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Spatial and ontogenetic variation in growth of nursery-bound juvenile lemon sharks, *Negaprion brevirostris*: a comparison of two age-assigning techniques

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Synopsis

We compared growth rates of the lemon shark, *Negaprion brevirostris*, from Bimini, Bahamas and the Marquesas Keys (MK), Florida using data obtained in a multi-year annual census. We marked new neonate and juvenile sharks with unique electronic identity tags in Bimini and in the MK we tagged neonate and juvenile sharks. Sharks were tagged with tiny, subcutaneous transponders, a type of tagging thought to cause little, if any disruption to normal growth patterns when compared to conventional external tagging. Within the first 2 years of this project, no age data were recorded for sharks caught for the first time in Bimini. Therefore, we applied and tested two methods of age analysis: (1) a modified 'minimum convex polygon' method and (2) a new age-assigning method, the 'cut-off technique'. The cut-off technique proved to be the more suitable one, enabling us to identify the age of 134 of the 642 previously unknown aged sharks. This maximised the usable growth data included in our analysis. Annual absolute growth rates of juvenile, nursery-bound lemon sharks were almost constant for the two Bimini nurseries and can be best described by a simple linear model (growth data was only available for age-0 sharks in the MK). Annual absolute growth for age-0 sharks was much greater in the MK than in either the North Sound (NS) and Shark Land (SL) at Bimini. Growth of SL sharks was significantly faster during the first 2 years of life than of the sharks in the NS population. However, in MK, only growth in the first year was considered to be reliably estimated due to low recapture rates. Analyses indicated no significant differences in growth rates between males and females for any area.

Introduction

The lemon shark, *Negaprion brevirostris* (Poey 1868), is a large, placentally viviparous coastal species, which inhabits three widely separated regions: the western Atlantic from New Jersey to Brazil, the eastern Pacific from Baja California (including the Sea of Cortez) to coastal Colombia, and the eastern North Atlantic, off West Africa (Bigelow & Schroeder 1948, Springer 1950, Compagno 1984). The lemon shark is one of 39 shark species protected by the National Oceanic and Atmospheric Administration (NOAA 2000) Secretarial Fisheries Management Plan, and is considered overfished in Atlantic and Gulf waters of the United States (NMFS 2001).

Knowledge of growth parameters in the juvenile stage is critical for the development of population models for both sharks and teleosts. Such population models can be valuable tools to identify critical life-stages both for management and for evaluating anthropogenic effects on population growth and viability (Holt 1998).

In the western North Atlantic, lemon sharks have a 10–12 month gestation period, with mating in spring and early summer (Bigelow & Schroeder 1948, Springer 1950, Compagno 1984) followed by parturition the subsequent year, between April and July (Henningsen & Gruber 1985). The reproductive cycle is biennial (Feldheim et al. 2001), as has been proposed for other carcharhinid sharks, e.g. *Carcharhinus limbatus* (Castro 1996). In shallow nursery grounds female lemon sharks give birth to 4–18 young (Compagno 1984, S. Gruber unpublished data) ranging from 50–68 cm total length (TL) at birth (Gruber & Stout 1983, Brown & Gruber 1988, S. Gruber unpublished data). Lemon sharks spend their early years in inshore nursery grounds (Henningsen & Gruber 1985, Gruber 1988, Gruber et al. 1988, Feldheim et al. 2001), which apparently offer selective advantages of low predation rates and abundant food (Branstetter 1990). Recent estimates of natural mortality (Gruber et al. 2001) within the first year of life ranged between 39 and 60%.

The juvenile life interval of the lemon shark has been investigated over the past 2 decades in nursery areas at Bimini, Brazil and the Florida Keys. Henningsen & Gruber (1985) calculated growth rates of juvenile lemon sharks to be 8.36 cm yr^{-1} in the Florida Keys and 8.25 cm yr^{-1} in Bimini by successfully marking and recapturing 259 juveniles. These tagging procedures used metal dart-tags, which caused an estimated 10% decrease in growth and an increase in mortality of juvenile lemon sharks (Manire & Gruber 1991). Tetracycline markings were used by Brown & Gruber (1988) as a time mark to validate the counts of growth rings in the vertebrae of recaptured lemon sharks. They then demonstrated that a von Bertalanffy growth curve suitably describes the relation between counts of growth rings in the vertebrae of recaptured lemon sharks and Precalcaudal length (PCLs) (46–226 cm) for both sexes in Bimini and the Florida Keys ($n = 110$). This allowed predictions of age at maturity of 11.6 years for males and 12.7 years for females, based on size at maturity of about 175 cm and 185 cm PCL for males and females respectively (Compagno 1984). Estimates of growth rate in the juvenile lemon shark using the described von Bertalanffy growth curve suggest that within the first 4 years of life PCL growth rates range between 13.0 and 15.4 cm yr^{-1} (for sharks in Bimini and the Florida Keys).

In preliminary studies during 1990, we attempted to collect and mark all the juvenile lemon sharks in the North Sound (NS) nursery at Bimini using Passive Integrated Transponder (PIT, Digital Angel Corp.) tags, which caused no apparent adverse affect-relative to metal dart-tags on growth (Manire & Gruber 1993), thus allowing growth rates to be more accurately measured. In May 1995, we initiated an annual shark-tagging project using PIT tags at Bimini and in July 1998 a similar project was started in the Marquesas Keys (MK), Florida.

One of the objectives of this study was to compare spatial and ontogenetic variation in growth of nursery-bound juvenile lemon sharks during the years 1995–2001 at Bimini and 1998–2000 at the MK. To do this, we applied two age-assigning techniques, the 'minimum convex polygon' and the 'cut-off' method. Both of these were evaluated to assign ages to lemon sharks of unknown age. Three separate nurseries were examined: two in the Bimini lagoon complex, the NS and Shark Land (SL), and one in the MK (Figure 1). Despite the close proximity of the NS and SL populations, we considered these nurseries to be distinct since high site attachment was clearly demonstrated in tracking experiments with free-ranging juvenile lemon sharks (Morrissey & Gruber 1993, Gruber et al. 2001, Sundström et al. 2001).

The work undertaken for the present study was part of a more extensive multidisciplinary investigation examining the conservation biology of the lemon shark and the role of nursery areas in its early life-history (Feldheim et al. 2001, Gruber et al. 2001, Feldheim et al. 2002a,b). We will show that growth in new born to 2 year old lemon sharks is relatively slow, linear, site specific and independent of sex.

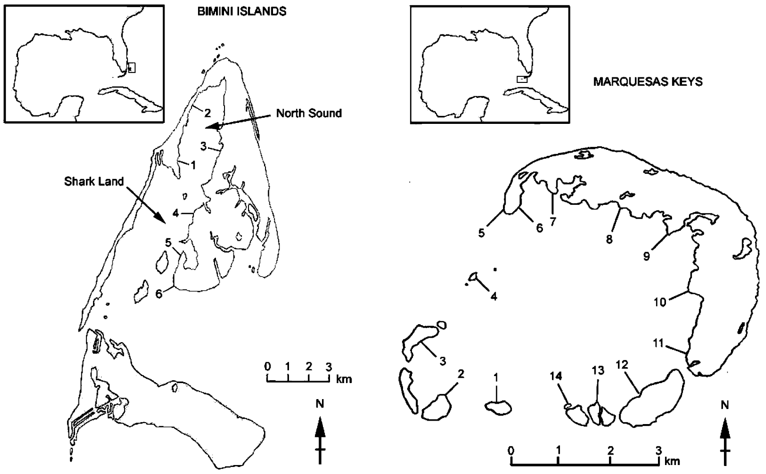

Figure 1. Map of Bimini Islands and the Marquesas Keys showing the three study sites, and the location of gill-net sets. Note: length of gill nets are not to scale. Inset shows relationship of Bimini and the Marquesas Keys (in box) to Florida coast.

Methods

Study sites

The main study sites were three nurseries, two located in a shallow lagoon surrounded by the mangrove-fringed islands of Bimini, Bahamas, (25°43.70′N, 79°18.00′W) and a third at MK Florida (Figure 1). The Biminis are located 85 km directly east of Miami, Florida, situated on the western edge of the Great Bahama bank. In an ecosystem study, Jacobsen (1987) showed that the restricted tidal flushing of the NS causes greater fluctuation in local water temperature and salinity than in SL. More recent field observations taken in the NS indicate that summer rains change salinity from 40 to 28%, and the temperature from 36 to 16°C within 1 h (S. Gruber unpublished data).

The MK Florida are located approximately 35.4 km west of Key West (82°07.40′W, 24°34.13′N). This nursery site is also mangrove-fringed, however the circular lagoon formed by the mangroves is more ‘open’ (to the waters of the Gulf of Mexico) than the Bimini nurseries (see Figure 1). While the Bimini nurseries are shallow throughout, the MK site has numerous deep channels running through the lagoon. Together these physical characteristics reduce salinity and temperature fluctuations in the MK nursery.

Lemon shark capture

We collected juvenile lemon sharks using ‘tag and hold’ marking experiments (Manire & Gruber 1991). Nets were set within the shallow waters (0–120 cm at low tide) of Bimini lagoon using three 180 m long, 2 m deep gill nets, constructed of 5 cm square mesh monofilament. Starting in 1995, we sampled the nurseries annually, always starting in the NS and always within the same 21-day period in late May to mid June until June 2001. This period coincided with the end of the pupping season, enabling neonates to be accurately identified by their open umbilical scars. Although the main pupping season was over, it is possible that further parturition of neonates occurred, in which case they would not have been caught until the subsequent year. Because lemon sharks are apparently more active at night (Nixon & Gruber 1988, Morrissey & Gruber 1993), generally swim within 50 m of shore (Morrissey & Gruber 1993), and avoid nets during the daytime (Gruber et al. 2001), we set nets at dusk perpendicular to the shore for a period of 12 h.

In both nurseries at Bimini, we set gill nets simultaneously at three sites (Figure 1) for up to 6 nights. Sampling of each population was judged to be complete when the catch per unit effort had effectively dropped to zero. Gruber et al. (2001) showed that 99% of all sharks within the nursery are captured within 6 nights. We monitored gill nets continuously and immediately removed sharks caught in the nets and transported them to a central holding pen as described in Gruber et al. (2001). We measured each shark to the nearest millimetre (PCL, fork length (FL), and TL) weighed it to the nearest 0.1 kg, sexed, and scanned it for the presence of a PIT tag. If no PIT tag was present, one was inserted intramuscularly below the first dorsal fin (see Manire & Gruber 1991). At the end of sampling each nursery we released sharks from the holding *pen en masse*. From 1997 onwards, we identified neonates by the presence of an open, partially closed or recently closed umbilical scar (Newman & Grant unpublished data).

Due to the greater size of the MK nursery area, we set gill nets at up to 14 locations (Figure 1) for 2 consecutive nights per site, again using the 'tag and hold method' (repetition of technique used). Annual sampling for 30 days took place within July and August, approximately 2 months after sampling in Bimini. Sampling in MK began in July 1998, 4 years after sampling commenced in Bimini and continued until August 2000.

Age determination

Exact determination of age at first capture was not always possible because the umbilical scar, which is the most reliable indicator of neonate status, heals and closes rapidly (approximately 1 and 2 months, respectively). Additionally, some individuals were not captured and tagged until age-1 or older; either because they were not caught in our nets, or as a result of parturition occurring after the sampling period. As we did not begin to evaluate condition of the umbilical scar until the third year of the study, we had no absolute means to recognise neonates born in 1995 and 1996. Since only sharks of known-age could be included in the analysis we used two age-assessing techniques in an attempt to assign ages to sharks of unknown-age: (1) the minimum convex polygon technique (adapted from Worton 1987) and (2) the cut-off technique (adapted by MJB for this study). We determined the more suitable method by (a) comparing the relative success of each technique at assigning known-age sharks to their correct age-class and (b) then assigning ages to unknown-age sharks and determining whether the results for estimated length-at-age or the estimated growth rates of the assigned sharks varied significantly from those obtained for known-aged sharks. The techniques are outlined below.

Minimum convex polygon technique

Allocation of individual sharks to the age-0 class was based on initial PCL and first year's growth. Initial PCLs of known neonates were plotted against their PCL at the day of recapture approximately 1 year later and the smallest (convex) polygon was drawn around the data points. This area, known as the 'minimum convex polygon' maps the area in which unknown-aged sharks would be expected to fall if they were in fact age-0 sharks when first tagged, permitting allocation of age-0 status to previously unknown aged sharks (for an illustration of this process, see Figure 2).

Cut-off technique

This technique allocated an individual shark to the age-0 class if it had less than a 5% chance of lying within the normal length–frequency distribution for lemon sharks aged one and older while at the same time falling with 95% confidence in the neonates normal length distribution. The critical boundary length was calculated by determining the lower confidence interval for age-1 and older age-classes (NS = 48.80 cm, SL = 49.94 cm) because this value was lower than that ensuring 95% confidence of lying in the neonate normal distribution.

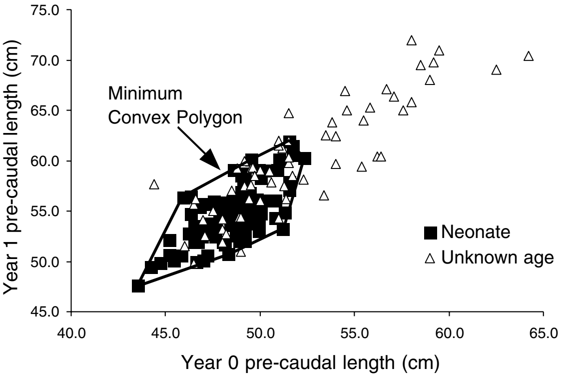

Figure 2. Use of the Minimum Convex Polygon technique for identifying unknown aged sharks. The example illustrates the polygon devised for juvenile sharks from Shark Land.

Table 1. Summary of final growth data for all juvenile shark age classes the North Sound (NS), Shark Land (SL) and Marquesas Keys (MK), illustrating the number of neonates and unknown aged sharks caught each year between 1995 and 2001, and the number of sharks assigned-age-0 status by the cut-off technique (and modal analysis in MK).

Location	Sampling year	Sharks tagged		Assigned age-0 status	Annual absolute growth (cm)							
		Neonates	Unknown age		n	0–1	n	1–2	n	2–3	n	3–4
NS	1995	0	88	29	–	–	–	–	–	–	–	–
	1996	0	61	9	11	6.0 ± 1.1	–	–	–	–	–	–
	1997	19	75	23	8	3.9 ± 0.4	7	4.7 ± 1.2	–	–	–	–
	1998	28	43	0	14	4.3 ± 0.5	6	4.7 ± 1.0	6	5.0 ± 0.8	–	–
	1999	41	17	1	13	6.6 ± 0.6	8	8.6 ± 1.2	3	9.4 ± 0.8	–	–
	2000	11	25	1	18	5.0 ± 0.3	8	5.2 ± 0.6	3	4.7 ± 1.0	2	8.3
	2001	34	11	3	1	5.0	8	5.4 ± 0.4	2	8.3	1	9.5
SL	1995	0	83	35	–	–	–	–	–	–	–	–
	1996	0	71	21	10	7.2 ± 0.8	–	–	–	–	–	–
	1997	44	47	7	10	7.1 ± 0.8	7	7.1 ± 1.2	–	–	–	–
	1998	43	29	0	27	7.0 ± 0.4	3	8.7 ± 0.5	2	5.1	–	–
	1999	53	28	1	17	7.7 ± 0.5	9	8.9 ± 0.9	0	–	–	–
	2000	61	40	1	26	6.4 ± 0.5	3	6.5 ± 0.6	1	9.9	0	–
	2001	35	24	3	25	4.8 ± 0.3	11	6.3 ± 0.8	3	4.1 ± 1.9	0	–
MK	1998	13	42	34	8	~20	–	–	–	–	–	–
	1999	23	31	29	3	~20	–	–	–	–	–	–
	2000	42	35	19	18	~20	–	–	–	–	–	–

Growth rate analysis

Growth rates of juvenile lemon sharks were compared using: (1) absolute annual growth, and (2) proportional annual growth rates. Absolute growth is the actual annual growth measured in cm increase in PCL. Comparisions were also made using proportional growth, found by calculating the percent annual increase in PCL. Proportional annual growth was used as it allowed us to determine if shark size affects subsequent growth (i.e., allowed the comparison of growth rates in sharks of different sizes).

Neither of the two age-assigning techniques described were applied to the MK sharks data due to the low number of recaptures, i.e. sharks known to be age-1 or older (n = 3). However, age-0 sharks caught at the Marquesas could be readily distinguished from older size classes because of large size differences (no overlap between age-0 and age-1 length–frequency distributions). In contrast, Bimini populations showed considerable overlap, accordingly length provided no reliable distinction between age groups. Thus in the Marquesas, age-0 sharks growth rates were inferred by examining the differences between the first and second modes on their length–frequency distribution.

Comparisons of initial PCL and subsequent growth (using one-way ANOVA, *t*-tests, *z*-tests, and Tukey's pairwise comparison (TPC)) were made between sexes, within each of the three nurseries for all age-classes and between cohorts for each different age-class within each nursery.

Results

Between May 1995 and June 2001, we tagged 1 011 neonate and juvenile sharks in Bimini (Table 1). The annual tagging project still continues, but sampling in 2001 provided the last cohort of sharks to be analysed in this study. Of the sharks tagged in Bimini 369 were identified as neonates (NS = 133, SL = 236) due to the presence of an open umbilical scar. However, the umbilical scars of the remaining sharks were closed when they were first captured so their ages were unknown (NS = 322, SL = 320). Assigning ages to these sharks was problematic due to the high degree of overlap in sizes between age-classes and the

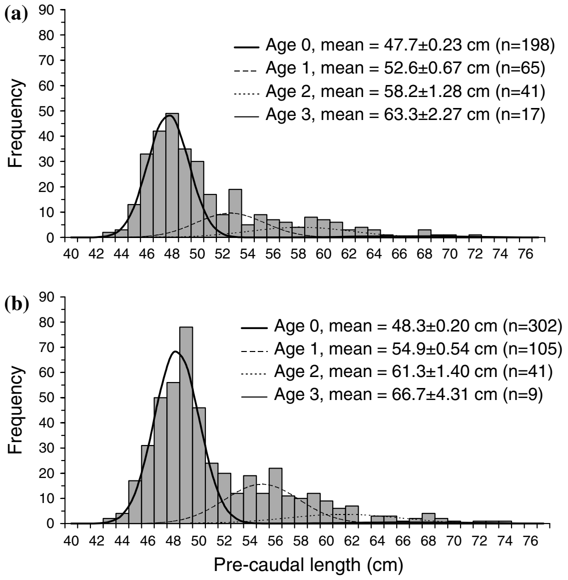

Figure 3. Length–frequency distributions of all sharks captured from 1995 to 2001 at Bimini using length-at-age data obtained from the cut-off technique combined with known-aged shark data for (A) the NS (age-0 sharks normal distribution plotted without one low outlier of 40.5 cm; age 4 normal distribution not shown as consists of only six individuals with mean of 71.6 ± 8.19 cm) and (B) SL (age-0 distribution plotted without two high outliers of 58.3 cm and 59.2 cm; one shark aged-5 was caught measuring 82.2 cm not shown).

evident increasing variation in length with age (Figure 3).

In the MK we tagged 190 juvenile sharks between July 1998 and August 2000, of which 78 were neonates. Results contrasted sharply with Bimini and indicated no overlap between age-class sizes, so unknown-aged sharks were identified as age-0 sharks due to the large, visible size difference from 1-year-olds (the neonate modal distribution was completely separated from the age-1 modal distribution–see Discussion).

Effectiveness of age-assigning techniques

Evaluation of the condition of umbilical scars did not begin until year 3 of the study, so there was no way to recognise neonates of the 1995 and 1996 cohorts. Without these data sets the total analysable data set would have been reduced from 7 to 5 years and the number of estimated 1 yr+ sharks and therefore valuable growth rate data would have been considerably diminished, as only growth rates of known aged sharks would have been included in the analysis. Therefore, the development of an effective age-assigning technique was undertaken to allow the inclusion of previously unknown-aged sharks in the analysis.

The cut-off method assigned a greater percentage of known aged-0 sharks (neonates) to their correct age class (74.3%) compared to the minimum convex polygon technique (35.0%). It also assigned a smaller proportion of known age-1 sharks wrongly to the age-0 class (Table 2). Therefore, since the cut-off technique minimised type I and type II errors it was selected and used throughout the study. We thus were able to assign age-0 status to 134 (NS = 66, SL = 68) of the previously 642 unknown-aged sharks. The cut-off method also assigned-ages to a greater proportion of unknown-aged sharks that were caught more than once. This increased the data set for which annual growth values were available by more than 50%. Multiple comparisons (*t*- and *z*-tests) for the NS and SL revealed no significant differences between PCLs, absolute annual growth, or proportional growth rates for known aged sharks and for those assigned to age-0 by the cut-off technique ($p > 0.05$). The only exceptions were the PCLs of assigned-age-0 sharks in the NS, which were significantly smaller than the PCLs of known age-0 sharks. Because growth results obtained from assigned-age sharks were not significantly different from those of known-age sharks, we combined both data sets to incorporate more individuals over a larger range of ages (Table 3). Figure 3 shows the resulting length–frequency distributions for all known- and assigned-aged sharks from 1995 to 2001 in the NS and SL. No significant differences were found between the growth and PCLs of known-aged male and female sharks within any of the three nursery areas or age-classes (*t*-tests, $p > 0.05$). Consequently, for the purpose of this study all data for male and female sharks were combined.

Initial lengths of known-aged sharks

Initial lengths of known 0-aged sharks (neonates) were available for 133 pups in the NS, 236 at SL and 78 sharks at Marquesas. We compared neonate PCLs from the three nurseries (Figure 4), and one-way ANOVA, ($p < 0.001$) and TPC showed that

Table 2. Ability of the minimum convex polygon and cut-off techniques in assigning age-0 status to known aged-0 and age-1 sharks and in assigning age-0 status to unknown-age sharks captured more than once. (Allocation of age-0 status to sharks known to be age-2+ did not occur using either technique).

Location	n	% Assigned age-0 status	
		Cut-off technique	Minimum convex polygon technique
Known Year 0			
North Sound	133	66.2	28.6[a]
Shark Land	236	78.8	38.6[b]
Known Year 1			
North Sound	38	2.6	5.3
Shark Land	91	3.3	4.4
Unknown Age captured > once			
North Sound	75	41	35
Shark Land	72	38	35

[a] Only assigned sharks which were used to define the polygon (n = 38).
[b] Only assigned sharks which were used to define the polygon (n = 91).

Table 3. Comparison of juvenile lemon shark growth rates between the North Sound (NS), Shark Land (SL) and Marquesas Keys (MK)using combined neonate and assigned-age shark data (n in brackets shows sample size before addition of age-assigned sharks).

Age (yr)	Location	n	Comparing growth rates between areas					
			Absolute growth			Proportional growth		
			Mean (cm)	*t*-test results		Mean (%)	*t*-test results	
0	North Sound	65 (38)	5.0 ± 0.3	<	$p < 0.001$	10.9 ± 0.6	<	$p < 0.001$
	Shark Land	115 (91)	6.5 ± 0.2	>		13.4 ± 0.4	>	
	Marquesas Keys	29 (2)	~20[a]	[b]	–	~39.5[a]	[b]	–
1	North Sound	37 (18)	5.8 ± 0.5	<	$p < 0.05$	11.1 ± 0.9	<	$p < 0.05$
	Shark Land	33 (21)	7.4 ± 0.5	>		13.7 ± 0.8	>	
2	North Sound	14 (4)	6.4 ± 0.7	=	$p = 0.13$	11.4 ± 1.3	=	$p = 0.32$
	Shark Land	6 (3)	5.4 ± 1.3	=		8.9 ± 2.0	=	
3	North Sound	3 (0)	8.7 ± 1.0	[c]	–	13.8 ± 1.7	[c]	–
	Shark Land	0 (0)	–	–			–	

[a] Estimated by differences between modes of age-0 and age-1 sharks.
[b] Marquesas Keys growth was more than triple that in NS and SL.
[c] Statistical comparison not possible.
t-tests results: < significantly slower, > significantly faster, = not significantly different.

the MK neonates were significantly longer (mean PCL = 52.4 ± 0.3 cm) than neonates from either Bimini nursery (NS mean PCL = 48.0 ± 0.3 cm and SL mean PCL = 48.4 ± 0.3 cm); however, MK neonates were sampled two months later than Bimini neonates. In the NS we found a significant difference between the neonate PCLs of some cohorts (one-way ANOVA, $p < 0.001$); TPC revealed that neonates caught in the years 2000 and 2001 were significantly smaller than neonates caught in both 1995 and 1996. In the SL nursery, a significant difference was found between the neonate PCLs of some cohorts (one-way ANOVA, $p < 0.05$); TPC analysis showed that neonates caught in the year 2001 were significantly smaller than neonates caught in 1997. A comparison of neonate PCLs between the MK cohorts revealed that they were significantly different as well (one-way ANOVA, $p < 0.001$); TPC showed that neonates caught in the year 2000 were significantly smaller (mean PCL = 51.0 ± 0.6 cm) than those captured in all other years (mean PCL = 54.0 ± 0.9 cm).

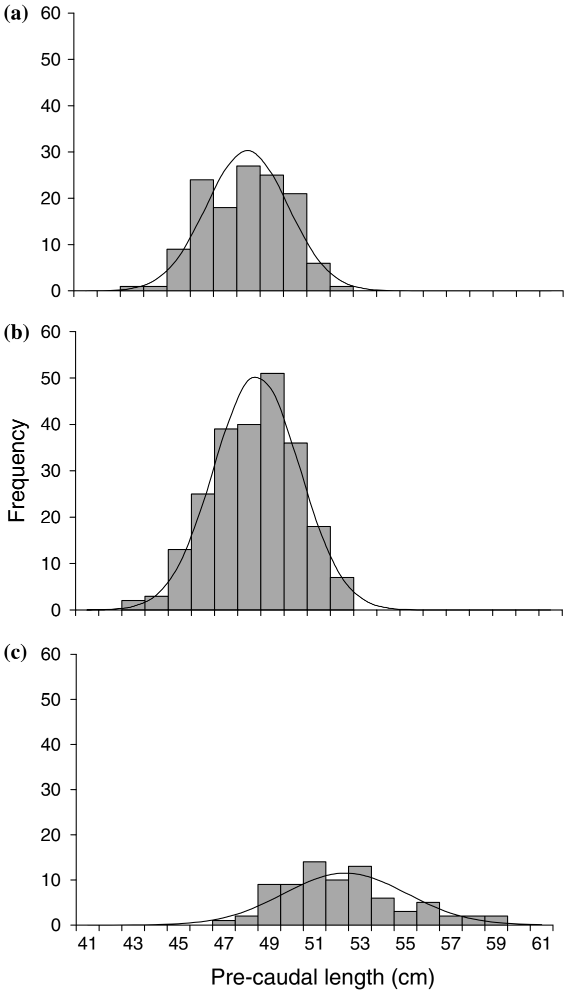

Figure 4. Length–frequency distribution of neonate *Negaprion brevirostris* for years from 1997 to 2001: (a) the NS (n = 133) the line represents a normal distribution with a mean of 47.95 cm and a standard deviation of 1.75 cm; (b) SL (n = 234) the line represents a normal distribution with a mean of 48.32 cm and a standard deviation of 1.85 cm (not including two larger outliers); and (c) Marquesas (n = 78) line represents a normal distribution with a mean of 52.35 cm and a standard deviation of 2.70 cm.

Spatial variation in growth

Absolute growth of age-0 sharks in Bimini was significantly greater in SL (6.5 ± 0.2 cm yr^{-1}) than in the NS (5.0 ± 0.3 cm yr^{-1}) (Table 3). The same applied to the absolute growth of age-1 sharks, in their second year juveniles grew 7.4 ± 0.5 cm yr^{-1} in SL and 5.8 ± 0.5 cm yr^{-1} in the NS. In both instances proportional growth rates were also significantly greater in SL (Table 3). However, in their third year sharks showed no significant differences in either absolute growth or in proportional growth rates between SL and NS (Table 3). A comparison of fourth year growth rates was not possible due to insufficient data for the age-3 age class (n = 0 for SL and n = 3 for NS).

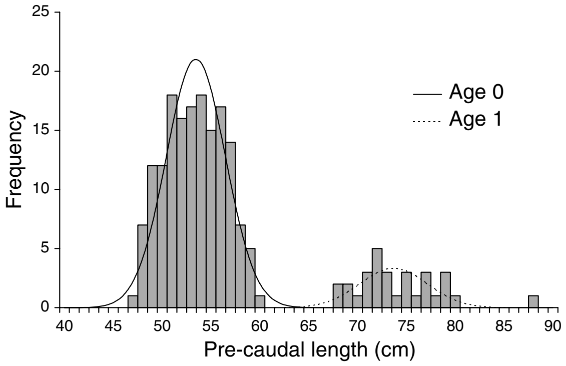

Figure 5. Length–frequency distribution of all Marquesas sharks from 1998 to 2001, normal distributions plotted using all sharks. Each line represents a normal distribution: for Year 0 (n = 160) with a mean of 53.5 cm and a standard deviation of 3.03 cm; and for Year 1 (n = 29) with a mean of 73.9 cm and a standard deviation of 3.55 cm. The high outlier of 88.5 cm is the only definite Year 2 (or older) shark.

Of the 186 sharks tagged in the MK only four were recaptured, three after 1 year, and one shark after 2 years. Two of the sharks that were recaptured after 1 year had been neonates when first caught; at age-1 they had a mean PCL of 71.3 ± 2.3 cm, exhibiting growth of 15.0 cm yr^{-1} and 16.4 cm yr^{-1} respectively (mean = 15.7 ± 0.7 cm yr^{-1}). As the initial age of the other two recaptured sharks was unknown, their growth information was discarded.

None of the MK neonates fell outside of the first modal class shown on the length–frequency distribution of all sharks captured (Figure 5) and no-age 1+ sharks fell within it. Therefore, it was assumed that this first modal class related to a distinct cohort composed of age-0 sharks. No significant difference was found between the PCLs of MK neonate sharks (n = 78, Figure 4c) and the unknown-aged MK sharks within the first distinct modal distribution (n = 82) shown on Figure 5 (*t*-test, $p < 0.001$). So the second, distinct cohort

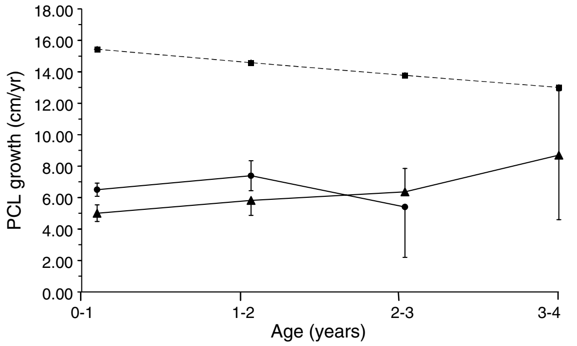

Figure 6. Comparison of juvenile shark's mean absolute growth (shown with the 95% confidence intervals for the means) for both the NS and SL (sexes combined) using data from combined known-aged and assigned-age sharks (using cut-off technique); and growth predicted for both sexes combined from Brown & Gruber (1988) according to the von Bertalanffy equation: $L_t = L_\infty(1 - e^{-K(t-t_0)})$, where L_t = PCL at time t, L_∞ = maximum theoretical length = 317.65 cm. K = growth coefficient = 0.057 and t_0 = theoretical age at 0 length = −2.302 yr (▲ = NS, age-0 mean PCL = 47.7 cm; ● = SL, age-0 mean PCL = 48.3 cm; ■ = growth predicted from von Bertalanffy equation, age-0 mean PCL = 39.0 cm).

of larger sharks (n = 29) was assigned to age-1, because the only lemon shark recaptured in the MK after 2 years had a PCL much greater than any other captured shark in the MK. Using the length–frequency characteristics of the two cohorts, now identified as comprising age-0 and age-1 individuals respectively, we estimated that age-0 sharks grew approximately 20 cm in the 12 months between sampling periods at the MK.

Ontogenetic variation in growth

A comparison between absolute annual growth for NS sharks ages 0–3, showed a significant difference in growth between some ages (Figure 6; one-way ANOVA, $p < 0.05$). TPC revealed that growth of age-3 sharks (8.7 ± 1.0 cm yr^{-1}) was significantly greater than growth of age-0 sharks (5.0 ± 0.3 cm yr^{-1}). However, there was no significant difference between proportional growth rates between sharks of all ages in the NS (one-way ANOVA, $p = 0.80$). There were no significant differences between absolute annual growth for sharks in SL aged 0–2 (Figure 6; one-way ANOVA, $p = 0.08$). No growth data were available for age-3 sharks in SL. However, proportional growth was significantly different between some ages (one-way ANOVA, $p < 0.05$); TPC showed growth of age-0 sharks in SL was significantly greater than age-2 sharks.

In 2001 only a single age-0 shark from the year 2000 cohort was recaptured in the NS; in all other years on average 12.8 age-0 sharks were recaptured. A comparison of growth of age-0 sharks between the other NS cohorts (1995–1999) revealed that absolute and proportional growths were significantly different between cohorts (one-way ANOVA, $p < 0.05$). TPC showed that absolute growth in 1998 was significantly greater than growth in 1996 and 1997. A comparison of proportional growth rates also showed that growth of age-1 sharks was greatest in the 1998 cohort (one-way ANOVA, $p < 0.05$). We found no other significant growth differences between cohorts, neither for age-1 nor for age-2 sharks (one-way ANOVA, $p > 0.09$).

In SL a comparison of growth of age-0 sharks between all cohorts from 1995 to 2000 revealed that absolute and proportional growth were also significantly different (one-way ANOVA, $p < 0.001$ and $p < 0.01$ respectively). TPC showed that absolute and proportional growth in 2000 were significantly less than in all other years. Comparisons of absolute and proportional growth between SL cohorts for both ages 1 and 2 sharks revealed no significant differences except in age-2 sharks, where proportional growth was significantly greater in 1998 than in 1999 (one-way ANOVA, $p < 0.05$).

Discussion

Our results demonstrate that the growth of juvenile male and female lemon sharks did not differ significantly either in Bimini or the MK. Juveniles of other carcharhinid sharks such as the sandbar shark, *Carcharhinus plumbeus* (Sminkey & Musick 1995); the oceanic whitetip shark, *C. longimanus* (Lessa et al. 1999); and the blacktip shark, *C. limbatus* (Wintner & Cliff 1996) also show similar growth between sexes. Brown & Gruber (1988) also further demonstrated that growth rates between lemon shark sexes are nearly identical throughout life. They reported a von Bertalanffy growth parameter K of 0.055 and 0.060 for males and females respectively.

MK neonate sharks were significantly larger than the Bimini neonates. This might have been because they were sampled 2 months later, and had time to grow approximately 4 cm in the interval since birth. The 4 cm estimate is based on a MK growth rate of approximately 20 cm yr^{-1}. Nevertheless, if both areas had been sampled simultaneously the MK neonates would still have been approximately 1.5 cm longer than the Bimini sharks. Possible explanations as to why birth size might vary between nurseries could be: (1) the estimated growth of 4 cm is in error if sharks exhibit disproportionally faster initial growth, relative to their overall first years growth; (2) poorer ecological conditions in Bimini with respect to prey availability and/or increased abiotic stresses; (3) different levels of intraspecific competition; or (4) genetic differences as related to the philopatric tendencies of adult female lemon sharks. For example, if larger neonates were born in the MK compared to Bimini, these may develop into larger females, which eventually return to the MK and subsequently give birth to larger neonates (mother's size is positively correlated to offspring size, Feldheim et al. 2001). However, not enough information is presently available to select between these alternatives.

The significantly smaller sizes of MK neonates in 2000 may be the result of a larger juvenile population existing that year ($n = 80$) compared to the previous 2 years (1998 $n = 55$, 1999 $n = 55$). Consequentially, sharks may have been competing more strongly for equivalent biological resources in 2000. On the other hand fishing efficiency was increased in 2000 by sampling more than the initial 14 sites. Accordingly, the increased number of sharks caught could have simply been a consequence of more extensive sampling.

Our results showed that growth rates varied greatly between different nurseries. Although annual absolute growth rates did not differ significantly over the first 3 years within each nursery in Bimini, the SL population grew significantly faster than the NS population during the first 2 years. Furthermore, the only age-4 shark caught during the study was recaptured in the NS, possibly indicating a longer nursery residence period than evident in SL. In the MK, because of low recapture rates ($n = 4$), only the growth of age-0 sharks was estimated. The estimated first year growth of approximately 20 cm yr^{-1} was more than triple that obtained for sharks in Bimini (6.3 and 5.3 cm yr^{-1} for SL and the NS respectively). If size prompts emigration out of nurseries this may explain why so few sharks were recaught in the Marquesas.

Growth rates of 26 shark species were categorised by Branstetter (1990) using the Brody growth coefficient K and a measure where juvenile growth was expressed as the ratio of the first year's growth and length at birth. Branstetter (1990) classified the lemon shark as a species with slow growth, due to its low K value (0.05) and a first year's growth of 23% of birth length (BL). Most carcharhinid species have similarly slow growth rates with growth during the first year ranging from 20 to 60% of the BL, e.g. bull shark, *C. leucas* (22% BL) and sandbar shark, *C. plumbeus* (23% BL) (Branstetter 1990). Results from the present study suggest that the growth value for lemon sharks previously calculated by Branstetter (1990) was too high for 1995–2000 Bimini population since we found it to be 11 and 13% of BL for the NS and SL populations respectively. However, juvenile lemon sharks from the MK had a growth value of 28% BL, slightly greater than Branstetter's (1990) previous estimate. The great difference of % BL between Bimini sharks caught before 1990 and Bimini sharks caught after 1995, as well as the even greater difference in % BL between Bimini sharks caught after 1995 and the MK sharks caught after 1998 suggest, that the growth of age-0 sharks from both Bimini populations may have been reduced by natural biotic and/or abiotic pressures. These could have been present in the nursery areas at least since 1995 and were perhaps brought about by the ongoing anthropogenic factors associated with dredging, mangrove deforestation and development of the Bimini Islands (Gruber & Parks 2002).

Preliminary growth studies in Bimini published nearly 20 years ago (Henningsen & Gruber 1985) showed that average growth of juvenile lemon sharks was 8.25 cm yr^{-1}, a higher value than the 6.19 cm yr^{-1} reported in the present study, despite Manire & Gruber (1991) finding that earlier tagging method using metal dart-tags resulted in an estimated 10% decrease in growth rates. Henningsen & Gruber (1985) also reported the growth rate of the juvenile lemon sharks in the upper Florida Keys to be almost identical to that in Bimini (8.36 cm yr^{-1}), much lower than the 20 cm yr^{-1} estimate reported for the MK in this study. These results further suggest that there is a great deal of geographic variability in the growth of juvenile lemon sharks.

Within their respective cohorts absolute growth rates of age-1 and 2 sharks were not significantly different between each Bimini nursery. However, in 2000, absolute growth of the age-0 sharks in SL was significantly less than in all other years. In addition, only a single age-0 shark from the year 2000 cohort was recaptured, compared to an average 12.8 age-0 sharks recaptured in all other years. A possible cause could have been a massive sand dredging enterprise that began in February 2000 at the mouth of the NS, which eventually aims to extract over 2 000 000 cubic yards of fill from the lagoon (Gruber & Parks 2002). This dredging caused a deleterious change in water quality in both the NS and SL through increased sediment loading, which coincided with the reduced growth and survival rates of the juvenile sharks and the capture of the smallest neonates in the NS and SL. The adverse effects of the sedimentation were made worse by the dredging companies disregard for any mitigation devices such as protective booms, silt barriers or sedimentation traps (Gruber & Parks 2002). Comparisons of proportional growth rates between cohorts for each shark age-class in the NS and SL showed that significantly higher growth only occurred in the 1998 cohorts, which might indicate more favourable nursery conditions that year.

To conclude, significant differences in growth (absolute and proportional) of juvenile lemon sharks were evident between Bimini and the MK in the first year of life and between the NS and SL in the first 2 years of life. However, growth rates of juveniles within each Bimini nursery did not vary significantly between the first 3 years of life. Unfortunately, without complete information about environmental effects such as temperature and salinity changes on growth parameters, without data on the extent of human impact and without sound knowledge of the habitat itself it is not possible to ascertain why these differences exist. Therefore, future studies should attempt to assess environmental variables and their role in shaping juvenile recruitment-dynamics in these nurseries. Specifically, the anthropogenic impacts thought to be caused by dredging activities in the Bimini lagoon need to be investigated, since they may significantly affect future recruitment rates if they actually adversely influence the growth of age-0 lemon sharks. New research might compare variation in individual growth rates, as related to social interactions between juvenile lemon sharks (Gruber et al. 1988, Morrissey & Gruber 1993).

Considering the detailed growth data obtained in the present study for the first three years of the lemon sharks' life, a simple linear model best fits the lemon sharks' absolute growth-rate in Bimini. This is similar to Simpfendorfer's (2000) finding that a linear model best describes the first 5 years growth of juvenile dusky sharks, *C. obscurus*.

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