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Abiotic affinities and spatiotemporal distribution of the endangered smalltooth sawfish, *Pristis pectinata*, in a south-western Florida nursery

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Abstract. Understanding how endangered marine species rely on coastal habitats is vital for population recovery planning. The smalltooth sawfish (*Pristis pectinata*) is one of several critically endangered sawfishes worldwide known to use estuaries and rivers during their early life history. In a Florida estuary designated as critical habitat by the USA government, juveniles were monitored to characterise seasonality, recruitment, and habitat use. Stretched total length ranged from 671 to 2172 mm ($n = 137$, mean = 1248 mm). Sawfish were captured year round. Captures of neonates with embryonic rostral sheaths allowed refinement of the size at birth (671–812 mm) and confirmed a protracted timing of parturition (November–July), which peaked between April and May. Although sampling occurred throughout the estuary, five locations had the greatest catch rates. Most juvenile sawfish had an affinity for water <1 m deep, water >30°C, dissolved oxygen $>6\ \mathrm{mg\ L^{-1}}$, and salinity between 18 and 30. Greater catch rates for sawfish >1 year old were associated with shoreline habitats with overhanging vegetation such as mangroves. These results detail habitat use within a recognised nursery that can be used for conservation of the first endangered marine fish species in the USA.

Additional keywords: Caloosahatchee River, Charlotte Harbor, elasmobranch, habitat use, lower lethal temperature, Myakka River, ontogenetic niche shift, Peace River, Pristidae, ray, tag–recapture.

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Introduction

A variety of natural processes and anthropogenic activities, especially overfishing, is likely to lead to an increase in the number of marine endangered species. Thus, understanding the biology and ecology of vulnerable (e.g. K-selected species) and currently endangered marine species is vital for population maintenance, recovery planning, and sustaining overall ecosystem health. Often, studies are not conducted before species decline because of factors that include plasticity of commercial fisheries and market demand (fisheries change before regulatory agencies and scientists can react), lack of funding priority (funding sources tend to be reactive rather than proactive), or because of poorly monitored indirect effects such as by-catch. In the United States, the first endangered marine fish species, listed in 2003, was the smalltooth sawfish (*Pristis pectinata*). Like for many newly listed species, more information is now needed on life-history parameters and habitat use requirements to guide specific management actions.

Pristis pectinata is one of several sawfish species listed as *Critically Endangered* on the IUCN Red List of Threatened Species (Adams *et al*. 2006). Although it has been reported worldwide, primarily in tropical and subtropical habitats (Bigelow and Schroeder 1953; Last and Stevens 1994), many earlier reports are likely to be erroneous because recent analyses have indicated that *P. pectinata* is restricted to the Atlantic basin (Faria 2007). Because of low numbers of recent encounter reports, this species may be extirpated from much of its former range, including the eastern Atlantic (e.g. Africa) and south-western Atlantic coasts (e.g. South America), although thorough surveys are needed to confirm population status in these regions

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(Adams *et al*. 2006). Sawfish species worldwide have been only occasionally studied, but species-specific research is required for successful management because available studies indicate that different species have contrasting life-history strategies, ranging from diadromous to wholly marine (Thorson 1976; Peverell 2005; Thorburn *et al*. 2007, 2008; Whitty *et al*. 2009).

Historically, *P. pectinata* was found in the western Atlantic from the United States to northern Argentina, but decades of largely unintentional overfishing (large numbers were caught and killed as by-catch) have reduced its population and restricted its range (Seitz and Poulakis 2002; Poulakis and Seitz 2004). This observation prompted state protections in Florida (FWC 1999), federal listing on the United States Endangered Species List (NMFS 2003), and international protection on CITES Appendix I (NMFS 2009*a*). Despite the special concern for this fish, *P. pectinata* was not studied in detail before the population was reduced, making the implementation of conservation and recovery plans for this species difficult. Thus, research was initiated to determine basic biological, ecological, and life-history parameters. Today, the only known viable population occurs in USA waters off south and south-western Florida (Seitz and Poulakis 2002; Poulakis and Seitz 2004; Wiley and Simpfendorfer 2010). Encounter reports from the public and research data suggest that gravid females enter nurseries briefly for parturition and juveniles occupy the lower reaches of rivers, estuaries, and coastal bays for about their first 3 years (up to ~2.5-m total length; Simpfendorfer *et al*. 2008, 2010); adults typically occur in more open-water, marine habitats (Poulakis and Seitz 2004; Fig. 1).

Although encounter reports from the public and research data have been combined to define the general areas in which juvenile *P. pectinata* can still be found, the use of scientific approaches (e.g. random sampling, directed sampling) to determine fine-scale habitat and environmental affinities within specific areas has been a priority for researchers and managers in recent years (NMFS 2009*a*). The objective of the present ongoing, collaborative study is to quantify aspects of the biology and ecology of juvenile sawfish (e.g. timing of parturition, abiotic affinities) over long-term time scales in the Charlotte Harbor estuarine system, one of only two areas of USA federally designated critical habitat for juvenile *P. pectinata* (NMFS 2009*b*). It is imperative that detailed information on sawfish habitat use be obtained if assessments are to be made regarding habitat protection and population recovery. Specifically, the present study tested the following two null hypotheses: (1) juvenile *P. pectinata* are not affected by abiotic variables within the Charlotte Harbor estuarine system, and (2) juvenile *P. pectinata* do not use specific habitats within the Charlotte Harbor estuarine system.

Materials and methods

Study area

One of the largest estuaries in Florida, the 56-km-long, 700-km^2 Charlotte Harbor estuarine system (Hammett 1990), is a recognised nursery for *P. pectinata* (Seitz and Poulakis 2002). Juveniles occur most frequently in the following two areas of Charlotte Harbor: (1) the mouths of the Peace and Myakka rivers in the northern portion of the system (upper harbor) and (2) the Caloosahatchee River, in the southern portion of the system (Seitz and Poulakis 2002; Fig. 1). In the northern portion of the system, two undammed rivers flow through the cities of Port Charlotte and Punta Gorda (Stoker *et al*. 1989; Hammett 1992). The Caloosahatchee River is a highly altered, freshwater flow-managed estuarine area adjacent to the cities of Cape Coral and Fort Myers. Alterations include extensive canal systems in the lower portion of the river and water-control structures that the South Florida Water Management District uses to regulate freshwater flow into the estuary and manage water levels in Lake Okeechobee (Stoker 1992; Chamberlain and Doering 1998; Barnes 2005). Extensive beds of the waterplant *Vallisneria americana* were present in the river before 2000, but beds of this and other waterplants (e.g. *Halodule wrightii*, *Thalassia testudinum*) have been largely absent from the river during the past decade because of high salinities during extended drought conditions as well as periods of low light availability that are intolerable to these species (Hunt and Doering 2005; P. Doering, pers. comm.).

Tidal water exchange occurs between the estuary and the Gulf of Mexico through Boca Grande Pass (direct exchange with Charlotte Harbor proper), the mouth of San Carlos Bay (direct exchange with the mouth of the Caloosahatchee River), and four smaller inlets. The climate of the study area is subtropical, with distinct wet (June–November) and dry (December–May) seasons. Air temperatures range from a mean of 27°C during the summer wet season to ~15°C in December and January (annual mean = 22°C; frosts occasionally occur). Mean annual rainfall is ~1270 mm, half of which occurs from June to September in localised thunder-showers (Stoker 1986; Hammett 1990). Rainfall during the rest of the year is usually associated with the passage of frontal systems and tends to be more broadly distributed. Tropical cyclones produce the most severe weather and have the potential to cause significant short-term effects, such as hypoxia (Stevens *et al*. 2006), and long-term effects, including the opening and closing of narrow direct connections between the ocean and the estuary through the barrier islands such as passes or inlets (Weisberg and Zheng 2006; see Fig. 1). Water temperature typically ranges from 12°C to 36°C, salinity ranges from 0 to 38.7, and dissolved oxygen values range from 1.0 mg L^{-1} to 16.7 mg L^{-1} (Poulakis *et al*. 2003).

Field sampling

From November 2004 to December 2009, two complementary sampling methods (random and directed) were used to capture and release *P. pectinata* in the Charlotte Harbor estuarine system. Some additional data collection occurred before and after this time period (e.g. neonate captures, cold kill event during January 2010) and these data were included where relevant.

Monthly random sampling (e.g. aimed at detecting long-term changes in relative abundance) was conducted year-round during the day by using a 183 × 3-m centre-bag haul seine with 38-mm stretched nylon mesh. The seine was deployed by boat in a rectangular shape along the shoreline and retrieved by hand, encompassing a bottom area of 4120 m^2. The study area was divided into 1 × 1 cartographic grids (1 nautical mile^2), and grids containing water depths between 0 and 3 m were selected as the sampling universe. This sampling area was then subdivided into sections to facilitate sampling logistics and to ensure broad coverage of the estuary. Grids to be sampled

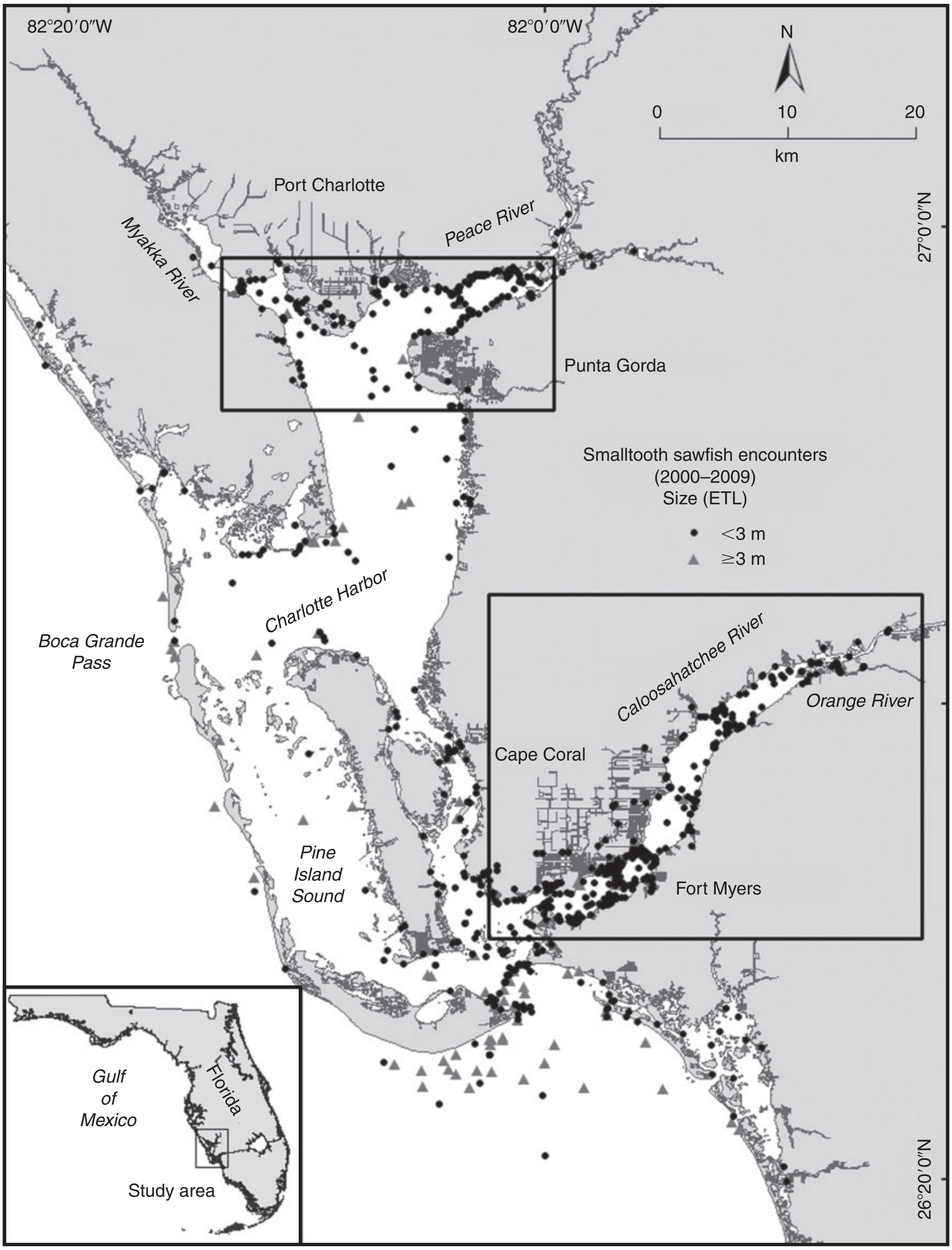

Fig. 1. Map of *Pristis pectinata* encounters reported by the public, 2000–2009. Dots represent sawfish <3 m estimated total length (ETL; $n = 1097$; mostly juveniles); triangles represent sawfish ≥3 m ($n = 99$; adults that are thought to enter the estuary only occasionally, primarily for parturition). Data are from the National Sawfish Encounter Database and update the information in Seitz and Poulakis (2002) that first identified these nursery areas. Scientific sampling was concentrated in the boxed areas because the majority of juvenile reports originated there. Lake Okeechobee is the largest natural lake in Florida and is located to the east of the map area (see inset). San Carlos Bay is located at the south-western corner of the Caloosahatchee River boxed area.

during each month were randomly selected from within each section. Each selected grid was then subdivided into microgrids by using a 10×10 cell overlay, and sample sites were randomly selected from these microgrids (i.e. microgrids represented sample sites). In total, 31 hauls per month were conducted throughout the estuarine system, including eight in the lower Caloosahatchee River, where the public has reported seeing and catching sawfish (Seitz and Poulakis 2002; Fig. 1).

Monthly directed sampling (targeting *P. pectinata*) was conducted year-round by using several types of gear, often targeting areas in which sawfish had been recently encountered by the public. Two to three directed sampling trips were conducted per month, primarily in the Caloosahatchee River. Gill-nets were the primary sampling gear for directed sampling, although other types of gear were used depending on location, habitat, and season to increase the likelihood of capturing the endangered *P. pectinata*. Sampling gear included the 183-m haul seines previously described; 45-m (50-yard), 91-m (100-yard), and 183-m (200-yard) gill-nets, all with 152-mm (6-in) stretched monofilament mesh; and a 762-m (2500-ft) nylon longline, with 227-kg (500-lb) monofilament gangions and as many as 50 15/0 non-offset circle hooks baited with striped mullet (*Mugil cephalus*). Gill-nets typically soaked for 1 h and were set primarily in creeks, canals, and embayments where haul seines would have been less effective. When the water was turbid, gill-nets were deployed and checked when fishes of any type were seen in the net or every 0.5 h, whichever came first. When water temperatures exceeded 30°C, gill-nets were checked every 20 min as a precautionary measure and to comply with our research permit. When the water was clear, we actively searched for sawfish and used both gill-nets and seines to catch sawfish that we could see. Longlines were fished for 1 h in the deepest portions of the study area, but were not used extensively because juveniles were being targeted.

Because the present study was conducted as a part of, and in conjunction with, the State of Florida's ongoing fisheries-independent monitoring program, all fish caught were processed according to standard protocols (see Casey *et al*. 2007), in addition to detailed data collection specifically for *P. pectinata*. This approach allowed staff to characterise both the biological and physical settings in which sawfish were found, while also monitoring populations of various economically important fish and invertebrate species which may be important prey for *P. pectinata* in this estuarine system. Accordingly, all fish and selected invertebrate species (e.g. blue crab, stone crab, penaeid shrimp, horseshoe crab) were identified to the lowest practical taxon, sexed (if possible externally), counted, and released alive. If necessary, a random subset of these species (20–40 specimens per sample) were measured to the nearest millimetre (sharks: precaudal length; rays: disc width; teleosts: standard length; crabs: carapace width; penaeid shrimp: postorbital head length). Detailed morphometrics and meristics were recorded for *P. pectinata* (e.g. stretched total length (STL; used for lengths in the present paper), rostrum length, rostral tooth count per side, rostral tooth length, disc width, and outer clasper length for males). Clasper length and clasper calcification are useful for determining maturity in males. Sawfish were assessed for overall health (e.g. external surface condition, broken rostral teeth), and a fin clip was taken for DNA analysis (e.g. Feldheim *et al*. 2010). Photographs and video were used to document the health of the sawfish as well as the normal tagging, handling, and release procedures.

Captured *P. pectinata* were tagged with a variety of tag types and released at or near the site of capture. Passive integrated transponder (PIT; 12-mm 134.2-kHz Super Tag II; Biomark®, Boise, Idaho, USA) tags were injected beneath the skin on the left side at the base of the first dorsal fin. These tags contain a microchip that can be detected and its unique number identified by an electronic reader carried by researchers. The advantage of PIT tags is that they should remain with the sawfish for life. Brightly coloured rototags (Dalton®, Henley on Thames, UK) printed with tagging hotline information on one side and a unique tag number on the other, were attached to the first dorsal fin. Anglers who encountered these tags could call the hotline and report their catch and location information. Most *P. pectinata* were also tagged on the second dorsal fin with another rototag to which an acoustic tag had been attached with a cable tie and covered with epoxy (see movement results in Simpfendorfer *et al*. 2010, 2011). Acoustic tags were attached externally to comply with our research permits.

The following physicochemical and habitat variables were recorded with each sample: water depth along the gear and at the bag of the net (if applicable), water temperature (°C), dissolved oxygen (mg L^{-1}), salinity (values are unitless on the basis of the Practical Salinity Scale of 1978), observations of shoreline inundation, tide level, and shoreline and bottom vegetation (presence/absence, type, and % coverage). Values for physicochemical variables were calculated by averaging the surface and bottom values for each sample.

Data analysis

Lengths and locations of *P. pectinata* captured during all sampling were plotted and combined with logistic regression and habitat suitability curves to analyse catch data and address null hypotheses (see detailed descriptions of each analysis below). Monthly length frequencies were presented with two and three size classes because of the rapid growth rates of juveniles and specific management needs. Age was estimated and presented by size class as follows: $\leq$1.5-m STL = $<$1-year old, $>$1.5-m STL = $>$1-year old, following Simpfendorfer *et al*. (2008). Juveniles were also assigned to size classes defined in the USA government's (NOAA Fisheries) Smalltooth Sawfish Recovery Plan (NMFS 2009*a*), as follows: $<$1-m STL = very small juvenile, 1–2-m STL = small juvenile, and $>$2-m STL = large juvenile. All *P. pectinata* $>$2 m (up to 2.2 m) captured during the study were still juveniles according to known life-history data and observed clasper sizes and lack of calcification (Simpfendorfer *et al*. 2008). Size at maturity for females is unknown; however, if they follow the pattern exhibited by most elasmobranchs, they mature when larger than males (Simpfendorfer *et al*. 2008). Only data from directed sampling was used in the logistic regression and habitat suitability analyses because directed sampling was most likely to catch a sawfish; however, random sampling and encounter data from the public complemented the directed sampling and supported conclusions drawn from the overall analysis (e.g. hotspots).

Logistic regression was used to determine the factors that influenced the probability of catching at least one *P. pectinata* in a sample. Full models were constructed for (1) all sawfish captured, (2) sawfish <1 year old, and (3) sawfish >1 year old; each model included four environmental variables and their interactions (maximum water depth, water temperature, dissolved oxygen, salinity), year, month, and gear type, as well as three shoreline habitat variables (overhanging vegetation, seawall and/or riprap (artificial shorelines), non-overhanging vegetation) and was simplified by using a stepwise elimination procedure. To refine the logistic regression models, non-significant ($P > 0.05$) variables were removed one at a time, in the order of decreasing *P*-value and the regressions were run again until only significant variables remained. Although recorded, bottom type and bottom vegetation were not included in the models because most of the samples occurred over unvegetated sand and/or mud bottoms. The overhanging vegetation category was represented mostly by native red mangroves (*Rhizophora mangle*) and included non-native Brazilian pepper trees (*Schinus terebinthifolius*). The non-overhanging vegetation category included beaches and open water.

Habitat suitability curves were constructed to explain regression model results and to characterise patterns of habitat selection along four gradients of environmental variability related to maximum water depth, water temperature, dissolved oxygen, and salinity. An electivity index (*E*) was calculated for each variable to investigate whether *P. pectinata* exhibited affinity or avoidance responses, as follows:

$$E = (r_i - p_i)/(r_i + p_i),$$

where r_i is the proportion of samples in which the species was caught in environmental variable *i*, and p_i is the proportion of environmental variable *i* in all samples (Ivlev 1961; Wiley and Simpfendorfer 2007). The electivity index ranges from -1 to 1; negative values indicate avoidance, 0 is neutral, and positive values indicate affinity. Data for each variable were divided into equal intervals and interval ranges were chosen to produce the smoothest curves. An advantage of these curves is that they take into account non-uniform (i.e. directed or non-random) sampling across environmental gradients.

Results

In total, 137 juvenile *P. pectinata* were captured and released (20 during random sampling and 117 during directed sampling), including 27 recaptures. Most samples contained one or two individuals, although some samples contained as many as seven. Also, as many as 14 sawfish, not including recaptures, were caught at one location in a relatively short period (3 months). STL ranged from 671 to 2172 mm (mean = 1248 mm) for all sawfish combined, from 671 to 2160 mm (mean = 1218 mm) for males, and from 690 to 2172 mm (mean = 1271 mm) for females (Fig. 2). Sawfish were captured in all months, and were most commonly captured between February and September (Fig. 3). Captures of the smallest juveniles (<1 m), including neonates with embryonic rostral sheaths in November, March, and April, allowed us to refine the size range at birth (671–812 mm) and document protracted timing of parturition (November–July). Complete or partial rostral sheaths are a good indicator of recent birth because tag–recapture data showed that the sheath disappeared in less than 2 weeks. Only four *P. pectinata* were captured with portions of the sheath because it disappeared so quickly; however, on the basis of known growth rates (Simpfendorfer *et al*. 2008) and captures of individuals <900 mm, the peak period for parturition was April and May. The probability of catching a sawfish was 1.4% in the random sampling ($n = 496$ sets) in the mouth of the Caloosahatchee River and 14.6% in directed sampling with primarily gill-nets ($n = 459$ sets) throughout the nursery areas.

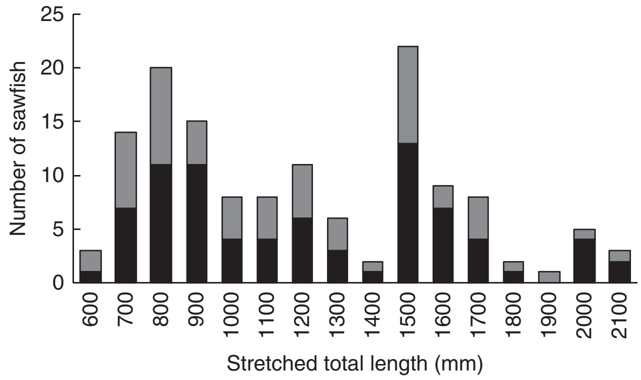

Fig. 2. Length-frequency of juvenile *Pristis pectinata* ($n = 137$) collected during the study, including recaptures. Females are shown in black ($n = 79$) and males are shown in grey ($n = 58$).

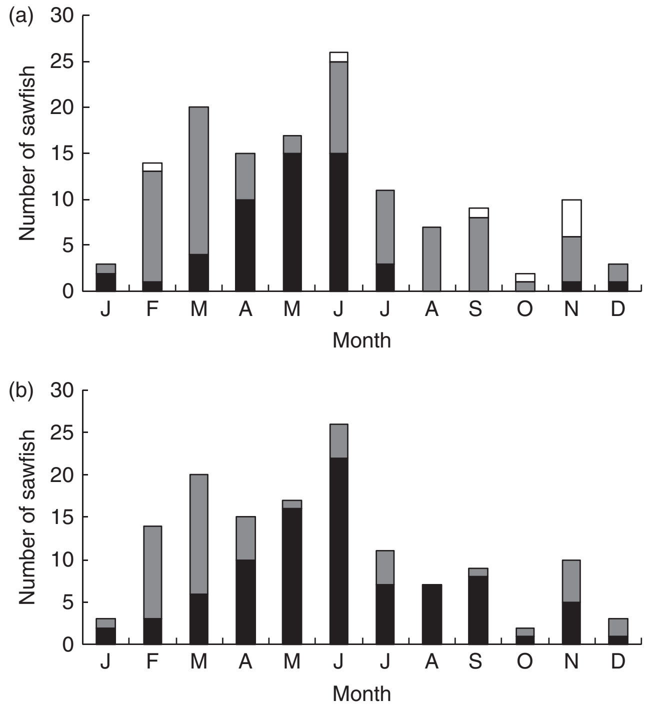

Fig. 3. Monthly length frequencies of *Pristis pectinata* ($n = 137$) collected during the study. (*a*) Size classes correspond to the USA government's (NOAA Fisheries) Smalltooth Sawfish Recovery Plan (NMFS 2009*a*), in which sawfish <1-m stretched total length (STL) are very small juveniles (black), those 1–2-m STL are small juveniles (grey), and those >2-m (up to 2.2-m) STL are large juveniles (white). This presentation shows the protracted period during which neonates entered the nursery. (*b*) Size classes correspond to ontogeny on the basis of estimated growth rates (Simpfendorfer *et al*. 2008) used in data analyses, in which ≤1.5-m STL is <1-year old (black) and >1.5-m STL is >1-year old (grey). Both graphs contain the same data, including recaptures.

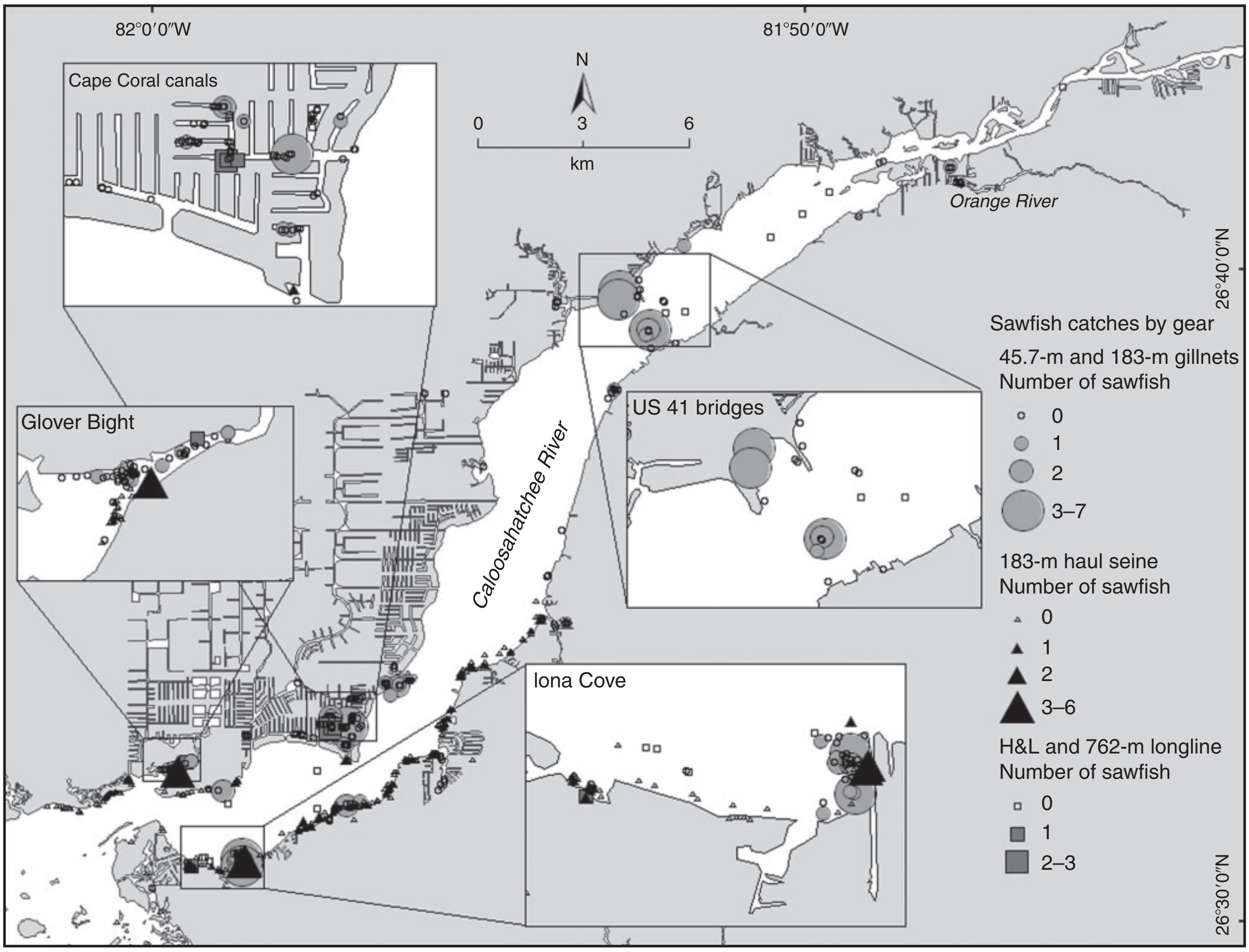

Fig. 4. *Pristis pectinata* research sampling and capture sites in the Caloosahatchee River during the study (see Fig. 1). Major sites (i.e. hotspots) where sawfish were captured, tagged, and released are shown in the insets. H&L = hook and line.

Most *P. pectinata* ($n = 100$; 70%) were captured in the Caloosahatchee River, and the remainder were captured in the upper harbor near the mouths of the Myakka and Peace rivers – the three major freshwater inputs to the Charlotte Harbor estuarine system (Fig. 1). Although extensive random sampling was conducted throughout the system (1778 samples; includes the entire estuarine area in Fig. 1), sawfish captures from all sampling techniques occurred primarily in the following five areas: Iona Cove, Glover Bight, Cape Coral canals, near the US 41 bridges in the Caloosahatchee River, and the Harborview area in the Peace River (Figs 4, 5). Because of relatively high intra- and inter-annual capture rates, these areas are referred to as hotspots. In general, there was more rainfall early in the study (2005–2006) and drought later in the study (2007–2009). These conditions affected the distribution of sawfish in the Caloosahatchee River (Fig. 6). For example, the hotspot near the US 41 bridges was not identified until the 2007 drought.

Pristis pectinata were captured in a wide range of physicochemical and habitat conditions (Table 1). The logistic regression models identified various combinations of water depth, water temperature, dissolved oxygen, and salinity as influencing the probability of catching a sawfish (Table 2). Thus, environmental electivity indices were examined and showed that, in general, juvenile *P. pectinata* (both size classes combined) had an affinity for water <1 m deep, water >30°C, moderate to high dissolved oxygen concentrations ($>6\,\text{mg}\,\text{L}^{-1}$), and salinities of 18–30; sawfish avoided water <18°C, dissolved oxygen $<6\,\text{mg}\,\text{L}^{-1}$, and salinity >30 (Fig. 7). Electivity indices for all sawfish and only individuals <1 year old tracked closely for all variables, whereas individuals >1 year old avoided water <0.5 m deep. The first mode (salinities of 3.1–9.0) of the bimodal salinity electivity curve was the result of several sawfish captured near the mouth of the Caloosahatchee River during low-salinity (strong freshwater-flow) periods. The habitat variable (overhanging vegetation/artificial shorelines/non-overhanging) was significant for sawfish >1 year old because of higher catch rates of this size class in samples associated with overhanging shoreline vegetation such as red mangroves (Fig. 8). Month was also significant in the model for the larger size class because of larger catches during February and March (Fig. 3).

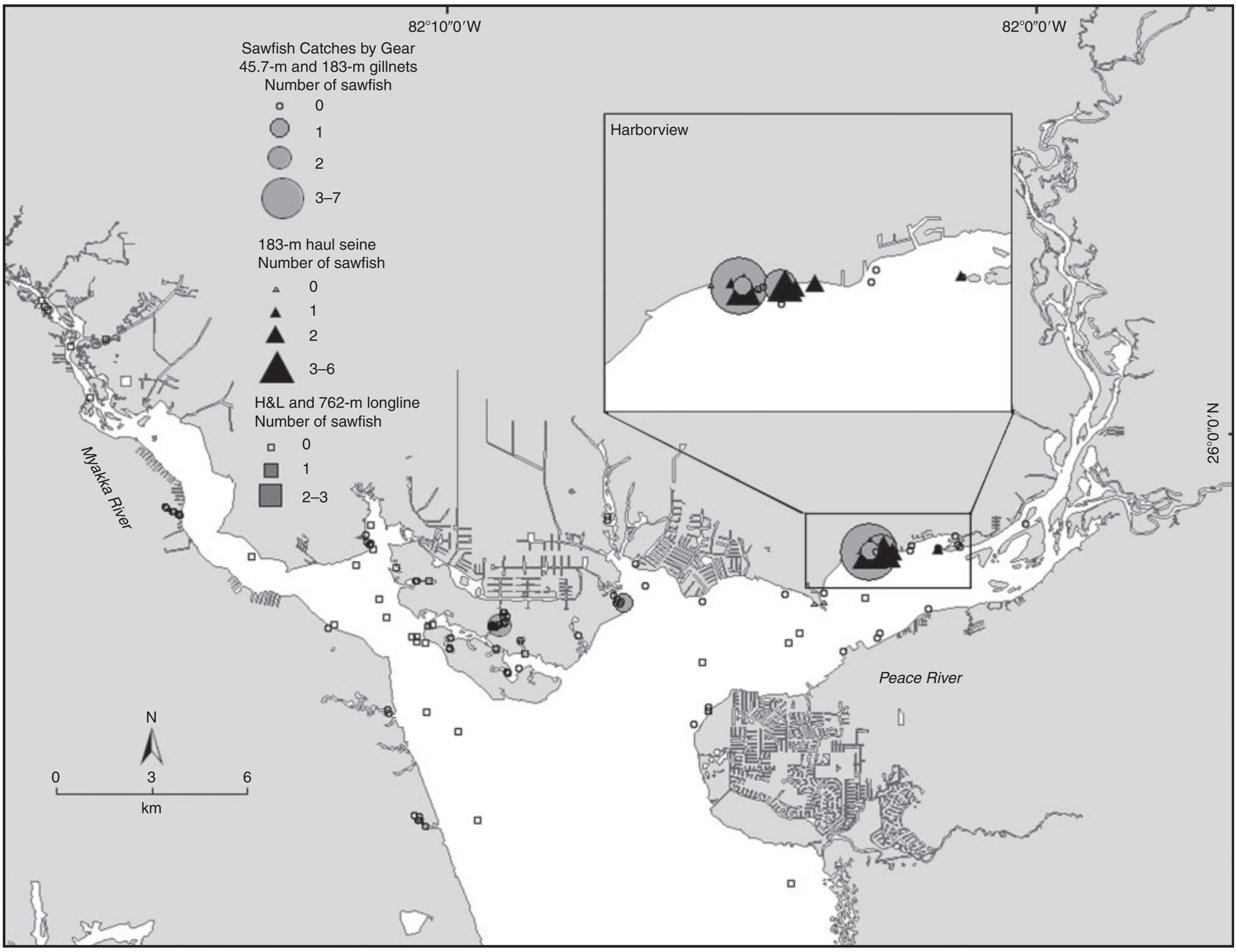

Fig. 5. *Pristis pectinata* research sampling and capture sites in the upper harbor during the study (see Fig. 1). The major site (i.e. hotspot) where sawfish were captured, tagged, and released in the Peace River is shown in the inset. H&L = hook and line.

Over the entire 5-year study, only two *P. pectinata* mortalities were reported by the public: one in our study area (17 June 2009, Caloosahatchee River, 1877 mm) and one in south Florida (20 April 2009, Florida Bay, 4327 mm); necropsies revealed no obvious causes of death. However, in January 2010, water temperatures across Florida decreased substantially following the passage of multiple cold fronts. For example, water temperatures in the Peace River fell to 8°C, stayed below 12°C for 3 days, and below 15°C for 13 days. At least 15 juveniles and one adult *P. pectinata* were found dead across Florida during this time. Cold water temperatures certainly caused the death of these sawfish and some individuals of other fish species (e.g. common snook, *Centropomus undecimalis*) known to be sensitive to these conditions.

Discussion

Spatial considerations within the nursery: the hotspot concept

Heupel *et al*. (2007) defined nursery areas for sharks and their relatives by using the following three criteria: (1) juveniles are more commonly encountered in the area when compared with other areas, (2) juveniles have a tendency to remain for extended periods, and (3) the area or habitat is used by juveniles repeatedly across years. Using this definition and applying multiple lines of evidence, including the data presented in the current paper, the tidal reaches of the Caloosahatchee River and upper Charlotte Harbor, including the Peace River, qualify as nursery areas for *P. pectinata*. The following two distinct lines of evidence support Criterion 1: first, we sampled extensively throughout the Charlotte Harbor estuarine system (from >1700 randomly selected sites) and caught juvenile *P. pectinata* only in the vicinity of the river mouths; and second, most encounters reported by the public were in the same areas (Fig. 1). Support for Criterion 2 comes from recapture and acoustic data that have shown that juveniles remain in the vicinity of the river mouths continuously for several months to more than a year (Simpfendorfer *et al*. 2011). For example, even with the external tag-attachment method (lower retention time compared with internal placement), data from acoustic monitoring showed that juveniles remain in the study area for as long as 473 days (Simpfendorfer *et al*. 2011). Support for Criterion 3 comes from

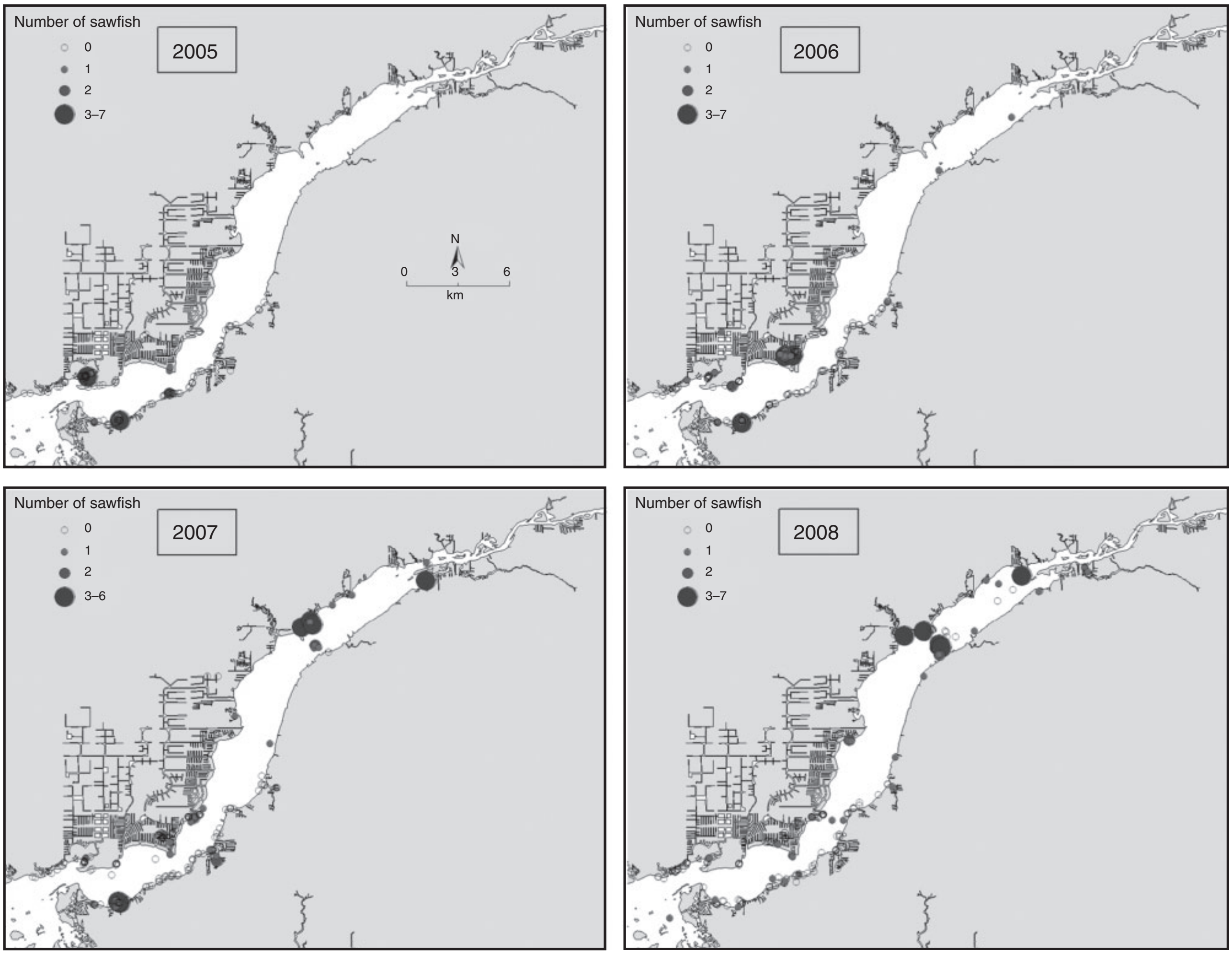

Fig. 6. All *Pristis pectinata* sampling and capture sites, including encounter reports from the public, in the Caloosahatchee River, 2005–2008. The centre of *P. pectinata* abundance was farther downriver in 2005 and 2006 (wet years) and farther upriver in 2007 and 2008 (drought years).

Table 1. Summary of mean ± s.e. (range in parentheses) water depth and physicochemical variables (mean of surface and bottom) during *Pristis pectinata* sampling

Variable	All directed sets	Sets with sawfish	Sawfish ≤1.5 m (<1-year old)	Sawfish >1.5 m (>1-year old)
Maximum water depth (m)	1.6 ± 0.04 (0.1–6.3)	1.2 ± 0.08 (0.1–2.9)	1.2 ± 0.10 (0.1–2.9)	1.1 ± 0.10 (0.4–2.4)
Water temperature (°C)	26.5 ± 0.20 (11.6–33.7)	26.9 ± 0.53 (18.2–33.7)	27.3 ± 0.61 (18.2–33.7)	26.5 ± 0.74 (18.2–33.6)
Dissolved oxygen (mg L^{-1})	6.6 ± 0.08 (1.4–13.5)	7.5 ± 0.22 (4.2–13.5)	7.4 ± 0.26 (4.2–13.5)	7.9 ± 0.26 (5.0–10.9)
Salinity	17.9 ± 0.44 (0.1–37.3)	19.7 ± 1.03 (0.3–32.6)	18.5 ± 1.23 (0.3–32.6)	21.8 ± 1.29 (6.7–30.6)

reports of consistent encounters with juveniles every year for more than a decade (Seitz and Poulakis 2002; Poulakis and Seitz 2004; Wiley and Simpfendorfer 2010).

Within the broader nursery area, as defined by Heupel *et al.* (2007), it is apparent that specific hotspots or microhabitats are disproportionally more important to juvenile *P. pectinata* in certain years or across multiple years. For example, in the present study, Glover Bight and Iona Cove, located near the mouth of the Caloosahatchee River, were hotspots primarily during periods of low salinity (high rainfall, freshwater releases out of Lake Okeechobee); habitats much farther upriver (~20 km) near the US 41 bridges (Figs 4, 6), in contrast, became important primarily during periods of high salinity (the dry season and droughts). Unexpectedly, during one year, even a seawall canal system was a hotspot. Thus, dynamic conditions and all available habitats used by juvenile *P. pectinata* during their nursery residency, including heavily developed areas such as those around the Caloosahatchee River, must be considered when gauging natural and anthropogenic effects (Sklar and Browder 1998). Tag–recapture data revealed that individual

Table 2. Summary of significant ($P < 0.05$) factors from the logistic regression models for predicting the probability of capturing at least one *Pristis pectinata* in a sample

Factor	d.f.	Wald χ^2	P
All sawfish (Wald $\chi^2 = 53.2$, $P < 0.0001$, $R^2 = 0.16$, d.f. = 7)			
Temperature	1	14.7	0.0001
Maximum water depth	1	11.2	0.0008
Dissolved oxygen	1	8.7	0.0032
Dissolved oxygen × salinity	1	10.0	0.0016
Water depth × temperature	1	7.8	0.0051
Water depth × dissolved oxygen	1	7.4	0.0065
Water depth × salinity	1	4.5	0.0344
Sawfish ≤1.5 m (<1-year old) (Wald $\chi^2 = 29.7$, $P < 0.0001$, $R^2 = 0.07$, d.f. = 3)			
Dissolved oxygen	1	23.3	<0.0001
Temperature	1	5.9	0.0165
Water depth × dissolved oxygen	1	12.5	0.0004
Sawfish >1.5 m (>1-year old) (Wald $\chi^2 = 34.4$, $P < 0.0001$, $R^2 = 0.12$, d.f. = 6)			
Maximum water depth	1	23.1	<0.0001
Temperature	1	8.3	0.0040
Habitat	1	4.6	0.0311
Month	1	4.3	0.0377
Water depth × dissolved oxygen	1	19.2	<0.0001
Water depth × salinity	1	8.5	0.0035

sawfish were captured in multiple hotspots and were present in most hotspots during a variety of freshwater flow conditions (wet season or dry season). This implies that habitat use by juvenile *P. pectinata* is probably influenced by a variety of physical conditions other than salinity, including temperature, dissolved oxygen, water depth, and shoreline vegetation. Further, on the basis of documented fast growth rates during the nursery residency (Simpfendorfer *et al.* 2008), food availability and successful acquisition of the food (e.g. shallow water may increase feeding success) probably also play primary roles in microhabitat selection. Determining why specific sites within a nursery (i.e. hotspots) are used regularly by *P. pectinata* will be an important part of the long-term assessment of habitat use in the federally designated critical habitat areas.

Abiotic effects, ontogenetic effects, and fitness

A common basic theme in fish biology is that fishes have fast growth rates during their early life histories and slower growth rates as adults (e.g. Jones 2002). Elasmobranch fishes tend to have slower growth rates when compared with teleost fishes, although exceptions exist and many endogenous (e.g. genetics) and exogenous (e.g. food, abiotic variables) factors affect individual species and populations (Cortés 2004). Temperature and food availability are the two environmental factors that have the greatest influence on growth and survival (Jones 2002) and as such, these factors are likely to be major influences on habitat use. Juvenile *P. pectinata* had an affinity for warm water and water with high dissolved oxygen concentrations; these conditions probably promote fast early growth rates (juveniles double in size during their first year) and rapid metabolism (Simpfendorfer *et al.* 2008). The juvenile growth model with the best representation of seasonal growth, although subtle, indicated that growth was fastest from June to September (Simpfendorfer *et al.* 2008), which corresponds to the warmest time of the year. Neonate *P. pectinata* are born primarily in the spring (April–May) when water temperatures are increasing and temperatures potentially remain above 30°C (the important threshold identified by the electivity analysis in the present study) during the day at least through September. Sawfishes are not obligate ram ventilators (i.e. they do not have to constantly move forward to get oxygen to their gills) and *P. pectinata* were captured in waters with a broad range of dissolved oxygen values, although this species may decrease its activity and metabolic rates when dissolved oxygen concentrations are low (Carlson and Parsons 2001). Dissolved oxygen concentrations are often correlated with water temperature, and juvenile *P. pectinata* may move within the nursery to reside in areas with adequate food resources and favourable environmental conditions that maximise growth during their nursery residency (~3 years).

Extreme low water temperature or low dissolved oxygen events can have acute effects on *P. pectinata*. Unlike juvenile cownose rays (*Rhinoptera bonasus*) and sandbar sharks (*Carcharhinus plumbeus*), which must migrate out of temperate nurseries like Chesapeake Bay with the onset of winter (Smith and Merriner 1987; Grubbs 2010), *P. pectinata* remain in their subtropical nurseries year-round (Seitz and Poulakis 2002; Simpfendorfer *et al.* 2011; the present study). Residency in shallow subtropical nurseries has the advantage of reduced predation risk; however, it leaves juveniles susceptible to periods of decreased water temperatures following the passage of strong cold fronts. On the basis of data collected during January 2010, 8–12°C approximates the lower lethal temperature for *P. pectinata* in Florida, depending on water depth and exposure time. The mortalities (at least 15, probably more) across southern

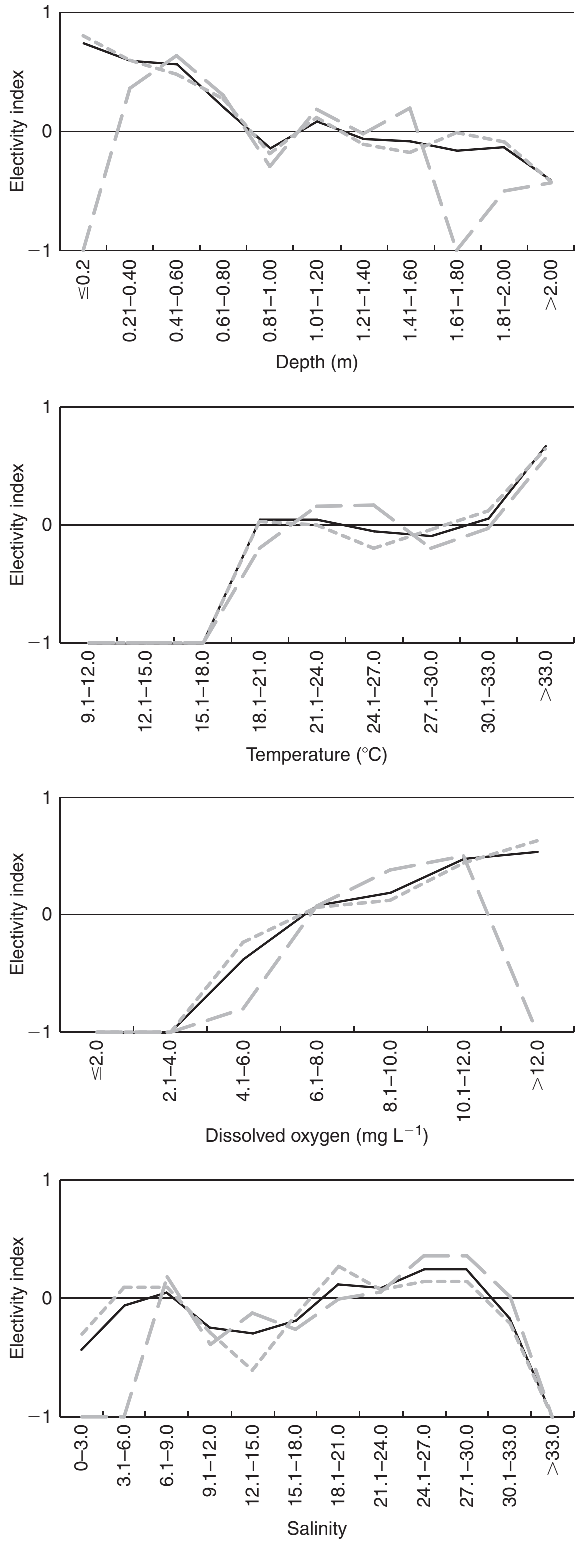

Fig. 7. *Pristis pectinata* electivity indices for water depth (m), water temperature (°C), dissolved oxygen (mg L^{-1}) and salinity. The black line indicates all sawfish combined, the small dotted line indicates sawfish <1 year old, and the large dotted line indicates sawfish >1 year old. Negative values indicate avoidance, 0 is neutral, and positive values indicate affinity.

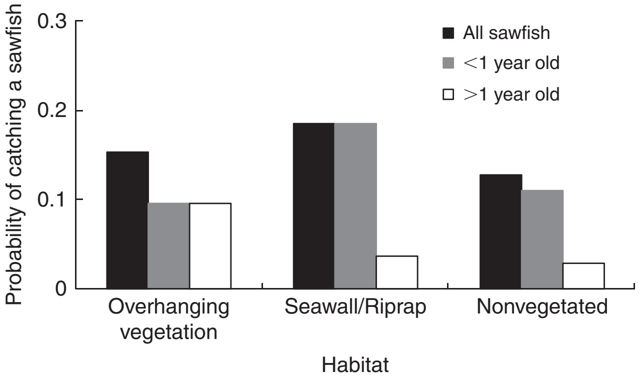

Fig. 8. Probability of catching *Pristis pectinata* in different habitat types. Overhanging vegetation includes red mangroves and Brazilian pepper; non-vegetated habitats include beaches and open water. Habitat was significant in the logistic regression model for sawfish >1 year old, suggesting that larger sawfish are more abundant along shorelines with overhanging vegetation.

Florida during this period highlighted the long-term and range-wide threat of cold weather to *P. pectinata* populations and recovery. Hotspots such as Glover Bight that include access to deeper water (>2 m, more stable temperatures) and shallow creeks or flats that warm up during the day may provide thermal refuges to juvenile *P. pectinata* (especially neonates born early between November and February) during cold weather because large numbers of individuals (at least 12) have been observed there when temperatures approached 12°C (G. R. Poulakis, pers. obs.). Further, these temperatures probably influenced the historical range of the species and may have prompted southerly movements by larger individuals that Bigelow and Schroeder (1953) reported from higher latitudes (North Carolina to New York) during the summer. Periodic midsummer hypoxia in the nursery or aperiodic hypoxia after the passage of tropical weather systems (Stevens *et al.* 2006; Turner *et al.* 2006; Heithaus *et al.* 2009) could also cause mortality and delay recovery.

Rapid early growth of *P. pectinata* maximises juvenile survival and contributed to observed ontogenetic differences in habitat use (Simpfendorfer *et al.* 2008, 2010). The smallest, youngest (<1-year old) juvenile *P. pectinata* tended to occur in shallower water than did the larger, older (>1-year old) juveniles. Similarly, Whitty *et al.* (2009) studied juvenile freshwater sawfish (*Pristis microdon*) in a riverine environment with passive acoustic telemetry, and observed more individuals <1 year old in shallower water (<0.6 m) than individuals >1 year old. This ontogenetic difference reflected variations between the size classes in movement between sections of the river separated by shallow runs during the dry season. Whitty *et al.* (2009) suggested that avoidance of predators by the <1 year old *P. microdon* is a likely explanation that this age class remains in shallow water. This interpretation was supported during the present study by direct observation of neonate *P. pectinata* in water <0.1 m deep among red mangrove prop roots when a shark was seen feeding nearby (G. R. Poulakis, pers. obs.). Simpfendorfer *et al.* (2010) also observed small juvenile sawfish among red mangrove prop roots in two cases to the south of our study area. Indirect support comes from depth-recording acoustic tags that showed the presence of sharks in deeper water of the study area during the day (Heupel *et al*. 2010).

Juvenile *P. pectinata* were more often associated with higher salinities than were other elasmobranchs found in the system (Simpfendorfer *et al*. 2005; Collins *et al*. 2008) and they also exhibited a propensity for remaining in nursery areas when salinities decreased. Simpfendorfer *et al*. (2011) reported a slightly narrower salinity-affinity range for juveniles within the system; however, this range was primarily based on an extended low-salinity period (2005–2006), whereas the salinity affinity range of 18–30 reported here included both low-salinity and high-salinity periods (wet and dry years, 2005–2009). The first mode (salinities of 3.1–9.0) of the bimodal salinity electivity curve in the present study was the result of several individuals captured near the mouth of the Caloosahatchee River during periods of low salinity caused by increased freshwater flow (see Simpfendorfer *et al*. 2011). Thus, the water conditions observed during the capture of these sawfish probably does not reflect an affinity for low salinity, but rather tolerance, because they remained in the river rather than egressing to the open bay to find higher salinities. This single observation probably explains the relatively minor contribution of salinity to the logistic regression models. The reluctance of sawfish to leave the Caloosahatchee River despite low salinities (supported by acoustic monitoring data; Simpfendorfer *et al*. 2011) may have important implications for long-term *P. pectinata* population fitness and species management because at least two year classes are vulnerable to increases in the energetic cost of osmoregulation, changes in prey availability, changes in predation pressure, and localised disturbances (e.g. cold temperatures, harmful algal blooms, hypoxia).

Predation on juvenile *P. pectinata* appears to be low over a broad range of salinities. Predation risk may not increase during periods of decreased salinity when *P. pectinata* are concentrated at the mouth of the river, because bull sharks (*Carcharhinus leucas*), the primary potential predator of juvenile sawfish caught during our sampling in the system, move out of the river during periods of high freshwater flow with no time lag (Heupel and Simpfendorfer 2008). In addition, juvenile bull sharks were most commonly caught in salinities between 7 and 17.5 in our study area (Simpfendorfer *et al*. 2005), whereas juvenile *P. pectinata* were more often associated with higher salinities (18–30). Other predators may enter the river during high-salinity periods (e.g. lemon shark, *Negaprion brevirostris*) or low-salinity periods (American alligator, *Alligator mississippiensis*); however, evidence of possible attacks on sawfish from the catch data do not exist (e.g. large jaw-shaped wounds). Collectively, these differences may be related to selection pressure to minimise interactions between these top predators (e.g. competition, predation). Research on *P. pectinata* and their potential predators is needed in other rivers and estuaries to determine whether similar growth rates and nursery site specificity (use of hotspots) are observed on a broad scale, especially during periods of decreased salinity. These comparisons may lead to site-specific management considerations.

Management

Communication between scientists and the public has been vital to the success of *P. pectinata* research in the United States. Early use of sawfish encounter data from the public included identification of the current range and location of nursery areas in Florida as well as anthropogenic effects on this endangered species (e.g. Seitz and Poulakis 2002; Seitz and Poulakis 2006). In the present study, continued collection of these encounter data translated directly into tagging events because we sometimes focussed our sampling in areas with recent sightings (within days or even hours). The combination of random sampling (almost 2000 samples estuary-wide, sawfish that were captured in these samples were in or near hotspots), directed sampling, and encounter reports from the public was valuable for identifying abiotic affinities, corroborating nursery hotspots, and providing information on the status of the species to the public. Publicly derived data also contributed greatly to the official designation of two broad critical-habitat areas for juvenile *P. pectinata* (NMFS 2009*b*). Long-term continuation of this public–scientist–management relationship is crucial, given the extended recovery time that is projected for this species (~100 years; NMFS 2009*a*). Similar databases could be developed and maintained for *P. pectinata* (in the eastern and south-western Atlantic) and for other highly recognisable fishes such as sawfish species in other parts of the world.

Understanding patterns of habitat use by a species is important for understanding population dynamics, intra- and interspecific interactions (e.g. competition, predation), and healthy ecosystem structure (Morris 2003). Although ontogenetic shifts in habitat use (change in niche during growth) are common in fishes, they tend to be more subtle in chondrichthyans than in teleosts because of differences in reproductive strategies (Grubbs 2010). Changes in habitat selection and use within nurseries have been linked to feeding as well as the risk of predation and involve many aspects of development and behaviour (e.g. prey selection, metabolism; Heithaus 2007). The present study has provided evidence that improves our understanding of habitat use by juvenile *P. pectinata*. Testing our two null hypotheses revealed juvenile abiotic affinities as well as ontogenetic shifts in habitat use associated with water depth and shoreline vegetation between juveniles $<$1 year old and those $>$1 year old. Similar observations were noted by Whitty *et al*. (2009) for *P. microdon*, which has a similar life-history strategy. These data may also be useful for management of the dwarf sawfish, *Pristis clavata*, because it uses both estuarine and marine habitats (Last and Stevens 1994).

Future research should determine the generality of these findings on a variety of spatial scales because populations of the same species can live in different environments and vary in their habitat preferences (Morris 2003). Investigation of dietary links by using stable isotope studies may help explain the ontogenetic habitat shifts observed in sawfishes that have been studied because size-specific shifts in food types are common (Werner and Gilliam 1984). For species that use riverine and estuarine habitats, analysis of acoustic monitoring and abiotic data collected during a variety of freshwater flow regimes could provide further insight into the reasons for these shifts (e.g. temporal lags, rate of salinity change). Further, knowing whether juvenile *P. pectinata* are behaving similarly in multiple nurseries with different geomorphologies and hydrologic conditions is vital for successful protection and management of the species. For example, understanding how *P. pectinata* fits into the conceptual ecological models being developed for Charlotte Harbor and the Ten Thousand Islands–Everglades regions (e.g. Barnes 2005; Davis *et al*. 2005) will be important as the Comprehensive Everglades Restoration Plan is implemented over at least the next 20 years. Collectively, achieving these goals for sawfishes worldwide will ensure long-term recovery of these *Critically Endangered* species.

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