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Spatial Distribution and Long-term Movement Patterns of Cownose Rays *Rhinoptera bonasus* Within an Estuarine River

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Abstract Passive acoustic telemetry was used to monitor the movements of cownose rays (*Rhinoptera bonasus*) within the Caloosahatchee River estuary in Southwest Florida. Twelve rays were tracked within the river between January 2004 and May 2005 for periods up to 234 days. Linear home range was calculated for all individuals and ranged between 0 and 18.4 km (daily) and 1 and 22.3 km (overall). Ray position within the river was compared to changing water quality parameters throughout the study. Although home range size did not increase with increasing salinity, individuals did occur farther upriver with decreasing flow rates and increasing salinity. There were no differences detected between day and night distribution patterns. Movement and presence patterns demonstrated significant use of the estuarine river over all months, indicating that cownose rays in southwest Florida may not undertake long seasonal migrations as established for other parts of their range.

Keywords Cownose ray · *Rhinoptera bonasus* · Movement patterns · Salinity · Acoustic telemetry

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Introduction

Extensive development in coastal areas and the ensuing human demand for fresh water often result in alteration of natural estuarine conditions by the regulation and modification of associated rivers. Consequently, river fauna are frequently subject to rapid changes in hydraulic variables such as flow, temperature, and salinity. These parameters have been repeatedly demonstrated to affect how fish utilize waterways and connected estuarine habitat (i.e., Collins et al. 2002; Cooke et al. 2004; Kraus and Secor 2005; Brewer et al. 2006; Childs et al. 2008; Heupel and Simpfendorfer 2008). Estuaries by definition are subject to fluctuations in water quality that result from converging fresh and salt water and are key habitat for many species (Able 2005). Understanding how organisms use these systems is essential for wildlife and natural resource management, and animal response to anthropogenic modifications in water flow is a critical component to proper management.

Cownose rays (*Rhinoptera bonasus*) occur in coastal waters of the western North Atlantic from Massachusetts to Brazil and throughout the Gulf of Mexico (Bigelow and Schroeder 1953). This species feeds extensively within estuarine systems (Orth 1975; Smith and Merriner 1985; Blaylock 1992; Collins et al. 2007a) and, as an apex predator of benthic fauna, occupies an important role in the estuarine food chain (Smith and Merriner 1985; Blaylock 1993; Collins et al. 2007a; Myers et al. 2007). A mobile and pelagic batoid, cownose rays complete large-scale oceanic migrations (Rogers et al. 1990; Schwartz 1990; Grusha 2005), but they are also regularly observed within estuaries and are known to frequent the lower reaches of coastal rivers (Clark 1963; Schwartz 1965; Snelson and Williams 1981; Smith and Merriner 1987; Blaylock 1993; Silberhorn et al. 1996). As euryhaline elasmobranchs, cownose rays can tolerate salinities as low as 5–7 (Thompson and Verret 1980; Smith and Merriner 1987).

It is suspected that cownose rays are present throughout the year within estuaries along the southwest coast of Florida (Collins et al. 2007b), but movement patterns and behavioral response to environmental changes within coastal rivers has not previously been investigated. Comparing animal movement to changing abiotic parameters can provide a greater understanding of how behavior can be used to select for certain environmental conditions and indicate the biological or physiological benefits provided within specific areas.

Foraging cownose rays are frequently implicated in the destruction of commercial shellfish (Smith and Merriner 1985; Blaylock 1992; Peterson et al. 2001; Myers et al. 2007). Consequently, this fish is often considered a nuisance species, prompting solicitations for a cownose ray fishery (Fisher and Lacey 1991; Blaylock 1993; Fisher, personal communication). Like most elasmobranchs, cownose rays are late to reach maturity and demonstrate low fecundity (Compagno 1990). These features combined with the gregarious nature of the species increase susceptibility to overfishing, habitat destruction, and other impacts (Heppel et al. 1999).

Combining animal movement patterns with corresponding water quality data allows for predictions regarding long-term patterns, home ranges, and response of individuals to changing environmental factors (e.g., Kieffer and Kynard 1996; Heupel et al. 2004; Geist et al. 2005; Heupel and Simpfendorfer 2008). These data are essential to the implementation of conservation or management strategies. The Caloosahatchee River on the southwest coast of Florida historically acted as a seasonal discharge from Lake Okeechobee. It has been modified over time to serve year-round as part of the Intracoastal Waterway and is currently an outlet for water management districts to control the freshwater supply for much of southwest Florida. This paper explores the extent of cownose ray activity within this riverine habitat and aims to identify effects of changing environmental conditions on this species' use of the area.

Materials and Methods

Study Location

The Caloosahatchee River runs between Lake Okeechobee and southern Charlotte Harbor, Florida (Fig. 1). This river provides substantial fresh water input to the Caloosahatchee Estuary and lower Charlotte Harbor, and river conditions are monitored and adjusted by the South Florida Water Management District (SFWMD). During periods of high rainfall (typically through summer), excess water from Lake Okeechobee is drained, increasing river flows and making much of the lower reaches of the river oligohaline (salinity 0–5). Discharges from the lake vary over time but can reach levels as high as 480 $m^3 s^{-1}$ (SFWMD). During Florida's dry season (usually winter), the lower reaches of the river fluctuate from mesohaline (salinity 5–18) to polyhaline (salinity 18–30). Temperatures within the river typically range between 15°C and 32°C annually.

Cownose rays were tracked in the lower estuarine portion of the Caloosahatchee River (approximately 27 km of river habitat; Fig. 1). The upper reaches of the monitored area are characterized by relatively natural shoreline, while areas near the river mouth are highly developed with extensive canal systems and shoreline modifications. Benthic habitat within the Caloosahatchee River is primarily mud or sand and supports extensive populations of invertebrate benthic fauna (Estevez 1981, 1986).

Field Methods

An array of 20 VR2 acoustic receivers (Vemco/Amirix Ltd.) was deployed in August 2003 to passively monitor the movement of elasmobranchs within the study area. Methods for deploying receivers follow those described by Heupel and Hueter (2001) and Simpfendorfer et al. (2008). Each receiver recorded the date, time, and identity of tagged individuals that swam within the detection range of the unit. Receivers were single-frequency omnidirectional units and were visited monthly to download data, maintain equipment, and record water quality. During each download, surface and bottom temperature, salinity, and dissolved oxygen were measured at each receiver station using an YSI 85 water quality meter.

Cownose rays were collected in 200-m (11- or 30-cm stretch mesh) entanglement nets. Individuals were sexed, weighed to the nearest 0.1 kg, and measured to the nearest centimeter (straight disc width, SDW). Cownose rays were defined as mature (>70 cm SDW) or immature (<70 cm SDW) based upon degree of clasper calcification in males or minimum size at pregnancy in females within Charlotte Harbor (Collins, unpublished data). Size at maturity conservatively agreed with that established for individuals in the

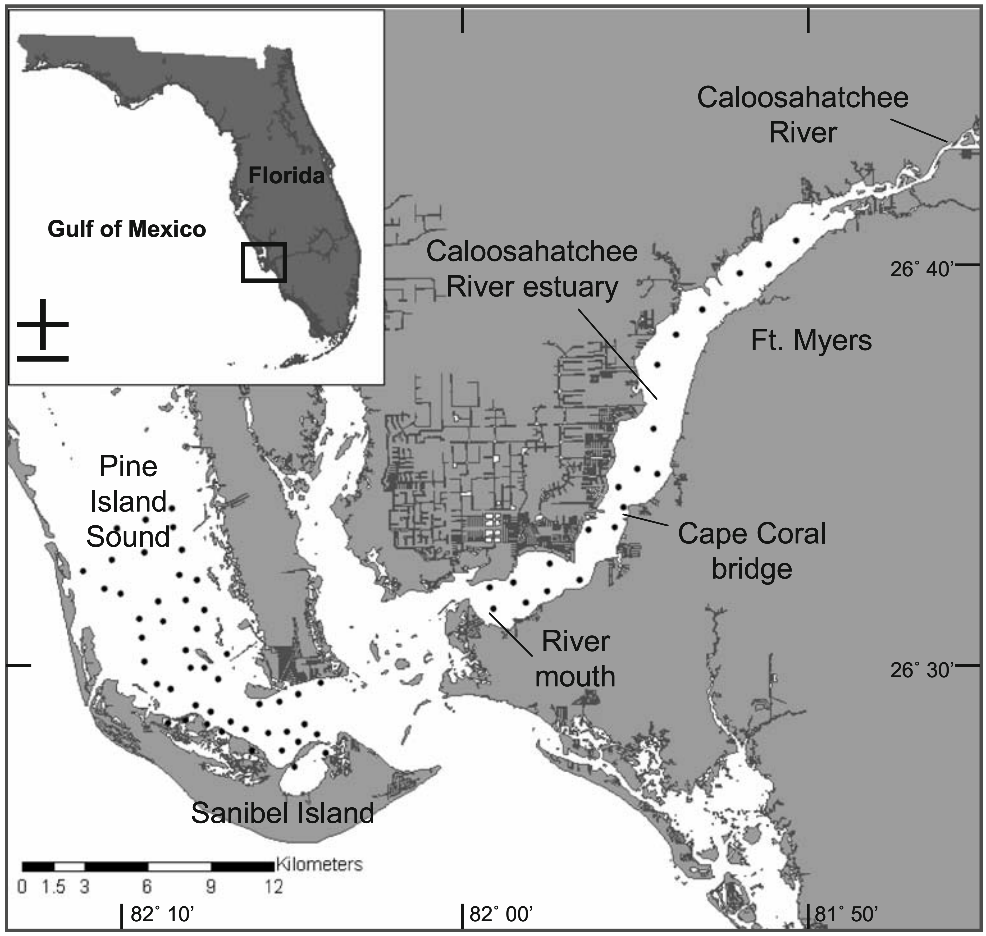

Fig. 1 Study site in the Caloosahatchee River estuary. *Filled circles* indicate locations of acoustic receiver stations, within the river as well as adjacent Pine Island Sound. *Inset*: location of study site in Florida

northern Gulf of Mexico (approximately 65 cm disc width; Neer and Thompson 2005). Prior to release, rays were fitted with acoustic transmitters measuring 8×28 mm (Vemco V8, Vemco Ltd., Nova Scotia, Canada) that had an expected battery life of 250 days and operated on 69 kHz. Transmitters were externally attached by a cinch tag (Floy Tags, Seattle, WA, USA) inserted through the spiracular cartilage. Transmitters were coded to allow individual identification and were set to pulse randomly once every 90–180 s. Random repeat rates allowed multiple individuals to be monitored simultaneously within a given area without signal overlap. Average detection distances for V8 transmitters were tested within the Caloosahatchee River and determined to be 450 m, with a maximum detection distance of 800 m (Heupel, unpublished data). Transmitters were determined to have minimal effects upon ray behavior or health (Collins et al. 2007b). All rays were released in good condition immediately after tagging within 500 m of capture location.

Data Analysis

Daily mean flow and salinity values were obtained from the SFWMD, who continuously monitored water quality via permanently deployed instruments at several locations throughout the river. Flow was classified at the Franklin Locks, upstream of the study area (35 km from the river mouth), and salinity values were obtained from instrumentation deployed at the Cape Coral Bridge (10.5 km from the river mouth). As an approximate midpoint within the study area, salinity values at Cape Coral were used as an index of daily salinity regimes.

Data recorded at receivers were analyzed to determine presence, home range, and movement patterns of cownose rays within the Caloosahatchee River estuary. Daily presence was defined by at least two detections of an individual for that day on any receiver within the river and presence histories were plotted by day to provide a visual timeline of animal residency within the study area. Sporadic detection of individuals outside of the Caloosahatchee River was also recorded and plotted, facilitated by a complementary study in the adjacent Pine Island Sound region (Fig. 1).

The number of cownose rays present within the river was assessed for each day and compared to mean daily river flow and salinity. The location of each cownose ray was estimated every 30 min using the river distance algorithm described by Simpfendorfer et al. (2008). This algorithm used data from the hydrophone array to estimate the distance between centers of activity calculated for each

30-min period and the river mouth, to estimate individual location on a linear scale. The 30-min position estimates were also used to generate daily minimum, maximum, and mean river distance (distance from the river mouth) for individual cownose rays. Daily activity space and monthly home ranges were also calculated on a linear scale as the difference between the maximum and minimum river distance for the time period.

To investigate the relationship between environmental conditions and cownose ray location within the river, daily mean river distances were compared to daily mean values of flow and salinity. Regression analysis was used to examine the relationship between an individual's river distance and salinity or flow rate.

The number of detections per hour by location within the river was assessed for each tracked individual over its total monitoring period to define any diel differences in detection patterns. Each detection recorded for an individual was assigned to one of 24 bins based upon the hour of the detection. Under a hypothesized equal distribution of detections over a 24-h period, Chi-squared tests were performed to determine whether the observed proportion of detections differed significantly from an expected even distribution. Significant differences from expected values would indicate that individuals were more frequently detected (and possibly more active) at specific times of the day. To determine whether detection numbers were higher during day or night hours, hourly detections were divided into day or night for each individual. "Day" was defined as 06:00–18:59 EST, and "night" was 19:00–05:59 EST. Total detections during day and night were summed for each individual and compared using Chi-squared tests to determine whether an individual had significantly more detections during day or night hours.

Results

Transmitters were fitted to cownose rays in January 2004 (n=1), June 2004 (n=1), July 2004 (n=5), October 2004 (n=1), and January 2005 (n=4). The two rays fitted with transmitters in June and October 2004 were initially caught in Pine Island Sound (Collins et al. 2007b, Fig. 1) but were then detected within the river in July and October 2004 and remained for 33 and 39 days, respectively (Table 1). All but one individual were mature, ranging from 710 to 810 mm SDW (mean SDW=770 mm). The single immature ray (ID 268) was a 490-mm female. Seven of the rays caught and tagged in the Caloosahatchee River were detected intermittently by receivers in the river and Pine Island Sound (Fig. 2a). Monitored individuals were present during all seasons of the year for periods extending from 12 to 234 days (mean=90 days). When salinity fell below 5, cownose rays typically moved out of the river and into Pine Island Sound, stayed near the river mouth (within the first 2 km), or disappeared from detection range completely (Fig. 2b).

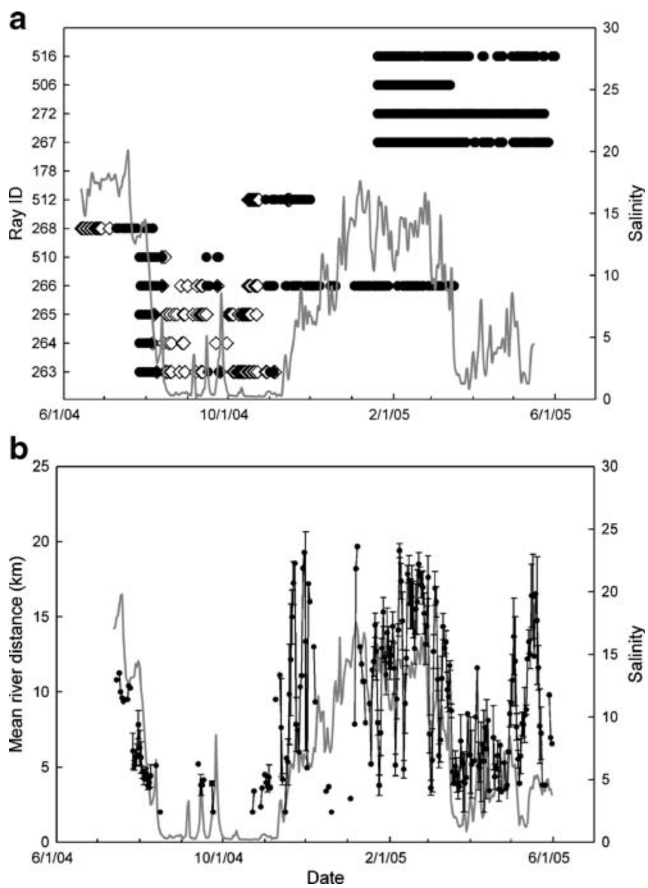

Fig. 2 **a** Relationship between salinity and presence of cownose rays. *Filled circles* designate detection within the Caloosahatchee River; *open diamonds* designate detection in Pine Island Sound, and gaps indicate periods of no detection. **b** Mean location of all individuals within the river. *Solid gray line* designates salinity on both graphs

Linear home ranges of cownose rays were 1–22.3 km (mean=3.5 km). Home range was variable among individuals but was not related to duration of residence (r=0.520, p=0.101; Table 1). Analysis of monthly home range for all individuals combined revealed larger home ranges during winter and spring (January–June) than summer and autumn (July–December; Fig. 3). Increasing home range through time is not believed to be ontogenetic since all but one individual were adult at the time of capture.

Daily activity space for individuals was variable but was typically less than 6 km (Fig. 4). The location of individuals along the length of the river was also variable (Fig. 5) with cownose rays detected over almost the entire monitored portion of the river during the course of the study. No significant differences in activity or river location between day and night were evident (χ^2=21.155, df=21, p=0.449) suggesting no diel pattern in individual locations within the river. Examination of change in river location showed

Table 1 Presence and home range data for all cownose rays monitored within the Caloosahatchee River

Transmitter ID Number	Date captured (m/d/y)	Date of last detection (m/d/y)	Sex	Size (mm, SDW)	Days monitored (n)	Mean daily activity space (km)	Total home range (km)
178	1/21/04	4/25/04	F	760	96	3.98	22.1
268[a]	6/14/04	8/6/04	F	490	33	1.07	9.3
263	7/27/04	11/4/04	F	800	101	1.75	9
264	7/27/04	9/13/04	F	810	62	3.25	7.5
265	7/27/04	8/7/04	M	730	12	4.10	9
510	7/27/04	9/24/04	M	760	60	3.51	7.5
266	7/28/04	3/17/05	F	800	234	1.99	20.9
512[a]	10/16/04	12/1/04	M	740	39	4.70	22.3
267	1/20/05	5/26/05	F	785	127	4.59	18.4
272	1/20/05	5/23/05	M	760	124	3.73	18.4
506	1/20/05	3/14/05	M	710	54	3.69	18.4
516	1/20/05	5/31/05	M	710	132	3.96	22.3

[a] Indicates individuals originally captured in Pine Island Sound

individuals typically moved less than 3 km upriver or downriver from 1 day to the next. This suggests contiguous use of regions of the river with expanded use of the available habitat through time rather than large-scale rapid movement upriver or downriver. Changes in individual 30-min center-of-activity locations also revealed that short-distance movements (0–1 km) were most common. Large-scale movements were rare, although individuals were recorded traveling distances as great as 15 km within 30 min (Fig. 6).

Detections by the farthest upriver receivers were rare, indicating that the acoustic array provided adequate coverage of utilized habitat within the river. Final detections (a detection followed by at least 24 h of no detection) were typically from the middle of the river (suggesting use of connected canals) or at the river mouth (indicating departure from the river). There were no cases where a final detection occurred on an upriver receiver.

Over the course of the study, temperatures ranged from 14.4°C to 32.4°C; salinity fluctuated between 0.2 and 21, and river flow varied between 0 and 374 $m^3 s^{-1}$. Cownose rays were present under all of these environmental conditions. Salinity was negatively correlated with river flow (salinity decreased with increasing flow; r=0.769, p<0.0001). Examination of mean location of individuals within the river in relation to flow rate revealed a weak negative correlation (slope=−0.0009, r=0.387, p<0.0001). Individuals tended to remain near the river mouth when flow rate was high but were detected throughout the study area when flow was low (c. 57 $m^3 s^{-1}$; Fig 7a). Examination of salinity in relation to ray location revealed that individuals moved farther upriver when salinity increased (Fig. 7b). Although locations of individuals within the river varied at midrange salinities (8–15), there was a significant correlation between location and

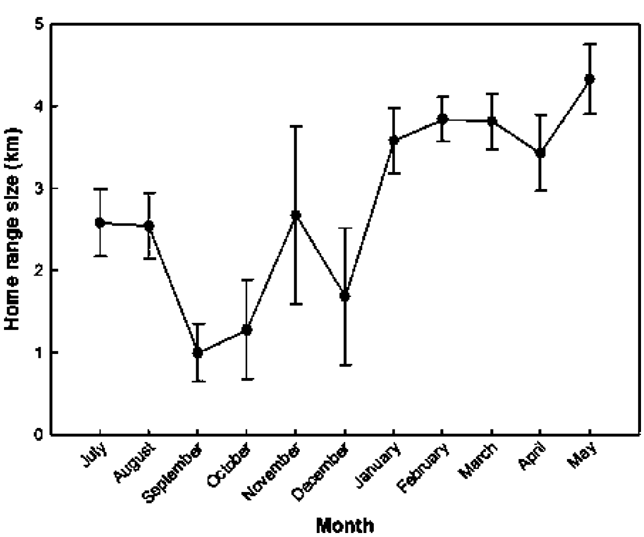

Fig. 3 Mean monthly home ranges for cownose rays monitored within the Caloosahatchee River

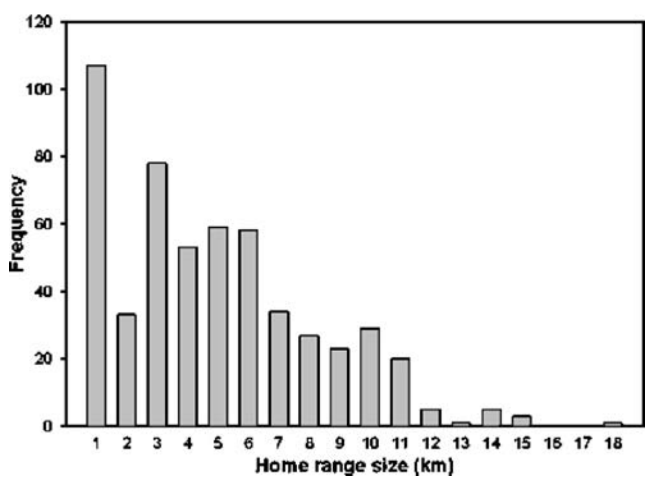

Fig. 4 Frequency of daily activity space for cownose rays monitored within the Caloosahatchee River

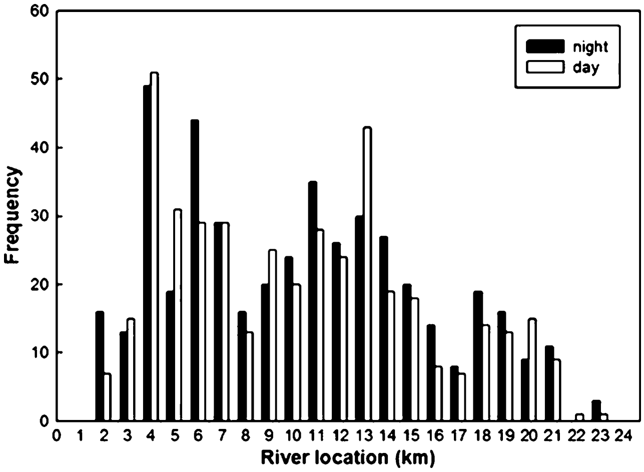

Fig. 5 Frequency of detection for cownose rays allocated by location within the river (kilometer from mouth) and classified as day or night detections

salinity (slope=0.465, r=0.522, p<0.0001). Mean river distance was negatively correlated with river flow (analysis of variance, ANOVA, F=33.758, df=193, p<0.0001) and positively correlated with salinity (ANOVA, F=76.877, df=206, p<0.0001) suggesting these factors played a role in ray distribution within the river. Analysis of home range size in relation to flow rate (slope=−0.0001, r=0.138, p=0.0027) revealed a weak relationship while comparison to salinity (slope=0.048, r=0.100, p=0.054) revealed no significant relationship. Despite being statistically significant, the relationship with flow only explained 2% of the variation and therefore other unidentified factors are likely more important in explaining the variation in home range. Although salinity and flow may have affected an individual's position within the river, they did not affect the amount of area an individual used.

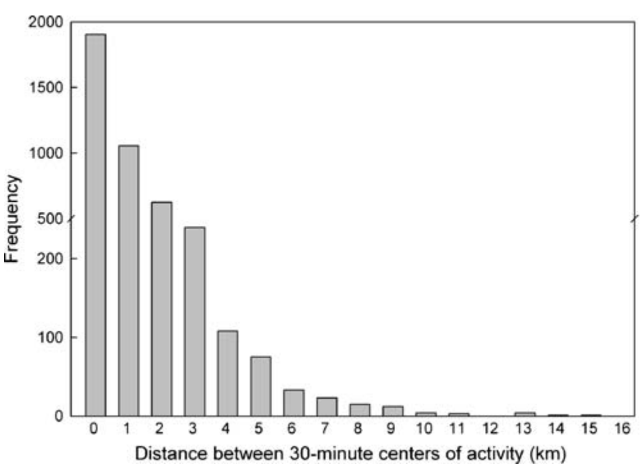

Fig. 6 Distance traveled upriver or downriver based on 30-min center-of-activity locations shown as number of kilometers traveled and the frequency of occurrence within the dataset

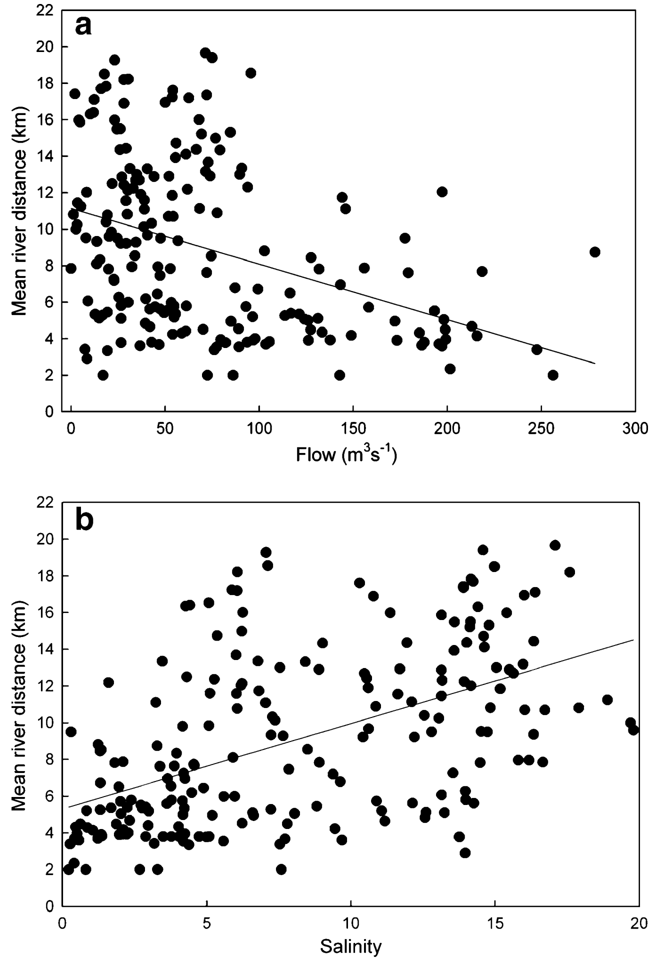

Fig. 7 Relationship between the distribution of tagged cownose rays within the Caloosahatchee River and flow (**a**) and salinity (**b**). Plots show the daily mean river location for all tagged cownose rays and the flow or salinity level when individuals were present

Discussion

Monitoring the presence and movement of cownose rays within the Caloosahatchee River revealed that many individuals were present over long-term periods but that the extent of river area utilized was affected by changing environmental conditions. Residency periods averaged approximately 3 months, with a maximum presence of nearly 8 months. In contrast to tracking results from adjacent Pine Island Sound where cownose rays were largely transient (Collins et al. 2007b), individuals within the Caloosahatchee River were present year-round and exhibited long-term use of the area. This result supports similar reports of resident populations in other regions such as Venezuela and North Carolina (Smith 1907; Smith and Merriner 1987) but contradicts research that predicts coordinated long-distance seasonal movement of cownose rays (Schwartz 1990; Neer et al. 2007).

Similar to the findings in this study, Smith and Merriner (1987) reported cownose rays as common within Chesapeake

Bay tributaries. Individuals were recorded as far upstream as 24 km in the York, 38 km in the Potomac, and 45 km in the Rappahannock rivers, and schools were reported to remain in river systems through summer. Blaylock (1992) also reported that cownose rays occurred regularly in pound net surveys within the Rappahannock and Potomac rivers. These data suggest that use of riverine systems adjacent to estuaries is common for this species and that these areas may function as long-term or critical habitat.

Examination of ray movements within the Caloosahatchee River revealed that daily activity spaces were typically small with individuals using less than 6 km of the river on most days. Daily linear activity spaces as large as 18 km were observed but were rare. Use of relatively small areas compared to the amount of available habitat on a daily scale was similar to findings for cownose rays in Pine Island Sound where individuals were reported to typically use less than 5 km^2 within a single day (Collins et al. 2007b). Other ray species such as the Hawaiian stingray, *Dasyatis lata* (Cartamil et al. 2003), and round stingray, *Urobatis halleri* (Vaudo and Lowe 2006), have smaller home range areas (c. 1 km^2), presumably based on the benthic nature of these species. These more benthic-associated ray species are known to spend long periods resting on the bottom, as opposed to cownose rays which are a semipelagic and more mobile species. The amount of river area used per day by cownose rays (~1–5 km) was similar to that used by juvenile bull sharks within the same habitat (Heupel, unpublished data), suggesting that movements of cownose rays are more similar to pelagic species than those of more sedentary ray species.

Although daily activity spaces were consistently small, monthly home ranges varied widely over time. Home ranges within the river were smaller during summer but increased during winter. Causal factors (i.e., changing water temperature, flow, salinity, or individual variability) for this difference in home range size were difficult to determine. The majority of individuals tracked during July–December (the smaller home range period) left the area or stopped transmitting before the coldest months of the year. Individuals tracked January–June (larger home range period) were mostly composed of newly caught individuals tagged in January 2005. However, at least one individual tagged in July remained through winter and exhibited a similar pattern to newly released individuals. Rays were detected over larger spans of the river during winter months, which may be related to the increased salinity values that accompany reduced freshwater flow. Additionally, detection in the upper reaches of the river (where salinity values are lowest) was minimal during summer months. This suggests that changes in home range may have a seasonal component, but additional investigation is necessary.

Although diel changes in activity patterns have been noted for other ray species (e.g., Standora and Nelson 1977; Bray and Hixon 1978; Cartamil et al. 2003; Vaudo and Lowe 2006), day–night activity patterns of cownose rays within the Caloosahatchee River were not significantly different. It is therefore likely that movement patterns of this species within the study area are unrelated to diel cycle and controlled by other factors. Hopkins and Cech (2003) reported that temperature and salinity affected the distribution of several elasmobranchs, including the bat ray (*Myliobatis californica*). Temperature was associated with bat ray presence in Tomales Bay, where individuals were observed to leave the area when water temperatures declined below 10°C (Hopkins 1993; Hopkins and Cech 1994). Matern et al. (2000) suggested that bat rays moved into warmer water during the day as a means of behavioral thermoregulation. Vaudo and Lowe (2006) related increased round stingray activity to increasing water temperature. Results of these studies imply the behavioral consequences of abiotic factors and suggest multiple cues can affect the movement and distribution of ray species within various habitats.

Water temperature has also been suggested as a causal factor for the movement and migration of cownose rays (e.g., Schwartz 1990; Neer 2005). Blaylock (1992) and Smith (1980) attributed the spring-time appearance of cownose rays (at Cape Hatteras in April and Chesapeake Bay in May) as a response to the northward movement of the 15–16°C surface isotherm. Neer (2005) reported that cownose rays in northern Florida were rarely caught at temperatures below 15°C. Neither this study nor the complimentary study in Pine Island Sound (Collins et al. 2007b) revealed significant seasonal movement patterns. However, the minimum temperature recorded over the study period was only 14.4°C. Lethal minimum temperature for the cownose ray is 12°C (Schwartz 1964). The lack of evidence for a seasonal departure from this southwest Florida estuary suggests that the local minimum water temperatures may not trigger movement of cownose rays away from the region. This supports the suggestion by Collins et al. (2007b) that movement may be more closely related to other factors such as prey availability, predator avoidance, or reproduction.

Although water temperature did not appear to affect the distribution of cownose rays within the Caloosahatchee River, drastic reductions in salinity resulted in a distinct departure, especially from the upper reaches of the study area. At increased river flow rates (and, consequently, decreased salinity), cownose rays moved toward the river mouth where tidal influence was presumably greatest. As cownose rays are large and muscular swimmers, river velocity (as governed by the freshwater flow rates) is probably not a major factor in determining their distribution. Blaylock (1992) reported that cownose rays have a swimming velocity of 0.29 m/s which should allow them to outswim even the highest flows recorded in the river during this study. Concentrated activity near the river mouth during periods of high flow is similar to the findings of Smith and Merriner (1987) and Blaylock (1989), who reported that cownose rays aggregated in the eastern portion of Chesapeake Bay where salinities were highest due to tidal flow.

Locations of home ranges within the river were significantly related to the surrounding abiotic conditions. Based on their known swimming ability, it is suspected that decreasing salinity (and potentially increasing turbidity) caused downriver movement of cownose rays during periods of freshwater release. When salinity decreased to 5 or less, rays left the Caloosahatchee River and many were subsequently recorded within Pine Island Sound where salinity was higher. Heupel and Simpfendorfer (2008) found that juvenile bull sharks also moved toward the mouth of the Caloosahatchee River when river flow rate was high. However, bull shark movements may have been an effect of prey response to flow changes rather than direct physiological effects of changing salinity (Heupel and Simpfendorfer 2008). As cownose rays feed primarily upon sessile benthic invertebrates (Smith and Merriner 1985; Collins et al 2007a), it is more likely that behavioral osmoregulation (rather than prey distribution) determined cownose ray position within the river.

Large schools of cownose rays have been reported in dilute waters hundreds of kilometers inland from the Atlantic Ocean (Smith and Merriner 1987) indicating active hyperosmotic regulation of body fluids (Scholnick and Magnum 1991). This physiological ability to withstand variable salinity regimes permits cownose rays to exploit a wider range of habitats, where benefits may include increased prey availability, decreased predation, or reduced competition. Extended residence of cownose rays within the Caloosahatchee River indicates that this region provides an important habitat for this species. Nutrient-rich rivers support a wide variety of benthic fauna. If competition for benthic prey is slight, year-round residence could provide a foraging advantage to cownose rays within the Caloosahatchee River. Additionally, if suspected ray predators such as large carcharhinids are generally absent from coastal rivers (Heupel and Simpfendorfer, unpublished data), then these areas may provide an ideal refuge and allow individuals to concentrate energy into feeding, growth, and other behaviors rather than predator avoidance.

Results of this study in conjunction with those of recent others (Collins et al. 2007a, b; Neer and Thompson 2005; Neer et al. 2007) are providing additional insight into the ecology of cownose rays. In general terms, cownose rays have evolved as batoids which feed predominantly on large bivalves and undertake large-scale and coordinated migrations. These studies have shown that at least a portion of the cownose ray population within the Gulf of Mexico may remain resident in southwest Florida, feeding opportunistically on a variety of benthic organisms. It is clear that cownose rays may have varying life history strategies within different regions, and further research is warranted for comparison to these findings.

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