

Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary

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Abstract The use of a coastal estuary by bonnethead sharks, *Sphyrna tiburo*, was examined by acoustic monitoring, gillnet sampling and tag-recapture studies. Acoustic monitoring data were used to define the residency and movement patterns of sharks within Pine Island Sound, Charlotte Harbor, Florida. Sharks were monitored for periods of 1–173 days with individuals regularly moving in and out of the detection range of the acoustic system. Patterns of movement could not be correlated with tidal level or time of day. Home range sizes within the Pine Island Sound population were typically small with individuals using core areas on a daily basis. However, core areas shifted within the study site over time resulting in eventual usage of most of the available habitat. Gillnet sampling revealed that *S. tiburo* were abundant in shallow water near seagrass beds, but that presence of individuals at specific sites was variable. Tag-recapture data showed that most individuals remained within the Pine Island Sound region over time and did not appear to undergo long coastal migrations. The movement and residence patterns of *S. tiburo*

suggest that individuals are resident within the estuary, but do not show site fidelity to specific areas within the estuary.

Keywords Home range · Presence · Habitat use · Shark

Introduction

The introduction of concepts such as ‘Essential Fish Habitat’, ‘Critical Habitat’ and ‘Marine Protected Areas’ into fisheries management has driven a need for information on habitat use of fish species. This, combined with advances in telemetry systems, has resulted in research to define habitat use becoming an increasingly important topic in marine science. Understanding how much area an individual uses over the course of a day, month or year is vital to understanding the biology and life history of a species. These data are important for both biological and management purposes.

The bonnethead shark, *Sphyrna tiburo*, is a common resident of coastal and estuarine waters of the tropical and subtropical Western Atlantic and Eastern Pacific (Compagno 1984). The population size, demographics (e.g. Cortés and Parsons 1996; Lombardi-Carlson et al. 2003), growth rate (e.g. Parsons 1993a; Carlson and Parsons 1997; Lombardi-Carlson et al. 2003), reproductive

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biology (e.g. Parsons 1993b; Manire et al. 1995) and feeding ecology (Cortés et al. 1996) of this species has been well studied by numerous investigators. Despite a good understanding of its life history there is little detailed information available on its habitat use and residency patterns. Work by Myrberg and Gruber (1974) described the behavior of a group of captive *S. tiburo*, but little else has been published. The bonnethead shark is part of the small coastal shark cluster monitored by the National Marine Fisheries Service and therefore information on its diet, movement patterns and behavior may be important for future management of this species.

To identify habitat use of a species, data on the presence, location and movement patterns of individuals must be collected. Historically these types of data were collected by conducting mark-recapture studies or by examining catch rates in different types of habitat (e.g. Olsen 1953; Smith and Abramson 1990; Musick et al. 1993; Kohler and Turner 2001; Simpfendorfer and Heupel 2004). This approach has provided a large amount of data about the presence of fish species. However, the advent of radio, acoustic, archival and satellite tracking technology has provided researchers new avenues for examining the residency of target species within a specific habitat (e.g. Wilkerson and Fisher 1997; Meyer et al. 2000; Block et al. 2001; Boustany et al. 2002; Young and Isley 2002; Sims et al. 2003; Wetherbee et al. 2003). More recently researchers have begun to use acoustic monitoring technology to simultaneously provide long-term data about the presence and movement patterns of groups of individuals within a population (e.g. Heupel and Hueter 2001; Starr et al. 2001; Lowe et al. 2003; Heupel et al. 2004; Ohta and Kakuma 2005).

Acoustic monitoring has been used to examine a wide array of biological, ecological and fisheries questions regarding a species (e.g. Starr et al. 2001; Heupel and Simpfendorfer 2002; Lowe et al. 2003; Heupel et al. 2004; Ohta and Kakuma 2005). This technology is typically applied to species that are easily accessed and are likely to remain within a defined geographic region. The predominance of bonnethead sharks along coastal Florida and the lack of data on their movement

patterns make this species an ideal candidate for acoustic monitoring studies.

Anecdotal and unpublished data from Florida suggest that *S. tiburo* may not move far during the course of a summer season (May to November) and that individuals may show site fidelity to specific regions within estuaries. The purpose of this research was to examine the residency and movement patterns of *S. tiburo* within a large estuarine system on the Gulf of Mexico coast of Florida during summer seasons to better define the behavior of this species within its natural habitat. Data from multiple sources were utilized and the results compared to determine differences between each type of analysis. The primary source of data was an acoustic monitoring study carried out between 2002 and 2004. Additional data were obtained from gillnet surveys carried out in the same area over a 10 year period (1995–2004) and from tag-recaptures of animals released during gillnet surveys. Results from all of these sources were integrated to provide a comprehensive picture of how *S. tiburo* use a large estuarine system.

Material and methods

Study site

Pine Island Sound is a large semi-enclosed coastal lagoon in lower Charlotte Harbor, Florida (Fig. 1). The boundaries of the study site are defined by the barrier islands; Captiva and Sanibel on the west side and Pine Island on the east side of the sound. The shore of the sound is mostly undeveloped, with sections of the barrier islands consisting of protected park or National Wildlife Refuge lands. Mangroves are the dominant shoreline vegetation, with red mangroves, *Rhizophora mangle*, the most common species. Pine Island Sound is dominated by muddy substrates with large seagrass beds in areas where water depth is less than 2 m. Approximately 20% of the monitored area (36 km²) has seagrass coverage (Fig. 1). Seagrass beds consist of three main species: manatee grass, *Syringodium filiforme*, turtle grass, *Thalassia testudinum*, and shoal grass, *Halodule wrightii*. Depths range from 1 to 7 m

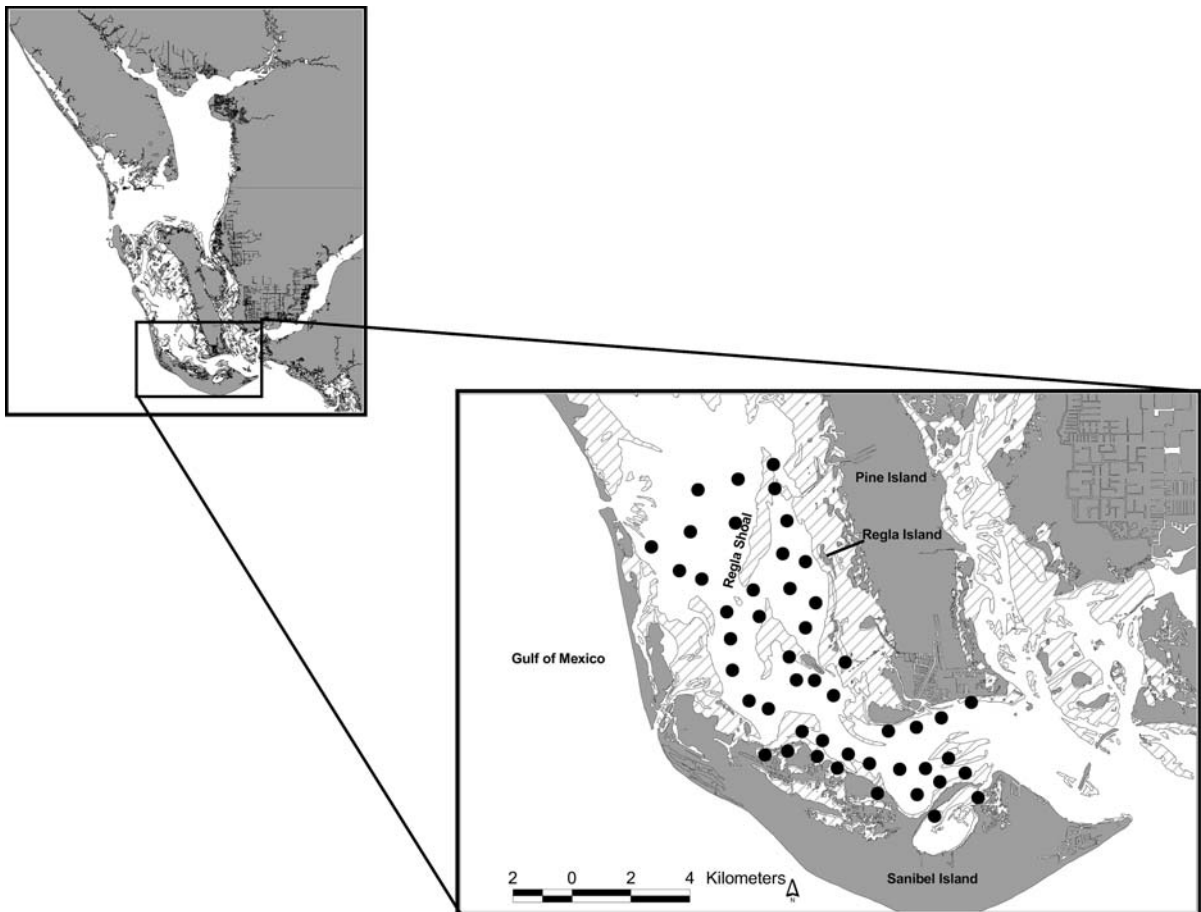


Fig. 1 Map of Pine Island Sound in the lower portion of Charlotte Harbor, Florida. Study site is indicated on the wider Charlotte Harbor map. Points indicate the location

of acoustic receivers within the study site. Crosshatch indicates seagrass beds. Relevant landmarks are labeled

with most of the area 3 m or less. Greatest depths within the study site are within the intracoastal waterway navigation channel that runs through the middle of the study region. The open water area of Pine Island Sound is approximately 304 km², with approximately 184 km² monitored during the course of this study.

Environmental conditions within Pine Island Sound can vary dramatically due to freshwater input from the Caloosahatchee River and several connections to the Gulf of Mexico. The Caloosahatchee River runs from Lake Okeechobee to San Carlos Bay (adjacent to Pine Island Sound) and is used to drain water from the lake and therefore can have very high flow rates during the summer wet season. Changes in flow rate in the river result in variable salinity conditions within

the study site. Water quality (temperature, salinity and dissolved oxygen) within the study site was recorded at each receiver station every time data were downloaded (every second week) to characterize the conditions within the study site during the study period.

Acoustic monitoring

A series of 49 VR2 acoustic hydrophones (Vemco Ltd.) were deployed within the study site to passively track the movement of sharks (Fig. 1) from April to November of 2003 and 2004. Receivers were removed from the study site during winter months (December–March) based on a lack of bonnethead shark captures during winter gillnet sampling efforts (MML unpublished data).

Bonnethead sharks are known to be seasonal residents of estuaries in this region suggesting that monitoring during winter months would be unproductive and not cost effective.

Methods for deploying hydrophone stations were identical to those previously described by Heupel and Hueter (2001). Hydrophones recorded the time, date and identity of sharks fitted with acoustic transmitters that swam within range of the units. Hydrophone stations were single frequency, omnidirectional receivers and had an approximate detection range of 800 m within Pine Island Sound (Heupel unpublished data). Range testing over multiple days within the study site showed that detection regions ranged up to 1,200 m within the study site. Probability of receiving signal detection over 1,000 m declined somewhat, so a conservative area of approximately 800 m detection range was used. This detection range allowed sharks to often be detected at more than one station simultaneously. The data analysis section provides detailed methods on how hydrophone data were processed.

Sharks were captured by gillnet, weighed, measured, tagged with a dart tag, and surgically fitted with a Vemco RCODE 16×65 mm transmitter for passive monitoring via the hydrophone array. Transmitters were surgically implanted into the abdominal cavity of all sharks. A 2–3 cm incision was made to allow transmitter insertion and was sutured using two running stitches in both the muscle and skin layers using suture silk and disposable needles. Surgical procedures were typically completed in less than 5 min. All passively monitored animals were in good condition upon capture and released in good condition within 10 min of landing on the vessel. Transmitters were coded with a unique pulse series for each shark, operated on 69.0 kHz at randomly spaced intervals between 45 s and 75 s, and had a battery life of at least 18 months. Random signal transmission times prevented more than one signal continuously overlapping and blocking detection by a hydrophone station.

Data analysis

Data from the hydrophone stations were used to examine the residence and movement patterns of

S. tiburo within the study site. Residency of all tagged sharks was assessed on a daily basis, with individuals considered present in the study site if a signal was detected on any receiver in the array on a given day. Residency histories were plotted by day to provide a visually interpretable timeline of animals present in the study site. The number of continuous days that individuals were resident in the study site was calculated (each time they entered the study site). To compare the number of continuous days present between years the data were log transformed and a *t*-test performed.

The acoustic monitoring data was examined to determine the potential influence of changes in water depth associated with the tidal cycle on the movements of *S. tiburo* or the performance of the equipment. The number of detections in 30-min periods was calculated for individual sharks. The tidal height for each 30-min period was then calculated from standard US tide tables for Galt Island, Pine Island Sound using Maptech Tides and Currents software. Tidal heights were divided into 20 cm bins and the number of detections in each bin was summed across all days that an individual was monitored. A χ^2 square goodness-of-fit test was then used to compare the frequency of the binned data with the frequency of all tidal heights during the period each individual was monitored. Statistically significant differences in frequency distributions would indicate that signal detection occurred differently at different tidal heights. The existence of differences would have several interpretations. For example, increased detections at higher tidal levels may suggest that greater water depth increased the detection range of receivers which would have enabled greater detection of individuals on shallow grass beds. Alternatively, increased frequency of detections at lower tidal heights would suggest that individuals may be moving onto shallow seagrass areas at higher tidal heights (and be less likely to be detected by the receivers) and moving back into more open waters at lower tides.

To examine for differences in movement patterns at different times of the day a similar approach to that used with the tidal data was applied. The number of detections in one hour bins was summed for individual sharks. χ^2 goodness-of-fit tests were used to compare the

frequency of detections to an even distribution (i.e. assuming an equal number of detections in each hour). Significant differences indicated that individuals were more frequently detected at particular times of the day, potentially identifying diel patterns of behavior.

The center of activity location of each tagged *S. tiburo* within Pine Island Sound was calculated every 30 min using a mean position algorithm (Simpfendorfer et al. 2002). Center of activity locations represent an average location for a specific 30-min period, and differ slightly from tracking data that typically provide a point estimate on a shorter interval (e.g. 15 min). The error of mean position estimates, relative to real time locations, has been calculated at approximately 225 m for small sharks (Simpfendorfer et al. 2002). The distance between consecutive centers of activities was calculated using standard geometric formulae. This distance was not a measure of the rate or distance moved, but rather an indicator of the linearity of movement. When a shark had a movement pattern that involved repeated use of the same area for a period greater than an hour the distance between consecutive centers of activity would be small. Alternatively, when a shark had a movement pattern that involved directional movement, the distance between consecutive centers of activity was large.

Home ranges of individual sharks were calculated based on center of activity locations using 50% and 95% fixed kernel estimates to examine the utilization of space within the home range area. Kernel estimates were made using the Animal Movement Extension for ArcView (Hooge and Eichenlaub 2000). Changes in home range over time were investigated by examining daily, weekly, and entire season home range sizes for individual sharks. Linear regression was used to determine if there was a relationship between the size of total season home ranges and length of residency. We used two-factor analysis of variance (ANOVA) to test for differences in log-transformed daily and weekly home range sizes between years and sexes.

During the course of this study several individuals returned to the study site in subsequent years. Two of the individuals from the 2003 population returned in 2004 and were treated as

return animals in 2004. One individual fitted with a transmitter in 2002 during a pilot study for this project returned in 2003 and 2004 and was treated as a return animal in both years. Data from return animals were treated the same as data from new individuals in the study. However, return animal data were also used to look for differences in movement patterns or habitat use across years by the same individual. Single factor ANOVA was used to test for differences in log-transformed daily and weekly home range sizes between years for returning animals (i.e. those present in both 2003 and 2004).

Gillnet surveys and tag-release data

Monthly, random stratified, fishery-independent sampling by gillnet was conducted in the shark nursery areas of Charlotte Harbor from 1995 to 2004 (with the exception of 1996 and 1998). The sampling spanned March to October but was confined to summer months (May–September) in 1999 and later. Two geographically fixed 10 km² grids (Pine Island [PI] and Long Point [LP]) were regularly sampled based upon previous exploratory surveys that revealed sub-areas with relatively high catch per unit effort of juvenile blacktip sharks, *Carcharhinus limbatus*. Grid depths ranged from 0.7 m to 4.9 m and averaged 2.1 m. For quantitative assessment of relative abundance, standardized sets were conducted each month in five of the ten 1×1 km² blocks for each of the two grids. In all, 386 quantitative sets were made using #208 (0.52 mm diameter) monofilament, 4 5/8" (11.8 cm) stretch mesh, 366×3 m weighted gill nets, used because of their relatively high selectivity for small sharks and relatively low bycatch of other species. At the end of each one-hour set, all shark catch was identified, sexed, categorized by stage of maturity (neonate, young-of-the-year, older juvenile, or mature), measured and weighed, and live sharks were tagged and released using nylon-barbed dart tags (Hallprint Ltd.). In addition to the random stratified sampling within the two grids, ad-hoc gillnet sampling also took place within the study site using the same style of net and set times.

Catch per unit effort (CPUE) of each set from both types of gillnet sampling were calculated by

dividing the number of *S. tiburo* caught by the soak time of the net (the time from the first float entering the water to the time that the last float came out of the water). Male and female CPUE were also calculated for each set. For the random stratified sampling, single factor ANOVA was used to test for differences in log-transformed CPUE between individual grid squares. For the ad-hoc sampling, maps of zero, low (1–10 sharks/set), medium (11–20 sharks/set) and high (>20 sharks/set) CPUE were generated in ArcView 3.3 to identify areas where *S. tiburo* were most commonly caught for comparison to data from acoustic monitoring data.

The period at liberty of recaptured sharks was calculated, and the distance between the point of release and recapture calculated using standard geometric formulae. Maps of release and recapture locations were plotted in ArcView 3.3 for comparison to acoustic monitoring and gillnet survey data.

Results

Acoustic monitoring

Over the two years, a total of 36 bonnethead sharks were fitted with acoustic transmitters in Pine Island Sound (2003: 18, 2004: 18) (Table 1) plus one shark that returned in 2003 and three that returned in 2004 for a grand total of 19 individuals monitored in 2003 and 21 in 2004. Monitored sharks ranged in size from 61 cm to 107 cm total length (TL). No effort was made to collect even numbers of each sex and individuals were tagged as they were captured regardless of sex. In 2003 the 19 sharks consisted of six females and 12 males and in 2004 the 21 sharks included 11 females and 10 males. Of the sharks that returned in subsequent years one was female and two were male.

Two of the sharks fitted with transmitters in 2004 died within a few days of release and were not included in further analyses. Remaining monitored sharks were present within the study site for periods of 1–173 days (mean=49 days). Individual sharks were never present for the entire period acoustic receivers were deployed in

the study site, with sharks leaving the array area for varying periods of time (Fig. 2). Individual sharks were continuously present within the study site for periods ranging from 1 to 89 days. The mean number of days continuously present was 7. There was no significant difference in the mean period of continuous residence time between years (t -test, $t=-0.816$, $P=0.416$).

Detailed analysis of the acoustic monitoring data was restricted to individuals that were present within the array area for more than 7 days and were detected throughout the monitoring period. This resulted in the analysis of data from eight individuals released in each year plus the animals that returned in subsequent years (i.e. 2003:9, 2004:11).

Examination of detection of sharks based on tidal state generally showed no difference between the frequency of detections and tidal height frequency (Table 2). This indicated that most individuals were heard by receivers at all stages of the tide, suggesting that sharks did not change movement patterns based on tide stage and that receivers performed equally well at all tidal stages. Three of the monitored individuals did show a significant difference between reception frequency and tidal height frequency (Table 2). Two of these individuals (tag numbers 471 and 472) were detected less often than expected during high tides. Once water levels increased above 1.4 m and 1.6 m detections for these two individuals decreased. The opposite pattern was observed for the third individual (tag number 464) that was detected more often than would have been expected during high tides when water depths were over 1.6 m. Although these three individuals showed significant relationships with tidal stages the pattern was not consistent and therefore no overall pattern of movement based on tide was identified.

Analysis of shark detections within the study site based on time of day showed significant differences by hour of day for all individuals (Table 3). However, there was no consistent pattern within the data. Some individuals (2 out of 20) showed increased detections during the day while others (13 out of 20) showed peaks at night and yet others showed no pattern of detection (5 out of 20). Based on these results it appears

Table 1 Biological data for bonnethead sharks monitored within Pine Island Sound

Year	ID	Size	Sex	Repro stage	Fate	Days monitored	Return
2002	335	72	M	Mat	S	2002: 76; 2003: 93; 2004: 79	2003, 2004
2003	354	73	F	Imm	S	8	N
2003	355	76	M	Mat	S	49	2004
2003	356	70	M	Mat	L	3	N
2003	357	81	M	Mat	S	13	N
2003	358	71	M	Imm	S	26	N
2003	370	93	M	Mat	S	76	N
2003	371	75	M	Mat	S	27	N
2003	372	82	F	Imm	S	30	N
2003	373	86	F	Mat	L	5	N
2003	374	76	M	Mat	S	24	N
2003	375	84	M	Mat	L	7	N
2003	376	88	F	Mat	L	10	N
2003	377	72	M	Mat	L	7	N
2003	382	79	M	Mat	S	25	N
2003	383	75	F	Imm	L	9	N
2003	384	71	M	Mat	L	11	N
2003	389	107	F	Mat	S	65	2004
2003	404	84	M	Mat	L	2	N
2004	454	68	M	Imm	D	0	U
2004	457	86	M	Mat	D	0	U
2004	458	83	F	Imm	L	7	U
2004	459	77	F	Imm	S	56	U
2004	460	71	M	Mat	L	4	U
2004	461	70	F	Imm	S	92	U
2004	462	68	M	Imm	L	4	U
2004	463	76	M	Mat	S	8	U
2004	464	75	F	Imm	L	12	U
2004	466	74	M	Mat	S	173	U
2004	467	63	F	Imm	S	8	U
2004	468	79	M	Mat	L	3	U
2004	469	90	F	Mat	L	2	U
2004	470	80	M	Mat	L	1	U
2004	471	79	F	Imm	S	75	U
2004	472	61	F	Imm	L	28	U
2004	473	81	F	Imm	L	16	U
2004	474	84	F	Mat	L	1	U

ID indicates transmitter number; reproductive stage is indicated as immature (Imm) or mature (Mat); fate of the individual is defined as (S): apparent survival, (L): individuals that left the acoustic array region, or (D): individuals that died within the study site; and return indicates whether individuals returned to the study site in a subsequent year (denoted by the year of return) or if they did not return (N), and (U) indicates unknown since the acoustic array was not deployed in 2005

that individuals may have differing patterns of movement during the day that increase or decrease their chance of detection by receivers, but that those patterns are highly variable and cannot be described for the population as a whole.

Analysis of the distances between 30-min centers of activity revealed that the majority were close to the previous locations, with sharks generally moving less than 1 km (Fig. 3). The minimum distance calculated between point locations was 0 km for individuals that remained within the same proximity over the course of an hour. The

maximum distance between locations was 10.3 km with a mean distance of 0.3 km. Since the mean distance was much less than the distance a bonnethead shark could swim in 30 min (an 80 cm animal swimming at 1 body length per second would swim 2.4 km in a straight line) this indicates that *S. tiburo* had little directionality to their movement. Such a movement pattern would result in individuals tending to remain in the same location.

Daily 50% kernel home ranges were between 0.001 and 14.67 km² (mean=1.64 km²) in both

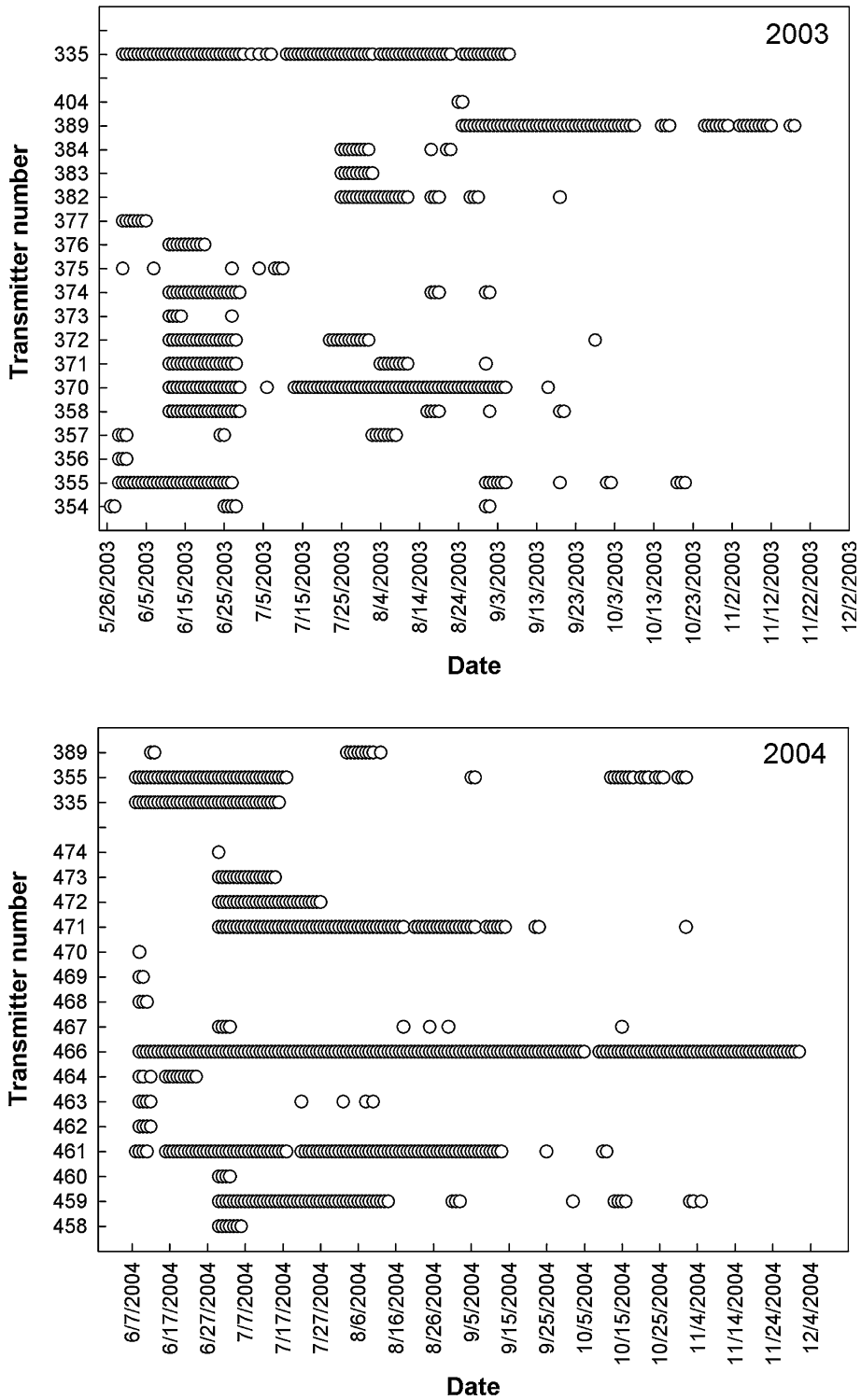


Fig. 2 Presence–absence of bonnethead sharks monitored within Pine Island Sound during 2003 and 2004

Table 2 χ^2 and *P* values based on shark presence versus tidal state

Transmitter number	χ^2 value	<i>P</i> value
2003		
355	12.13	0.9997
358	15.15	0.9967
370	25.93	0.8043
371	23.33	0.8940
372	32.32	0.5007
374	17.50	0.9876
382	20.19	0.8868
389	29.78	0.4771
335	20.67	0.9534
2004		
458	17.66	0.9906
459	25.85	0.8407
461	47.32	0.0642
464	64.35	< 0.0001
466	13.80	0.9992
471	91.38	< 0.0001
472	99.40	< 0.0001
473	18.21	0.9877
335	22.16	0.9411
355	12.92	0.9996
389	24.14	0.8393

Three sharks showed significant relationships to tide level and are indicated in bold

years, suggesting use of small core areas by individual *S. tiburo* in the short-term (Table 4, Fig. 4a). Calculation of daily 95% kernel estimates showed that although some individuals used a large portion of the study site (74.41 km²) most home ranges were of a small size (mean=8.31 km²) (Fig. 4b). There were no significant differences between 50% and 95% daily kernel home ranges when compared to sex of the individual (ANOVAs 50%: *P*=0.736; 95%: *P*=0.749) or by year (ANOVAs 50%: *P*=0.442; 95%: *P*=0.288). Examination of data from 2003 and 2004 for returning sharks also showed no difference in home range size by year (ANOVAs 50%: *P*=0.285; 95%: *P*=0.778) (Fig. 4a=50% kernel, 4b=95% kernel).

Weekly home range sizes were significantly larger than daily home ranges (*t*-test, 50% *t*=−7.92, *P*<0.001; 95% *t*=−3.05, *P*=0.001) (Table 4) suggesting that sharks did not maintain strict core areas that are used repeatedly day after day, but were more likely to have a home range that changes location over time. Most weekly home range sizes were small for both 50 (Fig. 4a)

and 95% (Fig. 4b) kernels during the course of the study. There was no significant difference in weekly home range size between males and females (ANOVAs 50%: *P*=0.447; 95%: *P*=0.481). Examination of mean weekly home range size by year revealed that they were generally larger in 2003 than in 2004 (Fig. 5). This increase in size was also reflected in a significant difference in 95% weekly kernel home range sizes between years (ANOVA, *P*=0.046). However, there was no significant difference in 50% weekly home range size between years (ANOVA, *P*=0.119). Examination of data from 2003 and 2004 for returning sharks showed a significant difference in weekly home range size by year for both 50% and 95% kernel estimates (ANOVAs 50%: *P*=0.034; 95%: *P*=0.035), with home range sizes greater in 2003 than 2004 in all instances.

There were no significant differences in total combined day or night home range sizes (ANOVAs, 50%: *P*=0.930; 95%: *P*=0.933). Total day and total night home range sizes were nearly identical for both 50% (day: 2.31 km², night:

Table 3 χ^2 and *P* values based on the number of detections per shark vs. time of day

Transmitter number	χ^2 value	<i>P</i> value	Period of highest detections
2003			
355	1549	0	Night
358	962	0	Night
370	2283	0	Night
371	243	0	No pattern
372	1099	0	Night
374	797	0	Night
382	1135	0	Night
389	845	0	Night
335	2232	0	Night
2004			
458	547	0	No pattern
459	735	0	No pattern
461	1572	0	Night
464	698	0	Day
466	2463	0	Day
471	5166	0	Night
472	1073	0	No pattern
473	490	0	Night
335	667	0	No pattern
355	2659	0	Night
389	392	0	Night

All sharks showed significant relationships to time of day and the pattern of detections are listed

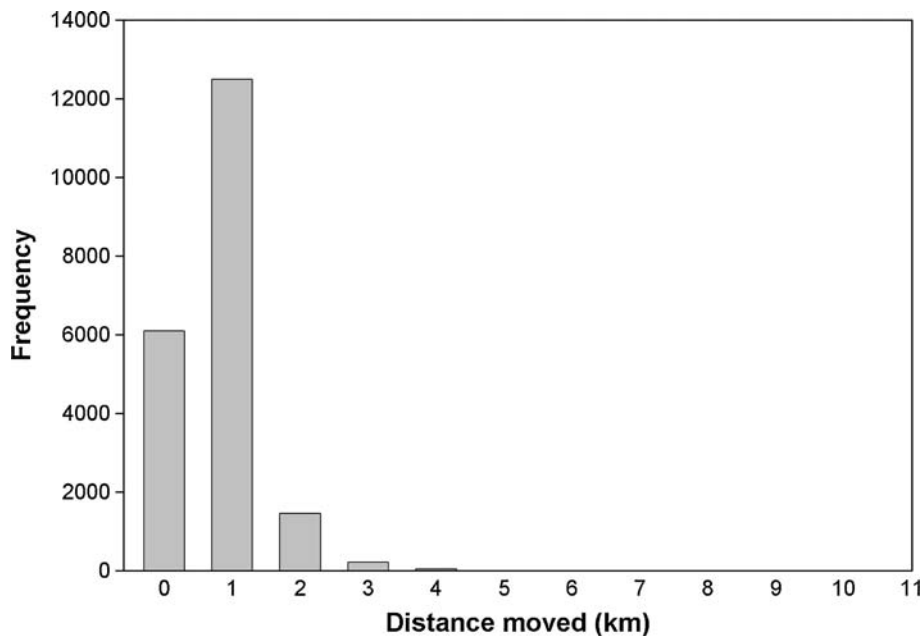


Fig. 3 Frequency histogram of linear distance between 30 min calculated locations of individual bonnethead sharks within Pine Island Sound

Table 4 Fixed kernel home ranges calculated for daily, weekly and total length of residency in Pine Island Sound by bonnethead sharks

	Daily home ranges		Weekly home ranges		Total home ranges	
	50%	95%	50%	95%	50%	95%
Minimum	0.001	0.008	0.016	0.042	0.24	1.22
Maximum	14.67	74.41	9.73	96.88	6.34	60.31
Mean	1.64	8.31	1.74	14.13	1.95	18.62

2.36 km²) and 95% (day: 20.63 km², night: 20.15 km²) kernel calculations. There was also no relationship between total home range size and residence time within the study site (ANOVA, $P>0.05$).

Gillnet surveys

A total of 1,388 *S. tiburo* were collected from 386 random stratified gillnet sets in the Pine Island (PI) and Long Point (LP) grids (Fig. 6a) between 1995 and 2004. Sharks were captured in all 20 sampled grids within the study site (Fig. 6b). Highest mean CPUE values appeared to be in areas near seagrass beds and lowest in areas of deeper water (>3 m). Catch per unit effort values for these sets ranged from 0.34 to 1.30 sharks/net hour and there were significant differences

between sampling grids (ANOVA, $P=0.0047$). Locations of catches by sex showed that females were caught in greater number in the LP 0, LP 1, LP 2, PI 1 and PI 2 grids (Fig. 6c). There were also significant differences in female CPUE between grids (ANOVA, $P=0.000$), but no significant difference between grids for males ($P=0.498$). Males were most commonly caught at LP 1, PI 1 and PI 2, were more common at PI 7, PI 8 and LP 4 than females, but less abundant at LP 0 (Fig. 6d). Although there was a slight difference in where males and females were collected, the sex ratio from these sets did not differ significantly from 1:1 (χ^2 test, $P=0.07$).

Ad-hoc sampling was generally directed at seagrass beds near the edges of islands to target *S. tiburo*. A total of 1,088 individuals were collected in 271 sets. Catches in these targeted

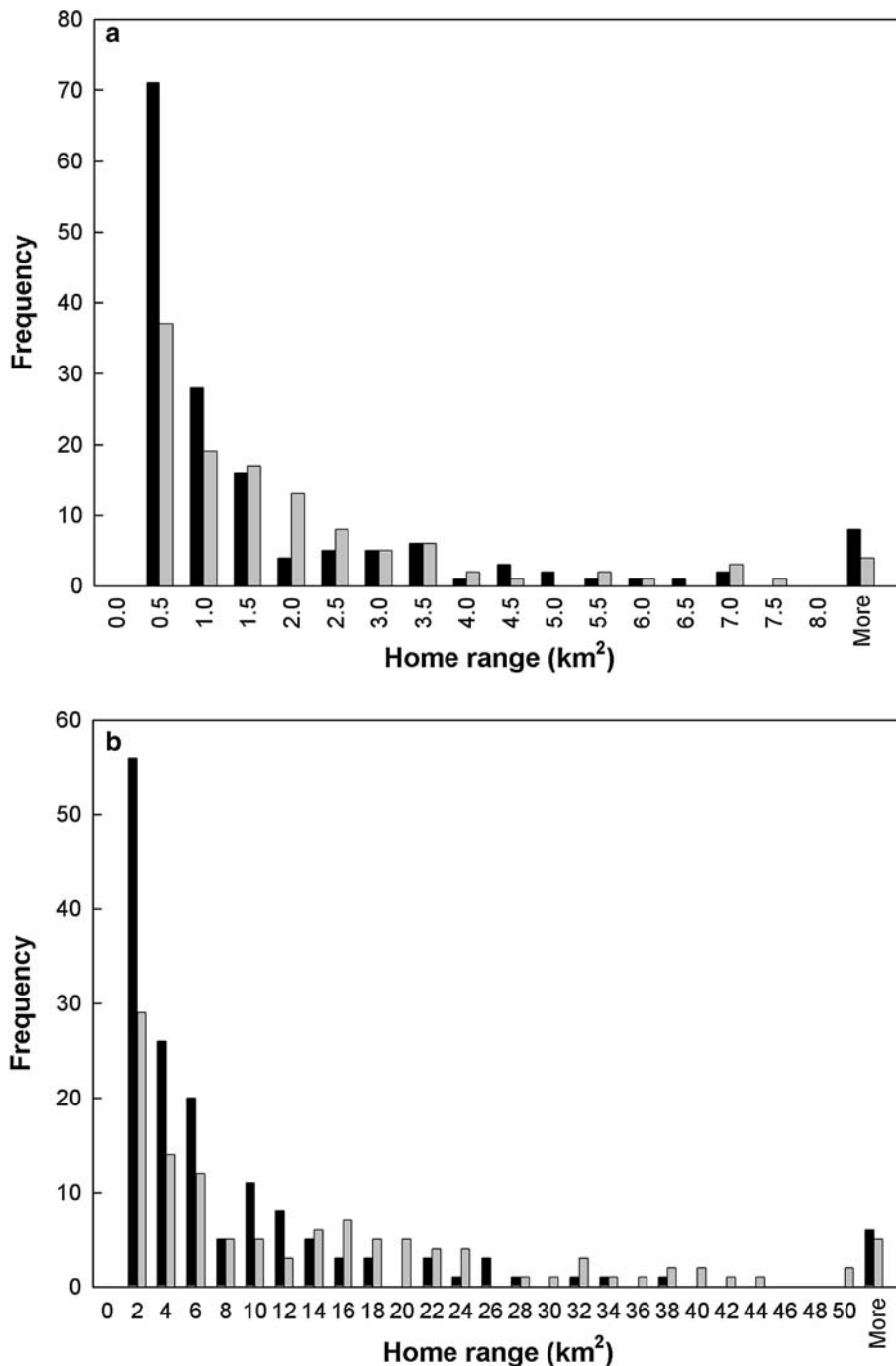


Fig. 4 Daily (dark bars) and weekly (light bars) home range size calculations for bonnethead sharks monitored within Pine Island Sound during 2003 and 2004 where (a) 50% kernel estimates and (b) 95% kernel estimates

efforts appear to be variable even among similar sites. For example, Fig. 7a displays the locations where no *S. tiburo* were captured during targeted fishing. These locations directly overlap with

locations where low (1–10), medium (11–20), and high (>21) numbers of *S. tiburo* were collected (Fig. 7b–d). This suggests that although sharks were commonly present in these regions, they

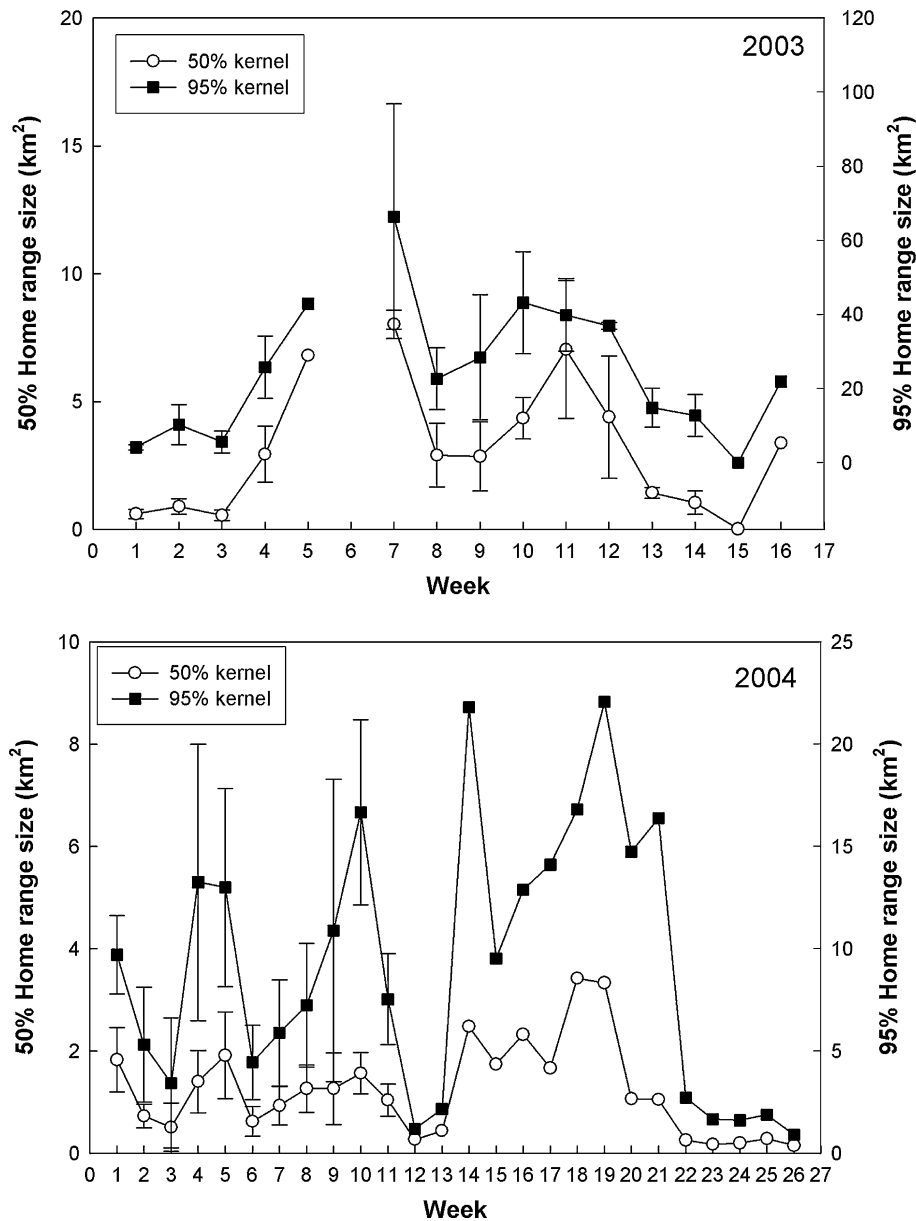


Fig. 5 Weekly mean home range sizes (50% and 95% kernel estimates) for bonnethead sharks monitored within Pine Island Sound during 2003 (top) and 2004 (bottom). Bars indicate standard error

were not permanent residents and cannot always be found in the same locations. Sets with moderate or high CPUE occurred at three locations in the study site—two embayments on the eastern shore of Sanibel Island and the seagrass beds around Regla Island and Regla Shoal (Fig. 7c, d). Sex ratios and capture locations based on sex were not examined from this data set since a large amount of this sampling was directed at collecting

large females for reproductive studies. Based on this bias greater numbers of females (767) were collected than males (321).

Tag-recapture data

A total of 1,505 *S. tiburo* were tagged and released within Pine Island Sound, of which 47 were recaptured. Days at liberty for recaptured sharks

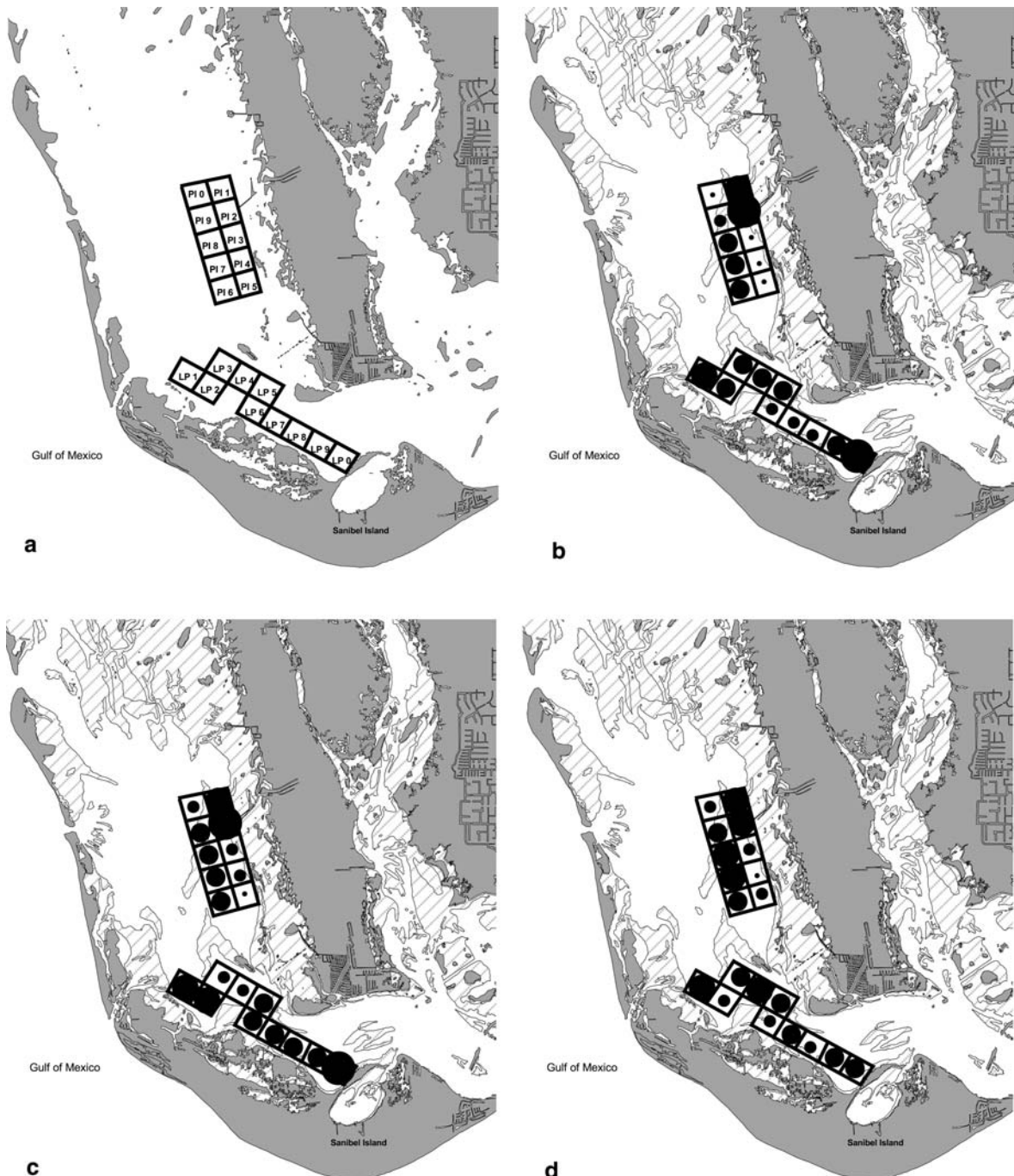


Fig. 6 Catch per unit effort (CPUE) data from random stratified gillnet sampling within Pine Island Sound where: (a) Pine Island (PI) and Long Point (LP) sampling grids within the study site; (b) capture of all bonnethead sharks

with size of dot representative of CPUE for that grid square; (c) CPUE for females only within the two grid sites; and (d) CPUE for males only within the two grid sites

ranged from 1 to 916 days (mean: 187 days; median: 78 days). Recapture distances were typically small (mean: 9.9 km; median: 2.8 km), but

did range from 0 to 185 km. Seven sharks were recaptured the year after initial tagging and six were recaptured two years post-tagging. Only one

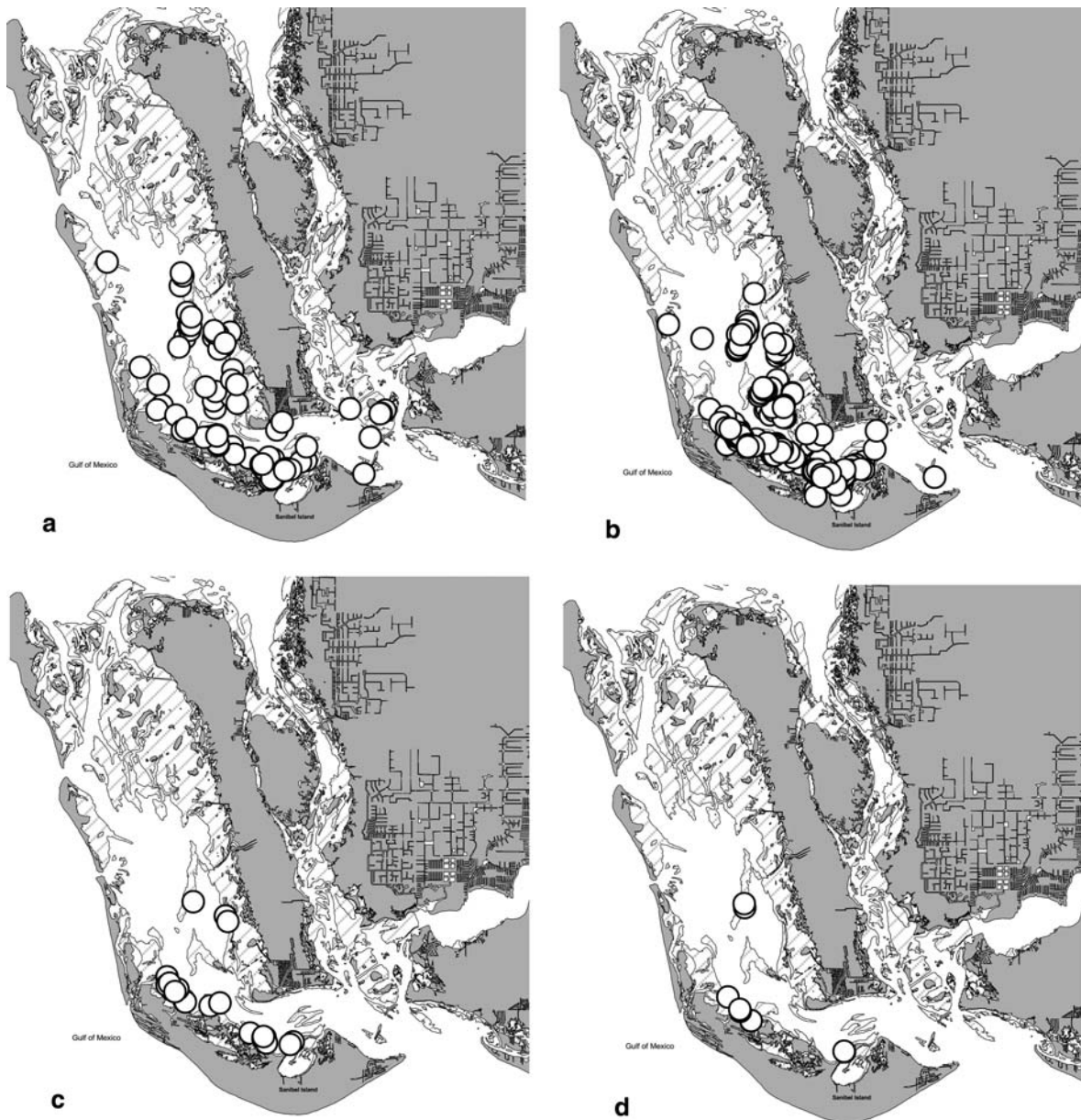


Fig. 7 Catches of bonnethead sharks targeted in ad-hoc sampling within Pine Island Sound where: **(a)** locations where zero bonnethead sharks were captured during sampling; **(b)** locations where 1–10 sharks were captured

during sampling; **(c)** locations where 11–20 sharks were captured during sampling; and **(d)** locations where >21 sharks were captured during sampling efforts

recapture was made outside of the greater Charlotte Harbor estuary (recaptured in Yankeetown, Florida) and only seven were recaptured outside of Pine Island Sound (Fig. 8). There was no relationship between recapture distance and time at liberty (Fig. 9), with most individuals being recaptured within one year of initial release.

Discussion

Acoustic monitoring of *S. tiburo* movement patterns within Pine Island Sound revealed that individuals were present within the estuarine system for variable periods of time between the study months of April through November. Most

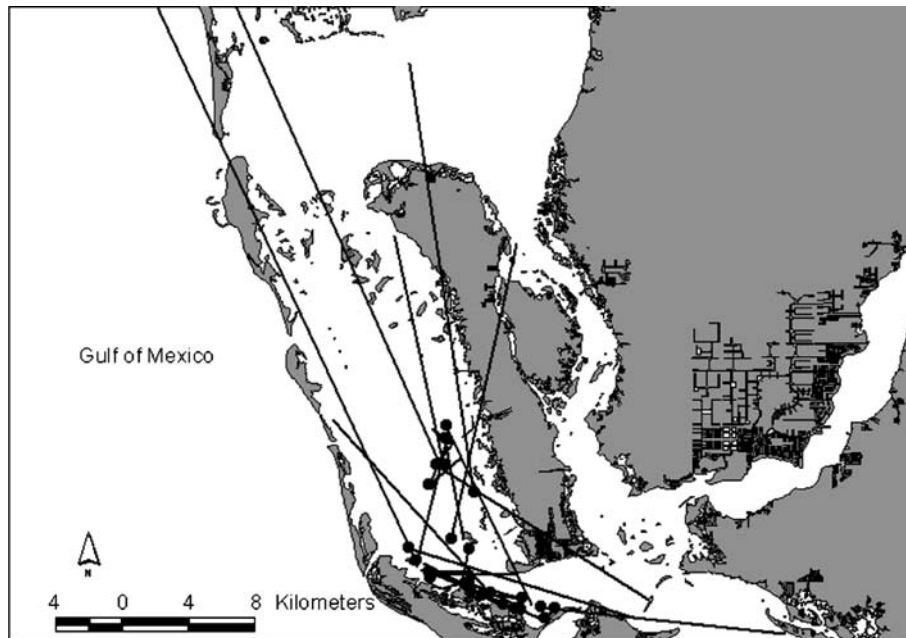


Fig. 8 Map of original tagging and recapture locations of 36 bonnethead sharks within Pine Island Sound. Most individuals were recaptured within Pine Island Sound with only a few individuals recaptured in Charlotte Harbor and one individual recaptured 185 km distant from the study site

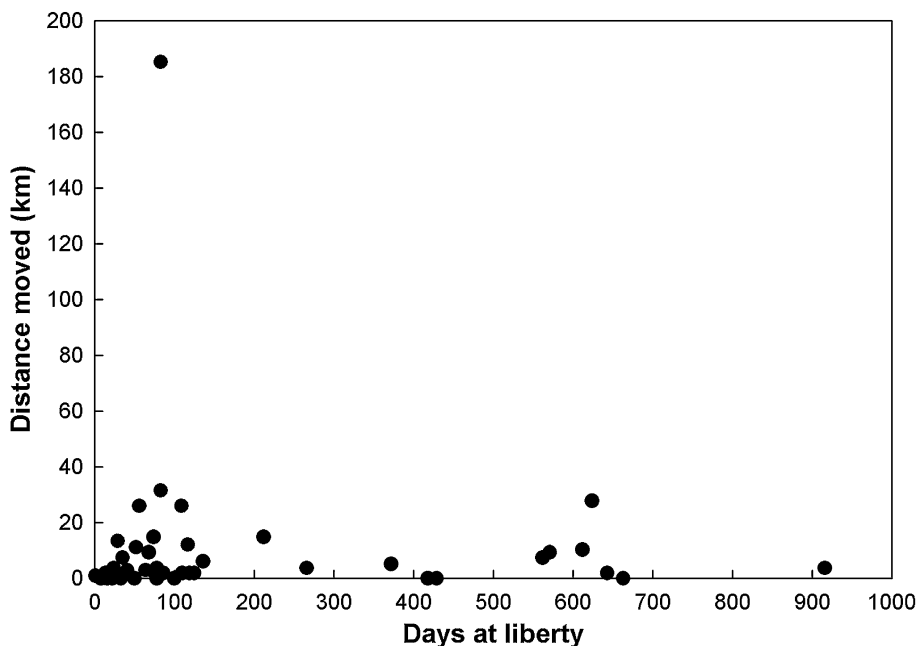


Fig. 9 Distance moved by recaptured sharks originally tagged within Pine Island Sound. Recapture distances through time are shown

individuals were present for periods of weeks or months, with some present for almost the entire monitoring period of a particular year. Although

many sharks used the area over the long-term, they were rarely continuously present within the study site. Individuals were recorded in the area

for up to 173 days, although those days were not necessarily contiguous, with individuals normally moving in and out of the study area. Some long-term continuous presence was observed with at least one individual present for 89 days straight. More commonly, however, individuals were present for continuous periods less than 10 days.

Loss of contact with sharks occurred when individuals moved beyond the coverage of the acoustic array and was the result of several different movement patterns. Firstly, individual *S. tiburo* may have remained within the estuarine system but either moved into areas north of the array or into extremely shallow waters over seagrass beds where signal detection was difficult, if not impossible. In these situations the recorded residency pattern was a conservative estimate of the time that individuals remained within the estuary. In other cases sharks may have moved out of the estuary into the Gulf of Mexico. Without further expansion of the acoustic array it was not possible to estimate the proportion of each of these movement patterns.

There have been few other long-term studies of sharks in estuarine systems with which to compare the results from *S. tiburo* in Pine Island Sound. Heupel and Hueter (2001) and Heupel et al. (2004) demonstrated that neonate blacktip sharks, *Carcharhinus limbatus*, were typically present continuously within an estuarine nursery area after birth in late spring until they migrated south for winter. Like *S. tiburo*, however, some *C. limbatus* quickly left the study area and were never recorded again. The variable dependence on specific areas thus may be a feature of sharks that inhabit estuarine systems, possibly as a survival strategy given the variability in quality of these systems (e.g. Holland et al. 1993; Heupel and Simpfendorfer 2002; Lowe 2002).

Although sharks did swim into areas outside the detection range of the acoustic receivers, there was no evidence that this occurred as a result of changes in water level associated with tidal heights. The lack of a relationship to tidal height provides useful information on both shark movement patterns and equipment performance. A consistent loss of detection during low tides would have suggested that sharks were distributed in shallow water where detection was more

difficult during these periods, or that reduced signal detection occurred as a result of lower water levels. The data therefore suggest that the equipment performed equally well at all tidal heights. This finding was confirmed by range tests conducted within the study site that showed no variation with tidal state (Heupel unpublished data). Conversely, there was no decrease in detections on the high tide that would have suggested sharks were using shallow grass bed areas during high tides and moving into deeper water (where the probability of detection was higher) as the water drained off of shallower areas. Although a small number of sharks did show a correlation between detection rate and tidal state, these results were inconsistent across individuals and did not reveal a reliable pattern. Thus the movements of *S. tiburo* appear to be independent of tidal movements.

No consistent movement or behavioral patterns were observed relative to the time of day. However, the majority of sharks were detected more at night than during the day. Further research will be required to understand the differences in behavioral patterns that led to the observed data. Although significant relationships between shark detection and time of day were found for most individuals, none of these relationships revealed a consistent or repeated pattern. This result contrasts with those from juvenile and adult scalloped hammerhead sharks, *Sphyrna lewini*, that showed clear diel patterns, with aggregation at day-time refuges and dispersal at night (Klimley et al. 1988; Holland et al. 1993). Although there were no detectable patterns in movement based on tidal state or time of day, examination of distance moved over time suggests that *S. tiburo* often remained in a confined region over the short-term. The distance between consecutive centers of activity was mostly less than 500 m, suggesting that *S. tiburo* normally had little directionality to their movements. This indicated that they were probably swimming slowly and re-using specific sections of habitat. This behavior is consistent with previously described movement patterns of captive *S. tiburo* (Myrberg and Gruber 1974). Captive bonnethead sharks were reported to typically swim at a slow rate, displaying a behavior Myrberg and

Gruber (1974) labeled ‘patrolling’. Patrolling was the most common mode of swimming and was consistent by hour per individual. Field observations made in the current study appear to support the captive observations of Myrberg and Gruber (1974). The conclusions based on the distances between centers of activity were also supported by the tag-recapture distances from conventionally tagged sharks. Most recaptures occurred a short distance from their release location even after long periods at liberty, suggesting limited movement.

Limited movement on the short-term was also supported by daily home range analyses where small core areas were used over the course of a day. However, the location of core areas was not consistent through time. Individuals appeared to use a small area of the study site each day, but the location of that core area ranged within the total monitored area. This is different to other previous studies of shark movement patterns that have shown consistent repeated movement patterns within the same location (e.g. Morrissey and Gruber 1993; Heupel and Hueter 2001; Heupel et al. 2004). Previous studies of juvenile lemon sharks, *Negaprion brevirostris*, revealed that sharks had consistent, repeated movement patterns within the same location (Morrissey and Gruber 1993). In this study young lemon sharks repeatedly swam a lap-like pattern in shallow waters. Studies of juvenile blacktip sharks also revealed repeated use of a restricted portion of a nursery area (Heupel and Hueter 2001; Heupel et al. 2004). Blacktip sharks heavily used one section of a nursery early in the season before expanding their home range size and increased use of the area. Individual *S. tiburo* maintained fairly consistent daily home range sizes, but moved the location of that home range rather than expanding the total area used like blacktip sharks. Thus the movements of bonnethead sharks appear to be much more variable than those reported for other shark species. However, although individual daily core areas moved throughout the study site, *S. tiburo* did re-use areas within the study site over the course of a summer season.

There were no differences in home range sizes based on sex or the number of days individuals

were present within Pine Island Sound suggesting consistent behavior patterns across sexes and over time. Home range sizes in 2003 were consistently higher than those calculated for 2004. This difference in home range size was possibly due to environmental changes within the study site. The summer of 2003 was an unusually wet season causing large fluctuations in salinity due to runoff from the Caloosahatchee River. Salinity levels declined to below 16 ppt during the summer causing monitored sharks to leave the area, presumably due to an inability to tolerate lower salinity levels. Due to the variability of environmental conditions within this area detailed analysis of the effects of these changes was beyond the scope of the present text, but will be examined in detail in subsequent publications of this data set.

Home range sizes for *S. tiburo* were generally small, but were comparable to those calculated for other small mobile sharks. Morrissey and Gruber (1993) found activity spaces of juvenile lemon sharks ranged from 0.23 to 1.26 km². Holland et al. (1993) found that small scalloped hammerhead sharks had activity spaces ranging from 0.46 to 3.52 km². Finally, Heupel et al. (2004) found that daily home ranges of juvenile blacktip sharks ranged from 0.019 to 13.0 km². All of these sharks were of a similar size to the bonnethead sharks monitored in the present study which showed comparable core areas, with daily 95% kernel home range sizes averaging 8.31 km² (0.008–74.41 km²). Home range size was fairly continuous through time for monitored bonnethead sharks with no obvious patterns of increasing or decreasing home range size with increased monitoring time.

During the course of this study three acoustically tagged *S. tiburo* returned to the study site in a subsequent year or years. Return individuals were of both sexes, suggesting philopatric behavior was not confined to one sex. All individuals that returned used similar, but not identical areas within the study site in subsequent years. This suggests that although sharks were philopatric to Pine Island Sound, they were not site specific enough to return to an individual seagrass bed. One of the return individuals had been fitted with a transmitter during pilot studies in 2002. This individual was monitored during the summer of 2002 and

returned in both 2003 and 2004. Its home range size and use of the area was similar in all three years this individual was present. Return individuals, however, represented a small proportion of the population fitted with transmitters suggesting this population may have low rates of philopatry or high levels of over-wintering mortality.

Results of gillnet sampling and tag-recapture studies suggest that bonnethead sharks are common residents of Pine Island Sound. Catch data suggest that individuals can be caught in a variety of regions ranging from seagrass beds to deeper water. Although bonnethead sharks were captured reliably within the study site they were rarely caught in large groups (>20 individuals). This result suggests that sharks move individually or in small groups and do not aggregate in large numbers within the study site as has been reported for scalloped hammerhead sharks (e.g. Clarke 1971; Holland et al. 1993; Klimley and Nelson 1984; Klimley et al. 1988). This finding is consistent with acoustic data which did not show any evidence of aggregation or individuals closely associated through time. Myrberg and Gruber (1974) also reported that bonnethead sharks can often be observed in small groups in shallow waters, but did not report any aggregation behavior. Although Myrberg and Gruber (1974) did report social interactions and evidence for a dominance hierarchy in their captive population, no evidence of territoriality or social interactions were observed based on telemetry data. Fine scale movements of sharks cannot be determined via acoustic monitoring, but the exclusion of an individual from one region and the continuous residence of another may suggest home range defense or territoriality. No evidence for this type of behavior was observed. In addition, core areas of individuals tended to shift through time, further indicating a lack of territoriality.

The compilation of several different data sets in this study provided a unique opportunity to examine this population of bonnethead sharks from several perspectives. Results from the various data sets were complimentary and provided a robust account of shark presence, distribution and movements. Based on the data it is clear that *S. tiburo* were common residents of lower Pine Island Sound during the spring, summer and fall

(April–November) months. Sharks could be collected in most areas of the study region, but were not always found in the same places. Gillnet data showed that the same locations fished repeatedly produced variable results for shark presence. Telemetry data also supported this concept by showing changes in daily home range location through time. Bonnethead sharks appeared to be long-term seasonal residents of this region and when targeted could often be found moving in shallow waters over seagrass beds. However, individuals were also collected in deeper waters and appear to be ubiquitous in this region. Recapture data also suggest that sharks remain within the region during the spring and summer months and will return during these same months in subsequent years.

Mark recapture data for the Pine Island Sound population of *S. tiburo* suggest that individuals do not move far and that distance traveled is not related to time at liberty. However, tag-recapture data also suggest that at least some individuals can and do migrate large distances. One individual originally tagged in Pine Island Sound was recaptured approximately 185 km north of its original capture location. This individual was captured in the early summer (May) and was recaptured 83 days later in late July. If this individual was undergoing a north–south migration along the Florida coast it may have originally been captured in Pine Island Sound on its way north. A lack of additional long distance tag recaptures suggest that such larger movements may be fairly rare and that only a small proportion of the population disperses along the Florida coast. Limited dispersal along the coast could account for clinal variation in reproductive and growth parameters of *S. tiburo* observed along the Gulf coast of Florida (e.g. Parsons 1993b; Lombardi-Carlson et al. 2003).

Regardless of occasional large scale movements out of the region, the current data suggest that bonnethead sharks are primarily resident within local estuaries. However, sharks were not attached to specific sites within these estuaries. Individuals generally remained within the estuary, but over time utilized most of the available area. This behavior is different from that recorded for scalloped hammerhead sharks.

Holland et al. (1993) described the movement patterns of juvenile scalloped hammerhead sharks in a nursery area in Hawaii. During their studies they found that young *S. lewini* showed high fidelity to geographically stable daytime core areas. Individuals returned to these consistent daytime areas over time, but exhibited wider activity spaces after dark. Based on these observations Holland et al. (1993) suggested that individuals may aggregate during the day in specific regions to avoid predation and disperse at night to feed. There was no evidence in the current study that *S. tiburo* were increasing their activity space after dark, in fact no difference could be found in home range size when comparing day to night. Previous studies of scalloped hammerhead sharks by Klimley and Nelson (1984) and Klimley et al. (1988) revealed that adult sharks also grouped at a specific geographic feature. Sharks were described as refuging at a seamount during the day and dispersing at night, similar to the patterns described by Holland et al. (1993) for juvenile *S. lewini*. Movement to and from the seamount was rhythmical and individuals appeared to show fidelity to their site of capture (Klimley and Nelson 1984; Klimley et al. 1988). Further examination of this behavior revealed that the presence of sharks at this geographic feature coincided with increased sea surface temperature suggesting that environmental conditions played a role in shark presence (Klimley and Butler 1988). Although examination of environmental conditions was not part of the current study, it is clear that *S. tiburo* do not show the same type of diel movement or behavior patterns reported for juvenile and adult *S. lewini*.

On the basis of the data collected in this study it is difficult to identify the factors that account for the movement patterns of *S. tiburo* in Pine Island Sound and why these are different to those observed in other shark species. Although large sharks (including lemon and bull sharks, *Carcharhinus leucas*) are present within Pine Island Sound (Simpfendorfer et al. 2005; Heupel unpublished data), *S. tiburo* do not appear to aggregate or display anti-predation behavior (e.g. the diel refuging pattern seen in young *S. lewini*). Consecutive monitoring of large bull and lemon sharks within Pine Island Sound showed

bonnethead sharks using the same areas as these potential predators. Bull sharks were commonly recorded in shallow regions (ca. 1 m) suggesting they are capable of using similar habitats to bonnethead sharks (Heupel unpublished data). Bonnethead sharks were not observed to avoid areas commonly used by either lemon or bull sharks. Based on the presence of large sharks and the lack of apparent avoidance behavior it appeared that bonnethead sharks were not selecting habitat based on predator distribution or as a means of predator avoidance as has been reported for other species (e.g. Holland et al. 1993; Heupel and Hueter 2002; Heupel and Simpfendorfer 2005). Since predation risk did not appear to be a factor in movement patterns, use of the study site may be a result of the distribution and abundance of their prey. Cortés et al. (1996) reported that bonnethead sharks in southwest Florida feed primarily on crustaceans, especially blue crab, *Callinectes sapidus*. Blue crabs are common residents of Florida estuaries and are widely distributed (Steele and Bert 1994). A specialized diet based on a common, resident crustacean provides bonnethead sharks an opportunity to feed in most of Pine Island Sound. There is no need for individuals to seek out or follow groups of prey or target specific habitat types. Simply patrolling the benthos for crabs is probably an effective means of finding prey. A prey capture scenario such as this would account for the distribution and movement patterns observed in the current study and would also account for the dominant type of swimming behavior described by Myrberg and Gruber (1974).

Summary/Conclusion

The results of this study suggest that *S. tiburo* are long-term residents of coastal estuarine systems. Individuals spend large amounts of time within specific regions while using a large portion of the available habitat. Some individuals may be resident, or nearby, throughout the winter season and do not appear to undertake long coastal migrations. Philopatric behaviors have also been observed suggesting that individuals will continue to use these regions over

several years or possibly throughout their life. The implications of this finding may be broad-reaching since this species is currently managed by the National Marine Fisheries Service as part of the small coastal shark cluster. Fidelity to specific regions or estuaries means that individuals may not disperse in great numbers, therefore localized depletion of a population could have long-term effects within that region. In addition, pollution or loss of habitat may affect the reproductive potential of the population causing long-term decline in abundance within the region (e.g. Gelsleichter et al. 2005). Thus the movement patterns observed in this study and other previously collected life-history data suggest that bonnethead shark populations will require a localized management approach to ensure that sharks are not heavily exploited in one portion of their range causing long-term or permanent population level depletion.

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