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Early growth and juvenile population structure of lemon sharks *Negaprion brevirostris* in the Atol das Rocas Biological Reserve, off north-east Brazil

R. H. A. Freitas*, R. S. Rosa*†, S. H. Gruber‡ and B. M. Wetherbee§

**Departamento de Sistemática e Ecologia, CCEN, Universidade Federal da Paraíba, João Pessoa – PB, CEP: 58059-900, Brazil, ‡Bimini Biological Field Station and University of Miami, Rosensteil School of Marine and Atmospheric Science, Miami, FL 33149-1098, U.S.A. and §Department of Biological Sciences/University of Rhode Island, Kingston, RI 02881, U.S.A.*

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Lemon sharks *Negaprion brevirostris* were sampled in the Atol das Rocas, a nursery area, on nine occasions from March 1999 to October 2003, during which 157 individuals were tagged and 35 were recaptured. The male : female sex ratio of captured individuals was 1 : 1·12. Mean ± s.d. growth rates were 24·7 ± 3·4 cm year^{-1} in total length (L_T), 20·7 ± 3·2 cm year^{-1} in fork length, and 19·5 ± 2·7 cm year^{-1} in precaudal length. There was no significant difference in growth rates between males and females. Mean ± s.d. increase in mass was 2565 ± 762 g year^{-1}. The von Bertalanffy growth parameters estimated by the Fabens method based on L_T were: $k = 0{\cdot}077$, $L_\infty = 399{\cdot}9$ cm and $t_0 = -2{\cdot}16$. Despite the large variation of environmental conditions, particularly of tidal range and currents, and the lack of protective mangrove cover in the nursery area at Atol das Rocas, juvenile lemon sharks grew relatively faster than at other nurseries. Such rapid growth could be a response to abundant food availability or high risk of predation by adults that enter the nursery area.

Key words: Carcharhinidae; Chondrichthyes; Fabens method; nursery; tag-recapture.

INTRODUCTION

The lemon shark *Negaprion brevirostris* (Poey) is distributed in the western Atlantic Ocean, from New Jersey (U.S.A.) to southern Brazil, including the Gulf of Mexico and Caribbean Sea. This species is also found on the west coast of Africa, off the Cape Verde Islands and from Dakar (Senegal) south to Ivory Coast; and on the eastern Pacific Ocean, from Baja California (Mexico) to Ecuador (Compagno, 1984; S.H. Gruber, pers. obs.). In Brazil, it is distributed from Pará State (north) to Rio de Janeiro State (south-east), and is also present at Atol das Rocas and in the Fernando de Noronha Archipelago, off the north-eastern coast of Brazil (Soto, 2001).

†Author to whom correspondence should be addressed. Tel.: +55 83 2167765; fax: +55 83 2167025; email: rsrosa@dse.ufpb.br

The lemon shark can be considered a K-strategist, characterized by slow growth, late age at maturity and low fecundity (Gruber & Stout, 1983; Gruber *et al.*, 2001). Like other carcharhinid sharks, it is viviparous, with a litter size varying from four to 18 and a gestation period lasting from 10 to 12 months (Compagno, 1984; S.H. Gruber, pers. obs.). Size at birth varies from 55 to 67 cm in total length (L_T) and the maximum adult size is 340 cm L_T (Compagno, 1984; Sundström *et al.*, 2001). Sexual maturity occurs at *c.* 11·6 years of age for males and 12·7 years for females in the coastal waters of Bimini, Bahamas (Brown & Gruber, 1988).

Many species of sharks have specific nursery grounds where the young are born and live for the first weeks, months, or years of their lives (Castro, 1993). Nursery areas of lemon sharks are known to occur in bays and shallow lagoons with seagrass dominated flats, frequently fringed by mangroves, in the coastal waters of Florida and the Bahamas (Gruber *et al.*, 1988).

The Atol das Rocas is perhaps the southern most nursery for lemon sharks (Feldheim *et al.*, 2001; Oliveira, 2001), but differs from other studied nursery grounds, in that it has no mangrove or seagrass habitats and experiences a large tidal flux. Young lemon sharks that utilize Atol das Rocas as a nursery area are therefore subjected to a wider range of abiotic conditions and reduced availability of shelter from predators than at other known nursery locations.

Tag-recapture experiments have been used to determine growth rates and to estimate parameters of the von Bertalanffy growth functions (VBGF) for several shark species (Grant *et al.*, 1979; Natanson *et al.*, 1999; Merson & Pratt, 2001). Lemon shark growth rates based on tag-recapture data have been reported by Gruber & Stout (1983), Manire & Gruber (1991), Morrissey & Gruber (1993) and Oliveira (2001). Only Brown & Gruber (1988), however, provided a length-at-age growth relationship, *i.e.* the VBGF estimated using tetracycline validated vertebral centra. The only study to examine the population structure of lemon sharks based on tag-recapture data in the southern Atlantic was that of Oliveira (2001) at Atol das Rocas. The purpose of the present study was to examine the growth of juvenile lemon sharks and the juvenile population structure at the Atol das Rocas, Brazil, based on a 5 year study using mark-recapture methods.

MATERIALS AND METHODS

STUDY SITE

A population of lemon sharks occurs at Atol das Rocas (Gadig, 1994; Rosa & Moura, 1997), but curiously, the species is rarely seen along the Brazilian coast (Gadig, 1994) even though there is abundant habitat. Atol das Rocas, the only atoll in the western South Atlantic Ocean, is located on the north-east coast of Brazil (3°52′ S; 33°49′ W) (Oliveira-Filho & Ugadim, 1976). Atol das Rocas was the first marine protected area in Brazil, established as a Biological Reserve in 1979 (Silva *et al.*, 2002). Inside the atoll there are two small sandy islands (Farol Island and Cemitério Island), a central lagoon, as well as natural pools on the rocky periphery, formed during low tides (Fig. 1). Diel tidal ranges often exceed 2·5 m in spring tides.

Farol Island is J-shaped and contains a small tidal creek, Baía da Lama, *c.* 600 m long, with a maximum width of 35 m, and a maximum depth of 1·8 m at its mouth. The water temperature in the creek varies from 26 to 30°C. There is an inflowing current into this creek during rising tide, when it becomes accessible to juvenile lemon sharks. They enter

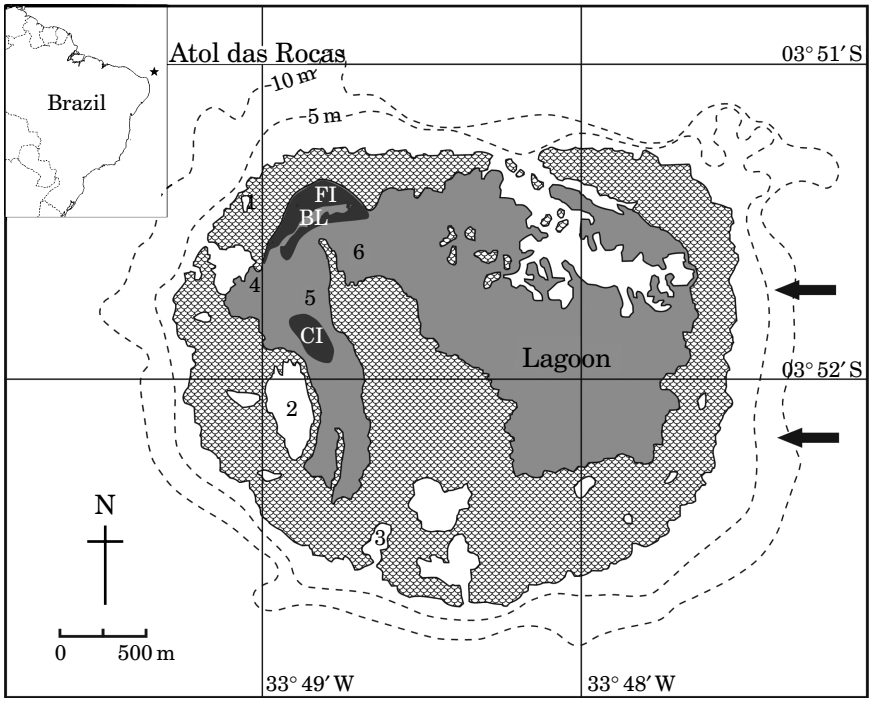

FIG. 1. Location of the Atol das Rocas Biological Reserve off Brazil (insert) and map of the study site, showing the sampled locations: BL, Baía da Lama; 1, Farol Pool; 2, Cemiterio Pool; 3, Podes Crer Pool; 4, Barretinha; 5, lagoon, north of Cemiterio Island; 6, lagoon, south of Farol Island, CI, Cemiterio Island; FI, Farol Island; ⟵, prevailing wind direction; ---, the 5 and 10 m isobaths (▨, Reef platform; ■, permanent island; ▩, shallow sandy bottom; □, sea water).

the creek in groups and remain until the direction of the tidal current is reverses. They then exit the creek with the outgoing tidal flow. The occurrence of an estimated 20–60 young lemon sharks at the mouth of Baía da Lama with the rising tide provides an opportunity for capture of many individuals over a short time period (Oliveira, 2001).

SAMPLING

Nine sampling trips to Atol das Rocas, each lasting *c*. 20 days, occurred during March 1999, March 2000, September 2000, March 2001, November 2001, August 2002, March 2003, May 2003 and October 2003. Juvenile lemon sharks were captured using monofilament gillnets (2 m depth with 10 cm stretched-mesh), dip-nets and longline fishing gear (30 circular hooks with barbs removed) at the locations indicated in Fig. 1. Although lemon sharks of all size classes are found at the atoll, the present study was limited to juveniles due to the low numbers of adults visiting the site and to the difficulty of catching and handling large lemon sharks in such a remote location. Captured lemon sharks were sexed and L_T, fork length (L_F), and precaudal length (L_{PC}) were measured to the nearest mm. In Brazil L_T is used most commonly, but elsewhere L_F and L_{PC} are used most often and deemed more consistent expressions of size than L_T. The relationships among the three measurement are provided in Table I.

When possible, lemon sharks were weighed to the nearest 100 g on a hanging scale and condition of the umbilical scar was noted. A passive integrated transponder (PIT) identification tag (Digital Angel Inc.^{TM}) was inserted into the epaxial musculature just

TABLE I. Linear regression of length measurements from 192 juvenile lemon sharks captured in the Atol das Rocas

	Linear regression	r^2	P
L_{PC} and L_T	$L_{PC} = 0{\cdot}16 + 0{\cdot}77\ L_{PC}$ or $L_T = 0{\cdot}39 + 1{\cdot}29\ L_{PC}$	0·99	<0·01
L_F and L_T	$L_F = 0{\cdot}29 + 0{\cdot}85\ L_T$ or $L_T = 0{\cdot}28 + 1{\cdot}17 L_F$	0·99	<0·01
L_{PC} and L_F	$L_{PC} = -0{\cdot}050 + 0{\cdot}91 L_F$ or $L_F = 0{\cdot}15 + 1{\cdot}10 L_{PC}$	1	<0·01

L_T, total length; L_F, fork length; L_{PC}, precaudal length.

below the first dorsal fin (Manire & Gruber, 1991; Morrissey & Gruber, 1993; Feldheim *et al.*, 2001). Lemon sharks were always scanned for PIT tags immediately after capture.

GROWTH RATES

When the time-interval between capture and recapture (time-at-liberty) is short, measurement errors are potentially larger than growth that has occurred during that time interval (Casey *et al.*, 1985). Lemon sharks captured multiple times during one trip and those captured in March 2003 and recaptured in May 2003 (*c.* 60 days-at-liberty) were not used for growth-rate estimates. For recaptured lemon sharks with times at liberty >60 days, a growth rate was calculated for each interval. A mean annual growth rate was calculated from all adequate recaptures, and outlier values were replaced by the mean, as suggested by Tukey (1977). For length based growth rates, such procedure was only adopted when all three-length measurements (L_T, L_F and L_{PC}) presented simultaneous outlier values. Outlier values were disregarded in subsequent growth analyses.

GROWTH PARAMETERS

The Fabens (1965) method was used to estimate the VBGF parameters for both sexes. This method is given by a non-linear function: $L_r = L_c + (L_\infty - L_c)\ (1 - e^{-kt})$, where: L_r = the length at recapture, L_c = the length at release (capture), t = time-at-liberty, k = von Bertalanffy growth constant, and L_∞ = theoretical maximum attainable length.

This function was fitted to the recapture data by using Statistica 4·0 (non-linear estimation module), as in Simpfendorfer (2000). The theoretical size at age 0 (t_0) was estimated by solving the function: $t_0 = t + (k^{-1})\{\ln[(L_\infty - L_t)L_\infty^{-1}]\}$ where: L_t = the mean size at birth and $t = 0$.

The $L_t \pm$ S.D. in the present study was 61·15 ± 1·90 cm in L_T and 47·62 ± 1·42 cm in L_{PC}, obtained from six lemon sharks with completely open umbilical scars.

The VBGF parameters were used to backcalculate the age of all captured lemon sharks, as given by the function: age $= -\{(-t_0) + (k^{-1})\ln[(L_\infty - L_t)L_\infty{}^{-1}]\}$

The theoretical maximum longevity was estimated by the function described by Fabens (1965): longevity $= 5\ (\ln 2)k^{-1}$.

STATISTICAL ANALYSIS

The Statistica 4·0 package was used for the statistical analyses, except for the Q-test, which was performed according to Zar (1999). Data were interpreted considering $\alpha = 0{\cdot}05$. The normality of the data (test of Komolgorov–Smirnov) and homogeneity of variances (test of Levene) were tested prior to t-tests and linear regression.

RESULTS

A total of 347 juvenile lemon sharks were captured throughout the 5 year study, 35 of which were recaptures of tagged individuals and 155 recaptured within the same sampling trip ('over-recaptures'), resulting in an effective tagging of 157 lemon sharks (Table II). The recapture rate was 22·3%.

All lemon sharks were caught with gillnets or dip-nets with the exception of 11 individuals which were caught with longline gear (four in March 1999 and seven in March 2000) and all others. Lemon sharks were captured at a variety of sites within the perimeter of the atoll, including the pools (16% of captures at sites number 1, 2 and 3 in Fig. 1), central lagoon (6% of captures at sites number 4, 5 and 6 in Fig. 1), but predominantly in the Baía da Lama (78% of captures at BL in Fig. 1), where lemon sharks gathered with the rising tide.

POPULATION STRUCTURE

The sex ratio for each sampling trip is shown in Table II. Among the 157 individuals tagged in the Atol das Rocas, 73 were male and 82 were female with the sex of two individuals not determined, resulting in a male : female sex ratio of 1 : 1·12. Among the 35 individuals recaptured, 18 were male and 17 were female (1 : 0·96) and there was no significant difference (χ^2, d.f. = 1, $P > 0{\cdot}05$) in the sex ratio between all the captured and all the recaptured individuals.

The size class distribution of all lemon sharks collected is shown in Fig. 2. Lemon sharks in the 60·1–70 cm size class were most abundant (34%), followed by the 70·1–80 cm size class (18%) and 80·1–90 cm (16%). The smallest juvenile specimen captured was 57·9 cm L_T, the largest was 157 cm L_T, with the mean ± s.d. being 83·8 ± 22·3 cm. Lemon sharks with completely or partially open umbilical scars were captured during each of four sampling trips in March and the one in May 2003, but not during any other trips.

TABLE II. Total captures (*C*), number of individuals captured (*N*), recaptures (*R*), number of tagged individuals (*T*), over-recaptures (*OR*) and sex ratio of juvenile lemon sharks in the Atol das Rocas

Date	*C*	*N*	*R*	*T*	*OR*	F	M	%F	%M
March 1999	39	30	0	30	9	20	10	67	33
March 2000	80	49	0	49	31	25	24	51	49
September 2000	46	37	10	27	9	17	20	46	54
March 2001	12	10	1	9	2	4	6	40	60
November 2001	19	10	4	6	9	5	5	50	50
August 2002	30	12	0	12	18	6	4	60	40
March 2003	40	13	3	10	27	6	7	46	54
May 2003	44	18	8	10	26	9	9	50	50
October 2003	37	13	9	4	24	7	6	54	46
Total	347	192	35	157	155				

Two unsexed specimens.
F, female; *M*, male.

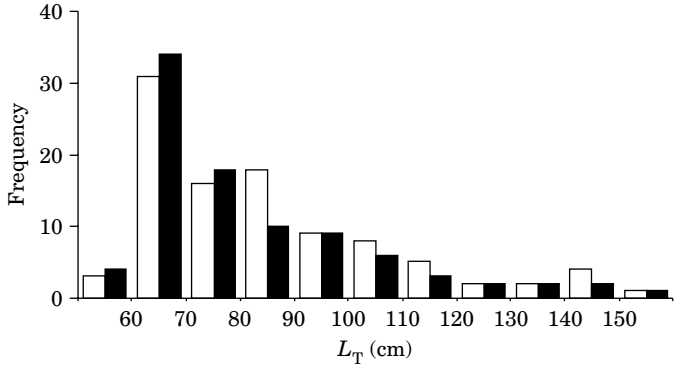

FIG. 2. Total length frequency distribution for size classes of 190 juvenile lemon sharks (□, females; ■, males) captured in the Atol das Rocas during this study.

When sampling trips were grouped into 3 month periods (quarters) the L_T differed significantly among quarters (Kruskal–Wallis, d.f. = 3, $P < 0{\cdot}01$). Size (L_T) of individuals collected in the first quarter (in March of the years 1999, 2000, 2001 and 2003) did not differ from that of individuals collected in the second quarter (May 2003) ($Q_{calc} = 1{\cdot}37 < Q_{0{\cdot}05,4} = 2{\cdot}64$), but was significantly lower than those of the third (September 2000 and August 2002) ($Q_{calc} = 3{\cdot}98 > Q_{0{\cdot}05,4} = 2{\cdot}64$) and fourth quarters [November 2001 and October 2003 ($Q_{calc} = 3{\cdot}73 > Q_{0{\cdot}05,4} = 2{\cdot}64$)]. The L_T of individuals captured in the second quarter was also significantly lower than those of the third ($Q_{calc} = 3{\cdot}78 > Q_{0{\cdot}05,4} = 2{\cdot}64$) and fourth quarters ($Q_{calc} = 3{\cdot}86 > Q_{0{\cdot}05,4} = 2{\cdot}64$), whereas size from the third and fourth quarters did not differ significantly ($Q_{calc} = 0{\cdot}67 < Q_{0{\cdot}05,4} = 2{\cdot}64$) (Fig. 3).

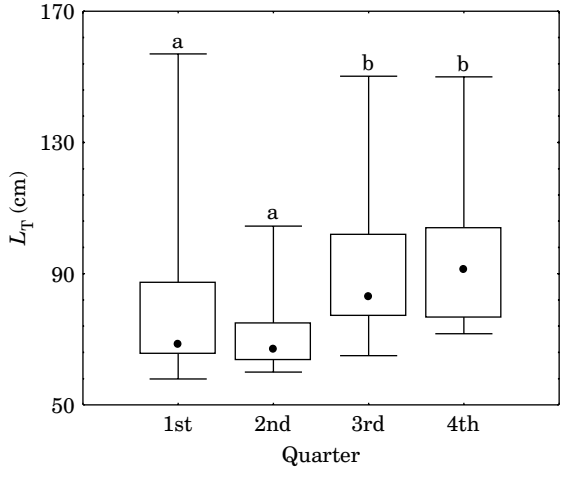

FIG. 3. Median (•), 25–75% (□) and minimum and maximum (T) total length of juvenile lemon sharks captured in the Atol das Rocas in the four quarters of the year. Different lower case letters represent significant difference with Kruskal–Wallis and Q tests.

GROWTH RATES

Of the 35 recaptures, seven occurred within 59–61 days-at-liberty and therefore were excluded from growth rate calculations. The time-at-liberty for recaptured lemon sharks ranged from 159 to 974 days. One individual recaptured for a second time exhibited a prominent scar on the dorsal fin, apparently caused by the loss of a Rototag used by Oliveira (2001), and this second recapture was excluded from the growth analyses due to the negative effect on growth possibly caused by that mark.

Average growth rates between tag and recapture are shown in Table III. A mean ± s.d. growth for L_T was the highest of the three estimates at 24·7 ± 3·4 cm year^{-1}, followed by L_F at 20·7 ± 3·2 cm year^{-1} and L_{PC} at 19·5 ± 2·7 cm year^{-1}. There were no significant differences in any of the growth rates between males and females (*t*-test, d.f. = 24, $P = 0{\cdot}27$ for L_T, $P = 0{\cdot}10$ for L_F and $P = 0{\cdot}16$ for L_{PC}). For nine individuals, 11 mass measurements were obtained throughout the study. Initial mass varied from 1300 to 2800 g, and final mass ranged from 2300 to 6200 g, yielding a mean ± s.d. growth rate of 2565 ± 762 g year^{-1}.

GROWTH PARAMETERS

Application of the Fabens (1965) method to tag and recapture data obtained in the present study estimated VBGF parameters for both sexes of $k = 0{\cdot}077$, $L_\infty = 399{\cdot}9$ cm and $t_0 = -2{\cdot}16$ ($r = 0{\cdot}99$) based on L_T (Fig. 4) and $k = 0{\cdot}162$, $L_\infty = 182{\cdot}6$ and $t_0 = -1{\cdot}87$ ($r = 0{\cdot}98$) based on L_{PC}. The backcalculated maximum longevity for the species was 45 years.

DISCUSSION

Lemon sharks were commonly over-recaptured in this study, as shown in Table II. The number of over-recaptures would have been higher if sampling in successive days had been adopted at the Baía da Lama, where, given the recurrent behaviour of lemon sharks, there was a high chance of sampling the same individuals. Repeated short-term recaptures of the same individuals were considered both unnecessary for the goals of this project and stressful to the

TABLE III. Mean ± s.d. annual growth rates in total length (L_T), fork length (L_F) and precaudal length (L_{PC}) of males, females, and total individuals of juvenile lemon sharks recaptured in the Atol das Rocas

		Growth rates (cm year^{-1})		
	n	L_T	L_F	L_{PC}
Males	13	25·4 ± 3·7	21·8 ± 3·3	20·3 ± 2·7
Females	13	23·9 ± 3·2	19·7 ± 3·0	18·8 ± 2·8
Total	27[1]	24·7 ± 3·4	20·7 ± 3·2	19·5 ± 2·7

[1]Outlier values of 14·6, 12·1 and 11·3 cm year^{-1} in L_T, L_F, and L_{PC} respectively, of one female specimen.

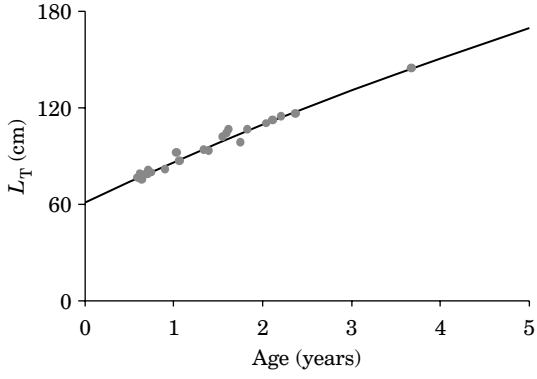

FIG. 4. The von Bertalanffy growth curve based on data from 28 juvenile lemon sharks recaptured in the Atol das Rocas. [•, for each lemon shark, the age at recapture (= age at capture from VBGF + time-at-liberty]. The curve was fitted by: $y = 61{\cdot}15 + (399{\cdot}9 - 61{\cdot}15)\,[1 - e^{(-0{\cdot}077x)}]$.

lemon sharks. The large number of over-recaptures indicates a high degree of site fidelity by the juvenile lemon sharks at Atol das Rocas, an expected behaviour considering the small size of the atoll. High site fidelity at Atol das Rocas was also reported by Oliveira (2001) and observed in juvenile lemon sharks from Bimini, Bahamas (Gruber *et al.*, 1988; Morrissey & Gruber, 1993; Sundström *et al.*, 2001). The degree of site fidelity, however, was greater compared to Bimini, as practically the entire juvenile population could be found at the highest tides, day after day in the Baía da Lama.

The recapture rate (22·3%) obtained in the present study was lower than that of Gruber *et al.* (1988) at Bimini (*c.* 35%), but was comparable to Oliveira (2001) at Atol das Rocas (23·3%). These differences are probably attributable to the greater sampling effort exerted at Bimini and also might be due to differential survival rates at the two locations. The recapture rate at Atol das Rocas can still be viewed as fairly high and indicative of high site fidelity of the lemon sharks. Such high recapture rate is also possibly related to the isolated geographic location and small size of the atoll, and to the concentration of juvenile lemon sharks in restricted areas such as Baía da Lama, which increases the chance of their capture. Other tag-recapture studies with lemons sharks resulted in lower recapture rates, ranging from 5·0 to 10·1% (Kohler & Turner, 2001).

The relatively large number of recaptures provides a good opportunity to examine growth rates based on tag and recapture methods and yields information on movements of juvenile lemon sharks within the atoll. Individuals were repeatedly captured at Baía da Lama at high tide, but the same individuals were often recaptured at other sites during intermediate and low tides, including pools and the main lagoon. Conversely, individuals tagged at these other sites were also recaptured at Baía da Lama. Such data indicate that lemon shark home ranges cover much of the atoll. Inferences about movement patterns are limited because tag-recapture studies usually provide few locations for each individual over a long time span. A more detailed study on the movement patterns of young lemon sharks using telemetry at the atoll has been completed and confirms the inferences of site fidelity based on tagging results.

POPULATION STRUCTURE

The recorded sex ratio was *c.* 1 : 1 during all sampling trips except in March 1999, when inexplicably twice as many females were captured. Oliveira (2001) also reported a male to female sex ratio near to 1 : 1 for his captures of lemon sharks at Atol das Rocas (47 males and 46 females). Since the sex ratio calculated for all captured individuals did not differ significantly from those of recaptured individuals, the selective mortality per sex due to capture and tagging of animals was minimal or non-existent. Smith & Abramson (1990) obtained similar results from tag-recapture of leopard shark *Triakis semifasciata* Girard in San Francisco Bay, U.S.A.

Based on predicted age estimates for all captured lemon sharks according to parameters of the VBGF in the present study the juvenile lemon shark population sampled at Atol das Rocas consisted of 65% of young-of-the-year and 22% age 1 year lemon sharks (Fig. 5). Larger juvenile sharks, possibly older than 4 years of age, occasionally were observed in dives at the pools (pers. obs.). Therefore, Atol das Rocas is both a primary nursery (where parturition occurs and neonates live) and secondary nursery (where juveniles occur before reaching maturity) (Castro, 1993; Merson & Pratt, 2001).

The similarity of sizes of lemon sharks during the first and second quarters at Atol das Rocas and increased size during the third and fourth quarters, most likely reflect a protracted parturition period occurring during the first two quarters, but not during the last two. The smallest lemon sharks (*c.* 60 cm L_T) were observed during the first two quarters, minimum sizes of 65 and 72 cm were observed during the third and fourth quarters respectively. Oliveira (2001) also captured 60 cm L_T lemon sharks early in the year (February) at Atol das Rocas. These records of minimum size of lemon sharks, along with observations of open or partially open umbilical scars in March and May, suggest that parturition in the south-western Atlantic at Atol das Rocas occurs between February and April, possibly into early May. In contrast, parturition of this species in the north-western Atlantic is reported to occur from April to July (Gruber & Stout, 1983; Compagno, 1984).

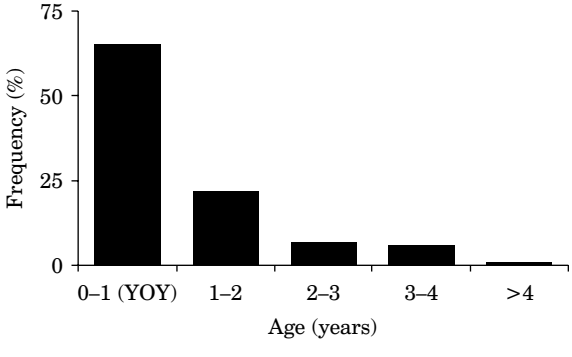

FIG. 5. Age class composition based on the von Bertalanffy growth model of 192 juvenile lemon sharks captured in the Atol das Rocas during this study.

GROWTH RATES

Differences in growth rates between sexes have been observed for young dusky sharks *Carcharhinus obscurus* (Lesueur) (Simpfendorfer, 2000), but apparently, no such differences occur in young bonnethead sharks *Sphyrna tiburo* (L.) (Parsons, 1993), sandbar *Carcharhinus plumbeus* (Nardo) (Sminkey & Musick, 1995) and lemon sharks (Manire & Gruber, 1991; present study). When both young and adult are concomitantly analysed, some carcharhiniform species, such as the Australian blacktip *Carcharhinus tilstoni* (Whitley) and *S. tiburo*, exhibit different growth between sexes (Davenport & Stevens, 1988; Parsons, 1993), while others, such as the sandbar, blacktip *Carcharhinus limbatus* (Valenciennes), whitetip *Carcharhinus longimanus* (Poey), blue *Prionace glauca* (L.) and night sharks *Carcharhinus signatus* (Poey) exhibit similar growth (Casey *et al.*, 1985; Wintner & Cliff, 1996; Lessa *et al.*, 1999, 2004; Santana & Lessa, 2004). In the majority of these species, including sharks of both growth patterns, females usually grow larger than males. Although no difference in growth rates between sexes was observed in the present study, sampling the adult population would be necessary to confirm if such condition persists through all life stages.

The L_T of juvenile lemon sharks used in growth rate calculation in this study (mean $\pm$ S.D. $75{\cdot}4 \pm 11{\cdot}1$ cm) was significantly higher than that obtained by Oliveira (2001), ($68{\cdot}2 \pm 7{\cdot}1$ cm, *t*-test, d.f. $= 36$, $P < 0{\cdot}05$). Although slightly larger lemon sharks were examined in the present study, which might be expected to grow at as lower rate than the smaller lemon sharks examined by Oliveira, the mean $\pm$ S.D. L_T growth rate obtained in the present study ($24{\cdot}7 \pm 3{\cdot}4$ cm year^{-1}, independently of sex) was significantly higher than that obtained by Oliveira (2001) ($12{\cdot}6 \pm 3{\cdot}9$ cm year^{-1}, *t*-test, d.f. $= 36$, $P < 0{\cdot}01$). The results of the two studies suggest that Rototag reduced the growth of the neonate and juvenile lemon sharks at Atol das Rocas by almost 50% when compared with the PIT-tag. It is possible that the Allflex Rototag used by Oliveira (2001) was too large for juveniles, and affected their hydrodynamics, or promoted infections and algal growth. Manire & Gruber (1991) reported that juvenile lemon sharks tagged with large external tags (M-type dart tags) grew 10% more slowly than fish tagged with PIT-tags. Tag choice may be an important consideration in tag-recapture studies with sharks. The PIT-tags have proven effective since they apparently have little or no effect on behaviour, health or growth of tagged sharks (Manire & Gruber, 1991; present study), and are shed at lower rates when compared with some external tags (Feldheim *et al.*, 2002). Further evidence of the negative effect on growth promoted by Rototags is suggested by data collected when the present study and that of Oliveira (2001) overlapped in time. Between March 2000 and September 2000, the L_T of sharks tagged in the present study (mean $\pm$ S.D. $72{\cdot}0 \pm 13{\cdot}2$ cm) did not differ from that reported by Oliveira (2001) (*t*-test, d.f. $= 16$, $P = 0{\cdot}43$). The growth rate obtained in the present study for this period (mean $\pm$ S.D. $24{\cdot}3 \pm 2{\cdot}3$ cm year^{-1} L_T), as well as for the entire study, was significantly higher than the growth rate calculated for lemon sharks over the same period of time by Oliveira (2001) (*t*-test, d.f. $= 16$, $P < 0{\cdot}01$).

Morrissey & Gruber (1993) reported a mean L_{PC} growth rate of $6{\cdot}7$ cm year^{-1} from seven juvenile lemon sharks at Bimini, fitted with internal telemetry

transmitters. Juveniles with PIT-tags in that same location have shown L_{PC} growth rates of *c.* 6·0 cm year^{-1} (S.H. Gruber, unpubl. data). At Marquesas Keys in Florida, however, the mean ± S.D. growth rate for juvenile lemon sharks, also tagged with PIT, was 17·1 ± 4·3 cm year^{-1} in L_{PC} (Manire & Gruber, 1991), closer to the rate of 19·5 ± 2·7 cm year^{-1} obtained in the present study. Environmental conditions at Bimini may result in slower growth of the species than at other locations.

Atol das Rocas is a more stable environment than either Bimini or Marquesas in terms of seasonal variations in water temperature, but is much more variable in tidal fluctuation. Differences in growth rate of young lemon sharks at different locations are at least to some degree probably related to food availability since rate of consumption directly influences growth rate (Cortés & Gruber, 1994). Gruber & Stout (1983) reported growth rates of 2051 g year^{-1} and 23·4 cm year^{-1} in L_{PC}, for young lemon sharks maintained in captivity and fed *ad libitum* for 89 days. These growth rates are close to the value obtained in the present study (mean ± S.D. 2565 ± 762 g year^{-1} and 19·5 ± 2·7 cm year^{-1}), suggesting that food availability is not a limiting factor in the Atol das Rocas. The lack of mangrove shelter and fewer locations that offer refuge from large adults at Atol das Rocas may also influence growth rate if selection pressure exerted by adults favours rapidly growing juveniles.

GROWTH PARAMETERS

Simpfendorfer (2000) reported linear growth for juvenile dusky sharks in Australia during their first 5 years of life. The linear model also fits the present data well (high linear correlation of L_T increment and time interval at liberty with $P < 0{\cdot}01$; $r^2 = 0{\cdot}95$) because growth was measured over a short time and age span. Growth represented by with the VBGF, however, probably represents a better model of growth over the entire life span of lemon sharks at Atol das Rocas. As lemon sharks increase in size, their rate of growth decreases and linear models generally do not describe the relationship between age and growth as well as the VBGF (Simpfendorfer, 2000).

Estimates of the VBGF parameters by Brown & Gruber (1988) in L_{PC} ($k = 0{\cdot}057$, $L_\infty = 317{\cdot}7$ cm and $t_0 = -2{\cdot}30$), using tetracycline validated vertebral centra at Bimini, differ from those of this study ($k = 0{\cdot}162$, $L_\infty = 182{\cdot}6$ and $t_0 = -1{\cdot}87$). These differences could be due to the largest lemon sharks captured in the present study being estimated at 4 years of age, whereas Brown & Gruber (1988) captured individuals estimated to be 8·3 years-old. Additionally, juvenile lemon sharks apparently grow three times faster in Atol das Rocas than in Bimini.

Males and female lemon sharks mature at 225 and 240 cm L_T respectively (Compagno, 1984). Using the parameters of VBGF for L_T obtained in the present study and Compagno's (1984) size estimates, the predicted age at maturity is *c.* 8·6 years for males and 9·7 for females. Although such estimates predict maturity at earlier ages than those estimated by Brown & Gruber (1988), of 11·6 years for males and 12·7 years for females, they are reasonable, since the juveniles at Atol das Rocas grow faster than in Bimini and consequently should reach maturity earlier. Overall, the VBGF parameters estimated in this study are

somewhat limited because that they are based only on data from young lemon sharks, and only by additional sampling of the other age classes, can a more complete picture be reached.

Along with the Fernando de Noronha Archipelago, Atol das Rocas is possibly one of the few nurseries for the lemon shark in the western South Atlantic, and as such, it should be protected to maintain the local population.

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