MOLECULAR ECOLOGY

Molecular Ecology (2009) 18, 3500–3507 doi: 10.1111/j.1365-294X.2009.04289.x

Long-term natal site-fidelity by immature lemon sharks (*Negaprion brevirostris*) at a subtropical island

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Abstract

Although many sharks begin their life confined in nursery habitats, it is unknown how rapidly they disperse away from their natal area once they leave the nursery. We examine this issue in immature lemon sharks (*Negaprion brevirostris*) from the time they leave the nursery (~ age 3) at a subtropical island (Bimini, Bahamas), through to the onset of sexual maturity (~ age 12). From 1995 to 2007 we tagged and genotyped a large fraction of the nursery-bound sharks at this location (0–3 years of age, $N = 1776$ individuals). From 2003 to 2007 we sampled immature sharks aged from 3 to 11 years ($N = 150$) living around the island and used physical/genetic tag recaptures coupled with kinship analysis to determine whether or not each of these 'large immature sharks' was locally born. We show that many island-born lemon sharks remain close to their natal area for long periods (years) after leaving the nursery; more than half of the sampled sharks up to 135 cm total length (~6 years old) were locally born. The fraction of locally born sharks gradually declined with increasing shark size, indicating that dispersal is relatively slow and does not primarily occur after sharks reach a threshold size. Local conservation measures (e.g. localized fishery closures, marine protected areas) can therefore help protect island-born lemon sharks even after they leave the nursery habitat.

Keywords: conservation, dispersal, elasmobranch, fishery closure, marine protected area, natal philopatry

Received 20 January 2009; revision received 28 May 2009; accepted 2 June 2009

Introduction

Very little is known about how mobile marine animals disperse from their natal area with ontogeny, even though this process has important ramifications for population dynamics, stock structure and conservation (Avise 2004). The paucity of information about this process stems from difficulties that arise when attempting to follow aquatic individuals of known geographic natal origin as they develop. Part of the problem is that it is difficult to elucidate natal origins of individuals in marine species without first sampling them during their earliest life stages (i.e. hatchlings, larvae or neonates), because even modest straying by adults can prevent the development of genetic characters diagnostic for different breeding populations (Waples 1998). All of these difficulties are especially acute in studies of long-lived, potentially highly mobile taxa, such as large chondrichthyan fishes (e.g. sharks, batoids).

Detailed information on how sharks disperse from their natal area could be very useful for management

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and conservation, given that many shark species are threatened by overexploitation (Manire & Gruber 1990; Robbins *et al.* 2006; Myers *et al.* 2007). It is well established that many coastal sharks begin their life confined to specific nursery habitats within their natal area (e.g. Castro 1993; hereafter referred to as the 'nursery-bound phase'), which has validated investments in spatial fishery closures targeting the earliest life-stages (e.g. Garla *et al.* 2006; NOAA/NMFS 2006). In contrast, adult sharks are often highly mobile (e.g. Springer 1960; Gruber *et al.* 1988), which has typically resulted in calls for broader scale, often transboundary management. Much less is known about the dispersal of immature sharks during the period from when they leave the nursery through to the onset of sexual maturity. While there has been considerable emphasis on the conservation of nursery-bound sharks, an increased investment in protecting immature individuals after they have left the nursery would significantly benefit shark populations. This is because population growth in sharks is especially sensitive to variation in the survival of this demographic (Cortes 2002).

The lemon shark, *Negaprion brevirostris*, is a large-bodied [to 340 cm total length (TL)], placental livebearer that occurs in disjunct Western Atlantic, Eastern Atlantic and Eastern Pacific populations (Compagno 1984). Adult lemon sharks are highly mobile, which weakens genetic population structure throughout the Western Atlantic even though adult females exhibit seasonal fidelity to particular nursery areas for parturition (Feldheim *et al.* 2001, 2002a). In contrast, newborn and small juvenile lemon sharks (<90 cm TL) are typically restricted to shallow habitats in their natal nursery area, ostensibly to avoid larger predatory sharks and to exploit nearshore prey resources (e.g. Morrissey & Gruber 1993; Wetherbee *et al.* 2007). Nursery use by lemon sharks has been especially well documented at Bimini (Bahamas), a subtropical island cluster where neonates are found in high densities on shallow, nearshore flats after having been born in the spring (Gruber *et al.* 2001). Individuals remain within their natal nursery during their first 2–3 years of life and expand their home-range into a wider variety of deeper habitats around the islands as they approach ~90 cm TL and become less vulnerable to predators and need to exploit larger prey (Morrissey & Gruber 1993; Franks 2007).

After leaving the nursery habitat around age 3, lemon sharks from Bimini take about 9 more years to reach sexual maturity, which occurs when they reach ~230–240 cm TL (Brown & Gruber 1988). Whereas large immature lemon sharks of all sizes and ages are common around Bimini throughout the year, the natal origins of these individuals are unknown, making it impossible to characterize how they disperse from their natal area with age. It is possible that all surviving locally born lemon sharks stay close to Bimini until they reach sexual maturity. Alternatively, they may be highly dispersive after leaving the nursery and rapidly mix between different islands, since Bimini is within 15–150 km of other islands utilized by immature lemon sharks. It is also possible that dispersal from Bimini occurs gradually, or occurs after large immature sharks reach a certain threshold size. If sharks strictly remain close to their birthplace until maturity or many individuals disperse only gradually, then we would expect that a high fraction of immature lemon sharks living around Bimini would have been born in the local nurseries. If immature lemon sharks born at Bimini (and elsewhere) are typically dispersive soon after leaving the nursery or after reaching some other specific threshold size, we would expect that sharks in this size range occurring at any given location would consist of a mixture of individuals from different nursery areas. Our primary objectives were therefore to estimate the proportion of locally born individuals among the large immature sharks living around Bimini and to determine how this parameter changed according to shark size.

Materials and methods

Bimini, Bahamas (25°44N, 79°16W) is a cluster of low-lying, subtropical islands and cays located on the western edge of the Great Bahamas Bank, ~ 86 km due east of Miami, Florida. There are two major islands, North and South Bimini, which enclose a shallow, mangrove-fringed lagoon that is a birthing and nursery area for lemon sharks (Fig. 1). Most nursery-bound lemon sharks inhabit two parts of the lagoon-North Sound (NS) and Sharkland (SL), primarily in shallow water (<1 m) close to extensive mangrove forests that comprise most of the north and east portions of North Bimini (Fig.1). A smaller population of nursery-bound sharks occur along the exposed, mangrove-lined south coast of South Bimini ('South Bimini': SB), as well as a small embayment on the north coast of South Bimini ('Pirate's Well': PW) and in a network of tidal creeks in the mangroves of the eastern part of North Bimini between Bonefish Hole and East Wells to the north ('Bonefish Hole': BH; Fig.1).

Nursery-bound lemon sharks are highly accessible to sampling during the first 3 years of their life in Bimini because they are concentrated in a relatively narrow strip of shallow nearshore areas (Gruber *et al.* 2001). The survey and tagging protocol for nursery-bound lemon sharks conducted off Bimini from 1995 to 2007 is described in detail elsewhere (Gruber *et al.* 2001; Feldheim *et al.* 2002a; DiBattista *et al.* 2008a). Briefly, a very large portion of every cohort was captured and held in captivity during intensive gillnet sampling conducted in

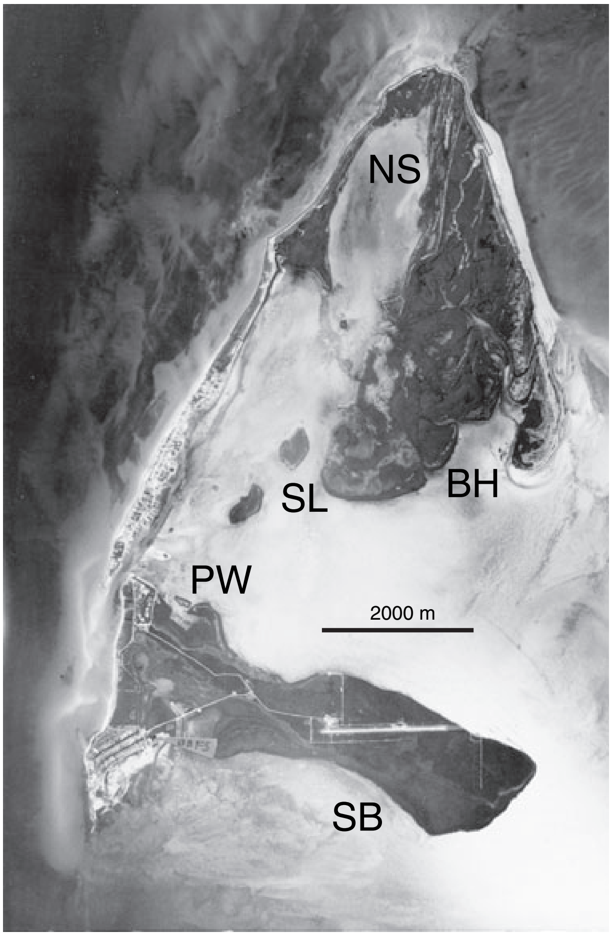

Fig. 1 The location of the study area (Bimini, Bahamas). Locations of each specific nursery are shown on the map: the major nurseries that were sampled with 99% efficiency: NS, North Sound and SL, Sharkland; the peripheral nurseries that were sampled less extensively: BH, Bonefish hole; PW, Pirate's Well; SB, South Bimini.

NS and SL over 3 weeks in the early summer each year. Gillnets (100 m long) were set perpendicular to shore at six sites within these nurseries, each of which was sampled for 6–10 fishing nights until an estimated 99% of all 0, 1 and 2-year-old sharks in the area were captured (Gruber *et al.* 2001; Feldheim *et al.* 2002a; DiBattista *et al.* 2008a). We were therefore able to sample the majority of individuals born in these nurseries from 1993 onwards. Individuals in peripheral nurseries (PW, BH, SB) were collected with gillnets sporadically throughout the year. A small piece of fin tissue was taken from each shark for DNA analysis and stored in 20% DMSO. Each individual was measured [total length (TL), fork length (FL) and precaudal length (PCL)] and a passive integrated transponder (PIT; Destron Fearing Inc.) tag was injected into the musculature at the base of its first dorsal fin (Gruber *et al.* 2001; Feldheim *et al.* 2002a; DiBattista *et al.* 2008a). Captured sharks were released after about 12 days captivity, both to ensure recovery and to avoid recapture within the same annual sampling session (Gruber *et al.* 2001; Feldheim *et al.* 2002a; DiBattista *et al.* 2008a).

Larger, older immature lemon sharks (i.e. >90 cm TL) that were no longer obligated to shallow nursery habitats were sampled within 3 km of Bimini from 2003 to 2007. These sharks are more dispersed and occur in deeper water than nursery-bound sharks so it is not possible to sample them with the same level of efficiency. Therefore, to obtain a representative sample of this age group living around Bimini we first opportunistically sampled sharks from 90 to 100 cm TL (~3–4 years old) collected during our gillnet sampling in the nursery. These sharks are no longer confined to the nursery but sometimes utilize these habitats during high tides. Sharks larger than 100 cm TL are infrequently found in the nursery habitat and were instead primarily captured on bottom longline fishing gear that was set twice a month in the deeper parts of the lagoon or within 3 km of the islands. After standard body measurements were taken, a hand-held tag reader (Destron Fearing Inc.) was used to scan for a PIT tag applied during earlier nursery area sampling. A piece of fin tissue was taken for later DNA analysis. All sharks were immediately released after being processed.

All of the immature lemon sharks larger than 90 cm TL (hereafter referred to as 'large immature sharks') that were captured from 2003 to 2007 were categorized as either 'locally born' or 'putative migrant'. To avoid including sharks that may have been born prior to 1993 we only used sharks >200 cm TL if they were caught from 2005 to 2007. This allowed for sharks to be up to 12 years old at these sizes, which is consistent with validated age-growth data from this population (Brown & Gruber 1988). Of the sharks used in this study, any that were traceable to a Bimini nursery by a PIT tag were immediately assigned to the 'locally born' category. Multilocus microsatellite genotypes (11 loci, 7–49 alleles/locus) were used to individually identify sharks that had potentially shed their PIT tag. These genotypes were resolved on an automated DNA Analyzer (ABI 3730, Applied Biosystems Inc.) following PCR amplification. All laboratory procedures, primer sequences and population genetic data have been previously described in Feldheim *et al.* 2001, 2002a and DiBattista *et al.* 2008b.

The program Identity 4 (http://www.uni-graz.at/~sefck/) was used to scan microsatellite genotypes of all large immature individuals against the genotypes of all sampled sharks collected from 1995 to 2007. The probability of identical genotypes arising between different individuals at all 11 loci was previously shown to be extremely low (1.11×10^{-15}; DiBattista *et al.* 2008a). Any 'untagged' large immature shark sampled from 2003 to 2007 that genetically matched a previously sampled nursery-bound shark was therefore considered to be the same individual. It was then assigned to the 'locally born' category.

A fraction of the large immature sharks not immediately assigned to the locally born category were actually locally born individuals but had escaped our 1995–2007 sampling efforts. To estimate this we used a kinship approach to directly identify sharks that may have been missed. This approach was based on the premise that if an individual escaped tagging during its nursery-bound phase, there was a high probability that some of its littermates did not. The 11 loci used in this study have previously been shown to be robust for resolving full-sibling, half-sibling and unrelated lemon sharks (Feldheim *et al.* 2002a; DiBattista *et al.* 2008a,b). We therefore used the maximum likelihood program KinGroup ver. 1.0505 + (Konovalov *et al.* 2004) to identify full-sibling clusters among all of the putative migrants from the 2003 to 2007 large immature sharks and the 1995–2007 nursery-bound sharks. We first identified likely full-sibling clusters from the pooled genotypes using the 'Descending Ratio' algorithm (Konovalov *et al.* 2004). We then verified each putative full-sibling cluster that contained at least two nursery-bound sharks born in the same year and at least one large immature shark, using the 'Exhaustive Descent' algorithm (Konovalov *et al.* 2004). If a large immature shark clustered as a full-sibling with two or more nursery-bound sharks sharing a birth year we assumed that they were all littermates. We then assigned the large immature shark to the 'locally born' category. Although littermates can frequently be half-siblings due to recurrent multiple paternity in Bimini's lemon sharks (Feldheim *et al.* 2002a), we elected not to use this relationship for the determination of natal origin because paternal half-siblings can be born at different islands in the same year as a result of polygynous mating.

Variation in the proportion of locally born individuals relative to migrants according to shark size and sex was tested using a logit link generalized linear model (GLM) appropriate for binomial data:

$$\log\left(\frac{p_i}{1-p_i}\right) = \beta_o + \beta_1 L_i + \beta_2 L_i^2 + \beta_3 S_i + \beta_4 S_i L_i + \varepsilon_i$$

where p_i is the probability that shark i is locally born, L_i is the total length of shark i and S_i is its sex, the β terms are the estimated regression parameters and ε_i is an error term. The significance of the regression parameters was determined with a Chi-squared test. The analysis was conducted in S-PLUS 8.0 (Venables & Ripley 1997).

Results

Between 1995 and 2007, 1776 nursery bound lemon sharks were tagged and genotyped at Bimini, primarily in the NS and SL nurseries where the overall sampling efficiency was previously estimated to be 99% (Gruber *et al.* 2001; Feldheim *et al.* 2002a; DiBattista *et al.* 2008a). Sampling efficiency in the smaller, peripheral nurseries over this period was unknown. A few exhaustive sampling sessions recently conducted at these sites indicate their collective size is probably about 30–40% of NS/SL combined and that we probably sampled ~30–40% of individuals born in these areas over the study period (S. H. Gruber unpublished).

Between 2003 and 2007, 150 large immature lemon sharks were captured in a variety of habitats within 3 km of Bimini and were used in the subsequent analyses. Their TLs ranged from 90 to 232 cm (estimated ages 3–11 years based on TL); mean size was 135.7 cm TL (SD = 37.3 cm). There were 84 males and 66 females in the sample. Thirty-eight individuals were immediately recognized as being locally born from a PIT tag applied during nursery area sampling. Following microsatellite genotyping and analysis, seven more individuals lacking a readable PIT tag matched a previously sampled nursery-bound individual. In all seven cases, the gender and size of the individual were also appropriate given phenotypic data collected during tagging. These individuals were thus considered to be a recapture and reassigned to the 'locally born' category. This is equal to a PIT tag failure rate of 15.5% in this group, which is similar to that recorded for younger lemon sharks tagged for 1–2 years (12.8%; Feldheim *et al.* 2002b). Finally, two or more full-sibling littermates were identified for another 32 large immature sharks using KinGroup, indicating that these individuals were locally born but had escaped sampling during the nursery-bound phase. Once these were reassigned to the 'locally born' category, the total number of large immature sharks living around the islands that were locally born was conservatively estimated to be 77 out of 150 sharks (51.3%).

The logistic regression indicated that the probability of a sampled shark having been born locally declined significantly with total length (Table 1). For example, a shark of 95 cm TL would have a 75% probability of being locally born, while a shark of 205 cm TL would have only a 14% probability (Fig. 2). The gradient of the relationship was shallow (slope = −0.024 in logit space, Fig. 2), indicating a gradual change in this probability. There was no obvious inflection point in the relationship, but sharks were equally likely to be locally born or putative migrants at 135 cm TL. The TL squared, sex and sex × TL terms were not significant.

Table 1 Analysis of deviance for a generalized linear model of the probability of a sampled shark being locally born, given its total length (L), sex (S), total length squared (L^2) and the interaction between total length and sex (L × S).

	d.f.	Deviance	Residual d.f.	Residual deviance	Pr(Chi)
NULL			149	207.84	
L	1	27.33	148	180.51	<0.001
S	1	1.35	147	179.16	0.25
L^2	1	0.05	146	179.10	0.82
L × S	1	0.35	145	178.75	0.55

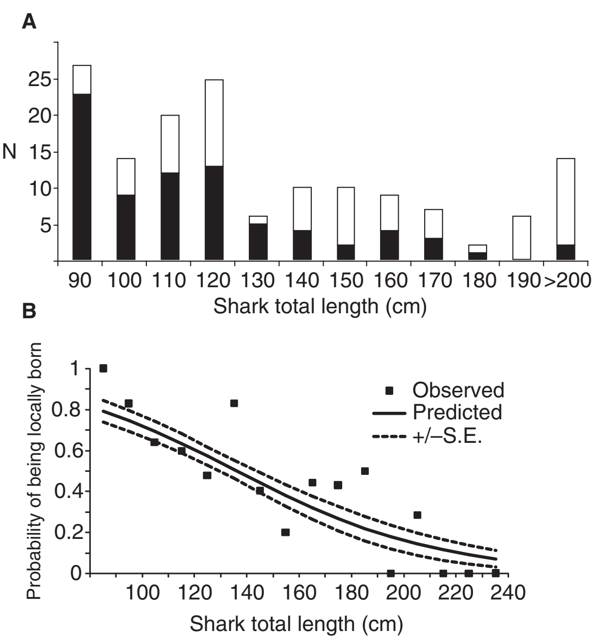

Fig. 2 A. Length frequency histogram for large immature lemon sharks (*N* = 150) sampled between 2003 and 2007 within 3 km of the Bimini Islands, Bahamas. Solid portions of the bars show the individuals that were born in the local nursery areas. Open portions of the bars show sharks that could not be traced back to the local nurseries and are therefore putative immigrants. B. Fraction of sharks known to be locally born in each length range (points), combined with the predicted fraction of sharks locally born in the centre of each length range (e.g. at 95 cm for the 90–100 cm category) according to a logistic regression model with length as the only explanatory variable (line) plus and minus one standard error (dashed lines). Note that raw, not binned, TL data were used for the actual model.

Discussion

Slightly over half of the large immature lemon sharks sampled around Bimini originated from the local nurseries, verifying that many individuals stay close to their birthplace for several years after they leave the confines of the nursery. Our procedure for determining whether a large immature lemon shark was born at Bimini is predicated upon it either having been caught locally during its nursery-bound phase or being full-siblings with at least two other individuals that met this criterion. Any locally born shark that did not meet either of these criteria would be misclassified as a migrant in this study. While we acknowledge that this occasional misclassification makes our estimate of the fraction of locally born individuals among the large immature sharks living around Bimini highly conservative, it did not obscure the general behavioural patterns that we were interested in examining.

Prior acoustic tracking studies show that nursery-bound sharks gradually increase the scale of their movements as they grow beyond ~ 90–100 cm TL, eventually leaving the nursery and entering deeper, more exposed coastal habitats around Bimini (Franks 2007). Tracking of large immature lemon sharks above these sizes revealed long-term site-fidelity and year round residency to Bimini, although the natal origins of these individuals were not known (Gruber *et al.* 1988; Sundstrom & Gruber 1998; Sundstrom *et al.* 2001; S. H. Gruber unpublished). When coupled with our findings, this indicates that many individuals born at the Bimini islands remain in their natal area for several years after leaving the nursery habitat, rather than frequently leaving and then returning to it (e.g. Hueter *et al.* 2005).

There was a gradual but significant decline in the proportion of locally born individuals with size. One way to interpret this finding is that fewer large sharks appear to be locally born because they are born prior to the beginning of our nursery sampling programme and therefore neither they (nor there littermates) were available for tagging and DNA sampling while in the nursery. We discount this explanation for two reasons: first, sharks born as early as 1993 would be included in our nursery sampling, which allows the largest immature sharks included in the study (i.e. >200 cm TL) to be 12–14 years old in 2005–2007 and still have been in the nursery when our sampling began. This is appropriate and reasonably conservative given previous age and growth data for this population (Brown & Gruber 1988) and recent recaptures of tagged sharks in this age range (S. H. Gruber unpublished). Second, the relationship between length and probability of being locally born was still highly significant when we took a more conservative approach and eliminated all sharks larger than 180 cm TL from the analysis.

While most lemon sharks up to 135 cm TL (~ 6 years old) living around Bimini come from the local nurseries, sharks larger than this size are primarily born elsewhere. Several possible movement scenarios would be consistent with this pattern. First, sharks could gradually increase the scale of their movements with age, initially remaining centred in their natal area. Second, sharks could have a small, constant probability of permanently leaving their natal area at any age, so that the fraction of sharks that remain in the natal area declines with age. Third, a 'random walk' movement model could also account for a gradual reduction in locally born sharks with age. Some combination of these scenarios could also occur, making it difficult to resolve this process further without more detailed movement data. Regardless of the precise dispersal scenario, these results show that many lemon sharks born at Bimini disperse gradually from these islands rather than immediately after emigrating from the confines of nursery habitat. The absence of a strong inflection point in the relationship between size and probability of being locally born also indicate that there is not a sudden, mass emigration of sharks from the natal area after they reach a specific threshold size.

Why would dispersal from Bimini by locally born immature lemon sharks occur only gradually? In the absence of additional movement data, we can speculate that the costs or risks associated with dispersal act to slow this process. This could be related to the insular nature of the island coupled with the presence of large predatory sharks in the surrounding deeper habitats (e.g. Chapman & Gruber 2002). Also, we could speculate that some of the typical drivers of shark migration [e.g. seasonal changes in water temperature, changes in prey availability (Springer 1960; Castro 1993; Reyier *et al.* 2008)] are not sufficient to trigger rapid dispersal from the islands. Sea temperatures off subtropical Bimini are hospitable year round for immature lemon sharks and there is also a resident community of subtropical fish species that are potential prey-items.

It is intuitive that concentrated fishing pressure or destruction of nursery habitat could drastically reduce the survivorship and local abundance of nursery-bound lemon sharks at Bimini and elsewhere (e.g. Gruber & Parks 2002). It is perhaps not as intuitive to resource managers that this can also reduce the abundance of larger sharks, given the popular perception that large sharks are highly mobile. The present study demonstrates that the local nurseries are the most important source of 90–135 cm TL lemon sharks living around the islands. Thus, any sustained reduction in the survivorship of nursery-bound sharks would also be expected to propagate through cohorts to eventually reduce the local abundance of these older, larger individuals in the immediate vicinity of the islands. This issue is cause for local concern given that these larger immature lemon sharks are a numerically important upper-level predator around these islands (Gruber *et al.* 1988) and their local depletion may trigger cascading effects in this insular ecosystem (Manire & Gruber 1990; Stevens *et al.* 2000; Myers *et al.* 2007).

These results indicate that many immature lemon sharks stay close to their natal area for a significant period after emigrating from the nursery habitat in Bimini. An important question is: Are these results broadly applicable to sharks that breed at tropical islands or are they unique to Bimini's lemon sharks? Lemon sharks breed at a number of subtropical and tropical islands throughout their range, including areas less isolated than Bimini (e.g. the Florida Keys, DiBattista *et al.* 2008b) and much more remote oceanic islands (e.g. Atol as Rocas, Brazil, Wetherbee *et al.* 2007). If it is the insular nature of Bimini that is primarily responsible for the site-fidelity of immature lemon sharks born there, then this characteristic will not be unique to Bimini and should be even more pronounced at more isolated locations.

Acoustic telemetry tracking of immature sharks from other species at have typically revealed that site-fidelity is a common behaviour even after the nursery-bound phase at tropical islands (McKibben & Nelson 1986; Chapman *et al.* 2005; Garla *et al.* 2006; Lowe *et al.* 2006). However, the natal origins of the tracked sharks in these studies are generally not known. Given our results, it is a reasonable hypothesis that site-fidelity commonly observed in immature sharks at tropical islands may often also reflect long-term fidelity to their natal area. Recent studies suggest that some tropical shark populations may exhibit more localized population dynamics than anticipated for such large, potentially mobile animals (e.g. Robbins *et al.* 2006). In addition, several genetic studies suggest that gene flow in shark populations is often restricted between insular locations (Duncan *et al.* 2006; van Herwerden *et al.* 2008). It is possible that these population genetic and demographic characteristics are related in part to a tendency for many individual sharks born in insular locations to stay close to their natal area for extended periods.

Localized fishery closures and marine protected areas (MPAs) are increasingly used for marine conservation, but their ability to protect large, mobile apex predators is not well known (Chapman *et al.* 2005; Sale *et al.* 2005). Up until now localized shark fishery closures and MPAs around nursery areas have primarily been employed to increase the survivorship of newborn sharks, although they can also protect vulnerable adult females as they concentrate in these coastal, nearshore areas to give birth (Garla *et al.* 2006; NOAA/NMFS 2006; DiBattista *et al.* 2008b). Our findings suggest that localized shark fishery closures or fixed MPAs around insular nursery areas also have the potential to increase the survivorship of many older immature lemon sharks for a substantial period (years) after they leave the nursery. In this regard, these local, spatially focused conservation measures could help enhance insular lemon shark populations by helping many individuals survive through much of their long and vulnerable immature phase, a life-stage that is critically important for sustaining shark populations (Cortes 2002).

This study illustrates how island-born lemon sharks can maintain a long-term spatial connection with their natal area even after they leave the confines of the nursery habitat. Future studies employing a combination of tagging, tracking and molecular analysis should further elucidate the connections that other shark species maintain with their natal area during different stages of their life. This information will provide important insights into shark population biology and how local measures can contribute to the restoration and conservation of these vulnerable apex predators.

Acknowledgments

This research was supported by the National Science Foundation Biological Oceanography Program under grant OCE-0623283 to S.G and K.F.; the Institute for Ocean Conservation Science at Stony Brook University from the Pew Charitable Trust (S.G.) and The Roe Foundation (D.C.). This study was also funded in part by a Natural Sciences and Engineering Research Council of Canada postgraduate fellowship to J.D.D, as well as by grants from the the Bimini Biological Field Station, the National Fish and Wildlife Foundation, Florida Sea Grant, National Geographic Society, University of Illinois at Chicago Research Foundation, Québec-Océan, and PADI's Project AWARE. Genetic data were collected in the Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution operated with support from the Pritzker Foundation. We also thank Rose Mann and Lacey Hoover for their kind efforts to secure private funding, and we are indebted to the Hoover Foundation, and Drs Tadashi and Toshi Fujino, for generous private support. We gratefully acknowledge the following corporate support: Mario Aiello, Davey Marine; the late Dan Schaad of Mercury Division, Brunswick Corporation; The Carolina Skiff corporation; Digital Angel Corporation (Destron), especially Sean Casey; Andrea Obrian, Bimini Island Air; and Cathy Bosch of Pelican Products. This research was carried out under a permit from the Department of Fisheries of the Commonwealth of the Bahamas (Michael Braynan, director). Thanks to the numerous students and volunteers who braved inclement conditions to help sample our this population so thoroughly over the past 13 years. Thanks to Debra Abercrombie and three anonymous reviewers for invaluable comments on the manuscript.

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Demian D. Chapman combines field ecology with molecular data to better understand dispersal and reproduction in marine vertebrates, with a particular emphasis on how these processes influence genetic variation and relate to the conservation of threatened populations. Elizabeth A. Babcock is a fisheries biologist specializing in quantitative methods for assessing and managing fisheries for which traditional fisheries data are lacking, including Bayesian stock assessment and ecosystem based management methods. Samuel H. Gruber has studied sharks for the past 40 years and is interested in fully resolving the life-history and ecology of the lemon shark as a model species. This study formed part of Joseph D. DiBattista's recently completed PhD thesis on quantitative genetics and the evolution of mating systems, using a natural population of lemon sharks as a model system. Joseph now hopes to explore more general questions on dispersal and connectivity among marine habitats. Bryan Franks studies the movement patterns and habitat use in elasmobranchs, especially during their early life-stages. Steve Kessel is interested in the movements and population dynamics of sharks. Tristan Guttridge's research interests are focused on the mechanisms and functions of group living in sharks and teleost fish. Ellen K. Pikitch's current research focus is ecosystem-based fisheries management and the conservation of critically-threatened or ecologically important fish (sharks, sturgeon, forage fish). Kevin A. Feldheim studies the evolution and ecology of a wide range of aquatic and terrestrial species using molecular data, but has a particular interest in mating systems and natal homing in sharks.