

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

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25 **Abstract**

26 Sharks are a globally threatened group of marine fishes that often breed in their natal
27 region of origin. There has even been speculation that female sharks return to their exact
28 birthplace to breed (“natal philopatry”), which would have important conservation
29 implications. Genetic profiling of lemon sharks (*Negaprion brevirostris*) from 20
30 consecutive cohorts (1993-2012) at Bimini, Bahamas showed that certain females
31 faithfully gave birth at this site for nearly two decades. At least six females born in the
32 1993-1997 cohorts returned to give birth 14-17 years later, providing the first direct
33 evidence of natal philopatry in the chondrichthyans. Long-term fidelity to specific
34 nursery sites coupled with natal philopatry highlights the merits of emerging spatial and
35 local conservation efforts for these threatened predators.

36 **Introduction**

37 Philopatry has been defined as the return of individuals to the locality or region
38 where they were born to reproduce (Mayr 1963; Secor 2002). This phenomenon has been
39 demonstrated in several marine vertebrates, including pinnipeds (Baker et al. 1995;
40 Hoffman and Forcada 2012), bony fishes (Thorrold et al. 2001; Rooker et al. 2008) and
41 sea turtles (Bowen & Karl 2006; Lohmann et al. 2013). When common to both sexes, this
42 behavior contributes to the development of closed populations where intrinsic
43 reproduction and recruitment are more important determinants of population dynamics
44 than immigration (Harden Jones 1968; Secor 2002). For this reason, philopatry is
45 fundamental to the stock-unit concept in fisheries management and is an important

46 consideration in conservation planning for threatened and endangered species (Harden
47 Jones 1968; Secor 2002).

48 One important property of philopatry is its geographic specificity, which
49 quantifies how closely individuals return to the site of their birth. This property helps
50 determine the scale at which populations may become closed and therefore identifies the
51 most appropriate scale of stock assessments and management actions. For example,
52 rapidly maturing, anadromous salmonids often return to their exact birthplace (i.e.,
53 tributary) to reproduce, which we hereafter refer to as “natal philopatry” (Harden Jones
54 1968). In many late-maturing marine organisms, however, individuals usually return to
55 their natal region of origin but not necessarily to their exact natal locality within this
56 region. We hereafter refer to this as “regional philopatry.” Female sea turtles, which
57 mature after a decade or more, are known from population genetic analyses to exhibit
58 regional philopatry, but most of these studies lack the resolution necessary to determine
59 whether they nest any closer than hundreds or even thousands of kilometers from the
60 beach where they hatched (Bowen & Karl 2007; Lohmann et al. 2013, but see Lee et al.
61 2007). There may be reduced geographic specificity in late-maturing species, compared
62 to rapidly maturing ones, simply because of the long time elapsed between birth and first
63 reproduction. One mechanism for homing animals that has been proposed is that they
64 imprint on the geomagnetic field at their birthplace and use this information to relocate to
65 this site when it comes time for them to reproduce (Lohmann et al. 2008). Since local
66 characteristics of the geomagnetic field change over time, navigational error is expected
67 to increase as time elapses between imprinting and the return migration (Lohmann et al.
68 2008; Putman et al. 2013).

69 Sharks are typically late-maturing marine fishes in which regional philopatry by
70 females has been inferred from population genetic data for several species (e.g., Keeney
71 et al. 2005; Chapman et al. 2009a; Tillett et al. 2012). There has also been conjecture that
72 finer-scale natal philopatry also occurs in this group (Hueter et al. 2004). Many coastal
73 sharks conform to a life-history model proposed by Springer (1967) in which adults are
74 segregated from juveniles for most of the year but females make seasonal migrations to
75 discrete coastal nursery areas for parturition. Juveniles either remain in their natal nursery
76 area for several years (in subtropical and tropical regions [e.g., Chapman et al. 2009b]) or
77 return there on a regular basis after having seasonally migrated to avoid low water
78 temperatures (in warm temperate regions [e.g., Reyier et al. 2008]), before moving into
79 habitat used by subadults and adults. Maternally inherited mitochondrial DNA is
80 commonly structured between nursery sites separated by at least 1,000 km in coastal
81 sharks, providing evidence that females give birth in their natal region of origin (Keeney
82 et al. 2005; Portnoy et al. 2010; Tillett et al. 2012). Recent observations that sibling
83 blacktip reef sharks give birth in the same nursery areas in French Polynesia provide
84 indirect evidence of natal philopatry (Mourier & Planes 2013). To date, however, there is
85 no direct evidence that female sharks return to give birth in their exact natal nursery area.
86 This is not surprising given the logistical difficulties associated with tracking late-
87 maturing, mobile marine animals from their birthplace to where they reproduce.

88 Studies of lemon sharks (*Negaprion brevirostris*) in the largest nursery area
89 (North Bimini) in the Bimini islands, Bahamas (Fig. 1) have offered clues that natal
90 philopatry may occur in sharks. Lemon sharks are large apex predators that mature at
91 total lengths (TL) of 230-240 cm, reached at age 12 or greater (Brown & Gruber 1988).

92 Telemetry studies show that lemon sharks < 90 cm TL are strongly site attached to their
93 natal nursery area and remain in < 1 m depth, typically within 300 m of shore (Morrissey
94 & Gruber 1993). In Bimini they do not even move between disjunct patches of nursery
95 habitat occurring in North and South Bimini (Fig. 1), let alone venture away from these
96 islands (Gruber et al. 2001). Once individuals exceed a size of ~ 90 cm TL (age 3 or more
97 years) they are less constrained to their inshore natal nursery habitat but remain in the
98 lagoon and coastal areas of Bimini, gradually dispersing from the islands as they grow
99 (Chapman et al. 2009b). Most (> 90%) subadult individuals approaching maturity that are
100 captured at Bimini are born elsewhere, indicating movement between Bahamian islands,
101 or further afield, occurs during this stage (Chapman et al. 2009b). Adult lemon sharks
102 only occur in Bimini in the spring (April-June), with individuals being recaptured or
103 tracked as far as 1,000 km from the site of tagging (Fig. 1; Kohler et al. 1998; Feldheim
104 et al. 2001; Supporting Information). Despite their mobility and the range of appropriate
105 nursery habitat available within 200 km of Bimini (Andros, Berry Islands; see Supporting
106 Information), adult females of uncertain natal origin repeatedly return to Bimini to give
107 birth, typically on a two-year reproductive cycle (Feldheim et al. 2002a, 2004). Juvenile
108 lemon sharks that are experimentally displaced several kilometers away from Bimini
109 rapidly navigate back to the exact part of the island where they were caught (Edrén &
110 Gruber 2005), suggesting that they have an innate ability to home to this site.

111 Here we analyze genetic profiles of individual lemon sharks sampled from 20
112 consecutive cohorts (1993-2012) in Bimini to look for the first direct evidence of natal
113 philopatry in sharks. We use both physical captures and genetic reconstructions of adult
114 female sharks to examine natal philopatry at this site. We also provide new insights into

115 the temporal and spatial fidelity of females that repeatedly give birth within the nursery at
116 Bimini.

117 **Methods**

118 *Sampling and genotyping of sharks*

119 Newborn and juvenile (< 90 cm TL) lemon sharks were intensively sampled in
120 the North Bimini nursery area annually from 1995 to 2012. Our analysis extends back to
121 the 1993 cohort, however, because we caught one and two-year old sharks in the 1995
122 sampling effort. Sampling occurred in June using 180 meter long, two meter deep
123 monofilament gillnets deployed perpendicular from shore. The South Bimini nursery was
124 also sampled opportunistically between 1996 and 2012. All captured sharks were
125 measured to the nearest 0.1 cm for pre-caudal length (PCL), fork length (FL), and TL,
126 sexed, tagged with a passive integrated transponder (PIT, Destron Fearing, South St.
127 Paul, MN, USA) tag and had a small piece of fin removed and stored in 20% DMSO for
128 genetic analysis. Individuals were released alive after a brief holding period (< 7 days).
129 We assume that any individual captured in the nursery that is < 90 cm was born locally
130 based on tagging and telemetry data collected at Bimini showing no emigration occurs
131 prior to this size (Morrissey & Gruber 1993; Gruber et al. 2001; Chapman et al. 2009b).
132 In many cases identifying the natal nursery is further strengthened when a group of
133 littermates are captured in the same nursery and/or when individuals or at least one of
134 their known littermates has an open umbilicus at first capture. The umbilicus closes
135 within ~ 30 days of birth in lemon sharks (S. Gruber unpublished data) and is therefore
136 diagnostic of a young-of-the-year shark. This feature was noted for all sharks captured
137 from 1997 onward (Feldheim et al. 2002a, 2004; DiBattista et al. 2009). All sampled

138 sharks were genotyped at 11 polymorphic microsatellite markers (Feldheim et al. 2002a,
139 2002b, 2004; DiBattista et al. 2008, 2009) followed by sibship and parental genotype
140 reconstruction employing the program COLONY version 1.2 (Wang 2004). In order to
141 reduce genotyping errors, a subset of all samples was rescored by an independent analyst.
142 Individuals that were homozygotes or had weak bands were re-amplified up to three
143 times (see DiBattista et al. 2008 for more information on details of quality control for this
144 dataset).

145 *Documenting natal philopatry*

146 Newborn and juvenile females that were sampled during 1995-1998 could reach
147 the age at first maturity in the later years of the study and were considered our pool of
148 potential returnees. We attempted to detect natal philopatry at Bimini using one of two
149 methods: the direct capture of gravid females entering the Bimini nursery for parturition
150 or detecting the offspring of returnees sampled in the 2008-2012 cohorts. Near term
151 females were targeted from mid-April to mid-May when they arrive at Bimini to give
152 birth. Targeted capture of adults is extremely labor-intensive and was only conducted in
153 2008. Adult lemon sharks approaching or leaving the shallow (<1.5 m) nursery area were
154 spotted by boat-based observers and captured by placing a dip-net in front of it to incite it
155 to bite. A tail rope was then applied, allowing the individual to be held straight alongside
156 the vessel for measurement of length (we report TL to the nearest 0.5 cm), fitted with a
157 National Marine Fisheries Service (NMFS) M-type dart tag (Kohler et al. 1998), and
158 tagged with a PIT tag unless they already had one, which would indicate a recapture. All
159 individuals were genotyped at eleven microsatellite loci as described previously
160 (Feldheim et al. 2002a, 2002b, 2004; DiBattista et al. 2008, 2009). Genetic tagging was

161 also used to determine if sharks had previously been captured and had shed their PIT
162 and/or NMFS tags (Feldheim et al. 2002b). The probability of two individuals having an
163 identical genotype at all 11 loci is estimated to be 1.11×10^{-15} (Feldheim et al. 2002b).

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

183 for the second run for males and females respectively. The probability was lower for the
184 second run to account for the additional candidate females from the 1993-1998 cohorts.

185 *Long-term fidelity to specific parturition sites*

186 Using COLONY, we continued to reconstruct parental genotypes from the 2008-
187 2012 cohorts to extend our understanding of how long individual females may exhibit
188 philopatry to certain nursery areas. We also determined whether females used the same
189 discrete patches of nursery habitat that are separated by ~ 5.5 km (North versus South
190 Bimini, Fig. 1) as opposed to using them randomly upon reaching the Bimini islands. It is
191 important to highlight that the females analyzed to answer these questions are too old for
192 us to know whether or not they are also exhibiting natal philopatry.

193 **Results**

194 The potential pool of philopatric individuals was composed of all females
195 captured and tagged from the 1993-1998 Bimini cohorts. We know from recapture
196 information that 128 of them survived to at least age two, but only a small number of
197 these are likely to have survived to maturity (see Supplementary Information). Directly
198 recapturing these returnees provided the strongest evidence of natal philopatry. Two large
199 (> 240 cm TL) females were captured in the North Bimini nursery area during the 2008
200 parturition season (Table 1). Neither of these had previously been detected as parents at
201 Bimini. The first was confirmed to be gravid at the time of capture through an ultrasound
202 examination. It lacked a readable PIT tag, but its multilocus microsatellite genotype
203 matched an individual sampled by us in the first year of the study, 1995, when it was 80.0
204 cm TL (PIT tag number 222D503E69; estimated age 2 years). The COLONY-derived
205 pedigree for 1995 revealed that this shark had six littermates in the Bimini nursery at the

206 time, bolstering evidence that Bimini is its natal site. Subsequent parentage analysis in
207 COLONY for the 2008 Bimini cohort detected one sampled offspring of this female. This
208 neonate (TL=55.5 cm) was captured in June 2008, less than 4 km from where its mother
209 had been captured about 13 years earlier. The second large female caught in 2008 carried
210 a readable PIT tag (4142485114), which had been applied in 1997 at Bimini when the
211 female was a newborn (65.2 cm TL, open umbilicus). This individual was recaptured in
212 the Bimini nursery in 1998 (age 1, 75.7 cm TL) and 1999 (age 2, 90.3 cm TL). We did
213 not, however, sample any of its offspring in 2008. As such, the female may have still
214 been immature or only newly mature when captured or all of its 2008 offspring died prior
215 to being sampled. This female did give birth to four newborns in 2012 based on
216 COLONY results.

217 Four more likely cases of natal philopatry were discovered during examination of
218 the reconstructed parental genotypes from COLONY based on the 2009-2012 cohorts
219 (Table 1). The reconstructed genotypes of two individuals were independently matched to
220 the genotypes of individuals from the 1993-1998 Bimini cohorts, which is highly unlikely
221 to occur by chance. In 2009, one reconstructed maternal genotype was independently
222 matched to the composite genotype of an individual that was sampled in 1995 (PIT tag
223 number 2236163951) that was 71.0 cm TL at the time of capture and likely two years old.
224 The COLONY-derived pedigree for 1995 revealed one littermate of this individual in
225 Bimini, further reinforcing that Bimini was its natal site. Four of its offspring were
226 captured in the 2009 sampling event while an additional individual belonging to this litter
227 was caught in 2010 as a one-year-old. An additional maternal genotype reconstructed
228 from seven offspring in the 2012 pedigree independently matched the genotype of an

229 individual captured in 1997 (2242401964). This female was 70.9 cm TL at time of
230 capture and pedigree analysis indicated it had three full siblings, all of which were born
231 in 1995.

232 The two remaining cases were inferred when these individuals were included as
233 candidate parents in COLONY. One individual (224238692D) was initially caught at
234 Bimini in 1997 as a newborn (65.7 cm TL with an open umbilicus). It gave birth to four
235 offspring in 2011, three caught as newborns in 2011 and one caught as a one-year-old in
236 2012. Another female (4142342365), captured in 1997 as a newborn (62.5 cm TL with an
237 open umbilicus), gave birth to three offspring in 2012.

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

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

252 at South Bimini) where the female in question exhibited fidelity to one island or the
253 other.

254 **Discussion**

255 Here we provide the first direct evidence that some female sharks return to their
256 natal nursery area to give birth (i.e., natal philopatry). Although there are only six cases
257 documented here, we stress the challenges of directly observing this behavior in late-
258 maturing marine species. There is a great deal of additional nursery habitat on the Great
259 Bahama Bank within ~ 200 km radius of Bimini for females to use. When coupled with
260 how few of the females we tagged from 1993-1997 that are likely to have survived and
261 the high proportion of the “new” females giving birth in 2012 that were born there (three
262 of six), it is reasonable to hypothesize that this behavior may be common among adult
263 female lemon sharks at Bimini. If this is indeed the case, natal philopatry will have
264 important implications for long-term sustainability of local nursery areas. Continued
265 sampling will enhance the probability of detecting additional returning females and
266 document whether or not the ones we have detected now start returning on a regular
267 cycle, as the older females of uncertain natal origin have been shown to do at this and an
268 additional site (Fig. 2, Feldheim et al. 2002a, 2004; DiBattista et al. 2008).

269 Previous population genetic studies of large coastal sharks have typically found
270 structure in mitochondrial gene regions over distances of > 1,000 km (Dudgeon et al.
271 2012) and a few have even found structure on finer scales (Tillett et al. 2012). Philopatry
272 to the natal nursery or natal region is frequently discussed as a potential cause of this
273 structure, but it is important to keep in mind the inherent limits of genetic markers for
274 testing natal philopatry at any spatial scale. First, an absence of structure does not

275 eliminate the possibility that natal philopatry is common. A small amount of
276 contemporary or historical straying can provide enough gene flow to preclude genetic
277 differentiation, as can recent founding events or incomplete lineage sorting (Thorrold et
278 al. 2001). Second, the presence of structure can be caused by processes other than natal
279 philopatry, such as biological limitations on dispersal capability or geophysical barriers to
280 gene flow. The advance of the present study is that it directly shows individuals returning
281 to their natal nursery. Future studies on other sharks should employ methods that can
282 together provide direct evidence of natal philopatry (tagging, telemetry or
283 biogeochemical tracers) and couple them with locally focused population genetic studies
284 to further elucidate the geographic specificity of natal philopatry and degree of local
285 population structure in coastal sharks.

286 The existence of decadal fidelity to nursery sites and natal philopatry by female
287 sharks may lead to some level of population isolation on fine geographic scales.
288 Assessment models that assume large, panmictic regional populations are unlikely to be
289 accurate in forecasting stock status if the population is more structured, especially when
290 the structure is due to behavior of the critically important adult females (Hueter et al.
291 2004). Models that take the spatial distribution of fishing effort and population structure
292 into account are more appropriate tools for predicting the population dynamics of these
293 species. They could also often benefit from investments in local, spatially explicit
294 conservation measures, such as time-area fishery closures around nursery areas while
295 females are concentrated in these locations to give birth or the establishment of
296 permanent shark fishery closures over large areas. Conversely, any negative ecological
297 impact stemming from the depletion of these large predators (Heithaus et al. 2008) could

298 potentially materialize more rapidly and on a much more local geographic scale than
299 resource managers might assume based on the mobility of sharks. Overall, it is becoming
300 increasingly clear that these imperiled predators have a complex population structure, and
301 some species can benefit from investments in local conservation measures nested within
302 broader international efforts.

303 Although it is well established that several marine taxa exhibit regional
304 philopatry, much less is known natal philopatry, especially for late-maturing taxa such as
305 sharks and sea turtles (Bowen & Karl 2007; Lohmann et al. 2012). It has been proposed
306 that late-maturing species home back to their natal region to reproduce but either cannot,
307 given changes in the geomagnetic field, or do not, given alternative nursery habitats in
308 the region, navigate back to the exact location (Lohmann et al. 2008, 2013). Here, we
309 provide extremely rare direct evidence of this type of geographically exact natal
310 philopatry in a late-maturing marine species, suggesting that sharks are capable of doing
311 so even when there is extensive alternative nursery habitat nearby. Coastal sharks,
312 however, have important advantages over sea turtles when it comes to imprinting on and
313 navigating back to their natal location. Sharks can spend from months to years in, or
314 close proximity to, their natal area (Chapman et al. 2009b), and, in more migratory
315 species, sometimes return to it as part of their seasonal migratory cycle (Hueter et al.
316 2004). These traits may allow them to continually refine their ability to relocate the site
317 even as the geomagnetic field and other parameters change over time (Lohmann et al.
318 2008; Putman et al. 2013). In contrast, sea turtles immediately leave their natal beach for
319 an extended oceanic phase and do not return until more than a decade has passed
320 (Lohmann et al. 2013). Despite potential differences between taxa in geographic

321 specificity, our findings support the emerging paradigm that natal philopatry is
322 widespread in mobile marine vertebrates (Cury 1994).

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434 **Data Accessibility:**

435 Microsatellite data will be deposited into Dryad.

436 **Author Contributions:**

437 SHG, MVA, EKP, DDC, KAF contributed funding support and materials to the project.

438 All fieldwork was organized by SHG. Samples and field data were collected by SHG,

439 DDC, SAK, JDD, and KAF. Data collection and analysis was performed in the labs of

440 KAF, APH, MVA, and DDC. Tracking data were compiled by SAK and SHG.

441 Microsatellite data analysis was performed by KAF, JDD, and DDC. Survivorship

442 analysis was performed by EAB. KAF, JDD and DDC wrote the paper. All other authors

443 edited the manuscript.

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445 **Figure legends**

446 **Fig. 1.** A synthesis of the movements of tagged or transmitterd subadult or adult female

447 lemon sharks in the southeastern United States and The Bahamas. Long distance

448 recapture locations for lemon sharks that were fitted with external tags are shown as

449 white triangles, with the tagging location shown as a black circle: 1= a subadult female

450 tagged in Bimini in 2006 that was recaptured by a fishermen at Jupiter, FL in 2008

451 (National Marine Fisheries Service), 2= recaptures of individuals tagged as juveniles and

452 recaptured at much larger sizes, 3= Pop-off satellite tag deployment, six weeks after

453 female gave birth in Bimini. The thick white lines, in both the main figure and the upper

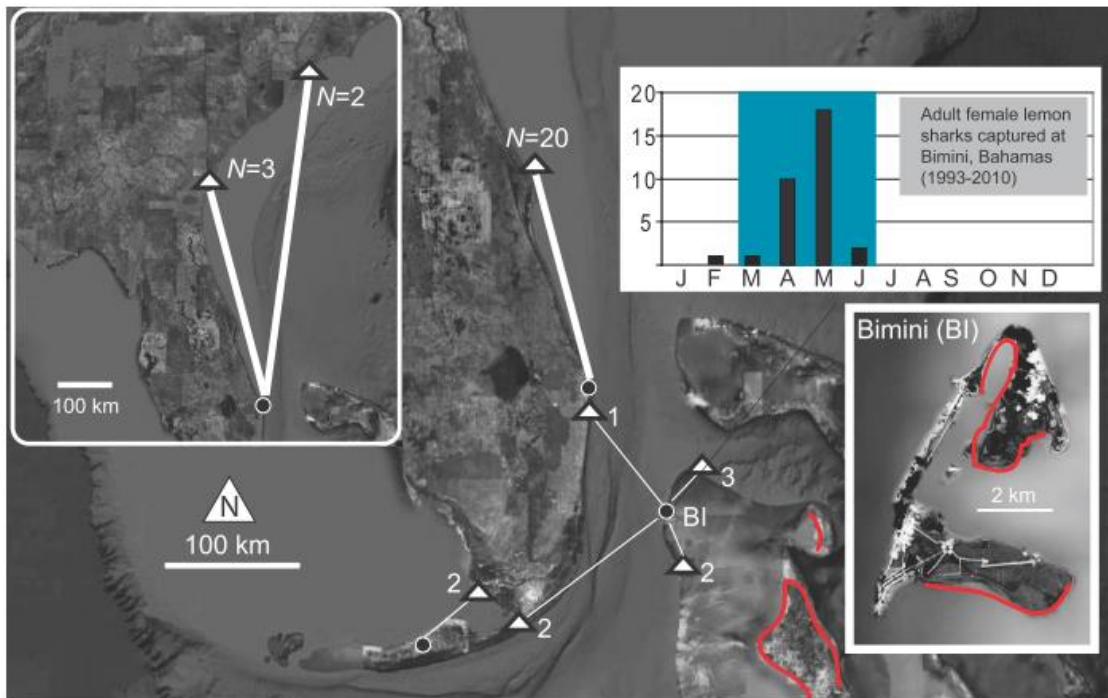
454 left inset, show minimum dispersal distance recorded for sharks fitted with internal

455 acoustic transmitters that were detected in Vemco receiver arrays from 2008-2011

456 (Supporting Information). Shark capture location (Jupiter, Florida) is shown by the black

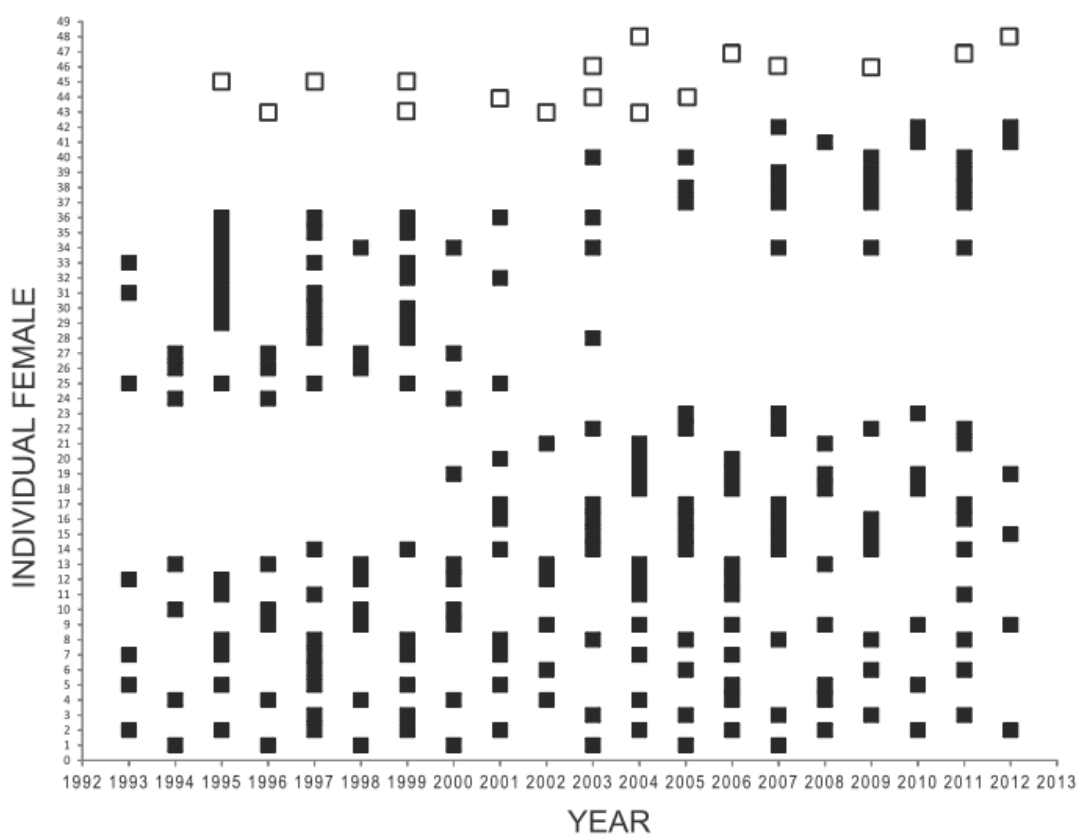
457 circle, the locations where detections were recorded are shown as white triangles. The

458 number of transmittered sharks recorded making these movements is provided, all of
 459 which were within 1 year of release. Inset (top right): Seasonal presence of adult female
 460 lemon sharks captured off Bimini (1993-2010). Capture effort was similar every month
 461 throughout the study. The blue area indicates the months when newborn sharks are also
 462 observed. Inset (bottom right): Map of Bimini, the red area highlights nursery habitats on
 463 both the North and South Islands. Red area highlighted in the main figure represents
 464 other nursery habitat available to lemon sharks within 200 km of Bimini.
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471 **Fig. 2.** Philopatric behavior of genetically reconstructed adult female lemon sharks at
 472 Bimini, Bahamas from 1993 to 2012. A black box above a year indicates that the female
 473 gave birth at North Bimini while an open box above a year indicates the female gave
 474 birth at South Bimini. For simplicity, we only included females that gave birth at least
 475 three times (N=46), with the exception of two philopatric females that gave birth at the
 476 south nursery twice (females 47 and 48).



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483 **Table 1.** Summary of females that exhibited natal philopatry to the Bimini nursery. ID
 484 represents the PIT tag number of each female. The individual with two PIT tag IDs was
 485 retagged with 45722E0A51 in 2008, as its original tag was not readable. Year of birth
 486 indicates the year females were born at Bimini. Year of parturition represents the year
 487 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 (# 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)

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