Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks

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Abstract

Sharks are a globally threatened group of marine fishes that often breed in their natal region of origin. There has even been speculation that female sharks return to their exact birthplace to breed ('natal philopatry'), which would have important conservation implications. Genetic profiling of lemon sharks (*Negaprion brevirostris*) from 20 consecutive cohorts (1993–2012) at Bimini, Bahamas, showed that certain females faithfully gave birth at this site for nearly two decades. At least six females born in the 1993–1997 cohorts returned to give birth 14–17 years later, providing the first direct evidence of natal philopatry in the chondrichthyans. Long-term fidelity to specific nursery sites coupled with natal philopatry highlights the merits of emerging spatial and local conservation efforts for these threatened predators.

Keywords: natal philopatry, nursery habitat, shark conservation

Introduction

Philopatry has been defined as the return of individuals to the locality or region where they were born to reproduce (Mayr 1963; Secor 2002). This phenomenon has been demonstrated in several marine vertebrates, including pinnipeds (Baker *et al.* 1995; Hoffman & Forcada 2012), bony fishes (Thorrold *et al.* 2001; Rooker *et al.* 2008) and sea turtles (Bowen & Karl 2007; Lohmann *et al.* 2013). When common to both sexes, this behaviour contributes to the development of closed populations where intrinsic reproduction and recruitment are more important determinants of population

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dynamics than immigration (Harden Jones 1968; Secor 2002). For this reason, philopatry is fundamental to the stock-unit concept in fisheries management and is an important consideration in conservation planning for threatened and endangered species (Harden Jones 1968; Secor 2002).

One important property of philopatry is its geographical specificity, which quantifies how closely individuals return to the site of their birth. This property helps determine the scale at which populations may become closed and therefore identifies the most appropriate scale of stock assessments and management actions. For example, rapidly maturing, anadromous salmonids often return to their exact birthplace (i.e. tributary) to reproduce, which we hereafter refer to as 'natal philopatry' (Harden Jones 1968). In many late-maturing

marine organisms, however, individuals usually return to their natal region of origin, but not necessarily to their exact natal locality within this region. We hereafter refer to this as 'regional philopatry'. Female sea turtles, which mature after a decade or more, are known from population genetic analyses to exhibit regional philopatry, but most of these studies lack the resolution necessary to determine whether they nest any closer than hundreds or even thousands of kilometres from the beach where they hatched (Bowen & Karl 2007; Lohmann *et al.* 2013; but see Lee *et al.* 2007). There may be reduced geographical specificity in late-maturing species, compared with rapidly maturing ones, simply because of the long time elapsed between birth and first reproduction. One mechanism for homing animals that has been proposed is that they imprint on the geomagnetic field at their birthplace and use this information to return to this site when it comes time for them to reproduce (Lohmann *et al.* 2008). As local characteristics of the geomagnetic field change over time, navigational error is expected to increase as time elapses between imprinting and the return migration (Lohmann *et al.* 2008; Putman *et al.* 2013).

Sharks are typically late-maturing marine fishes in which regional philopatry by females has been inferred from population genetic data for several species (e.g. Keeney *et al.* 2005; Chapman *et al.* 2009a; Tillett *et al.* 2012). There has also been conjecture that finer-scale natal philopatry also occurs in this group (Hueter *et al.* 2004). Many coastal sharks conform to a life history model proposed by Springer (1967) in which adults are segregated from juveniles for most of the year but females make seasonal migrations to discrete coastal nursery areas for parturition. Juveniles either remain in their natal nursery area for several years (in subtropical and tropical regions [e.g., Chapman *et al.* 2009b]) or return there on a regular basis after having seasonally migrated to avoid low water temperatures (in warm temperate regions [e.g. Reyier *et al.* 2008]), before moving into habitat used by subadults and adults. Maternally inherited mitochondrial DNA is commonly structured between nursery sites separated by at least 1000 km in coastal sharks, providing evidence that females give birth in their natal region of origin (Keeney *et al.* 2005; Portnoy *et al.* 2010; Tillett *et al.* 2012). Recent observations that sibling blacktip reef sharks give birth in the same nursery areas in French Polynesia provide indirect evidence of natal philopatry (Mourier & Planes 2013). To date, however, there is no direct evidence that female sharks return to give birth in their exact natal nursery area. This is not surprising given the logistical difficulties associated with tracking late-maturing, mobile marine animals from their birthplace to where they reproduce.

Studies of lemon sharks (*Negaprion brevirostris*) in the largest nursery area (North Bimini) in the Bimini islands, Bahamas (Fig. 1), have offered clues that natal philopatry may occur in sharks. Lemon sharks are large apex predators that mature at total lengths (TL) of 230–240 cm, reached at age 12 or greater (Brown & Gruber 1988). Telemetry studies show that lemon sharks < 90 cm TL are strongly site attached to their natal nursery area and remain in < 1 m depth, typically within 300 m of shore (Morrissey & Gruber 1993). In Bimini, they do not even move between disjunct patches of nursery habitat occurring in North and South Bimini (Fig. 1), let alone venture away from these islands (Gruber *et al.* 2001). Once individuals exceed a size of ~90 cm TL (age 3 or more years), they are less constrained to their inshore natal nursery habitat but remain in the lagoon and coastal areas of Bimini, gradually dispersing from the islands as they grow (Chapman *et al.* 2009b). Most (>90%) subadult individuals approaching maturity that are captured at Bimini are born elsewhere, indicating movement between Bahamian islands, or further afield, occurs during this stage (Chapman *et al.* 2009b). Adult lemon sharks only occur in Bimini in the spring (April-June), with individuals being recaptured or tracked as far as 1000 km from the site of tagging (Fig. 1; Kohler *et al.* 1998; Feldheim *et al.* 2001; Supporting Information). Despite their mobility and the range of appropriate nursery habitat available within 200 km of Bimini (Andros, Berry Islands; see Supporting Information), adult females of uncertain natal origin repeatedly return to Bimini to give birth, typically on a two-year reproductive cycle (Feldheim *et al.* 2002a, 2004). Juvenile lemon sharks that are experimentally displaced several kilometres away from Bimini rapidly navigate back to the exact part of the island where they were caught (Edrén & Gruber 2005), suggesting that they have an innate ability to home to this site.

Here, we analyse genetic profiles of individual lemon sharks sampled from 20 consecutive cohorts (1993–2012) in Bimini to look for the first direct evidence of natal philopatry in sharks. We use both physical captures and genetic reconstructions of adult female sharks to examine natal philopatry at this site. We also provide new insights into the temporal and spatial fidelity of females that repeatedly give birth within the nursery at Bimini.

Methods

Sampling and genotyping of sharks

Newborn and juvenile (<90 cm TL) lemon sharks were intensively sampled in the North Bimini nursery area
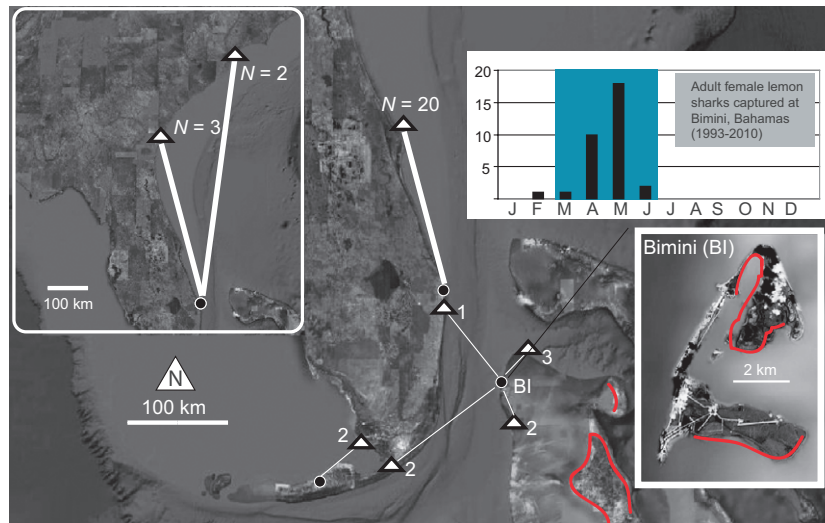
Fig. 1 A synthesis of the movements of tagged or transmittered subadult or adult female lemon sharks in the southeastern United States and The Bahamas. Long distance recapture locations for lemon sharks that were fitted with external tags are shown as white triangles, with the tagging location shown as a black circle: 1 = a subadult female tagged in Bimini in 2006 that was recaptured by a fishermen at Jupiter, FL in 2008 (National Marine Fisheries Service), 2 = recaptures of individuals tagged as juveniles and recaptured at much larger sizes, 3 = Pop-off satellite tag deployment, 6 weeks after female gave birth in Bimini. The thick white lines, in both the main figure and the upper left inset, show minimum dispersal distance recorded for sharks fitted with internal acoustic transmitters that were detected in Vemco receiver arrays from 2008 to 2011 (Supporting Information). Shark capture location (Jupiter, Florida) is shown by the black circle, the locations where detections were recorded are shown as white triangles. The number of transmittered sharks recorded making these movements is provided, all of which were within 1 year of release. Inset (top right): Seasonal presence of adult female lemon sharks captured off Bimini (1993–2010). Capture effort was similar every month throughout the study. The blue area indicates the months when newborn sharks are also observed. Inset (bottom right): Map of Bimini, the red area highlights nursery habitats on both the North and South Islands. Red area highlighted in the main figure represents other nursery habitat available to lemon sharks within 200 km of Bimini.

annually from 1995 to 2012. Our analysis extends back to the 1993 cohort, however, because we caught one- and two-year-old sharks in the 1995 sampling effort. Sampling occurred in June using 180-metre-long, two-metre-deep monofilament gillnets deployed perpendicular from shore. The South Bimini nursery was also sampled opportunistically between 1996 and 2012. All captured sharks were measured to the nearest 0.1 cm for precaudal length (PCL), fork length (FL) and TL, sexed, tagged with a passive integrated transponder (PIT, Destron Fearing, South St. Paul, MN, USA) tag and had a small piece of fin removed and stored in 20% DMSO for genetic analysis. Individuals were released alive after a brief holding period (<7 days). We assume that any individual captured in the nursery that is <90 cm was born locally based on tagging and telemetry data collected at Bimini, showing no emigration occurs prior to this size (Morrissey & Gruber 1993; Gruber *et al.* 2001; Chapman *et al.* 2009b). In many cases, identifying the natal nursery is further strengthened when a group of littermates are captured in the same nursery and/or when individuals or at least one of their known littermates has an open umbilicus at first capture. The umbilicus closes within ~30 days of birth

in lemon sharks (S. Gruber unpublished data) and is therefore diagnostic of a young-of-the-year shark. This feature was noted for all sharks captured from 1997 onwards (Feldheim *et al.* 2002a, 2004; DiBattista *et al.* 2009). All sampled sharks were genotyped at 11 polymorphic microsatellite markers (Feldheim *et al.* 2002a,b, 2004; DiBattista *et al.* 2008, 2009) followed by sibship and parental genotype reconstruction employing the program COLONY version 1.2 (Wang 2004). To reduce genotyping errors, a subset of all samples was rescored by an independent analyst. Individuals that were homozygotes or had weak bands were reamplified up to three times (see DiBattista *et al.* 2008 for more information on details of quality control for this data set).

Documenting natal philopatry

Newborn and juvenile females that were sampled during 1995–1998 could reach the age at first maturity in the later years of the study and were considered our pool of potential returnees. We attempted to detect natal philopatry at Bimini using one of two methods: the direct capture of gravid females entering the Bimini nursery for parturition or detecting the offspring of

returnees sampled in the 2008–2012 cohorts. Near-term females were targeted from mid-April to mid-May when they arrive at Bimini to give birth. Targeted capture of adults is extremely labour-intensive and was only conducted in 2008. Adult lemon sharks approaching or leaving the shallow (<1.5 m) nursery area were spotted by boat-based observers and captured by placing a dip-net in front of it to incite it to bite. A tail rope was then applied, allowing the individual to be held straight alongside the vessel for measurement of length (we report TL to the nearest 0.5 cm), fitted with a National Marine Fisheries Service (NMFS) M-type dart tag (Kohler *et al.* 1998) and tagged with a PIT tag unless they already had one, which would indicate a recapture. All individuals were genotyped at eleven microsatellite loci as described previously (Feldheim *et al.* 2002a,b, 2004; DiBattista *et al.* 2008, 2009). Genetic tagging was also used to determine whether sharks had previously been captured and had shed their PIT and/or NMFS tags (Feldheim *et al.* 2002b). The probability of two individuals having an identical genotype at all 11 loci is estimated to be 1.11×10^{-15} (Feldheim *et al.* 2002b).

COLONY-reconstructed maternal genotypes generated from juveniles captured between 2008 and 2012 were used to determine whether any females born in the early years of our study (1995–1998) came back to Bimini to give birth. Females giving birth at Bimini often return for parturition every 2 years (Feldheim *et al.* 2002a, 2004). As such, we have several maternal ($N = 89$) and paternal ($N = 352$) genotypes that we previously reconstructed from our 1993–2007 cohorts. We included these genotypes as candidate parents in our COLONY runs. We then ran two separate runs of COLONY for each of the 2008–2012 cohorts. In the first run for each cohort, we used these previously reconstructed adult genotypes for the male and female genotype input. Newly reconstructed parental genotypes obtained from the 2008–2012 COLONY results were compared to all female sharks born at Bimini between 1993 and 1998 ($N = 249$). Any matches were considered to be the same individual. COLONY does not fully reconstruct genotypes for adults when there is either monogamy or when there are few offspring sampled from each litter (Wang 2004). Therefore, for the second COLONY run, we also included all female sharks born at Bimini between 1993 and 1998 in the candidate female file. For every run, we used the default parameters in COLONY, with female polygamy and male monogamy [as is generally the case at Bimini (Feldheim *et al.* 2002a, 2004)]. Allelic dropout was set at 0, and error rate was set at 0.005. The probability that a parent was in the pool of candidates was set at 0.005 and 0.2 for the first run and 0.005 and 0.1 for the second run for males and females, respectively. The probability was lower for the second run to account for the additional candidate females from the 1993–1998 cohorts.

Long-term fidelity to specific parturition sites

Using COLONY, we continued to reconstruct parental genotypes from the 2008–2012 cohorts to extend our understanding of how long individual females may exhibit philopatry to certain nursery areas. We also determined whether females used the same discrete patches of nursery habitat that are separated by ~ 5.5 km (North versus South Bimini, Fig. 1) as opposed to using them randomly upon reaching the Bimini islands. It is important to highlight that the females analysed to answer these questions are too old for us to know whether or not they are also exhibiting natal philopatry.

Results

The potential pool of philopatric individuals was composed of all females captured and tagged from the 1993–1998 Bimini cohorts. We know from recapture information that 128 of them survived to at least age two, but only a small number of these are likely to have survived to maturity (see Supplementary Information). Directly recapturing these returnees provided the strongest evidence of natal philopatry. Two large (>240 cm TL) females were captured in the North Bimini nursery area during the 2008 parturition season (Table 1). Neither of these had previously been detected as parents at Bimini. The first was confirmed to be gravid at the time of capture through an ultrasound examination. It lacked a readable PIT tag, but its multilocus microsatellite genotype matched an individual sampled by us in the first year of the study, 1995, when it was 80.0 cm TL (PIT tag number 222D503E69; estimated age 2 years). The COLONY-derived pedigree for 1995 revealed that this shark had six littermates in the Bimini nursery at the time, bolstering evidence that Bimini is its natal site. Subsequent parentage analysis in COLONY for the 2008 Bimini cohort detected one sampled offspring of this female. This neonate (TL=55.5 cm) was captured in June 2008, less than 4 km from where its mother had been captured about 13 years earlier. The second large female caught in 2008 carried a readable PIT tag (4142485114), which had been applied in 1997 at Bimini when the female was a newborn (65.2 cm TL, open umbilicus). This individual was recaptured in the Bimini nursery in 1998 (age 1, 75.7 cm TL) and 1999 (age 2, 90.3 cm TL). We did not, however, sample any of its offspring in 2008. As such, the female may have still been immature or only newly mature when captured or all of its 2008 offspring died prior to

Table 1 Summary of females that exhibited natal philopatry to the Bimini nursery. ID represents the PIT tag number of each female. The individual with two PIT tag IDs was retagged with 45722E0A51 in 2008, as its original tag was not readable. Year of birth indicates the year females were born at Bimini. Year of parturition represents the year each female returned to the Bimini nursery to give birth to its own young

ID	Method of detecting natal philopatry	Year of birth	Year of parturition (no. of pups)
222D503E69/ 45722E0A51	Direct capture followed by parentage assignment	1993	2008 (1)
4142485114	Direct capture (2008); Genotype reconstruction and parentage assignment (2012)	1997	2012 (4)
2236163951	Genotype reconstruction and parentage assignment	1993	2009 (5)
224238692D	Parentage assignment	1997	2011 (4)
2242401964	Genotype reconstruction and parentage assignment	1995	2012 (7)
4142342365	Parentage assignment	1997	2012 (3)

being sampled. This female did give birth to four newborns in 2012 based on COLONY results.

Four more likely cases of natal philopatry were discovered during examination of the reconstructed parental genotypes from COLONY based on the 2009–2012 cohorts (Table 1). The reconstructed genotypes of two individuals were independently matched to the genotypes of individuals from the 1993–1998 Bimini cohorts, which is highly unlikely to occur by chance. In 2009, one reconstructed maternal genotype was independently matched to the composite genotype of an individual that was sampled in 1995 (PIT tag number 2236163951) that was 71.0 cm TL at the time of capture and likely 2 years old. The COLONY-derived pedigree for 1995 revealed one littermate of this individual in Bimini, further reinforcing that Bimini was its natal site. Four of its offspring were captured in the 2009 sampling event, while an additional individual belonging to this litter was caught in 2010 as a one-year-old. An additional maternal genotype reconstructed from seven offspring in the 2012 pedigree independently matched the genotype of an individual captured in 1997 (2242401964). This female was 70.9 cm TL at time of capture, and pedigree analysis indicated that it had three full siblings, all of which were born in 1995.

The two remaining cases were inferred when these individuals were included as candidate parents in COLONY. One individual (224238692D) was initially caught at Bimini in 1997 as a newborn (65.7 cm TL with an open umbilicus). It gave birth to four offspring in 2011, three caught as newborns in 2011 and one caught as a one-year-old in 2012. Another female (4142342365), captured in 1997 as a newborn (62.5 cm TL with an open umbilicus), gave birth to three offspring in 2012.

Consideration of the 2012 cohort provides preliminary insight into how important natal philopatry is among females using Bimini for parturition. Fifteen females produced this cohort, nine of which had previously used Bimini for parturition and are therefore too old to have been born in the 1993–1997 cohorts. It remains unknown whether any of them were born at Bimini. Of 6 'new' (i.e., previously undocumented) females giving birth in North Bimini in 2012, three (50%) were born there (Table 1).

Some females have been returning to Bimini to give birth to their young for the entire course of this study (1993–2012, Fig. 2). In addition, we found that females give birth at discrete locations within the Bimini nursery on a regular basis (Fig. 2). Females returning to Bimini give birth either at the North island ($N = 59$, e.g. females 1–42 in Fig. 2) or at the South island ($N = 6$, e.g. females 43–48 in Fig. 2). There are no examples of a female using both islands for parturition; *without exception*, females were faithful to one nursery site or the other across multiple returns to Bimini. If we consider each philopatric event for every female in our study, there are 268 birthing events (246 at North Bimini and 22 at South Bimini) where the female in question exhibited fidelity to one island or the other.

Discussion

Here, we provide the first direct evidence that some female sharks return to their natal nursery area to give birth (i.e. natal philopatry). Although there are only six cases documented here, we stress the challenges of directly observing this behaviour in late-maturing marine species. There is a great deal of additional nursery habitat on the Great Bahama Bank within ~ 200 km radius of Bimini for females to use. When coupled with how few of the females, we tagged from 1993 to 1997 that are likely to have survived and the high proportion of the 'new' females giving birth in 2012 that were born there (three of six), it is reasonable to hypothesize that this behaviour
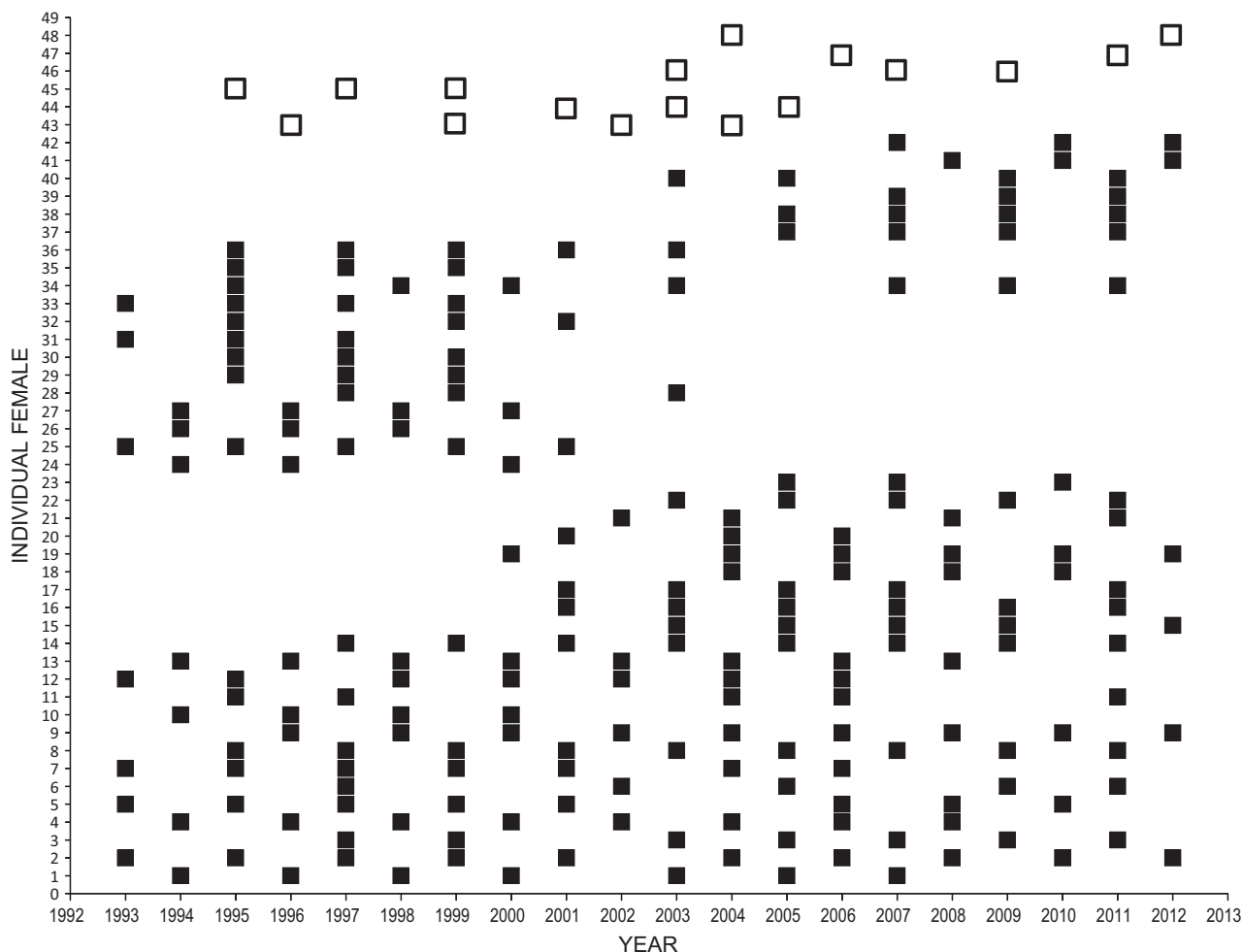
Fig. 2 Philopatric behaviour of genetically reconstructed adult female lemon sharks at Bimini, Bahamas, from 1993 to 2012. A black box above a year indicates that the female gave birth at North Bimini, while an open box above a year indicates the female gave birth at South Bimini. For simplicity, we only included females that gave birth at least three times ($N = 46$), with the exception of two philopatric females that gave birth at the south nursery twice (females 47 and 48).

may be common among adult female lemon sharks at Bimini. If this is indeed the case, natal philopatry will have important implications for long-term sustainability of local nursery areas. Continued sampling will enhance the probability of detecting additional returning females and document whether or not the ones we have detected now start returning on a regular cycle, as the older females of uncertain natal origin have been shown to do at this and an additional site (Fig. 2, Feldheim *et al.* 2002a, 2004; Di-Battista *et al.* 2008).

Previous population genetic studies of large coastal sharks have typically found structure in mitochondrial gene regions over distances of >1000 km (Dudgeon *et al.* 2012), and a few have even found structure on finer scales (Tillett *et al.* 2012). Philopatry to the natal nursery or natal region is frequently discussed as a potential cause of this structure, but it is important to keep in mind the inherent limits of genetic markers for testing

natal philopatry at any spatial scale. First, an absence of structure does not eliminate the possibility that natal philopatry is common. A small amount of contemporary or historical straying can provide enough gene flow to preclude genetic differentiation, as can recent founding events or incomplete lineage sorting (Thorrold *et al.* 2001). Second, the presence of structure can be caused by processes other than natal philopatry, such as biological limitations on dispersal capability or geophysical barriers to gene flow. The advance of the present study is that it directly shows individuals returning to their natal nursery. Future studies on other sharks should employ methods that can together provide direct evidence of natal philopatry (tagging, telemetry or biogeochemical tracers) and couple them with locally focused population genetic studies to further elucidate the geographical specificity of natal philopatry and degree of local population structure in coastal sharks.

The existence of decadal fidelity to nursery sites and natal philopatry by female sharks may lead to some level of population isolation on fine geographical scales. Assessment models that assume large, panmictic regional populations are unlikely to be accurate in forecasting stock status if the population is more structured, especially when the structure is due to behaviour of the critically important adult females (Hueter *et al.* 2004). Models that take the spatial distribution of fishing effort and population structure into account are more appropriate tools for predicting the population dynamics of these species. They could also often benefit from investments in local, spatially explicit conservation measures, such as time-area fishery closures around nursery areas, while females are concentrated in these locations to give birth or the establishment of permanent shark fishery closures over large areas. Conversely, any negative ecological impact stemming from the depletion of these large predators (Heithaus *et al.* 2008) could potentially materialize more rapidly and on a much more local geographical scale than resource managers might assume based on the mobility of sharks. Overall, it is becoming increasingly clear that these imperiled predators have a complex population structure, and some species can benefit from investments in local conservation measures nested within broader international efforts.

Although it is well established that several marine taxa exhibit regional philopatry, much less is known about natal philopatry, especially for late-maturing taxa such as sharks and sea turtles (Bowen & Karl 2007; Lohmann *et al.* 2013). It has been proposed that late-maturing species home back to their natal region to reproduce but either cannot, given changes in the geomagnetic field, or do not, given alternative nursery habitats in the region, navigate back to the exact location (Lohmann *et al.* 2008, 2013). Here, we provide extremely rare direct evidence of this type of geographically exact natal philopatry in a late-maturing marine species, suggesting that sharks are capable of doing so even when there is extensive alternative nursery habitat nearby. Coastal sharks, however, have important advantages over sea turtles when it comes to imprinting on and navigating back to their natal location. Sharks can spend from months to years in, or close proximity to, their natal area (Chapman *et al.* 2009b), and, in more migratory species, sometimes return to it as part of their seasonal migratory cycle (Hueter *et al.* 2004). These traits may allow them to continually refine their ability to relocate the site even as the geomagnetic field and other parameters change over time (Lohmann *et al.* 2008; Putman *et al.* 2013). In contrast, sea turtles immediately leave their natal beach for an extended oceanic phase and do not return until more than a decade has passed (Lohmann *et al.* 2013). Despite potential differences between taxa in geographical specificity, our findings support the emerging paradigm that natal philopatry is widespread in mobile marine vertebrates (Cury 1994).

Acknowledgements

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Data accessibility

Microsatellite, morphological and catch data: Dryad doi:10.5061/dryad.1q9r8.

Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1 Supporting information describing movements of lemon sharks in Florida and The Bahamas and estimates of the number of female sharks born between 1993–1998 surviving to adulthood and the nursery habitat available to them as adults.

Table S1 Maximum-recorded dispersal distances (km) and years of return to tagging site for adult lemon sharks fitted with acoustic transmitters and acoustic transmitters off Jupiter, Florida.

Fig. S1 Islands with lemon shark nursery habitat on the Great Bahama Bank, Bahamas.