Environ Biol Fish
DOI 10.1007/s10641-014-0296-x

Towed-float satellite telemetry tracks large-scale movement and habitat connectivity of myliobatid stingrays

Matthew J. Ajemian · **Sean P. Powers**

Received: 8 September 2013 / Accepted: 24 June 2014

Abstract Batoids are important mesopredators whose high mobility and extensive migrations can link seemingly distant food webs in coastal ecosystems. Despite this recognition, our knowledge of the movement patterns of many species is limited due to the logistical challenge of tracking these animals on multiple scales. Smart Positioning or Temperature (SPOT) satellite-linked transmitters allow for precise, multi-scale tracking of species that regularly use surface waters. To date, SPOTs have been predominantly used on sharks, with only a single application to a batoid. Given the epipelagic nature of myliobatid stingrays, we examined the potential for towed-float SPOT transmitters to monitor large-scale movements of two representative species: the Cownose Ray (*Rhinoptera bonasus*; $n=15$) and Spotted Eagle Ray (*Aetobatus narinari*; $n=9$). Tracking data identified several consistent outmigration patterns of Cownose Rays along the Mississippi-Alabama shelf and seasonal variation in movement rates along barrier island habitats. We also documented sex-related differences in movement rates and habitat use of Spotted Eagle Rays along the Bermuda platform, where males exhibited significantly higher movement rates than females and more transient behavior between inshore lagoons and outer coral reefs. Both Cownose and Spotted Eagle Rays were shown to exhibit connectivity among several habitat types along continental shelves in their respective locales, demonstrating future challenges to the management of these species over large spatial scales. While reductions in tag size and improved tethering techniques would undoubtedly broaden the applicability of towed-float satellite telemetry to other species and sizes, our work highlights the strong potential for this technology to provide insights into the spatial ecology and habitat use of myliobatid rays.

Keywords Elasmobranch · Myliobatidae · Satellite telemetry · Cownose Ray · Spotted Eagle Ray · SPOT

Introduction

Several species of marine vertebrates connect widely separated ecosystems via large-scale movements such as seasonal migrations. Elasmobranchs are considered exemplary agents of this type of ecosystem connectivity, yet to date the majority of quantitative movement studies have been focused on apex predatory sharks (Hammerschlag et al. 2011). Despite their hypothesized capacity to undertake long-distance migrations, there has been little effort to delineate the role of batoid

M. J. Ajemian · S. P. Powers
Department of Marine Sciences, University of South Alabama,
307 N University Blvd, Mobile 36688 AL, United States

M. J. Ajemian · S. P. Powers
Center for Ecosystem-based Fisheries Management, Dauphin Island Sea Lab,
101 Bienville Blvd, Dauphin Island 36528 AL, United States

M. J. Ajemian (✉)
Harte Research Institute for Gulf of Mexico Studies, Texas A&M University – Corpus Christi,
6300 Ocean Drive, 78401 Corpus Christi, TX, USA
e-mail: Matt.Ajemian@tamucc.edu

mesopredators in linking disparate habitats. This is especially true of myliobatid (Cownose and Eagle Ray) stingrays, which have relatively unknown movement patterns despite their demonstrated foraging effects in many marine systems (Hines et al. 1997; Peterson et al. 2001; Ajemian et al. 2012). Because the impacts of these mobile rays on benthic communities are largely dependent on their long-term residency and exchange rates among these habitats, further research is needed on their fine-scale movement across large marine landscapes. Further, the declining status of myliobatid stingrays in the Gulf and Caribbean (Cuevas-Zimbrón et al. 2011; Tagliafico et al. 2012) and hypothesized negative effects on fisheries along the U.S. eastern seaboard (Peterson et al. 2001; Myers et al. 2007) further emphasizes the urgency of these habitat use and connectivity data. This information will be crucial for the effective conservation and management of these highly mobile species and their associated benthic feeding habitats.

Unlike sharks, myliobatid stingrays (and most batoids) are generally not included in coordinated large-scale mark-recapture tagging programs. Thus, biotelemetry has become the principal tool for examining movement in these taxa over the past few decades. Acoustic telemetry studies have provided considerable data on the movement patterns and habitat use for a variety of batoid species, including changes in day vs. night activity, predator–prey interactions and movement directionality (Silliman and Gruber 1999; Matern et al. 2000; Cartamil et al. 2003; Klimley et al. 2005; Vaudo and Lowe 2006; Collins et al. 2007, 2008; Dewar et al. 2008; Ajemian et al. 2012). However, as with all acoustic approaches, the extent of animal tracking in these previous studies was restricted to the confines of passive acoustic arrays or tracking efforts from manual approaches. Furthermore, due to the maintenance requirement of large passive arrays, these studies tend to be expensive and labor-intensive despite the relatively low cost of acoustic tags.

The limitations of acoustic technology and the rather large-bodied nature of myliobatid stingrays have led to attempts to implement satellite biotelemetry to track the movements of these mobile species. Though considerably more expensive per unit, satellite telemetry offers the advantage of tracking animals on unrestricted spatial scales. To date, nearly all satellite telemetry studies conducted on myliobatid stingrays have utilized pop-up satellite archival tags (PSATs). While there are examples of several recent PSAT deployments on other large batoids, (Le Port et al. 2008; Wearmouth and Sims 2009; Canese et al. 2011; Croll et al. 2012), PSAT studies on myliobatid stingrays have been met with a number of logistical and technical challenges (Blaylock 1990; Grusha and Patterson 2005). Blaylock (1990) and Grusha and Patterson (2005) first investigated the feasibility of using PSATs on Cownose Rays (*Rhinoptera bonasus*) though Grusha (2005) produced the only known data on large-scale movements of this species. Unfortunately, other than the pop-off locations, the majority of the archived spatial data were deemed unreliable as they produced unfeasible position estimates from geolocation algorithms (Grusha 2005). Riding et al. (2009) investigated the use of buoy-based satellite telemetry on the New Zealand Eagle Ray (*Myliobatis tenuicaudatus*) utilizing short-term Global Positioning Devices (GPDs) to record positions to an onboard unit tethered to the animal. Due to the constraints of GPD technology, these researchers were required to re-locate the device and/or manually detach the device from a free-swimming animal in order to retrieve the data. Despite high accuracy of positions, deployments were limited to <30 h (Riding et al. 2009). In sum, there have been no studies capable of combining accurate, remote tracking of myliobatid stingrays on scales relevant to migration or large-scale habitat connectivity.

Given the short-term success in tracking New Zealand Eagle Rays with buoy-based GPDs, following Riding et al. (2009) we investigated the use of real-time towed-float satellite transmitters to track the large-scale movements of two species of myliobatid stingrays, the Cownose Ray (*R. bonasus*) and Spotted Eagle Ray (*Aetobatus narinari*). Both species represented strong models for towing surface-transmitting tags as they are relatively large (up to 20 kg for cownose; >100 kg for Spotted Eagle Ray; Bigelow and Schroeder 1953), regularly use surface waters at both inshore and offshore locales (Smith and Merriner 1987; Ajemian et al. 2012), and commonly forage in shallow waters of the coastal zone (Smith and Merriner 1985; Silliman and Gruber 1999; Collins et al. 2007; Schluessel et al. 2010; Ajemian and Powers 2012, 2013; Ajemian et al. 2012). These characteristics provided opportunities to track these animals over a suite of behavioral modes (e.g., feeding, transiting) and habitats. Furthermore, the spatial ecology of both species remains relatively unknown throughout the majority of their ranges, and thus provided an opportunity to understand the role of these animals in connecting disparate ecosystems. For example, while the movement behavior of Cownose Rays has been well documented within estuaries of southwest Florida (Collins et al. 2007, 2008), migration habitats are poorly known from the rest of the Gulf of Mexico and across a continuum of habitats. We thus implemented a satellite tagging program to further elucidate movement patterns from the northern Gulf of Mexico, where these rays were hypothesized to undertake more seasonal migrations. Spotted Eagle Ray movement behavior has also been poorly studied and has concentrated on acoustic approaches to document habitat use in restricted lagoons (Silliman and Gruber 1999; Ajemian et al. 2012). Though its simple presence in the isolated islands of Bermuda has been considered representative of the species' ability to migrate over large spatial scales (Bigelow and Schroeder 1953), there are no empirical studies documenting Spotted Eagle Ray movement patterns beyond 1's of kilometers.

We elected Smart Positioning or Temperature (SPOT) transmitters (SPOT5; Wildlife Computers, Inc.) to allow for precise, multi-scale tracking of these epipelagic stingrays. To date, SPOTs and other satellite-linked transmitters have been predominantly used on sharks (reviewed by Hammerschlag et al. 2011), and sea turtles (reviewed by Godley et al. 2008), with recent applications to humpback whales (Fossette et al. 2014) and manta rays (Graham et al. 2012). Graham et al. (2012) is the only other published study to apply this technology to a pelagic batoid and successfully tracked large-scale movements of large mantas up to several months at a time. Our study represents the first attempt to implement this technology to track the large-scale movements of smaller-bodied myliobatid stingrays.

Methods

Tag retention study

To determine the feasibility of using Wildlife Computers © SPOT5 towed-float tags on myliobatid stingrays, we conducted an initial captive study using Cownose Rays. Mature Cownose Rays [*n*=21; >80 cm disc width (DW); 8–15 kg; Neer and Thompson 2005] were captured from local nearshore waters of the Mobile and Perdido Bay estuaries and transported in plastic tubs of ambient seawater to the Claude Peteet Mariculture Center in Gulf Shores, Alabama. All rays were kept in a single 50 × 25 m pond with free-flowing seawater pumped from the nearby Gulf of Mexico. During the 30 day study period, pond temperatures ranged from 25 to 30 °C and salinities were generally 30 psu. Pond depth ranged from 0.5 to 2.0 m with a bottom mainly composed of mixed sand and silt. Rays were fed to satiation daily with a mixture of cut fish and shrimp.

Eleven rays were fitted with non-functional versions of SPOT5 towed-float tags and allowed to swim freely around the experimental pond with ten "control" rays, which received no tag treatment. Tags were secured to the rays using one of five methods: 1) Spiracular Tube, 2) Dart Bridle, 3) Tail Suture; or 4) Through-wing Disc-bridle (Fig. 1). Spiracular attachments (method 1) involved a segment of Silastic^{TM} tube that ran through the most medial portion of the spiracular cartilage and laterally across the dorsal region of buccal cavity and around the head. A strand of monofilament was run through the inside of the tube and crimped to a swivel above the head to secure the tether attachment. This design kept the attachment medial to spiracular openings and allowed for uninhibited movement of the valves during respiration. Dart bridles (method 2) were inserted into the dorsal musculature of the rays' pectoral fin in the "trunk" region posterior to the spiracles and anterior to the dorsal side of the peritoneal cavity. Tail

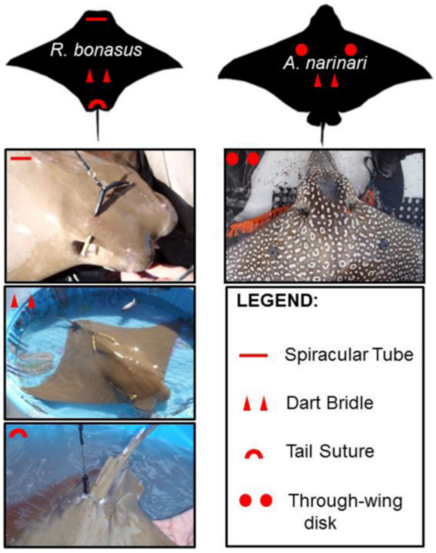

Fig. 1 Diagram of various attachment points and techniques for tethering towed-float SPOT5 transmitters to myliobatid rays. Symbols indicate the tether type and locations relative to a silhouette of a Cownose (left) and Spotted Eagle Ray (right). Symbols are superimposed on photographs of individuals fitted with transmitters in the field

sutures (method 3) also utilized a segment of monofilament inside a tube that was inserted around the base of the tail, medial to the pectoral fin insertion and crimped back on itself on the dorsal side anterior to the dorsal fin. Through-wing disc bridles (method 4) involved the same Silastic^{TM} and monofilament material run dorsoventrally through the pectoral fin. Tubes were secured to the exterior portion of the pectoral fin using neoprene discs and crimps. Monofilament bridles were crimped to the main swivel and tag attachment. All tethers were connected to the transmitter via a double-barrel swivel with a 50 cm length of coated aircraft cable (54 kg breaking strength) provided by the manufacturer.

During the trial period, animals were checked daily for behavioral changes and photographed, measured, and inspected on a weekly basis. We noted initial scarring around dart tag insertion sites, but these generally healed within a week. No mortality associated with tagging treatment was observed over the 30 day period. Furthermore, all tagged and control rays continued to school together and exhibited normal behaviors. Due to species-specific differences in head morphology and overall size, for field deployments we elected to use spiracular attachments on Cownose Rays only and restricted through-wing disc attachments to much larger and thicker-bodied Spotted Eagle Rays.

Equipment preparation

The Wildlife Computers © SPOT5 tag utilizes a small ARGOS cricket transmitter and can transmit locations for approximately 280 day on a single AA cell battery. Locations are determined when the wet/dry sensor of the satellite tag breaks the water surface (becoming momentarily dry) and transmits a signal to an ARGOS satellite. Satellite-based positioning is implemented using Doppler-shift algorithms based on a series of consecutive transmissions. The positively buoyant SPOT5 towed-float model is composed of epoxy and syntactic hydrodynamic foam and weighs 120 g in air. For all deployments, tags were programmed to transmit during all days of the year at all hours of the day, but were restricted to a daily maximum of 250 total transmissions. Once deployed, tags checked for dry conditions at 0.25 s intervals. When dry, the transmitter began a fast repetition rate of 45 s and then switched to a slow repetition rate of 90 s after 10 successive dry transmissions. Because it is not possible to program SPOT tags to detach after a certain amount of time, we used corrodible crimps and tackle to tether our tags and ensure eventual detachment from the animal.

Field deployments

We deployed SPOT tags on 11 female and 4 male Cownose Rays between fall 2009 and spring 2011. Animals were captured in near shore waters either off Dauphin Island (n=13) or Perdido Pass (n=2), Alabama using 10 cm mesh monofilament gillnets set in 2–4 m water depth, or actively set 6.35 mm mesh bag seines in waters < 1 m when water clarity was sufficient. In Bermuda, we tagged 4 female and 5 male Spotted Eagle Rays between fall 2009 and summer 2010. Spotted Eagle Rays were captured using a 100 m (6.35 mm mesh) haul seine after visually sighting the animals near the water surface and encircling them with the net. All Spotted Eagle Rays were captured and released within Harrington Sound and Flatts Inlet.

During tagging procedures, animals were kept submerged in a 1.0 m diameter plastic tub (Cownose Rays <100 cm DW) or restrained on deck with running ambient seawater over the gills (Spotted Eagle Rays and Cownose Rays >100 cm DW). All individuals were measured for DW (mm), weighed to the nearest 0.1 kg, photographed, fitted with a plastic cinch-up loop identification tag (Hallprint, Inc.) through the spiracular cartilage and fitted with a satellite transmitter. The total time for these tagging procedures did not exceed 10 min. Geographic coordinates were taken with a handheld GPS at tagging sites. Where possible, photos of the animals swimming with transmitters were taken underwater upon release (Fig. 2).

Data analyses

Transmissions from satellite tags were detected by a combination of National Oceanic and Atmospheric Association polar-orbiting environmental satellites (POES), METOP-A, METOP-B, and Saral. Collectively, these satellites scanned the regions in the northwest Atlantic Ocean and data from satellite tags were downloaded weekly from the ARGOS system (CLS America, Inc.). We estimated detachment time based on temporal patterns in SPOT transmission behavior. Specifically, we defined detachment day at the first of three consecutive days where tags transmitted their full daily allotment by 06:00 (or mean daily transmit hour of approximately 3; Fig. 3). This technique was

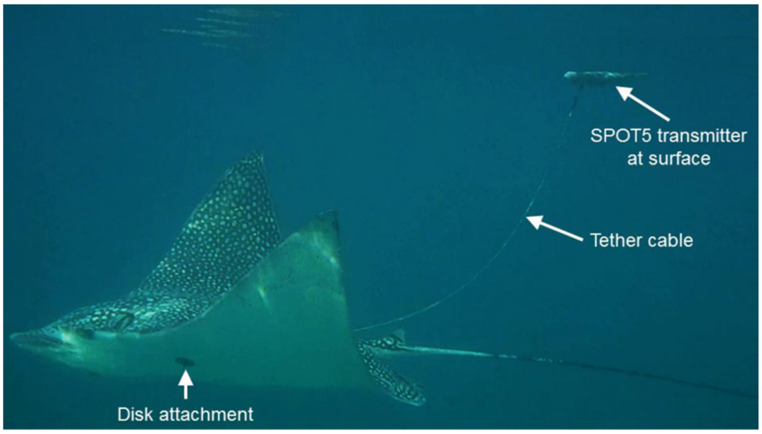

Fig. 2 Underwater photo of a Spotted Eagle Ray in upstroke transporting a SPOT5 towed-float transmitter in Harrington Sound, Bermuda. The disc attachment (left ventral side visible) secured the tether cable to the animal. The upper portion of the transmitter is not visible as it is exposed above the water surface

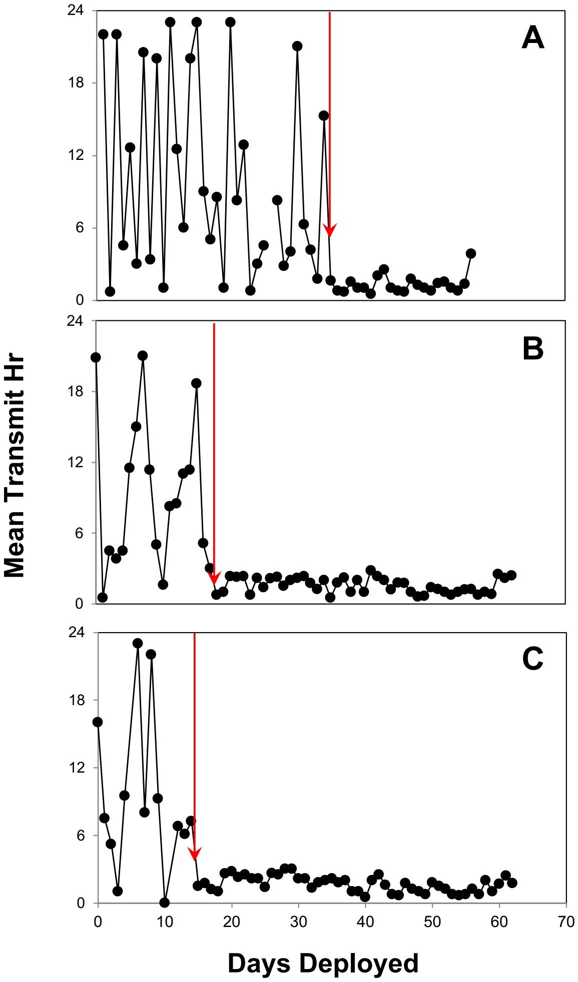

Fig. 3 Line-scatter plots displaying transmission behavior of SPOT5 towed-float transmitter field deployments on 3 representative Spotted Eagle Rays (A – SER-02, B – SER-04, C – SER-03). Mean Transmit hour is plotted by deployment day (i.e., days since release). Red arrow indicates the estimated detachment time of the tag

recently demonstrated for the field deployments of SPOT5 towed-float tags attached to Whale Sharks (*Rhincodon typus*) (Hearn et al. 2013).

Position estimates of tagged individuals were filtered using least-squares methods and ranged in location quality (Z, B, A, 0, 1, 2, and 3). Due to our need for high quality location data for habitat use, we solely used position estimates with location classes of 1 (500–1500 m error radius), 2 (250–500 m error radius), and 3 (<250 m). Position estimates were plotted in ArcGIS 10.0 (ESRI, Inc.) to quantify habitat use and movement behaviors of rays. Following Domeier et al. (2012) daily rates of movement (ROM) were determined between successive days of high quality transmissions (location quality$\geq$1) that were maximally 2 days apart. We summed these individual movements to derive a total distance moved for each individual as well as a maximum ROM based on the highest value from all individual ROM values. We compared mean ROM between sexes for Spotted Eagle Rays using t-tests. Cownose Rays were excluded from the analysis as sample sizes were biased towards female rays, though we did inspect variation in ROM by season (spring=March-May, fall=November-December, and summer=August-September) for this species. For both species, linear regressions were run to examine the potential for animal size as a predictor of ROM. All data were checked for normality and homogeneity of variances prior to running t-tests and regressions. Statistical analyses were performed in SigmaPlot 12.0 (Systat Software, Inc.) with an α=0.05.

To examine potential diel surface behavior of satellite tagged rays, we performed a likelihood chi-square analysis on the observed number of detections recorded during each hourly interval with FishTel 1.4 telemetry analysis program (LabView, Inc.). This program accounted for individual variability among rays (replicates) and determined a selection ratio (w_i) for each hour of the day using the formula:

$$w_i = o_i/\pi_i$$

where o_i=proportion of the detections at hour i, and π_i= proportion of time units (we assumed this to be the same across all individuals). A w_i value larger than 1 indicates a positive selection for the resource and a value less than 1 indicates avoidance (Manly et al. 2002). We verified uniform satellite coverage over the course of the day in both the northern Gulf of Mexico and Bermuda through inspection of satellite pass predictions from the ARGOS website.

Results

Tag retention

Retention rates of towed-float transmitters ranged between 1 and 349 days and depended on the tether type used for each species (Table 1). We found the highest retention of SPOT tags for Cownose Rays using a spiracular attachment (Mean±standard error; M=72.0±31.6 days), whereas the highest mean retention on Spotted Eagle Rays was found using through-wing disc attachments (M=127.8±70.9 days). Tag retention using stainless steel dart-bridles varied markedly between and within species (M=47.3±36.1 day for Cownose Rays; M=18.5±6.8 days for Spotted Eagle Rays).

Cownose Ray movements

Cownose Rays demonstrated connectivity between shelf and inshore waters of the northern Gulf of Mexico (Fig. 4a). However, core regions of use included the immediate waters off Dauphin Island, Fort Morgan, Perdido Pass, and nearshore areas of the Mississippi-Alabama barrier islands (Fig. 4). Two large female rays released in November 2009 (CNR-01, CNR-02) displayed movements along barrier islands of Alabama and Mississippi, including excursions into Mississippi Sound. Several position estimates were made at inlet passes of this region, including Mobile Pass, Petis Bois Pass, Horn Island Pass and Dog's Keys Pass (Fig. 4). Two individuals (CNR-03, CNR-05) tagged west of Mobile Pass also displayed movement parallel to shore along the Ft. Morgan peninsula. One female released from Dauphin Island (CNR-02) was tracked westward to Dog's Keys Pass, just west of Horn Island, Mississippi. This individual eventually moved southwestwardly into Barataria Bay, Louisiana, where the tag was apparently shed 17 days after release. Three individuals (CNR-01, CNR-02, CNR-03) tagged in fall of 2009 and 2010 evaded surface waters in mid-December, remained submerged throughout winter, and re-appeared in spring off the edge of the Mississippi-Alabama shelf near 29° N latitude. When these individuals began transmitting in the spring, transmissions were continuous, suggesting tags were at the surface and most likely shed from the animals. Two large female rays tagged in November 2011 (CNR-13, CNR-14) off Perdido Pass also displayed initial movements to the west and southwest before detaching by Mississippi Delta waters. CNR-15, tagged off Dauphin Island in late November 2011, made similar movements, but reported through late January 2012 near the Mississippi-Alabama shelf edge. Animals tagged in late-summer 2011 south of Dauphin Island remained close to this region for several days at a time (Fig. 4).

Maximum daily rates of movement for Cownose Rays were variable, ranging from 1.3 – 50.1 km/day (Table 1). There was no significant relationship between ray size and either maximum ROM (linear regression; $F_{1,14}$=0.089; p=0.770; R^2=0.456) or mean ROM (linear regression; $F_{1,14}$=1.43; p=0.252; R^2=0.100). Male Cownose Rays appeared to have generally slower movement rates ($M_{♂}$=11.3±4.9 km/day) than females ($M_{♀}$=22.5±3.4 km/day), though sample sizes were limited. Seasonal comparisons of movement rates showed Cownose Rays were most active in fall (M=23.5± 5.8 km/day), less active in summer (18.1±2.4 km/day), and least active in spring (9.6±4.9 km/day). Log-likelihood chi-square tests indicated significant differences in diel surface activity by hour in Cownose Rays (χ^2=391.36, d.f. = 299; p<0.001). Specifically, Cownose Rays elected to be within surface waters (w_i >1) during three major intervals: 07:00–09:00, 13:00–15:00, and 18:00–21:00 (Fig. 5a).

Spotted Eagle Ray movements

In Bermuda, most Spotted Eagle Rays exhibited high fidelity to release sites within waters of Harrington

Table 1 Deployment characteristics of all Cownose (CNR) and Spotted Eagle Rays (SER) fitted with towed-float SPOT5 transmitters. Transmitters from individuals marked with an asterisk (*) were recovered after detachment, and two asterisks (**) represent animals fitted with recovered transmitters. Tether Type abbreviations: D = dart bridle, T = tail suture, S = spiracular tube, and W = through-wing disc. Total distance is cumulative distance traveled between all position estimates. ROM = rate of movement

Animal ID	Tagging Date	Tether Type	Disc Width (mm)	Weight (kg)	Sex (M/F)	Track Days	Total Distance (km)	Mean ROM (km/day)	Max ROM (km/day)
CNR-01*	11/14/2009	D	842	9.0	F	155	225.5	8.1	23.2
CNR-02	11/14/2009	D	1011	17.0	F	17	211.3	10.5	15.2
CNR-03*	11/8/2010	D	995	19.5	F	145	267.5	6.4	22.3
CNR-04*	11/8/2010	D	808	6.8	M	121	149.2	0.8	1.3
CNR-05	3/30/2011	D	842	9.0	M	29	31.9	2.6	4.7
CNR-06*	4/18/2011	D	872	10.5	F	26	17.7	3.8	14.4
CNR-07*	8/11/2011	T	875	10.0	M	4	75.3	22.4	22.4
CNR-08	8/17/2011	T	900	12.5	M	7	43.6	8.2	16.4
CNR-09	9/15/2011	D	980	18.5	F	16	88.9	8.6	27.2
CNR-10	9/15/2011	D	920	17.0	F	1	3.3	5.5	14.1
CNR-11**	9/21/2011	D	1020	22.0	F	3	14.0	8.1	17.4
CNR-12**	9/21/2011	T	950	17.0	F	1	3.7	10.9	10.9
CNR-13	11/14/2011	S	964	15.5	F	27	228.2	14.5	33.6
CNR-14	11/14/2011	S	1025	20.0	F	133	148.5	19.0	19.0
CNR-15**	11/22/2011	S	840	9.0	F	56	166.7	13.6	50.1
SER-01*	10/16/2009	D	1590	46.5	F	2	1.7	1.2	1.2
SER-02	10/21/2009	D	1320	36.0	M	35	25.3	3.2	16.7
SER-03	10/22/2009	D	1320	38.0	M	20	30.0	4.5	13.2
SER-04	10/27/2009	D	1270	33.5	F	17	14.5	2.3	9.3
SER-05*	7/15/2010	W	1530	N/A	F	37	12.3	1.6	12.3
SER-06	7/16/2010	W	1320	35.5	M	2	1.4	8.0	10.7
SER-07	7/21/2010	W	1290	N/A	M	243	8.0	2.4	12.2
SER-08*	7/22/2010	W	1255	21.5	F	8	7.3	1.8	4.1
SER-09**	7/22/2010	W	1300	31.0	M	349	432.4	10.1	14.8

Sound, Flatts Inlet, and adjacent waters of the North Sound (Fig. 6). However, we documented multiple excursions to coral reef areas fringing the North Sound (Fig. 6). For example, we estimate SER-02 departed and returned to Harrington Sound on at least three separate occasions. SER-03 exhibited similar transient behavior, including an offshore excursion to a reef location and back into Harrington Sound within a 4 d period. After returning to Harrington Sound for approximately 1.4 d, SER-03 reported along another reef area where we suspect the tag had detached. SER-04 (female) did not appear to leave the Harrington Sound region for the first few weeks of deployment, but rapidly transited to "The Reefs" shortly thereafter where we expect the tag to have also detached. Individuals released in Harrington Sound in 2010 were also observed to move outside of this inshore lagoon. For example, both males SER-05 and SER-07 made excursions to the North Sound and/or coral reefs before returning Harrington Sound. Only a single female (SER-08) was observed to move into Great Sound and likely utilized the north-facing shoreline to transit from Harrington Sound to this larger protected water body (Fig. 6).

There was no significant relationship between Spotted Eagle Ray size and either maximum (linear regression; $F_{1,8}=1.05$; $p=0.340$; $R^2=0.130$) or mean (linear regression; $F_{1,8}=1.15$; $p=0.318$; $R^2=0.141$) ROM. Male Spotted Eagle Rays exhibited significantly greater maximum ROM ($M_{♂}=13.5\pm1.9$ km/day) than females ($M_{♀}=6.7\pm2.5$ km/day) (two-sample *t*-test; t= 2.36, d.f. = 7, p<0.05). No major differences in movement rates were observed between rays tagged in

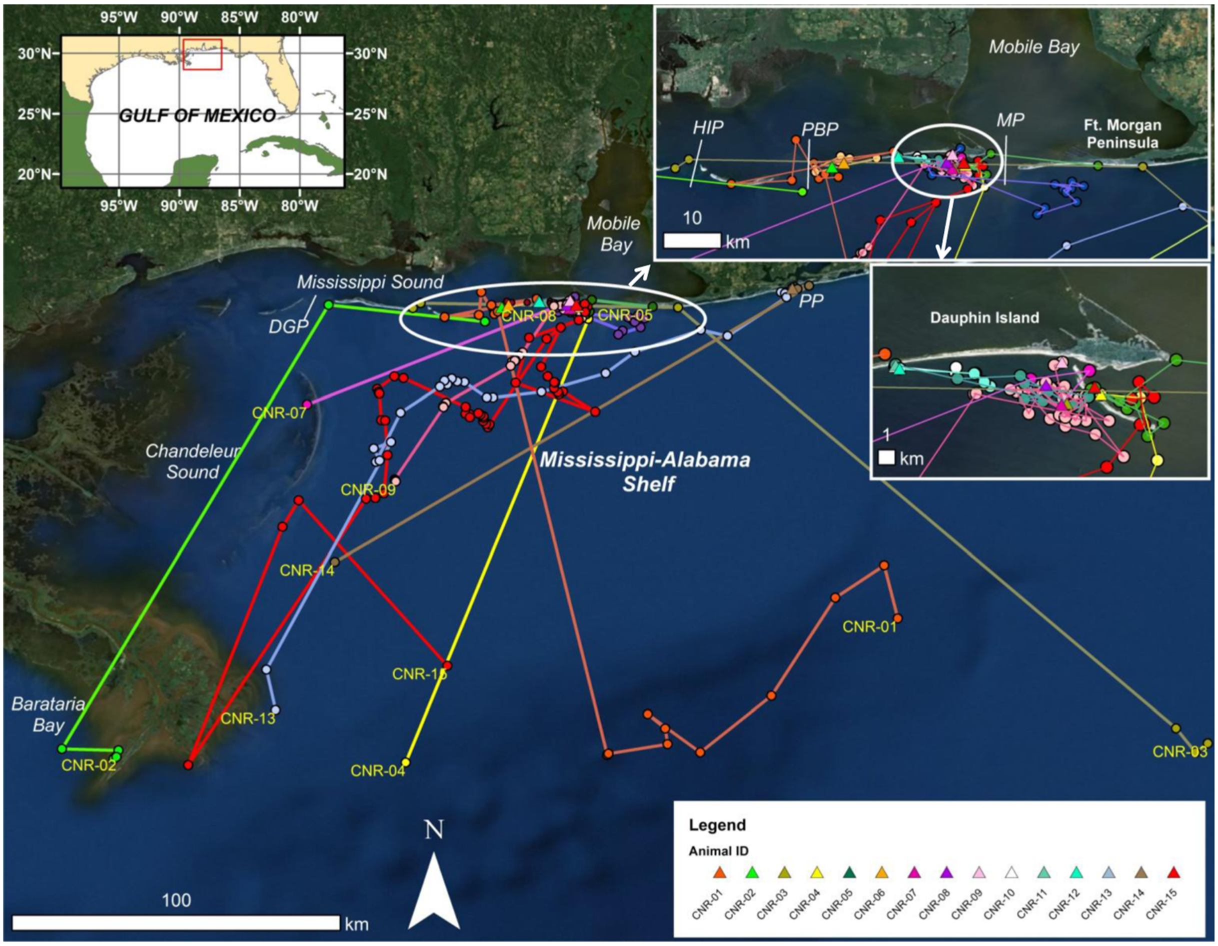

Fig. 4 Multi-scale display of minimum movement paths and position estimates of Cownose Rays (n=15) fitted with SPOT5 towed-float transmitters in the Northern Gulf of Mexico (2009–2011). Individuals and paths are coded by color, with release sites displayed as triangles. Individuals that moved >10 km from release sites are also labelled with text next to final position estimate. Major passes along barrier islands are labelled (from west to east): DGP = Dogs Keys Pass; HIP = Horn Island Pass, PBP = Petis Bois Pass, MP = Mobile Pass, PP = Perdido Pass)

November 2009 (M=10.1±3.3 km/day) and July 2010 (M=10.8±1.8 km/day). Log-likelihood chi-square tests indicated significant differences in surface activity by hour in Spotted Eagle Rays (χ^2=295.53, df=184; p<0.001). Specifically, Spotted Eagle Rays elected to be within surface waters during hours 01:00–04:00, and again between 18:00 and 21:00 (Fig. 5b).

Discussion

Real-time surface transmitting tags such as the Wildlife Computers SPOT5 towed-float model are highly capable of tracking the movements and habitat use of free-ranging myliobatid stingrays in coastal and open ocean waters. Our novel application of this technology on two species indicates towed-float telemetry can track movement patterns on multiple temporal and spatial scales, from 1's to 100's of kilometers, and from days to several months at a time. As such, future applications of this technology could involve studies that identify ray emigration routes from coastal systems, general dispersal behavior, and interactions between ray aggregations and oceanographic surface features.

Tag retention

Our study identified multiple challenges associated with tethering towed-float transmitters to highly mobile myliobatid rays. Although transmitter retention rates

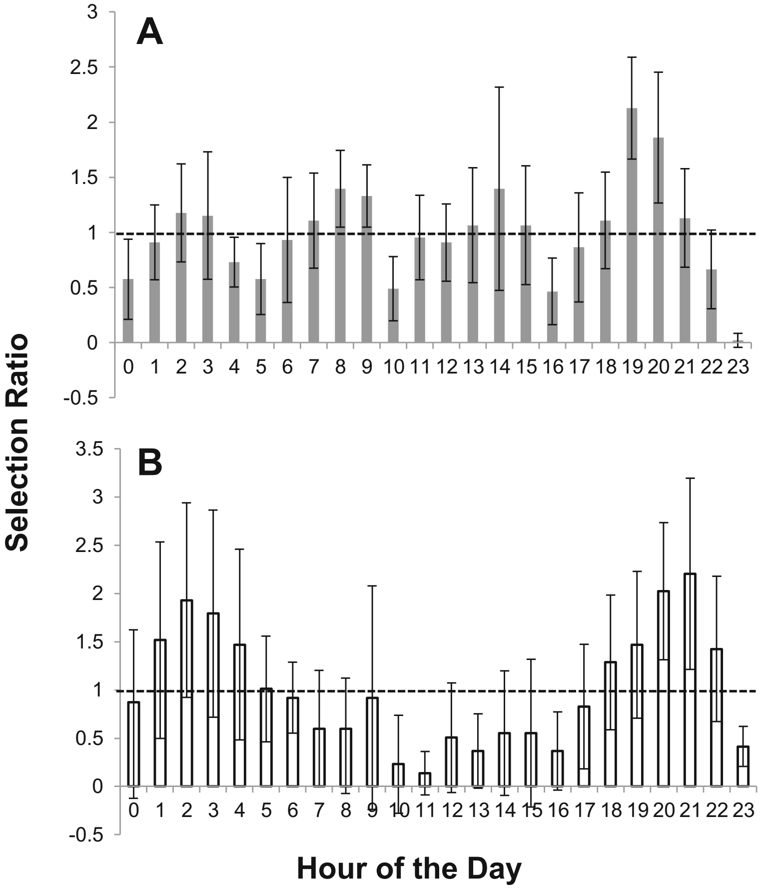

Fig. 5 Plots of hourly transmission behavior of satellite-tagged Cownose Rays (A; N=15) and Spotted Eagle Rays (B; N=9). On both charts a horizontal dashed line is displayed at a value of 1, as values above this level indicate selection and those below represent avoidance (Manly et al. 2002)

exceeded those from the only other application of towed-float satellite telemetry to a batoid (Graham et al. 2012), we had the advantage of conducting animal instrumentation experiments under more controlled settings, which enabled us to test multiple tethering techniques. While we could not replicate all tethering techniques on both species of myliobatid stingrays, our work suggested that stainless steel-headed dart tags, inserted intramuscularly, were not the most effective means of anchoring towed-float transmitters to these species. Intramuscular dart tags have been applied to several species of elasmobranchs for both long-term mark-recapture studies (Kohler and Turner 2001) and anchoring of PSATs to large sharks (Hammerschlag et al. 2011). Within our study, we found divergent retention rates of dart-bridled SPOT5 transmitters between Spotted Eagle Rays and Cownose Rays, possibly linked to behavioral and environmental differences between the two species. Though the cause for the behavior is not currently known, Spotted Eagle Rays commonly breach surface waters in many parts of their range (Silliman and Gruber 1999). We observed this behavior regularly in Harrington Sound and suspect it may have contributed to detachment of tethers given the strong drag likely imposed on the dart-bridle upon exiting and re-entry into the water. Moreover, this species was more often exposed to complex environments like coral reefs, which may have further contributed to tag shedding as individuals may have swam near these structures. Recovered SPOT5 units originally tethered with dart-bridles typically had missing or bent stainless dart heads. For this reason, we recommend spiracular attachments (Cownose Rays) or through-wing tether attachments (Spotted Eagle Rays) for future studies using this technology on myliobatid rays. We envision reductions in the size of the towed-float will improve overall retention and allow this technology to be applied over a larger size range of myliobatid rays.

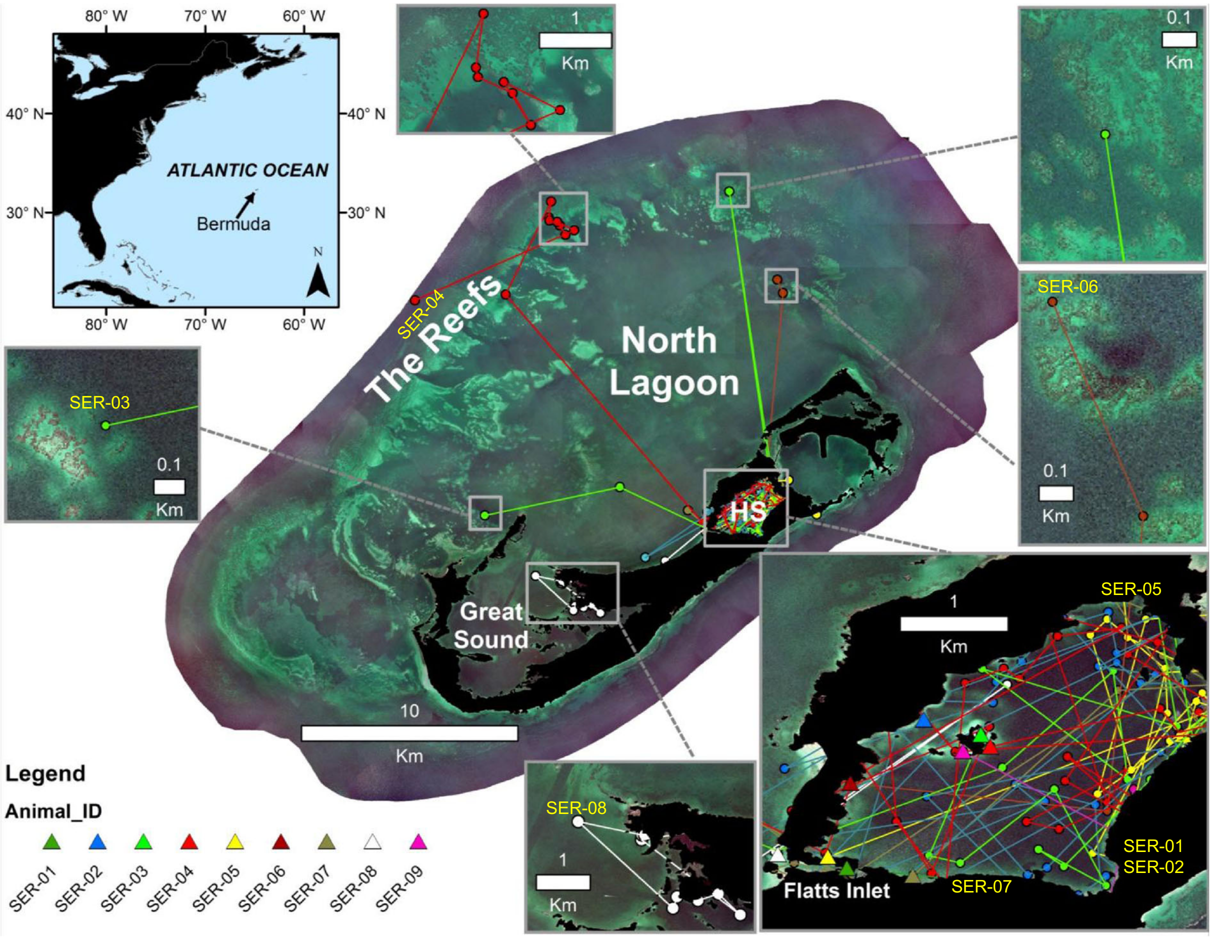

Fig. 6 Multi-scale display of minimum movement paths and position estimates of Spotted Eagle Rays (n=9) fitted with SPOT5 towed-float transmitters in Bermuda (2009–2010). Individuals and paths are coded by color, with release sites depicted as triangles. Gray boxes represent areas of interest that are expanded outside of the central map of the Bermuda platform. Major areas of interest of interest are labelled (HS = Harrington Sound). Individual ID is placed on final position estimate. Imagery provided by Bermuda Department of Conservation Services

Cownose Rays in the northern Gulf of Mexico

Our satellite tracks of Cownose Rays off coastal Alabama supplement a growing body of knowledge on the habitat use of this species. Movements between near shore and inshore waters of the Mobile Bay and Mississippi Sound systems confirm the association of this species with productive coastal estuaries of the Gulf of Mexico (Rogers et al. 1990; Craig et al. 2010). Further, the multiple tracks of individuals within shallow waters of the Gulf Islands National Seashore corroborate aerial observations of large schools of Cownose Rays observed along this barrier island chain (Rogers et al. 1990; Ajemian 2011). The shallow sandflats associated with these barrier islands house productive assemblages of crustaceans and bivalves that represent important food resources to these rays as they arrive in springtime (Ajemian and Powers 2012, 2013). Our finding of low relative movement rates during the spring season may thus be explained by prolonged periods of foraging in these productive benthic habitats. Contrastingly, elevated movement rates during the fall may be indicative of deteriorating environmental conditions (i.e., reduced temperature) causing Cownose Rays to migrate southwardly to more tolerable habitats. Despite being significantly smaller than Spotted Eagle Rays, movement rates of cownose were overall much higher with peaks in surface activity during multiple portions of the day. These findings contrast with Collins et al. (2007), who found no distinct overall activity pattern using acoustic telemetry in a confined coastal lagoon. Our concentrated tagging efforts along open barrier islands systems and inclusion of much larger and mature individuals may account the differences observed in diel behavior between the two studies. Future work should attempt to apply towed-float transmitters to Cownose Rays over a larger estuarine gradient to clarify these differences.

It has been hypothesized that Gulf of Mexico Cownose Rays comprise a single population that migrates in a clockwise direction beginning in Mexico during winter, the northern Gulf during spring, and southwest Florida in the fall (Schwartz 1990). However, this hypothesis has been challenged by multiple studies. Rogers et al. (1990) examined Cownose Ray distribution throughout the Gulf of Mexico from aerial surveys and found seasonality in densities, but did not notice an eastward expansion along the northern Gulf of Mexico as suggested by Schwartz (1990). Moreover, in southwest Florida, acoustic monitoring studies found Cownose Rays were year-round residents that did not migrate seasonally, though it was suggested that rays from the northern Gulf of Mexico could exhibit these behaviors (Collins et al. 2007, 2008). Our data from satellite tracked Cownose Rays support seasonality in this species, but also refute Schwartz's (1990) hypothesis. Tracks from several individuals appear to converge on a common northeast-southwest outmigration path along the 20–30 m isobaths of the Mississippi-Alabama shelf during late fall. Despite these consistent outmigration patterns, Cownose Rays in the northern Gulf of Mexico did not appear to leave the confines of Mississippi-Alabama shelf. This finding, as well as the observation of CNR-15 tracked near the shelf edge through January 2012, supports a relatively short-term departure (December – February) from coastal waters as noted in regional gillnet and aerial surveys (Ajemian 2011). Unfortunately, due to the surfacing requirement of the SPOT5 transmitters, we are limited in our conclusions of overwintering location and behavior of Cownose Rays in the northern Gulf of Mexico. However, given our observations of multiple resurfacing tags in spring along the Mississippi-Alabama shelf edge, we suspect these animals may seek refuge in sub-surface waters of this region during the winter months and thus have relatively limited migrations. This hypothesis would starkly contrast findings by Grusha (2005), who found Cownose Rays seasonally migrate over long distances between north-central Florida and the mid-Atlantic Bight. Such potential differences in migratory patterns could explain variability in life history patterns between Cownose Rays of the US east coast (Smith and Merriner 1986) and the Gulf of Mexico (Neer and Thompson 2005; Poulakis 2013), though further work is clearly needed to confirm these relationships.

Spotted Eagle Rays in Bermuda

Our satellite telemetry data on Spotted Eagle Rays complemented previous findings on habitat use and residency patterns from acoustically tagged individuals in Harrington Sound (Ajemian et al. 2012). When used as a proxy for surface habitat use, transmission patterns from SPOT5 tags confirmed a bimodal distribution in vertical habitat use, with two peaks in surface activity (02:00 and 21:00) that were negatively correlated with the depth of acoustically tagged animals from an earlier study (Fig. 7). These converging patterns could be representative of shallow water use by Spotted Eagle Rays during these darker and cooler periods and increased use of benthic habitats (i.e., movement out of surface waters) for foraging during the midday period. Matern et al. (2000) suggested that bat rays (*Myliobatis californica*) in Tomales Bay, California, preferentially foraged in intertidal flats during the midday as this was the most energetically favorable (i.e., warmest) period for excavating benthic prey. In Harrington Sound, Bermuda, where intertidal flats are scarce, Spotted Eagle Ray prey (calico clam, *Macrocallista maculata*) are distributed along a deeper depth of 7.5 m, on average (Ajemian et al. 2012). Acoustically tagged rays travel to these depths during midday, concomitant with the timing of minimal surface activity from satellite tracked individuals. Thus, similar to bat rays in Tomales Bay, Spotted Eagle Rays may take advantage of these temporarily warmer conditions during midday to forage in productive benthic environments of Harrington Sound.

Our application of towed-float satellite telemetry revealed novel connections between coral reef habitats and Harrington Sound by Spotted Eagle Rays. While previous acoustic tagging work in the region demonstrated regular egress of these animals from Harrington Sound, the acoustic array was spatially restricted and thus prevented comprehension of additional habitats exploited by rays on the Bermuda platform. Our observations of offshore reef use by satellite-tagged Spotted Eagle Rays are supported by several sightings from recreational divers (J. Clee, REEF database, pers. comm), and demonstrates potential ecosystem

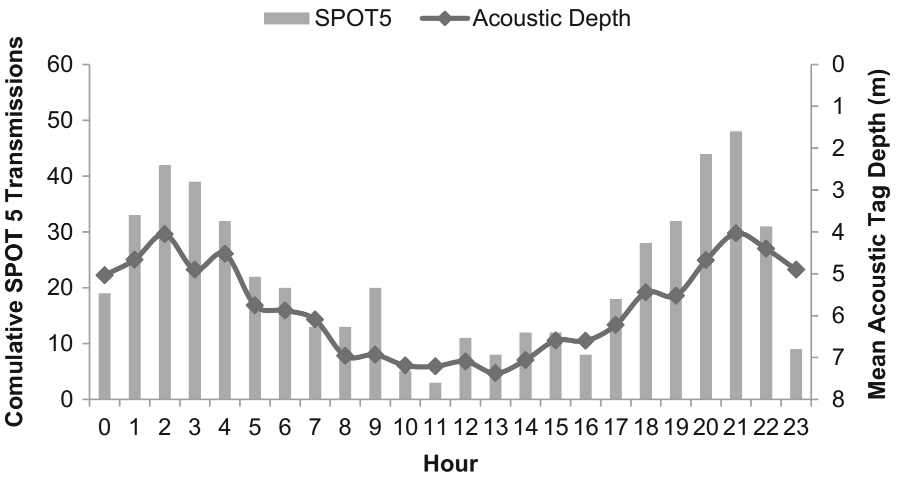

Fig. 7 Dual plot showing vertical bars of cumulative SPOT5 transmissions by hour for Spotted Eagle Rays tagged 2009–2010, and a line-scatter of mean hourly acoustic transmitter depth from Spotted Eagle Rays monitored in Harrington Sound in 2008. Acoustic data are derived from Ajemian et al. (2012)

connectivity between coral reefs and inshore soft-sediment lagoons of Bermuda. To date, elasmobranch habitat connectivity has been described in the context of ontogenetic changes in habitat use of populations (e.g., Chin et al. 2013), without an appreciation of how individuals may connect habitats on finer temporal and spatial scales. Adult Spotted Eagle Rays may thus serve as a model predator to test future hypotheses related to benthic habitat connectivity and spatial subsidies (sensu Heithaus et al. 2010). Future work should concentrate on the frequency and extent of these habitat exchanges.

We only documented round-trip movements from Harrington Sound to the reef in male Spotted Eagle Rays (*n*=4). In addition, overall movement rates of males were, on average, twice those of females. These differences in the distribution and movement behavior between sexes also corroborate our previous acoustic monitoring study in this region, which showed female Spotted Eagle Rays tended to remain in Harrington Sound for significantly longer periods than more transient males (Ajemian et al. 2012). In addition, multiple (*n*=4) female-only inter-annual recapture events within Harrington Sound suggest the region is used over several years by mature female rays (Ajemian et al. 2012). The consistent use of the sound may be linked to the abundance and availability of benthic prey, which may be important to large females preparing for parturition.

Several marine species, including elasmobranchs, show differential habitat use patterns between sexes (Wearmouth and Sims 2008). In fact, sexual segregation is so commonly utilized among elasmobranchs that it is often considered a generality in these fishes (Grubbs 2010). Habitat use differences between sexes may be linked to differences in temperature preference, foraging grounds, and/or reproductive behaviors (Wearmouth and Sims 2008). For many species, mature females utilize shallower and more turbid inshore environments as these represent productive and protected pupping areas for their newborns (Heithaus 2007). Though far from a eutrophic estuary, Harrington Sound typically experiences warmer temperatures and more frequent phytoplankton blooms than the surrounding areas of the Bermuda islands (Thomas 2003). With their larger size and higher energetic demands of gestation, mature female Spotted Eagle Rays may elect to remain in Harrington Sound where food resources are more abundant and pups are protected from sharks, while males exploit habitats where resources are of higher quality (Wearmouth and Sims 2008). One female captured in Harrington Sound in September 2008 aborted live pups, indicating the individual was very close to parturition (M.J. Ajemian, pers. obs). Further, small young-of-the-year Spotted Eagle Rays were regularly observed in Great Sound (M.J. Ajemian, pers. obs), where we tracked a single mature female in July 2010. Further survey work is needed across the inshore region of the Bermuda islands to confirm whether Harrington and/or Great sounds serve as pupping grounds for this protected species.

Despite our observations of movements among various coastal lagoons and reefs of the Bermuda islands, we did not document any Spotted Eagle Ray movement off the Bermuda platform. This finding suggests that this species may be resident to the Bermuda islands, which is consistent with the isolated nature of this assemblage of volcanic pedestals. Limited data from the National Marine Fisheries Service Cooperative Shark Tagging Program indicate other species of elasmobranchs (e.g., Galapagos Shark, *Carcharhinus galapagensis*) tend to be similarly restricted to the Bermuda platform (Kohler et al. 1998). However, a growing satellite tag data set suggests that Tiger Sharks (*Galeocerdo cuvier*) exhibit seasonal transitions between Bermuda and other islands of the subtropical and temperate North Atlantic, including evidence of multiple inter-annual returns to waters fringing the Bermuda platform (B. Wetherbee, unpublished data). Consequently, there is likely some variability in fidelity to the Bermuda Islands among elasmobranch taxa of the region.

General conclusions

Our use of towed-float satellite telemetry revealed novel insights into the spatial ecology and habitat use of two species of myliobatid rays. While still seemingly restricted to the insular shelves of the Atlantic, both individual Cownose and Eagle Rays exchange between productive coastal habitats (i.e., estuaries and lagoons) and more oligotrophic shelf waters in their respective ecosystems. Additional research is needed to identify both biotic and abiotic triggers of these habitat shifts as they have the potential to affect local ecological (food web, nutrient) dynamics in these disparate ecosystems. Such findings also highlight the need for more ecosystem-based approaches to managing these highly mobile species as they traverse multiple habitats in relatively short time scales.

The successful deployments and transmission behaviors of SPOT5 transmitters on Cownose and Spotted Eagle Rays were likely enhanced by the pelagic behavior of these two species. As such, this type of transmitter may not be as effective at capturing periods of high benthic use (e.g., shellfish feeding grounds) by these animals, especially when these regions of interest are located in relatively deep waters. Thus, we still encourage acoustic telemetry approaches or integration of archival and surface-transmitting satellite technology to help unravel these potential fine-scale movement patterns of myliobatid rays while at depth.

Acknowledgments This study was conducted in accordance with the laws of the State of Alabama and under IACUC protocols (Permit # 05043-FSH) approved by the University of South Alabama. All Spotted Eagle Rays were collected under special permit # SP090608, issued by the Bermuda Government Department of Environmental Protection. All efforts were made to minimize animal suffering during tagging procedures. Collection of Spotted Eagle Rays would have been impossible without the field and logistical assistance of Marine Ops staff of the Bermuda Aquarium, Museum and Zoo (BAMZ; C.T. Flook and C. Bridgewater, K. Smith), members of the Fisheries Ecology Lab at the Dauphin Island Sea Lab (M. Kenworthy, K. Gregalis, C. Hightower, L.M. Showalter, C. Pabody, N. Bawden, L. Dodd, S. Chutkan, A. Brown, A. Kroetz, M. Schrandt), as well as interns and students from BZS/BAMZ (C. Grenfell, J. Rosser, D. Young, and R. Fisher). Funding for this project came from the Gulf of Mexico Research Initiative Small Grants for Exploratory Research and the Bermuda Zoological Society. We are indebted to W.T. Driggers III, C. Jones, I. MacDonald, and T.J.T. Murdoch for advice on tag placement, animal handling, and general logistical support. Save Our Seas Foundation provided financial support for this publication and others in this special issue. Special thanks go to Gregg Poulakis for his insightful comments on the manuscript, as well as the input of an additional anonymous reviewer. This is Contribution #217 of the Bermuda Biodiversity Project (BBP), Bermuda Aquarium, Natural History Museum and Zoo, Department of Conservation Services.

References

Ajemian MJ (2011) Foraging ecology of large benthic mesopredators: effects of myliobatid rays on shellfish resources. University of South Alabama, Dissertation

Ajemian MJ, Powers SP (2012) Habitat-specific feeding by Cownose Rays (*Rhinoptera bonasus*) of the northern Gulf of Mexico. Environ Biol Fish 95:79–97

Ajemian MJ, Powers SP (2013) Foraging effects of Cownose Rays along barrier islands of the northern Gulf. J Exp Mar Biol Ecol 439:119–128

Ajemian MJ, Powers SP, Murdoch TJT (2012) Estimating the potential impacts of large mesopredators on benthic resources: Integrative assessment of Spotted Eagle Ray foraging ecology in Bermuda. PLoS ONE 7:e40227. doi:10.1371/journal.pone.0040227

Bigelow HB, Schroeder WC (1953) Fishes of the western north Atlantic. Sawfishes, guitarfishes, skates, rays, and chimeroids. Memoirs of the Sears Foundation for Marine Research 1, Part 2. Yale University, New Haven, Connecticut.

Blaylock RA (1990) Effects of external biotelemetry transmitters on behavior of the Cownose Ray *Rhinoptera bonasus* (Mitchill 1815). J Exp Mar Biol Ecol 141:213–220

Canese S, Cardinali A, Romeo T, Giusti M, Salvati E, Angiolillo M, Greco S (2011) Diving behavior of the giant devil ray in the Mediterranean Sea. Endanger Species Res 14(2):171–176. doi:10.3354/esr00349

Cartamil DP, Vaudo JJ, Lowe CG, Wetherbee BM, Holland KN (2003) Diel movement patterns of the Hawaiian stingray, *Dasyatis lata*: implications for ecological interactions between sympatric elasmobranch species. Mar Biol 142:841–847

Chin A, Heupel MR, Simpfendorfer CA, Tobin AJ (2013) Ontogenetic movements of juvenile blacktip reef sharks: evidence of dispersal and connectivity between coastal habitats and coral reefs. Aquat Conserv 23:468–474. doi:10.1002/aqc.2349

Collins AB, Heupel MR, Motta PJ (2007) Residence and movement patterns of Cownose Rays *Rhinoptera bonasus* within a south-west Florida estuary. J Fish Biol 70:1–20

Collins AB, Heupel M, Simpfendorfer C (2008) Spatial distribution and long-term movement patterns of Cownose Rays *Rhinoptera bonasus* within an estuarine river. Estuaries 31:1174–1183. doi:10.1007/s12237-008-9100-5

Craig JK, Gillikin PC, Magelnicki MA, May LN (2010) Habitat use of Cownose Rays (*Rhinoptera bonasus*) in a highly productive, hypoxic continental shelf ecosystem. Fish Oceanogr 19:301–317

Croll DA, Newton KM, Weng K, Galván-Magaña F, O'Sullivan J, Dewar H (2012) Movement and habitat use by the spine-tail devil ray in the Eastern Pacific Ocean. Mar Ecol-Prog Ser 465:193–200. doi:10.3354/meps09900

Cuevas-Zimbrón E, Pérez-Jiménez J, Méndez-Loeza I (2011) Spatial and seasonal variation in a target fishery for Spotted Eagle Ray *Aetobatus narinari* in the southern Gulf of Mexico. Fisheries Sci 77:723–730. doi:10.1007/s12562-011-0389-9

Dewar D, Mous P, Domeier M, Muljadi A, Pet J, Whitty J (2008) Movements and site fidelity of the giant manta ray, *Manta birostris,* in the Komodo Marine Park, Indonesia. Mar Biol 155:122–133. doi:10.1007/s00227-008-0988-x

Domeier ML, Nasby-Lucas N, Lam CH (2012) Fine scale habitat use by white sharks at Guadalupe Island, Mexico. In: Domeier ML (ed) Global Perspectives on the Biology and Life History of the Great White Shark. CRC Press, Boca Raton, pp 121–132

Fossette S, Heide-Jørgensen M, Jensen MV, Kiszkad J, Bérubée M, Bertrandf N, Vélyg M (2014) Humpback whale (*Megaptera novaeangliae*) post breeding dispersal and southward migration in the western Indian Ocean. J Exp Mar Biol Ecol 450:6–14

Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: where have we been and where do we go next? Endanger Species Res 3:1–20

Graham RT, Witt MJ, Castellanos DW, Remolina F, Maxwell S, Godley BJ, Hawkes LA (2012) Satellite Tracking of Manta Rays Highlights Challenges to Their Conservation. PLoS ONE 7:e36834. doi:10.1371/journal.pone.0036834

Grubbs RD (2010) Ontogenetic shifts in movements and habitat use. In: Carrier JC, Musick JA, Heithaus MR (eds) Sharks and their relatives II: Biodiversity, adaptive physiology, and conservation. CRC Press, Boca Raton, pp 319–350

Grusha DS (2005) Investigation of the life history of the Cownose Ray, Rhinoptera bonasus (Mitchill 1815). Thesis, College of William and Mary

Grusha DS, Patterson MR (2005) Quantification of drag and lift imposed by pop-up satellite tags and estimation of the metabolic cost to Cownose Rays (*Rhinoptera bonasus*). Fish B-NOAA 103:63–70

Hammerschlag N, Gallagher AJ, Lazarre DM (2011) A review of shark satellite tagging studies. J Exp Mar Biol Ecol 398:1–8

Hearn AR, Green JR, Espinoza E, Peñaherrera C, Acuña D, Klimley AP (2013) Simple criteria to determine detachment point of towed satellite tags provide first evidence of return migrations of whale sharks (*Rhincodon typus*) at the Galapagos Islands, Ecuador. Anim Biotelem 1:1–11

Heithaus MR (2007) Nursery areas as essential shark habiats: a theoretical perspective. In: McCandless CT, Pratt HL Jr, Kohler NE (eds) Shark nursery grounds of the Gulf of Mexico and east coast waters of the United States. American Fisheries Society Symposium 50:3–13

Heithaus MR, Frid A, Vaudo J, Worm B, Wirsing AJ (2010) Unraveling the ecological importance of elasmobranchs. In: Carrier JC, Musick J, Heithaus MR (eds) Sharks and their relatives II: biodiversity, adaptive physiology, and conservation. Boca Raton, CRC Press, pp 611–637

Hines AH, Whitlach RB, Thrush SF, Hewitt JE, Cummings VJ, Dayton PK, Legendre P (1997) Nonlinear foraging response of a large marine predator to benthic prey: eagle ray pits and bivalves in a New Zealand sandflat. J Exp Mar Biol Ecol 216:191–210

Klimley AP, Kihslinger RL, Kelly JT (2005) Directional and non-directional movements of bat rays, *Myliobatis californica*, in Tomales Bay, California. Environ Biol Fish 74:79–88

Kohler NE, Turner PA (2001) Shark tagging: a review of convential methods and studies. Environ Biol Fish 60:191–223

Kohler NE, Casey JG, Turner PA (1998) NMFS cooperative shark tagging program, 1962–93: an atlas of shark tag and recapture data. Mar Fish Rev 60(2):1–87

Le Port A, Sippel T, Montgomery JC (2008) Observations of mesoscale movements in the short-tailed stingray, *Dasyatis brevicaudata* from New Zealand using a novel PSAT tag attachment method. J Exp Mar Biol Ecol 359(2):110–117. doi:10.1016/j.jembe.2008.02.024

Manly BFH, McDonald LL, Thomas DL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Dordrecht

Matern SA, Cech J, Joseph J, Hopkins TE (2000) Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: evidence for behavioral thermoregulation? Environ Biol Fish 58:173–182

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean. Science 315(5820):1846–1850. doi:10.1126/science.1138657

Neer JA, Thompson BA (2005) Life history of the Cownose Ray, *Rhinoptera bonasus*, in the northern Gulf of Mexico, with comments on geographic variability in life history traits. Environ Biol Fish 73:321–331

Peterson CH, Fodrie FJ, Summerson HC, Powers SP (2001) Site-specific and density-dependent extinction of prey by schooling rays: generation of a population sink in top-quality habitat for bay scallops. Oecologia 129:349–356

Poulakis GR (2013) Reproductive biology of the Cownose Ray in the Charlotte Harbor estuarine system, Florida. Mar Coast Fish Dynam Manag Ecosyst Sci 5:159–173. doi:10.1080/19425120.2013.795509

Riding TAC, Dennis TE, Stewart CL, Walker MM, Montgomery JC (2009) Tracking fish using buoy-based GPS telemetry. Mar Ecol-Prog Ser 377:255–262. doi:10.3354/meps07809

Rogers C, Roden C, Lohoefener R, Mullin K, Hoggard W (1990) Behavior, distribution, and relative abundance of Cownose Ray schools *Rhinoptera bonasus* in the northern Gulf of Mexico. Northeast Gulf Sci 11:69–76

Schluessel V, Bennett MB, Collin SP (2010) Diet and reproduction in the white-spotted eagle ray *Aetobatus narinari* from Queensland, Australia and the Penghu Islands, Taiwan. Mar Freshw Res 61:1278–1289

Schwartz FJ (1990) Mass migratory congregations and movements of several species of Cownose Rays, genus *Rhinoptera*: a world-wide review. J Elisha Mitchell Sci Soc 106:10–13

Silliman WR, Gruber SH (1999) Behavioral biology of the Spotted Eagle Ray, *Aetobatus narinari*. Bahamas J Sci 11:713–720

Smith JW, Merriner JV (1985) Food habits and feeding behavior of the Cownose Ray (*Rhinoptera bonasus*). Estuaries 8(3): 305–310

Smith JW, Merriner JV (1986) Observations on the reproductive biology of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay. Fish B-NOAA 84:871–877

Smith JW, Merriner JV (1987) Age, growth, movements and distribution of the Cownose Ray, *Rhinoptera bonasus*, in Chesapeake Bay. Estuaries 10(2):153–164

Tagliafico A, Rago N, Rangel S, Mendoza J (2012) Exploitation and reproduction of the Spotted Eagle Ray (*Aetobatus narinari*) in the Los Frailes Archipelago, Venezuela. Fish B-NOAA 110:307–316

Thomas MLH (2003) Marine Ecology of Harrington Sound Bermuda. Bermuda Zoological Society, Bermuda

Vaudo JJ, Lowe CG (2006) Movement patterns of the round stingray *Urobatis halleri* (Cooper) near a thermal outfall. J Fish Biol 68:1756–1766

Wearmouth VJ, Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and mammals: behavior patterns, mechanisms and conservation implications. Adv Mar Biol 54:101–170

Wearmouth VJ, Sims DW (2009) Movement and behaviour patterns of the critically endangered common skate *Dipturus batis* revealed by electronic tagging. J Exp Mar Biol Ecol 380:77–87. doi:10.1016/j.jembe.2009.07.035