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Homing ability of young lemon sharks, *Negaprion brevirostris*

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Synopsis

We carried out the first experimental study testing an elasmobranch's ability to return home. We displaced juvenile lemon sharks, *Negaprion brevirostris,* 4–16 km from their observed home ranges at Bimini Islands, Bahamas during daylight and at night. We tracked all sharks except one back to the Bimini Islands and most returned to their home ranges observed before displacement. Even sharks displaced to a site closer to another island with suitable habitat for young lemon sharks returned to their home ranges at Bimini Islands. Sharks displayed a preferred compass direction (PCD) toward the east as their first swimming direction after release, suggesting an innate sense of direction. This bearing was followed shortly afterwards by a home-oriented direction. Swimming speeds prior to reaching shore were approximately twice as fast than the usual cruising speed reported for juvenile lemon sharks. The return of young (0–2 years), inexperienced sharks to their original home range indicate high site fidelity and an ability to home.

Introduction

Homing, as it applies to orientation and navigation in animals, has been defined in many ways. Gerking (1959) established a general definition of homing in fishes, stating that 'homing refers to the choice that a fish makes between returning to a place formerly occupied instead of going to other equally probable places'.

Homing is widespread among fishes (Hasler et al. 1958, Grunning 1959, Schmidt-Koenig 1975, Leggett 1977, Quinn & Dittman 1992) and other vertebrates (Wallraff et al. 1982, Luschi et al. 1998), but it has yet to be experimentally demonstrated for any elasmobranch species. Much of the homing research has been conducted using terrestrial animals – mainly birds and, in particular, the homing pigeon (Wallraff et al. 1982, Papi 1986, 1990). Like birds, fishes are highly mobile in three dimensions. Thus, Wallraff (1984) suggested that birds and fishes might have similar mechanisms of orientation when using similar environmental clues.

While methods such as mark-recapture, telemetry, and the observation of seasonal abundance patterns can provide insight into migration and orientation (Baker 1978, Quinn 1984, Nelson 1990), only displacement experiments can conclusively resolve questions concerning the ability to orient and navigate (Baker 1978).

Displacement involves removing an animal from its known home range and releasing it far enough away to be in unfamiliar surroundings. According to Morrissey & Gruber (1993a, b) juvenile lemon sharks confine their activity to water depths up to 50 cm near mangrove-fringed shorelines where they are born. The mangrove root system provides a nursery, feeding ground and a haven from predators. One important consideration when displacing an animal could be that the animal is transported so far from home that the motivation to return is essentially lost which could prevent homing. In addition to the confounding effects of motivation, the farther an animal is taken from its home, the greater the probability that small, initial navigational inaccuracies will cause it to miss the home area if and when it tries to return (Baker 1978). Finally, the longer a small lemon shark remains in open water, the greater its chances of falling prey to larger sharks which are common in the study area (Morrissey & Gruber 1993a).

Lemon sharks are believed to be philopatric (Hueter 1998, Feldheim et al. 2001, 2002) and the females are believed to return to their natal nursery to give birth (Gruber 1982). To return to its natal ground, an animal must have homing mechanisms. As a first step in addressing philopatry, we carried out an experimental study to determine whether young lemon sharks returned home when experimentally displaced. Part of the findings in the present study is included in a review paper on ultrasonic telemetry studies on sharks (Sundström et al. 2001).

Materials and methods

Study area

We carried out this study in the waters around Bimini, Bahamas, a cluster of three subtropical islands on the western edge of Great Bahamas Bank, approximately 86 km east of Miami, Florida. The Bimini Islands are low in elevation, have areas covered with mangroves and are arranged in a triangle enclosing Bimini Lagoon (Figure 1). The lagoon covers an area of about 21 km^2 with a tidal range of 0.75–1.0 m and an mean depth of 1 m at mid-tide (Bathurst 1967). The Gulf Stream, approximately 80 km wide and 750 m deep, flows northward about 2 km west of Bimini Islands, with a velocity up to 1.7 m s^{-1}. There is a prevailing east southeast current and a southeastern wind of 5–15 kt in the area.

We conducted homing tests mainly on the expansive sand banks lying to the north, south and east of the Bimini Islands. While contiguous with the sharks' home ranges, these offshore areas lack

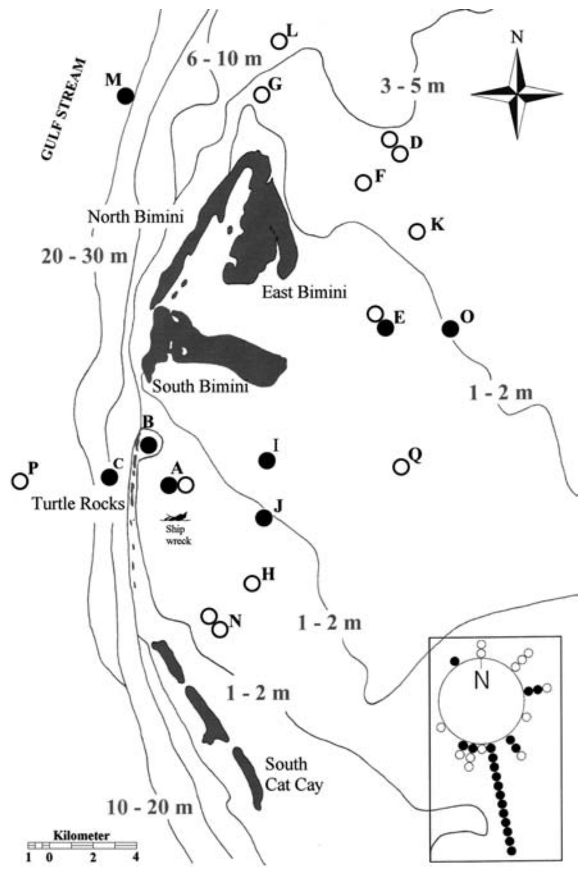

Figure 1. Map of the Bimini Islands complex showing the water dept around the islands and Cat Cays, the closest larger islands to Bimini, consisting of two small cays. Seventeen release sites (A–Q) are marked for the two groups of displaced sharks from South Bimini (closed circles) and East Bimini Lagoon (open circles). Twelve sharks from South Bimini were released at site A, the only site with more than two releases. The circle diagram illustrates the distribution of the release sites in relation to the direction of the sharks' home ranges.

the resources and conditions for survival of juvenile lemon sharks.

The Cat Cays, approximately 13 km south of the Bimini Islands, are the closest habitable islands for these sharks (see Figure 1). The southernmost island in the group has an area of less than 4 km^2 and possesses physical and biological resources (personal observations) similar to those described for Bimini Islands by Morrissey & Gruber (1993a); thus it could support a population of young lemon sharks. To determine whether lemon sharks were using the site, we set gill nets in the island's very small mangrove area and caught two individuals: a young-of-the-year and a 3–4 year old (age estimated following Brown & Gruber 1988). Additionally, we observed several subadult lemon sharks at the island.

Telemetry equipment

We attached ultrasonic (70–79 kHz) cylindrical transmitters (XTAL-87; Sonotronics Inc.) measuring 16 × 66 mm to the base of the first dorsal fin of the sharks. Each transmitter was individually coded by a unique pulse interval and frequency. When two or more sharks were heard at the same time, it was thus possible to distinguish them by ping interval and frequency. Transmitter weight in water was 9 g and with two 2 × CR1/3N, 6 V batteries, the nominal life with continuous transmission was 40 days. Transmitter output was monitored with direct-conversion type manual receivers (USR-5; Sonotronics Inc.). The receiver was attached to a directional hydrophone (DH-2 Sonotronics Inc.). The hydrophone had a sensitivity of 84 dB (re 1 microbar at 1 m) and a beam width of ±6° at half power points (Sonotronic specifications). The range of each transmitter was calibrated to approximately 300 m on a calm day in water 1.5 m deep over a flat sand bottom.

Sample size

We conducted homing trials on 32 individual lemon sharks (13 males and 19 females), 1.4–5.1 kg (mean weight 2.6 kg ± 1.0), ranging in precaudal length (L_{PC}) from 50.0 to 76.9 cm (mean length 60.6 cm ± 7.8). Based on their L_{PC} the sharks were estimated to be between 0 and 2 years old (Brown & Gruber 1988). We chose juvenile sharks for the study because they: (1) are numerous in the study area; (2) maintain well known and relatively small home ranges (Morrissey & Gruber 1993b); and (3) could be captured, handled, and transported as required by the experimental protocol.

Capture of the sharks

We captured juvenile lemon sharks in 90-m long × 1.4-m deep, bottom-set, monofilament gill nets (square mesh size of 50 mm), deployed perpendicular to the shore line. We allowed each captured shark to recover for a period of more than 12 h in a 3 m diameter, fenced pen, placed near the capture site. We then recaptured sharks with dip nets, fitted them with a transmitter and released them after a minimum 2 h recovery after attachment of a transmitter. They were tracked over several days to determine their home ranges and recaptured for displacement trials (see below).

Tagging procedures

We implanted a sub-dermal miniature, passive-integrated transponder tag (PIT tag, Destron Fearing Inc.), shown to induce little stress compared with other commonly used tags (Manire & Gruber 1991), intramuscularly below the shark's first dorsal fin for later identification.

For transmitter attachment, we placed the shark in a trough made from 150 mm diameter PVC pipe cut in half, 120 cm long and with enough water to cover the body. This way the shark could be handled easily and still ventilate its gills. To attach the transmitter, we made two holes through the fin base of the fin by piercing the first dorsal fin with a 2.5 mm (lumen diameter) hypodermic needle. We threaded a 7 kg – test monofilament line through each hole of the fin base and through the end of the transmitter. We secured the monofilament line to the transmitter with metal crimps. We attached a thin plastic backing plate covered with a piece of neoprene with the monofilaments on the other side of the fin. The shark's dorsal fin was thus sandwiched between the transmitter and the plastic plate. The monofilaments were melted into a knot on the plastic-plate side where two thin corrodible discs of mild steel prevented the monofilaments from pulling through the fin. In case a shark was to disappear, the transmitter would eventually fall off because the hole in the metal plates would eventually rust through allowing the monofilaments to pull through the backing plate and the fin. The tagging procedures were carried out without any anesthesia. We released all sharks at the capture site after a minimum 2 h recovery from surgery in the fenced pen.

Home range

We recorded the sharks' location opportunistically in relation to tide close to the mangroves using a handheld GPS (Global Positioning System) for at least 3 days prior to any displacement. While we tracked some sharks continuously, we relocated others every 4–6 h. We recaptured telemetered juveniles with the gill net, replaced them in the pen and fed them prior to displacement. The displacement trials were weather-dependent and thus, some sharks remained in the pens for several days before being displaced. We fed these individuals 200 g cut fish once every 48 h.

Displacement

We carried out displacement trials between October 1997 and August 1998. We used a 4-m skiff to displace sharks 4–16 km from their home range and subsequently track them. Transportation to the displacement site took 20–45 min. To reduce stress during transport, we placed sharks in a 100 l container of continuously aerated seawater, which was partially exchanged with new water every 5 min. The container was not covered during transportation.

Geographic distributions of the release sites were chosen randomly to maximize coverage, though displacement trials to the Gulf Stream were limited due to the precaution with the small tracking vessels in the Stream day as well as night. The circle diagram in Figure 1 shows the distribution of release sites in relation to the direction of the sharks' observed home ranges. We released 12 sharks at site A. We released only one or two sharks at 16 other release sites (Figure 1). We displaced three sharks to a point closer to Cat Cay than to Bimini Islands (release sites H and N, Figure 1).

Once a displacement site was reached, the shark was handed to a diver who released it in an arbitrary direction. Two divers at the surface then followed and observed the shark for approximately 30 min to observe its behavior during the early stages of orientation for 22 of 32 sharks. Sharks released at night carried a chemical 'light stick', a plastic cylinder of 25 × 3 mm attached to the transmitter, so that the shark's position could be observed by divers from a distance. Divers reported the compass bearings of the shark every time its direction changed. While divers followed the shark, the tracking vessel stayed within a distance of 5–30 m of the divers until the 30 min was up or the divers lost visual contact with the shark, at which time the tracking vessel took over. During displacement trials the tracking vessel followed each shark continuously, if possible, until it reached the border of its previously observed home range. Some sharks were tracked for longer to ensure that they stayed in their home range and did not just move through it. Subsequently all sharks were recaptured and had their transmitter removed. The position of the vessel was recorded every 5 min using a handheld GPS receiver. Special care was taken to maintain a 'buffer zone' of at least 100 m between shark and skiff to lessen any effects on the shark's behavior (Banner 1967, Stasko & Buerkle 1975, Myrberg 1978) except during the first 30 min. (i.e. when divers were in the water). This 'buffer-zone' could be maintained relatively precisely because the transmitter signal has an echo effect if the shark came within 100 m of the hydrophone.

Collection of environmental data

The direction and speed of the current were determined at the time of release using a propeller-type current meter (General Oceanics Inc.). While tracking was in progress, water depth was measured with a 2 m long graduated pole every 15 min. Water depths beyond 2 m were estimated by the observer. Cloud cover and wind direction and speed were recorded every hour using a hand-held anemometer (Davis Instruments Inc.).

Statistical analysis

Homing behavior of an individual was assessed by (1) the 'first swimming direction' of the shark immediately after release until the first change of course, which normally occurred within the first 1–2 min; (2) 'subsequent bearing', defined as the bearing between the release site and the position of the shark 1 h after release; (3) 'first straight bearing', determined by tracking vessel is defined as the first course of half an hour duration that did not deviate more than 5% from a straight line; (4) the rate of movement (ROM) between GPS fixed points; (5) the total time for the shark to return to its home range; (6) a regression analysis between displacement distance and homing time; and (7) success in returning to the home range.

We analyzed variables 1–3 using circular statistics to compare the distributions of vectors in relation to the release sites and geographic north. We used the Rayleigh Statistic (Batschelet 1981) to test whether each shark's compass bearings differed significantly from random. Circular statistics were also used to test the shark's orientation within the first hour of release. We divided the compass direction for each shark into 10-min intervals. The mean vector (r) was then calculated for each shark using the following equation:

$$r = (x^2 + y^2)^{-1}$$

where

$$x = \sum_{i=1}^{n} \cos v_i / n$$

$$y = \sum_{i=1}^{n} \sin v_i / n$$

v_i is the swimming direction for each 10-min interval and n is the number of those intervals. Vector values near 1 represent a straight course.

We used ArcView 3.1 to map the location of the sharks. We used all locations for each shark in the home range calculation due to limited days of data collection. We calculated home range size using the adaptive kernel method (Seaman & Powell 1996) using the ArcView extension HRE v. 0.9 (Rodgers & Carr 1999)[1]. We calculated a minimum convex polygon and the 50 and 90% probability contours of the home ranges.

We calculated movement rates of each shark by dividing the distance traveled between each fix point by the time it took to traverse that distance. This is referred to as point-to-point swimming speed, or rate-of-movement (ROM). A major problem when estimating ROM involved the accuracy of fixing a shark's position. The position of the tracking vessel was only an approximation of the shark's true position. With GPS fixes and a directional hydrophone, the accuracy of the shark's position could be established to within about 200 m. As sharks are not always likely to swim in straight lines between fix-points, ROM is an underestimation of the actual swimming speed. We calculated average ROM using 5-min intervals between fixes for each shark from release until the shark reached the shore of Bimini (open water) and along the shoreline of Bimini until the shark reached its home range (near shore). By dividing ROM with the shark total length (TL), the speed is given in body lengths per second (bl s^{-1}).

Results

Tracking records

Sharks were either caught in East Bimini Lagoon (EBL) or south of South Bimini (SB). They maintained shore-fringing home ranges with broad overlap. Figure 2 shows examples of home ranges of three individuals (shark #1, #10 and #14), with no overlap. Home ranges were only calculated for

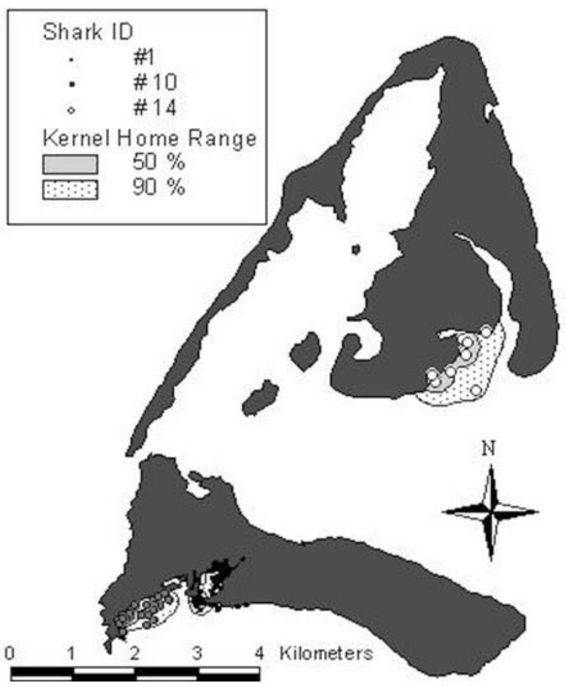

Figure 2. The 90 and 50% Kernel home ranges of three sharks: #1 (filled circles), #10 (filled triangles) and #14 (open circles). Each point represents the individual sharks' location recorded opportunistically in relation to tide close to the mangroves for at least three days prior to any displacement. More locations were collected for the sharks at South Bimini than in East Bimini Lagoon.

[1]Rodgers, A.R. & A.P. Carr. 1999. HRE: The Home Range Extension for Arc View. Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, Canada. http://www.blueskytelemetry.com/hre.asp#dataa.

12 sharks, nine from SB and three from EBL, due to limited data for the rest of the sharks. The average 90% probability Kernel home range was 0.51 km^2 (0.11 SE, n = 120). Sharks at SB had a much smaller home range (0.35 km^2, SE = 0.11, n = 9) than sharks in EBL (0.97 km^2, SE = 0.07, n = 3). These differences in home range size could have been caused by the limited data set for each shark in the EBL. Kernel estimators are very sensitive to outliers and tend to overestimate home range from smaller samples of locations (Seaman & Powell 1996). The data set for EBL sharks contained 11–12 locations for each shark, whereas the data set for SB sharks contained between 10 and 90 locations for each shark.

All but one shark (#31), released in the Gulf Stream, were tracked to the Bimini Islands, 22 within 12 h (Table 1). We tracked five to other areas around the islands, while 26 (81%) returned to their previously observed home ranges,.

Thus, although we attempted to estimate homing time for the 26 sharks that returned to their previously observed home range, we only obtained precise estimates of homing time for 12 individuals (eight females and four males). A linear regression model predicting displacement distance as a function of homing time for these 12 sharks showed that homing time increased with displacement distance (homing time = 64.135 × displacement distance (km)−33.479). The intercept was −33.479

Table 1. Recruitment data for 33 lemon sharks (*Negaprion brevirostris*).

Shark ID	Sex	L_{PC}	Weight (bls)	Displacement distance (km)	Time to shore (h:min)	Time to HR (h:min)
# 1	M	50.0	3.00	4,23	05:52	< 12:32
# 2	F	60.0	5.50	3,91	11:51	27:50
# 3	M	60.5	5.25	4,22	< 13:40	< 13:40
# 4	F	56.0	4.25	4,20	< 11:39	< 11:39
# 5	F	56.0	4.25	4,26	02:58	04:20
# 6	F	74.0	11.0	4,00	01:40	01:40
# 7	M	60.5	5.75	4,09	03:55	04:35
# 8	M	54.9	4.20	4,09	04:49	04:49
# 9	M	58.6	5.00	3,99	< 12:40	< 12:40
# 10	F	61.0	4.50	6,08	< 3:36	< 03:36
# 11	F	57.3	4.00	4,26	09:37	< 24:35
# 12	F	57.3	4.00	4,08	06:20	< 22:00
# 13	M	76.3	11.25	5,90	01:10	< 9:12
# 14	F	57.8	5.75	8,01	09:28	09:28
# 15	F	58.5	5.25	6,12	04:33	05:03
# 16	F	76.9	10.00	6,26	< 33	< 33
# 17	M	58.0	5.40	7,45	03:09	06:39
# 18	F	57.3	5.50	9,30	10:11	–
# 19	F	67.4	5.75	4,78	02:40	02:40
# 20	F	61.5	5.50	6,34	06:33	07:58
# 21	M	51.3	3.50	4,76	< 46:51	< 46:51
# 22	F	61.6	5.00	9,46	02:04	–
# 23	M	51.5	3.50	8,84	< 185:35	–
# 24	F	60.0	5.30	7,65	03:58	04:18
# 26	F	56.0	4.40	10,02	< 117:21	< 117:21
# 27	M	59.4	5.50	11,31	< 47:51	–
# 28	F	69.4	7.70	16,08	< 165:16	< 165:16
# 29	M	63.6	6.60	15,87	< 141:38	< 141:38
# 30	F	54.9	4.00	12,96	09:38	11:33
# 31	M	51.5	3.50	13,40	–	–
# 32	F	70.5	8.20	13,10	07:54	–
# 33	M	52	3.40	8,89	11:28	11:28

L_{PC} = precaudal length.

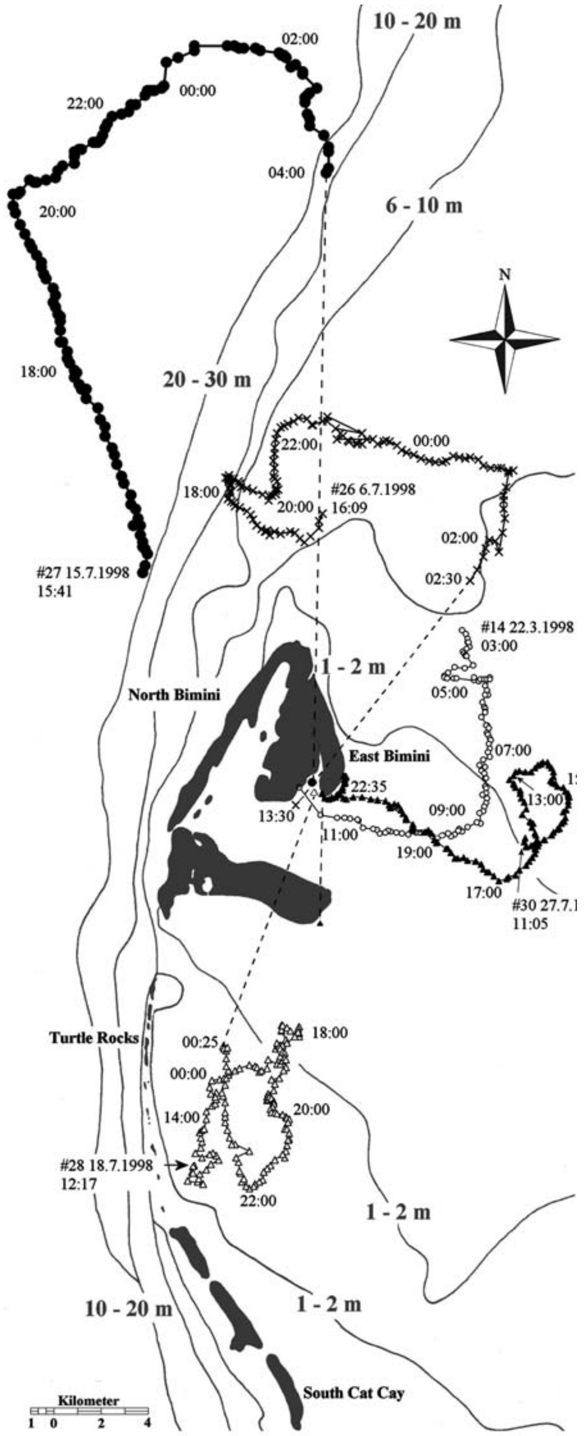

Figure 3. Homing path of five lemon sharks – #14 (open circles), #26 (crosses), #27 (filed circles), #28 (open triangles) and #30 (filed triangles). Shark #30 was caught near the pond south of South Bimini (SB) and shark #14, 26, 27 and 28 were caught in East Bimini Lagoon (EBL). Each track point represents a fix point with an interval of 5 min. The broken line on the graph indicates that the trackers lost the transmitter signal of #26, 27 and 28 but the sharks were later found in EBL. Shark #30 was tracked to EBL but the transmitter was later relocated on the sand bottom at the southeast corner of SB. Release sites are marked with shark number, release date and time of release.

± 273.29 (95% CI, $p = 0.79$, n = 12). The slope was 64.135 ± 0.007 (95% CI, $p = 0.01$, n = 12). Sample size was too small to compare homing times between males and females, so we did not attempt to do this.

Homing performance did not appear to depend on body size based on the very poor correlation between body size of the sharks and time to shore ($R^2 = 0.001$). Examples of homing behavior are shown in Figure 3. We chose these sharks to show the homing tracks from five different release sites. Many homing tracks were terminated before the sharks reached their home ranges at Bimini Islands as contact with the sharks were lost due to rains or rough sea and high ambient noise. Search teams were subsequently sent out to search for the sharks around the Bimini Islands. Shark #14 (open circles) was displaced 8 km northeast of its home range in EBL (release site D, Figure 1) at 3:00 h and returned within 10 h back to EBL where it was subsequently caught. Shark #26 (crosses), also caught at EBL, were released 4.25 km north of the Bimini Islands (release site L, Figure 1) at 16:06 h. The shark swam further north and east for 8 h before it reverted the course and swam towards Bimini. However, at 02:30 h, contact with the shark was lost due to rough seas and high ambient noise. It was relocated and recaptured in EBL 5 days later. Shark #28 (open triangles) was caught in EBL and displaced 6 km south of SB (16 km from its observed home range) closer to Cat Cay than the Bimini Islands (12:17 h, release site H, Figure 1). This shark was heading south for the first 20 min where it turned around and swam north–northeast for approximately 5 h. The shark then changed course again, assuming a southern course for 4½ h. The shark changed its course once again, at the same latitude, as previously, to a northerly course straight towards SB but contact with the shark was lost due to rain and high ambient noise. It was relocated and recaptured in EBL a week later. Shark #30 (filled triangles) was caught at SB and displaced 6.7 km

East of the Bimini Islands at 11:20 h (release site O, Figure 1). The shark swam in a clockwise circle north of its release site followed a straight course towards East Bimini. The shark was still in EBL 2 days later but recapture of the shark failed. The transmitter was relocated 2 days later on the sandy bottom at the southeast corner of SB, 7 days after transmitter attachment. No monofilament was attached to the transmitter, which might indicate that the transmitter had fallen of by it self as the shark swam towards its home range at SB. Shark #27 (filled circles), originally caught at SB, was displaced 5.6 km northwest of North Bimini (at 15:41 h, release site M, Figure 1), 11.3 km from its observed home range. The shark showed a clear northerly course but changed its heading 20 km northwest of Bimini, moving directly northeast. By 04:00 h the next morning, the shark had reversed course and was heading south toward Bimini. However, at that time, contact with the shark was lost due to rough seas and high ambient noise. It was relocated in EBL the next day at 15:30 h where several visuals on the shark were made. Attempt to recapture the shark failed. We relocated the transmitter 2 days later in EBL, but visuals showed that we were tracking a much bigger shark of approximately 120 cm with the transmitter inside. We found the transmitter package with monofilament and backing plate a week later on the sandy bottom of EBL proving that shark #27 had been eaten and all the tissue around the transmitter package had been digested. We still choose to show this track, as this was the furthest a shark traveled from Bimini and still returned.

Both sharks displaced to the Gulf Stream (#27 and #31) followed a clear northerly course, probably influenced by the strong northerly current. The Gulf Stream track of shark #31, a young-of-the-year, was terminated 32 km north of North Bimini and the shark's transmitter was never heard again. In contrast, the Gulf Stream track of shark #27, possibly 2 years old, was aborted 17 km north of the islands because of bad weather. However, this shark returned to Bimini after moving out of the Gulf Stream current and onto the shallow banks (see Figure 3). Shark #31 may have been too small to make headway against the current so that if it ever did reach shallow water, it may have been too far away from Bimini to orient toward the islands properly. Alternatively, a predator may have taken it.

We tracked seven of the 12 sharks caught at SB and released at site A continuously until they reached the shore of SB (Figure 4). All sharks but #6, which followed a more direct course to its previously observed home range, swam toward the southeast point of SB before returning along the shore to their previously observed home ranges.

Water current determined at the time of release did not show a unidirectional current. During most tracks a prevailing eastern wind was recorded up to 30 cm s^{-1}. Tracking was not possible under stronger wind conditions due to rough sea. In general a decline in water depth was observed with most tracks, as the shark got closer to shore but sometimes the sharks had to cross areas with deeper waters to get closer to shore.

Non-homers

The transmitter signal of the shark that was not tracked to the Bimini Islands (#31) was last heard 32 km north of the Islands. The tracking vessel aborted the trial, due to safety precautions, as radio communications with Bimini Islands was lost. We tracked five sharks to other location at Bimini than their previously observed home ranges. Shark # 18, caught in EBL and displaced 9.3 km south of SB was tracked to the little lagoon at SB within 13 h. After 2 days we recaptured the shark, removed its transmitter and transported it back to EBL. Shark # 22, caught at SB and displaced 9.5 km to the east of Bimini was tracked to EBL within 2 h. After 2 days we recaptured the shark, removed its transmitter and transported it back to SB. It is uncertain if these two sharks would have returned to their previously observed home ranges on their own. Shark #23, caught at SB was displaced 8.8 km south east of SB. We terminated the track 21 h later 16.3 km southeast of SB as the tracking boat got out of radio contact with the Bimini Islands. We heard the transmitter at EBL a week later but with out any sight of the shark. We relocated the transmitter a month later on the sandy bottom in the deep channel along the inside of North Bimini where bigger sharks are often seen. This indicates that the shark could have been eaten by a bigger one and the transmitter was later regurgitated. It is well documented that sharks commonly eat other sharks (van der Elst 1979, Compagno 1984, Harvey 1989). It is

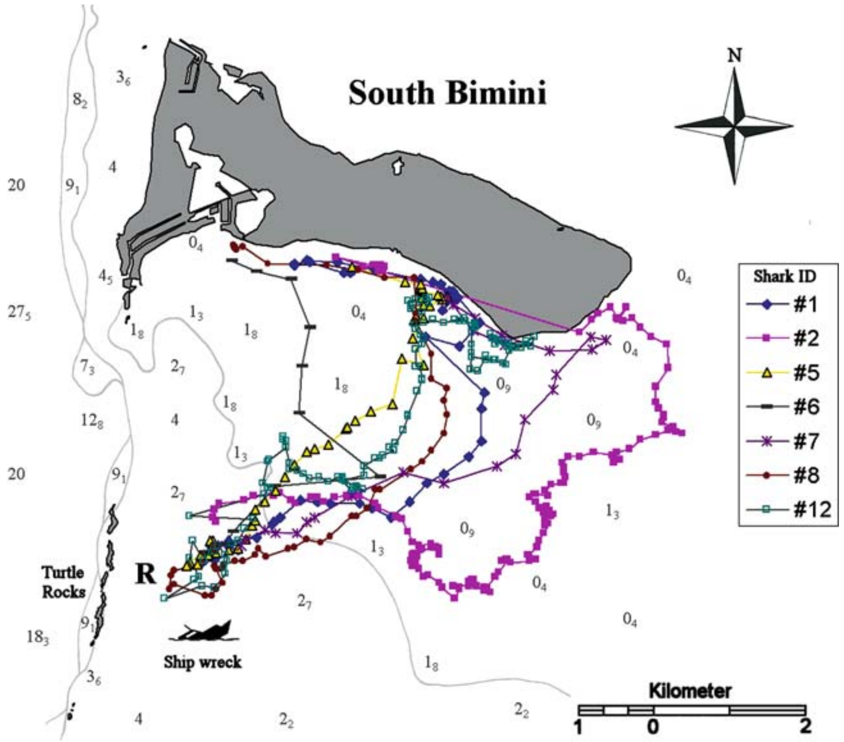

Figure 4. Homing path of seven sharks caught at South Bimini, released at site A and tracked continuously until the shore was reached. Shark #6 swam directly to its home range while the rest swam toward the south-east corner of South Bimini before returning along shore to their home ranges. Release site is marked with 'R'. Water depths are indicated in meters (eg. 2_7 equals 2.7 m).

uncertain when shark #23 could have been eaten. Shark #32 caught at EBL and released closer to Cat Cay that Bimini Islands was tracked to the pond at SB within 11 h. We relocated the transmitter six days later in the pond at SB in the sea grass bed where it had fallen of the shark. It is therefore uncertain if this shark has returned to its previously observed home range in EBL.

Observation by divers

We followed 22 of the 32 displaced sharks and divers observed them for 30 min after release – 10 at night and 12 during daytime. The sharks typically dove straight to the bottom and swam along the sea floor. The 10 sharks released at night made vertical movements, oscillating between the surface and the bottom. However, only two of 12 sharks released during the daytime showed this behavior. One of these sharks, displaced to the Gulf Stream, made frequent dives to 10–20 m depth but quickly returned to the surface after each dive. Divers were not believed to affect the swimming direction of the sharks as some sharks turned 180° and swam underneath the divers toward the bottom after release. Divers also observed that sharks swimming at the bottom would change their course and swim underneath them. There was no evidence of trauma-induced influence on the ROM following release. That is, there were no consistent patterns in change of ROM with time elapsed followed release.

During horizontal swimming all sharks swam in a zigzag pattern around a general heading, changing to a new course after approximately 2–10 min. This zigzag swimming pattern was observed both at the surface and at the bottom.

Orientation

Figure 5 shows the circular orientation for the sharks' first swimming direction, subsequent bearing and first straight bearing. To equalize the statistical distribution of the release sites, we

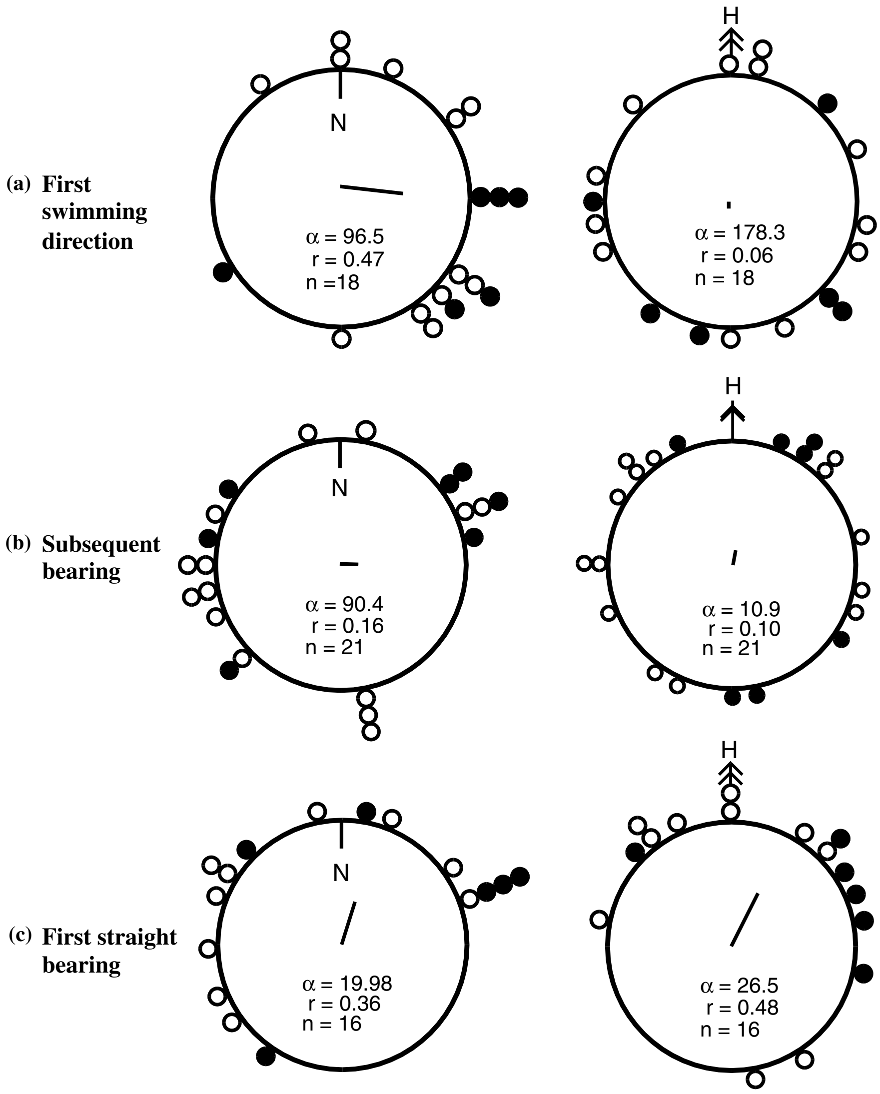

Figure 5. Orientation behaviour of juvenile lemon sharks from South Bimini (filled circles) and East Bimini Lagoon (open circles) in relation to geographic north (N, left diagram) and the sharks home ranges (H, right diagram) with mean vector (r, central line). Orientation behaviours are shown for the very first swimming direction as observed by divers (a), subsequent orientation within the first hour of release (b), and first straight bearing followed by the sharks (c). The average bearing is indicated by 'α'. See text for more details on pooled data and definition of first straight bearing.

pooled data from the 12 sharks released at site A so that only the mean vector from these sharks was used for comparisons with sharks released at the other sites. Thus, a maximum of 21 sharks is represented in Figure 5. The diagrams show the swimming direction of each shark in relation to both geographic north (diagrams on the left) and the shark's home range (diagram on the right). Sharks caught at SB are illustrated with filled circles while sharks caught at EBL are illustrated with open circles. The sharks' first swimming direction (Figure 5a, n = 18) as reported by divers showed a significant preferred compass direction (PCD) toward the east (diagrams on the left, $z = 3.96$, $p < 0.05$, Raleigh test, n = 18), whereas there was no homeward component for their first swimming direction (diagrams on the right). Subsequent bearings, recorded within the first hour after release (Figure 5b, n = 21), showed a random orientation with respect to both geographic north and the sharks' home direction. However, the first straight bearing (Figure 5c, n = 16) showed a homeward orientation with an angular deviation of 26.5° (± 58.6°) from the center of the sharks home ranges ($z = 3.63$, $p < 0.05$, Raleigh test, n = 16). A straight bearing was only found for seven of the 12 sharks released at site A. These seven sharks showed no homeward component in the first straight bearing. However, they displayed a skewed orientation, with a significant ($z = 4.66$, $p < 0.01$, Raleigh test, n = 7) angular deviation of 73.4° (± 34.7°) from the centers of their home ranges (Figure 6b). All sharks headed in a northeast direction, with an average angular degree of 61.8° (± 27.8°, $z = 5.45$, $p < 0.01$, Raleigh test, n = 7, Figure 6a). The one shark caught in EBL and released at site A showed very similar behaviour with its first straight bearing (open circles in Figure 6).

The compass direction recorded within the first hour after release for each of the 32 sharks was divided into 10-min intervals. The mean vector (r) was then calculated to give the shark's orientation at the time of release. The average mean vector for sharks released at night was found to be 0.46 while that for sharks released during daylight was 0.63. The difference was not quite statistically significant ($t = 2.00$, t-test, $p = 0.055$, df = 30). Thus, sharks released at night seem to have changed course more frequently than those released during the day. The average mean vectors for orientation within the first hour after release were compared with the degree of cloud cover and moon phase to examine possible effects of the sun or night sky on the initial heading. Cloud cover or moon phase did not seem to affect behavior after release during either daytime or nighttime, and we found no correlation between the return time and cloud cover.

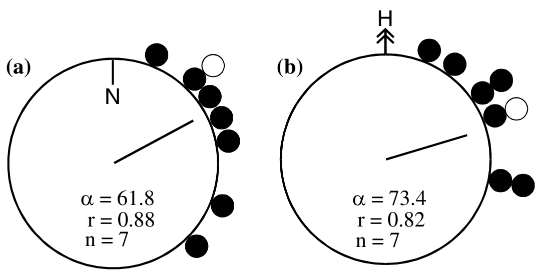

Figure 6. The orientation of the first straight bearing by seven lemon sharks caught at South Bimini and displaced to release site A south of South Bimini (filled circles). The first straight bearing for this group of sharks varies from the rest of the sharks displaced (see Figure 5c) by not being home-oriented but deviating with 73.4 (± 34.7°) degrees from their home ranges (*H*) ($z = 5.45$, $p < 0.01$, Raleigh test). The sharks headed in northeast direction (61.8° ± 27.8°, $z = 4.66$, $p < 0.01$, Raleigh-test). Only one shark caught at East Bimini was released at site A (open circles).

Rate of movement (ROM)

We calculated mean ROM in body-length per second (bl s^{-1}) for each individual shark using 5-min intervals between fix points. The mean ROM of all sharks was 0.77 (± 0.09) bl s^{-1} before the sharks reached the shore of Bimini Islands. Only 15 sharks were tracked along the shore of Bimini Islands before they reached their home ranges. For those sharks a separation of the tracking sequences into 'open water' and 'near shore' revealed a significant higher ROM in 'open water' than 'near shore' ($t = 3.03$, $p < 0.01$, paired t-test, n = 14). Mean ROM was 0.77 (± 0.07) bl s^{-1} in 'open water' and 0.58 (± 0.13) bl s^{-1} after the shore was reached. We found no diurnal difference in ROM.

Discussion

The fact that most (81%) of these very young (0–2 years), inexperienced sharks returned to their original home range suggests high site fidelity and implies that they have an innate ability to home.

During an attempted recapture, we chased shark #4 out of its home range. We did not record the transmitter signal in that area for the following 6 days, but as the search area was progressively enlarged, we finally detected this shark at EBL, where we caught the shark and removed its transmitter. A week later, we recaptured the shark in its previously observed home range at SB. Also shark #30 caught at SB was tracked to EBL but we later found its transmitter at SB. These two observations suggests that sharks can move to other areas of Bimini Islands and return home, suggesting that lemon sharks possess a homing behavior as defined by Gerking.

Even though six sharks did not return to their precise home ranges, all but one returned to the islands of Bimini. As sharks were recaptured and transmitters were removed shortly after the shore of Bimini was reached it is difficult to say if these sharks eventually would have found their way home. Because there was greater probability to miss the island if the sharks were choosing their headings on a random basis, simply making landfall at Bimini Islands suggests that 31 of 32 lemon sharks, or 97% of them, exhibited a homing behavior.

Several laboratory studies of swimming speed in juvenile and subadult lemon sharks showed average cruising speed between 0.2 and 0.4 bl s^{-1} (Nixon & Gruber 1988, Bushnell et al. 1989, Scharold & Gruber 1991). Sundström & Gruber (1998) recorded a mean burst speed of 1.0 bl s^{-1} for subadult lemon sharks (150–200 cm TL), about three times the cruising speed. Since territorial behavior has not been observed in lemon sharks (Morrissey & Gruber 1993b), bursts of speed likely indicate either an escape response or an attack on prey (Gruber et al. 1988). According to Morrissey & Gruber (1993a), excursions away from restricted home ranges could be fatal as juvenile sharks could fall prey to bigger sharks. It is therefore possible that the mean open water ROM (0.77 bl s^{-1}) of the displaced sharks, which is an underestimation of their actual swimming speed, reflects the sharks' effort to escape from open, unprotected areas and return to their sheltered home ranges. The average ROM of 0.58 bl s^{-1} after the shore was reached does not necessarily mean the sharks were swimming slower but possibly exhibiting a meandering swimming pattern in and out of the mangrove root system too fine to be accurately traced by the tracking vessel. It could also indicate that the sharks felt safe from predators and had slowed down their swimming speed but were still searching for their home ranges.

Morrisey & Gruber (1993b) made an extensive home range study on juvenile lemon sharks in Bimini. They used a modification of the minimum convex polygon method and found a positive correlation between the sharks activity space and their size

$$y = 0.06x - 2.6,$$

where y equals the shark's activity space and x the shark's precaudal length, L_{PC}. Entering the mean L_{PC} for our sharks of 52 cm we get a mean activity space of 0.52 km^2 which is similar to our value estimated using the Kernel home range method. Morrisey & Gruber also found that the sharks maintained shore fringing home ranges similar to our findings. The differences in home range size between sharks at SB and in EBL could be due to the bigger area of low water depth and small mangrove patches in EBL in contrast to the narrow shore fringing mangrove areas south of SB. The differences could also be a result of the fewer data point used for the Kernel home range calculation in EBL.

The repeated nocturnal surfacing behavior demonstrated by many of the sharks might enable them to observe low light intensity celestial cues. Changes in water temperature in the water column could also be an explanation for the vertical movements. Thermoregulatory behavior has been suggested to occur in juvenile lemon sharks in Bimini lagoon (Morrisey & Gruber 1993a) as well as in *Carcharhinus isodon* (Castro 1993) and in *Prionace glauca* (Carey & Scharold 1990). This behavior might be more prevalent at night as other sensory cues such as sun light or polarity are not present. As water temperatures in the present study were only measured approximately 10 cm below the surface it is not possible to draw any conclusion. Another possibility is that these sharks were disoriented by the presence of a light stick on their dorsal fins. Further studies are needed for a better understanding of these vertical movements.

We observed a PCD for the first swimming direction of the sharks after release (Figure 5a), suggesting an innate sense of direction. A polarization towards a PCD is found for the initial bearing of displaced pigeons in relation to their loft (Wallraff 1978). Homing pigeons released at distant sites symmetrically distributed around their loft, depart preferably in a direction that points toward home. However, they do so only in the total mean, i.e., when the vanishing bearing of all the release sites are taken together. At the single release site the pigeons often deviate considerably from the true homeward direction. Unlike homing pigeons, we found that the mean PCD for all sharks was not related to the direction of their home ranges, but was instead related to a certain compass direction (96.5 degree, Figure 5a). Wallraff (1978) who studied the PCD in homing pigeons believes that PCDs develop upon some unknown environmental conditions at the pigeons' home site. He also believes that PCDs are not only curious effects superimposed on the homing process, but an unavoidable expression of its functional structure. Weather the behavior observed in pigeons and sharks are controlled by the same mechanisms are unknown.

This compass direction changes quickly to become random as the sharks began orienting towards home. It is interesting that the sharks released at the same site south of SB (release site A, Figure 1), only 4 km from their home ranges, kept this highly significant PCD for their first straight bearing (Figure 6). These sharks were still not homeward-oriented, but rather were oriented toward the southeast point of SB. As we only had one site with multiple releases we can not rule out the presence of site-specific influence affecting the sharks' first swimming direction at this site. More release sites with multiple releases would show if the sharks at a particular release site would keep a PCD for their first straight bearing or we have to search for physical factors that characterizes the local environment. Local water currents might have caused these 'non-homeward' northeast movements of the sharks away from release site A. According to Strong & Gruber[2] water current seemed to play a role in initial orientation of sharks in a pen. The prevailing water currents in the area are flowing east–south–east. The water current might carry sensory cues such as olfactory, essential for homing migration in salmon (Cooper & Hirsh 1982, Hasler 1983, Hasler & Scholz 1983, reviewed in Hara 1994), trout (Halvorsen & Stabell 1990), American eels (Barbin 1998) and radiated shanny (Goff & Green 1978). Another possibility is that the sharks were simply using water depth gradient in their orientation towards the shoreline. If these sharks had followed a more direct rout towards their home ranges they would needed to travel through deeper water. (see Figure 4). Nevertheless, three sharks displaced close to Cat Cays shows that not all tracks could simply be explained by a tendency to move toward shallow water as these sharks should have moved toward the Cat Cays, instead they returned to Bimini Islands.

[2]Strong, W.R. & S.H. Gruber. 1994. Homeward orientation in displaced juvenile lemon sharks, *Negaprion brevirostris*. Abstracts of the American Society of Ichthyologists. Los Angeles, CA [on line]. Available from the Internet URL http://www.flmnh.ufl.edu/fish/Organizations/AES/abst94c.htm,

Sensitivity to infrasound, or low-frequency linear acceleration, may be an important sensory ability to fishes (Sand & Karlsen 2000), cephalopods (Packard et al. 1990) and crustaceans (Heuch & Karlsen 1997) in, for instance, courtship and prey-predator interactions. Sand & Karlsen (2000) hypothesize that migratory fishes may use the infrasound pattern in the ocean for orientation and navigation by detecting changes in surface wave pattern associated with altered water depth and distant land formation. It is possible that infrasound could be used to help the sharks in the present study to orient towards the islands.

Knowing that lemon sharks possess a homing ability will contribute to an unified understanding of one of the more remarkable attributes of these animals: the presumed ability of the female lemon shark to return to their natal nursery to give birth to their own pups, more than 12 years later.

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