

Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (*Negaprion brevirostris*)

S. T. Kessel^{1,2,*}, D. D. Chapman³, B. R. Franks⁴, T. Gedamke⁵, S. H. Gruber⁴,
J. M. Newman⁶, E. R. White⁷, R. G. Perkins²

¹Great Lakes Institute for Environmental Research, University of Windsor, 401 Sunset Ave, Windsor, ON N9B 3P4, Canada

²School of Earth and Ocean Sciences, Cardiff University, Cardiff, CF10 3AT, UK

³School of Marine and Atmospheric Science, Stony Brook University, Stony Brook, NY 11794, USA

⁴Bimini Biological Field Station Foundation, South Bimini, Bahamas

⁵National Oceanographic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL 33149, USA

⁶Dyko Enterprises Incorporated, 205 Golfview Drive, Jupiter, FL 33469, USA

⁷Department of Biology, University of Victoria, Victoria, BC V8P 5C2, Canada

ABSTRACT: Understanding how and why animals are distributed through time and space has always been a fundamental component of ecology and is an essential prerequisite for effective conservation and/or management. However, for highly mobile K-selected species, behavioural predictability is rarely considered over appropriate scales relative to life history. To address this point, a multidisciplinary approach combining telemetry, external tagging, physical assessment, environmental monitoring and genetic analysis was adopted to determine a spatial framework for the movements of adult lemon sharks *Negaprion brevirostris* at multiple spatial and temporal scales from 2007 to 2011. Lemon sharks (n = 83) were tracked with passive acoustic telemetry, revealing a winter residency in the southeast Florida region. Detections from individuals recorded within the core winter habitat for >20 d (n = 56) were incorporated into generalized linear mixed-effects models to investigate the influence of water temperature, photoperiod, moon phase, month and year on presence. The findings of this study suggest a temperature driven 'migration-residency' model for mature lemon shark distribution across the USA eastern seaboard. Lemon sharks are distributed across a wide geographical area in the summer months and migrate south concentrating off southeast Florida in the winter, with this pattern repeated each year. From comparative genetic analysis and the absence of any evidence of mating behaviour during the winter residency period, mating and parturition most probably occur in May/June between northern Florida and the Carolinas. This study highlights the importance of determining the specific dynamics and proximate causes of animal movement and distribution over appropriate spatial and temporal scales relative to life history.

KEY WORDS: Lemon shark · Acoustic telemetry · Seasonal residency · Seasonal migration · Temperature preference · GLMM

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Animal movement defines not only the distribution and abundance of organisms but also the dynamics of many ecological processes at population, commu-

nity and ecosystem levels. Thus, quantifying why and how factors influence movement is a fundamental goal in animal ecology, providing the key for predicting the responsiveness of populations to future change (Bestley et al. 2013). Many organisms that

exhibit a high level of mobility throughout, or for a proportion of, their life-span display a level of repeatability in their movements, which can vary over different scales among species and individuals (Morales & Ellner 2002). The predictability of the timing and distribution of animal groups can greatly influence their vulnerability to directed harvest (Block et al. 2011), but can also greatly aid management/conservation feasibility (Costello et al. 2010). However, conservation and management strategies for highly mobile species rarely account for how animals are spatially connected over the different stages of their annual distribution (Martin et al. 2007). This common strategic shortfall greatly reduces the effectiveness of these efforts in maximizing population persistence as intended and can result in regional population declines of varying magnitude (Sutherland 1998). For many species, a lack of knowledge of annual patterns in geographical distribution has made it virtually impossible to incorporate year-round dynamics when developing conservation and management strategies (Martin et al. 2007). These year-round dynamics can denote the geographical scope of conservation needs as well as identify specific areas of importance that require increased attention to ensure longevity for particular groups and populations (Schneider 1994). While great advances have been made in understanding such behaviours for terrestrial animals, aquatic and particularly marine animals have often proven more difficult to investigate due to the dynamic nature of their habitats (Block et al. 2011, Koslow & Couture 2013). Policy makers are increasingly adopting spatial management as an evolving paradigm for ocean policy (Costello et al. 2010). With increasing concern over the exploitation of marine animals (Pauly et al. 2005), and in particular top predators, it is more important than ever to increase our knowledge of their spatial ecology.

Sharks are one such top predator that are greatly impacted by overfishing, with one-quarter of all chondrichthyan fishes estimated to be threatened with extinction, based on IUCN Red List criteria (Dulvy et al. 2014). Improving conservation and management potential for sharks is essential for preventing regional biodiversity loss, extinctions and disruptions to ecosystem services (Block et al. 2011, Worm et al. 2013). Sharks of the family Carcharhinidae (requiem sharks) constitute an important fraction of upper trophic-level biomass in both coastal and pelagic habitats and compose a substantial component of global shark landings (Anderson 1990, Matsunaga & Nakano 1999, Clarke 2008, Morgan et al.

2009, Worm et al. 2013). Yet, despite their ecological and economic importance, a thorough understanding of the behaviour and life history of many carcharhinids is lacking. One exception is the lemon shark *Negaprion brevirostris*, which has been intensively studied in the western Atlantic region over the past 4 decades (e.g. Cohen & Gruber 1977, Gruber 1984, Brown & Gruber 1988, Morrissey & Gruber 1993b, Motta et al. 1997, Feldheim et al. 2001a, 2002, Sundström et al. 2001, DiBattista et al. 2007, Chapman et al. 2009, de Freitas et al. 2009, Newman et al. 2010).

A large-bodied, coastal species, lemon sharks exhibit many features that typify carcharhinid biology, such as placental viviparity, slow growth, delayed maturation, use of nursery grounds, natal homing and a piscivorous diet (Gruber 1982, Brown & Gruber 1988, Cortes & Gruber 1990, Feldheim et al. 2004, 2014, Chapman et al. 2009). For 'K-selected' species such as the lemon shark, the adult life-stage containing the breeding portion of the animal's life history is considered the most important for sustaining population stability (Hoenig & Gruber 1990, Musick et al. 2000, Kinney & Simpfendorfer 2009, Feldheim et al. 2014). Although the lemon shark has been intensively investigated, our understanding of the adult life-stage has largely been extrapolated from studies on juveniles (e.g. Feldheim et al. 2001a, 2002, 2004). Thus, our understanding of the lemon shark's adult stage is limited given ontogenetic changes in ecology, behaviour and physiology. This lack of information represents a lacuna in the otherwise comprehensive understanding of lemon shark life history and can confuse or impede effective management decisions for this commercially targeted species. In 2001, recreational divers reported the presence of aggregations of large lemon sharks on natural and artificial reefs at depths 20 to 35 m off Jupiter, Florida, USA. Sharks were observed and photographed swimming or resting on the bottom in large, often polarized groups estimated to be between 50 and 100 individuals. This presented an opportunity to study large numbers of adult lemon sharks with the goal of gathering direct information on the adult phase of their life cycle.

Seasonal spatial variation and migration behaviour is experiencing a global decline, particularly for large species in the terrestrial environment where anthropogenically sourced interruptions to migration pathways are common (Alerstam 2008). In the marine environment, physical barriers to migration pathways are less common and more easily deviated by large, highly mobile species. Thus, any future evolu-

tion of spatial behaviour in a large, highly mobile marine species, such as the lemon shark, is more likely to be driven by changes to resource availability and environmental conditions. The specific aim of this study was to assess the physical and behavioural characteristics of lemon sharks with respect to their current and potential future spatial ecology. Therefore, the following research questions were articulated: (1) Are the observed sharks sexually mature? (2) To what extent is their residence and migration driven by breeding behaviour? (3) What is the timing of, and what are the environmental factors driving, lemon shark seasonal residency and distribution in the southeast Florida region? (4) Do the same individuals return to the region annually or biennially? (5) What is the seasonal distribution of lemon sharks outside of their winter residence in southeast Florida? (6) Where do these lemon sharks give birth? Given the inherent difficulties of studying large mobile predators in the dynamic marine environment, it was necessary to adopt a multi-disciplinary research approach.

MATERIALS AND METHODS

Study site

The core area of field work for this study was the south-eastern coast of Florida, USA, between Delray Beach (26° 28' N, 80° 02' W) to the south and Port St. Lucie (27° 14' N, 80° 07' W) to the north, stretching offshore ~7 km (Fig. 1). All lemon sharks reported in this study were captured and tagged in this core area. Further details relating to the bathymetry, seascape and habitats of this region are provided below (see 'Passive acoustic telemetry').

Shark capture and transmitter implantation

All sharks were captured between February 2006 and April 2012, using rigs consisting of free-floating individ-

ual lines and baited 20/0 circle hooks set to drift within 2 to 3 m of the substrate. Once hooked and secured alongside a small vessel, the sharks were processed. Individuals were held straight, and precaudal (PCL), fork (FL) and standard total length (TL) were measured to the nearest 0.5 cm. To estimate maturity in males, the length (to nearest mm) of the inner margin of the right clasper was measured, plot-

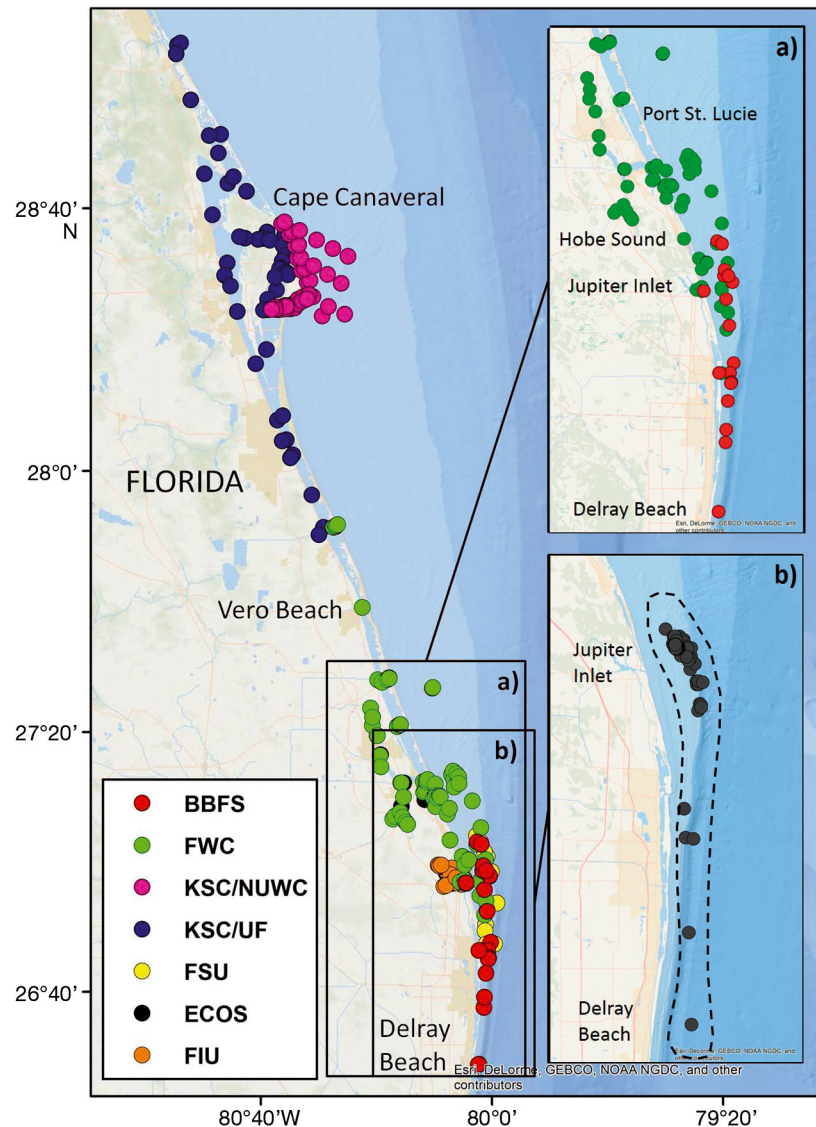


Fig. 1. Florida Atlantic Coastal Telemetry (FACT) acoustic array spanning from Cape Canaveral (north) to Delray Beach (south) deployed and maintained by BBFS: Bimini Biological Field Station; FWC: Florida Fish and Wildlife Commission; KSC: Kennedy Space Centre; NUWC: Naval Underwater Warfare Centre; UF: University of Florida; FSU: Florida State University; ECOS: Environmental Council Of States; FIU: Florida International University. Inset (a) shows core lemon shark monitor array composed of BBFS and FWC receivers, the detections from which were used for data analysis; inset (b) shows area targeted during fishing efforts (boundary represented by dashed line) and specific capture locations of all 83 sharks that received acoustic tags (grey circles)

ted against PCL and compared with similar measurements of 58 mature males from Florida and the north-western Bahamas. All sharks were tagged at the base of the first dorsal fin with a NMFS M-type dart tag (Kohler & Turner 2001), and a passive integrated transponder microtag (PIT, RFID; Destron Fearing®) was injected under the skin on the opposite side. Six individuals were issued with Pop-off Satellite Archival Tags (PSAT; Wildlife Computer MK10®), from which only locational data will be presented for the purposes of this study. A $\sim 3 \times 3$ mm skin sample was taken from a fin for genetic extraction. All lemon sharks judged to be in good condition, based on skin coloration, received a V16-6H coded acoustic transmitter (Vemco®) internally implanted into the coelom (Holland et al. 1999, Carlisle & Starr 2009). During the surgical procedure, sharks were held in tonic immobility (Watsky & Gruber 1990, Speed et al. 2011). The transmitter, which represented <1% bodyweight for all individuals, was inserted into the body cavity through a ~ 3 cm ventral incision just anterior of either pelvic fin. Incisions were closed with a single central silicone-coated, braided, polyester suture (Ti-Cron 2818-89). Prior to each surgery, all surgical equipment including the transmitter was sterilised with a 10% betadine solution. The duration of the procedure was about 2 to 4 min for each individual. Nominal battery life for the V16-6H tags was 36 mo until 2008, after which it was improved to 84 mo, and nominal transmission delays were 90 to 360 s. Standard tagging procedures were reported following Thiem et al. (2011), with a typical at-vessel handling time of <15 min. Upon release, all 86 sharks swam off vigorously.

Passive acoustic telemetry

An array of 19 acoustic receivers (VR2 and VR2W; Vemco®) was deployed along the coast between Delray Beach (26° 28' N, 80° 02' W) and Hobe Sound, Florida (27° 03' N, 80° 02' W; Fig. 1). Receivers were moored at locations where repeated sightings and captures of lemon shark had been made, predominantly exposed natural and artificial reef sites. Additional receiver sites were located along the 20 to 30 m depth reef line, selected as potential transitional corridors between identified aggregation areas based on bottom characteristics and geographic position. Participation in a data-sharing network substantially increased the potential for detecting movements outside of the identified aggregation grounds. The Florida Atlantic Coastal Telemetry (FACT) array group

is currently composed of 8 research teams all using Vemco acoustic systems to track different marine species off Florida's coast (Fig. 1). Collectively, the group deployed ~ 300 VR2W acoustic receivers spanning a total of ~ 310 km of coastline, lagoons, inter-coastal waterways and rivers between Delray Beach and Cape Canaveral. Of these, an additional 52 receivers deployed by the Florida Fish and Wildlife Commission (FWC) were used to form the 71 receiver core array for this study (Fig. 1). Detecting sharks outside the FACT array area was facilitated by collaborating with another data-sharing group, the Atlantic Cooperative Telemetry (ACT) Network, estimated to have ~ 3000 monitors across the eastern seaboard (Dewayne Fox, ACT coordinator, pers. comm.). Thus, working with the FACT and ACT research groups significantly increased the probability of detecting local and meso-scale movements of tagged lemon sharks between the Florida Keys and USA–Canadian border.

Detection range testing of acoustic monitors

Various factors, including depth, temperature, turbidity and background noise, generate spatial and temporal variation in the range that an acoustic receiver is reliably able to detect and decode an acoustic transmission (Heupel et al. 2006, Heupel & Webber 2012, Kessel et al. 2014). To establish the effective detection range and to monitor its temporal variability, 3 V16-6H sentinel transmitters were deployed at fixed distances from 2 acoustic receivers at the most representative array location between February 2009 and December 2011. The sentinel tags transmitted a uniquely coded signal with a fixed delay of 900 s. The 2 receivers were separated by 300 m; thus, it was possible to test 4 linear distance parameters from the 3 transmitters at 150, 300, 600 and 900 m (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m514p175_supp.pdf). The detection range was defined as the distance at which 50% of sentinel tag transmissions were recorded over the course of the study, based on a logistic regression through the daily detection proportions at each distance parameter, as defined by Kessel et al. (2014).

Monitoring of environmental parameters

Water temperature was continuously monitored between September 2007 and July 2009 by attaching thermochron (iButton® #DS1921) temperature log-

gers to each acoustic monitor. In July 2009, these were changed to HOBO Pro V2 (Onset Computer Co.®) loggers for the remainder of the study. Currents at the receiver site of highest residence index (RI) were continuously monitored during the height of the winter aggregations (9 February to 12 April 2008), with an acoustic Doppler current profiler (Teledyne RDI Sentinel Workhorse ADCP®, 1200 kHz). Current speed and direction from the substrate to sea-surface were sampled every 24 s. Photoperiod (day length) and moon phase were obtained from the United States Navy Observatory (USNO) website (www.usno.navy.mil).

Filtering data for false detections

To remove false detections created by acoustic tag collisions (interference between multiple overlapping transmission; Heupel et al. 2006), the full database was filtered in R v. 2.15.1 (R Development Core Team 2012) using the following criteria. Detections of a given ID were considered false if they were recorded only once on a given receiver within a 1 h period, unless that same ID was recorded on another receiver that was within a distance the shark (at average swimming speed) could feasibly travel to within that same time frame. To identify adjacent receivers within a feasible swimming distance within 1 h, a time matrix was created (Ersts 2013) based on the number of seconds it would take a lemon shark to swim between each station based on 0.71 m s^{-1} average swimming speed (Sundström & Gruber 1998).

Data analysis

Analysis was restricted to individuals that were detected for at least 20 d on the 71 receivers of the core array (Fig. 1), following data filtering (reducing the number of sharks to $n = 56$). Seasonal residence between September 2007 and September 2011 was calculated by dividing the number of detections received each month by the number of acoustically tagged sharks available for detection in that month. Residence index (RI) was calculated as the mean number of days an individual shark was detected at each receiver station relative to the total number of days the shark was detected within the core array. To investigate environmental cues influencing lemon shark presence and absence in the study area, generalised linear mixed models (GLMM) with random and fixed effects were used (Bolker et al. 2009, Bond

et al. 2012, Kneebone et al. 2012, Dudgeon et al. 2013). The GLMM had fixed effects of (1) average daily water temperature (averaged across the core array), (2) photoperiod (day length), (3) moon phase (on an illumination scale from 0 to 1), (4) month and (5) study year. Shark ID was included in the model as a random effect to account for the non-independence amongst detections of the same individual shark (Bolker et al. 2009). Presence-absence was examined on a daily basis (a shark detected anywhere on the array in a given 24 h day was 'present') using a binomial error structure and logit link function. To account for temporal autocorrelation, explanatory variables were included that described the presence or absence of a particular shark in previous days (Brockwell & Davis 2002). For instance, a 4 d lag would indicate that the presence (or absence) $n - 4$, $n - 3$, $n - 2$ and $n - 1$ days ago is an important determiner of whether a shark was present (or absent) at time n . After determining the optimal time-correlation structure, it was possible to find the best-fitting model in regard to the fixed effects.

The Bayesian information criterion (BIC) was used to determine the time-correlation structure because BIC is typically more conservative, thus better at not over-fitting (Zuur et al. 2011). To find the best time correlation structure, the full model (all explanatory variables) was fit using different time lags. BIC was then used to rank these models with different time lags to determine the best time-correlation structure. After finding an optimal time lag of 13 d, a series of models by using all possible combinations of explanatory values were examined, while using this time lag for all models. These models were ranked according to BIC to find the best-fitting model (Table 1). In determining both the time-correlation structure and the best-fitting model, ranking by Akaike information criterion values yielded similar results. Estimates for the explanatory variables in the GLMM were then determined (Table 2). Significant relationships in the models with $p < 0.001$ were evaluated according to recommendations laid forth by Zuur et al. (2011). All analyses was implemented in R v.2.15.1 (R Development Core Team 2012) using the `lmer()` function in the `lme4` package (Bates et al. 2011).

Genetic analysis

Acoustic telemetry alone cannot demonstrate where individuals are giving birth. Population genetic analyses can offer insights into the relationship between a sample of adults and a sample of juveniles. If popu-

Table 1. Ranking of the 10 best generalised linear mixed models (GLMM) plus the null model. BIC: Bayesian Information Criteria; Pres: shark presence; Temp: daily average water temperature; (1IID) = random effect for shark ID

Model	BIC	Deviance
Pres~Temp + Photoperiod + Month + (1IID)	14947.11	14743.9
Pres~Temp + Photoperiod + Month + Year + (1IID)	14955.17	14740.67
Pres~Temp + Photoperiod + Moon + Month + (1IID)	14958.29	14743.79
Pres~Temp + Photoperiod + Moon + Month + Year + (1IID)	14966.34	14740.55
Pres~Temp + Photoperiod + (1IID)	14972.23	14780.31
Pres~Temp + Photoperiod + Year + (1IID)	14978.86	14775.65
Pres~Temp + Photoperiod + Moon + (1IID)	14983.18	14779.97
Pres~Temp + Photoperiod + Moon + Year + (1IID)	14989.77	14775.27
Pres~Temp + Month + (1IID)	15104.57	14912.65
Pres~Temp + (1IID)	15106.35	14925.72
NULL: Pres~(1IID)	15633.14	15463.58

Table 2. Model results for best-fit GLMM model based on BIC rankings. Note the time lag of 13 d is included in the model but not shown here. Parameter estimates, β , in terms of log odds ratio; Temp: daily average water temperature

	$\beta \pm SE$	Z	p
(Intercept)	2.848 \pm 0.346	8.22	<0.001
Temp	-0.136 \pm 0.013	-10.27	<0.001
Photoperiod (hours)	-0.321 \pm 0.025	-12.68	<0.001
Month	-0.049 \pm 0.008	-5.98	<0.001
Random effects			
Acoustic Tag ID estimated variance \pm SE: 0.139 \pm 0.373			

lation genetic analyses indicate that the adult and juvenile samples are differentiated, then it is unlikely that the 2 groups are related to one another. To address the question of where Jupiter females give birth, we conducted a population genetic analysis of a sample set that included adults from Jupiter and juvenile sharks in nearby nursery areas. Juvenile lemon sharks from 67 to 90 cm total length (n = 82) were sampled at 2 sites in Florida, one in the south of the core adult study area (Marquesas Key, 24° 34' N, 82° 07' W; n = 40) and one to the north (Cape Canaveral, 28° 27' N, 82° 31' W; n = 42). Marquesas Key juveniles are born at this location, while the Canaveral juveniles are born to the north and migrate to this location to overwinter (Reyier et al. 2008, Reyier et al. 2014). All juveniles had a small piece of fin removed and stored in 20% DMSO for genetic analysis. Genomic DNA was extracted from tissues from these individuals and 40 haphazardly selected adults from Jupiter using the Qiagen Blood and Tissue extraction kit (Qiagen®). Sequences from the entire mitochondrial control region (CR, 1080 bp) were PCR amplified using mitochondrial CR proline transfer RNA light strand forward primer Pro-L

(5'-AGG GRA AGG AGG GTC AAA CT-3') and ribosomal RNA heavy strand reverse primer 282 12S (5'-AAG GCT AGG ACC AAA CCT-3') (Keeney et al. 2003). Partial sequences from the mitochondrial ND2 gene (650 bp) were amplified using forward (5'-TGT ATT AAC CAT CCT AAT TTC AAG-3') and reverse (5'-GGT GTT AGG GCA GAA GGA TGG ATA-3') primers designed from GenBank Accession #U91418. For both loci, PCR was carried out in 50 μ l volumes containing 1 μ l

DNA template (~20 ng), 1X CoralLoad PCR Buffer, 200 μ M deoxynucleoside triphosphate (dNTPs), 1 U HotStar Taq DNA Polymerase (Qiagen) and 0.25 μ M forward and reverse primers. Cycling parameters included an enzyme activation step of 95°C for 15 min, 35 cycles of 94°C for 1 min, 50°C for 1 min, and 72°C for 2 min, and a final extension at 72°C for 10 min with a MultiGene thermal cycler (Labnet International®). PCR products were purified with ExoSAP-IT (Affymetrix®) and sequenced using the Big Dye Terminator v.3.1 cycle sequencing kit (Applied Biosystems®) with a Bio-Rad DYAD thermal cycler (Bio-Rad Laboratories). The resulting products were precipitated with 125 mM EDTA and 100% ethanol and run on an ABI 3730 DNA Analyzer (Applied Biosystems®). Resulting sequences were validated by eye and aligned in Geneious Pro v.5.1.7 (Drummond et al. 2010) where haplotypes of CR and ND2 were identified manually. Once separate haplotypes of ND2 and CR were identified for each individual, a new 'composite' sequence file was created with the contiguous sequence of the 650 nucleotides from ND2 followed by the 1080 nucleotides from CR, for a total of 1730 bp for each individual. To assess differentiation between the 3 samples, i.e. Jupiter adults and juveniles from Marquesas Key and Cape Canaveral, Φ_{ST} was calculated between each pair of samples using the program Arlequin 3.5 (Excoffier & Lischer 2010). The significance of each pairwise comparison was assessed using 10 000 permutations of the data.

RESULTS

Detection range testing conducted from February 2009 to December 2011 demonstrated an effective detection range for the receivers of 326 m. This is

based on the distance at which 50% of sentinel tag transmissions were detected (Kessel et al. 2014; see Fig. S2 in the Supplement).

Over the course of the study, 140 lemon sharks *Negaprion brevirostris* (65 male and 75 female) were caught and tagged with NMFS M-Type dart tags, ranging between 165 and 227 cm PCL (mean \pm SE = 198 ± 1.3 cm). All but 1 male exceeded the minimum size of maturity (166 cm PCL) listed for lemon sharks by Compagno (1984), and all but 3 males measured had calcified claspers that were large relative to body length (Fig. 2). None of the female lemon sharks had recent mating scars, and none of the male's claspers showed haematoma or broken capillaries, indicating that copulation had not recently occurred (Klimley 1980, Kajiura et al. 2000). In total, 83 lemon sharks (26 males, 57 females), ranging between 165 and 225 cm PCL (mean \pm SE = 197 ± 1.5 cm), received acoustic tags.

Between September 2007 and September 2011, the 71 receivers of the core array (Fig. 1) recorded 1 257 419 acoustic detections from the 83 tagged lemon sharks. Data filtering removed 2787 questionable detections. In each of the 4 research seasons, the number of detections per month divided by the number of acoustically tagged sharks peaked between December and April, which hereafter is referred to as the 'residency period' (Fig. 3, see Fig. S3 in the Supplement). During the residency period, 97.5% of total detections were recorded. The arrival and departure of lemon sharks from the study area was abrupt, with very few acoustic detections recorded in the months between successive residency periods. The residency period corresponded to the winter season, when water temperature in the study area was consistently below $\sim 24^{\circ}\text{C}$. Of the sharks tagged and detected in the 2008 season, 4 were detected in 1 season only, 8 were detected in 2 subsequent seasons, 10 in 3 subsequent seasons, and 1 in 4 subsequent seasons. Of the sharks tagged and detected in the 2009 season, 5 were detected in 1 season only, 6 were detected in 2 subsequent seasons, and 12 were

detected in 3 subsequent seasons. Of the sharks tagged and detected in the 2010 season, 9 were detected in 1 season only, and 7 were detected in 2 subsequent seasons.

According to the results of our GLMM, the model of best fit included Shark ID as a random effect, temperature, photoperiod and month (Tables 1 & 2). The

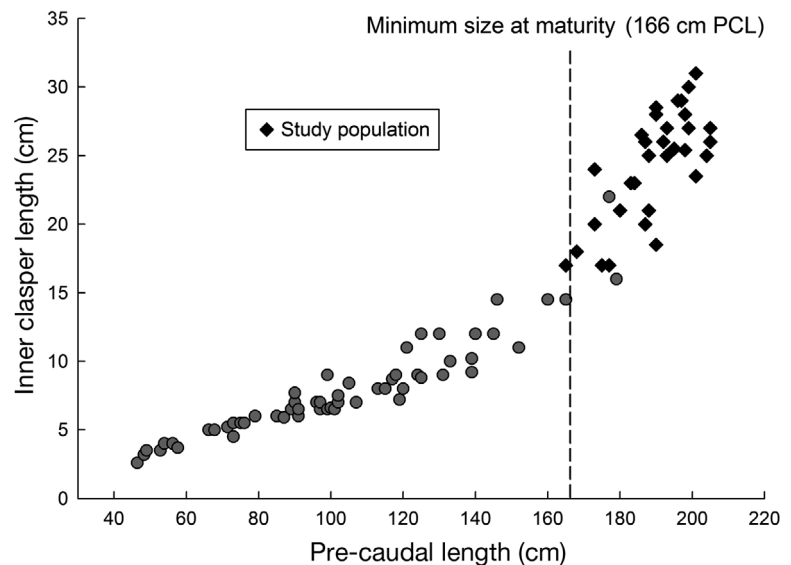


Fig. 2. Relationship between inner clasper length (ICL) and pre-caudal length (PCL) in 91 male lemon sharks from Florida and the western Bahamas (46.4–201 cm PCL). Males captured in the Jupiter study area are denoted by black diamonds. Minimum size of maturity (166 cm PCL) denoted by the dashed line

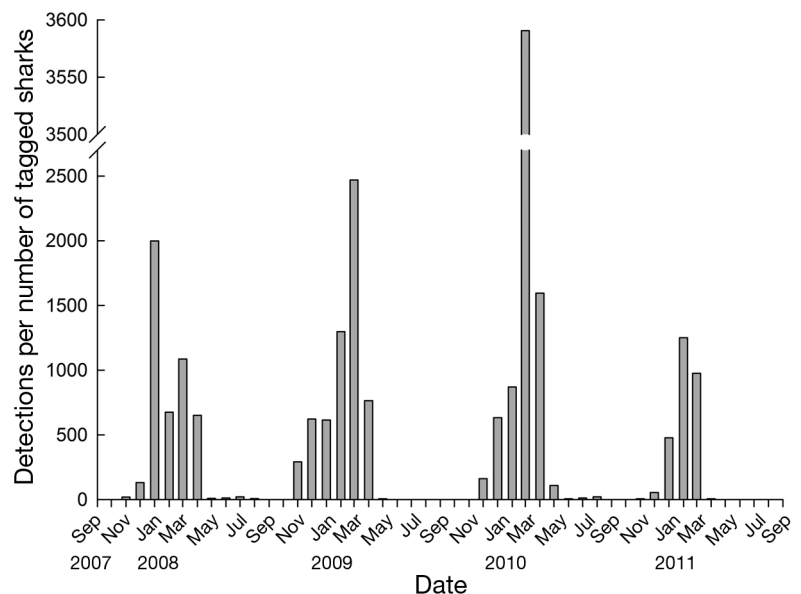


Fig. 3. Number of detections per month at the core array, normalised by the number of lemon sharks fitted with active acoustic transmitters potentially available for detection, from September 2007 to September 2011

models improved dramatically when temporal auto-correlation was accounted for. An optimal time structure of a 13 d lag was found. This showed that it was important to account for shark presence 13 d prior, 12 d prior, and so forth. Results of the GLMM demonstrated that water temperature was the most important factor in predicting lemon shark presence (Fig. 4, Tables 1 & 2). Photoperiod had an effect as well but is also weakly correlated with water temperature. Moon phase and study year had no significant effect in predicting lemon shark presence.

Mean RI for sharks detected on the core array for >20 d ($n = 56$) showed a strong site fidelity to the middle of the array (Fig. 5). This is particularly true for a centrally located artificial reef site, which showed by far the highest RI (0.42). During the residency period from December to April, at the site of highest RI, the majority of lemon sharks were acoustically recorded during daylight hours (Fig. 6). A steady increase was recorded from midnight until 07:00 h eastern standard time, with the highest number of detections received at or around sunrise. Detections then steadily decreased from 07:00 to 12:00 h and remained relatively stable from 12:00 to 17:00 h. Following this, at around sunset, there was a rapid decline from 17:00 to 20:00 h and a stable rate from 20:00 to 23:00 h. The consistent proportion of detections from sentinel tags at fixed distances, across all hours of the day, demonstrates that the detection pattern of acoustically tagged sharks represents a true behav-

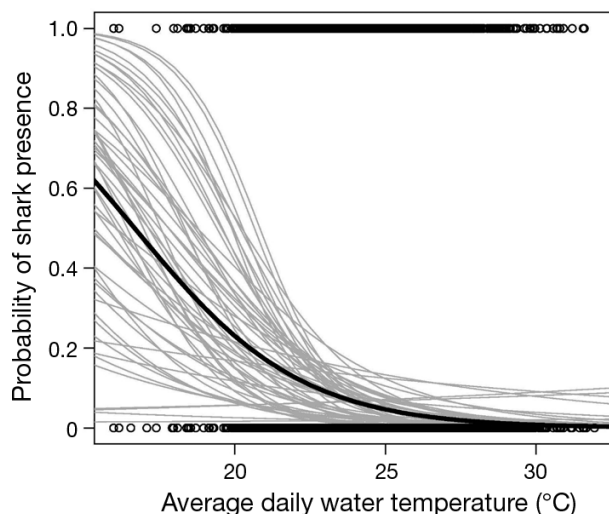


Fig. 4. Predicted probability of shark presence at different water temperatures based on GLMM. Each grey line represents a different individual shark ($n = 56$). The dark circles represent actual presence/absence data. The dark curve represents a mean prediction probability for all sharks

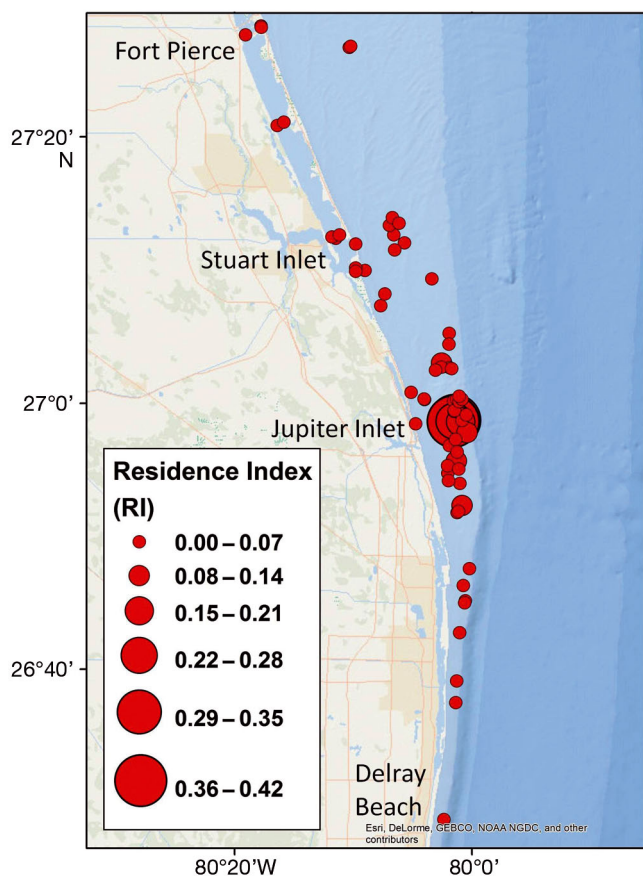


Fig. 5. Mean residence index (RI) by station for sharks that were detected on the core array for >20 d ($n = 56$). Sites with high RI values are composed of artificial reef sites on the 20–30 m depth reef line

our and is not an artefact of detection range variability (Payne et al. 2010).

Simultaneous monitoring of current and water temperature made it possible to assess presence or absence of lemon sharks at the site of highest RI in relation to these environmental parameters. From 6 to 18 March 2008, 7 of 15 acoustically tagged lemon sharks (46.7%) moved southward, relative to their predominant location within the array, then returned north around mid-March (Fig. 7). The southerly movement coincided with both a reduction in current strength from 600 to 5 mm s^{-1} and a drop in mean daily water temperature from 23 to 17°C. The return movement to the north coincided with both an increase in current strength and water temperature. However, subsequent comparable drops in current velocity (Fig. 7a) did not lead to a similar southward migration of lemon sharks. Both temperature and the presence of lemon shark were stable until the end of the residency period when all parameters were measured (Fig. 7b).

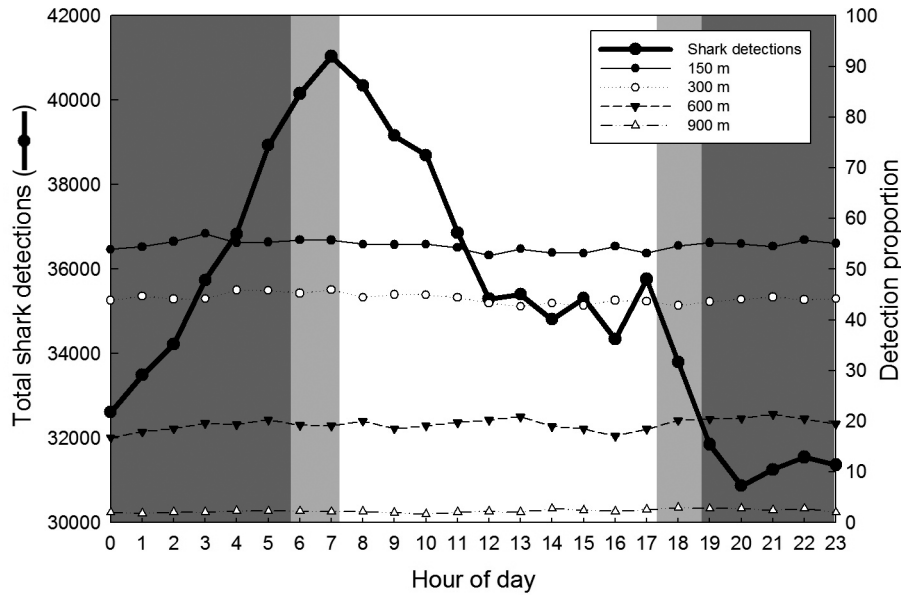


Fig. 6. Number of lemon shark detections (left-hand y-axis) at the receiver site of highest RI by hour of the day. Dark grey shading represents hours of darkness, light grey shading represents sunrise and sunset ranges from December to April, and no shading represents daylight hours. Right-hand y-axis represents detection proportions of fixed sentinel tags at 150, 300, 600 and 900 m horizontal distance from the receivers

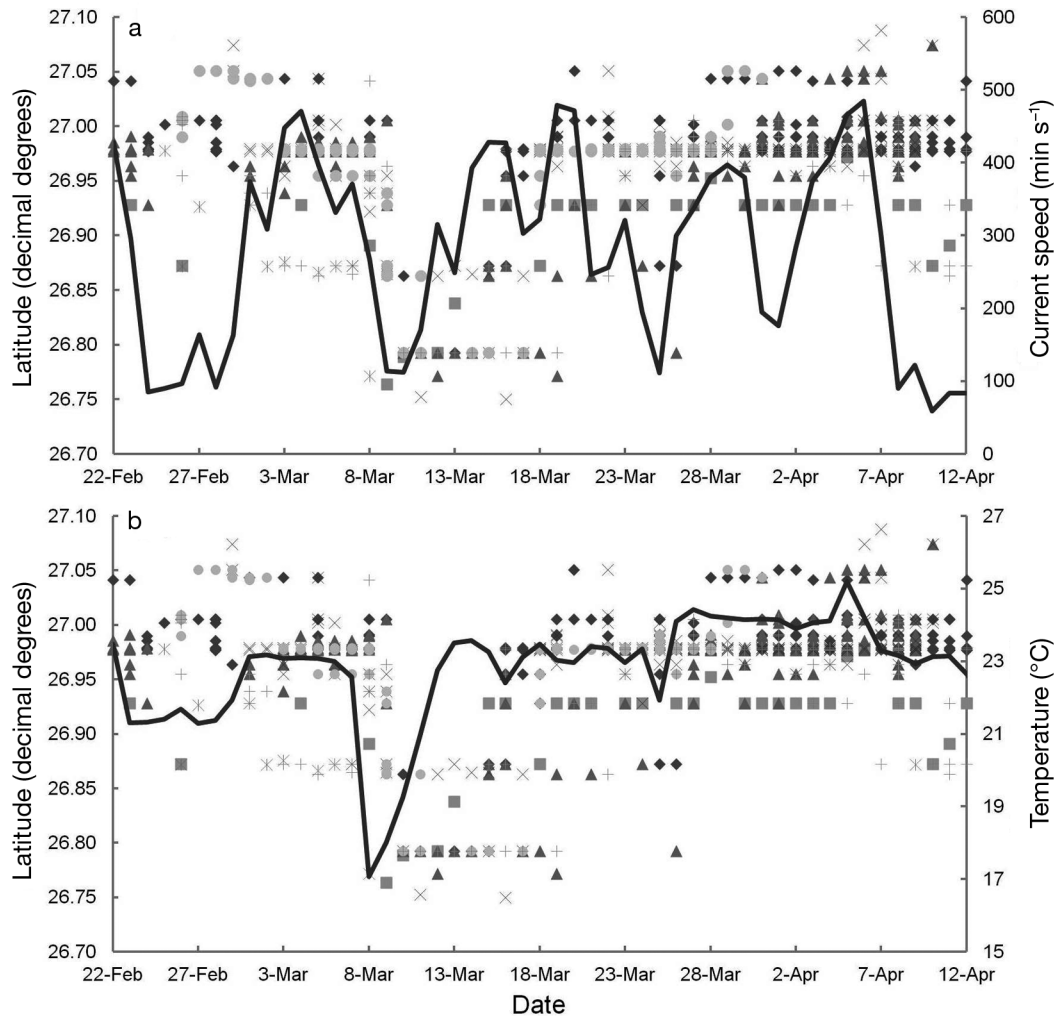


Fig. 7. Latitudinal movements of lemon sharks throughout the extent of the array coverage compared to (a) current speed and (b) average daily water temperature at the monitor sites of highest residence index (RI; latitude $26^{\circ}98'N$); unique symbols represent individual lemon sharks

During the residency period, tagged lemon sharks were predominately detected in southeast Florida waters, mostly within the core array coverage (Fig. 8). Three individuals were detected in waters of

Georgia during this time. In the summer months, May to August, tagged lemon sharks were recorded over a much larger geographical area to the north of the Jupiter array. This comprised a considerable por-

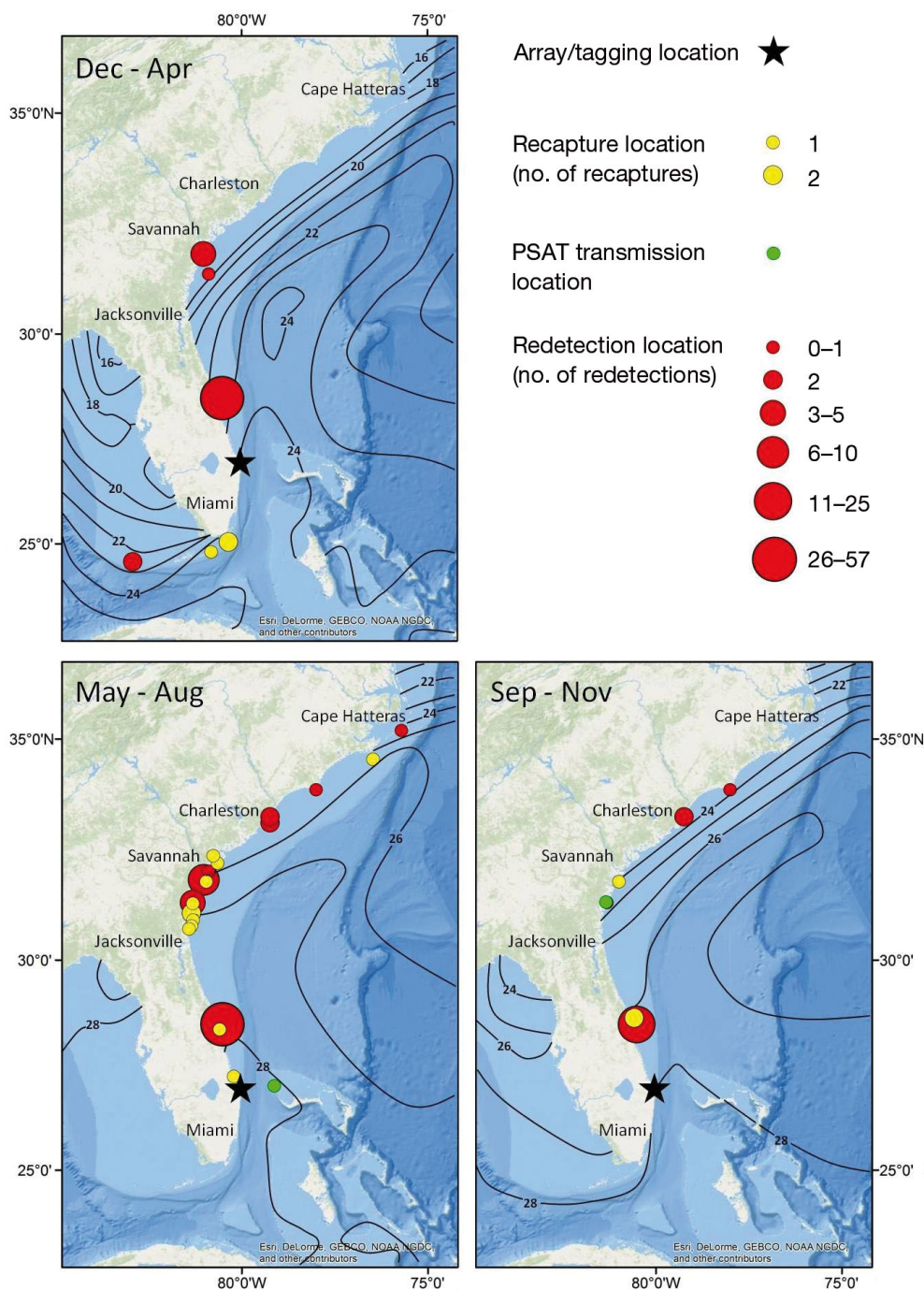


Fig. 8. Long distance transmitter detections and tag returns by time of year outside of the core array. Isobars are separated by 1°C and show northern extent of average sea surface temperature boundaries (www.noaa.gov). Yellow circles represent recapture locations, green circles represent pop-off satellite archival tag (PSAT) transmission locations, and red circles represent acoustic detection locations

tion of the USA eastern seaboard, spreading as far north as Cape Hatteras, North Carolina. One individual crossed the Gulf Stream into Bahamian waters, revealed by a PSAT pop-off location. From September to November, the tagged sharks still showed a relatively wide distribution to the north, but fewer individuals were recorded, suggesting they had begun their transition back to the southeast Florida region.

There were 17 unique haplotypes among 102 sampled lemon sharks. These haplotypes were not homogeneously distributed among sampling sites, with significant non-zero pairwise Φ_{ST} occurring between the Marquesas Key (MK) sample and both of the others, Cape Canaveral (CC) and Jupiter (JU) (MK-CC $\Phi_{ST} = 0.33$, $p < 0.00001$; MK-JU $\Phi_{ST} = 0.30$, $p < 0.00001$; Fig. 9). The Φ_{ST} between Cape Canaveral juveniles and Jupiter adults was not significantly different from zero ($\Phi_{ST} = 0.004$, $p > 0.64$; Fig. 9).

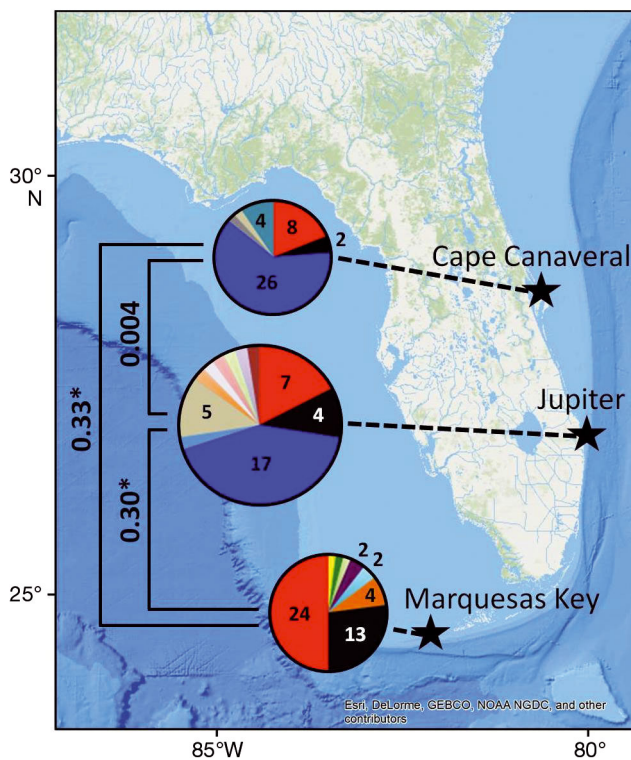


Fig. 9. Mitochondrial DNA haplotype frequencies for (from top to bottom) juvenile sharks sampled at Cape Canaveral ($n = 42$), adult sharks sampled at Jupiter ($n = 40$) and juvenile sharks sampled at Marquesas Key ($n = 40$). Black stars indicate the location of these sites; the pie charts show the haplotype frequencies (segments with no label have a value of 1). Pairwise Φ_{ST} between each sample is shown on the left.

*Significantly different values ($p < 0.0001$)

DISCUSSION

The present study describes the seasonal activity patterns of a large coastal species, the lemon shark *Negaprion brevirostris*, and attempts to describe the adult phase of this otherwise well studied species. Through capture, physical assessment, genetic sampling, passive acoustic telemetry and environmental monitoring, this study shows that lemon sharks primarily migrate from the north during the fall months, most probably driven by seasonal changes in water temperature, exhibit both short and long-term repetitive behaviour, are not actively mating during their winter residency, migrate northward in the spring as the water temperature warms and inhabit a considerably wider geographic area in the summer months. As such, evolution of spatial distribution and migration behaviour will be most accurately predicted in relation to changes in seasonal water temperatures.

The initial diver observations suggested that the lemon sharks aggregating off Jupiter were large enough to be adults, and this was confirmed, with the vast majority of individuals sampled above the minimum size of maturity (Brown & Gruber 1988). The residency period of these adult lemon sharks off the southeast Florida coast has clearly been identified as December through April, which was consistent across each of the 4 years assessed, 2008 to 2011. The burgeoning use of automated acoustic telemetry along the USA eastern seaboard allowed for the detection of lemon sharks well outside of the core study area, from as far south as the Dry Tortugas, Florida (minimum distance ≈ 490 km), and as far north as Cape Hatteras, North Carolina (minimum distance ≈ 1010 km). The wide geographical distribution of summer detections and recaptures shows that the winter residency of lemon sharks in southeast Florida represents a high concentration of individuals that seasonally inhabit a considerable geographical area. The timing of detections and recaptures outside of the study area show that the lemon sharks migrate northward following the winter residency period. Some individuals were recorded in the study area in the summer months, but the detections were much more sporadic than during the residency period.

The GLMM identified water temperature to be a very important environmental factor in predicting lemon shark presence and absence in this region (Fig. 4). Water temperature appeared in the top 10 best models (Table 1) and was highly significant (Table 2). Regionally, water temperature changes appear to be directly associated with localised latitu-

dinal movements of sharks between receiver sites. Other studies have similarly identified water temperature as a factor influencing the habitat use of coastal sharks (Carlisle & Starr 2009, Bessudo et al. 2011, Espinoza et al. 2011, Kneebone et al. 2012, Dudgeon et al. 2013), while other environmental variables have been found to exhibit an effect, such as prey abundance (Heupel & Hueter 2002, Torres et al. 2006, Barnett & Semmens 2012) salinity (Heupel & Simpfendorfer 2008, Ubeda et al. 2009) and dissolved oxygen (Carlson & Parsons 2001, Heithaus et al. 2009). Though the specific influence of these other potential factors is yet to be investigated in detail, the fact that both local movements during the residency period and the following meso-scale migrations are closely associated with changes in water temperature strongly suggests that water temperature primarily drives movements of lemon sharks across their annual distribution and is consistent with the results of Morrissey & Gruber (1993a) and Sundström et al. (2001), who documented the same behavioural association for immature lemon sharks. Similarly, Reyier et al. (2014) found water temperature to be the most probable factor influencing the winter distribution of juvenile lemon sharks off Cape Canaveral, which also exhibited temporary southward displacements in response to local declines in water temperature. Clearly, the residency period in southeast Florida coincides with the lowest annual water temperatures ($< 24^{\circ}\text{C}$) for the region. However, southerly movements to warmer waters during the residency period, coupled with the northward dispersal as latitudinal water temperature increases, indicates that these water temperatures represent the lower favoured tolerance for this species during the mature life stage. This increased understanding of this relationship could help to predict changes to timing and distribution in a changing climate.

Tagged lemon sharks of both sexes typically return to the study area between successive residency periods. The annual return of males to the aggregation site indicates that mature male lemon sharks display repeatability in the movement behaviour, which contradicts previous theories of nomadic mature males (Feldheim et al. 2002). The annual return of adult females to the Jupiter study area contrasts their identified biennial parturition periodicity (Feldheim et al. 2002, 2004, 2013, DiBattista et al. 2008). Other studies have noted that adult female sharks with biennial fecundity typically return to seasonal sites on an alternate year cycle; e.g. white shark *Carcharodon carcharias* aggregations at Guadalupe (Domeier & Nasby-Lucas 2007), sand tiger shark *Carcharias tau-*

rus aggregations at Wolf Rock, Australia (Bansemer & Bennett 2009), and nurse shark *Ginglymostoma cirratum* aggregations at the Dry Tortugas, Florida (Pratt & Carrier 2007). This pattern implies that use of these specific aggregation sites is related to the reproductive cycle of these sharks. The annual use of coastal waters off Jupiter, Florida, by adult females and the absence of any physical signs typical of carcharhinid courtship or copulation (e.g. fresh mating wounds on females, swollen claspers in males) suggest that lemon shark presence in the area is not driven by sexually motivated behaviour.

Several of the females sampled appeared to be gravid and many were near term, exhibiting very large girths, and pups could be felt to be moving when pressing a hand against the belly. Female lemon sharks may give birth on their northward migration. Genetic analysis demonstrated that the adults sampled in the Jupiter study area are significantly differentiated from juveniles sampled at the southern site in the Florida Keys but exhibit the same haplotype frequency as juveniles sampled to the north at Cape Canaveral. Cape Canaveral juveniles only overwintered at this site from December to February and migrated to north Florida, Georgia and the Carolinas in the spring and summer (Reyier et al. 2008, 2014). Since parturition takes place in spring in other locations (Feldheim et al. 2001b, 2002, 2004) and winter-captured individuals at Cape Canaveral have not been recorded with an open umbilicus (Reyier et al. 2008), it is probable these individuals are born in one or more of these northern regions during the spring or summer. It is therefore proposed that females documented off the coast of Jupiter give birth to the north of the overwintering area given that they exhibit the same haplotype frequency as the Canaveral-sampled juveniles and the timing and directionality of their annual migrations are very similar. It is highly improbable that females sampled off the coast of Jupiter primarily give birth to the south of the overwintering area in the Florida Keys, given the lack of movements into this area and the significant genetic differentiation observed between Marquesas Key juveniles and Jupiter adults.

RI analysis revealed that the central area of the array, just north of Jupiter Inlet, was the most commonly used area during the residency period (Fig. 5). Artificial reef sites along the submerged reef line were favoured with high RI values. It is most likely that the wintering lemon sharks are drawn to the elevated structure of these sites that may function as a point of association, concentrating individuals and facilitating predictable social interactions. This is a

behaviour similarly exhibited by sand tiger sharks *Carcharius taurus*, which are well documented to associate with distinct bottom structures, forming localised concentrations (Compagno 2001, Kneebone et al. 2012). As these sites appear to further concentrate lemon sharks that are already regionally concentrated from a considerably larger summer distribution (Fig. 8), it is suggested that the 15 to 30 m depth reef line extending from latitudes 26° 50' N to the south and 27° 04' N to the north may well constitute essential fish habitat (Kinney & Simpfendorfer 2009) for the adult life-stage of the lemon shark in USA waters. The use of the inter-coastal waterway habitat at, and to the north of, St. Lucie Inlet (Fig. 5) is a behaviour not previously documented for this species at the adult life-stage and may indicate adaptive potential to anthropogenic coastal alterations.

Lemon sharks resided at receiver sites primarily during daylight hours (Fig. 6), where, when undisturbed, they have been observed laying in polarized groups on the seafloor facing into the current (S. T. Kessel pers. obs.). Current associated polarization in resting groups was similarly observed for aggregating zebra sharks *Stegostoma fasciatum*, with the orientation facilitating respiration and reducing physiological costs (Dudgeon et al. 2013). Simultaneous monitoring of lemon sharks and detection range variability allows a confident conclusion that the observed diel pattern represents a true behaviour (Payne et al. 2010, Kessel et al. 2014). Active hunting has not been observed at the aggregation sites (video review, pers. obs. and pers. comm. with local sport divers 2008 to 2011), which, given the nocturnal reduction in detections, indicates that the lemon sharks are moving to areas not covered by the array at night to feed. Lemon sharks are well suited to nocturnal hunting, with good vision in low light conditions, and laboratory studies of juveniles show a nocturnal peak in activity (Cohen & Gruber 1977, Nixon & Gruber 1988, Cohen 1990). Daytime group resting and nighttime foraging over a larger geographical area is a common behaviour exhibited by elasmobranchs (Papastamatiou & Lowe 2012). More specifically, aggregations of scalloped hammerhead shark *Sphyrna lewini* near seamounts in the Gulf of California also primarily occur during daylight hours, dissolving at night as individuals or small groups depart to feed (Klimley & Nelson 1984, Klimley et al. 1988). The pattern of steadily increasing detections after midnight indicates that after the lemon sharks successfully forage, they begin to return to the artificial reefs to rest and digest their meals (Sims et al. 2006, Dudgeon et al. 2013), with possibly the last or

least successful individuals returning for the peak of detections at or around sunrise. The steady decline from 07:00 to 12:00 h may be the result of increasing anthropogenic disturbance throughout the day, particularly from SCUBA divers. Alternatively, this could be related to a social or physiological phenomenon. Further investigation is required to elucidate the causes driving this trend.

The findings of this study suggest a 'migration-residency' model for mature lemon shark movements and behaviour in the region. While this model requires further quantitative assessment, it is consistent with the data generated in this 4 yr study. It has been demonstrated that many of the lemon sharks using the southeast Florida region reside over a much larger area in northern coastal and estuarine areas during the summer months. As water temperatures drop in the early fall, they migrate southward, reaching the waters off Jupiter between November and early January. The continental shelf off Jupiter is narrow, and the warm Florida current flows closer inshore there than at any other part of the coast (Pillsbury 1891). Southward migrating lemon sharks probably stop and concentrate off the coast of Jupiter when they first encounter the warm temperatures of the Gulf Stream, where they then orient to bathymetric features such as shipwrecks and reef structure. Lemon sharks remained in this broad area until April. As water temperatures began to rise, they moved northward, reaching Cape Canaveral by April–May and then Georgia, South Carolina and North Carolina as water temperatures became favourable in the summer months. It is probable that the most northerly recorded distribution at Cape Hatteras is defined by the cold water-temperature boundary of the Northern Atlantic Recirculation Gyre. It is speculated that mating and parturition takes place in late May or June somewhere between northern Florida and the Georgia-Carolina area. Evidence from this study indicates that predicting the evolution of spatial and migration behaviour for mature lemon sharks in the northwest Atlantic will be strongly linked to climate change-driven temperature variations.

CONCLUSION

Repeated seasonal behaviour in adult sharks has important management implications, yet has been underemphasized in relation to protection of juvenile aggregations and nursery areas (Hoenig & Gruber 1990, Musick et al. 2000, Kinney & Simpfendorfer 2009). It is well established that predictable concen-

trated presence greatly increases a species' catchability (De Mitcheson et al. 2008). For lemon sharks in southeast Florida, this is particularly true for the centre of the study area, where they exhibited the highest site-fidelity. For slow-growing species with low fecundity, like the lemon shark, the adult life stages are the most critical for sustaining the population (Kinney & Simpfendorfer 2009). Thus, the predictable presence of adult lemon sharks around specific bathymetric features signals a high potential for overexploitation in our study area during the winter months. In recognition of this increased vulnerability, in March 2010, lemon sharks were listed as a prohibited species in Florida state waters¹. However, many areas of high site fidelity were recorded outside of state waters, demonstrating current management measures to be spatially insufficient. Limiting fishing pressure on predictable aggregations of adults will be an important component of restoration efforts for depleted shark populations. This study has highlighted the importance of determining the causes of adult shark seasonal residency and seasonal distribution to be able to predict the impacts of anthropogenic and environmental disturbance (e.g. fishing pressure and climate change, respectively) on shark behaviour and to assess the potential for downstream effects on shark population dynamics and the ecosystems they inhabit.

Acknowledgements. Funding was primarily provided by the Swiss Shark Foundation – Hai Stiftung, and additionally by the National Geographic Society, Bimini Biological Field Station Foundation and Guy Harvey Ocean Foundation. The authors thank Walt Stearns for bringing the aggregations to our attention and for assisting with field work. For logistical support and many hours of their personal time, thanks to Bill Parks, Cheryl Carroll, Joanne and John Fraser, Tony Grogan, Phil Bessler and John David Newman. David Fugate at the Florida Gulf Coast University provided equipment loans. Thanks to David Kerstetter and Jürg Brunnenschweiler für PSAT tag donations. All the many staff and volunteers, including those that gave boat time and diver reports, facilitated the field work element of this study. Eric D. Johnson, Paul Van Dam-Bates, Eric D. Stolen and Dale Webber provided statistical advice. Nigel Hussey and Aaron Fisk provided guidance and logistical support. We acknowledge all FACT and ACT members, particularly Joy Young with the FWC Tequesta Lab and Eric Reyier at Kennedy Space Centre, who provided us with lemon shark detections outside of our personal acoustic coverage. Finally, we thank the editor and 3 anonymous reviewers for their constructive comments on an early draft of the manuscript, which improved the current version.

¹See Florida Administrative Code, Section 68B-44.008 Final, effective 03/21/2010 (ID 8394203), www.flrules.org/gateway/ruleNo.asp?id=68B-44.008&Section=0

LITERATURE CITED

- Alerstam T (2008) No way home—The decline of the world's great animal migrations. *Science* 319:572–572
- Anderson ED (1990) Estimates of large shark catches in the Western Atlantic and Gulf of Mexico 1960–1986. In: Pratt HL Jr, Gruber SH, Taniuchi T (eds) *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries*. NOAA Tech Rep NMFS 90:443–454
- Bansemmer CS, Bennett MB (2009) Reproductive periodicity, localised movements and behavioural segregation of pregnant *Carcharias taurus* at Wolf Rock, southeast Queensland, Australia. *Mar Ecol Prog Ser* 374:215–227
- Barnett A, Semmens JM (2012) Sequential movement into coastal habitats and high spatial overlap of predator and prey suggest high predation pressure in protected areas. *Oikos* 121:882–890
- Bates D, Mächler M, Bolker B (2011) lme4: linear mixed-effects models using S4 classes. R package version 0.999375-42, <http://cran.R-project.org/package=lme4>
- Bessudo S, Soler GA, Klimley AP, Ketchum JT, Hearn A, Arauz R (2011) Residency of the scalloped hammerhead shark (*Sphyrna lewini*) at Malpelo Island and evidence of migration to other islands in the Eastern Tropical Pacific. *Environ Biol Fishes* 91:165–176
- Bestley S, Jonsen ID, Hindell MA, Guinet C, Charrassin JB (2013) Integrative modelling of animal movement: incorporating in situ habitat and behavioural information for a migratory marine predator. *Proc R Soc Lond B Biol Sci* 280(1750):20122262
- Block BA, Jonsen ID, Jorgensen SJ, Winship AJ and others (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* 475:86–90
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135
- Bond ME, Babcock EA, Piskitch EK, Abercrombie DL, Lamb NF, Chapman DD (2012) Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier Reef. *PLoS ONE* 7:e32983
- Brockwell PJ, Davis RA (2002) *Introduction to time series and forecasting*. Taylor and Francis, Oxford
- Brown CA, Gruber SH (1988) Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral centra. *Copeia* 747–753
- Carlisle AB, Starr RM (2009) Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. *Mar Ecol Prog Ser* 380:213–228
- Carlson J, Parsons G (2001) The effects of hypoxia on three sympatric shark species: physiological and behavioral responses. *Environ Biol Fishes* 61:427–433
- Chapman DD, Babcock EA, Gruber SH, DiBattista JD and others (2009) Long-term natal site-fidelity by immature lemon sharks (*Negaprion brevirostris*) at a subtropical island. *Mol Ecol* 18:3500–3507
- Clarke S (2008) Use of shark fin trade data to estimate historic total shark removals in the Atlantic Ocean. *Aquat Living Resour* 21:373–381
- Cohen JL (1990) Adaptations for scotopic vision in the lemon shark (*Negaprion brevirostris*). *J Exp Zool* 256:76–84
- Cohen JL, Gruber SH (1977) Spectral sensitivity and Purkinje shift in retina of lemon shark, *Negaprion brevirostris*

- (Poey). *Vision Res* 17:787–792
- Compagno LJ (1984) An annotated and illustrated catalogue of shark species known to date. In: FAO (ed) *Sharks of the world, Book 4*. FAO, Rome
- Compagno LJ (2001) *Sharks of the world: an annotated and illustrated catalogue of shark species known to date, Vol 2*. FAO, Rome
- Cortes E, Gruber SH (1990) Diet, feeding-habits and estimates of daily ration of young lemon sharks, *Negaprion brevirostris* (Poey). *Copeia* 204–218
- Costello C, Rassweiler A, Siegel D, De Leo G, Micheli F, Rosenberg A (2010) The value of spatial information in MPA network design. *Proc Natl Acad Sci USA* 107: 18294–18299
- de Freitas RHA, Rosa RS, Wetherbee BM, Gruber SH (2009) Population size and survivorship for juvenile lemon sharks (*Negaprion brevirostris*) on their nursery grounds at a marine protected area in Brazil. *Neotrop Ichthyol* 7:205–212
- De Mitcheson YS, Cornish A, Domeier M, Colin PL, Russell M, Lindeman KC (2008) A global baseline for spawning aggregations of reef fishes. *Conserv Biol* 22:1233–1244
- DiBattista JD, Feldheim KA, Gruber SH, Hendry AP (2007) When bigger is not better: selection against large size, high condition and fast growth in juvenile lemon sharks. *J Evol Biol* 20:201–212
- DiBattista JD, Feldheim KA, Thibert-Plante X, Gruber SH, Hendry AP (2008) A genetic assessment of polyandry and breeding-site fidelity in lemon sharks. *Mol Ecol* 17: 3337–3351
- Domeier ML, Nasby-Lucas N (2007) Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico). *Mar Biol* 150:977–984
- Drummond AJ, Ashton B, Buxton S, Cheung M and others (2010) Geneious 5.1.7. Available at www.geneious.com
- Dudgeon CL, Lanyon JM, Semmens JM (2013) Seasonality and site fidelity of the zebra shark, *Stegostoma fasciatum*, in southeast Queensland, Australia. *Anim Behav* 85:471–481
- Dulvy NK, Fowler SL, Musick JA, Cavanagh RD and others (2014) Extinction risk and conservation of the world's sharks and rays. *eLife* 3:e00590
- Ersts PJ (2013) Geographic Distance Matrix Generator (version 1.2.3). Available at http://biodiversityinformatics.amnh.org/open_source/gdmg (accessed 10 January 2013)
- Espinoza M, Farrugia TJ, Lowe CG (2011) Habitat use, movements and site fidelity of the gray smooth-hound shark (*Mustelus californicus* Gill 1863) in a newly restored southern California estuary. *J Exp Mar Biol Ecol* 401:63–74
- Excoffier L, Lischer HEL (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol Ecol Resour* 10: 564–567
- Feldheim KA, Gruber SH, Ashley MV (2001a) Population genetic structure of the lemon shark (*Negaprion brevirostris*) in the western Atlantic: DNA microsatellite variation. *Mol Ecol* 10:295–303
- Feldheim KA, Gruber SH, Ashley MV, McEachran JD (2001b) Multiple paternity of a lemon shark litter (Chondrichthyes: Carcharhinidae). *Copeia* 2001:781–786
- Feldheim KA, Gruber SH, Ashley MV (2002) The breeding biology of lemon sharks at a tropical nursery lagoon. *Proc Biol Sci* 269:1655–1661
- Feldheim KA, Gruber SH, Ashley MV, Orti G (2004) Reconstruction of parental microsatellite genotypes reveals female polyandry and philopatry in the lemon shark, *Negaprion brevirostris*. *Evolution* 58:2332–2342
- Feldheim KA, Gruber SH, DiBattista JD, Babcock EA and others (2014) Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. *Mol Ecol* 23:110–117
- Gruber SH (1982) Role of the lemon shark *Negaprion brevirostris* as a predator in the tropical marine environment: a multidisciplinary study. *Fla Sci* 45:46–75
- Gruber SH (1984) Bioenergetics of the captive and free ranging lemon shark. *Proc Am Assoc Zool Parks Aquar* 60:340–373
- Heithaus MR, Delius BK, Wirsing AJ, Dunphy-Daly MM (2009) Physical factors influencing the distribution of a top predator in a subtropical oligotrophic estuary. *Limnol Oceanogr* 54:472–482
- Heupel MR, Hueter RE (2002) Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. *Mar Freshw Res* 53:543–550
- Heupel MR, Simpfendorfer CA (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. *Aquat Biol* 1:277–289
- Heupel MR, Webber DM (2012) Trends in acoustic tracking: Where are the fish going and how will we follow them? *Am Fish Soc Symp* 76:219–231
- Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Mar Freshw Res* 57:1–13
- Hoenig JM, Gruber SH (1990) Life-history patterns in elasmobranchs: implications for fisheries management. In: Pratt HL Jr, Gruber SH, Taniuchi T (eds) *Elasmobranchs as living resources: advances in the biology, ecology, systematics and the status of the fisheries*. NOAA Tech Rep 90:1–16
- Holland KN, Wetherbee BM, Lowe CG, Meyer CG (1999) Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. *Mar Biol* 134:665–673
- Kajiura SM, Sebastian AP, Tricas TC (2000) Dermal bite wounds as indicators of reproductive seasonality and behaviour in the Atlantic stingray, *Dasyatis sabina*. *Environ Biol Fishes* 58:23–31
- Keeney DB, Heupel M, Hueter RE, Heist EJ (2003) Genetic heterogeneity among blacktip shark, *Carcharhinus limbatus*, continental nurseries along the U.S. Atlantic and Gulf of Mexico. *Mar Biol* 143:1039–1046
- Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. *Rev Fish Biol Fish* 24:199–218
- Kinney MJ, Simpfendorfer CA (2009) Reassessing the value of nursery areas to shark conservation and management. *Conserv Lett* 2:53–60
- Klimley AP (1980) Observations of courtship and copulation in the nurse shark, *Ginglymostoma cirratum*. *Copeia* 878–882
- Klimley AP, Nelson DR (1984) Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. *Behav Ecol Sociobiol* 15:45–54
- Klimley AP, Butler SB, Nelson DR, Stull AT (1988) Diel movements of scalloped hammerhead sharks, *Sphyrna*

- lewini* Griffith and Smith, to and from a seamount in the Gulf of California. *J Fish Biol* 33:751–761
- Kneebone J, Chisholm J, Skomal GB (2012) Seasonal residency, habitat use, and site fidelity of juvenile sand tiger sharks *Carcharias taurus* in a Massachusetts estuary. *Mar Ecol Prog Ser* 471:165–181
- Kohler NE, Turner PA (2001) Shark tagging: a review of conventional methods and studies. *Environ Biol Fishes* 60:191–224
- Koslow JA, Couture J (2013) Ocean sciences: follow the fish. *Nature* 502:163–164
- Martin TG, Chadés I, Arcese P, Marra PP, Possingham HP, Norris DR (2007) Optimal conservation of migratory species. *PLoS ONE* 2:e751
- Matsunaga H, Nakano H (1999) Species composition and CPUE of pelagic sharks caught by Japanese longline research and training vessels in the Pacific Ocean. *Fish Sci* 65:16–22
- Morales JM, Ellner SP (2002) Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology* 83:2240–2247
- Morgan A, Cooper PW, Curtis T, Burgess GH (2009) Overview of the U.S. east coast bottom longline shark fishery, 1994–2003. *Mar Fish Rev* 71:23–38
- Morrissey JF, Gruber SH (1993a) Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. *Environ Biol Fishes* 38:311–319
- Morrissey JF, Gruber SH (1993b) Home range of juvenile lemon sharks, *Negaprion brevirostris*. *Copeia* 425–434
- Motta P, Tricas T, Summers R (1997) Feeding mechanism and functional morphology of the jaws of the lemon shark *Negaprion brevirostris* (Chondrichthyes, Carcharhinidae). *J Exp Biol* 200:2765–2780
- Musick JA, Burgess G, Cailliet G, Camhi M, Fordham S (2000) Management of sharks and their relatives (Elasmobranchii). *Fisheries* (Bethesda, Md) 25:9–13
- Newman SP, Handy RD, Gruber SH (2010) Diet and prey preference of juvenile lemon sharks *Negaprion brevirostris*. *Mar Ecol Prog Ser* 398:221–234
- Nixon AJ, Gruber SH (1988) Diel metabolic and activity patterns of the lemon shark (*Negaprion brevirostris*). *J Exp Zool* 248:1–6
- Papastamatiou YP, Lowe CG (2012) An analytical and hypothesis-driven approach to elasmobranch movement studies. *J Fish Biol* 80:1342–1360
- Pauly D, Watson R, Alder J (2005) Global trends in world fisheries: impacts on marine ecosystems and food security. *Philos Trans R Soc Lond B* 360:5–12
- Payne N, Gillanders B, Webber D, Semmens J (2010) Interpreting diel activity patterns from acoustic telemetry: the need for controls. *Mar Ecol Prog Ser* 419:295–301
- Pillsbury JE (1891) The Gulf Stream off Jupiter Inlet and Cape Hatteras. The Equatorial Current. The Gulf Stream: methods of investigation and results of the research. Government Printing Office, Washington, DC
- Pratt HL Jr, Carrier JC (2007) The nurse shark, *Ginglymostoma cirratum* mating and nursery habitat in the Dry Tortugas, Florida. In: McCandless CT, Kohler HE, Pratt HL Jr (eds) Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. *Am Fish Soc Symp* 50, Bethesda, MD, p 225–236
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Reyier EA, Adams DH, Lowers RH (2008) First evidence of a high density nursery ground for the lemon shark, *Negaprion brevirostris*, near Cape Canaveral, Florida. *Fla Sci* 71:134–148
- Reyier EA, Franks BR, Chapman DD, Scheidt DM, Stolen ED, Gruber SH (2014) Regional-scale migrations and habitat use of juvenile lemon sharks (*Negaprion brevirostris*) in the US South Atlantic. *PLoS ONE* 9:e88470
- Schneider DC (1994) Quantitative ecology: spatial and temporal scaling. Elsevier Science, San Diego, CA
- Sims DW, Wearmouth VJ, Southall EJ, Hill JM and others (2006) Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *J Anim Ecol* 75:176–190
- Speed CW, Meekan MG, Field IC, McMahon CR and others (2011) Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. *Mar Ecol Prog Ser* 429:261–275
- Sundström LF, Gruber SH (1998) Using speed-sensing transmitters to construct a bioenergetics model for subadult lemon sharks, *Negaprion brevirostris* (Poey), in the field. *Hydrobiologia* 371–372:241–247
- Sundström LF, Gruber SH, Clermont SM, Correia JPS and others (2001) Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion Brevirostris*, around Bimini Islands, Bahamas. *Environ Biol Fishes* 60:225–250
- Sutherland WJ (1998) The importance of behavioural studies in conservation biology. *Anim Behav* 56:801–809
- Thiem J, Taylor M, McConnachie S, Binder T, Cooke S (2011) Trends in the reporting of tagging procedures for fish telemetry studies that have used surgical implantation of transmitters: a call for more complete reporting. *Rev Fish Biol Fish* 21:117–126
- Torres LG, Heithaus MR, Delius B (2006) Influence of teleost abundance on the distribution and abundance of sharks in Florida Bay, USA. *Hydrobiologia* 569:449–455
- Ubeda AJ, Simpfendorfer CA, Heupel MR (2009) Movements of bonnetheads, *Sphyrna tiburo*, as a response to salinity change in a Florida estuary. *Environ Biol Fishes* 84:293–303
- Watsky MA, Gruber SH (1990) Induction and duration of tonic immobility in the lemon shark, *Negaprion brevirostris*. *Fish Physiol Biochem* 8:207–210
- Worm B, Davis B, Kettemer L, Ward-Paige CA and others (2013) Global catches, exploitation rates, and rebuilding options for sharks. *Mar Policy* 40:194–204
- Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2011) Mixed effects models and extensions in ecology with R. Springer, New York, NY

Editorial responsibility: Nicholas Tolimieri,
Seattle, Washington, USA

Submitted: May 2, 2014; Accepted: July 23, 2014
Proofs received from author(s): October 20, 2014