Received: 1 April 2021 | Revised: 22 November 2021 | Accepted: 8 December 2021

DOI: 10.1002/aqc.3777

RESEARCH ARTICLE

WILEY

Commercial fishery bycatch risk for large juvenile and adult smalltooth sawfish (*Pristis pectinata*) in Florida waters

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Funding information
Disney Worldwide Conservation Fund; NASA Environmental and Medical Contract, Grant/Award Number: 80KSC020D0023; National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Grant/Award Number: NA16NMF4720062; National Science Foundation Graduate Research Fellowship Program, Grant/Award Number: 1449440; NOAA Fisheries Office of Protected Resources; U.S. Department of Commerce; US Bureau of Ocean Energy Management; Disney Conservation Fund

Abstract

1. Incidental catch of marine species can create ecological and economic issues, particularly for endangered species. The smalltooth sawfish (*Pristis pectinata*) is endemic to the Atlantic Ocean and listed as Endangered in the US Endangered Species Act. One of its major threats is bycatch mortality in commercial fisheries.
2. Despite the protection afforded by the US Endangered Species Act, smalltooth sawfish are still captured as bycatch in commercial fisheries. Acoustic and satellite tag data collected on 59 sawfish between 2011 and 2019 were analysed to assess commercial fishery bycatch risk for large juveniles and adults off Florida. This study focused on shrimp trawl, south-east coastal gillnet, and shark bottom longline fisheries, as these were identified in the recovery plan as having the greatest potential threats to recovery.
3. Bycatch risk associated with the shrimp trawl fishery was significantly higher than the other fisheries, indicating that this fishery currently poses the greatest threat to recovery.
4. Bycatch risk was concentrated in all seasons in the Gulf of Mexico adjacent to the lower Florida Keys for the shrimp trawl fishery, off Cape Canaveral in the south-east coastal gillnet fishery, and in the Atlantic Ocean adjacent to the Florida Keys in the shark bottom longline fishery.
5. Tagging location and sex were predictors of bycatch risk. Individuals tagged in Charlotte Harbor had the highest shrimp trawl bycatch risk. Females tagged in

south Florida tended to reside in the deepest water, which is where shrimp trawl effort is highest. Therefore, females may be at more risk in these deeper waters.
6. Results from this study indicate a year-round closure of waters off south-west Florida to the shrimp trawl fishery between Charlotte Harbor and the western Florida Keys would reduce sawfish bycatch, and thus mortality, which is in line with recovery plan goals.

KEYWORDS
acoustic monitoring, bycatch, commercial fisheries, conservation, elasmobranch, endangered species, satellite telemetry

1 | INTRODUCTION

Bycatch is defined in the USA as the incidental capture and subsequent discard of a non-targeted species (National Oceanic and Atmospheric Administration (NOAA), 2019). Many marine animals, including sea turtles, marine mammals, invertebrates, seabirds, elasmobranchs, and teleosts, are incidentally caught in commercial fisheries (Zollett, 2009; Kroetz, Mathers & Carlson, 2020). Bycatch creates both economic and ecological issues, including damage to gear, lost income, lost time, and mortality of non-target species. This can create negative ecosystem effects through loss of top predators, removal of large biomasses of important prey taxa, and cryptic mortality of threatened species (Zollett, 2009). Bycatch is of particular conservation concern for species with low intrinsic rates of population growth and small or threatened populations (Dulvy et al., 2008; Northridge et al., 2017).

Bycatch mortality is a major threat for many protected marine species, and numerous strategies have been used to mitigate this risk (Zollett, 2009). In 1994, amendments were made to the US Marine Mammal Protection Act to mitigate the impacts of bycatch mortality on marine mammals, and these protections were successful in ensuring the continued recovery of some threatened species (Johnson et al., 2005). Farmer et al. (2016) evaluated several bycatch mitigation options to reduce entanglement risk of North Atlantic right whales (*Eubalaena glacialis*) with black sea bass (*Centropristis striata*) pot gear and ultimately found time–area closures to be a viable option to decrease bycatch mortality. Turtle exclusion devices have led to a significant decrease in bycatch of sea turtles in trawl fisheries worldwide, and there is evidence that they may also mitigate bycatch risk for other non-targeted species (Zollett, 2009).

Sawfishes are among the most endangered elasmobranch families in the world, with all five species listed as Endangered or Critically Endangered on the International Union for the Conservation of Nature Red List of Threatened Species (Dulvy et al., 2016). The smalltooth sawfish (*Pristis pectinata*) is endemic to the Atlantic Ocean, historically occupying subtropical and tropical waters on both sides of the basin. In the western Atlantic, the species inhabited waters along the east coast of the USA from Florida at least as far north as North Carolina, the entire Gulf of Mexico, the Caribbean, including The Bahamas, and as far south as Uruguay (National Marine Fisheries Service (NMFS), 2009b). Sawfishes are benthic species with long, toothed rostra, making them prone to entanglement in fishing gear, particularly gear on the bottom. Since the Industrial Revolution, the range of smalltooth sawfish has declined dramatically due to fishing, habitat loss, and overexploitation (Carlson, Wiley & Smith, 2013). The range has contracted substantially, and there are only two known viable 'lifeboat' populations remaining (Dulvy et al., 2014): one centred in south-west Florida waters (NMFS, 2009a; Norton et al., 2012; Brame et al., 2019) and the other in The Bahamas (Guttridge et al., 2015).

In Florida, the smalltooth sawfish is incidentally caught in fisheries in state and federal waters. The smalltooth sawfish was prohibited from harvest in Florida in 1992 and listed as Endangered under the US Endangered Species Act in 2003 (NMFS, 2009b). Following the US Endangered Species Act listing, a team of experts was assembled to develop a recovery plan to outline major threats to the species, as well as goals and objectives. One of the major goals was to estimate the impact of commercial fisheries on recovery and the feasibility of policy implementation to mitigate fishery threats (NMFS, 2009b). The recovery plan identified the shrimp trawl fishery as the largest source of direct mortality and biggest potential threat to recovery, followed by the south-east coastal gillnet fishery and the shark bottom longline fishery. Like other commercial fisheries, shrimp trawling is prohibited in some state of Florida waters, including Everglades National Park and the Florida Keys National Marine Sanctuary, due to habitat considerations (e.g. to protect seagrass and hardbottom habitats or limits to fishing close to the shoreline) and conflicts with other fisheries (e.g. trap fishery for stone crabs, *Menippe mercenaria*). However, shrimp trawling is currently allowed elsewhere in state and federal waters. All coastal gillnetting was banned in state waters in 1994; longlining is also prohibited in state waters, but both gears are currently allowed in federal waters.

The shrimp trawl fishery is one of the most profitable fisheries in the USA, but also accounts for a large percentage of incidental catches. According to NMFS observer data, between 1998 and 2008, trawls were towed for an average of 3.9 h, with some trawls towed as long as 12.8 h. Shrimp trawling gear is deployed at an average depth of 73 m, with some gear being deployed as deep as 540 m. Both penaeid and rock shrimp are targeted by this fishery in the Gulf of Mexico and South Atlantic (Scott-Denton et al., 2012). Harrington, Myers & Rosenberg (2005) reported that shrimp trawls accounted for nearly half of all fishery bycatch in US waters. For this reason, in 1992 the NMFS Southeast Fisheries Science Center implemented a research plan in collaboration with the Gulf and South Atlantic Fisheries Foundation to collect bycatch data from the fishery (Scott-Denton et al., 2012). However, observer coverage on shrimp trawl vessels in the USA is extremely low (1–2% coverage), so bycatch impacts are still largely unknown (Scott-Denton et al., 2012).

The south-east coastal gillnet fishery targets sharks and teleosts and uses sink, strike, and drift gillnet gear. According to NMFS observer data gathered between 1998 and 2017, approximately 71% of coastal gillnets deployed were sink, 8% were strike, and 21% were drift. Sawfish are largely benthic; thus, the sink gillnets present the biggest threat because they sit on the bottom, where sawfish reside. The south-east coastal gillnet fishery targets Spanish mackerel (*Scomberomorus maculatus*), southern kingfish (*Menticirrhus americanus*), spiny dogfish (*Squalus acanthias*), mixed teleosts, and mixed sharks. Depending on target species, nets range from 14 to 3,246 m long with stretch mesh sizes between 3.2 and 38 cm and are deployed at depths from 1.2 to 110 m for durations between 0.05 and 91 h (Kroetz, Mathers & Carlson, 2020).

The shark bottom longline fishery has been monitored by NMFS observers since 1994, and approximately 200 fishers have US permits to target sharks in the Atlantic Ocean and Gulf of Mexico (Mathers et al., 2018). The observer coverage goal of this fishery is 5–10%, but there is 100% coverage on the four to six commercial shark-fishing vessels participating in the shark research fishery programme monitored by NMFS. Based on observer data from vessels not participating in the research programme, on average, mainlines averaged 7.2 km long (range 0.9–12.0 km), gear was deployed at depths between 3 and 21 m (average 16.4 m), and had between 47 and 401 hooks (average 289). The majority (63.6%) used 18/0 circle hooks, and the average soak time was 7.8 h. Vessels that participated in the research programme had mainline lengths ranging from 2 to 19.6 km (average 7.0 km), were deployed at depths between 4 and 158 m (average 31.4 m), and had between 112 and 300 hooks (average 247). The majority (51.9%) used 18/0 circle hooks, and the average soak time was 5.6 h (Mathers et al., 2018).

For this study, bycatch risk is defined as the probability of commercial fishing occurring in an area at the same time as sawfish are in that area. Minimizing interaction potential with commercial fisheries is important owing to high sawfish mortality rates from incidental catches, particularly in the shrimp trawl fishery (NMFS, 2009b). The toothed rostra of sawfish are prone to entanglement in nets, and bringing the entire animal on board to disentangle can be dangerous. This sometimes leads fishers to seriously harm or kill the sawfish. Breaking or removing the rostrum alters a sawfish's behaviour and usually leads to death (G. R. Poulakis, unpublished data; NMFS, 2009b; Morgan et al., 2016).

Our objective was to use long-term, wide-ranging passive acoustic monitoring and shorter term satellite telemetry data from large juvenile and adult smalltooth sawfish to determine how movement patterns and habitat use interact with commercial fishing effort of the shrimp trawl, south-east coastal gillnet, and shark bottom longline fisheries. Results can aid resource managers to reduce smalltooth sawfish bycatch and thereby facilitate population recovery.

2 | METHODS

2.1 | Acoustic receiver networks

Acoustic receivers for monitoring smalltooth sawfish were established within the Charlotte Harbor estuarine system, Everglades National Park, and the Florida Keys. The Charlotte Harbor array contained 51 receivers in the northern portion of the estuary in and around the Peace River, as well as 51 receivers in the southern portion of the system in and around San Carlos Bay and the Caloosahatchee River. The array in the Everglades National Park and Florida Keys region comprised 26 receivers maintained by co-authors that tagged sawfish. This study also used the Florida Atlantic Coast Telemetry (secoora.org/fact), Atlantic Cooperative Telemetry (theactnetwork.com), and Integrated Tracking of Aquatic Animals in the Gulf of Mexico (itagscience.com) arrays, which provided access to positive detection data from hundreds of additional receivers along both coasts of Florida (Figure 1). These receivers were maintained by various researchers and institutions, so receiver download schedules varied.

2.2 | Tagging

Sawfish were tagged primarily near where acoustic arrays were maintained for monitoring smalltooth sawfish. Large juveniles (>2 m stretch total length (STL)) and adults (>3.4 m for males; >3.7 m for females; Brame et al., 2019) were captured in Charlotte Harbor with rod and reel and drumlines. Rod and reel used 36–45 kg test braided or monofilament line with 9/0 non-offset circle hooks. Drumlines consisted of 20 kg concrete anchors and 5 m or 10 m gangions with 250 kg test monofilament line and 14/0 non-offset circle hooks. Drumlines soaked for 1 h and up to five were set at a time. Rod and reel gear was typically used during the drumline soaks. Sawfish were also tagged in the Florida Keys and portions of Everglades National Park using bottom longlines, almost always set in pairs, of 50 16/0 non-offset circle hooks fished for 1 h, rod and reel as already described, and shoreline gillnets 1.5 m deep, between 30.5 and 61 m long, with stretch mesh sizes either 7.6 cm or 10.2 cm. Ladyfish (*Elops saurus*) was the primary bait for all baited gears. Two sawfish were opportunistically tagged on the east coast; they were caught in the intake canal net at the Florida Power and Light nuclear power plant in St Lucie, Florida.

Captured sawfish were measured (rostrum length, pre-caudal length, fork length, and STL) and tagged with multiple tag types.

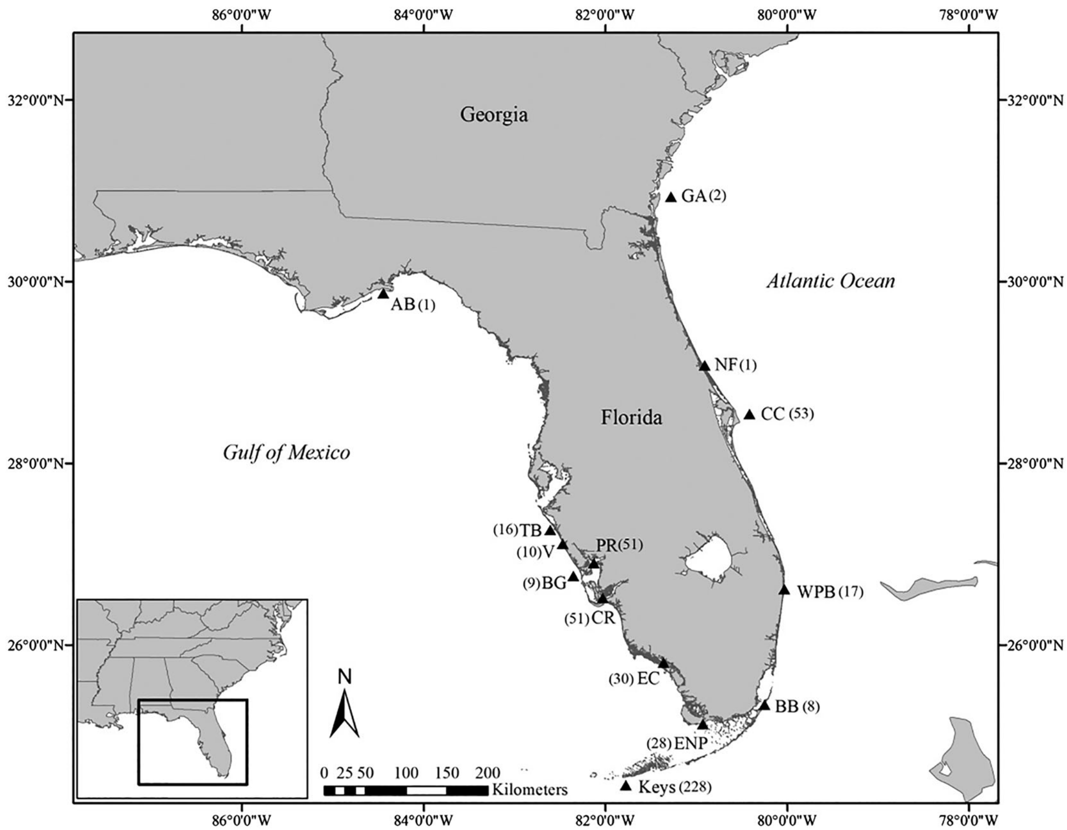

FIGURE 1 Map showing the centre of activity for each acoustic receiver region: Apalachee Bay (AB), Tampa Bay (TB), Venice (V), Peace River (PR), Caloosahatchee River (CR), Boca Grande (BG), Everglades City (EC), Everglades National Park (ENP), the Florida Keys (Keys), Biscayne Bay (BB), West Palm Beach (WPB), Cape Canaveral (CC), North Florida (NF), and Georgia (GA). The Peace River and Caloosahatchee River regions make up the Charlotte Harbor estuarine system. The number of receivers in each region is shown in parentheses

External tags included either small rototags (Dalton®, Newark, UK) or metal-tipped dart tags (FH-69, ©Floy Tag & Mfg Inc., Seattle, WA, USA) placed on or near a dorsal fin. Sawfish were also injected with a passive integrated transponder (PIT-tag; HPT12; Biomark® Inc., Boise, ID, USA) under the skin at the base of a dorsal fin for identifying individuals after external tag loss. Finally, a 69 kHz acoustic transmitter (Vemco/Innovasea V13-1L or a V16-6H) with either an estimated battery life of 4 years or 10 years was surgically implanted within the body cavity of some sawfish. These tags were programmed to emit unique acoustic sequences on a random delay once every 80–180 s (V13) or 70–150 s (V16). Surgery involved a 2–4 cm incision on the animal's ventral surface just anterior to the pelvic fins using a sterile, disposable scalpel and two or three dissolvable surgical sutures to close the incision after tag placement.

Other sawfish were tagged with multiple generations of pop-up archival transmitting (PAT) tags manufactured by Wildlife Computers (i.e. PAT2–4, Mk10-PAT, MiniPAT, PATF). These tags were programmed to pop off between 60 and 150 days depending on the type. Tags were rigged with either 136 kg monofilament leaders and a Pfleger Institute of Environmental Research nylon 'umbrella' dart or a modified harness consisting of 1.8 mm stainless steel cable surrounded by chafe tubing, then clear surgical tubing with polyolefin heat-shrinkable tubing at each end. Umbrella darts were inserted by making a small incision below the middle of the first dorsal fin approximately 5 cm below the fin base; the dart was inserted into the musculature, seating the anchor at a depth of 6–10 cm. For sawfish tagged with the modified harness, a small hole was made through the anterior portion of the base of the first dorsal fin where the free end of the harness assembly was threaded through to the opposite side of the dorsal fin. The free end of steel cable was then inserted into the open sides of two double copperlock crimps, which were closed, and excess cable was removed. The PAT tag trailed just behind the dorsal fin when the sawfish was released.

2.3 | Data processing

Acoustic data were first processed by removing any single detections within a 24 h period to avoid including false detections. The data were then binned by day to ensure data were not skewed by a few individuals spending significant time near a single receiver within a single day. The resulting data were used to calculate single-band kernel density rasters with a cell size of 0.05 decimal degrees (°) and populated by number of sawfish detected per day for each month using the Kernel Density tool in ArcMap v10.7.1 (Environmental Systems Research Institute, 2011).

Satellite data were processed by filtering geolocation point estimates using a maximum travelling speed of 110 km per day, which was based on maximum daily travelling distance calculated from acoustic detections. Papastamatiou et al. (2015) estimated that the average rate of movement of adult smalltooth sawfish actively tracked in Florida Bay was 1.2 km h^{-1} (28.8 km day^{-1}), and the maximum rate of movement was estimated to be 7.5 km h^{-1} (180 km day^{-1}). It was assumed, based on sawfish behaviour, that migrating sawfish likely move faster than the average rate of movement, but it is unlikely that the maximum rate of movement is sustainable for a full day. Thus, the maximum rate of 110 km day^{-1} is likely a reasonable proxy for maximum rate of movement over a 24 h period. All geolocation point estimates on land were also removed. After filtering, the point estimates were binned by month, and monthly kernel density rasters were created. To analyse space use, a combined activity raster was created by building a mosaic of the acoustic and satellite data for each month. This was accomplished using the Mosaic to New Raster tool in ArcMap by summing overlapping cells.

Smalltooth sawfish vulnerability to bycatch in commercial shrimp trawl, south-east coastal gillnet, and shark bottom longline fisheries was analysed by overlaying movements from acoustic and satellite tag data with fishing effort obtained from NMFS observer programmes. While target observer coverage was only 1–2% for the shrimp trawl fishery, 5–15% for the coastal gillnet fishery, and 5–100% of the total effort for the shark bottom longline fishery (Scott-Denton et al., 2012; Mathers et al., 2017; Mathers et al., 2018), these data were more reliable than logbook data. Logbook data are reported by spatial grid and data from Vessel Monitoring Systems (VMS), which makes it difficult to discern whether a vessel is actively fishing or just moving to a new location. Fishing effort was calculated using the number of hours each gear was deployed in a 30.8 km^2 area, which corresponds to the size of the NMFS's spatial grids. The shrimp trawl dataset contained 5,789 trawls and approximately 20,837 hr of fishing from 2005 to 2018. The south-east coastal gillnet dataset contained 2,480 sets and 7,022 h of fishing from 2005 to 2017. The shark bottom longline fishery dataset contained 8,915 sets and 28,173 h of fishing from 2005 to 2016.

Kernel density rasters were calculated for each fishery to assign a probability of fishing value to each cell. Fishing effort rasters for the shrimp fishery were calculated by creating lines between start and end coordinates of each trawl, and by excluding any trawls that were missing starting or ending coordinates. It is important to note that the spatial distribution of shrimping effort can change from year to year, and trawling often does not occur in a strictly linear path; however, given the sample size of trawls and the large spatial scale, this method provided an adequate approximation. Trawls were subsampled by month, and kernel density rasters with a cell size of 0.05 decimal degrees (°) were constructed from the resulting polyline features. For the coastal gillnet fishery, fishing effort rasters were created by subsampling by month and creating kernel density rasters with a cell size of 0.05 decimal degrees (°) from the deployment points. For the longline fishery, the kernel density raster was calculated by using only the starting locations, due to many missing or erroneous ending locations. Data were divided by month, and rasters with a cell size of 0.05° populated by soak time were created.

The relative sawfish-fishery bycatch risk rasters were calculated by multiplying the fishing effort rasters by the sawfish activity rasters to create fishery-specific relative bycatch risk rasters for each month across all years. Bycatch risk is a measure of the probability of a sawfish occurring in the same geographic location that fishing gear is being deployed in any given month. The rasters were normalized, and the risk values were assigned to detections in the acoustic dataset for corresponding months using the Extract to Points tool in ArcMap. Average bycatch risk across all individuals was calculated, and a series of Kruskal–Wallis tests were conducted to analyse the difference in risk across the three fisheries.

2.4 | Modelling bycatch risk

A linear mixed-effects model, fitted to optimize the restricted maximum likelihood (REML) criterion, was created where the response variable was bycatch risk for a specific fishery (as already defined herein). All possible combinations of the fixed effects STL, sex, and tagging location were added into the model along with the random effects of individual and month. The change in Akaike information criterion (AICc) values of all potential models for a specific fishery was compared to determine the best model (ΔAICc < 2; Anderson & Burnham, 2002). The AICc comparison was repeated for each of the three fisheries. Because only two sawfish were tagged off the Indian River Lagoon, compared with 19 in Charlotte Harbor, 10 in Everglades National Park, and 11 in the Florida Keys, they were excluded from the model.

2.5 | Analysis of vertical distribution

Fourteen (seven females and seven males) of the 17 satellite tags used in this study had viable depth data that could be used for analysis (i.e. daily depth measurements for at least 2 weeks). Although the maximum number of days depth data were collected on any one tag was 156, this study had coverage across all months when all tags were aggregated. The tags were programmed to record depth readings every 60 s. Data were combined into 4 h bins distributed in 12 discrete depth bins based on previous vertical distribution data, which were averaged to create histograms showing vertical movement for each sex. Histograms were also made showing vertical space use for each season using data from tags that had depth data for that season. These histograms were compared to seasonal histograms showing fishing depths for each fishery that depth data were recorded for. A linear mixed-effect model fit to maximize REML was run with sex and depth bin as fixed effects, month as a random effect, and percentage time as the response variable.

3 | RESULTS

Fifty-nine large juvenile and adult smalltooth sawfish were tagged in this study. Forty-two were tagged with acoustic tags between 2016 and 2019; 24 were female (mean 3.13 m STL) and 18 were male (mean 3.09 m STL) (Table 1). Seventeen were tagged with satellite tags between 2011 and 2017; seven were female (mean 3.43 m STL) and 10 were male (mean 3.94 m STL) (Table 2). No sawfish were tagged with both tag types.

3.1 | Acoustic monitoring summary

From May 2016 to September 2019, individuals were detected on 461 acoustic receivers ranging from off the coast of Brunswick, Georgia, to the lower Florida Keys and along the Gulf of Mexico to Apalachee Bay, Florida; these receivers were divided into regions (Figure 1; Graham et al., 2021). In general, sawfish moved north from the Keys in spring (March–May) on both Florida coasts and travelled to Charlotte Harbor on the Gulf coast and to Cape Canaveral on the Atlantic coast. Some detections (<1%) were recorded north of these areas in summer (June–August), but most detections occurred south of 27°N latitude on the Gulf coast and south of 29°N latitude on the Atlantic coast. Some individuals moved back to the Keys in the autumn (September–November) and winter (December–February), whereas some remained in Charlotte Harbor and the Keys year-round.

3.2 | Shrimp trawl fishing effort

Shrimp trawl effort varied temporally and spatially within state and federal waters (Figure 2). There was high effort during January and during June through August around the lower Keys and Marquesas Keys, particularly offshore on the Gulf side. There was also high effort between the lower Keys and Charlotte Harbor from January through May and from October through December. On the Atlantic coast, there was high effort off Cape Canaveral during January and north of Cape Canaveral to the Florida–Georgia border in September and November.

3.3 | South-east coastal gillnet fishing effort

South-east coastal gillnet fishing effort occurred in federal waters near Cape Canaveral for most of the year (Figure 2). There was also high effort around the Florida–Georgia border from February through May, as well as August. Gulf coast effort was limited to November and December.

3.4 | Shark bottom longline fishing effort

Longline effort was relatively high year-round in federal waters along both coasts (Figure 2). Gulf coast effort was concentrated in the warmer months and only occasionally extended south of Charlotte Harbor, usually during the winter. On the Atlantic coast, effort was also highest during the warmest months, but extended further south than the Gulf coast to the Florida Keys almost year-round.

3.5 | Bycatch risk

Bycatch risk for each fishery was examined seasonally (Figure 3). For the shrimp trawl fishery, risk was concentrated year-round off the Gulf side of the lower Florida Keys and Marquesas Keys. Gillnet risk was concentrated off Cape Canaveral for most of the year, but was negligible in winter and early spring because the sawfish were overwintering in the Florida Keys during this time. Risk for the longline fishery was concentrated year-round in the Atlantic Ocean adjacent to the Florida Keys. Risk associated with the shrimp trawl fishery was significantly higher than risk associated with the coastal gillnet fishery (Kruskal–Wallis test, $P < 0.001$, $\chi^2 = 4542.5$, $df = 36$) or the longline fishery (Kruskal–Wallis test, $P < 0.001$, $\chi^2 = 68.14$, $df = 305$). Risk for the longline fishery was significantly higher than the gillnet fishery (Kruskal–Wallis test, $P < 0.001$, $\chi^2 = 51{,}810$, $df = 210$).

3.6 | Modelling bycatch risk

A linear mixed-effects model was used to account for individual variation in bycatch risk and determine if there was variation across months. The best-fitting models from all three fisheries included sex × tagging location, length, and the random effects individual and month (Table 3). All three fixed effects variables were included in the best-fitting model, as well as the interaction between sex and tagging location.

3.6.1 | Shrimp trawl fishery

Both male and female sawfish tagged in Charlotte Harbor had the highest shrimp trawl bycatch risk, with the risk for males slightly higher (Figure 4). This is likely because all sawfish leaving and returning to this estuary swim through an area that has a high concentration of shrimp trawl effort. Risk was relatively low for sawfish tagged in Everglades National Park, including Florida Bay, and this risk was comparable between sexes. The random effect month showed that February, June, July, and August had higher than average risk. Trawl risk in October was not significantly different from in February or June (Tukey, $P = 0.79$, $P = 0.14$), but was significantly higher than all other months (Tukey, $P < 0.02$).

TABLE 1 Summary of all acoustic-tagged smalltooth sawfish (*Pristis pectinata*) including ID number, sex (F: female; M: male), maturity, stretch total length, tagging location, date tagged, date of first detection, date of last detection, days of study, and number of detections

ID	Maturity	Length (m)	Location tagged	Date tagged	Date of first detection	Date of last detection	Days of study	No. of detections
F1	Immature	2.12	CH	March 15, 2019	March 15, 2019	September 18, 2019	188	4,639
F2	Immature	2.13	CH	August 2, 2018	August 3, 2018	October 3, 2019	427	31,954
F3	Immature	2.16	Keys	August 10, 2017	March 11, 2018	June 26, 2018	108	35
F4	Immature	2.25	ENP	June 20, 2016	January 5, 2018	February 4, 2018	31	53
F5	Immature	2.27	CH	March 15, 2019	March 15, 2019	September 14, 2019	184	2,138
F6	Immature	2.34	CH	July 19, 2017	July 21, 2017	June 25, 2019	705	3,543
F7	Immature	2.38	CH	March 25, 2019	March 25, 2019	September 20, 2019	180	3,808
F8	Immature	2.43	CH	July 9, 2018	July 9, 2018	September 10, 2019	64	8,768
F9	Immature	2.46	CH	July 26, 2017	July 26, 2017	April 26, 2018	275	1,246
F10	Immature	2.57	CH	July 26, 2017	July 26, 2017	July 23, 2018	363	1,927
F11	Immature	2.58	CH	March 20, 2019	March 20, 2019	July 29, 2019	132	5,381
F12	Immature	2.69	CH	September 12, 2018	September 12, 2018	December 26, 2018	106	157
F13	Immature	3.18	ENP	March 30, 2017	November 16, 2017	June 22, 2019	584	864
F14	Immature	3.20	CH	August 11, 2017	August 15, 2017	May 21, 2019	645	1,940
F15	Immature	3.49	Keys	August 1, 2018	August 27, 2018	June 8, 2019	286	166
F16	Immature	3.55	Keys	April 11, 2017	April 16, 2017	February 3, 2018	294	1,279
F17	Mature	3.64	Keys	April 11, 2017	April 27, 2017	March 28, 2019	701	4,913
F18	Mature	3.71	PP	November 2, 2017	November 23, 2017	April 10, 2019	504	2,069
F19	Mature	3.92	Keys	April 1, 2017	April 1, 2017	May 25, 2019	785	755
F20	Mature	4.26	Keys	April 1, 2017	April 3, 2017	May 28, 2019	786	610
F21	Mature	4.38	Keys	May 21, 2016	May 21, 2016	June 1, 2019	1,107	3,122
F22	Mature	4.38	ENP	September 13, 2016	November 5, 2016	April 4, 2019	881	1,548
F23	Mature	4.42	ENP	April 2, 2017	May 12, 2017	March 19, 2019	677	791
F24	Mature	4.53	ENP	April 2, 2017	June 4, 2017	June 6, 2017	3	27
M1	Immature	2.11	CH	June 4, 2018	June 5, 2018	March 27, 2019	296	5,769
M2	Immature	2.35	CH	August 21, 2018	August 21, 2018	September 18, 2019	394	10,288
M3	Immature	2.35	CH	July 26, 2017	July 26, 2017	April 19, 2019	633	3,118
M4	Immature	2.48	CH	August 21, 2018	August 21, 2018	September 14, 2019	390	12,509
M5	Immature	2.59	ENP	November 9, 2016	January 21, 2018	June 16, 2019	512	277
M6	Immature	2.60	CH	October 23, 2018	October 23, 2018	April 24, 2019	184	237
M7	Immature	2.66	CH	April 18, 2019	April 18, 2019	September 26, 2019	162	2,615
M8	Immature	2.72	ENP	March 30, 2017	April 26, 2017	June 8, 2019	774	10,337
M9	Immature	2.76	CH	October 24, 2017	July 19, 2017	April 22, 2019	643	919
M10	Immature	2.90	CH	September 12, 2018	September 12, 2018	April 22, 2019	223	2,229
M11	Immature	2.93	Keys	July 20, 2016	August 22, 2016	June 10, 2019	74	4,284
M12	Mature	3.50	PP	September 17, 2017	September 24, 2017	August 12, 2018	323	638
M13	Mature	3.82	ENP	April 6, 2019	April 10, 2019	June 15, 2019	67	25
M14	Mature	3.83	Keys	April 1, 2017	April 1, 2017	June 17, 2019	808	689
M15	Mature	3.98	Keys	April 15, 2018	February 14, 2018	November 30, 2018	290	382

(Continues)

TABLE 1 (Continued)

ID	Maturity	Length (m)	Location tagged	Date tagged	Date of first detection	Date of last detection	Days of study	No. of detections
M16	Mature	3.98	ENP	April 2, 2017	April 26, 2017	April 7, 2019	712	388
M17	Mature	3.98	ENP	September 9, 2016	December 12, 2016	May 28, 2019	898	2,414
M18	Mature	4.07	Keys	April 14, 2017	April 15, 2017	July 2, 2017	79	1,143

Abbreviations: CH, Charlotte Harbor; PP, St Lucie Power Plant; ENP, Everglades National Park; Keys, Florida Keys.

TABLE 2 Summary of all satellite tagged smalltooth sawfish (*Pristis pectinata*) including identification number (ID), sex (F: female; M: male), and stretch total length

ID	Maturity	Length (m)	Used in bycatch analysis	Depth days analysed
F25	Immature	2.79	No	141
F26	Immature	2.83	No	133
F27	Immature	3.23	No	138
F28	Immature	3.52	Yes	156
F29	Mature	3.68	Yes	84
F30	Mature	3.68	Yes	140
F31	Mature	4.28	Yes	121
M19	Mature	3.65	Yes	N/A
M20	Mature	3.66	Yes	N/A
M21	Mature	3.71	Yes	141
M22	Mature	3.95	Yes	61
M23	Mature	3.95	Yes	62
M24	Mature	3.99	Yes	46
M25	Mature	4.03	Yes	N/A
M26	Mature	4.09	Yes	55
M27	Mature	4.12	Yes	150
M28	Mature	4.27	Yes	151

Abbreviation: NA, not analyzed.

February, March, June, and July were not significantly different from each other (Tukey, $P = 1.0$, $P = 0.90$, $P = 0.08$), but risk in February was significantly higher than in January, April, May, August, September, November, and December (Tukey, $P < 0.05$). Risk in June was significantly higher than in September and August (Tukey, $P = 0.04$, $P = 0.03$). Although risk was higher than average in July, there was no significant difference between risk in July and risk associated with any months with lower-than-average risk (Tukey, $P > 0.30$).

3.6.2 | South-east coastal gillnet fishery

Sawfish tagged in the Florida Keys had the highest bycatch risk from the south-east coastal gillnet fishery, with slightly higher risk for females (Figure 4). Sawfish tagged in Charlotte Harbor and Everglades National Park, including Florida Bay, had negligible risk in this fishery because these fish did not travel along the Atlantic coast where this fishery occurs. April, May, June, July, September, November, and December had gillnet bycatch risk, and there was no significant difference between these months (Tukey, $P > 0.42$).

3.6.3 | Shark bottom longline fishery

Average longline bycatch risk was highest for both males and females tagged in the Florida Keys, with both sexes having comparable risk (Figure 4). Risk in this fishery was low for both males and females tagged in Charlotte Harbor, and risk was comparable between sexes. Risk was higher for females tagged in Everglades National Park. Males tagged in Florida Bay had slightly higher risk than females. When examining the random effect of month, February, March, November, and December had higher than average risk. December and February had significantly higher risk than all other months except November and March (Tukey, $P < 0.01$). Although November and March had higher than average risk, this risk was not significantly higher than any months with below-average risk (Tukey, $P > 0.06$).

3.7 | Modelling vertical distribution

It is important to consider both the depth that fishing gear is deployed at and the depths that sawfish most commonly occupy when assessing bycatch risk. Although sawfish are benthic, they exhibit preferences for

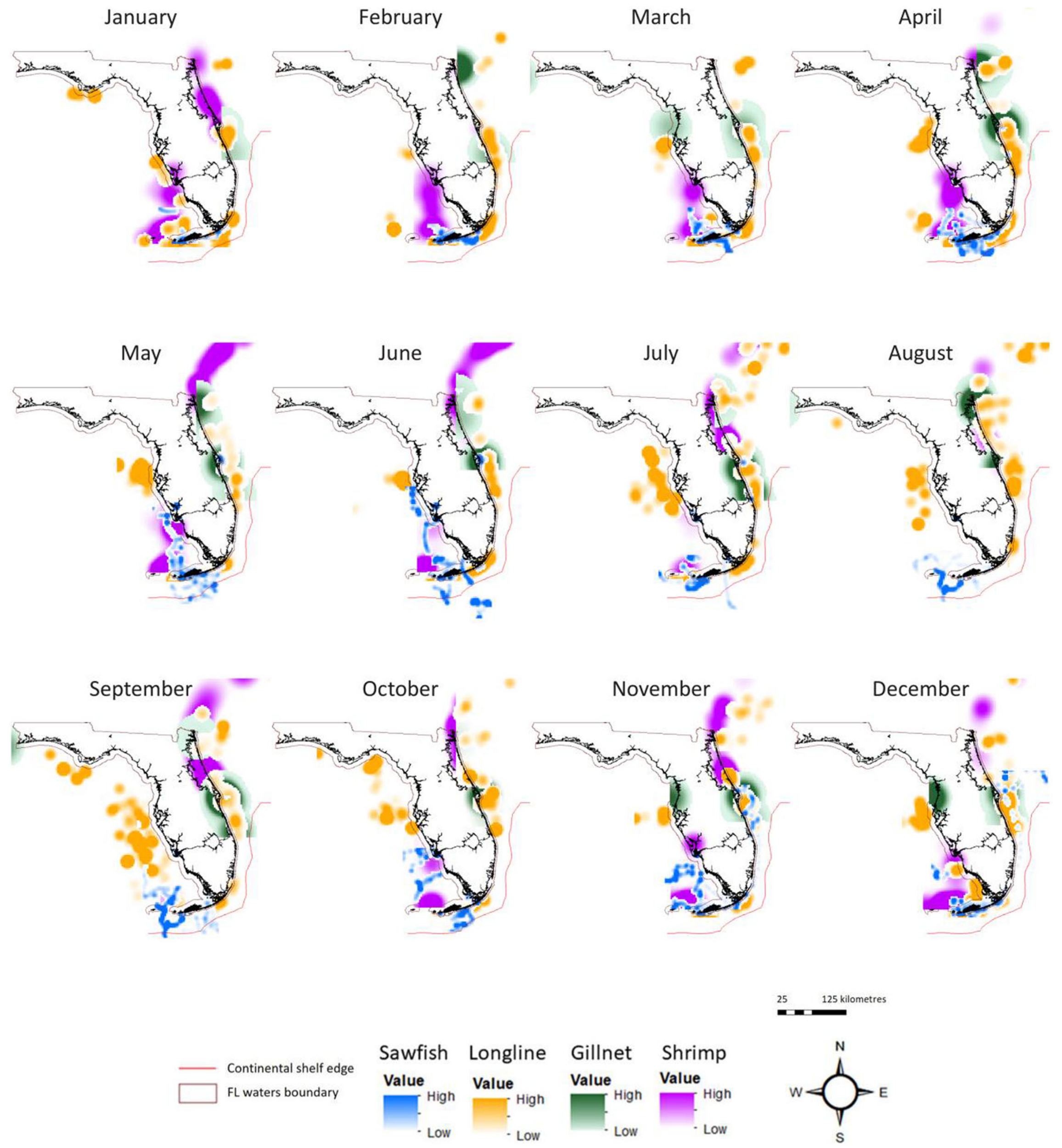

FIGURE 2 Smalltooth sawfish (*Pristis pectinata*) activity (blue) and fishing effort rasters for all three commercial fisheries. The edge of the continental shelf and the state–federal waters boundary are shown for reference

areas of certain depths. Therefore, a model was created to analyse the vertical distribution of sawfish activity (Table 2). Percentage time at depth was calculated to examine how the sexes moved along depth gradients and to model the time each sex spent at various depths. Sex was a good predictor of the percentage of time spent at depth (Table 4, Figure 5). Females spent the most time in 0–2 m and 30–100 m depth ranges. Males spent the most time in 0–2 m and 30–40 m. Both sexes spent a high percentage of time in the 0, 30, and 40 m depth ranges and a low percentage of time in the 4 and 8 m ranges. Although females spent a high percentage of time at about 100 m, males spent less time at this depth.

When analysing the vertical distribution of sawfish and the deployment depth of the gear, it became clear that whereas bycatch risk for females was highest in the shrimp trawl fishery, risk was not significantly different between the sexes in the other two fisheries (Figure 6). Both sexes spent most of their time in the extremes of their vertical range, remaining either very shallow or venturing deep, though females tended to venture deeper than males. Shrimp trawl effort was highest at depths greater than 100 m, and bycatch risk was highest for females that spent more time at these depths than males. Gillnet fishing effort occurred mostly between 4 and 30 m for both sexes, and risk was highest between 20 and 30 m. Most of the longline fishing effort occurred between 10 and 30 m, and this is also where bycatch risk was highest.

Elevated bycatch risk for females in the shrimp fishery was observed across seasons (Figure 7). Although the risk was comparable

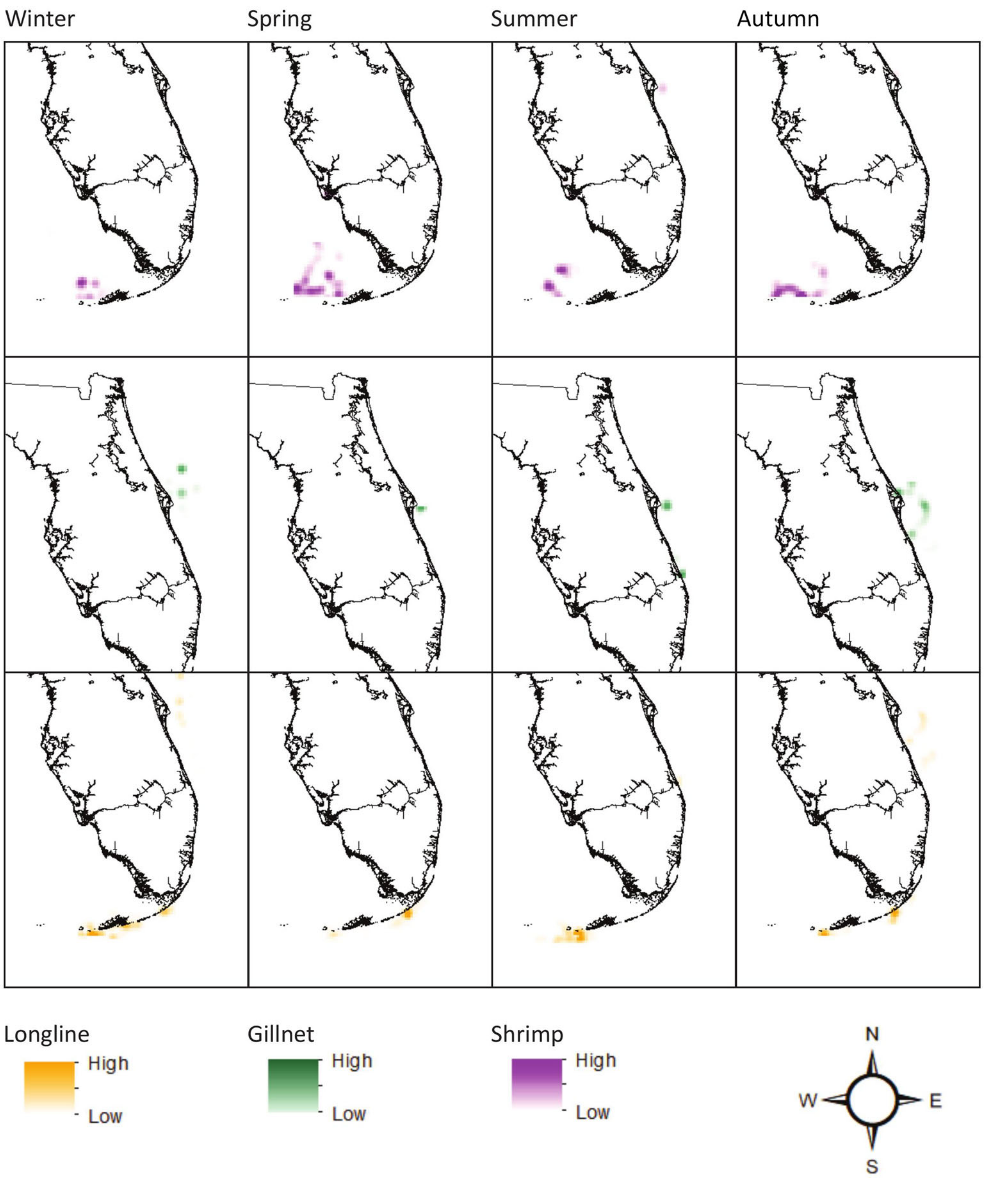

FIGURE 3 Shrimp trawl (top row), south-east coastal gillnet (middle row), and shark bottom longline (bottom row) bycatch risk rasters by season. Darker shades represent higher risk

TABLE 3 The two best-fitting bycatch risk models for each fishery with rank, number of parameters *K*, change in Akaike information criterion (ΔAICc), cumulative weight, and model formula. All models include the random effects month and individual

Rank	*K*	ΔAICc	Cumulative weight	Model
Shrimp trawl				
1	13	0.00	0.98	Av_Risk ~ Sex × Tagging location
2	14	8.11	1.00	Av_Risk ~ Sex × Tagging location + Length
South-east coastal gillnet				
1	13	0.00	0.89	Av_Risk ~ Sex × Tagging location
2	14	4.28	1.00	Av_Risk ~ Sex × Tagging location + Length
Shark bottom longline				
1	13	0.00	0.98	Av_Risk ~ Sex × Tagging location
2	14	7.37	1.00	Av_Risk ~ Sex × Tagging location + Length

between sexes for the remaining fisheries, risk fluctuated throughout the year. Most of the shrimp trawling effort occurred at depths of 20 m or more, which more heavily affected females. Risk in the shrimp fishery was highest in summer and autumn. Risk was highest in spring and summer for the coastal gillnet fishery. Risk in the longline fishery was lowest in autumn.

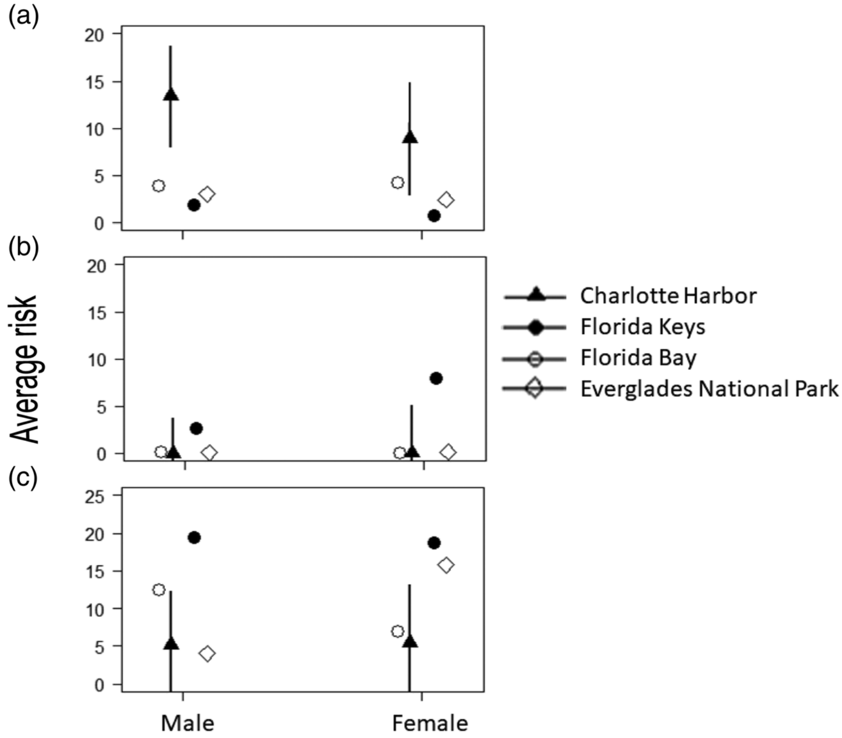

FIGURE 4 Average (a) shrimp trawl, (b) south-east coastal gillnet, and (c) shark bottom longline bycatch risk as a relative percentage probability by sex for acoustic-tagged smalltooth sawfish (*Pristis pectinata*). Bycatch risk was calculated by multiplying the probability of fishing occurring by the probability of a sawfish occurring in the same area

TABLE 4 The two best models for predicting smalltooth sawfish (*Pristis pectinata*) percentage time at depth with number of parameters *K*, change in Akaike information criterion (ΔAICc), cumulative weight, and model formula

Rank	K	ΔAICc	Cumulative weight	Model
1	26	0.00	1	Percentage Time ~ Sex × Bin + (1|Month)
2	15	45.65	1	Percentage Time ~ Sex + Bin + (1|Month)

4 | DISCUSSION

4.1 | Implications for management

This study identifies the spatial and temporal overlap between commercial fishery effort and large juvenile and adult smalltooth sawfish occurrence. Areas and times of overlap represent areas of increased bycatch risk and identify specific locations and times for resource managers to implement conservation measures. The results illustrate minimal overlap in the south-east coastal gillnet fishery, temporally limited overlap in the shark bottom longline fishery (four of 12 months), and substantial overlap in the shrimp trawl fishery—both temporally (nine of 12 months) and spatially. Given limited overlap of the south-east coastal gillnet and shark bottom longline fisheries with sawfish occurrence, additional regulations do not appear necessary for these fisheries at this time. In contrast, conservation measures to mitigate bycatch risk in the shrimp trawl fishery appear necessary to promote conservation of this species. Results from this study indicate a year-round closure of waters off south-west Florida to the south-east shrimp trawl fishery between Charlotte Harbor and the western Florida Keys (Figure 8) is warranted to ensure bycatch does not cause population decline.

Of the three fisheries examined, the shrimp trawl fishery is most likely to result in both bycatch and mortality of large juvenile and adult smalltooth sawfish. Although uncertainty was very high, in a recent assessment of the shrimp trawl fishery's effect on smalltooth sawfish, NMFS determined that 1,806 sawfish could be taken as bycatch in this fishery, with 50% of those resulting in mortality, over any running 5-year period (NMFS, 2021). These figures were estimated using current NMFS observer data and estimates of total effort from this fishery. Unfortunately, low levels of observer coverage (1–2%) result in high levels of uncertainty, as annual captures from 2008 to 2010 were estimated to be as low as 17 or as high as 162 animals per year (Carlson & Scott-Denton, 2011). Because the assessment based the bycatch value on the highest capture estimate (162 sawfish), it represents a worst-case scenario. To more accurately understand the effect of this fishery on smalltooth sawfish, increased observer coverage, especially in high-risk regions, and more information on total fishing effort is needed. Increased observer coverage combined with tagging of released animals could refine bycatch estimates and provide data on post-capture survivorship.

Traditionally, fishery observations have been conducted by trained people onboard vessels. However, increasing observer

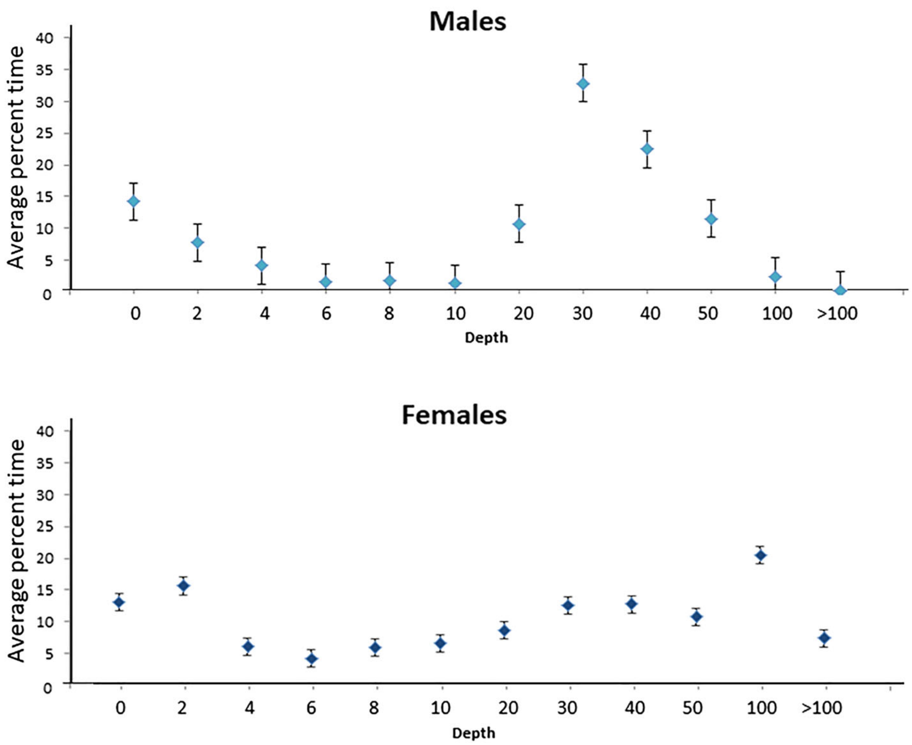

FIGURE 5 Average percentage time (with standard error bars) spent by smalltooth sawfish (*Pristis pectinata*) at 12 depth bins by sex. Note difference in *y*-axis scales

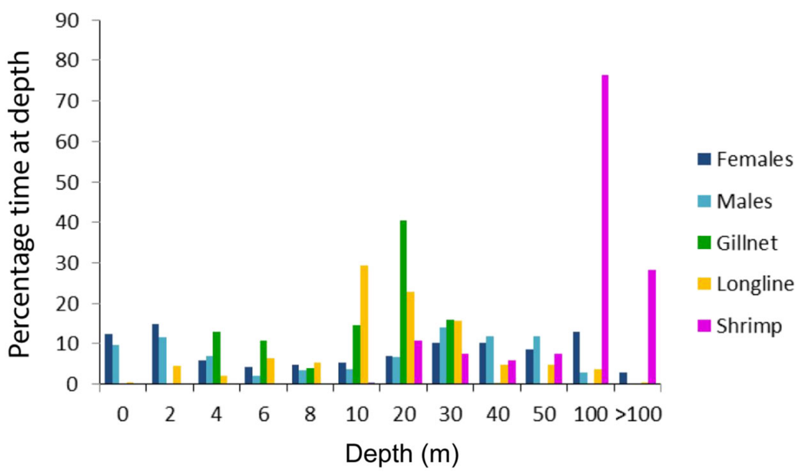

FIGURE 6 Percentage time at depth by smalltooth sawfish (*Pristis pectinata*) sex and fishing effort in the shrimp trawl, south-east coastal gillnet, and shark bottom longline fisheries

coverage to refine bycatch estimates can be costly, especially for rare captures like smalltooth sawfish. Electronic monitoring techniques, including the use of cameras, are improving and increasingly replacing human observers in some circumstances. For sawfish, electronic monitoring may be a cost-effective complement to onboard observers to help achieve sufficient coverage associated with bycatch reduction goals (Moncrief-Cox et al., 2020).

As mentioned, sawfish rostra are easily entangled in nets and are often difficult to disentangle. With shrimp trawl nets, risk to sawfish is exacerbated by relatively long tow times (4 h on average) that result in sawfish being dragged for extended periods. Because of these factors, shrimp trawls have substantially higher sawfish mortality rates than other gears do, including hooks and even stationary nets that do not drag the sawfish and allow for faster release. Further study is needed to determine the extent to which tow time restrictions coupled with safe release methods could increase post-release survivorship of sawfish and to evaluate the potential for such measures to facilitate recovery.

Bycatch risk varied throughout the year, with some months and specific areas having higher associated risks than others. This variation opens the possibility of time–area or seasonal closures. There is evidence that such closures can be an effective management strategy in mitigating bycatch in commercial fisheries with minimal effect on the fisheries (NMFS, 2003; O'Keefe, Cadrin & Stokesbury, 2014). One such success was a closure instituted in the Kuwait shrimp fishery, which significantly decreased bycatch, such as

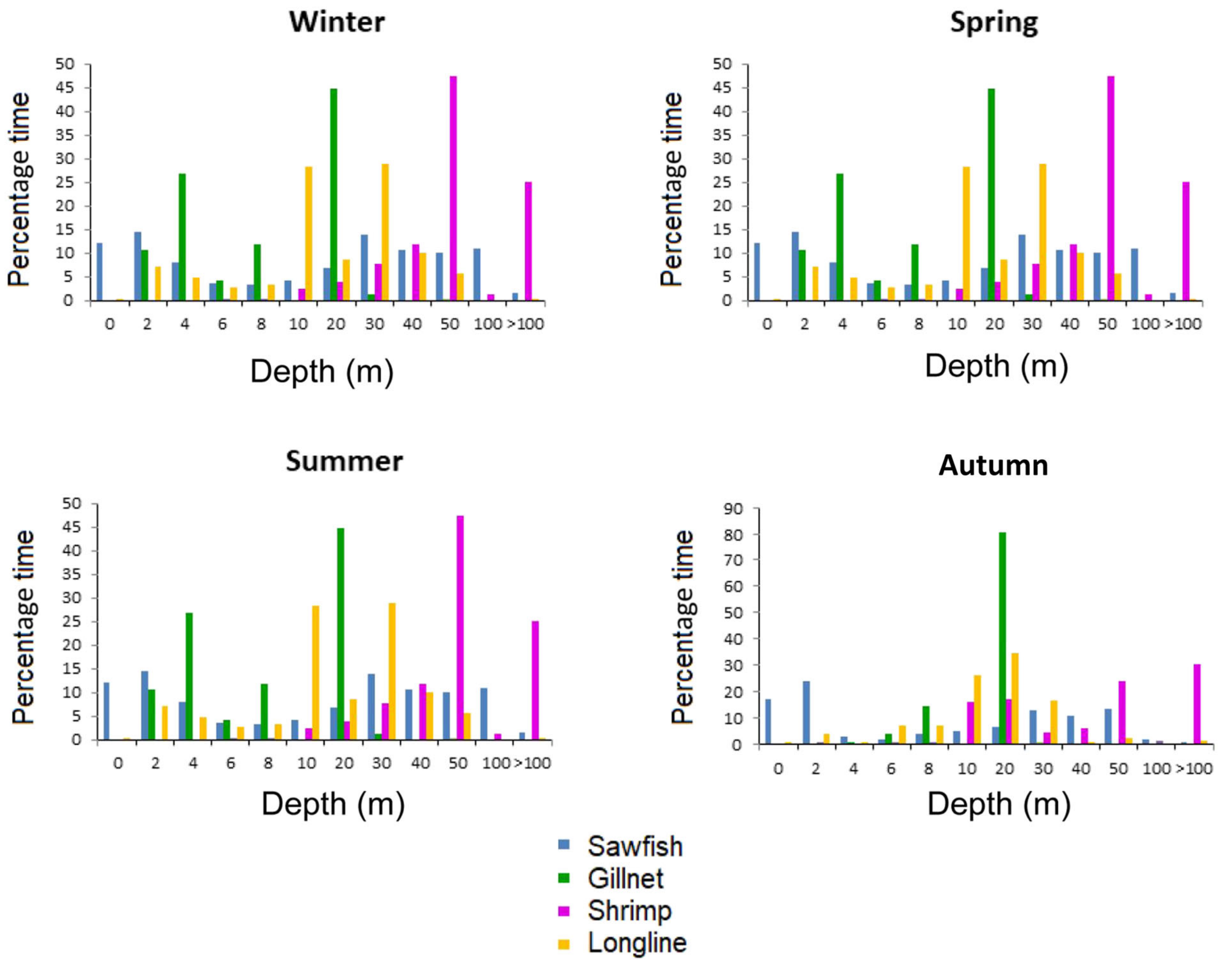

FIGURE 7 Smalltooth sawfish (*Pristis pectinata*) percentage time at depth (blue) with shrimp trawl (purple), south-east coastal gillnet (green), and shark bottom longline (yellow) percentage time spent fishing at depth. Winter: December–February; spring: March–May; summer: June–August; autumn: September–November. Note change in *y*-axis scale on autumn graph

of sea turtles and marine mammals, with a minimal loss of target catch (O'Keefe, Cadrin & Stokesbury, 2014). Closures have also been implemented to assist recovery of other elasmobranch species. For example, a seasonal closure off North Carolina was implemented to protect juvenile dusky (*Carcharhinus obscurus*) and sandbar (*Carcharhinus plumbeus*) sharks (NMFS, 2003). However, closures can cause negative socio-economic impacts on fishers or relocate the problem to another area as fishing efforts shift (O'Keefe, Cadrin & Stokesbury, 2014). Therefore, it is important that managers consider the overlap between target taxa (e.g. shrimp aggregations) and sawfish movements to understand how fishing effort displacement could affect the overall sawfish population.

4.2 | Additional considerations

It is important to address caveats associated with the relative bycatch risk metric and the statistical model used in this study. The sawfish activity raster was driven mostly by positive acoustic data, which are highly dependent on receiver coverage. Therefore, activity estimates were biased towards areas with higher receiver coverage. The satellite tag data may also be biased due to the uneven distribution of tagged males and females; however, by combining these two methods, these biases may have been minimized. Also, the relative risk metric is an estimate of bycatch likelihood and does not necessarily equate to capture or mortality risk. It simply represented the probability that a sawfish was in an area during a given month, multiplied by the probability of fishing occurring in that area during that month. There are other factors that could contribute to whether bycatch occurs, including time of day, tidal cycle, depth of gear deployment, and gear-specific catchability, which were not accounted for. In addition, the differing temporal scales between the fishing effort data and the sawfish activity data were also a source of potential bias. However, we believe the relative risk metric served as an adequate proxy to assess areas that were of highest risk to sawfish even if the true value of that risk was unknown. It is also useful for modelling purposes to determine which sawfish are spending the most time in these high-risk areas and which, therefore, are most likely to interact with the fisheries.

Notably, the size distributions of sawfish tagged in Charlotte Harbor, Florida Bay, and the Florida Keys differed. Sawfish tagged in

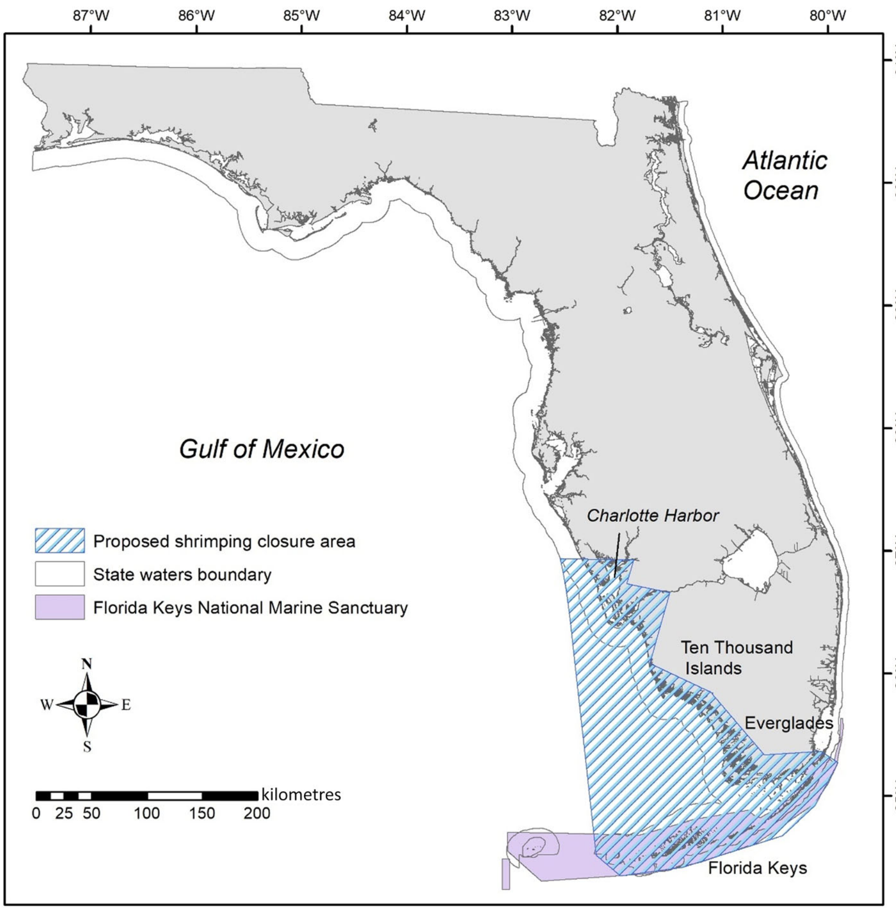

FIGURE 8 Proposed year-round closure area for the shrimp trawl fishery based on our analysis of where and when large juvenile and adult smalltooth sawfish (*Pristis pectinata*) would most likely interact with the fishery

Charlotte Harbor tended to be smaller than the sawfish tagged in the Florida Keys or Florida Bay. There is evidence of ontogenetic shifts in space use, so this skew in size class may have biased the data. However, sawfish larger than 2 m STL move from the shallowest waters of the nurseries along mangrove shorelines into deeper waters (>3 m) in Charlotte Harbor (G. R. Poulakis, unpublished data). Thus, the sawfish tagged in Charlotte Harbor spent more time within the estuary and did not move around as much. For this reason, bycatch risk differed between Charlotte Harbor and areas further south.

There was a significant difference in movement and associated bycatch risk between males and females depending on where they were tagged. In general, individuals tagged in Charlotte Harbor did not move as much as those tagged in south Florida, but both sexes tagged in Charlotte Harbor had the highest shrimp trawl bycatch risk, with the risk for males being slightly higher. Large females tagged in south Florida tended to reside in the deepest water, which is where shrimp trawl effort was highest. Therefore, females may be more vulnerable than males in the southernmost portions of Florida. We recommend that these sex-specific analyses be revisited as more fish are tagged and analysed, as more years of acoustic data are received from the 10-year tags that have been deployed, and as sex data are recorded from sawfish caught in shrimp trawls. Consistent funding is needed for acoustic tags, fisheries-independent and fisheries-dependent (e.g. NMFS observers, electronic monitoring) sampling, and continuation and expansion of acoustic monitoring, especially in the proposed shrimp trawling closure area.

To promote recovery of the smalltooth sawfish population, bycatch fishing mortality rates need to be minimized (NMFS, 2009b). A population viability analysis found that population growth remained stable at low levels (19 females per year) of fishing mortality but, not surprisingly, population growth declined when fishing mortality levels increased (Carlson & Simpfendorfer, 2015). Increasing observer coverage and acquiring more bycatch and survivability data for sawfish in these fisheries, especially the shrimp trawl fishery, would help managers focus future conservation measures. Regardless, management tools such as the proposed area closure are warranted to mitigate bycatch mortality in the shrimp trawl fishery now. The current study provides baselines for determining which areas and times are of highest risk to sawfish. This information will prove useful as policy-makers continue to monitor the smalltooth sawfish population and assess threats to recovery from various fisheries. With effective management practices, the smalltooth sawfish population can grow to eventually reach a healthy population size and expand to its historical range.

ACKNOWLEDGEMENTS

We thank all researchers, technicians, and institutions that have contributed to collecting the data used in this paper by maintaining acoustic receiver arrays. We thank M. Ajemian and M. McCallister for opportunistically tagging two sawfish near the St Lucie Power Plant under Endangered Species Permit number 15802. We thank A. Wooley and A. Court for assistance tagging sawfish in Charlotte Harbor and P. Stevens for providing two tags early in the study. We thank A. Brame for insightful comments and suggestions that improved the manuscript. This work was supported by funding from the US Department of Commerce, National Science Foundation Graduate Research Fellowship Program under grant no. 1449440, NOAA National Marine Fisheries Service through Section 6 (Cooperation with the States) of the US Endangered Species Act under grant award NA16NMF4720062 to the Florida Fish and Wildlife Conservation Commission, funding to FSU through the Northern Gulf Institute and the NOAA Fisheries Office of Protected Resources, the US Bureau of Ocean Energy Management, and NASA Environmental and Medical Contract (NEMCON) Contract #80KSC020D0023 as well as the Disney Conservation Fund. This research was conducted under Endangered Species Permit numbers 15802, 17787, 21043, and 22078 issued by NOAA Fisheries. Sawfish tagged by FSU were tagged under approval of FSU IACUC Protocol 1718. All data use conforms to SEFSC Data Confidentiality and 216-100 Protection of Confidential Fisheries Statistics Documents. A non-disclosure agreement was issued to R. Dean Grubbs. The senior author thanks N. Underwood, S. Burgess, and J. Elsner for their support of this work and assistance with R coding. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of institutions or data providers.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Research data are not shared.

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How to cite this article: Graham, J., Kroetz, A.M., Poulakis, G.R., Scharer, R.M., Carlson, J.K., Lowerre-Barbieri, S.K. et al. (2022). Commercial fishery bycatch risk for large juvenile and adult smalltooth sawfish (*Pristis pectinata*) in Florida waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1–16. https://doi.org/10.1002/aqc.3777