

Spatial ecology of juvenile lemon sharks (*Negaprion brevirostris*) in tidal creeks and coastal waters of Eleuthera, The Bahamas

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Abstract Fisheries exploitation and habitat alteration are threatening lemon shark (*Negaprion brevirostris*) populations because they use nearshore regions as nursery sites. As such, there is a need for information on the spatial ecology of juvenile lemon sharks to identify critical habitats that require protection, as well as to understand their basic ecology. The purpose of this study was to determine the habitat preferences and movement patterns of juvenile lemon sharks along a sub-section of coastline characterized by coastal flats and tidal creeks of Eleuthera, The

Bahamas. Eleven juvenile lemon sharks (766 ± 127 mm total length; mean \pm SD) were captured from various tidal creeks within the 23 km study area and were surgically implanted with acoustic transmitters. A series of 27 hydrophone receivers acted as a passive monitoring array to detect tagged individuals as they moved among habitats. Findings suggest that juvenile lemon sharks tagged in this study prefer shallow water habitats within tidal creeks, and typically display high site fidelity with occasional forays to alternate habitats or creeks. In fact, more

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than 90% of tagged lemon sharks had the greatest percentage of detections located at a receiver at or close to the location where they were tagged. There was no evidence of differences in diel or seasonal movement and habitat use. Knowledge gained from this study will be useful for directing future conservation and management strategies including coastal development plans and marine protected areas.

Keywords Lemon shark · Acoustic telemetry · Site fidelity · Nursery area

Introduction

Globally, sharks and other apex predatory fish species are in decline (Baum et al. 2003; Christensen et al. 2003; Baum and Myers 2004), largely as a result of life history characteristics that make them vulnerable to fisheries exploitation (i.e., slow growth, late maturity and low fecundity; Walker 1998; Kroese and Sauer 1998; Stevens et al. 2000). However, some shark species are also facing threats from habitat alteration associated with coastal development (Manire and Gruber 1990; Camhi et al. 1998). Species which use nearshore regions as nursery sites (e.g., Castro 1993) are particularly at risk as these habitats are essential for the growth and survival of juveniles and therefore the persistence of the population. Therefore, there is a need for information on the habitat selection and movement patterns of juvenile sharks in nursery habitats to identify critical areas that require protection, as well as to understand their basic ecology if shark stocks are to be managed successfully (Merson and Pratt 2001). To date, there have been reasonably few studies on the topic, although recent advances in biotelemetry have made such research feasible (Voegeli et al. 2001; Heupel et al. 2006).

Lemon sharks (*Negaprion brevirostris*) are an excellent example of a species that uses nearshore lagoons, bays, tidal creeks, and other coastal areas for juvenile habitat (see Wetherbee et al. 2007). This shark is common on Atlantic coasts from USA to Brazil, and possibly in some West African countries, and in the Pacific from Baja, California to Ecuador (Compagno 1984). Maturing between 11 to 13 years of age, or approximately 235 cm in total length (Brown and Gruber 1988; Castro 1993), successfully fertilized females will deliver 4–18 offspring in

nearshore areas (Compagno 1984). Neonates and juvenile lemon sharks are restricted to an area of about 6–8 km² during the first few years of their life, with their territory gradually increasing to 300 km² as it nears maturity (Gruber 1982). Adults expand their activity space to include deeper offshore waters, yet return to the coastal zone for the birth of their young (Gruber 1982). The early life history and spatial ecology of juvenile lemon sharks are better known than arguably any other shark species as a result of extensive work by Samuel Gruber and colleagues on a population at Bimini, The Bahamas (reviewed in Sundström et al. 2001). Bimini is a cluster of islands that enclose a shallow lagoon habitat which provides nursery grounds for juvenile lemon sharks (Correia et al. 1995). The collective research has revealed that juvenile lemon sharks in the Bimini lagoon demonstrate high site fidelity [i.e., temporal attachment of an individual to a space in its habitat (Carraro and Glastone 2006) and limited home ranges (Morrissey and Gruber 1993a, b; Gruber et al. 2001)]. Given this information, the degradation of coastal habitats has the potential to reduce the ability of these sharks to meet their requirements for growth and survival.

The increase in tourism development in the Bahamas and other countries in the Caribbean is changing the connectivity and structure of coastal habitats (Buchan 2000). At present, 60% of The Bahamas gross domestic product of 2.7 billion is based on tourism (Buchan 2000). Therefore, development of resorts, beaches, and leisure areas on coastal zones is in high demand. As development increases and coastal habitats become destroyed or fragmented, further information regarding lemon shark movement and activities will provide a better understanding of how critical these habitats are to this species. There is also increasing evidence that loss of apex predators from coastal environments may induce a number of cascades that could dramatically alter ecosystem structure and function (Jackson et al. 2001; Myers et al. 2007). Hence, sharks and shark habitat require protection from exploitation and habitat destruction. Furthermore, the World Conservation Union/Species Survival Commission (IUCN/SSC) rates lemon sharks as “Near Threatened”. As such, telemetric information on the spatial ecology of juvenile lemon sharks beyond the waters of Bimini (i.e., Sundström et al. 2001) will provide critical information needed to make informed decisions

regarding the conservation status and protection of lemon sharks (Cooke 2008).

Given the information above, the objective of this study was to document the habitat use and movement patterns of juvenile lemon sharks in nursery areas near Cape Eleuthera, Eleuthera, The Bahamas. Unlike the earlier work of Gruber and colleagues that focused primarily on a single, predominantly closed lagoon system and the use of manual tracking (but see Wetherbee et al. 2007), this study examines the movement of juvenile lemon sharks along a section of open coastline with a number of discrete tidal mangrove creek systems using a passive acoustic telemetry array. This work will enable us to evaluate the extent to which tagged individual juvenile lemon sharks exhibit site fidelity in a relatively open environment, where the possibility of long-distance movement exists. Furthermore, we will evaluate the diurnal and seasonal movement patterns of juvenile lemon sharks to reveal any temporal trends in their use of habitat.

Materials and methods

Study site and hydrophone array set-up

This study was conducted along a 23 km stretch of the north coast of Cape Eleuthera, Eleuthera, The Bahamas (N 24 50 05 and W 76 20 32) (Fig. 1). This section of coastline is comprised of tidal flats and four distinct tidal creek systems (Page Creek, Kemps Creek, Broad Creek, and Starved Creek). A variety of habitats including mangrove, seagrass, sand, algal plains and patch reefs with sharp calcium carbonate outcroppings throughout typically make up tidal creek and tidal flats ecosystems (Danylchuk et al. 2007). Two daily tidal cycles occurred and had a maximum daily range of 0.8 m.

A series of 27 hydrophone receivers (VR2 and VR2W models, Vemco Inc., Shad Bay, NS) were strategically placed at choke points (e.g., creek mouths) or deployed as curtains extending up to 1.5 km perpendicular to the shoreline along the study area to allow for the passive monitoring of transmitter-implanted lemon sharks (Fig. 1). Individual receivers were secured to a short piece of rebar anchored into a concrete block. Receivers in water greater than 1 m deep at low tide and in open water

were positioned vertically in the water column. In water <1 m deep at low tide and at narrow choke points, receivers were deployed horizontally or 5–10 degrees above horizontal, with the hydrophone oriented to maximize coverage and ensure continual submersion. Range tests determined that receivers located in water greater than 1 m had a radius coverage of 250 m, whereas receivers in shallow water (<1 m) had a radius coverage of as little as 30 m, due to shoreline confinement. Although the range of coverage for receivers in shallow water or positioned horizontally was considerably less, they did provide the necessary coverage to monitor choke points (e.g., creek mouths), such that data correction for receiver range was not required. Wind and wave conditions as well as water depth and tidal cycles influenced the detection range of individual receivers (Heupel et al. 2006). Even at slack low tides, all of the receivers were covered by at least 20 cm of water and had the potential to receive signals from tagged juvenile sharks. Receivers were deployed between November 2005 and May 2007 (5 in November 2005, 6 in February 2006, 15 in October 2006, and 1 in May 2007) as resources were available, and were visited regularly for downloading and cleaning.

Shark capture, tagging and passive monitoring

Juvenile lemon sharks were angled from Page, Kemps, and Broad Creek using conventional spinning gear and baited hooks (10–15 lb test, 5/0 or 7/0 circle hooks) between November 2005 and May 2007. Upon capture, tonic immobility was induced by restraining the shark and rapidly inverting it onto its back (see Watsky and Gruber 1990) to facilitate the implantation of an ultrasonic transmitter (model V16-4 L coded tags, 16 mm diameter, 52 mm long, 9 g, Vemco Inc., Shad Bay, NS). For implantation, a small (2–3 cm) incision was made to the left side of the ventral midline, anterior to the pelvic fins. The transmitter was inserted gently, and the incision was closed with 3 to 4 interrupted sutures using monofilament absorbable suture material (3-0 PDS II, Ethicon Inc., NJ). The total length of the shark (cm) was measured and sex was determined and recorded prior to release. The entire procedure took less than 5 min and fish recovered quickly and were released within 3 min. The monitoring period for this study was from the time of the first fish tagged (2 November 2005) to the last time receivers

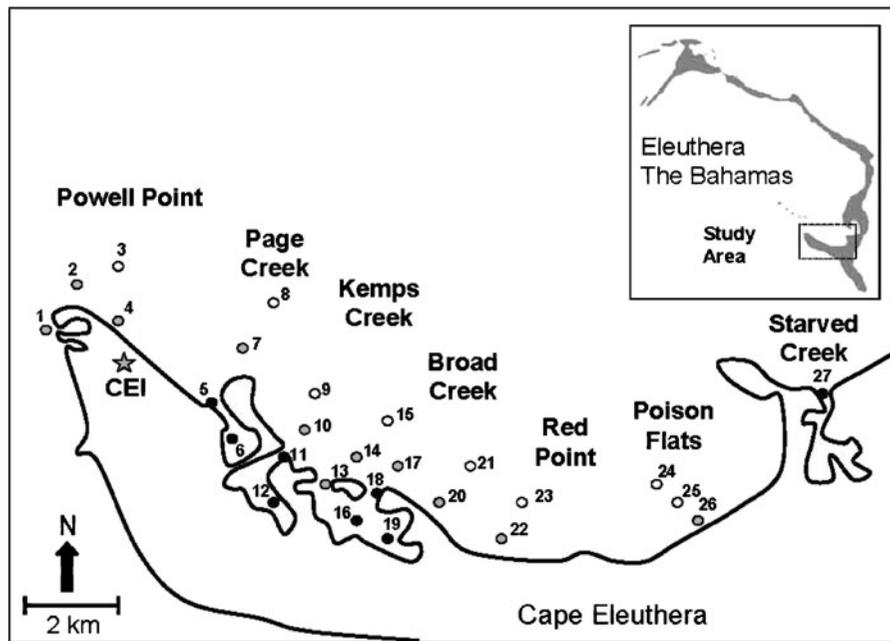


Fig. 1 Study area along the north coast of Cape Eleuthera, Eleuthera, The Bahamas, showing the locations of the 27 hydrophone receivers (numbered circles), and the various tidal creeks and tidal flats areas. ‘Within-creek’ receivers were designated as black circles, ‘nearshore’ receivers as grey circles, and ‘offshore’ receivers as white circles (see materials and methods for

a definition of each habitat zone). The inset map displays the entire island of Eleuthera with the study area highlighted. Note that receiver detection ranges were as little as 30 m at ‘within-creek’ receivers, whereas all other receivers typically had a radius coverage of 250 m or more

were downloaded (11 September 2007). All methods used in this study were in accordance with the policies of the Canadian Council on Animal Care as administered by the Carleton University Animal Care Committee (Protocol B07-03, 04).

Defining ‘site’ and other spatial extents

For the purpose of this study, ‘site’ is defined as the individual hydrophone receiver location. To elucidate trends in movement patterns at larger spatial scales, receiver locations were grouped into 7 ‘areas’ along the shoreline that were associated with one of the tidal creeks, points or flats (Powell Point, Page Creek, Kemps Creek, Broad Creek, Red Point, Poison Flats and Starved Creek) (Fig. 1). Receiver locations were also grouped into three habitat zones (i.e., within-creek, nearshore, and offshore). ‘Within-creek’ receivers were located in creek mouths or the backwaters of creeks; ‘near-shore’ receivers were located 200 m or less from shore but were outside of the creeks; and, ‘offshore’ receivers were located greater than 200 m from shore (Fig. 1).

Data analysis

For each receiver, the total number of detection records was tallied from the date of deployment to the last date downloaded (11 September 2007) to determine sites of high use. To account for the fact that not all receivers were deployed for an equal length of time and thus did not have equal opportunity for detecting the tagged juvenile lemon sharks, the total number of detections was divided by the number of days the receiver was deployed. The total number of detections per days deployed were compared for receivers in each of the three habitat zones (i.e., within-creek, nearshore, and offshore) using a repeated measures analysis of variance (ANOVA). Detection records were further sorted by transmitter identity, date, and time so that individual habitat preferences and movement patterns could be elucidated. Site fidelity was examined by comparing the sites most frequented to the location of tagging, as well as by calculating the minimum linear dispersal and median distance traveled by each juvenile lemon shark. The minimum linear dispersal is defined as the

straight line distance between the two most distant receivers which detected the individual (see Chapman et al. 2005). The median distance traveled was determined for each individual shark by calculating the distance between the receiver with the highest percentage of detections and all other receivers visited, and then taking the median of those distances. Distance measurements were made using Mapsource 6.13.7 (Garmin). Relationships between minimum linear dispersal, and median distance traveled with juvenile lemon shark size were examined using a linear regression. In addition, the minimum, maximum, and mean number of receivers individual lemon sharks visited daily was calculated for the study period.

Diel patterns of activity were examined by combining all detections of each juvenile lemon shark using a repeated measures ANOVA. Each day was evenly divided into four periods of equal time (i.e., sunrise, day, sunset, and night) as per Correia et al. (1995), and divisions were based on sunrise and sunset timing data from a weather station located on Cape Eleuthera. Seasonal movement patterns were determined by combining the total number of detections for each shark in the summer and winter seasons. Seasonal divisions were based on mean water temperatures recorded by data loggers (Hobo-H8 temperature logger, Onset Computer Corporation, $\pm 0.7^{\circ}\text{C}$ accuracy, range of -20°C to 70°C) deployed within the study tidal creeks. As a result, summer had mean water temperatures of 29°C and included 1 May to 31 October, and winter had a mean water temperature of 23° and included 1 November to 30 April. Comparisons between seasonal patterns were made using a t-test for paired samples. All statistical analyses on collected and derived data were completed using JMP 7.0.2 (SAS Institute, Cary, NC). Maximal type-1 error rates were set at $\alpha=0.05$.

Results

Eleven juvenile lemon sharks (77 ± 13 cm total length; mean \pm SD) were captured from the various tidal creeks and surgically implanted with transmitters (Table 1). The total number of days that tagged juvenile lemon sharks were monitored ranged from 11 to 601 days, with the total number of days detected ranging from 11 to 370 (Table 1). Individual lemon

sharks were detected between 935 to 49 498 times within the study period, with 282 735 detections logged in total (Table 1). The receiver with the most detections per days deployed was R11, which was located in the mouth of Kemps Creek (Fig. 2). Out of the five receivers that recorded the greatest number of detections per days deployed, four were located in within-creek habitats (Page, Kemps, and Broad Creek) (Fig. 2). Receivers to the west of Page Creek (R1–4) and to the east of Red Point (R23–27), as well as two offshore receivers (R15 and R21) all had less than one detection per days deployed. The receiver at the mouth of Starved Creek (R27), the most distant from the location of tagging sites, did not detect the presence of any tagged sharks during the study period (Fig. 2). Juvenile lemon sharks were detected at within-creek habitats significantly more frequently than in nearshore or off-shore habitats ($p<0.0001$; repeated measures ANOVA). There was no significant difference in the number of detections of juvenile lemon sharks with days individual receivers were deployed between nearshore and offshore habitats ($p>0.05$; repeated measures ANOVA).

Examination of data for individuals revealed that no juvenile lemon sharks utilized all four tidal creeks within the study area, and only one shark (4083) was not detected within any tidal creeks (Table 2). Four individuals (sharks 4071, 4085, 4093, and 2602) were detected at a ‘within-creek’ receiver at one creek exclusively. Four individuals (sharks 4072, 4084, 4091, and 2604) were detected within two of the tidal creeks on the north coast of Cape Eleuthera (Table 2). In each case, the two tidal creeks utilized were the two creeks closest to each other (i.e., Page and Kemps Creek or Kemps and Broad Creek). Movements between the mouths and/or upper reaches of Page, Kemps, and Broad Creek were undertaken by juvenile lemon sharks 4092 and 2603 (Table 2).

A strong degree of site fidelity was displayed by 91% tagged lemon sharks in this study, with the greatest percentage of detections located at a receiver at or close to the location where they were tagged. Sharks 4071, 4072, 4084, 4085, 4091, 4093, 2603, and 2602 were all detected most frequently at a within-creek receiver for the tidal creek where they were tagged. Two individual lemon sharks (4083 and 4092) had the highest percentage of detections at a nearshore receiver adjacent to their location of tagging. Lemon shark 2604 was tagged in Broad

Table 1 Summary of the tagging, monitoring, and biological data for the 11 juvenile lemon sharks used in this study

Date tagged	Location tagged	Transmitter ID	Total length (cm)	Sex	Date last detected	Total # of days from the time of tagging to the date last detected	Total # of days detected	Total # of detections
2-Nov-05	Broad Creek	4071	95	male	12-Nov-06	375	73	4,011
4-Nov-05	Broad Creek	4072	77	female	28-Jun-07	601	304	49,498
18-Feb-06	Kemps Creek	4083	86	male	4-May-06	76	34	1,856
18-Feb-06	Kemps Creek	4084	86	male	1-Aug-07	530	122	13,379
15-Apr-06	Page Creek	4085	69	female	4-Mar-07	335	279	26 550
29-Apr-06	Page Creek	4091	77	female	2-Mar-07	308	266	44 607
5-May-06	Broad Creek	4092	54	male	9-Sep-07	493	361	35,015
26-Aug-06	Kemps Creek	4093	64	male	4-Sep-07	375	370	32,252
20-Feb-07	Kemps Creek	2603	78	male	11-Sep-07	204	183	49,394
14-Apr-07	Broad Creek	2604	92	female	24-Apr-07	11	11	935
29-May-07	Kemps Creek	2602	65	male	8-Sep-07	103	103	25,238

Creek but had the highest percentage of detections at a nearshore receiver located by Powell Point (R04), with the second highest percentage of detections at a receiver adjacent to the tagging location. Trends in site fidelity were further examined by calculating the

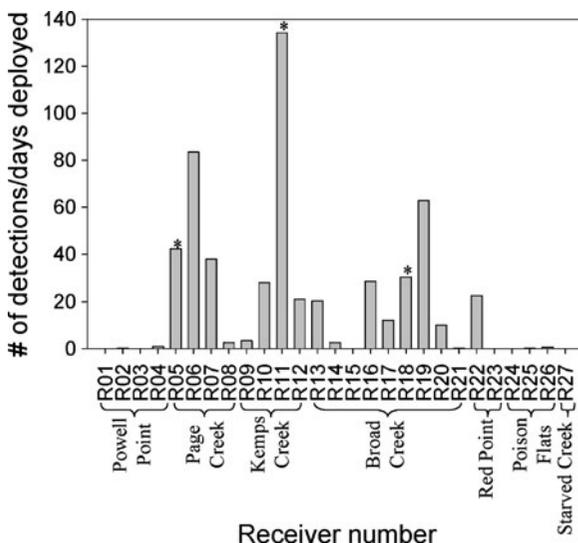


Fig. 2 The number of detections per days deployed of each receiver, located from west to east along the north coast of Cape Eleuthera. Note that receiver R27 is the only location without any detections of juvenile lemon sharks, whereas R01–R04, R15, R21, and R23–27 all had <1 detection/days deployed. An asterisk was placed above the closest receivers to where individual sharks were captured and tagged (see Table 1 for additional details)

minimum linear dispersal and the median distance traveled for each individual except shark 4083 as it was only detected at one receiver. The range in minimum linear dispersal was 648 to 14,094 m (Table 3). There was no significant relationship in the distance between the furthest receivers a shark was detected at and its body size ($p=0.216$). Median distance traveled ranged from 271 to 3,512 m (Table 3), and was not significantly related to the total length of the individual ($p=0.501$). The mean number of receivers that juvenile lemon sharks visited on a daily basis was three, but individuals ranged from visiting one site to 15 sites in 1 day (Table 3).

The number of detections at each receiver for each individual was combined to elucidate any temporal patterns in juvenile lemon shark movements. There was no significant difference in the number of detections between sunrise, day, sunset, and night ($p=0.118$; repeated measures ANOVA). A paired-sample t-test revealed no significant difference in the amount of detections of juvenile lemon sharks between summer and winter seasons ($p=0.959$).

Discussion

The use of a passive acoustic telemetry array proved to be an effective technique for monitoring the habitat use and movement patterns of juvenile lemon sharks along the north coast of Cape Eleuthera as there were

Table 2 Percentage of use of each tidal creek and flats area along the north coast of Cape Eleuthera Bahamas by the individual juvenile lemon sharks used in this study. Calculations took into account the number of days each receiver was

deployed, and the percentage of the detections each receiver logged for the individual. Note that all receiver locations are listed from west to east, and that empty fields indicate that the individual shark was not detected at that receiver

Area	Receiver #	Habitat zone	Transmitter ID											
			4071	4072	4083	4084	4085	4091	4092	4093	2603	2604	2602	
Powell point	R01	Nearshore								<1		<1		
	R02	Nearshore				<1				<1			13	
	R03	Offshore				<1				<1			1	
	R04	Nearshore				<1				<1		<1	27	
Page creek	R05	Within-creek	<1				33	33				<1		
	R06	Within-creek	<1				60	47	<1			<1		
	R07	Nearshore	<1		100	2	8	27	<1		3	3	2	
	R08	Offshore					<1	2	<1		<1	1	<1	
Kemps creek	R09	Offshore		<1		<1			<1	<1	1	1	3	4
	R10	Nearshore	<1	<1		5	<1	1	<1	12	14	4	15	
	R11	Within-creek		<1		54			<1	<1	83	43	6	78
	R12	within-creek				28			<1	<1	4	13		1
Broad creek	R13	Nearshore	5	4		6				12		8	6	
	R14	Nearshore	<1	<1						<1		2	<1	
	R15	Offshore		<1						<1		<1		
	R16	Within-creek	8	8		1				27		4	2	
	R17	Nearshore		11						1		1	5	
	R18	Within-creek	19	23		2				8		2	<1	
	R19	Within-creek	23	46						15		8		
	R20	Nearshore	22	7		1				1		<1	5	
	R21	Offshore	<1	<1		<1				<1		<1		
Red point	R22	Nearshore	23	<1		1				33		<1	20	
	R23	Offshore	<1	<1		<1							2	
Poison flats	R24	Offshore										<1		
	R25	Offshore	<1									<1		
	R26	Nearshore										1		
Starved creek	R27	Within-creek												

over 282 000 detections to base inferences on. Juvenile lemon sharks captured and tagged within tidal creeks exhibited a preference for shallow water habitats within the study area. Similar observations were made by Morrissey and Gruber (1993a, b) for juvenile lemon sharks in the Bimini lagoon area, as they had a penchant for habitats less than 50 cm in depth and close to shore. The mouth of Kemps Creek was the most highly utilized location within the study area. One possible explanation for the use of this particular area is simply geography. Kemps Creek is

immediately adjacent to both Page and Broad Creek and thus is closest for juvenile lemon sharks moving between tidal creeks. From a habitat perspective, the mouth of Kemps Creek has a deeper section that remains flooded at low tides whereas water levels at Page and Broad Creek become much shallower. Ultimately this would afford juvenile lemon sharks the opportunity to stay within-creeks and nearshore longer, potentially avoiding predation in deeper offshore areas. Certainly the use of shallow, nearshore coastal habitats by juvenile sharks is hypothesized to

Table 3 Minimum linear dispersal and median distance traveled by juvenile lemon sharks along the north coast of Cape Eleuthera, The Bahamas, along with a summary of the daily number of receivers individual lemon sharks visited during the study period

Transmitter ID	Minimum linear dispersal (m)	Median distance traveled (m)	Minimum # of receivers visited daily	Maximum # of receivers visited daily	Mean±SD # of receivers visited daily
4071	10,020	1,334	1	9	2.9±1.9
4072	3,701	954	1	12	4.2±1.7
4083	n/a	n/a	1	1	1
4084	8,317	1,838	1	9	2.8±1.9
4085	1,148	465	1	4	2.1±0.9
4091	1,268	927	1	7	2.7±1.5
4092	8,719	3,512	1	15	2.7±1.9
4093	648	271	1	4	1.9±0.9
2603	14,094	1,605	1	12	5.7±2.5
2604	8,317	4,783	2	13	6.6±3.8
2602	969	477	1	6	3.5±1.1

be driven largely by predator avoidance (Heithaus 2004), with the distribution of juvenile lemon sharks being no exception (Morrissey and Gruber 1993b).

With regards to distribution, lemon sharks have been found to exhibit high degrees of site fidelity in a lagoon habitat in Bimini, The Bahamas (Gruber et al. 1988; Morrissey and Gruber 1993a, b; Correia et al. 1995) as well as an atypical nursery habitat within Atol das Rocas, Brazil (Wetherbee et al. 2007). In the current study, 91% of the tagged individuals had the highest number of detections at or close to the location of tagging, and the majority of sharks (73%) utilized only one or two tidal creeks out of four available in the study area. Additionally, juvenile lemon sharks visited, on average, only three sites within the study area on a daily basis. The mean median distance traveled by juvenile lemon sharks in this study was 1,470 m. Morrissey and Gruber (1993a) found that juvenile lemon sharks had a mean activity radii of 496 m. Although these indices of site fidelity are not calculated in the same manner, it appears that juvenile lemon sharks on the north coast of Cape Eleuthera may utilize a large home range than those in Bimini lagoon. This may be further supported with observations of some individual juvenile lemon sharks visiting up to 15 sites on a daily basis. Although forays of up to 1,000 m offshore occurred by some individual juvenile lemon sharks in this study, they were infrequent. Morrissey and Gruber (1993a) also found juvenile lemon sharks would make forays beyond typical activity spaces in the Bimini lagoon. The authors suggested that individ-

uals establish home ranges of sufficient size to recover from repeated exploitation of resources and that shifts in site selection allowed for resource recovery in preferred areas.

Telemetry studies on young (Correia et al. 1995) and adult (Gruber 1984) lemon sharks found that activity level increased at sunset and/or night. Studies on other species of sharks such as grey reef sharks, *Carcharhinus amblyrhynchos*, and scalloped hammerheads, *Sphyrna lewini*, also found a similar trend in nocturnal activity (McKibben and Nelson 1986; Holland et al. 1993). In our study, no significant differences in the number of detections of juvenile lemon sharks were noted between the different diel periods (i.e., sunrise, day, sunset, night). These results are consistent with a study by Cortés and Gruber (1990) that found no diel patterns in the amount of food in young lemon shark stomachs despite the high variability in sampling times. Indeed, such diel patterns only appear to apply to lemon sharks over 120 cm, which are less dependent on shallow water refuges for protection from predators (Wetherbee et al. 2007). One of the reasons that we may not have observed diel patterns in activity may be due to the fact that the tidal creek areas contain highly productive and complex seagrass and mangrove habitats (see Beck et al. 2001) which may provide sufficient food resources and predator refuge such that there is no temporal variance in activity.

The high degree of site fidelity exhibited by juvenile lemon sharks in tidal creek habitats should

be considered in fisheries conservation and management plans as such apex predators play an important role in the trophic structure of marine ecosystems (Myers et al. 2007). Tidal creeks are particularly vulnerable to disturbance and appear to be critical habitats for this species. In fact, this study demonstrates that tidal creeks meet the three criteria necessary for an area to be identified as a nursery; a greater chance of juvenile lemon shark encounter in the area, high site fidelity, and repeated use of the site across years (Heupel et al. 2004). High site fidelity and K-selected life history strategies are not a favorable combination in light of increasing habitat loss and degradation as sharks are generally unable to adapt to rapidly changing environmental conditions (Gruber 1988; Manire and Gruber 1990; Camhi et al. 1998). Evidence for such effects on lemon shark populations has already been observed in the presence of mega-resort development on Bimini (Gruber and Parks 2002). However, the existence of site fidelity may mean that marine protected areas (MPAs) would be successful in protecting juvenile lemon sharks (Kramer and Chapman 1999). In fact, MPAs have been suggested as a conservation tool for young Caribbean reef sharks, *Carcharhinus perezi*, in Brazil (Garla et al. 2006). Continued research into the basic ecology of sharks in general is imperative for the protection of this unique group of species.

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References

- Baum JK, Myers RA (2004) Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecol Lett* 7:135–145
- Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA (2003) Collapse and conservation of shark populations in the Northwest Atlantic. *Science* 299:389–392
- Beck MW, Heck LK, Able KW, Childers DL, Eggleston DB, Gillanders BM, Hapler B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641
- Brown CA, Gruber SH (1988) Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral centra. *Copeia* 3:747–753
- Buchan KC (2000) The Bahamas. *Mar Pollut Bull* 41:94–111
- Camhi M, Fowler S, Musick J, Bräutigam A, Fordham S (1998) Sharks and their relatives: ecology and conservation. Occasional Paper of the IUCN Species Survival Commission Occas. Paper No. 20
- Carraro RW, Glastone W (2006) Habitat preferences and site fidelity of the Ornate Wobbegong shark (*Orectolobus ornatus*) on rocky reefs of New South Wales. *Pac Sci* 60:207–223
- Castro JI (1993) The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Environ Biol Fish* 38:37–48
- Chapman DD, Pikitch EK, Babcock E, Shivji MS (2005) Marine reserve design and evaluation using automated acoustic telemetry: a case-study involving coral reef-associated sharks in the Mesoamerican Caribbean. *Mar Technol Soc J* 39:42–55
- Christensen V, Guenette S, Heymans JJ, Walters CJ, Watson R, Zeller D, Pauly D (2003) Hundred-year decline of North Atlantic predatory fishes. *Fish Fish* 4:1–24
- Compagno LJ (1984) FAO species catalogue of the world, vol 4: sharks of the world. An annotated and illustrated catalogue of shark species known to date, part 2: carcharhiniformes. *FAO Fish Synop* 125:251–665
- Cooke SJ (2008) Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national and IUCN Red List threat assessments. *Endang Species Res* 4:165–185
- Correia J, De Marignac J, Gruber S (1995) Young lemon shark behaviour in Bimini Lagoon. *Bahamas J Sci* 10:2–8
- Cortés E, Gruber SH (1990) Diet, feeding habits and estimates of daily ration of young lemon sharks, *Negaprion brevirostris* (Poey). *Copeia* 1:204–218
- Danylchuk AJ, Danylchuk SE, Cooke SJ, Goldberg TL, Koppelman JB, Philipp DP (2007) Post release mortality of bonefish exposed to different handling practices during catch-and-release angling in Eleuthera, The Bahamas. *Fish Manag Ecol* 14:149–154
- Garla RC, Chapman DD, Wetherbee BM, Shivji M (2006) 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. *Mar Biol* 149:189–199
- Gruber SH (1982) Lemon sharks: supply-side economists of the sea. *Oceanus* 24:56–64
- Gruber SH (1984) Bioenergetics of the captive and free-ranging lemon shark. *AAZPA Annual Conference Proceedings*. 340–373
- Gruber SH (1988) Sharks of the shallows. *Nat Hist* 97:50–59
- Gruber SH, Parks W (2002) Mega-resort development on Bimini: sound economics or environmental disaster. *Bahamas J Sci* 5:2–18

- Gruber SH, Nelson DR, Morrissey JF (1988) Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. *Bull Mar Sci* 43:61–76
- Gruber SH, de Marignac JRC, Hoenig JM (2001) Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark-depletion experiments. *Trans Am Fish Soc* 130:376–384
- Heithaus MR (2004) Predator-prey interactions. In: Carrier JC, Music JA, Heithaus MR (eds) *Biology of sharks and their relatives*. CRC, Boca Raton, pp 487–521
- Heupel MR, Simpfendorfer CA, Hueter RE (2004) Estimation of shark home ranges using passive monitoring techniques. *Environ Biol Fish* 71:135–142
- Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Mar Freshw Res* 57:1–13
- Holland KN, Wetherbee BM, Peterson JD, Lowe CG (1993) Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia* 2:495–502
- Jackson JBC, Kirby MX, Bergner WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. *Env Biol Fishes* 55:65–79
- Kroese M, Sauer WH (1998) Elasmobranch exploitation in Africa. *Mar Freshw Res* 49:573–577
- Manire C, Gruber S (1990) Many sharks may be headed toward extinction. *Conserv Biol* 4:10–11
- McKibben JN, Nelson DR (1986) Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bull Mar Sci* 1:89–110
- Merson RR, Pratt HL Jr (2001) Distribution, movements and growth of young sandbar sharks, *Carcharhinus plumbeus*, in the nursery grounds of Delaware Bay. *Env Biol Fishes* 61:13–24
- Morrissey JF, Gruber SH (1993a) Home range of juvenile lemon sharks, *Negaprion brevirostris* (Poey). *Copeia* 2:425–434
- Morrissey JF, Gruber SH (1993b) Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. *Environ Biol Fish* 38:311–319
- Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315:1846–1850
- Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyan), and the implications for marine ecosystems. *ICES J Mar Sci* 57:476–494
- Sundström LF, Gruber SH, Clermont SM, Correia JPS, de Marignac JRC, Morrissey JF, Lowrance CR, Thomassen L, Oliveira MT (2001) Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Environ Biol Fish* 60:225–250
- Voegeli FA, Webber DM, Smale MJ, Andrade Y, O'Dor RK (2001) Ultrasonic telemetry, tracking and automated monitoring technology for sharks. *Environ Biol Fish* 60:267–281
- Walker TI (1998) Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Mar Freshw Res* 49:553–572
- Watsky MA, Gruber SH (1990) Induction and duration of tonic immobility in lemon shark, *Negaprion brevirostris*. *Fish Physiol Biochem* 8:207–210
- Wetherbee BM, Gruber SH, Rosa RS (2007) Movement patterns of juvenile lemons sharks *Negaprion brevirostris* within Atol das Rocas, Brazil: a nursery characterized by tidal extremes. *Mar Ecol Prog Ser* 343:283–293