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A subtropical embayment serves as essential habitat for sub-adults and adults of the critically endangered smalltooth sawfish

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ABSTRACT

Identifying essential habitat for large, mobile endangered species is difficult, particularly marine species where visual observations are limited. Though various methods of telemetry are available, each suffers from limitations and only provides satisfactory information over a specific temporal or spatial scale. Sawfish are one of the most imperilled groups of fishes, with every species worldwide listed as endangered or critically endangered. Whereas movements of juvenile sawfish are fairly well studied, much less is known about adults due to their rarity and the challenging environments they live in. Previous encounter records have identified Florida Bay in the Everglades National Park as a potentially important habitat for adults of the critically endangered smalltooth sawfish (*Pristis pectinata*). We used a combination of acoustic and satellite telemetry, as well as conventional tagging, to determine patterns of movement and residency by sub-adult and adult sawfish. Over short time periods, movements appeared primarily tidal driven with some evidence that animals moved into shallow water during the ebbing or flooding tides. Adult sawfish sexually segregated seasonally with males found by mangrove-lined canals in the spring and females predominantly found in outer parts of the bay. Males migrated from canals starting in late May potentially as temperatures increased above 30° C. Some males and females migrated north during the summer, while others may have remained within deeper portions of Florida Bay. Male sawfish displayed site fidelity to Florida Bay as some individuals were recaptured 1–2 years after originally being tagged. We hypothesize that mating occurs in Florida Bay based on aggregations of mature animals coinciding with the proposed mating period, initial sexual segregation of adults followed by some evidence of females moving through areas where males show seasonal residency, and a high percentage of animals showing evidence of rostrum inflicted injuries. The combination of methods providing movement data over a range of spatial and temporal scales reveals that sub-tropical embayments serve as essential habitat for adult smalltooth sawfish.

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1. Introduction

A critical component of conservation management is an understanding of the movements and habitat use of the species in question. Knowledge of an animal's spatial ecology can predict the ability of protected areas to conserve the species, and highlight the frequency and location of interactions between the species and human activity in addition to potential sources of mortality (e.g. Simpfendorfer et al., 2010, Lambertucci et al., 2014 and Nawaz et al., 2014). Large carnivores can be particularly challenging to conserve as they may move over large distances, often crossing protected area and even geo-political boundaries where conservation regulations may vary (Lambertucci et al., 2014; Yorio, 2009). For these animals it may be extremely difficult to provide complete protection over their entire life cycle, and instead managers must focus on protecting habitats important for foraging, mating, parturition, and juvenile development (e.g. Cooke, 2008, Lambertucci et al., 2014 and Yorio, 2009).

Conservation of large marine animals may be even more complicated as protected areas are usually small relative to the animal's scale of movements, and it is hard to identify the role of particular habitats to the animal's life cycle (Devitt et al., in press; Yorio, 2009). A variety of tools can be used to quantify the movements of marine species. The various forms of telemetry each provide data over a range of spatial and temporal scales, but each leaves data-gaps. Satellite telemetry for example can provide movement data over months to a year but the spatial resolution of animal locations may have large errors. Alternatively, acoustic telemetry can provide data with high spatial resolution (e.g. active tracking) but only over short time periods (days) or single point locations over months to years (passive telemetry). Studies that combine multiple forms of telemetry with a single species in a single location are rare (Holland et al., 2001; Meyer et al., 2010). Ultimately, to fully comprehend the role a habitat plays, movements must be measured over short and long time frames which combined with life history information can determine the potential function of that habitat.

The sawfishes are a group of large batoid elasmobranchs and are considered some of the world's most imperilled fishes (Dulvy et al., 2014). The characteristic rostrum is particularly susceptible to entanglement and is also a target in the curio trade. Sawfish also heavily use coastal habitats and are sensitive to issues associated with habitat modification, fisheries bycatch and pollution (Dulvy et al., 2014; Seitz and Poulakis, 2006; Simpfendorfer et al., 2010; Waters et al., 2014). Combined, these factors have led to precipitous declines in sawfish populations worldwide and currently all five species are listed as endangered or critically endangered by the International Union for the Conservation of Nature (IUCN) Red List (Dulvy et al., 2014).

The smalltooth sawfish (*Pristis pectinata*) reaches almost 600 cm in length and is the only species found regularly in the United States (Poulakis et al., 2014). While historic records are distributed along the US east coast as far north as New York, sawfish are now only found reliably along the coast of southern Florida and it is estimated that the population size may have declined to 5% of what it was at the time of European settlement (NMFS, 2000; Poulakis and Seitz, 2004; Simpfendorfer et al., 2010). These declines lead to smalltooth sawfish being classified as Critically Endangered by the IUCN (Carlson et al., 2014) and Endangered under the US Endangered Species Act in 2003 (NMFS, 2003). Due to the fragmented distribution of the species worldwide, smalltooth sawfish are considered one of the species most at risk of extinction having shown a range contraction of 81% (Dulvy et al., 2014).

However, southwest Florida still has a viable population of sawfish and is considered a 'lifeboat' due to the strict legal protections provided (Dulvy et al., 2014). Furthermore, despite the drastic reduction in population size, recent population viability models predict that due to rapid growth rates, sawfish populations can recover if the appropriate management plans are implemented (Carlson and Simpfendorfer, 2014; Simpfendorfer et al., 2008b). The spatial ecology of sawfishes in Florida has been studied using two basic methods: telemetry and encounter records from the public (e.g. Simpfendorfer et al., 2011 and Wiley and Simpfendorfer, 2010). These data show that there are ontogenetic shifts in movements and habitat use, with neonates and juveniles using rivers and estuaries as nursery grounds, and adults using coastal habitats (Carlson et al., 2014; Simpfendorfer et al., 2011; Waters et al., 2014; Wiley and Simpfendorfer, 2010).

Most information is regarding neonate and juvenile life stages as there are far fewer encounter records for individuals > 300 cm. Adults only make up 8% of reported encounters, primarily because they inhabit deeper murky water where they are less likely to be seen (Waters et al., 2014). Satellite tagged adults are more mobile than juveniles but still spend 96% of their time shallower than 10 m depth, and show relatively high levels of residency to areas of southern Florida (Carlson et al., 2014). There remains a considerable gap in our knowledge of the spatial ecology of adult sawfishes and it has already been recognized that this is an area where more research should be focused (Norton et al., 2012; Waters et al., 2014).

Adult sawfish encounters are frequently reported from Florida Bay, a large lagoonal estuary situated adjacent to the Everglades and the Florida Keys (Poulakis and Seitz, 2004; Waters et al., 2014). Florida Bay could be a key habitat for adult sawfish, but encounter data are only static in nature and do not trace the behaviour of individuals. Establishing if a habitat is important requires distinguishing it from transitory habitats and an understanding of the movements of individuals over multiple time scales. A combination of active and passive acoustic telemetry, satellite telemetry, and conventional tagging were used to determine how adult sawfish use Florida Bay over short (days) and medium (months) temporal scales. Our specific questions were (a) over short time scales, are sawfish movements related to diel and/or tidal periods? (b) how long do adult sawfish reside in the bay and do they show site fidelity? (c) does male/female behaviour differ? (d) what are the potential functions of Florida Bay to smalltooth sawfish?

2. Methods

2.1. Study site

Florida Bay is a large (2600 km^2), shallow embayment consisting of mud banks, deeper channels, large seagrass beds and extensive mangrove habitats. It is part of the Everglades National Park and there is extensive drainage into the bay from adjacent estuaries. The bay experiences strong tidal currents on a semi-diurnal cycle. The inner bay is characterized by much shallower water (often < 1 m) and mangrove lined coastal areas and canals. Sandy Key is a small island on the border of the outer bay where water depths slowly increase, although it is still adjacent to extensive shallow seagrass beds (Fig. 1). See Poulakis and Seitz (2004) for more details.

2.2. Tagging

Adult sawfish were caught using bottom longlines or rod and reel with ladyfish (*Elops saurus*) bait, and secured alongside the vessel where they could be measured and sexed. The animals were tagged with one or two types of transmitters (acoustic and/or satellite, see below). An external Hallprint M-type dart tag was inserted into the musculature below the dorsal fin, a fin clip was taken for DNA analysis, and the animal was released. Maturity of males was assessed by calcification of claspers, whereas females were considered mature if stretched total length (STL, the length from the tip of the rostrum to the end of the caudal fin bent down) was > 375 cm (Poulakis et al., 2014, J. Gelschleiter unpublished data).

2.2.1. Acoustic transmitters

Due to permitting restrictions we were not allowed to internally implant acoustic transmitters. Therefore, acoustic tags were externally attached to the first dorsal fin via two small drilled holes. Stainless steel leader was used to attach transmitters to the dorsal fin. Leader was encased in heat shrink tubing, and thin foam padding was placed between the transmitters and the dorsal fin to prevent any abrasion. The leaders were then sealed with copperlock crimps of dissimilar metal so that they would corrode, and eventually the whole transmitter would fall off the fin.

2.2.1.1. Active tracking. An adult female sawfish was tagged with a V16PT (Vemco ltd., Nova Scotia, 75 kHz) continuous pinger at Sandy Key on March 23rd 2011. The transmitter continuously emitted an acoustic signal approximately once per second. Sensors measured pressure (depth) and temperature, and these data were also transmitted via the acoustic signal. The signal was detected and converted into an audible ping and sensor readings via a hull-mounted directional hydrophone and VR100 receiver located on the tracking vessel. The tracking vessel attempted to remain with the sawfish at all times, but maintained at least a 10 m distance from the animal to prevent it from being startled. Geographic locations and sensor readings were taken every 5 min. Rate of Movement (ROM) was calculated by determining the distance moved every 5 min.

2.2.1.2. Passive telemetry. Sixteen adult sawfish were tagged with V16 RCode transmitters with a 50–90 s delay (69 kHz, Vemco Ltd.). Transmitters were detected by seven acoustic listening stations (VR2W) strategically placed throughout Florida Bay (Fig. 1). VR2Ws were deployed in locations where large numbers of sawfish encounters were reported and areas of importance identified from the active track. VR2Ws were attached to PVC pipes embedded within cement blocks, which were then connected via chain to sand-screws installed by divers. VR2Ws were retrieved and downloaded approximately every six months. All VR2W's were range tested by towing a V16 test tag behind a boat and slowly drifting up to 1000 m from the VR2W in four directions (N, E, S, W). Receiver performance was also evaluated using the metrics calculated from the VR2W meta-data. These included detection efficiency (what percentage of pulse trains are logged by the VR2W as actual detections), rejection coefficient (what percentage of detections are rejected by the VR2W due to invalid check sums, the pulses at the end of the synch), and finally the noise quotient (level of environmental noise or acoustic collisions, Simpfendorfer et al., 2008a). See Appendix A for details.

Data analysis. Cyclical patterns in sawfish movements were identified using fast Fourier transforms (FFT). The FFT decomposes time series data and searches for cyclical patterns which can be identified as peaks in a spectral density plot. For each individual, the number of detections that occurred during every hour of the monitoring period was determined, and a FFT was performed with Hamming window smoothing (Papastamatiou et al., 2009).

Generalized additive models (GAM) were used to determine the role of date and environmental conditions (temperature, salinity, dissolved oxygen) on the daily presence/absence of sawfish at East Cape Canal. Environmental data (daily means) were obtained from a monitoring station located within close proximity of East Cape Canal (station MK) and maintained by the National Park Service. However, oxygen concentration was highly correlated with temperature and was well above hypoxic levels so was not included in the analysis. GAMs were constructed with a binomial distribution and a cubic spline was fitted to the residuals. The serial correlation in the time series data were modelled using a continuous auto-regressive process of order 1 (AR1) with time as the position variable. Model fits were compared using Akaike Information Criteria (AIC), Bayesian Information Criteria (BIC) and maximum likelihood values. Due to differences in environmental profiles and detection spans, data from 2012 and 2013 were analysed separately. All analyses were performed using the *mgcv* package (Wood, 2006) in R (3.0.1).

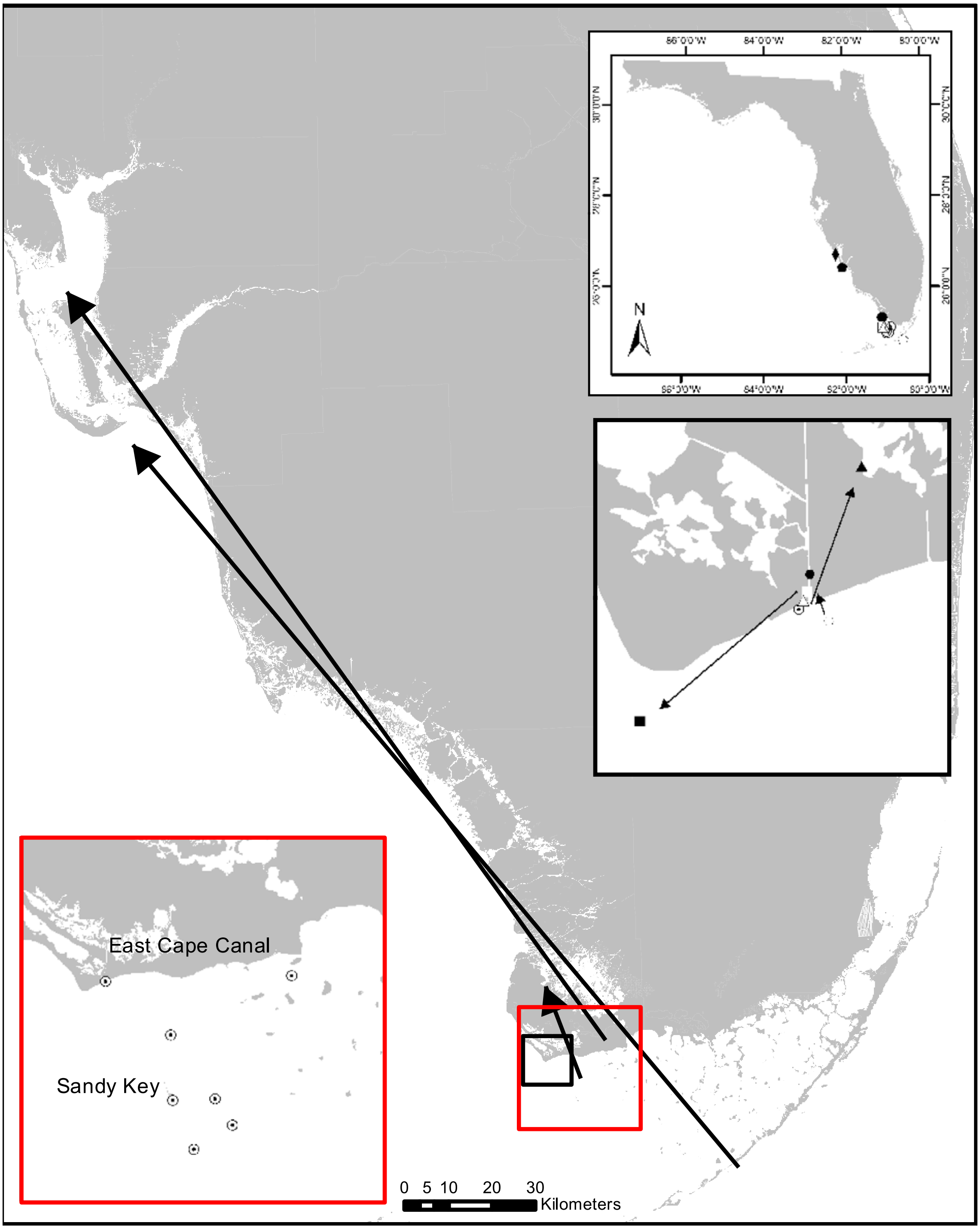

Fig. 1. The location of acoustic listening stations (bulls eye) in Florida Bay (lower left inset, square in main figure). Middle right inset shows satellite tagging deployment and pop-off locations for 'residential' individuals. Main figure shows tagging locations (satellite and acoustic) and pop-off or detection locations, for individuals that left the bay ('transients').

2.2.2. Satellite transmitters

Some animals were tagged with pop-up archival transmitting tags (MK 10 PATF, Wildlife Computers, Inc.) that archive temperature and depth but are also equipped with a Fastloc GPS to provide location if the tag breaks the water's surface. PATF tags were rigged with a modified harness consisting of 1.8 mm stainless steel cable surrounded by chafe tubing, with polyolefin heat-shrinkable tubing at each end. A small hole was made through the anterior portion of the first dorsal fin. The

Table 1
Smalltooth sawfish caught in Florida Bay from 2011 to 2013. Periods of cyclical detections (as determined by fast Fourier transforms) are given. ND not enough data to run FFT, NP no detectable cyclical patterns, and NT no transmitter applied. Sawfish in bold were only tagged with PATF satellite transmitters. Maximum distance is either between receiver detections (acoustic telemetry) or between satellite tag deployment and pop-off locations. Duration detection is time of first and last acoustic detection or satellite deployment duration. For double tagged animals, satellite tag deployment durations are in parenthesis. Ratio of # day detected to detection duration are also given.

Sawfish #	Stretch total length (cm)	Sex	Mature (Y/N)?	Location	Date tagged	Detection duration (d)	Max. dist. (km)	# days detected	Ratio (%)	Cyclical peaks
1 017[a]	420	F	Y	Sandy Key	23/2/11	–	–	–	–	–
1 251[a]	439	F	Y	Sandy Key	23/3/11	3	–	–	–	–
31 116	400	F	Y	Sandy Key	1/3/12	37	–	4	10.8	ND
31 117[b]	403	M	Y	East Cape	27/3/12	80 (30)	2.75	74	92.5	12 h
31 104	395	M	Y	Snake Bight	28/3/12	73		62	85	NP
31 108[b]	363	M	Y	East Cape	29/3/12	63 (60)	0.68	29	46	NP
31 105	372	M	Y	East Cape	29/3/12	10		10	100	ND
31 106	406	M	Y	East Cape	30/3/12	10		10	100	ND
31 110	374	M	Y	East Cape	30/3/12	111		67	60	12 h
31 107	379	M	Y	Sandy Key	31/3/12	8		5	63	ND
31 109	410	M	Y	Snake Bight	1/4/12	138		44	32	NP
31 111	389	M	Y	East Cape	27/4/12	43		36	84	12 h
31 113	378	M	Y	East Cape	27/4/12	72		38	53	16 h
29 087	383	F	Y	Sandy Key	23/3/13	58	25.5	8	14	ND
29 089	411	M	Y	East Cape	18/4/13	16		11	69	12 h
29 086	383	M	Y	East Cape	18/4/13	76		44	58	NP
29 090	423	M	Y	East Cape	18/4/13	63		53	84	12 h
29 088	431	M	Y	East Cape	19/4/13	48		33	75	12 h
1 701	224	M	N	East Cape	19/4/13	–		–	–	NT
103 435	399	M	Y	Sandy Key	13/3/12	46	9			
60 743	257	F	N	East Cape	23/4/13	62	2			
60 745	395	M	Y	Conch Channel	23/4/13	28	220			
60 746	395	M	Y	Out. Fl. Key	24/4/13	65	232			

[a] Animals were actively tracked.
[b] Animals were tagged with an acoustic transmitters (passive) and a PATF satellite transmitter.

free end of the harness assembly was threaded through the dorsal fin and the free end of steel cable was inserted into the open sides of two double copperlock crimps. The cable was pulled through the crimps to decrease the loop in the harness until the crimps rest just under the free rear tip of the dorsal fin. The crimps were then closed (crimped) to secure the harness in place and the excess steel cable was removed with wire cutters. The crimps and stainless steel leader were of dissimilar metals and the resulting electrolysis ensured the crimp would break down within six months and the leader would pull out of the sawfish. After 60 days the tags were programmed to release, float to the surface and transmit data to passing Argos satellites. Data transmission is power intensive and the number of data messages that can be transmitted is limited by the size of the tag's onboard battery pack. Depth and temperature data were summarised into 4 h bins to maximise the amount of successful data packet transmissions and also allow direct comparison to the previous study (Carlson et al., 2014). We classified sawfish into those whose tags released in the bay ('Residents') and those whose tags popped-off outside the bay ('Transients'). To examine differences in occupied depth bins between residents and transients, analysis of variance (ANOVA) was performed using the binned proportion of time spent as the dependent variable and temperature and depth bins as independent variables among tagged sawfish. Prior to analysis, the dependent data were transformed taking the arcsine of the square root to normalize the data. Violations of assumptions of normality were tested post hoc using normal probability and quantile–quantile plots of residuals.

3. Results

In total, 23 smalltooth sawfish were captured within Florida Bay (18 males, 5 females) that ranged in size from 224 to 439 cm STL (383 ± 52 cm mean (±1SD), Table 1). There was clear evidence of sexual segregation of adults, with more females caught in the outer bay (e.g. Sandy Key, 2 M: 4 F) and only mature males caught in the inner bay (14 M: 0 F). At East Cape Canal we also caught an immature male and female. Sawfish were caught in waters of 23.4–29.7 °C, salinities 37.0–40.0, and oxygen concentration 4.7–6.9 mg/L.

3.1. Acoustic transmitters

3.1.1. Active tracking

One mature female was tracked for nearly 40 h over a 72 h period (Fig. 2). The individual showed evidence of tidally related movements, swimming over warm shallow seagrass beds during the ebbing or flooding tide (73% of time ≤ 2 m,

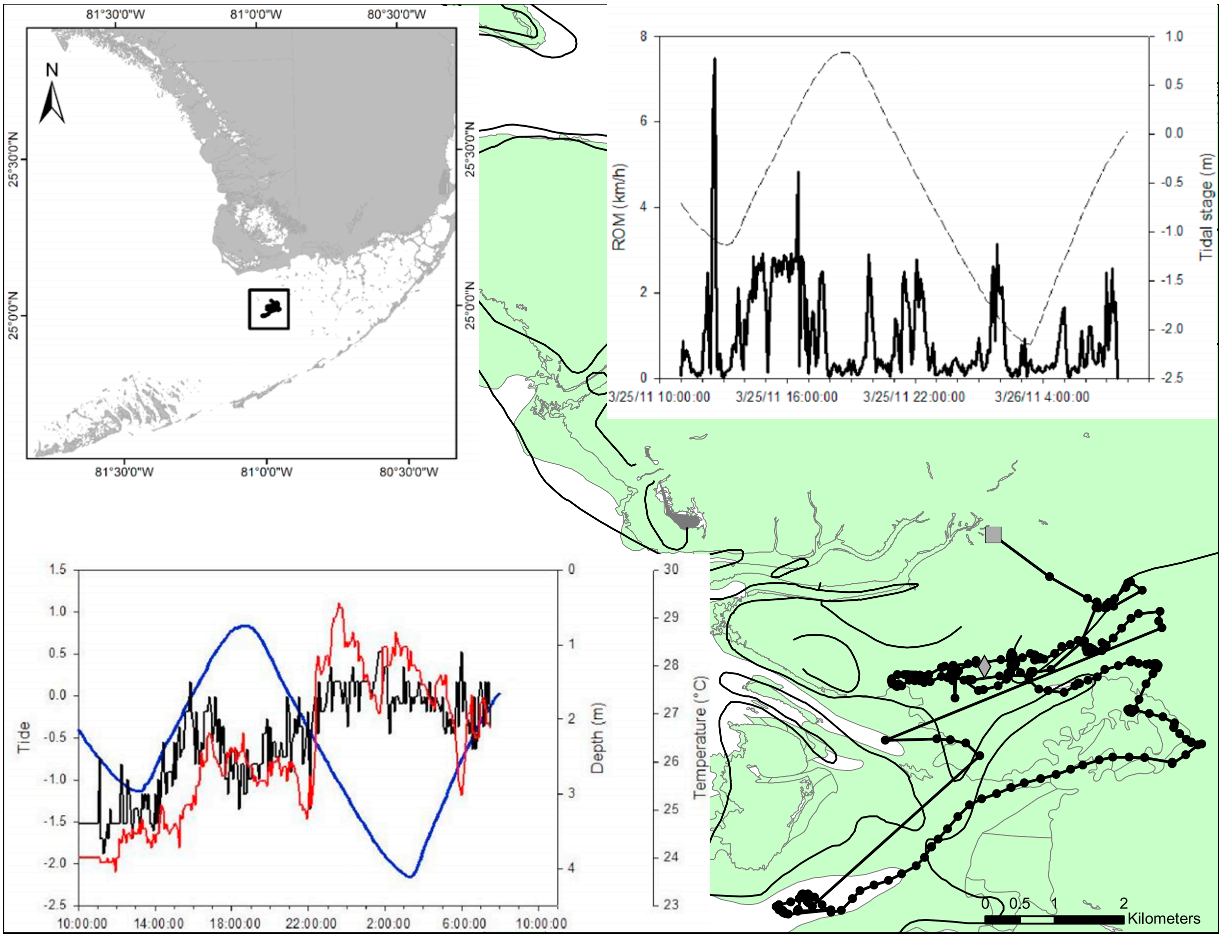

Fig. 2. Movements of a mature female smalltooth sawfish in outer Florida Bay, over a 70 h period. Changes in swimming depth (black) and water temperature (red) relative to tidal state (blue) are shown in lower left inset. Upper right shows change in rate of movement (black) against tidal state (dashed line). Grey square and diamond indicate the start and end points of the track, respectively. Green layers show seagrass beds and contour lines represent 1–2 m depth. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

76% of time $\geq$ 26.5 °C), and deeper cooler channels at slack tide (80% time $>$ 2 m, 98% time $<$ 26.5 °C). Overall, ROM was 1.1 $\pm$ 1.2 km/h (maximum 7.5 km/h) and was also related to tidal stage with 0 ROM during periods of slack tide (high or low, Fig. 2). The maximum displacement during the tracking period was 8 km (i.e. width of the activity space), and the same areas were visited over the two nighttime periods the animal was tracked.

3.2. Passive tracking

3.2.1. Receiver performance

Detection ranges were low, between 30 and 380 m and were not uniform around the receivers. Lowest detection ranges were for East Cape Canal (30–70 m), whereas the largest ranges were for the South Channel and Sandy Key receivers (37–380 m). There were some differences in receiver performance, although generally the receivers with the lowest performance (e.g. Snake Bight) had the highest number of detections (see Appendix A for details). We are confident that differences in detections between receivers reflect real differences in habitat use by adult sawfishes.

3.2.2. Movements

Sixteen individuals were detected over mean durations of 57 $\pm$ 37 days (range: 8–138 days, Fig. 3). While in the bay, animals were detected over 64 $\pm$ 28% of days. Residency was particularly high for males tagged inside the bay (detected for 71 $\pm$ 21% of days). Males showed high periods of residency to East Cape Canal, with some individuals being detected almost daily over periods of 1–3 months (Fig. 3). Five males were detected moving from the inner bay to the outer bay. Females acoustically tagged in the outer bay were detected for much shorter periods of time but were detected for brief periods in the inner bay. One female tagged by Sandy Key was detected for 7 consecutive days at East Cape Canal in late March and

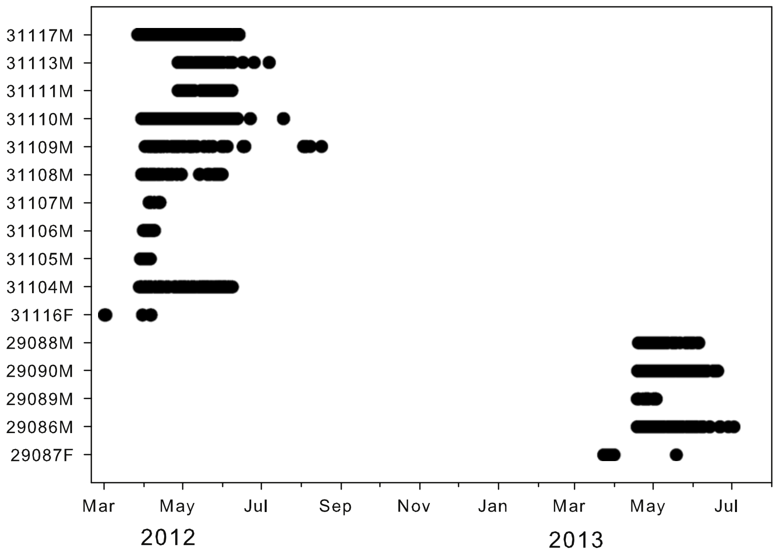

Fig. 3. Presence/absence plots for acoustically tagged individuals within Florida Bay. 'M' designates males, 'F' females. Note the first detection for each individual corresponds to the time when it was actually tagged.

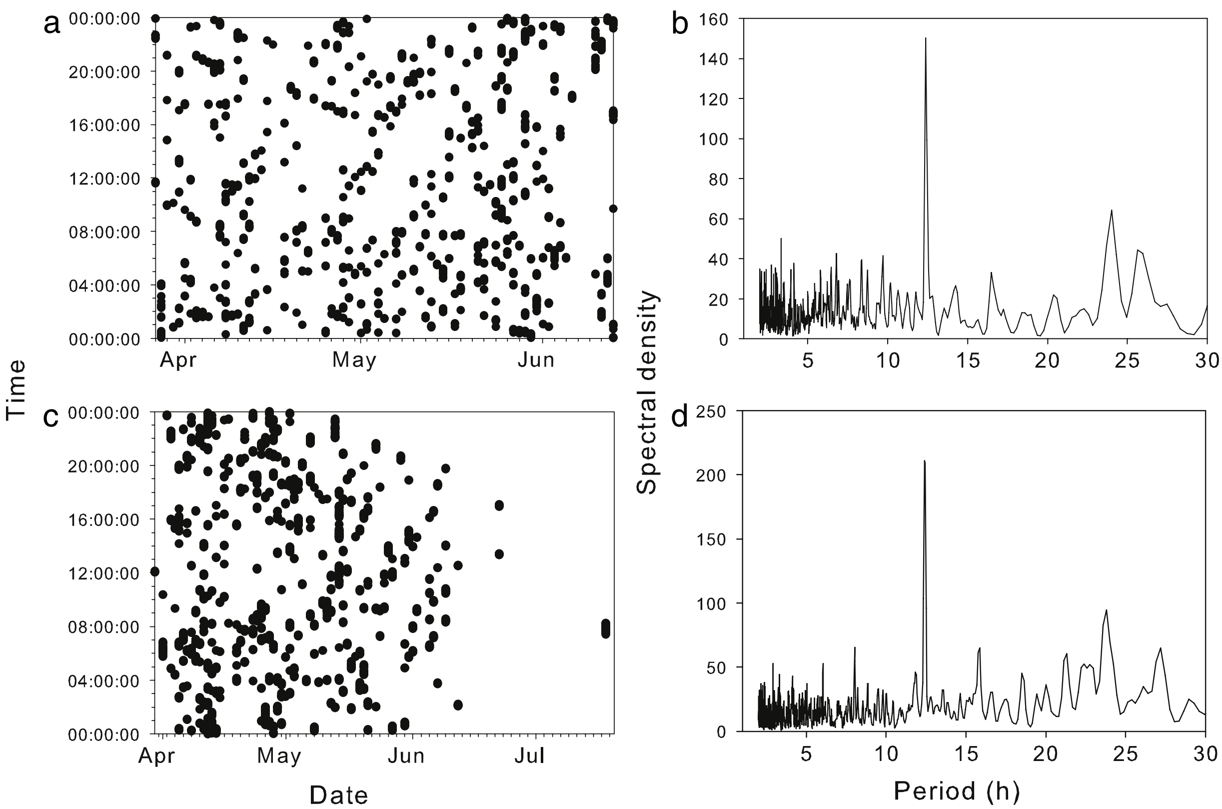

Fig. 4. Scatterplots of detections and associated fast Fourier transform for sawfish 31 117 (a, b) and 31 110 (c, d). Detections are for East Cape Canal.

then again in May. She was then detected by a series of receivers 37 km north, at Shark River from June 15–20 (M. Heithaus personal information). Out of the 11 individuals with enough data to perform FFT analysis, seven (64%) showed evidence of tidal movements, with 12 h peaks in the power spectrum (Fig. 4). No individuals showed any evidence of diel or crepuscular patterns of movement.

Environmental conditions within the bay (data from the National Park station) varied quite dramatically seasonally with temperatures of 15–35 °C, and salinities of 24–40 throughout the year. Oxygen concentration was highly correlated with

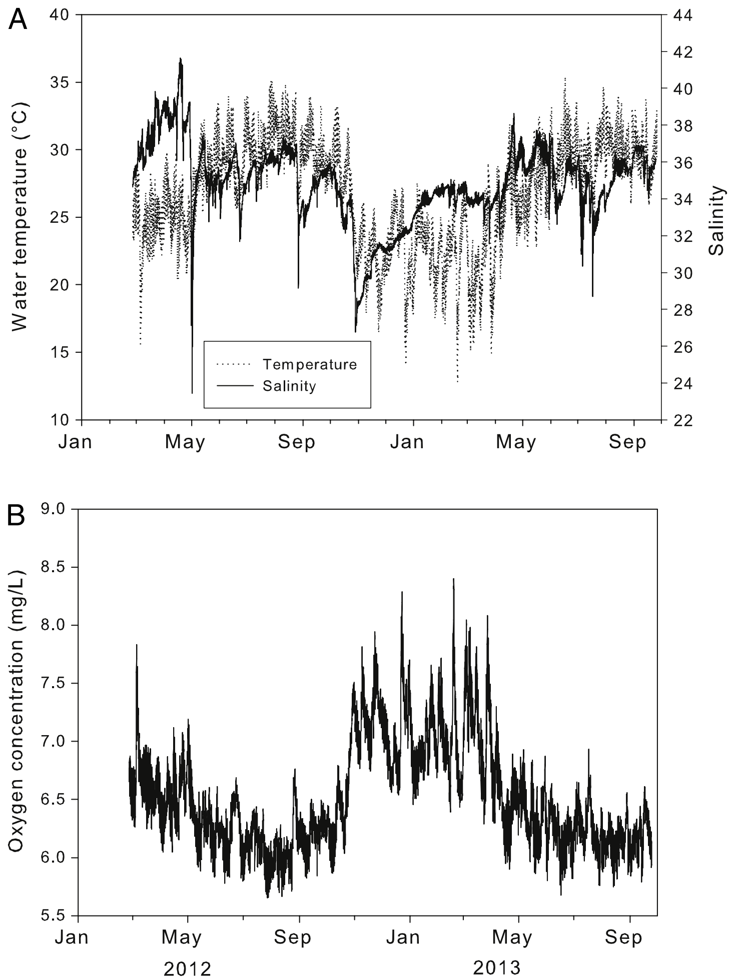

Fig. 5. Annual changes in water temperature, salinity (a) and dissolved oxygen (b) within Florida Bay.

Table 2
Results from GAMs for 2012 and 2013 for the influence of environmental variables on sawfish presence at East Cape Canal. Akaike Information Criteria (AIC), Bayesian Information Criteria (BIC) and maximum likelihoods (Max. Lik.) are given. Best fit models are in bold.

Index	Model	AIC	BIC	Max. Lik.
1 (2012)	Temperature + Salinity + Date	907.4	955.8	458.4
2	**Temperature + Date**	**904.2**	**949.4**	**458.7**
3	**Date**	**903.3**	**942.5**	**458.8**
1 (2013)	**Temperature + Salinity + Date**	**443.5**	**477.4**	**222.7**
2	**Temperature + Date**	**443.8**	**475.6**	**224.1**
3	**Salinity + Date**	**442.8**	**475.9**	**224.5**
4	Temperature	480.1	495.1	239.3
5	Salinity	510.3	527.7	254.8
6	**Date**	**442.3**	**472.5**	**225.2**

temperature but rarely decreased < 6 mg/L (Fig. 5). Environmental conditions can vary substantially throughout the bay, which may not be captured by the station data. All males started to leave East Cape Canal in May and going into June, although one individual was still detected in August. Although there was a clear seasonal departure from East Cape Canal, it was difficult to determine if this was only related to the time of year, or if it was also driven by temperature and possibly salinity. Although Date alone provided the best model fit, this was less than 1 AIC units from the next candidate model making them difficult to separate (Burnham and Andersen, 2002). Sawfish presence in 2012 started to decline at the end of May (150 days) and potentially at temperatures > 30 °C (Table 2, Fig. 6(A), (B)). In 2013, sawfish also started to leave the end of May but possibly also at temperatures > 30 °C and salinities < 36 (Table 2, Fig. 6(C), (D), (E)). Although no sawfish were detected returning to Florida Bay the following year, this was likely an artefact of tag loss, as two male sawfish were recaptured at East Cape canal after more than a year at liberty (both recaptured in May). An additional male was tagged in

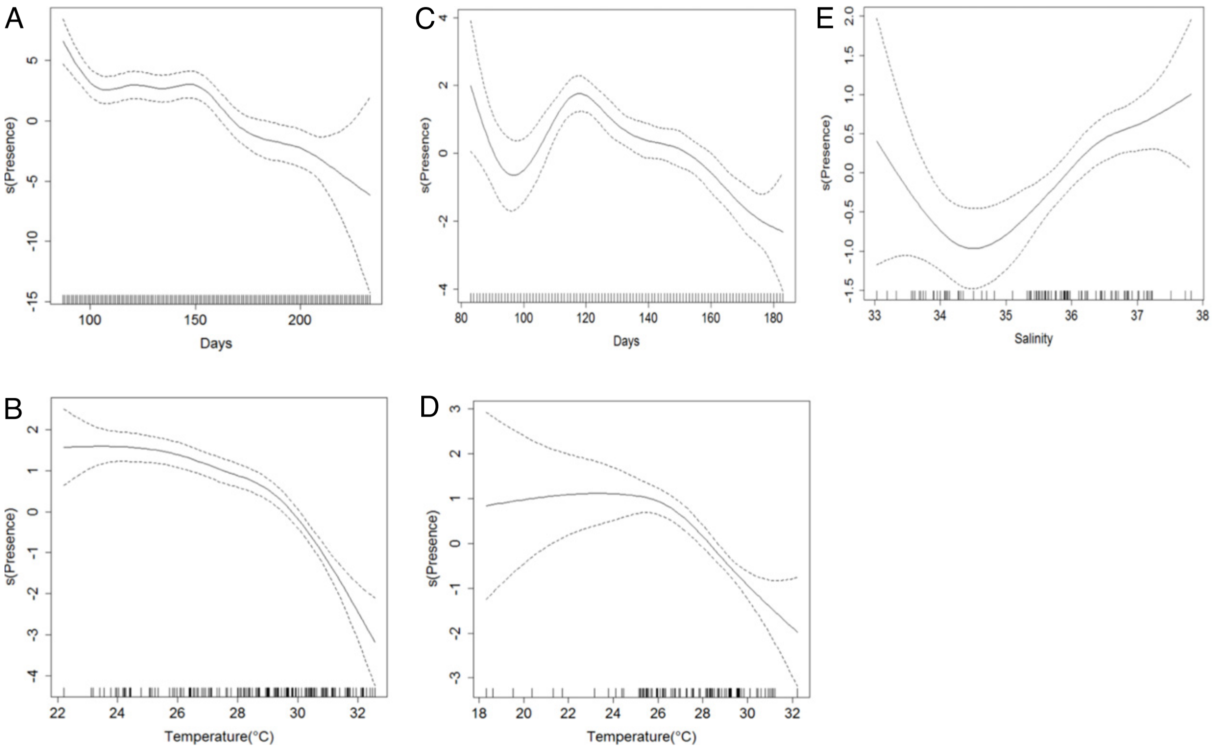

Fig. 6. Generalized additive model results of the effects of date (A), and temperature (B) on the presence of adult sawfish at East Cape Canal for individuals tagged in 2012. Days are numbered from the beginning of the year. Similar results from generalized additive models for effects of date (C), temperature (D) and salinity (E) for sawfish tagged in 2013. The initial decline in (C) at 100 days is due to a lag between the detection of a female in Feb/March and tagging of males in early April. Cubic splines have been fitted to data (means and confidence intervals).

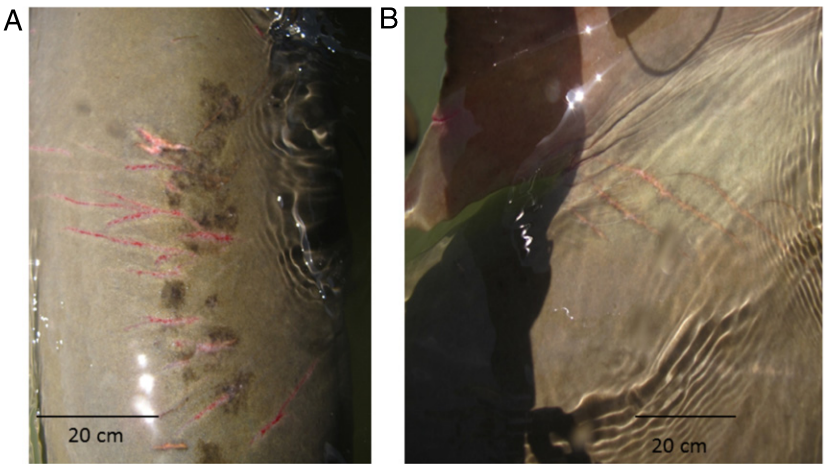

Fig. 7. Rostrum inflicted wounds on two male sawfish at East Cape Canal. (A) fresh wounds, and (B) healed wounds.

East Cape Canal in April 2012 and recaptured in Conchie Channel in September 2014 (Conchie Channel is within the inner bay and 11 km from East Cape Canal). All recaptured individuals had shed their acoustic tags. Females and males displayed scars which appeared to have been caused by the rostrum of other sawfish. Some males caught at East Cape Canal had fresh and/or healed scars (Fig. 7).

3.3. Satellite tagging

Six individuals were tagged with PATF satellite transmitters that were retained for 28–65 days. Two of those animals were also tagged with acoustic transmitters. Five tags were deployed in Florida Bay and reported, whereas an additional tag was deployed on an individual close to the Florida Keys (Fig. 1). Pop-off locations showed that sawfish either remained

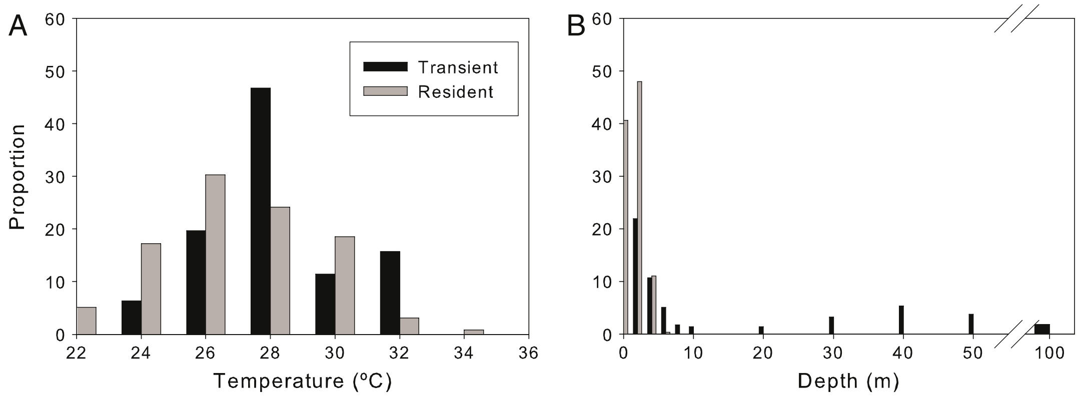

Fig. 8. Histograms of time at temperature (A) and time at depth (B) for satellite tagged sawfish that either remained within the bay ('resident') or migrated north ('transient').

within Florida Bay, or they migrated northwards during summer (Fig. 1). A mature male tagged in the inner bay, swam 220 km north before the transmitter popped off, and a male tagged off the Florida Keys had the tag release 232 km north (all releases were in the Gulf of Mexico). Other individuals showed much greater residency, with a mature male tagged in East Cape Canal having its tag pop-off 0.68 km from the tagging location, 60 days later (this was the same individual recaptured in Conchie Channel, two years later, Fig. 1). All GPS Fastloc locations were from within the bay during this period. Archival data for individuals whose tags released inside Florida Bay also suggested residency over the 1–2 month period as 99% of recorded depths were < 4 m and 94% of temperatures < 30 °C (Fig. 8). Animals that left Florida Bay and swam north performed deeper dives, in some cases diving to depths of 100 m, but 80% of depth recordings were < 10 m (Fig. 8). These wider roaming individuals spent 84% of their time in water < 30 °C. However, while sawfish exhibited significant differences among depth and temperature zones occupied ($p < 0.0001$) there was no difference ($p \geq 0.05$) in depth use between sawfish categorized as transient and residents. Sawfish categorized as transient occupied significantly ($p < 0.05$) warmer water zones than resident animals.

4. Discussion

By combining four methods of tagging we were able to gain insight into how adult smalltooth sawfish use Florida Bay and an understanding of just how important this habitat may be to adults of this species. We primarily captured adult individuals although some sub-adults were also captured which suggests that Florida Bay may serve several functions to sawfish including foraging and potentially mating sites.

Sawfish seasonally used certain habitats within Florida bay and adults showed clear patterns of sexual segregation. As suggested by encounter data, sawfish appeared to be more abundant during the spring and early summer (e.g. Poulakis and Seitz, 2004 and Waters et al., 2014). Female sawfish were predominantly caught on the outer parts of the bay, and seemed to arrive before males, whereas males were found in higher numbers by mangrove-lined canals within inner parts of the bay. Within these habitats there was evidence that sawfish movements were primarily driven by tides with animals moving into shallow water during the ebbing or flooding tides, but tending to rest at slack tide in deeper water. There was little evidence of diel movements, which agrees with studies of adult sawfishes (of several species) in other areas where movements were also tidally driven (Stevens et al., 2009). Similarly, satellite tagged smalltooth sawfish showed no evidence of diel vertical migrations (Carlson et al., 2014). Tidal movements in adults may be a response to periods when prey species are being forced out of protective habitats. During tracking, large numbers of smaller fishes and invertebrates were seen actively swimming during ebbing tides over seagrass beds and may provide an easy prey source. Tidal movements may also be related to behavioural thermoregulatory strategies associated with changes in water temperature, as suggested previously for adult sawfish (e.g. Sims et al., 2006 and Carlson et al., 2014). However, movements of juvenile smalltooth sawfish in estuaries and canals of the Everglades National Park were correlated with diel period and were not tidally driven (Hollensead et al., 2015).

Despite the clear seasonal departure of male sawfish from East Cape Canal starting towards the end of May, it was more difficult to determine the role of environmental conditions. There was some evidence that sawfish would leave the canal as temperatures > 30 °C and possibly if salinity < 36. Satellite tagging also suggested that adult sawfish rarely go into waters warmer than 30 °C although they were occasionally in water of 32–34 °C. Similarly, in a previous study, satellite tagged adults spent 65% of their time in waters of 22–28 °C (Carlson et al., 2014). Juvenile and neonate sawfish show similar preferences for temperature, avoiding waters > 30 °C, but use much lower salinities of 18–24 (Poulakis et al., 2011; Simpfendorfer et al., 2011).

It has been suggested that adult sawfish perform seasonal northward migrations in Florida waters (e.g. Waters et al., 2014), although tracking data to date have not identified such behaviour (Carlson et al., 2014). We obtained some evidence to support the migration theory as northward summer movements were observed from three individuals, but there were no southerly movements. However, no data were collected during late fall and winter when southerly movements would be predicted. Some individuals were recaptured in Florida Bay throughout the year, so a proportion of animals may use the bay year-round. Due to tag retention issues, it was not possible to quantify when individuals returned to the bay or at least to the East Cape Canal. At least three males returned to Florida Bay and presumably display site fidelity to this location. It may be that sawfish use partial migration where only a proportion of individuals migrate, with the decision to migrate based on sex, breeding status, and resource or body condition (e.g. Papastamatiou et al., 2013). This may likely be the case with smalltooth sawfish as females are hypothesized to reproduce on a biennial basis and hence only 50% of individuals should be pregnant each year (Poulakis et al., 2014). Additional long-term tagging may detect partial migration patterns.

Sexual segregation is seen in many groups of marine vertebrates although the function of this behaviour varies between and within the groups (Wearmouth and Sims, 2008). A frequent explanation for segregation in elasmobranch fishes is the social factors hypothesis (Wearmouth and Sims, 2008). This strategy may evolve when mating behaviour is energetically expensive and can lead to injury or even the death of the female. Elasmobranch fishes reproduce using internal fertilization and copulation often involves a female being mobbed by large numbers of males (Wearmouth and Sims, 2008). Hence, females are likely to avoid males outside of mating periods. However, while no adult female sawfish were caught in the inner bay, they were acoustically detected swimming into habitats used by males (Snake Bight and East Cape Canal), suggesting some overlap between the sexes during the late spring/early summer. Could this suggest mating is occurring in the bay? Generally it is thought that for most sharks and rays, males are more active during the mating season and will actively search for and locate females. While we never quantified activity, males appeared to show strikingly high residency to East Cape Canal from April to June (despite the low reception range of the receiver). The high frequency of individuals with rostrum wounds suggests agonistic interactions and possibly mating between individuals in the bay. One hypothesis is that mating may occur in or close to East Cape Canal and that sawfish perform behaviour similar to lekking (e.g. Emlen and Oring, 1977). Lekking occurs when males occupy small core territories with females moving through the location looking for mates, and may be beneficial for increasing encounter success. Lekking is commonly reported in birds, reptiles, and fishes but to the best of our knowledge has only been suggested for one other elasmobranch (Emlen and Oring, 1977; Wikelski et al., 1996; Jorgensen et al., 2012). Our mating hypothesis also correlates with what is known of reproductive physiology in sawfish. Based on blood testosterone levels in males and F prostaglandin levels in males and females, it is thought that mating occurs in the spring (Poulakis et al., 2014, J. Gelsleichter unpublished data). Finally, peak parturition is thought to occur from April to May, and the proposed one-year gestation period also suggests that mating occurs during a similar time period (Simpfendorfer et al., 2008b; Poulakis et al., 2011). However, our sample size of females was small and behaviour or activity was not recorded for either sex. An alternative explanation may be that mating occurred just prior to individuals arriving at Florida Bay, and that individuals used the bay to forage, or that individuals that visited Florida bay were in a 'non-breeding' year. Understanding the mating system of endangered animals is not trivial in its importance; reproductive skew, lekking and reproductive suppression can all reduce the effective population size (N_e) of a species and has consequences for conservation (Anthony and Blumstein, 2000).

Conserving large mobile animals is difficult as their movements frequently take them across protected area and geopolitical boundaries (e.g. Yorio, 2009, Lambertucci et al., 2014 and Heupel et al., 2015). Under these scenarios, it is vital that key habitats such as breeding or foraging sites are identified and protected (Yorio, 2009; Lambertucci et al., 2014). Florida Bay is an important area of recreational fishing activity and it is critical that outreach continues to ensure that fishers in the bay know how to respond to accidental captures, particularly in microhabitats such as East Cape Canal. Dockside interviews with anglers have previously highlighted that sawfish numbers in Florida bay may be increasing, so these interactions may not negatively affect conservation efforts (Carlson et al., 2007). Sawfish clearly cross and connect habitat realms, both between and within life stages, which require special consideration for conservation planning (Beger et al., 2010). There is a broad interface between life stages (juveniles prefer brackish estuaries, while adults prefer coastal waters) but also a diffuse connection within adults that move from deeper coastal to mangrove habitats. Future management may require a variety of spatial conservation prioritization techniques to account for these multiple forms of connectivity (Beger et al., 2010).

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2015.03.003.

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