution, the non-parametric Kruskal-Wallis test was employed to compare variability between sexes. Regression techniques were applied between the most important biometric variables (FL vs. TL and TL vs. TW), in order to obtain conversion equations. Subsequently, differences between line regressions by sex were tested by analysis of covariance (ANCOVA).

The abundance levels of *C. perezi* were investigated by calculating the index of catch per unit effort (CPUE; sharks 100-hooks⁻¹); where the fishing sets with no captures of this species corresponded to zero CPUE. The fishing operations within the central lagoon of the archipelago were excluded from this analysis because the species *C. perezi* is absent from this area (Tavares 2008). Mean CPUE and confidence limits (CL 95%) by year and by trimester were calculated by computing Monte-Carlo simulations with 2000 estimates of CPUE, randomly generated from a standard normal distribution (mean and sd from observed data; Grunkemeier & Wu 2004). Then, differences between years and between trimesters (years combined) were tested with a one-way analysis of variance (ANOVA I) and Tukey's pairwise comparison (TPC). Additionally, the vertical distribution of the relative abundance was explored by plotting CPUE values against catch depths; the level of correlation between these two variables was measured with the Pearson coefficient (*r*). The diet was analyzed quantitatively by applying the prey importance indices by number (%N), by occurrence (%O) and by weight (%W). The index of relative importance (%IRI), which incorporates the previous three indices and facilitates comparisons among the contributions of different prey, was estimated (Cortés 1997).

The indirect growth assessment was carried out by using the Bhattacharya (1967) method based on the statistical analysis of the modal groups observed in the length-frequency distribution (FAO-ICLARM, Fish Stock Assessment Tools II); this assumes that each normal component represents one age group or cohort. The separation index (SI) was used to

measure the goodness of the modal separation: $SI = |L_{i+1} - L_i| / [(s_{i+1} + s_i)/2]$, where L_i is the mean length of the distribution *i*, L_{i+1} is the mean length of distribution *i+1*, and *s* is standard deviation of the distributions. Only those values of SI >2 were considered as successfully separated by definition. Annual growth rates (cm year⁻¹) were estimated from the difference between successive mean lengths corresponding to identified age groups. The length and age groups generated from modal analysis were used to fit the von Bertalanffy growth function (VBGF): $L_t = L_\infty [1 - e^{-K(t-t_0)}]$, where L_t is the predicted length at time *t*, L_∞ is the mean asymptotic length, *K* is the growth rate parameter, and t_0 is the theoretical age at which length is zero. For the study area, the maximum lengths reported for *C. perezi* are 289 cm TL in males and 305 cm TL in females (Tavares 2005) and hence these sizes were used as L_∞ values in the VBGF. Growth was modeled by fixing the asymptotic length (L_∞) to estimate the parameters *K* and t_0 . The regression procedure was carried out by employing a Gauss-Newton algorithm of the Systat package that provides confidence limits (95% CL) of the parameters and the r-squared statistic (r^2). An F-test assessed differences in growth curves between sexes. Once growth parameters had been obtained, the individual age was derived for each male and female by applying the inverse VBGF: $t = |t_0 - 1/K| \times \log|1 - L_t/L_\infty|$. The statistical methods (significant if $p \leq 0.05$) used in the present study (without cited references) are fully described by Zar (1998).

Results

In total, 194 fishing sets (32,728 deployed hooks) were registered as fishing effort during monitoring of local shark fishing in 2001 and 2002. Catch data were lacking during some months of the study period (May, Nov and Dec 2001; Jan, May, Jun, Oct and Dec 2002) owing to the absence of either monitoring activities or shark fishing. The 803 sharks caught represented 13 species in 5 families, with the most important group being Carcharhinidae (93.3%). The contribution of *C. perezi* to annual shark catches represented 38.2% in 2001 and

35.8% in 2002. The spatial distribution of shark catches showed that *C. perezii* was primarily caught in areas close to the islands and bordering the archipelago, in waters between 3 m and 60 m in depth (Figure 1).

On the basis of specimens examined in this study, total length and total weight could be estimated by using the following conversion equations: $TL = 3.087 + |1.198 \times FL|$ ($n = 116$, $r^2 = 0.99$); $TW = |0.000002 \times TL|^{3.21}$ ($n = 244$; $r^2 = 0.97$). There were not significant differences between sexes for FL vs. TL or TL vs. TW (ANCOVA, $p > 0.05$). The annual and seasonal sex ratio of the *C. perezii* did not vary significantly from the expected proportion of 1:1 (Table I).

Table I. Catch numbers by sex (including results of χ^2 -test) of *Carcharhinus perezii* caught by the artisanal fishery in the Los Roques Archipelago National Park.

Sampled Periods	Catch		χ^2 -test	
	Males	Females	χ^2 value	p value
Years				
2001	120	124	0.03	0.87
2002	25	34	1.41	0.24
Years Combined				
Trimester 1	36	39	0.16	0.69
Trimester 2	21	18	0.59	0.44
Trimester 3	81	96	0.72	0.40
Trimester 4	7	5	2.78	0.10

Overall, 145 males (47.9%) and 158 females (52.1%) were caught during the study period. Analysis showed that length data were not normally distributed (Figure 2; Kolmogorov-Smirnov test, $p < 0.05$). Subsequent comparison of length composition between sexes showed no significant difference (Kruskal-Wallis test, $p > 0.05$). Males measured between 67 and 216 cm TL and females measured between 72 and 270 cm TL. In males, the smallest adult measured 149 cm TL, and the estimated mean length of the mature individuals was 180.8 cm TL ($n = 18$). In females, the smallest adult measured 154 cm TL, and the estimated mean length of the mature specimens was 182.6 cm TL ($n = 38$). In total, 17 neonates with sizes between 74 and 86 cm

TL (mean: 80.7 ± 3.2 sd) were observed during August and September months. Another 17 individuals (67-87 cm TL) had a recently closed umbilical scar and these were captured during the same months. Two gravid females (210 and 229 cm TL) were caught in April 2002, and these carried three (62-66 cm TL) and four (59-62 cm TL) embryos at an advanced stage of development, respectively. Assessment of the reproductive condition indicated that 88.6% of the *C. perezii* caught were immature. The body size were positively correlated to the depth of the waters in which the sharks were caught ($r = 0.77$; Figure 3). The capture of small juvenile *C. perezii* (< 100 cm TL) was primarily observed in depths < 20 m.

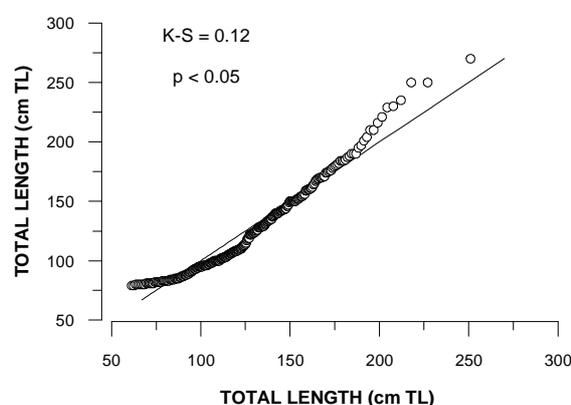


Figure 2. Normal quantile-quantile plot of the total length (TL cm) of *Carcharhinus perezii* caught by the artisanal longline fishery in the Los Roques Archipelago National Park. The Kolmogorov-Smirnov test indicated a significant difference ($p < 0.05$) from normality.

Monte-Carlo estimates of annual mean CPUE were 1.7 and 1.9 sharks 100-hooks⁻¹ in 2001 and 2002, respectively (Figure 4). Statistical analysis to test for differences in mean CPUE estimates was not significant for years (ANOVA, $p > 0.05$). In relation to the seasonal estimates by trimester, mean CPUE varied from a low of 1.1 sharks 100-hooks⁻¹ (trimester 2) to a high of 2.1 sharks 100-hooks⁻¹ (trimester 3). The only significant estimate (ANOVA, $p < 0.05$) was the CPUE in trimester 3 that was greater than the estimates observed in trimesters 1, 2 and 4. The vertical distribution of CPUE values estimated from the individual fishing sets showed that the abundance of *C.*

perezii appeared to be negatively correlated with depth ($r = -0.61$, Figure 3). The highest CPUE values (> 5 sharks 100-hooks⁻¹) were observed in zones with depths < 20 m.

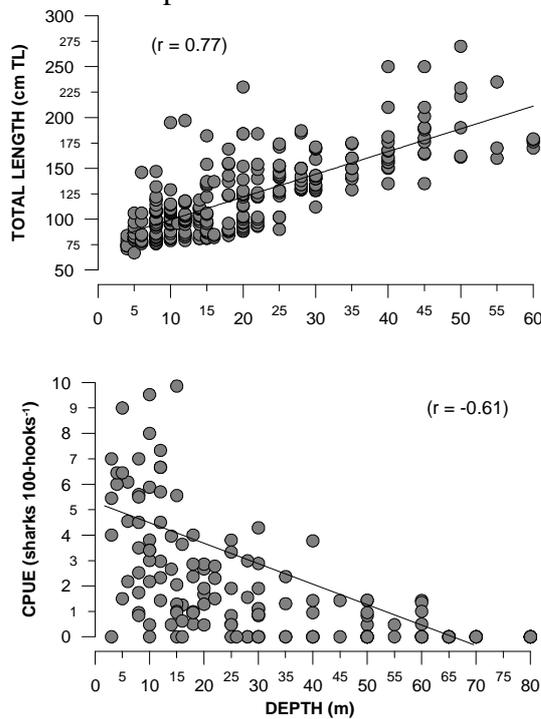


Figure 3. Individual lengths and relative abundance estimates (CPUE) in relation to depth of water column for *Carcharhinus perezii* caught by the artisanal longline fishery in the Los Roques Archipelago National Park.

Of 139 individuals (67-270 cm TL) examined for diet analyses, 77.7% had empty stomachs and 22.3% contained food items. A total of 10 families and 12 species of prey could be positively identified (Table II). Teleost fishes were the main prey group observed in stomachs (99.5% IRI), followed by cephalopods (0.5% IRI). However, a high proportion of teleost prey (70.1 %IRI) remained unidentified because of their advanced stage of digestion. Among teleosts, the more important components of the diet were members of the families Carangidae (*Caranx hippos* and *Caranx* spp.; 10.0% IRI), Lutjanidae (*Ocyurus chrysurus* and *Lutjanus* spp.; 6.9% IRI) and Belonidae (*Hemiramphus brasiliensis* and *Ablennes hians*; 5.4% IRI). The analysis also indicated that Carangidae also contributed the highest proportion by weight (32.7% W).

Analysis of the length-frequency distribution by sex (years combined) resulted in the successful separation of five modal

components or cohorts, from 0 to 4 years of age (Table III, Figure 5). When data for the two sexes were combined, the mean lengths ranged from 79.6 cm TL (group of age 0) to 178.7 cm TL (group of age 4), and growth rates varied from 31.6 to 17.4 cm year⁻¹ during the first four years of life (Table III, Figure 5). The von Bertalanffy growth model predicted similar estimates of the parameter K for males (0.16 year⁻¹) and females (0.15 year⁻¹) (Table IV). The estimated age groups for *C. perezii* catches ranged from 0 to 7 years for males and from 0 to 14 years for females (Figure 6). Statistical analysis indicated that growth curves did not differ significantly between males and females (F-test, $p > 0.05$).

Table II. Diet composition of *Carcharhinus perezii* in the Los Roques Archipelago National Park, expressed as percentage of prey items by numbers (%N), frequency of occurrence (%O), percent weight (%W) and percentage of relative importance (%IRI).

Prey item	Quantitative method			
	%N	%O	%W	%IRI
Teleosts				
Carangidae				
<i>Caranx</i> spp.	8.1	9.7	15.8	7.9
<i>Caranx hippos</i>	2.7	3.2	16.8	2.1
Lutjanidae				
<i>Ocyurus chrysurus</i>	8.1	9.7	10.6	6.1
<i>Lutjanus</i> spp.	2.7	3.2	3.8	0.7
Belonidae				
<i>Hemiramphus brasiliensis</i>	8.1	9.7	6.7	4.9
<i>Ablennes hians</i>	2.7	3.2	2.6	0.6
Haemulidae				
<i>Haemulon sciurus</i>	5.4	6.5	5.1	2.3
Scaridae				
<i>Scarus</i> spp.	2.7	3.2	0.8	0.4
<i>Scarus guacamaia</i>	2.7	3.2	7.3	1.1
Pomacentridae				
<i>Abudefduf saxatilis</i>	2.7	3.2	3.0	0.6
Mullidae				
<i>Mulloidichthys martinicus</i>	2.7	3.2	5.0	0.8
Aulostomidae				
<i>Aulostomus maculatus</i>	2.7	3.2	2.0	0.5
Sphyraenidae				
<i>Sphyraena barracuda</i>	2.7	3.2	8.3	1.2
Teleosts non-identified	43.2	38.7	10.0	70.1
Cephalopods				
Octopidae				
<i>Octopus vulgaris</i>	2.7	3.2	2.0	0.5

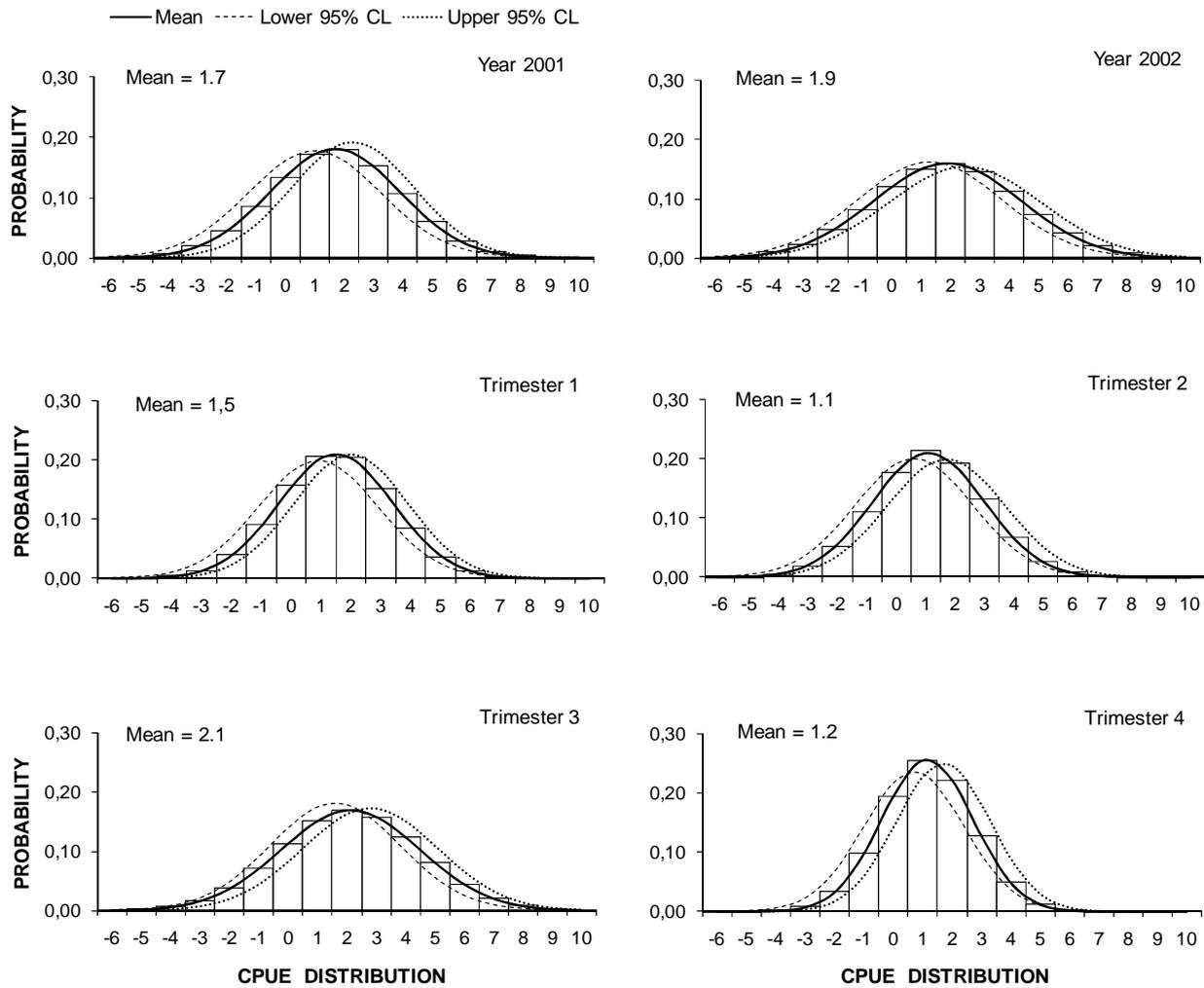


Figure 4. CPUE (sharks 100-hooks⁻¹) distributions by year and by trimester (years combined) estimated for *Carcharhinus perezii* caught by the artisanal longline fishery in the Los Roques Archipelago National Park. Also indicated are Monte-Carlo means of CPUE and 95% confidence limits (CL).

Table III. Results obtained from the Bhattacharya (1967) modal analysis applied to the length frequency distribution of *Carcharhinus perezii* caught by the artisanal longline fishery in the Los Roques Archipelago National Park. (sd = standard deviation, SI = separation index).

Bhattacharya Modal Analysis						
Sample	Age Group	Mean Length (cm TL)	sd	SI	Growth Rate	
					Year	cm year ⁻¹
Sexes combined	0	79.6	5.5	n.a	n.a	n.a
	1	111.2	8.2	4.6	1	31.6
	2	140.7	7.3	3.8	2	29.6
	3	161.3	3.6	3.8	3	20.6
	4	178.7	5.4	3.9	4	17.4
Males	0	78.0	4.3	n.a	n.a	n.a
	1	114.2	9.3	5.3	1	36.2
	2	140.0	9.7	2.7	2	25.8
	3	162.9	5.2	3.1	3	22.9
	4	181.2	4.2	3.9	4	18.3
Females	0	83.0	5.1	n.a	n.a	n.a
	1	108.8	9.2	3.6	1	25.8
	2	141.2	7.0	4.0	2	32.4
	3	159.7	3.1	3.6	3	18.5
	4	176.3	4.9	4.1	4	16.7

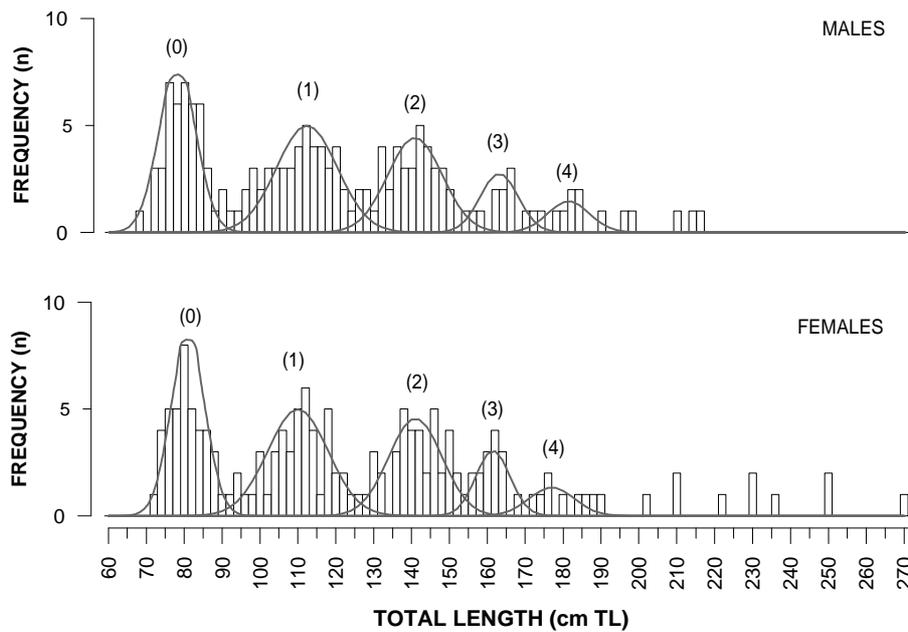


Figure 5. Length and age groups identified from the modal progression analysis of the length-frequency distribution of *Carcharhinus perezii* caught by the artisanal longline fishery in the Los Roques Archipelago National Park. Age groups from 0 to 4 years old are indicated.

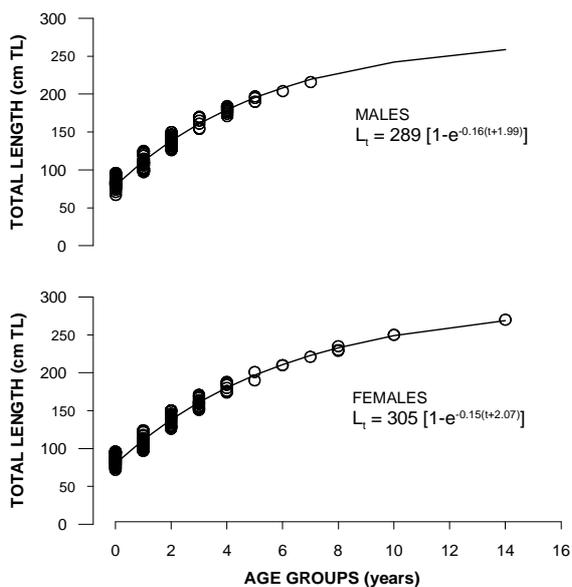


Figure 6. Von Bertalanffy growth curve fitted to length and age group data of *Carcharhinus perezii* caught by the artisanal longline fishery in the Los Roques Archipelago National Park.

Table IV. von Bertalanffy growth parameters estimated for *Carcharhinus perezii* caught by the artisanal longline fishery in the Los Roques Archipelago National Park. (95% CL = confidence limits of the parameters, r^2 = r-squared statistic).

von Bertalanffy Growth Function			
Parameter	Value	95% CL	r^2
Males			
L_{∞}	289	fixed value	0.95
K	0.16	0.15 - 0.17	
$-t_0$	1.99	2.10 - 1.68	
Females			
L_{∞}	305	fixed value	0.95
K	0.15	0.14 - 0.16	
$-t_0$	2.07	2.41 - 1.69	

Discussion

The results showed that *C. perezii* is a shark species frequently caught in the Los Roques Archipelago and its presence and abundance could keep relation with the presence of large expanses of coral reef structures. On the basis of personal observations, *C. perezii* is

seldom if ever observed in the main artisanal fisheries conducted along the continental shelf of Venezuela, and the occurrence of this species is limited to some areas characterized by their low to moderate human impact. In the Caribbean Sea, other studies have revealed that *C. perezii* is common on several oceanic insular

platforms, such as Glover's Reef Atoll, Belize (Pikitch *et al.* 2005), Las Aves Archipelago and La Blanquilla island, Venezuela (Tavares 2005), and San Andres, Providencia and Santa Catalina islands, Colombia (Ballesteros & Castro 2006). In the southwestern Atlantic Ocean, *C. perezii* has been also reported as one of the most important shark species occurring around the oceanic Brazilian islands of Fernando de Noronha Archipelago and Atol das Rocas (Garla *et al.* 2006a). All those study areas have two main characteristics in common: the existence of important coral reef formations; and their remoteness from the anthropogenic influence of the continental mainland coast. Considering that sharks are the top predators in the oceans and thus play an important role in marine ecosystems (Wetherbee & Cortés 2004), *C. perezii* must be a key species for the ecological maintenance of the oceanic insular areas in the Caribbean Sea.

In the present study area, catches of *C. perezii* were composed of a wide range of lengths, from neonates to large adults in both sexes. However, the sizes of adult males were below the maximum lengths reported for this species in Los Roques. Results also indicated that body sizes tend to increase with depth and hence these findings indicate that large adults usually inhabit or spend more time in deep zones (> 60 m). This conclusion is consistent with previous information obtained for the same study area, which showed that large adults of this species were commonly captured at depths of as much as 200 m (Tavares 2005). On the other hand, the capture of neonates and small juveniles *C. perezii* was restricted to zones of shallow water (3-20 m depth), indicating the importance of these areas close to shore as habitat for the early life-stages of this species. The studies conducted by Pikitch *et al.* (2005) and by Garla *et al.* (2006a) provided similar results in relation to the distribution of *C. perezii* according to ontogenetic development. Changes in habitat type with increasing length or age have been widely documented in sharks (Simpfendorfer & Heupel 2004). On the basis of the findings from all the above-mentioned studies of *C. perezii* (including the present work), a common distribution pattern appears to

be followed by this species. This pattern can be described as follows: neonates and small juveniles (< 130 cm TL) are primarily distributed along shallow fringing reefs close to islands (< 30 m depth); and large juveniles and adults commonly occur in deeper zones along ocean reefs bordering the insular shelves, although they can also make incursions into shallow areas, probably for feeding purposes during night hours. In the study area, the observed sex ratio (~1:1) and the length structure of *C. perezii* catches suggest the presence of a localized population in the Los Roques Archipelago. This conclusion is consistent with tag-recapture and telemetry data that have also suggested a non-migratory behavior in this species (Kohler *et al.* 1998, Chapman *et al.* 2005, Garla *et al.* 2006b).

Owing to the structure of the CPUE data (typically log-normal distribution), the use of Monte-Carlo simulations can be an alternative procedure to normalize the data. The CPUE analysis showed that abundance of *C. perezii* did not change significantly between sampled years. The higher mean CPUE observed during the third trimester was related to the birth period, which occurred during August and September. Previous seasonal CPUE estimates for *C. perezii* in the Los Roques Archipelago were highly variable (Tavares 2005), fact attributed to differences in the sources of fishing data. The information analyzed in that previous study came from the monitoring of fishing by medium-scale longline fleets operating around Venezuelan insular platforms and hence catch data were restricted to depth zones. Catches obtained in the present study can be considered a good representation of the population structure of *C. perezii*, since local shark fisheries exploit areas ranging from internal shallow waters to zones as deep as 80 m. The analysis revealed that higher CPUE values were also concentrated in the shallow zones (< 20 m) inhabited by the early life-stages. These nearshore reef zones sustain an abundant and diverse marine fauna, which makes them highly productive habitats (i.e. shark nursery areas) for the development of juvenile *C. perezii*. The species *C. limbatus* and *Negaprion brevirostris* also have nursery grounds in the Los Roques Archipelago;

however, the habitats used by the early life-stages of these two species are discretely partitioned within the insular area (Tavares 2008, 2009). The selection of a specific nursery habitat by sharks of each species helps to reduce the levels of competition and predation, and thereby leads to ecological benefits for the juvenile populations. The most recent insights regarding the complex process of shark nursery selection and habitat use are extensively discussed by Heithaus (2007) and Heupel *et al.* (2007).

The stomach contents were dominated by teleost remains, with members of the Carangidae, Lutjanidae and Belonidae being the ones most often identified. Although all teleost species that could be identified are common inhabitants of the reef zones of the Los Roques Archipelago, *C. perezii* appeared to prey mainly on those three specific groups of fishes. This pattern appears to be common in carcharhinids and the factors influencing shark feeding behavior were fully reviewed by Wetherbee & Cortés (2004). Those authors suggested that the presence of a specific prey in the diet of a particular predator might be related to the abundance of those prey species in distinct geographic areas or habitat types. However, it is necessary to take into account that prey that are easily captured could also dominate the diet of a particular shark species. Moreover, the use of separate habitats by different shark species (particularly by juvenile individuals) will avoid competition for food. Other studies conducted in Los Roques Archipelago showed that *C. limbatus* preyed primarily on Gerreidae fishes but also on clupeids when these were present in the area (Tavares & Provenzano 2000, Tavares 2008). The spatial distribution and diet composition of *C. limbatus* and *C. perezii* within the same insular area constitute a good example of habitat and dietary partitioning. The high percentage of empty stomachs observed in the present study, combined with the frequent occurrence of prey items in advanced stages of digestion, was probably a consequence of the fishing method used. Wetherbee & Cortés (2004) concluded that sharks attracted with bait (e.g. linehooks) generally had relatively empty stomachs. Consequently, stomachs obtained

from individuals caught by non-baited fishing methods (such as gillnets) would be most appropriate for diet analysis in sharks.

In the present study, the length frequency analysis appeared to provide a reasonable approximation of the annual growth rates of *C. perezii* during the first life stages, owing to the clear separation of the modal groups. Mean size estimates of mature males (180.8 cm TL) and females (182.6 cm TL) corresponded to age group of 4 years in both sexes. The information compiled by Cailliet & Goldman (2004) on the age and growth of elasmobranchs shows that, on average, the age at maturity is 9 years among sharks of the genus *Carcharhinus*. Also in Los Roques Archipelago, the species *C. limbatus* exhibits a rapid juvenile growth when compared with populations of the same species from other geographic areas (Tavares 2008). The factors that could be influencing this rapid growth observed in the study area are: (1) the constant and elevated temperature of the sea water, typical of the tropical regions; (2) the availability of prey and consequent food abundance; (3) the well conserved state of the marine ecosystems; and (4) the apparently low rate of competition as a result of the partitioning of nursery areas. In regard to the von Bertalanffy growth modeling, the K values obtained in this study (males: 0.16 year⁻¹; females: 0.15 year⁻¹) were within the range of faster-growing species (K > 0.1) given by Branstetter (1990). However, growth parameters estimated for *C. perezii* will have to be re-examined and verified through the use of other techniques such as tag-recapture or vertebral analysis, since stock evaluation requires precise and accurate age information in order to avoid inappropriate management decisions.

This study has demonstrated that a large proportion of the *C. perezii* individuals caught by the local shark fishery (88.6%) are immature; these are captured mainly in zones of shallow water (< 30 m depth) along the coral reefs bordering the islands or keys. These findings have led to recognition of the areas occupied by neonates and juveniles of this species in Los Roques Archipelago. The delineation and protection of shark nursery areas, as a

conservation measure, has received increased attention in recent years; this measure would be of significant benefit for the maintenance or recovery of the exploited shark populations. Nevertheless, Kinney & Simpfendorfer (2008) recently suggested that, for management purposes, protection of adult sharks beyond nurseries may be more important than protection of juvenile individuals within the nursery areas. In the case of the Los Roques Archipelago, the adult population of *C. perezi* appears not to be significantly affected by the artisanal fishery conducted in the area. Research must continue in order to increase biological knowledge of the most important species of sharks captured in the study area. However, considering the status of the Los Roques Archipelago as a national park, a closed season for shark fishing should be established in this area.

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References

- Baamonde, J. M. 2003. Origen y formación del archipiélago. Pp. 85-98. *In*: Zamarro, J. (Ed.). **Parque Nacional Archipiélago Los Roques**. Agencia Española de Cooperación Internacional, Caracas. 271 p.
- Ballesteros, C. A. & Castro, E. G. 2006. **La pesquería industrial de tiburones en el Archipiélago de San Andrés, Providencia y Santa Catalina: una primera aproximación**. Secretaria de Agricultura y Pesca, Colombia. Informe Técnico. 37 p.
- Bhattacharya, C. G. 1967. A simple method of resolution of a distribution into Gaussian components. **Biometrics**, 23:115-135.
- Branstetter, S. 1990. **Early life-history implications of selected carcharhinoid and lamnoid sharks of the Northwest Atlantic**. Technical Report, NMFS. 90:17-28.
- Bonfil, R. 1997. Status of shark resources in the southern Gulf of Mexico and Caribbean: implications for management. **Fisheries Research**, 29:101-117.
- Cailliet, G. M. & Goldman, K. J. 2004. Age determination and validation in chondrichthyan fishes. Pp. 399-447. *In*: Carrier, J. C., Musick, J. A. & Heithaus, M. R. (Eds.). **Biology of sharks and their relatives**. CRC Press, New York. 596 p.
- Camhi, M., Fowler, S., Musick, J., Bräutigam, A. & Fordham, S. 1998. **Sharks and their relatives: ecology and conservation**. IUCN/SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. 39 p.
- Castro, J. I. 1993. The shark nursery of Bull Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. **Environmental Biology of Fishes**, 38:37-48.
- Castro, J. I., Woodley, C. M. & Brudek, R. L. 1999. **A preliminary evaluation of the status of shark species**. FAO, Fishery Technical Report No 380. 72 p.
- Chapman, D. D., Pritchard, E. K., Babcock E. & Shivji, M. S. 2005. Marine reserve design and evaluation using automated acoustic telemetry: a case-study involving coral reef-associated sharks in the Mesoamerican Caribbean. **Marine Technology Society Journal**, 39(1):42-55.
- Compagno, L. J. V. 2002. Sharks. Pp. 357-505. *In*: Carpenter, K. E. (Ed.). **The living marine resources of the Western Central Atlantic: Introduction, mollusks, crustaceans, hagfishes, sharks, batoid fishes, and chimaeras**. FAO, Special Publication No. 5. 600 p.
- Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to

- elasmobranch fishes. **Canadian Journal of Fisheries and Aquatic Sciences**, 54:726-738.
- FAO. 2005. **Management techniques for elasmobranch fisheries of sharks**. FAO, Fisheries Technical Paper No. 474. 251 p.
- Garla, R. C., Chapman, D. D., Shivji, M. S., Wetherbee B. M. & Amorim, A. F. 2006a. Habitat of juvenile Caribbean reef sharks, *Carcharhinus perezi*, at two oceanic insular marine protected areas in the southwestern Atlantic Ocean: Fernando de Noronha Archipelago and Atol das Rocas, Brazil. **Fisheries Research**, 81:236-241.
- Garla, R. C., Chapman, D. D., Wetherbee, B. M. & Shivji, M. S. 2006b. Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. **Marine Biology**, 149:189-199.
- Grunkemeier, G. L. & Wu, Y. 2004. Bootstrap resampling methods: something for nothing? **Annals of Thoracic Surgeons**, 77:1141-1144.
- Heithaus, M. R. 2007. Nursery areas as essential shark habitats: a theoretical perspective. **American Fisheries Society Symposium**, 50:3-13.
- Heupel, M. R., Carlson, J. K. & Simpfendorfer, C. A. 2007. Shark nursery areas: concepts, definition, characterization and assumptions. **Marine Ecology Progress Series**, 337:287-297.
- Kinney, M. J. & Simpfendorfer, C. A. 2008. Reassessing the value of nursery areas to shark conservation and management. **Conservation Letters**, 1-8.
- Kohler, N. E., Casey, J. G. & Turner, P. A. 1998. NMFS Cooperative Shark Tagging Program, 1962-93: An atlas of shark tag and recapture data. **Marine Fisheries Review**, 60:1-86.
- Pikitch, E. K., Chapman, D. D., Babcock, E. A. & Shivji, M. S. 2005. Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). **Marine Ecology**, 302:187-197.
- Simpfendorfer, C. A. & Heupel, M. R. 2004. Assessing habitat use and movement. Pp. 553-572. *In*: Carrier, J. C., Musick, J. A. & Heithaus, M. R. (Eds.). **Biology of sharks and their relatives**. CRC Press, New York. 596 p.
- Stevens, J. D., Bonfil, R., Dulvy, N. K. & Walker, P. A. 2000. The effects of fishing on sharks, and chimaeras (chondrichthyans), and the implications for marine ecosystems. **ICES, Journal of Marine Sciences**, 57:476-494.
- Tavares, R. & Provenzano, F. 2000. Alimentación de los juveniles del tiburón Macuira, *Carcharhinus limbatus* (Valenciennes, 1839), en el Parque Nacional Archipiélago Los Roques, Venezuela. **Acta Biologica Venezuelica**, 20(1):59-67.
- Tavares, R. 2001. **Estudio sobre biodiversidad de tiburones en el Parque Nacional Archipiélago de Los Roques (Segunda Etapa)**. Oficina Nacional de Diversidad Biológica, Caracas. Informe Técnico No 2001-0074. 76 p.
- Tavares, R. 2005. Abundance and distribution of sharks in Los Roques Archipelago National Park and other Venezuelan oceanic islands, 1997-1998. **Ciencias Marinas**, 32:441-454.
- Tavares, R. 2008. Occurrence, diet and growth of juvenile blacktip sharks, *Carcharhinus limbatus*, in the Los Roques Archipelago National Park, Venezuela. **Caribbean Journal of Science**, 44(3):291-302.
- Tavares, R. 2009. Preliminary results from tag-recapture procedures applied to lemon sharks, *Negaprion brevirostris* (Poey 1868), at Los Roques Archipelago, Venezuela. **Proceedings of the Gulf and Caribbean Fisheries Institute**, 62:1-8.
- Wetherbee, B. M. & Cortés, E. 2004. Food consumption and feeding habits. Pp. 225-246. *In*: Carrier, J. C., Musick, J. A. & Heithaus, M. R. (Eds.). **Biology of sharks and their relatives**. CRC Press, New York. 596 p.
- Zar, J. 1996. **Biostatistical analysis**. Prentice Hall. New Jersey. 662 p.

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