

Long-term presence and movement patterns of juvenile bull sharks, *Carcharhinus leucas*, in an estuarine river system

Michelle R. Heupel^{A,D,F}, Beau G. Yeiser^A, Angela B. Collins^B, Lori Ortega^C and Colin A. Simpfendorfer^{A,E}

^ACenter for Shark Research, Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236, USA.

^BFlorida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 100 8th Avenue SE, Saint Petersburg, FL 33701, USA.

^CUniversity of South Florida, Environmental Science and Policy, 4202 E. Fowler Avenue, Tampa, FL 33620, USA.

^DSchool of Earth and Environmental Sciences, James Cook University, Townsville, Qld 4811, Australia.

^EFishing and Fisheries Research Centre, School of Earth and Environmental Sciences, James Cook University, Townsville, Qld 4811, Australia.

^FCorresponding author. Email: michelle.heupel@jcu.edu.au

Abstract. Elasmobranchs living in rivers and estuaries may be highly susceptible to environmental and anthropogenic changes to coastal habitats. To address this, patterns of movement of 67 juvenile bull sharks (*Carcharhinus leucas*) were examined in the Caloosahatchee River between 2003 and 2006 using an array of 25 acoustic receivers. Individuals were monitored for periods of 1–460 days with most present for periods of weeks to months. Individuals utilised the entire monitored section of the river (~27 km) and also moved upriver beyond the extent of the acoustic array. Daily activity spaces of individuals ranged from 0 to 14 km with most <5 km. Monthly mean home ranges were 0.9–5.6 km and although home-range sizes were consistent through time, location of individuals within the river changed through time. Individuals moved upstream during the day and downstream at night and this pattern persisted across years. Based on data collected from depth transmitters in 2006, individuals swam closer to the surface at night and remained in deeper water during the day, suggesting further diurnal patterns in habitat use. Long-term consistent use of this habitat by young *C. leucas* suggests this population is highly dependent on the Caloosahatchee River as a nursery area.

Additional keywords: acoustic monitoring, home range.

Introduction

Despite a broad range of studies, and although several elasmobranch species are known to utilise river environments, limited data are available on the movement patterns of elasmobranch species within rivers. The bull shark, *Carcharhinus leucas*, is common in estuarine and riverine habitats throughout tropical and subtropical environments around the world and has been recorded from numerous river and lake systems in the USA, Central America, South America, Africa, Australia, Papua New Guinea and Asia (Compagno 1984). *C. leucas* is one of the few elasmobranch species that is physiologically capable of residing in freshwater, but movements of individuals within these systems have rarely been explored. Recently, studies have examined the short-term movement of *C. leucas* in estuarine systems (Curtis 2008; Ortega 2008; Ortega *et al.* 2009), but detailed long-term movement data remain limited. This has restricted our understanding of how large seasonal changes in physical and environmental factors affect the occurrence and distribution of this important high-order predator. Improved information

on the relationship between environmental variables and animal movement will aid management of these habitats, which are coming under increasing pressure from urbanisation and coastal development.

Studies of *C. leucas* within US waters have primarily examined presence and distribution. For example, Snelson and Williams (1981) reported that *C. leucas* were present year-round within the Indian River Lagoon system (Florida). In a more detailed survey of this area, Snelson *et al.* (1984) reported that *C. leucas* were captured primarily in low-salinity basins, suggesting preferential use of these habitats. Recent telemetry research on *C. leucas* in the Indian River Lagoon (Curtis 2008) supports this result. In another study of *C. leucas* distribution, Simpfendorfer *et al.* (2005) identified distinct habitat partitioning within a south-west Florida estuary with neonate and young-of-the-year individuals occupying different habitats from older juveniles. In this study, salinity was an important factor, with younger individuals occurring within mesohaline regions and older juveniles utilising polyhaline regions.

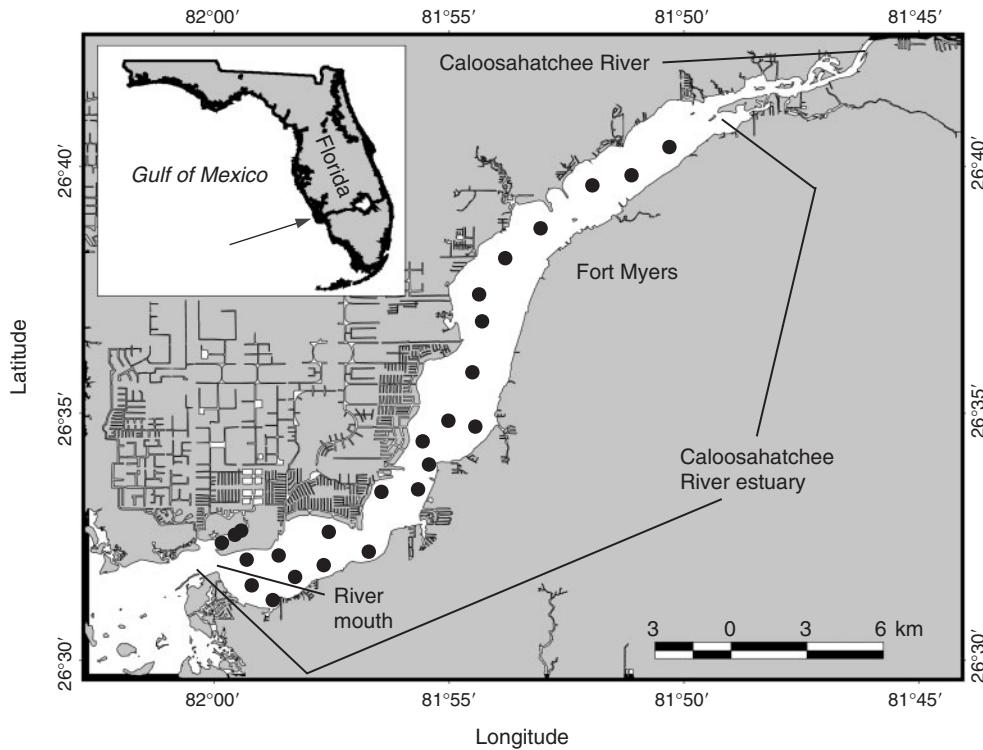


Fig. 1. The Caloosahatchee River estuary study site. Filled circles indicate locations of acoustic receiver stations. (Inset) Location of study site in Florida (arrow indicates location of the river).

Acoustic monitoring of *C. leucas* within the Caloosahatchee River suggested that young individuals occupied habitats based on environmental conditions (primarily salinity) within the river (Heupel and Simpfendorfer 2008). Similarly, research on *C. leucas* in Louisiana revealed low-salinity habitats to be important for this species (Blackburn *et al.* 2007). All of these studies indicate that *C. leucas* is not distributed uniformly through estuarine habitats and that environmental conditions affect how individuals use these regions.

Given the lack of detailed information on long-term movement patterns of *C. leucas* in riverine and estuarine habitats, and the importance of this information for resource management, the present study attempts to define space utilisation of young *C. leucas* within the Caloosahatchee River. The aims of the present study were to: (1) define temporal variation in habitat use patterns; (2) define daily activity space size and location; (3) define long-term home-range size and location; and (4) compare data among years and cohorts of individuals.

Materials and methods

Study area

The Caloosahatchee River ecosystem (26°35'S, 81°55'W) is part of south Florida's wetlands and is the major source of freshwater to the Caloosahatchee River estuary and southern Charlotte Harbor, Florida (Fig. 1). The river connects Lake Okeechobee to the south-west coast of Florida and has been substantially altered over the past 100 years (Doering and Chamberlain 1998). Habitat alterations include an artificial link to Lake Okeechobee,

intricate canal systems connected to the main river channel, two locks for boat passage and flow regulation dams.

Carcharhinus leucas movement was studied in the estuarine portion of the river (Fig. 1) and encompassed ~27 km of river habitat. Upper reaches of the Caloosahatchee River estuary have natural shoreline and native vegetation (primarily red mangroves, *Rhizophora mangle*). The habitat closer to the river mouth has been largely altered by urbanisation as evidenced by extensive canal developments and shoreline modifications (Fig. 1). Water depth within the river is variable with a maximum of 8 m in the dredged channel.

Field methods

A series of 25 VR2 acoustic receivers (Vemco Ltd, Halifax, NS, Canada) were deployed within the study site to passively track the movement of *C. leucas* (Fig. 1). Methods for deploying receivers have previously been described (Heupel and Hueter 2001; Heupel and Simpfendorfer 2008; Simpfendorfer *et al.* 2008). Acoustic receivers were deployed continuously from August 2003 until project completion in August 2007. Due to limited numbers of animals present in 2007, data presented here only reflect presence and movements through 2006. Receivers recorded the time, date and identity of individuals fitted with acoustic transmitters that swam within range of the receiver. Receivers were single frequency, omnidirectional units and had an approximate detection range of 800 m (Simpfendorfer *et al.* 2008). This detection range allowed individuals to be detected at more than one station simultaneously. The receiver array allowed individuals to be continuously monitored for the entire period

they were present within the study area. Data were downloaded from receivers and maintenance was performed monthly. At this time, temperature and salinity were measured at the surface and bottom of the water column using a water quality meter (YSI 85, Yellow Springs, OH, USA).

Sampling gear consisted of bottom-set longlines (400–800 m) consisting of 8-mm braided nylon rope anchored at both ends. Gangions were constructed of 1 m of braided nylon cord (5 mm) and 1 m of stainless steel wire leader. Mustad tuna circle hooks ranging in size from 12/0 to 16/0 were baited with frozen sea mullet (*Mugil cephalus*) and fresh hardhead catfish (*Arius felis*). Longline set periods ranged 0.5–2 h, but most were set for 1.5 h. All captured individuals were neonate or young-of-the-year juveniles (68–96 cm total length). Individuals were caught and fitted with acoustic transmitters soon after birth in June–August in each of the four study years, except 2004 when four individuals were fitted with transmitters in November. Captured *C. leucas* were weighed, sexed, measured, externally tagged with a dart tag and surgically implanted with a Vemco V16 RCODE transmitter (16 × 65 mm) in 2003–2005 or a V13P pressure-sensing transmitter (13 × 84 mm) in 2006. Each transmitter was coded with a unique pulse series and operated on 69.0 kHz at randomly spaced intervals between 45 and 75 s. Battery life for transmitters in 2003–2005 was at least 18 months (V16) and was ~12 months (V13) in 2006. Random signal transmission times prevented signal overlap from blocking detection by a hydrophone station. Over 4 years, a total of 67 *C. leucas* were monitored in the river (2003: 8 female, 10 male; 2004: 7 female, 11 male; 2005: 10 female, 10 male; 2006: 6 female, 5 male).

Data analysis

Data from receivers were used to examine the presence and movement patterns of *C. leucas* within the Caloosahatchee River. Presence of all tagged *C. leucas* was assessed daily, with individuals considered present in the study site if more than one signal was detected on any receiver in the array on a given day. Presence histories were plotted by day to provide a timeline of animals present in the study site. The number of consecutive days individuals were present in the study site was calculated (each time they entered the study site). To compare the number of consecutive days present between years, the data were $\log(x + 1)$ -transformed, normality checked by examination of Quantile–Quantile plots and a *t*-test performed. Presence histories were also examined to determine when individuals went upriver beyond the extent of the acoustic array. These forays upriver were noted, the number of excursions beyond the array counted and the number of days upriver recorded. Movement of individuals outside of the Caloosahatchee River was detected in 2003–2005 by a complementary acoustic monitoring study in the adjacent Pine Island Sound region (Heupel *et al.* 2006; Yeiser *et al.* 2008) that included more than 40 receivers. These data were added to presence graphs of individuals released in the Caloosahatchee River array.

The location of each individual was estimated every 30 min using the river distance algorithm described by Simpfendorfer *et al.* (2008). This algorithm used data from the receiver array to estimate the distance between a centre of activity calculated for each 30-min period and the river mouth, to estimate location

(referred to as river km). The distance between consecutive centres of activity was calculated using subtraction, so that upstream movements were identified by a negative value and downstream movements by a positive value. A factorial general linear model (GLM) was used to determine if there were differences in distances between centres of activity between diel period (day (0701 to 1900 hours) or night (1901 to 0700 hours)) or cohort (2003–2005). The 2006 cohort was excluded from this analysis due to reduced battery life and shorter tracking periods of the V13 tags.

Due to the linearity of the receiver array in the river system, traditional home range techniques (e.g. minimum convex polygon, kernel estimates) could not provide effective area-based home-range estimates. As a proxy for daily activity space and monthly home range, we examined the extent of the river used by an individual within a day (e.g. Collins *et al.* 2008). This was determined by subtracting the location (in river km) closest to the mouth from the location farthest upstream to determine the number of river km the individual utilised that day. Differences in home-range size among cohorts were tested using a GLM with cohort and month as factors and salinity (measured at river km = 10, see Heupel and Simpfendorfer 2008) and river location as covariates. Month was treated as an independent factor because of the overlapping occurrence of cohorts within the dataset. Home range values were normalised using a $\log(x + 1)$ -transformation and the form of the distribution checked by examination of Quantile–Quantile plots. The 2006 cohort was excluded from this analysis as the different acoustic tag type reduced tracking periods.

Pressure-sensing transmitters used in 2006 reported the depth of an individual in the water column with every transmission (every 45–75 s). Depth data were used to define patterns in swimming depth of individuals through time. A factorial GLM with hour and month as factors was used to examine the data and identify diel and monthly patterns in position within the water column. Day and night depth distributions were compared using a *t*-test assuming unequal variances.

Results

Shark presence

Over the course of the study, temperatures ranged from 14.4 to 34.1°C and salinity fluctuated between 0.1 and 34.7. Juvenile *C. leucas* were present year round and during all of these environmental conditions. Individuals from 2003 to 2005 were present for periods of 1–460 days (Table 1). While some individuals were only present for short periods, most individuals were present in the study site for continuous periods of weeks to months (Fig. 2). In 2006, when use of smaller, depth-sensing transmitters resulted in reduced battery life, individuals were present for periods of 1–252 days. Individuals were present in the study site for 2–363 consecutive days for the 2003–2005 cohorts and 1–81 days for the 2006 cohort (Table 1). During 2003–2005 when the adjacent Pine Island Sound acoustic array was in place, 19 of 36 (52.8%) individuals were recorded moving back and forth between the two study sites (Fig. 2). Movement to Pine Island Sound occurred mostly during the second wet season after tagging (and hence birth), when individuals were > 1 year old.

At least one individual also undertook a longer migration out of the Caloosahatchee River and along the Florida coast.

Table 1. Presence of *Carcharhinus leucas* within the Caloosahatchee River, south-west Florida showing the numbers of days individuals were monitored and the number of days individuals were consecutively present by year

Number in brackets indicates standard deviation. Year indicates when individuals were released and is not representative of a calendar year

	Days present			Consecutive days present		
	Min	Max	Mean	Min	Max	Mean
2003	3	379	144 (118)	3	234	9.8 (31)
2004	2	370	152 (118)	3	363	18.1 (45)
2005	2	460	202 (160)	2	158	17.2 (29)
2006	1	252	79 (70)	1	81	9.7 (17)

Shark number 3418 was released in the Caloosahatchee River on 21 June 2005. It remained in the river for 125 days until October 23 before leaving the area for 66 days. During this time, it was not detected on any other receivers and its location was unknown. In December 2005, it returned to the Caloosahatchee River and was present until November 2006 (351 days) until it left the river again and was subsequently detected on acoustic receivers located in a tidal creek in the western Florida Everglades (140 km south) in February and March 2007. This individual was detected back in the Caloosahatchee River in early April 2007 and remained in the river until the acoustic array was removed from the site in August 2007.

Detections on receivers at both ends of the acoustic array occurred in all years of the study and indicated individuals from all cohorts used the entire study region. There were also gaps in detections that occurred after individuals were detected on the receiver farthest upriver. This indicated that individuals moved farther upriver and beyond the extent of the array. Thirteen individuals (19.4% of releases) moved upriver beyond the extent of the acoustic array. Some of these excursions were validated by detection of *C. leucas* transmitter codes on receivers maintained by the Fish and Wildlife Research Institute to track snook (*Centropomus undecimalis*; R. Taylor, pers. comm.). Movements upriver beyond the array ranged from 1 to 141 days. The maximum number of days consecutively upriver beyond the array was 94, but most excursions were shorter (mean = 14 days). In all, 44 of these upriver trips totaling 597 days were observed for the 13 individuals. The majority of excursions ($n = 28$) occurred during March to May while the longest excursions occurred during January to March.

Activity space, home range and river location

The daily activity space of individuals ranged from 0 km (suggesting limited movement up or downstream and so detection by only one receiver) to 14 km. The majority of daily activity space values were <5 km for all cohorts (Fig. 3). Monthly mean home-range estimates were 0.9–5.6 km for all cohorts (Fig. 4). Home-range size differed significantly among cohorts ($F_{2,8137} = 119.43$, $P < 0.001$) and months ($F_{15,8137} = 10.510$, $P < 0.001$). Mean home range was highest for 2003 and 2004 cohorts and significantly lower for the 2005 cohort (Unequal N HSD *post hoc* test). There was also a significant interaction between cohort and month ($F_{30,8137} = 19.780$, $P < 0.001$), indicating that each cohort had different monthly home-range patterns. Both river location ($F_{1,8137} = 10.009$, $P = 0.0016$) and

salinity ($F_{15,8137} = 10.048$, $P = 0.0015$) were significant covariates for monthly mean home range. Home-range size increased with distance from the mouth of the river, but was also highly variable between individuals.

In all years, individuals were near the river mouth during September and were farther upstream in March to June (Fig. 5). The location of individual home ranges within the river (as measured by river km) was significantly different among cohorts ($F_{2,8137} = 217.47$, $P < 0.001$) and months ($F_{15,8137} = 210.60$, $P < 0.001$). There was also a significant interaction between cohort and month ($F_{30,8137} = 32.171$, $P < 0.001$), indicating that home ranges for each cohort were located in different parts of the river in each month. Salinity ($F_{1,8137} = 172.635$, $P < 0.001$) and home-range size ($F_{1,8137} = 10.009$, $P = 0.0016$) were both significant covariates.

Daily change in mean river location of individuals was typically very small, with most showing little or no change in location from one day to the next (Fig. 6). This suggested contiguous use of relatively small regions of the river by individuals, with expanded use of the available habitat through time rather than regular large-scale, rapid movement up- or downstream. Large-scale movements in short periods of time were rare, with 30-min movements >5 km recorded only 158 times (0.042% of occurrences). There were significant differences in the change in river location between day and night periods ($F_{1,12643} = 9.07$, $P = 0.003$), with mean daytime movements upstream (−0.013 km), and mean night-time movements downstream (0.016 km). There was no significant difference in the daily change in mean river location among cohorts ($F_{2,12643} = 1.21$, $P = 0.29$) and no interaction between time of day and cohort ($F_{2,12643} = 2.22$, $P = 0.11$), indicating a consistent day–night pattern of movement between cohorts.

Swimming depth

Swimming depths recorded for individuals in 2006 ranged from 0.1 to 6.1 m, with depths greater than 4.0 m rarely observed. Mean swimming depth was greater during the day (1.21 m) than at night (0.89 m) (t -test, $t_{26113} = 45.71$, $P < 0.001$; Fig. 7). There were significant differences in swimming depth between months ($F_{4,40798} = 439.15$, $P < 0.001$), hours of the day ($F_{23,40798} = 37.51$, $P < 0.001$) and hourly pattern by month ($F_{92,40798} = 13.89$, $P < 0.001$). Mean depths decreased from >1.0 m in June and July to ~0.75 m in September and October. The hourly pattern in depth showed shallowest swimming depths between midnight and 4 a.m., then a crepuscular increase to

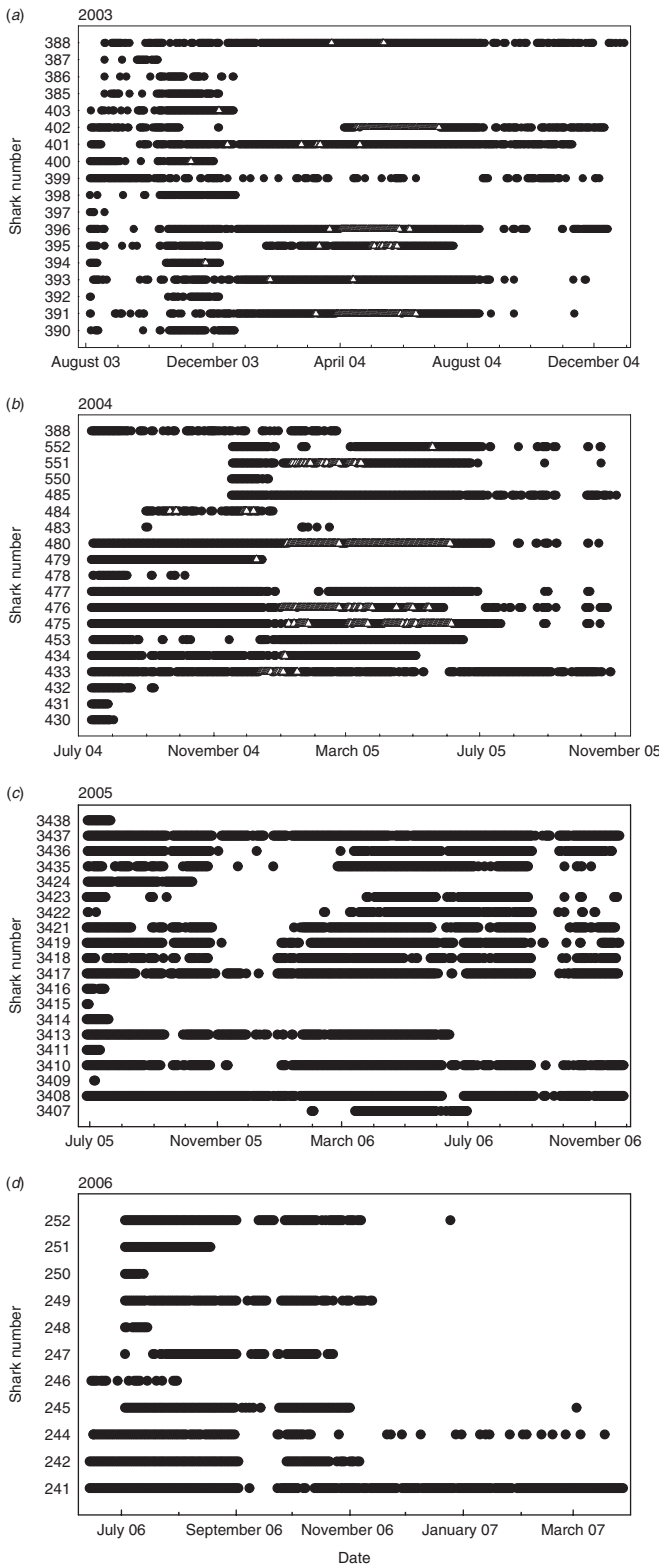


Fig. 2. Presence-absence of *Carcharhinus leucas* monitored in the Caloosahatchee River in (a) 2003 to (d) 2006. Filled circles indicate presence within the Caloosahatchee River and open triangles indicate detection within the adjacent Pine Island Sound array. Individuals were monitored for greater than 1 year for 2003–2005 cohorts as reflected by months monitored.

maximum mean depth at 8 a.m., and thereafter a slow decline in swimming depth (Fig. 8).

Discussion

Shark presence

Long-term acoustic monitoring of juvenile *C. leucas* in the Caloosahatchee River revealed that individuals were present year-round and used variable amounts of the available river habitat. Patterns of long-term residence were consistent among and across years, although some individuals did leave the study site permanently after shorter periods of time (days to weeks). When the adjacent Pine Island Sound acoustic array was in place (2003–2005), it was clear that if individuals left the river, they often only moved into Pine Island Sound before returning. This is similar to patterns observed in cownose rays (*Rhinoptera bonasus*) also tracked within the Caloosahatchee River (Collins *et al.* 2008). However, movement of at least one individual from the Caloosahatchee River to the Florida Everglades revealed that large movements do occur. Wiley and Simpfendorfer (2007) also demonstrated movements of young *C. leucas* from the Caloosahatchee River to the Everglades using conventional tagging. These observations indicate that a small portion of the population migrates south, but may return.

C. leucas regularly moved upriver beyond the acoustic receiver array and so their exact location could not be determined. However, it was assumed that their movement upriver was restricted by the Franklin Locks (river km 35), a fact confirmed by the Fish and Wildlife Research Institute that maintains receivers in this area. Movement of *C. leucas* beyond the array contrasted with data collected for *R. bonasus*, which did not move upriver beyond the array (Collins *et al.* 2008). This suggests that *R. bonasus* may have a narrower environmental tolerance than *C. leucas* and thus more restricted movement within river systems. The movement of *C. leucas* upriver beyond the array occurred only during periods of low freshwater inflow, typically from January to May. Movement farther upriver during periods of low freshwater input and increased salinity has already been reported for this population by Heupel and Simpfendorfer (2008) and these excursions may reflect a preference for mesohaline waters that occur well upriver during these periods.

Activity space, home range and river location

The activity space of individual *C. leucas* revealed that daily habitat use was typically <5 km. This is similar to use of this same habitat by *R. bonasus* that were reported to use <6 km of river in a given day (Collins *et al.* 2008). Although only measured in linear distance, the amount of space used by individuals falls within a similar range of activity space of actively tracked juvenile *C. leucas*. For example, active tracking of juvenile *C. leucas* in the Caloosahatchee River resulted in daily activity spaces ranging from 1.2 to 4.3 km² (Ortega *et al.* 2009) with similar tracking results reported from the Indian River Lagoon including activity spaces of 0.02–3.49 km² (Curtis 2008). Examination of monthly home-range estimates revealed usage of consistently small areas (0.9–5.6 km) with individuals within a cohort appearing to behave similarly. Similarity in the amount of space used in relation to data from other studies (i.e. Curtis 2008; Ortega *et al.* 2009) and consistency in the size of area used by individuals

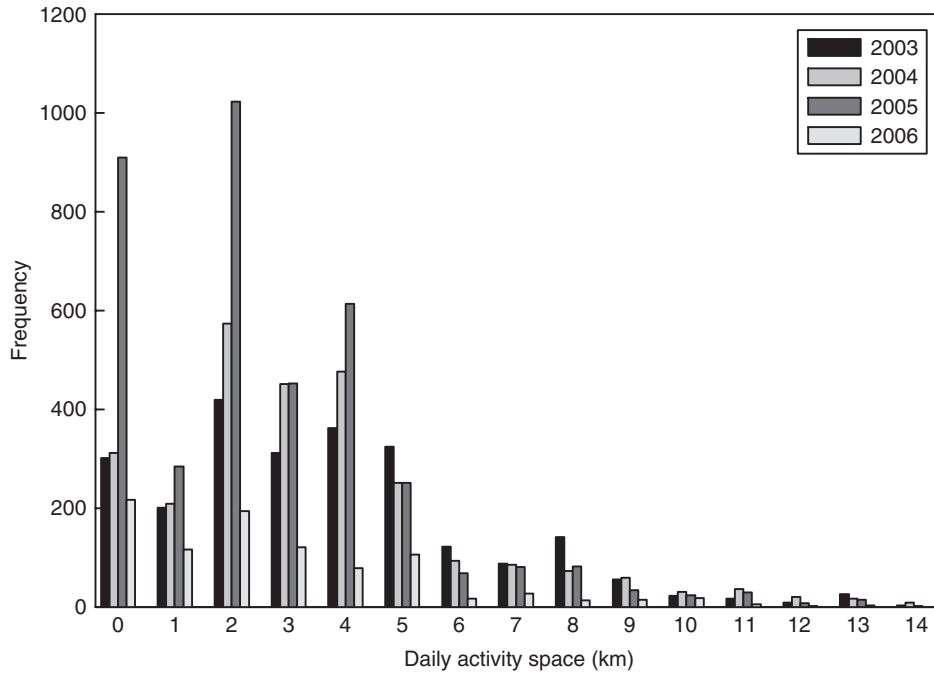


Fig. 3. Size of daily activity space for juvenile *Carcharhinus leucas* monitored within the Caloosahatchee River from 2003 to 2006.

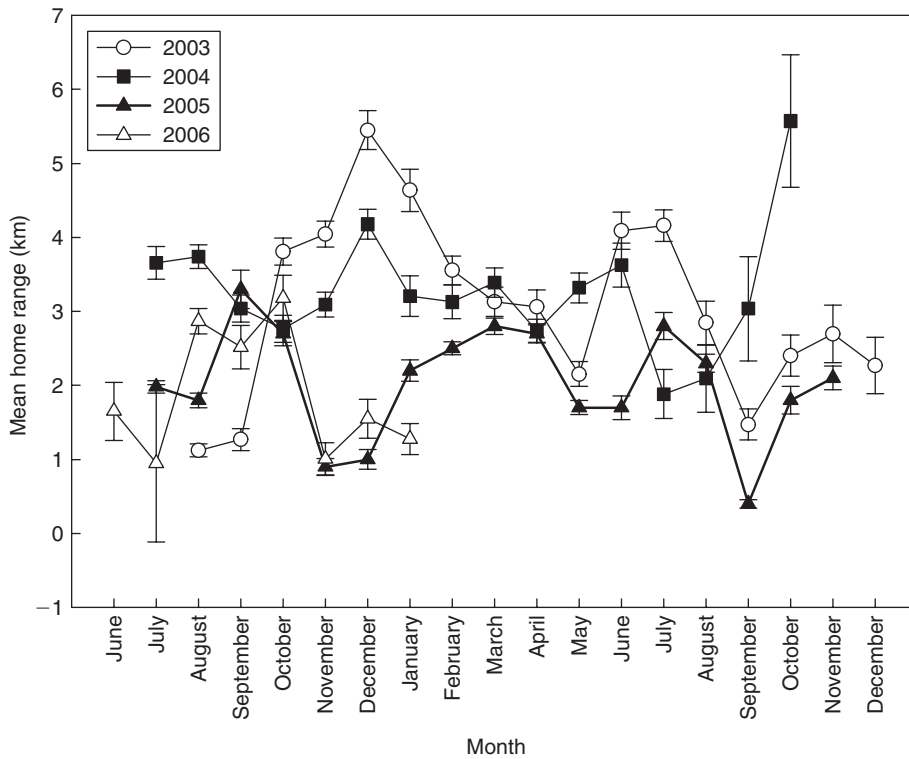


Fig. 4. Mean monthly linear home-range estimates for juvenile *Carcharhinus leucas* within the Caloosahatchee River. Bars indicate standard error. Symbol type indicates the year individuals were released with monitoring extending beyond 1 year as shown by months.

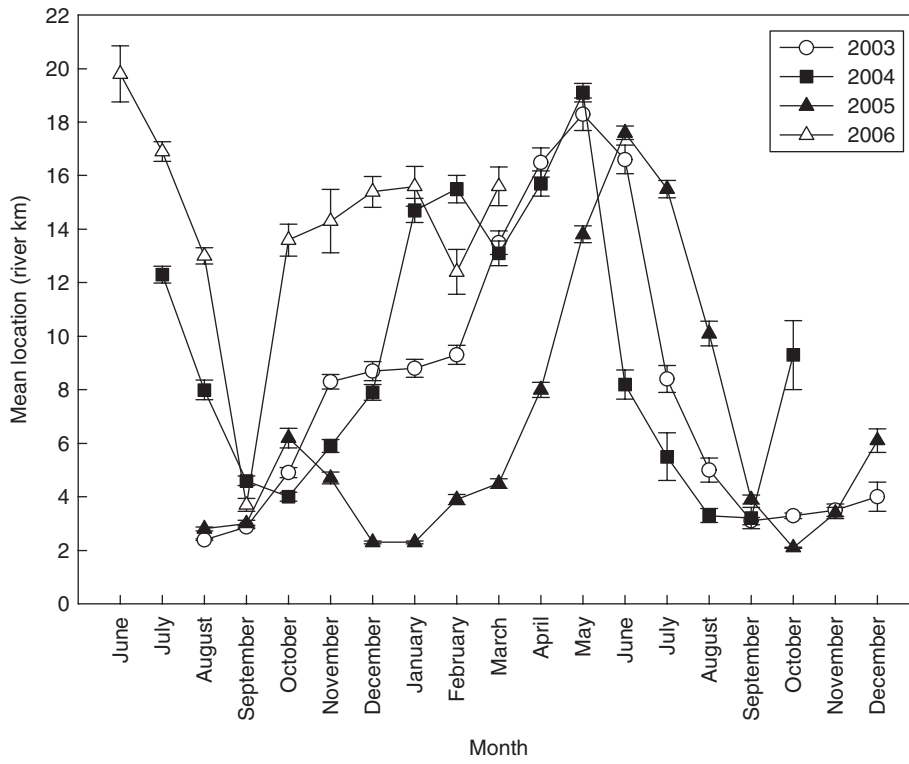


Fig. 5. Mean river location (distance from the mouth of the river) of juvenile *Carcharhinus leucas* revealing patterns in use of the Caloosahatchee River. Bars indicate standard error. Symbol type indicates the year individuals were released with monitoring extending beyond 1 year as shown by months.

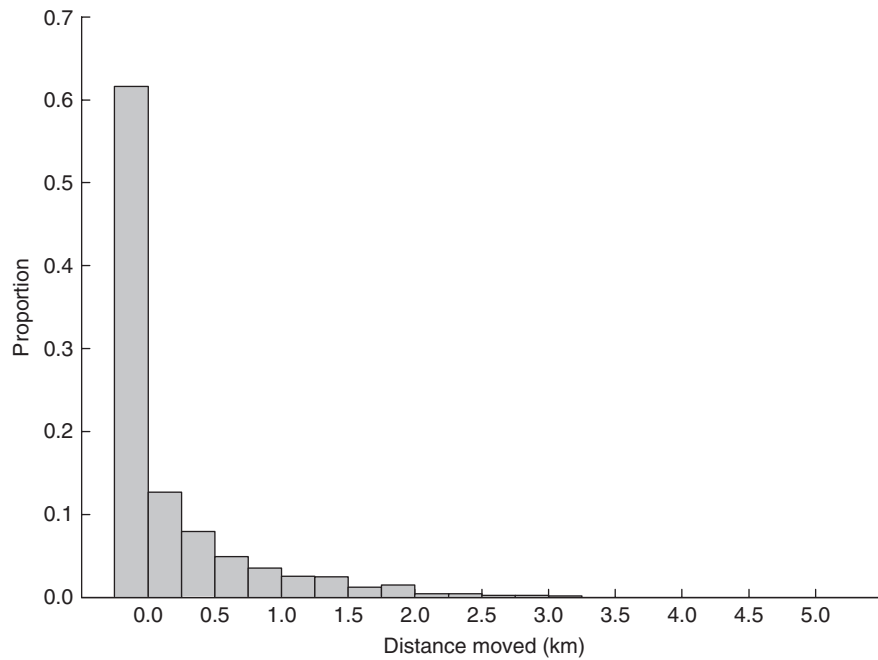


Fig. 6. Distance moved between 30-min centres of activity by juvenile *Carcharhinus leucas* from three cohorts (2003–2005) in the Caloosahatchee River. Far left bar represents the proportion of observations where there was no difference between consecutive 30-min centres of activity.

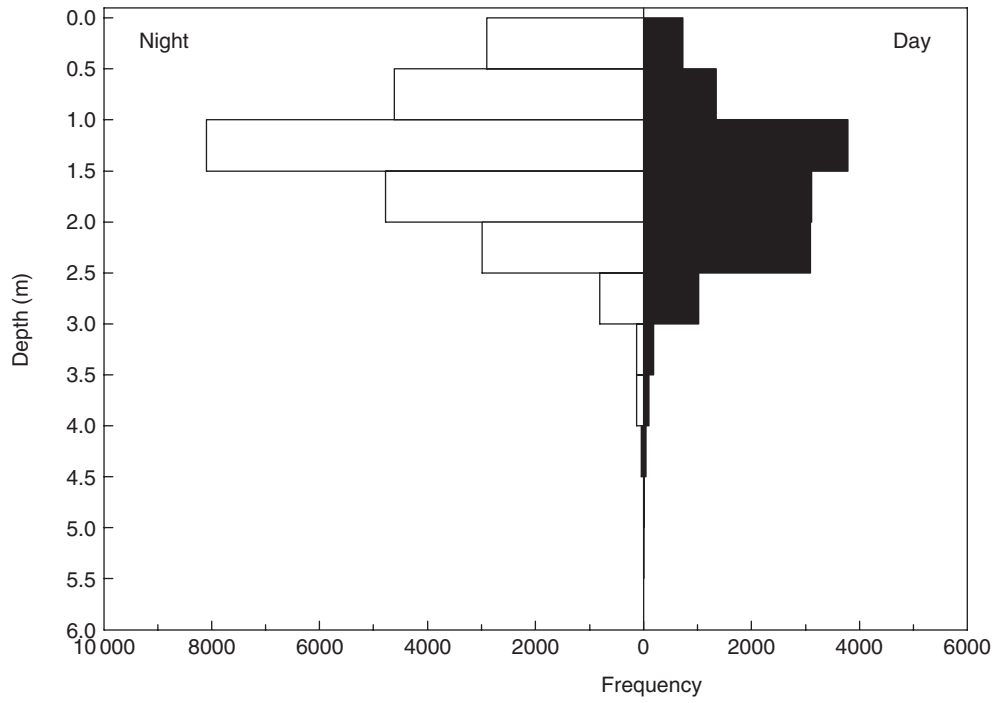


Fig. 7. Night (open bars) and day (filled bars) depth distributions of age 0 *Carcharhinus leucas* monitored in the Caloosahatchee River in 2006.

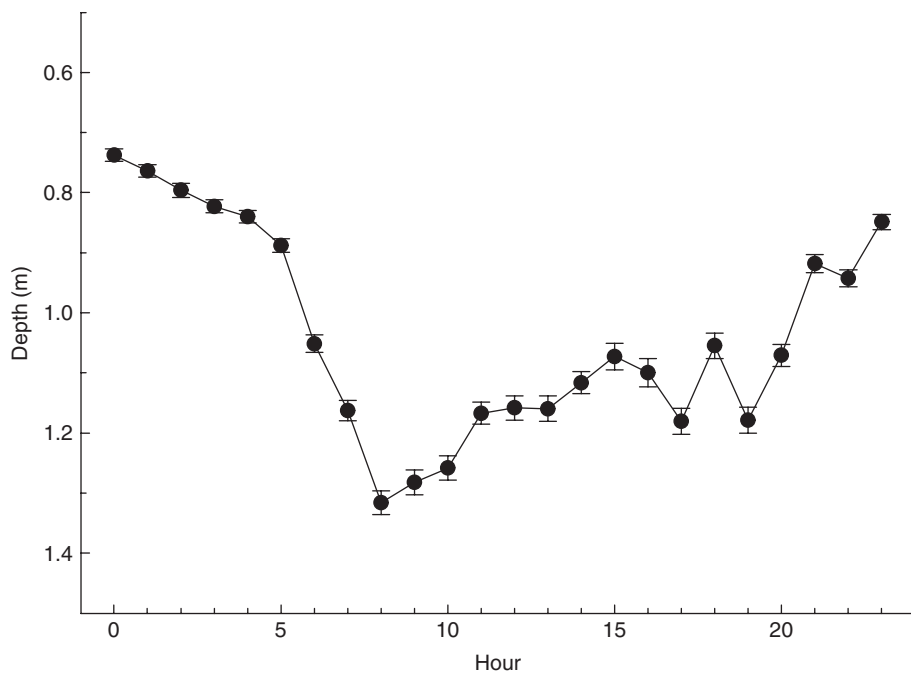


Fig. 8. Mean hourly depth of age 0 *Carcharhinus leucas* in the Caloosahatchee River in 2006 based on data from acoustic telemetry tags. Error bars represent standard error.

suggests use of this amount of space may be typical for young *C. leucas*.

Despite consistency in home-range size over time, location within the river changed through time with individuals moving up- and downstream throughout the year. This usage was consistent with the findings of Heupel and Simpfendorfer (2008) and revealed movement upstream during the dry winter and spring months (February–June) and movement closer to the river mouth during the wet summer and autumn months. This movement is likely related to changes in environmental conditions as described by Heupel and Simpfendorfer (2008). Although the location of individuals within the river changed seasonally, the amount of space used (daily activity space and monthly home-range size) did not change. This suggests that although *C. leucas* location within the river may be influenced by environmental conditions, the amount of space used by individuals does not change.

Diel patterns

Analysis of movements between centres of activity showed a tendency for juvenile *C. leucas* to move upstream during the day and downstream at night. This pattern was consistent between cohorts and is consistent with results of active tracking within the same area (Ortega *et al.* 2009). Since the magnitude of movements between day and night were very similar, there was no net movement up- or downstream over time. However, it is unclear why individuals would move up- or downstream on a diel cycle. The diel nature of this movement indicates that tidal transport, salinity change, or other tidally related factors did not play a role in this behaviour. This would suggest environmental conditions are unlikely to have triggered this pattern and it may be driven by some other external driver such as prey movement.

Depth data from the 2006 cohort showed that individuals swam closer to the surface at night and deeper during the day. This result is similar to that reported by Ortega *et al.* (2009) based on active tracking of juvenile *C. leucas* in the Caloosahatchee River. However, not all tracking studies of *C. leucas* have reported diel differences in depth distribution. Curtis (2008) reported that juvenile *C. leucas* in the Indian River Lagoon remained primarily within 1 m of the water surface and that there was no diel difference in depth used. This lack of diel behaviour, however, may reflect the shallow depths where individuals were tracked in the Indian River Lagoon. Ortega (2008) suggested diel patterns in *C. leucas* depth were based on use of habitat closer to the shoreline (and thus shallower) at night. This suggests that some behavioural patterns may be at work and that depth within the water column may be a factor of water depth where an individual is present rather than directed movement up or down in the water column. However, the current study could not resolve distance to the shore, and so could not test this hypothesis.

Response to environmental conditions

Year-round presence of juvenile *C. leucas* within this region is unique as many coastal shark species migrate from summer regions to winter grounds. For example, juvenile blacktip (*C. limbatus*) and sandbar sharks (*C. plumbeus*) in south-east USA are known to migrate south towards warmer waters during colder months of the year (Castro 1993; Grubbs *et al.* 2007;

Heupel 2007). This result is similar to those reported for juvenile *C. leucas* in the Indian River Lagoon (Snelson *et al.* 1984; Curtis 2008). Lack of movement out of the Caloosahatchee River during winter months suggests *C. leucas* may have different environmental tolerances than related species in adjacent habitats. Interestingly, Collins *et al.* (2008) reported that *R. bonasus* also remained resident in the Caloosahatchee River during winter months. This species is known to be migratory in most of its range (Schwartz 1990) and move out of inshore, coastal regions during winter months (Smith and Merriner 1987). Collins *et al.* (2008) hypothesised that water temperatures within the Caloosahatchee River did not get low enough to trigger migration of *R. bonasus* within the system. Curtis (2008) reported that *C. leucas* moved out of the northern Indian River Lagoon when water temperatures fell below 20°C. In contrast, water temperatures in the Caloosahatchee River dropped as low as 14°C with no apparent response. Based on these results, it appears that *C. leucas* in the Caloosahatchee River behave differently to *C. leucas* in other habitats. It is unclear why these differences occurred in such similar habitats but may have been related to the movement of prey species or some other variable. This difference may provide advantages to young *C. leucas* in the Caloosahatchee River by allowing individuals to forego migratory behaviour, which potentially shunts energy from growth and exposes them to predation risk in open coastal waters.

Despite changes within the environment, data indicate that juvenile *C. leucas* in the Caloosahatchee River are capable of tolerating most conditions. Changes in temperature, river flow rate and salinity did not affect the amount of space individuals used within the river, although the location of individuals within the system shifted with environmental parameters. This suggests consistent use of space by *C. leucas* despite the variable environmental conditions they are exposed to in estuarine and river habitats. Thus, *C. leucas* appears to be very adaptable and long-term presence within this habitat suggests they are highly dependent on the Caloosahatchee River as juvenile habitat. High habitat dependence and movement over a restricted area could make juvenile *C. leucas* vulnerable to exploitation and to extreme negative alterations to habitat including loss of prey populations. Despite the adaptive ability of *C. leucas*, careful management of river and estuarine systems, which act as nursery areas, is integral to their survival in these habitats. This information may be valuable for future management of *C. leucas* populations and provide a greater understanding of how this species will cope with changes in habitat and environmental conditions in the future.

Acknowledgements

The authors thank Mote Marine Laboratory staff who helped with field efforts for this research including M. Amato, T. Wiley and J. Morris. The authors also thank the numerous volunteer student interns for their assistance during this project including: B. Fulcher, L. Abdelmessih, M. McKenzie, C. Friess, K. Kovitvongsa, A. Lemons, D. Walker and G. Kirkilas; and two anonymous referees for their comments on the text. This research was funded in part by the Mote Scientific Foundation, South Florida Water Management District and the National Shark Research Consortium (NOAA Fisheries). P. Doering and K. Haunert from the South Florida Water Management District provided information on the Caloosahatchee River system and access to water quality data. Treatment of all animals in this study was conducted under ethical

guidelines and approval for procedures was granted to M. R. Heupel by the MML IACUC Committee.

References

- Blackburn, J. K., Neer, J. A., and Thompson, B. A. (2007). Delineation of bull shark nursery areas in the inland and coastal waters of Louisiana. *American Fisheries Society Symposium* **50**, 331–343.
- Castro, J. I. (1993). The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Environmental Biology of Fishes* **38**, 37–48. doi:10.1007/BF00842902
- Collins, A. B., Heupel, M. R., and Simpfendorfer, C. A. (2008). Movement patterns and spatial distribution of cownose rays *Rhinoptera bonasus* within an estuarine river as determined through passive acoustic telemetry. *Estuaries and Coasts* **31**, 1174–1183. doi:10.1007/S12237-008-9100-5
- Compagno, L. J. V. (1984). FAO species catalogue, Volume 4. Sharks of the world: an annotated and illustrated catalogue of shark species known to date, Part 2. Carcharhiniformes. *FAO Fisheries Synopsis* **125**, 478–481.
- Curtis, T. H. (2008). Distribution, movements, and habitat use of bull sharks (*Carcharhinus leucas*, Müller and Henle 1839) in the Indian River Lagoon system, Florida. M.Sc. Thesis, University of Florida, Gainesville.
- Doering, P. H., and Chamberlain, R. H. (1998). Water quality in the Caloosahatchee Estuary, San Carlos Bay and Pine Island Sound. In 'Proceedings of the Charlotte Harbor Public Conference and Technical Symposium, Punta Gorda, FL'. pp. 793–806. Charlotte Harbor National Estuary Program Technical Report No. 98–02.
- Grubbs, R. D., Musick, J. A., Conrath, C. L., and Romine, J. G. (2007). Long-term movements, migrations, and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. *American Fisheries Society Symposium* **50**, 63–86.
- Heupel, M. R. (2007). Exiting Terra Ceia Bay: examination of cues stimulating migration from a summer nursery area. *American Fisheries Society Symposium* **50**, 265–280.
- Heupel, M. R., and Hueter, R. E. (2001). Use of a remote acoustic telemetry system to monitor shark movements in a coastal nursery area. In 'Electronic Tagging and Tracking in Marine Fisheries'. (Eds J. R. Sibert and J. L. Nielsen.) pp. 217–236. (Kluwer Academic Publishers: Dordrecht, The Netherlands.)
- Heupel, M. R., and Simpfendorfer, C. A. (2008). Movements and distribution of young bull sharks (*Carcharhinus leucas*) in a variable estuarine environment. *Aquatic Biology* **1**, 277–289. doi:10.3354/AB00030
- Heupel, M. R., Simpfendorfer, C. A., Collins, A. B., and Tyminski, J. P. (2006). Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. *Environmental Biology of Fishes* **76**, 47–67. doi:10.1007/S10641-006-9007-6
- Ortega, L. A. (2008). Movement and distribution of juvenile bull sharks, *Carcharhinus leucas*, in response to water quality and quantity modifications in a Florida nursery. M.Sc. Thesis, University of South Florida, Tampa.
- Ortega, L. A., Heupel, M. R., van Beynen, P., and Motta, P. (2009). Movement patterns and water quality preferences of juvenile bull sharks (*Carcharhinus leucas*) in a Florida estuary. *Environmental Biology of Fishes* **84**, 361–373. doi:10.1007/S10641-009-9442-2
- Simpfendorfer, C. A., Freitas, G. G., Wiley, T. R., and Heupel, M. R. (2005). Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a southwest Florida estuary. *Estuaries* **28**, 78–85. doi:10.1007/BF02732755
- Simpfendorfer, C. A., Heupel, M. R., and Collins, A. B. (2008). Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 482–492. doi:10.1139/F07-180
- Snelson, F. F., Jr, and Williams, S. E. (1981). Notes on the occurrence, distribution, and biology of elasmobranch fishes in the Indian River Lagoon System, Florida. *Estuaries* **4**, 110–120. doi:10.2307/1351673
- Snelson, F. F., Jr, Mulligan, T. J., and Williams, S. E. (1984). Food habits, occurrence, and population structure of the bull shark *Carcharhinus leucas*, in Florida coastal lagoons. *Bulletin of Marine Science* **34**, 71–80.
- Schwartz, F. J. (1990). Mass migratory congregations and movements of several species of cownose rays, genus *Rhinoptera*: A world-wide review. *Journal of the Elisha Mitchell Scientific Society* **106**, 10–13.
- Smith, J. W., and Merriner, J. V. (1987). Age and growth, movements and distribution of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay. *Estuaries* **10**, 153–164. doi:10.2307/1352180
- Wiley, T. R., and Simpfendorfer, C. A. (2007). The ecology of elasmobranchs occurring in the Everglades National Park, Florida: implications for conservation and management. *Bulletin of Marine Science* **80**, 171–189.
- Yeiser, B. G., Heupel, M. R., and Simpfendorfer, C. A. (2008). Residence and movement patterns of bull (*Carcharhinus leucas*) and lemon (*Negaprion brevirostris*) sharks within a coastal estuary. *Marine and Freshwater Research* **59**, 489–501. doi:10.1071/MF07181

Manuscript received 30 January 2009, accepted 18 May 2009