Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary

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Between July 2003 and November 2004, 21 cownose rays *Rhinoptera bonasus* were tagged and tracked within Pine Island Sound estuary, Florida, using passive acoustic telemetry. Residence time of individuals ranged between 1 and 102 days. No relationship was detected between ray activity and tidal stage or time of day. Minimum convex polygons (MCP) and kernel utilization distributions (KUD) were calculated over several time frames to demonstrate the extent of an animal's home range and core areas of use. Total MCPs ranged between 0·81 and 71·78 km^2 (mean = 22·01 km^2), with daily MCPs as large as 25·8 km^2. Total 95% KUDs ranged from 0·18 and 62·44 km^2 (mean = 22·63 km^2), while total 50% KUDs were smaller, ranging from 0·09 to 9·68 km^2 (mean = 3·33 km^2). Both MCP and KUD areas exhibited a positive relationship with residence time and *R. bonasus* size. As mobile, pelagic swimmers capable of traversing large distances, these data show that cownose rays travel extensively throughout this estuary, yet may remain within very small areas for extended periods. © 2007 The Authors

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INTRODUCTION

Atlantic cownose rays *Rhinoptera bonasus* (Mitchill, 1815) are believed to be highly migratory, transient and seasonal residents of coastal and inshore waters. They have at times been observed travelling in groups numbering thousands of individuals (Clark, 1963; Blaylock, 1989; Rogers *et al.*, 1990), and large shoals are frequently reported within estuaries and along beaches (Clark, 1963; Smith & Merriner, 1985; Blaylock, 1989, 1992; Rogers *et al.*, 1990). Schwartz (1965, 1990) suggested that *R. bonasus* in the Gulf of Mexico make up a separate population from those in the western Atlantic and that each population displays a unique migration pattern in response to seasonal changes in water temperature. He hypothesized that the Atlantic population moves north

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and south along the coast from New England to South America, based on results from a study where cownose rays tagged in Chesapeake Bay were recaptured as far south as Venezuela and Brazil (Schwartz, 1965). This hypothesis has recently been partially supported using satellite tags to track the movements of *R. bonasus* from Virginia to the east coast of Florida (D. Grusha, pers. comm.). The population in the Gulf of Mexico was suggested to travel clockwise from the Yucatan peninsula to Florida (Schwartz, 1990), but there are no quantitative data available to support this hypothesis. Alternately, it has been proposed that some *R. bonasus* may reside in coastal estuaries and simply move offshore to warmer water during colder months (Smith & Merriner, 1987) rather than take part in extensive autumn and spring migrations. In either case, cownose rays are believed to be highly mobile, short-term residents of inshore waters, but little quantitative data are available concerning movement patterns of individual *R. bonasus*.

As benthic predators, batoids play an important ecological role (Orth, 1975; Valentine *et al.*, 1994; Peterson *et al.*, 2001). Large schools of foraging *R. bonasus* have been implicated in commercial shellfish predation as well as seagrass habitat destruction along the eastern coast of the U.S.A. (Orth, 1975; Merriner & Smith, 1979; Peterson *et al.*, 2001). Damage caused by cownose rays has incited calls to manage the population by instating a fishery (Fisher & Lacey, 1991; R. A. Fisher, unpubl. data). Determining and interpreting the movement patterns of cownose rays would be beneficial, not only to understanding their use of coastal habitats and role within the ecosystem as upper-level predators, but also to estimate the impact of a possible fishery upon the species.

Most tracking data that are available for rays consist of short-term or intermittent manual tracking data (Blaylock, 1992, 1993; Gilliam & Sullivan, 1993; Silliman & Gruber, 1999; Matern *et al.*, 2000; Cartamil *et al.*, 2003), and minimal data exist regarding the movement patterns of cownose rays. The advent of passive acoustic monitoring technology has allowed the movements of multiple animals to be continuously tracked over extended time frames (Klimley *et al.*, 1988; Meyer *et al.*, 2000; Heupel & Hueter, 2001; Voegeli *et al.*, 2001; Heupel *et al.*, 2004) permitting predictions regarding long-term patterns, home ranges and response of individuals to environmental factors (Heupel *et al.*, 2004). The objectives of this study were to investigate *R. bonasus* within a south Florida estuary using passive acoustic telemetry to gain a better understanding of their seasonal residency, movement patterns and potential effect on the benthic community.

MATERIALS AND METHODS

STUDY AREA

Charlotte Harbor is a large estuary on the south-west coast of Florida (between 27°05′ and 26°27′ N; 81°50′ and 82°30′ W). This research was conducted in Pine Island Sound, located in lower Charlotte Harbor (Fig. 1). The shore of Pine Island Sound is largely undeveloped including state and federally protected areas (National Wildlife Refuge). The aquatic habitat within the sound varies from shallow sand and mud flats to seagrass beds and deep channels. Depths within the sound are generally shallow

FIG. 1. Map of Pine Island Sound and its location along the south-west coast of Florida. Hatched areas indicate seagrass beds and bathymetry contour indicates depths >4 m. ▲, hydrophone station locations.

(<3 m), but range from 0 to 10 m with a tidal range of 0·7 to 1·8 m. Seagrass beds are typically found in areas <2 m deep and consist of three main species: manatee grass *Syringodium filiforme*, turtle grass *Thalassia testudinum* and shoal grass *Halodule wrightii*. Pine Island Sound experiences significant freshwater input from the Caloosahatchee River that causes salinity to vary widely (15–37 over the course of the study; unpubl. data). Temperature within the sound ranged between 20 and 33° C over the course of the study period (unpubl. data).

ACOUSTIC ARRAY

An array of acoustic hydrophones (Vemco VR2 receivers) deployed within Pine Island Sound from April to November of 2003 and 2004 was used to track movements of *R. bonasus* within the study site. The main array system within Pine Island Sound consisted of 40 hydrophones deployed in open water areas (Fig. 1) allowing for a total monitoring area of *c.* 184 km^2. Data were downloaded manually from hydrophones every 2–3 weeks.

STUDY SPECIES

Cownose rays were collected in 200 m (110 or 300 mm stretch mesh) or 400 m (110 mm stretch mesh) tangle nets. Individuals were sexed, weighed to the nearest 0·1 kg and measured to the nearest cm (straight disc width, W_{SD}). Cownose rays were defined as mature (>70 cm W_{SD}) or immature (<70 cm W_{SD}) based upon degree of clasper calcification in males or minimum size at pregnancy in females within Charlotte Harbor (unpubl. data). Sizes conservatively agreed with those established for *R. bonasus* in the northern Gulf of Mexico (*c.* 65 cm disc width) (Neer & Thompson, 2005). Prior to release cownose rays were fitted with acoustic transmitters measuring 8 × 28 mm (Vemco V8; Vemco Ltd, Halifax, Nova Scotia, Canada) that had an expected battery life of 250 days and operated on 69 kHz. 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 continuous signal overlap. Detection distances for V8 transmitters within Pine Island Sound were tested within the region and determined to be 450 m (average) with a maximum detection distance of 800 m (unpubl. data). Wax coated transmitters were externally attached to rays by a cinch tag (Floy Tags, Seattle, WA, U. S. A.) inserted through the spiracular cartilage. All cownose rays were released in good condition within 500 m of their capture location.

To determine effects of transmitter attachment and retention time, four *R. bonasus* were housed together in a circular saltwater tank (8700 l) at Mote Marine Laboratory for 16 months. Three of the captive cownose rays were fitted with 'dummy' transmitters, equal in all physical aspects to field transmitters. One captive cownose ray was not tagged and acted as a control. All four cownose rays were monitored for changes in physical appearance or behaviour. Cownose ray swimming and feeding behaviours were qualitatively assessed daily, and each individual was photographed, weighed and measured monthly.

DATA ANALYSIS

Residence time

The residence of cownose rays within Pine Island Sound was examined by determining the number of days individuals were present within the study site. Individuals were considered present when greater than two detections were recorded for that individual within a single day. Daily presence data were analysed to determine the number of consecutive days that an individual was resident (continuous presence), as well as the total number of days that it was detected within the study area. The number of days present (both continuous and total) within the study area was tested for differences based on sex and maturity stage using *t*-tests.

Activity patterns

Number of detections per hour were 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 groups based upon the hour of the detection. χ^2 tests (Microsoft Excel, 2003) were performed to determine whether the observed proportion of detections differed from an expected even hourly distribution. Significant differences from expected values would show individuals were more

frequently detected at specific times of the day. To determine whether detection numbers were higher during day- or night-time hours, hourly detections were divided into day (between 0600 and 1859 hours) or night (between 1900 and 0559 hours). Day and night total detections were summed for each individual and compared using the χ^2 test. Similar to examination of detections per hour, the number of detections at various tidal stages (in 200 mm increments of tidal height) were analysed to define effects of tidal variation on individual detections. Tide data were obtained for Galt Island, Pine Island Sound, using the programme Tides and Currents (Nautical Software, Inc., Portland, OR, U.S.A.). χ^2 tests were used to compare the frequency of detections per tidal stage with the frequency of all tidal heights during the periods individuals were monitored. Significant differences in the distribution of detections would indicate that an individual was detected more frequently at specific tidal heights.

Home range analyses

Detection data from *R. bonasus* were processed using a custom-written FORTRAN programme (Simpfendorfer *et al.*, 2002). This programme used a mean position algorithm to calculate position estimates, or 'centre of activity' locations (COA), for monitored individuals every 30 min. Simpfendorfer *et al.* (2002) compared real time location data from small sharks *Carcharhinus limbatus* (Müller & Henle, 1839) to mean position estimates and calculated an error of *c.* 225 m using this method. Processed data were used for all of the following analyses to define individual locations and movements through time.

Calculated COAs through time were used to define home range and activity space. Minimum convex polygons (MCP) and kernel utilization distributions (95 and 50% KUD) (Worton, 1989) were calculated for each individual using the Animal Movement Analyst Extension (AMAE) in ArcView 3·2 GIS (Hooge & Eichenlaub, 2000). Minimum convex polygons were used to demonstrate the extent of an animal's range over a given period, while KUDs illustrated the utilization of space within that range (Worton, 1987). Changes in the extent of an individual's range over time were assessed by examining daily, 3 day, 7 day, 30 day and total MCPs. To detect changes in the utilization of the study site over time, KUDs were also examined over 3 day, 7 day, 30 day and total monitoring periods. Daily KUDs were not calculated because most cownose rays did not have enough detections over a single day to calculate an accurate utilization distribution. Unpaired *t*-tests were used to determine if there were sex or size differences in home ranges within each time period (*e.g.* 3, 7, 30 or all days) for both estimators. To determine whether the size of an animal's range depended upon the number of days it was present, total MCPs and KUDs were compared to length of residency using linear regression. To determine whether home range was related to animal size, linear regression was used to compare activity spaces to W_{SD}.

Daytime and night-time KUDs were calculated for each examined time period to identify whether individuals exhibited diel changes in home range size or distribution. Paired *t*-tests were used to detect differences in size of day- *v.* night-activity spaces. Day and night KUDs were then compared between immature and mature *R. bonasus* using unpaired *t*-tests to determine whether maturity had an effect on the size of day- and night-utilization distributions.

The distance between consecutive centres of activity was calculated using standard geometric formulae. Distances between consecutive 30 min COA locations were used to examine linearity of movement and define the net movement of an individual between detections. Calculated distances were used to define the minimum distance travelled between consecutive centres of activity and indicate whether cownose rays were generally stationary or moved large distances over short periods. Linear regression was used to detect relationships between cownose ray size and distance moved, and unpaired *t*-tests were used to detect size or sex differences in mean distances moved over time.

All data were tested for normality and homogeneity of variances, and statistical tests (significance level, $P < 0.05$) were performed using Statistica (StatSoft, 1999 edition; StatSoft, Inc., Tulsa, OK, U.S.A.) or Sigma Plot (Systat Software, Inc., version 9.0; Systat, Inc., San Jose, CA, U.S.A.).

RESULTS

Twenty-one *R. bonasus* (15 male and six female) were monitored using passive acoustic telemetry between July 2003 and November 2004 within Pine Island Sound. Four *R. bonasus* were monitored in 2003 and 17 were monitored in 2004. Monitored *R. bonasus* ranged in size from 49 to 90 cm W_{SD}. Twelve were mature (eight male and four female), and nine were immature (seven male and two female). No tagging effects were observed in three captive *R. bonasus* (two mature and one immature) held for >16 months in captivity. Transmitters were retained in captive cownose rays for periods of 156, 187 and 457 days. Tagging sites displayed some necrosis, but transmitters were not dislodged and no negative effects on animal feeding or health were observed.

RESIDENCE TIME

Residence time was highly variable among individuals (Fig. 2). Although some cownose rays were resident for extended lengths of time, others only remained within the study site for brief periods. In 2003, all *R. bonasus* were tagged in July. One left the study area in July, two left in August and one remained through to October. In 2004, cownose rays were captured in June, July, August and October, and left the study area in June, July, August, October and November. One cownose ray tagged in July 2004 (number 266) and another tagged in October (number 512) were still in the estuary upon removal of equipment from Pine Island Sound on 30 November 2004. Two *R. bonasus*
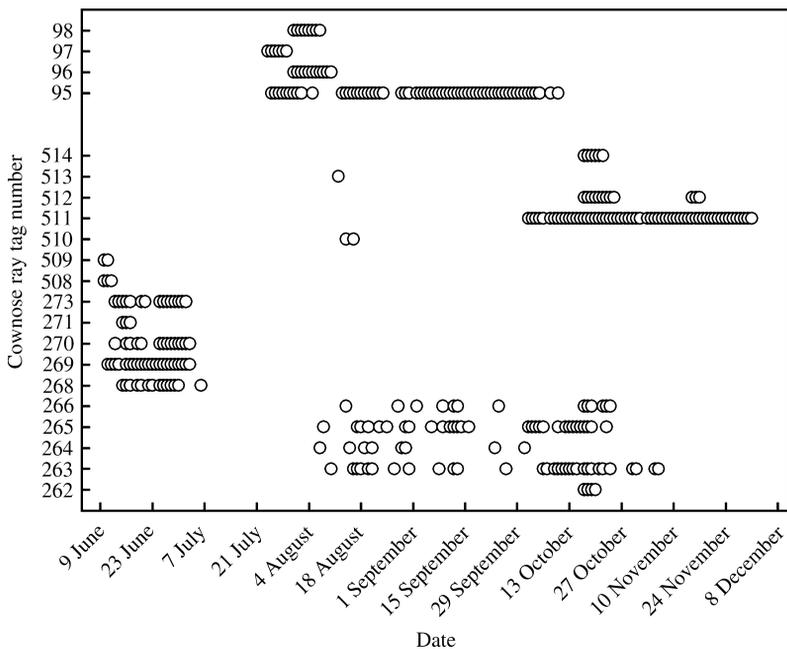

FIG. 2. Daily presence of *Rhinoptera bonasus* monitored within Pine Island Sound between June 2003 and November 2004. 2003 animals (numbers 95–98) are listed at the top and separated by a gap in the *y*-axis.

fitted with transmitters in 2004 were within the study area for <2 days and were excluded from all further analyses.

Total monitoring periods ranged between 1 and 102 days [Fig. 3(a)]. The mean total monitoring period for all *R. bonasus* over both years was 32 days. Total monitoring periods varied between years from 7 to 78 days in 2003
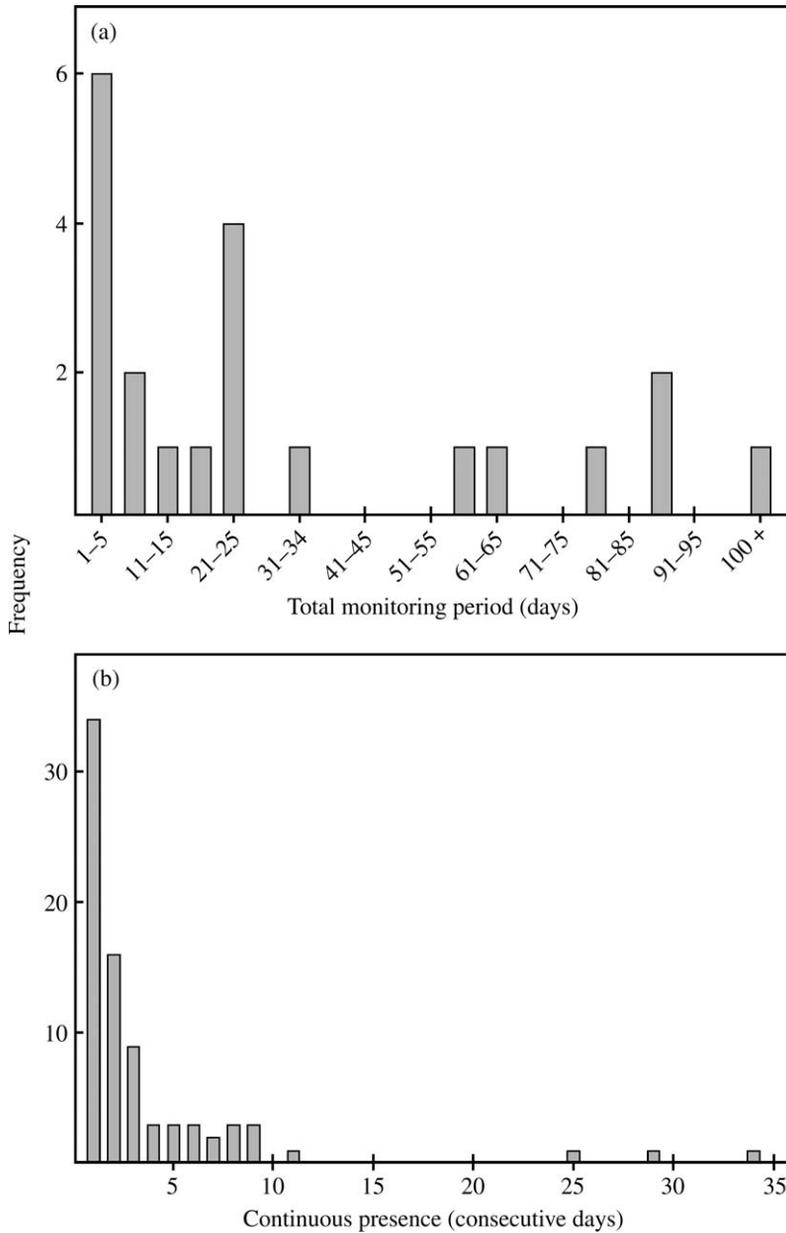

FIG. 3. Frequency histogram of residency times for *Rhinoptera bonasus* monitored in Pine Island Sound: (a) total monitoring period and (b) periods of continuous presence.

(mean = 26·0 days) and 1 to 102 days in 2004 (mean = 33·0 days). Females remained within the monitoring area for longer periods than males (mean male = 27·7 and female = 78·0 days) (*t*-test, d.f. = 19, $P < 0.05$). There were no differences between the total residence time of mature (mean = 50·7 days) and immature cownose rays (mean = 30·6 days) (*t*-test, d.f. = 19, $P > 0.05$). Periods of continuous presence ranged from 1 to 34 days in 2003 (mean = 8·0 days) and 1 to 29 days in 2004 (mean = 3·0 days). Most periods of continuous presence, however, were between 1 and 3 days [Fig. 3(b)].

ACTIVITY PATTERNS

The variability in detection rates between individuals indicated that there were no consistent behavioural patterns that demonstrated a relationship in the distribution of detections to hour or tidal stage. Detections were expected to be equally distributed over all hours and tidal stages. Nineteen individuals (those present for >2 days) were tested for differences in the number of hourly detections. Observed presence by hour differed from expected for all but one of the 19 individuals (χ^2, d.f. = 23, $P < 0.01$), but there was no consistent pattern in detection differences. Four juvenile cownose rays that were tagged together in 2004 had similar hourly detections, with substantially more detections from 0600 to 1200 hours than at other times of the day [Fig. 4(a)]. The remaining 15 individuals did not reveal similar hourly detection patterns [Fig. 4(b)]. Six individuals had higher detection numbers during the day, six had higher numbers of night-time detections and seven showed no pattern (Table I).

Analysis of detections by tidal height showed no differences between observed and expected detection rates for any *R. bonasus* (χ^2, d.f. = 34, $P > 0.05$), which suggests that tidal stage did not influence behaviour patterns. This result also indicates that hydrophones were capable of recording equally well at all stages of the tide.

HOME RANGE ANALYSES

Minimum convex polygons

Daily MCPs for all cownose rays ranged between <0·01 and 25·78 km², with a mean of 5·25 km². Most daily MCPs were <5 km² for both mature and immature individuals (Fig. 5) and did not differ in area between the two groups (*t*-test, d.f. = 60, $P > 0.05$). Mature cownose rays displayed larger 3 day MCP areas (*t*-test, d.f. = 14, $P < 0.001$) and smaller 30 day MCP areas (*t*-test, d.f. = 3, $P < 0.001$) (Fig. 6). There were no differences between mature and immature *R. bonasus* 7 day (*t*-test, d.f. = 9, $P > 0.05$) or total MCP areas (*t*-test, d.f. = 17, $P > 0.05$) (Fig. 6). Although a consistent relationship with state of maturity was not detected, largest MCP sizes were observed in individuals >60 cm W_{SD}. MCP sizes were generally larger for mature animals over all examined time frames, with the exception of the 30 day period (Fig. 6). This discrepancy was most likely due to the small number of animals that were present within the study area for 30 consecutive days and two large 30 day ranges for immature individuals.

Total MCPs for all *R. bonasus* ranged between 0·81 and 71·78 km² (mean = 22·01 km²). Total MCPs showed an increase with longer residence (linear
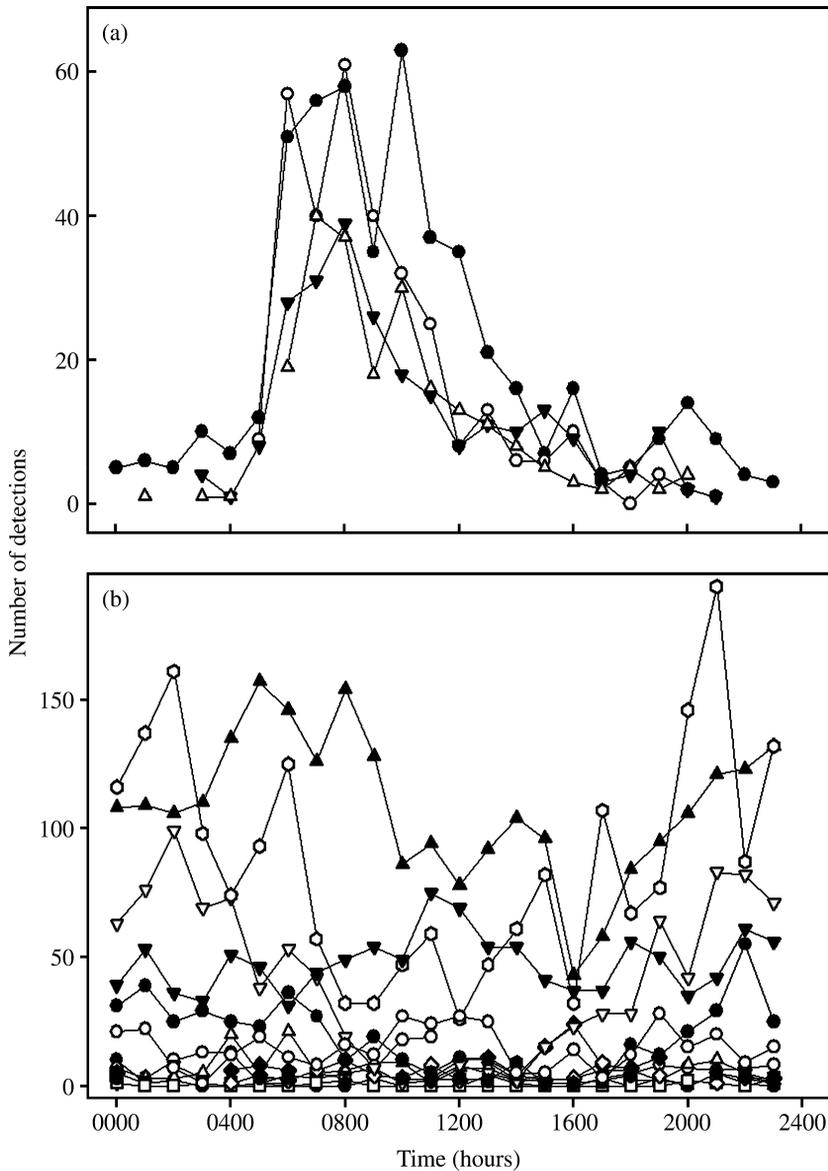
FIG. 4. Similar patterns in hourly detections observed for (a) four immature *Rhinoptera bonasus* tagged together and (b) no distinct pattern in hourly detections emerged for the remaining 17 tracked cownose rays.

regression, $r^2 = 0.63$, $n = 19$, $P < 0.05$). Although females remained within the study site for longer periods than males, no differences were detected between sexes in MCP area over any time frame (*t*-tests, 3 day: d.f. $= 17$, $P > 0.05$; 7 day, d.f. $= 9$, $P > 0.05$; total, d.f. $= 17$, $P > 0.05$). Sex based differences between 30 day monitoring periods could not be tested because only one female was present within the study area for 30 consecutive days.

TABLE I. Results for χ^2 analysis of the proportion of detections for *Rhinoptera bonasus* within Pine Island Sound by time of day (daytime *v.* night-time detections)

Cownose ray tag number	Time of day for highest number of detections
95	Night***
96	Night***
97	No pattern
98	No pattern
262	Night**
263	No pattern
264	Night***
265	No pattern
266	No pattern
268	Day***
269	Day***
270	Day***
271	No pattern
273	Day***
508	Day***
509	Day***
511	Night***
512	Night***
514	No pattern

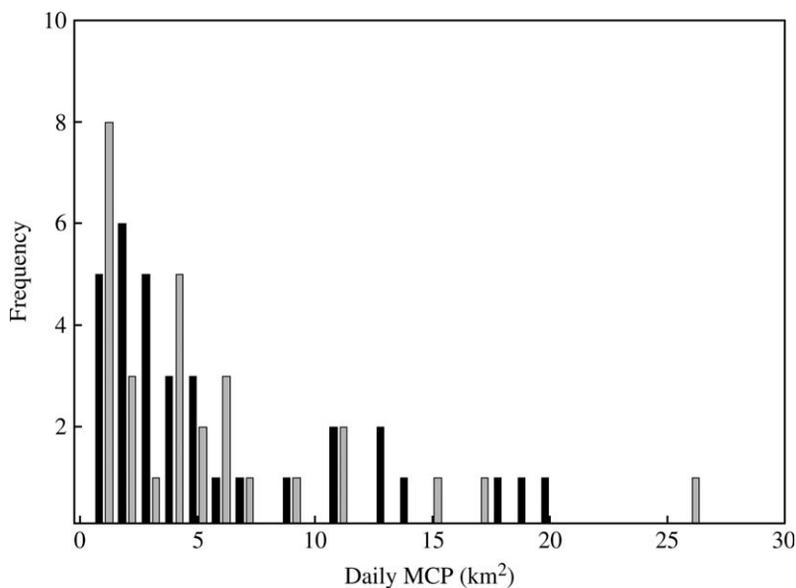$**P < 0.01$; $***P < 0.001$.

FIG. 5. Frequency histogram representing the size of daily minimum convex polygons (MCPs) for immature (■) and mature (▨) *Rhinoptera bonasus*. There were no significant differences detected between mature and immature daily MCP areas (*t*-test, $P > 0.05$).
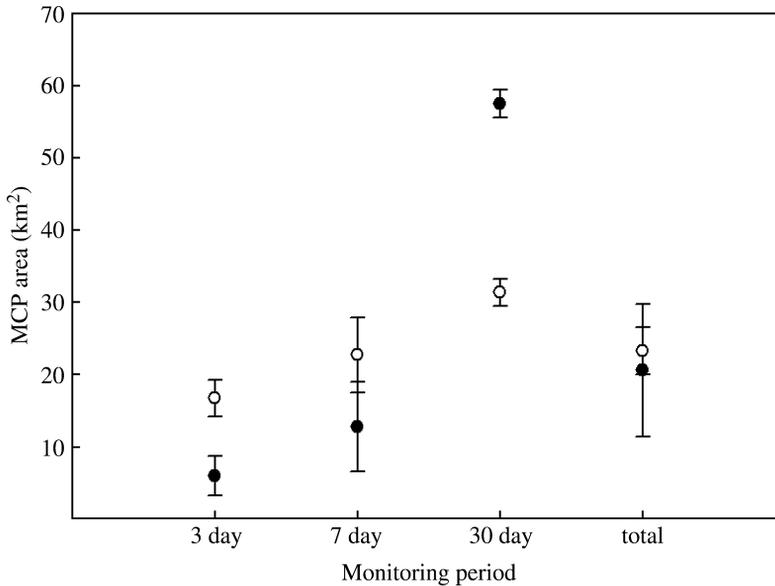
FIG. 6. Mean minimum convex polygon (MCP) areas for immature (●) and mature (○) *Rhinoptera bonasus* over all monitoring periods (3 day, 7 day, 30 day and total). Mature cownose rays had larger MCPs over the 3 day monitoring period ($P = 0.01$) and smaller MCPs over the 30 day monitoring period ($P < 0.001$). No significant differences were detected in MCP area over the 7 day or total monitoring periods ($P > 0.05$).

Kernel utilization distributions (KUDs)

Mature *R. bonasus* had larger 95 and 50% KUDs than immature cownose rays over all time frames except the 30 day period (*t*-tests, 3 day: d.f. $= 17$, $P < 0.01$; 7 day, d.f. $= 9$, $P < 0.05$; 30 day, d.f. $= 3$, $P > 0.05$; total, d.f. $= 17$, $P < 0.01$) (Fig. 7). Similar to MCPs, largest KUDs occurred for individuals >60 cm W_{SD}. Total 95% KUDs ranged between 0.18 and 62.44 km^2 (mean $= 22.63$ km^2), while total 50% KUDs were smaller and ranged between 0.09 and 9.68 km^2 (mean $= 3.33$ km^2). Both 95 and 50% KUDs increased with W_{SD} (linear regression, $r^2 = 0.84$, $n = 19$, $P = 0.01$ and $r^2 = 0.88$, $n = 19$, $P < 0.001$ for 95 and 50% KUDs, respectively) (Fig. 8). Total KUD areas also increased with total monitoring periods (linear regression, $r^2 = 0.67$, $n = 19$, $P = 0.01$ and $r^2 = 0.62$, $n = 19$, $P = 0.03$ for 95 and 50% KUDs, respectively). No differences were detected between males and females for either the 95 or 50% KUD areas over the 3 day (*t*-test, d.f. $= 17$, $P > 0.05$) or 7 day (*t*-test, d.f. $= 9$, $P > 0.05$) time frames. Males, however, had larger total 50% KUD areas than females (*t*-test, d.f. $= 17$, $P < 0.001$). Differences between 30 day KUD areas could not be calculated because only one female *R. bonasus* was present for 30 consecutive days.

No differences ($P > 0.05$) were detected between the sizes of daytime and night-time KUDs for immature or mature cownose rays over any time frame. Mature cownose rays, however, had larger night-time 95% KUDs than immature rays over all time frames except the 30 day period (*t*-tests, 3 day, d.f. $= 8$, $P < 0.05$; 7 day, d.f. $= 7$, $P < 0.05$; 30 day, d.f. $= 3$, $P > 0.05$; total, d.f. $= 15$, $P = 0.01$). Night-time 50% KUDs did not differ between maturity levels.
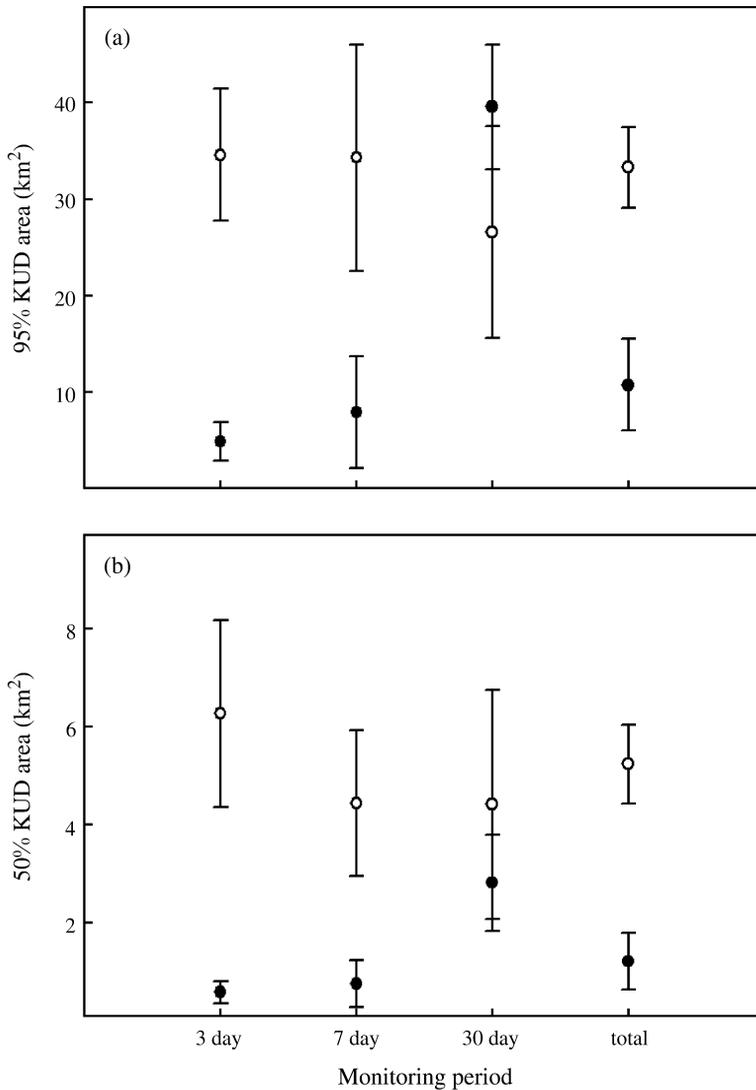
FIG. 7. Mean (a) 95% and (b) 50% Kernel utilization distribution (KUD) areas for immature (●) and mature (○) *Rhinoptera bonasus* over all monitoring periods (3 day, 7 day, 30 day and total).

Distance between consecutive centres of activity (COAs)

Analysis of the distances between 30 min centres of activity revealed that the majority of consecutive COAs were in close proximity. Movement distances ranged from 0 to 13 km, but mean distances per individual ranged between 0·1 and 0·7 km (Fig. 9). Mature *R. bonasus* displayed larger distances between consecutive centres of activity (0·50 km) than immature rays (0·26 km) (*t*-test, d.f. = 16, $P = 0.01$), and distances generally increased with disc width (linear regression, $r^2 = 0.64$, $n = 17$, $P = 0.01$) (Fig. 9). Movements over large distances
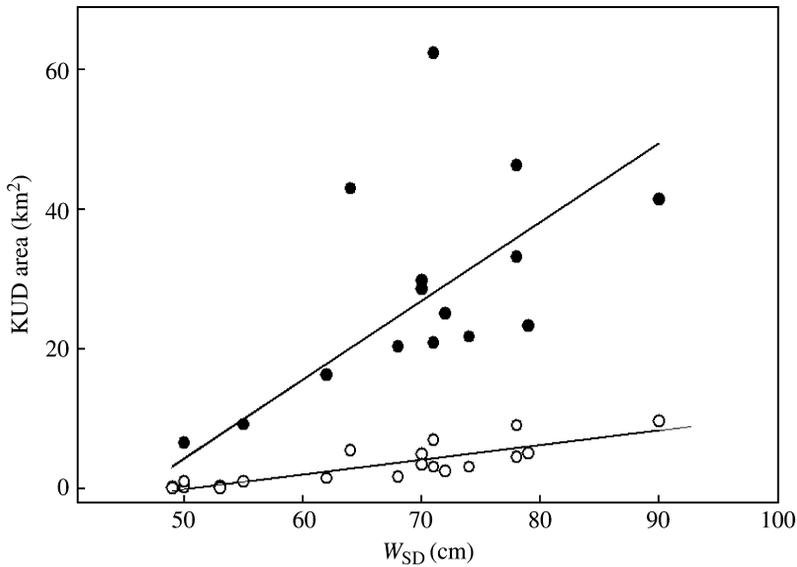
FIG. 8. Total 95% (●) and 50% (○) Kernel utilization distribution (KUD) areas compared with *Rhinoptera bonasus* straight disc width (W_{SD}) (cm). Both KUD areas get significantly larger as W_{SD} increases. For 95% KUD, the curve was fitted by $y = 1·13x − 52·10$ and for 50% KUD, the curve was fitted by $y = 0·21x − 10·69$.
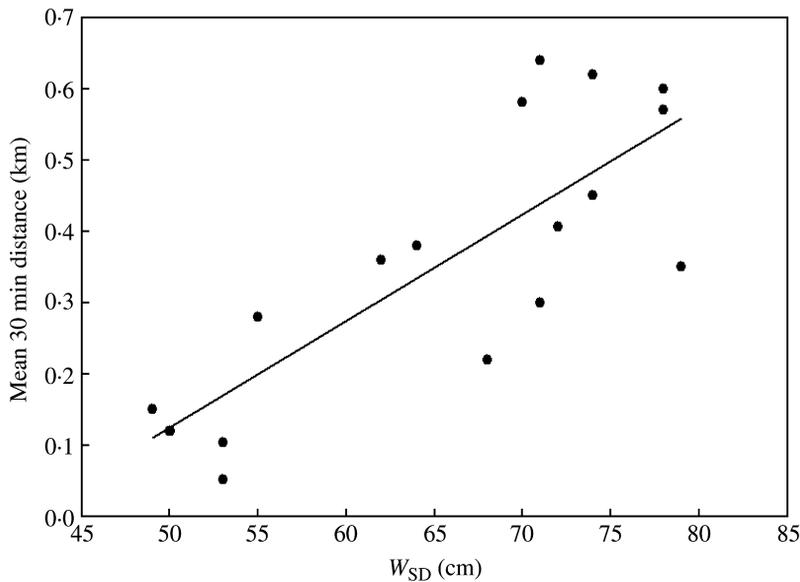

FIG. 9. Mean distance moved over 30 min intervals and *Rhinoptera bonasus* straight disc width (W_{SD}). The curve was fitted by $y = 0·02x − 0·62$.

were not common, with the majority of rays travelling between 0 and 2 km within a 30 min period (Fig. 10).

DISCUSSION

Acoustic monitoring of *R. bonasus* within Pine Island Sound revealed that cownose rays utilize the area for extended periods but demonstrate considerable interindividual variability in their habitat utilization. Cownose rays were detected within the estuary for varying lengths of time, but detection of individuals was usually not continuous, with most cownose rays monitored for ≤2 consecutive days. This suggests intermittent and transient use of the monitored area. Loss of contact with individuals could be the result of movement out of the study area or into shallow water regions where detection was improbable. Utilization of intertidal and subtidal shallow flats has been well documented for many ray species (Smith & Merriner, 1985; Snelson *et al.*, 1988; Matern *et al.*, 2000), so it is possible that individuals were not exiting the study site but simply moving into shallow water and out of detection range.

Although data from most individuals suggested transient use of the study site, some remained within the area for extended periods. Seven of 21 tracked cownose rays were monitored for at least 1 month, and three were detected within the array for >3 months. This demonstrates that some *R. bonasus* did remain resident within the estuary for extended lengths of time. The majority of *R. bonasus*, however, were monitored for shorter periods suggesting no
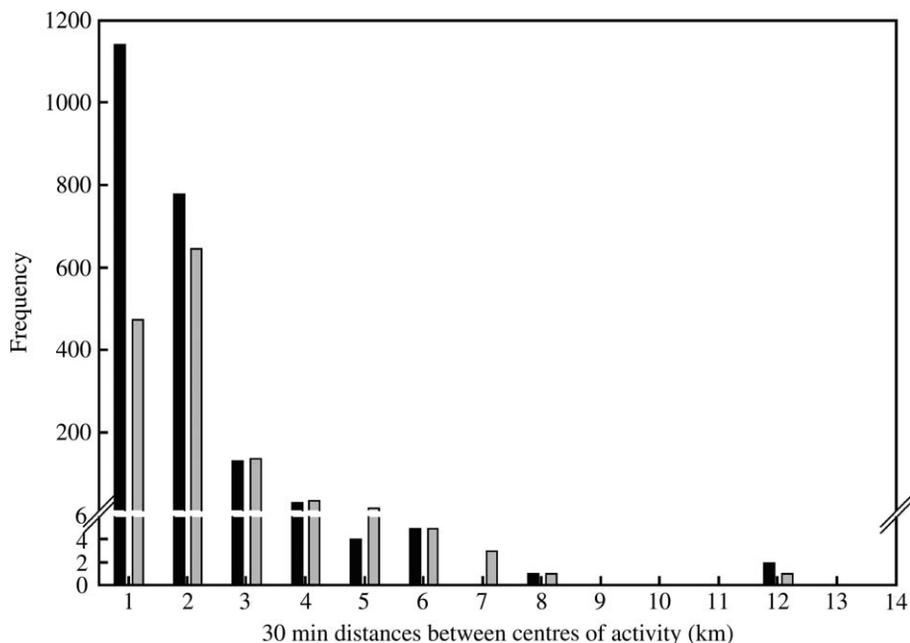

FIG. 10. Frequency histogram of mean distance moved over 30 min intervals for immature (■) and mature (▨) *Rhinoptera bonasus.*

consistent pattern of residency. Although minimal tracking data are available for batoids, these results are similar to those from other studies of bottom feeding elasmobranchs. Bat rays *Myliobatis californica* Gill, 1865, in Tomales Bay, California, U.S.A., were documented within 1 km of their initial tagging site after periods of 106, 359 and 583 days during a tag-recapture study (Hopkins & Cech, 2003). Recapture data, however, were gathered from only three out of 257 tagged bat rays, similar to the results of this study where a small number of tracked individuals were resident in the area while the remainder moved out of the region.

There was no distinct relationship between activity patterns and tidal stage, contrasting with existing research on cownose rays. Smith & Merriner (1985, 1987) reported that cownose rays in Chesapeake Bay moved into intertidal zones to feed during high tide. If this occurred in Pine Island Sound, however, there would have been an absence of detections during high tide because these shallow areas were not within detection range of the hydrophone array. In Chesapeake Bay, cownose rays feed primarily upon bivalves (Smith & Merriner, 1985) and are observed foraging in shallow sand or mud flats made accessible during high tide. The diet of *R. bonasus* in Charlotte Harbor consists primarily of small crustaceans (cumaceans) and polychaetes that are abundant within the sand and mud bottom of the estuary (Collins *et al.*, 2007). Therefore, it may not be necessary for individuals to move into the shallower seagrass areas to feed as demonstrated for *R. bonasus* in Chesapeake Bay (Orth, 1975; Smith & Merriner, 1985).

Similar to the present study, Matern *et al.* (2000) did not observe tidal correlations while tracking bat rays in Tomales Bay but did note a distinct diel pattern that they attributed to behavioural thermoregulation. Although no distinct diel activity pattern emerged for cownose rays in Charlotte Harbor, there was a general trend of less detection between 1200 and 1800 hours over both years of this study. This may be explained by cownose rays moving into canal systems or shallow areas, and thus out of detection range during warmer periods. Cownose rays may be responding to increased prey availability in shallow areas during warmer hours of the day. Alternatively, movement into shallow water could serve as a means of predator avoidance. Large bull *Carcharhinus leucas* (Müller & Henle, 1839) and hammerhead sharks *Sphyrna* spp. are known to feed upon batoids (Snelson *et al.*, 1984; Chapman & Gruber, 2002) and both species regularly occur throughout Charlotte Harbor (Simpfendorfer *et al.*, 2005; unpubl. data).

Examination of home-range sizes demonstrated that movement patterns and habitat use were not consistent across individual *R. bonasus*. Minimum convex polygons can overestimate home-range size (Kernohan *et al.*, 2001) but are useful to illustrate boundaries and the extent to which an animal travels. Daily MCP areas between individuals varied greatly over the course of this study ($<1–26$ km^2), but the majority were between 1 and 5 km^2 suggesting individuals generally used a small portion of the estuary within a single day. This is comparable to activity space estimates for bonnethead sharks *Sphyrna tiburo* (L., 1758) tracked within Pine Island Sound, which had a mean daily activity space of $8·31$ km^2 (Heupel *et al.*, 2006). In Charlotte Harbor, the diet of individual *R. bonasus* was typically dominated by a single prey type (*i.e.* swarms of

cumaceans *Cyclaspis* sp. or hundreds of the polychaete *Pectinaria gouldii*), suggesting that they are feeding on clumped or aggregated prey (Collins *et al.*, 2007). In areas of high prey density, small activity spaces could be explained by a lack of need to traverse large areas to find sufficient food.

Total MCP size for *R. bonasus* increased with monitoring period, suggesting that individuals expand the area utilized over time. Maximum total MCP recorded was 71.78 km^2 which falls within the range of MCPs recorded for other coastal elasmobranchs. Lemon sharks *Negaprion brevirostris* (Poey, 1868) have displayed activity spaces ranging from 9 to 93 km^2 over intermittent tracking periods of 1–8 days (Gruber *et al.*, 1988), and juvenile sandbar sharks *Carcharhinus plumbeus* (Nardo, 1827) tracked for periods between 2.5 and 70 h had MCPs ranging from 1.1 to 333.9 km^2 (Rechisky & Wetherbee, 2003).

Mean MCP areas tended to increase with animal size, but differences based on maturity were only detected over the 3 and 30 day time frames. Although the power of the test was decreased by the low *n*, and these results should be interpreted with caution, mature *R. bonasus* had larger MCPs over 3 day periods and smaller MCPs over 30 day periods. This result is confounding because of the correlation of MCP area W_{SD}. The reversal of trend for the 30 day data is probably the result of a small sample size and large home ranges calculated for two juvenile individuals over that period. These two individuals, although nearing maturity, had much larger 30 day home ranges than any other immature or mature individual. As individuals get larger and become reproductively active, the increased energetic demands and resulting need to consume greater quantities of food may contribute to increased activity space. In addition, sexually mature animals may extend their ranges in search of mates. Although female cownose rays remained within the study area for longer periods than males, there were no differences for MCP areas between sexes.

The KUD is more descriptive than the MCP, illustrating the use of space within a home range and differentiating areas of intense use from those that are only briefly occupied (Worton, 1987). Based on KUD analysis *R. bonasus* demonstrated 95% usage areas ranging between 0.1 and 62.44 km^2 (mean $=$ 17.89 km^2) over monitoring periods of 1–3 days. These values are generally larger than those obtained for the more stationary, benthic myliobatiform *Dasyatis lata* (Garman, 1880), which exhibited 95% KUDs between 0.62 and 2.77 km^2 during manual tracking over 31–74 h periods (Cartamil *et al.*, 2003). In contrast, values observed for *R. bonasus* were much smaller than juvenile *C. plumbeus*, which exhibited 2.8 to 315.4 km^2 95% KUDs over manual tracking periods up to 70 h (Rechisky & Wetherbee, 2003). As midwater swimmers, myliobatid rays like *R. bonasus* are typically more mobile than the predominantly sedentary dasyatid rays (Bigelow & Schroeder, 1953). As *R. bonasus* tend to feed on clumped or aggregated benthic prey (Collins *et al.*, 2007) and spend long periods foraging in one location (Smith & Merriner, 1985; Sasko, 2000), they may exhibit smaller home range sizes than a species that is continuously mobile such as the sandbar shark (*C. plumbeus*).

Although 95% KUDs tended to expand over time, 50% KUDs were more stable. This suggested that individuals maintained a consistent small area that was used repeatedly, indicating individuals concentrated large amounts of time within these restricted core areas. This is probably related to the distribution of

prey within Charlotte Harbor, but a thorough explanation requires additional research.

Rhinoptera bonasus monitored during this study were active diurnally and nocturnally, as daytime and night-time activity spaces were not different for any individual. This differs from patterns observed in other bottom feeding elasmobranchs. *Dasyatis lata* showed larger activity spaces during the night than during the day (Cartamil *et al.*, 2003). Similarly, both the Pacific electric ray *Torpedo californica* Ayres, 1855, and the Pacific angel shark *Squatina californica* Ayres, 1859, have been documented as nocturnal, covering much larger distances between dusk and dawn than during daylight hours (Standora & Nelson, 1977; Bray & Hixon, 1978). Mature *R. bonasus* had larger night-time 95% KUDs than immature rays over all time periods, but total daytime 95% KUD comparison showed no difference between size groups. This indicates that mature animals were utilizing larger areas within their range during the night-time hours, while immature animals remained within more confined spaces. This behaviour could be attributed to increased predation risk for smaller individuals.

In this study, there was no distinct seasonal departure of tagged cownose rays as would be expected if they were undertaking seasonal migrations (Schwartz, 1990). Cownose rays were still present in Pine Island Sound at the end of November 2004 and were detected in another portion of the estuary in January 2005, suggesting that cownose rays were not migrating out of the area for the winter even though water temperatures had declined to 16° C (unpubl. data). In addition, *R. bonasus* were tracked in the Caloosahatchee River (adjacent to Pine Island Sound) in January to May of 2004 and 2005 as part of another project (unpubl. data), and an additional 18 *R. bonasus* were also captured in north Charlotte Harbor between November 2003 and March 2004 (Collins *et al.*, 2007). These data suggest that *R. bonasus* are resident within Charlotte Harbor during winter months and do not provide evidence for a seasonal departure (or widespread migration, as hypothesized by Schwartz, 1990).

Hopkins & Cech (2003) noted that the departure of bat rays from coastal California during winter months was not as pronounced in more southern counties where water temperatures were warmer. Cownose rays in the northeast Gulf of Mexico have been reported at temperatures between 15·5 and 33·6° C (Neer, 2005). Based on these results, it seems possible that water temperatures in Charlotte Harbor were not low enough to trigger seasonal migration and that individual movements may be related to other factors (*e.g.* prey availability, mating or predator avoidance). This concept is supported by reports of a resident population of cownose rays in Venezuela (Smith & Merriner, 1987) and year-round presence of *R. bonasus* in coastal North Carolina (Smith, 1907). It is possible that *R. bonasus* inhabiting the south-west coast of Florida, where water temperatures rarely drop below 15° C, simply move offshore to warmer, deeper water when necessary and can easily return to inshore waters when temperatures increase. Whether or not *R. bonasus* in more northern portions of the Gulf of Mexico follow a particular migration route should be determined by further research.

While it is important to keep in mind that the power of statistical tests performed was reduced by a low sample size, these data suggest that *R. bonasus* in

south-west Florida do not undertake a seasonal mass migration. Individuals remained resident within Charlotte Harbor for months and displayed high variability in activity spaces. As highly mobile, pelagic swimmers, *R. bonasus* displayed the ability to move large distances over short periods, but many remained within relatively confined home ranges. These data did not provide evidence for a relationship between *R. bonasus* movement and time of day or tidal stage, and it is more likely that movements are driven by biotic factors such as prey availability or predator avoidance. Movement patterns do not appear to be predictable for this population as a whole, but indicate that Pine Island Sound provides a suitable environment for *R. bonasus* to remain resident for extended periods, while also serving as a transient stopping ground for numerous individuals. These results provide insight to *R. bonasus* use of a south Florida estuary and allow predictions regarding the impact of this species on similar environments.

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