

Spatiotemporal dynamics of spawning aggregations of common snook on the east coast of Florida

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ABSTRACT: Data collected to determine specific reproductive traits, including spatial and temporal patterns, are an area of need for improved understanding of factors that contribute to productivity in fish populations. We used passive acoustic telemetry to study the movements of 271 common snook *Centropomus undecimalis* on the east coast of Florida from 2008 to 2011 to assess spatial dynamics during the spawning seasons. Common snook were detected in 6 inlets from Port Canaveral to Palm Beach Inlet during the summer months when water temperature exceeded 23°C, with peak densities between July and August. Individual residency times in an aggregation were over 7.5 times shorter than the spawning season which, together with asynchronous arrival dates and frequent migrations away from the aggregation, indicates high rates of turnover. Nearly half of the tagged common snook were observed at multiple (2 to 5) spawning sites during a single season and showed varying degrees of fidelity to a spawning site. Area of residence, sex and size are influential factors in spawning traits of common snook. Females migrated earlier, made more trips, and spent longer periods in aggregations compared to males. Larger fish showed greater site fidelity to a single aggregation site. Each year a portion of the population was not detected in an inlet, implying that some common snook skip spawning or that spawning may occur outside of inlets. Findings highlight the need for a combined approach to management that includes updating the stock assessment, using more accurate measures of spawning effort and the protection of spawning areas from physical disturbance.

KEY WORDS: Acoustic monitoring · Fish spawning · Fisheries management · Reproductive patterns · *Centropomus undecimalis*

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INTRODUCTION

Many fish species periodically migrate to specific locations at predictable times to form short-term spawning aggregations (Claydon 2004). In catadromous fishes such as common snook *Centropomus undecimalis*, sexually mature adults travel from fresh and euryhaline water to coastal marine areas to spawn in aggregations, after which the fertilized eggs and larvae are swept inshore into brackish swamps and creeks (Gilmore et al. 1983, Russell & Garrett 1985, Peters et al. 1998, Tucker 2005). Because these fishes depend on high salinity water for successful fertilization of eggs, it is likely that all reproductive activity for the year is confined to the

spawning aggregations in marine areas (Edwards & Henderson 1987, Shapiro et al. 1993). For these and other species that aggregate to spawn, and specifically those individuals within a population that do not spawn annually, the persistence of spawning aggregations is vital for population maintenance (Heyman & Kjerfve 2008).

Fish spawning aggregations (FSAs) are vulnerable to overexploitation due to the predictability of their timing and the high density of fish within the aggregation (e.g. Johannes 1978, Sadovy et al. 1994). Heavy fishing pressure on FSAs decreases spawner abundance, decreases the mean size of spawners, alters population sex ratios, and depletes or disperses the aggregation (Craig 1969, Sadovy & Eklund 1999,

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Sala et al. 2001, Ames 2004). For example, a spawning aggregation of camouflage grouper dispersed in 7 d after anglers harvested 4000 individuals from the aggregation (Rhodes & Tupper 2008). Recovery of the FSA after a 7-yr moratorium on fishing was minimal. While this may represent an extreme case, the potential exploitation of FSAs has become a special concern for management agencies and highlights the need to understand aggregation dynamics (Coleman et al. 1996, Sadovy & Domeier 2005, Robinson et al. 2011).

The effects of fishing pressure on FSAs are influenced by several factors including the number of spawning sites, spatial distribution of spawning sites, length of spawning season, distance of migration, participation rates, fraction of the population spawning, and residence time in the aggregation (Smedbol & Stephenson 2001, Murua et al. 2003, Cardinale et al. 2011). Traditional tag and recapture studies are limited by time and distance between release and recapture points and thus provide inconclusive data when examining finer-scale movements (Domeier & Colin 1997). Vast improvements in technology including the use of archival and real time data loggers, stable isotopes, genetic markers, and otolith microchemistry now allow researchers to track and infer movement (McKenzie et al. 2012). In recent years, the migrations of common snook have been examined on the Gulf and Atlantic coasts of Florida in the United States using acoustic telemetry methods. Movement data from acoustic tagging of common snook show high intra-annual site fidelity to individual spawning sites (Atlantic stock: Lowerre-Barbieri et al. 2003; Gulf stock: Adams et al. 2009). However, in both of these studies the number of tagged individuals ($n < 30$) and receivers ($n < 12$) were limited. A greater sample size and more expansive array that include multiple aggregation sites may provide new insights into the movements and spawning traits of common snook.

Common snook are euryhaline fish that in the western Atlantic inhabit waters of coastal rivers and estuaries out to the continental shelf (Marshall 1958, McMichael et al. 1989). While adult common snook can be found in all aquatic habitats in their range, juveniles are generally confined to rivers and estuaries (Gilmore et al. 1983, Peters et al. 1998). Common snook are protandrous hermaphrodites, reaching sexual maturity as males at 169 to 222 mm total length (TL) with observed transition into sexually mature females between 264 and 876 mm TL during the fall following the spawning season (Taylor et al. 2000). Females exhibit batch spawning with a group-synchronous ovary type and a protracted spawning season of 5 to 7 mo from late spring to early autumn

(Tucker & Campbell 1988, Taylor et al. 1998). Females may spawn every 1 to 3 d with hydration of oocytes during the afternoon and early evening (Taylor et al. 1998). On the east coast of Florida, spawning aggregations of common snook have been documented in Palm Beach, Jupiter, and Fort Pierce inlets (Tucker & Campbell 1988, Taylor et al. 1998). Histological samples of gonads indicate that all fish present in an inlet during the spawning season are capable of spawning (Lowerre-Barbieri et al. 2003). Recent studies on migration frequency to spawning sites suggest, that at least for common snook on the Gulf coast of Florida and the similar barramundi *Lates catcarifer*, nearly half of the population does not spawn annually (Milton & Chenery 2005, Trotter et al. 2012). However, little is known about the migration frequency of common snook on the east coast of Florida, which varies geographically from the Gulf coast. Specifically, the east coast has a larger number of artificial coastal features than the Gulf coast of Florida (Adams et al. 2009).

Consideration of reproductive dynamics is the core of understanding how a population will respond to disturbances such as the fishing of aggregations (Chambers & Trippel 1997). In Florida, anglers frequently target spawning aggregations of common snook. The current harvest season for common snook on the Atlantic coast of the United States coincides with the reproductive season for 3 mo, or half the spawning season. In 2011, 69% (1630 individuals) of the total harvest of common snook was taken from inland waters during the spawning season, i.e. 15 April to 15 October (www.st.nmfs.noaa.gov/recreational-fisheries/index). A better understanding of the movement patterns and the factors that contribute to individual variability in reproductive effort will improve conservation and management of the species (Claydon 2004).

This study aims to provide insight into the population and individual spawning dynamics of common snook on the east coast of Florida using telemetry data. We investigated how spawning dynamics vary across time, space, and among environmental and physiological factors. Our hypotheses were: (1) *Population level*: Spawning aggregations of common snook reach peak density as a response to lunar phase, water temperature, time and inlet. (2) *Individual level*: Spawning traits vary between sizes, areas of residence, years and among sexes. (3) *Individual level*: Spawning status, whether the individual has spawned or not, is dependent on size, sex and area of residence. We then examined the implications of our results for fisheries management.

MATERIALS AND METHODS

Study area

This study was conducted along the eastern coast of the Florida peninsula from Ponce Inlet south through Delray Beach (between 29° 04' N, 80° 55' W and 26° 28' N, 80° 02' W). This includes a range of coastal environments that were categorized into 5 general habitat types: (1) *Rivers* are narrow (<1 km between shorelines) waterways that are headwaters to the river mouth. (2) *Estuaries* extend from river mouths to inlets and include connecting waterways between inlets. Estuaries are characterized by open waterways and lagoons with >1 km distance between shorelines. The estuaries are bound by the mainland and barrier islands of Florida that provide a unique passageway through (3) *inlets* connecting inshore and nearshore areas. These inlets are well defined by landmasses (barrier islands) that constrict water flow tidally between estuaries and nearshore/offshore habitats. Our (4) *nearshore* extended from the beach out to 1.6 km, and (5) *offshore* was any area east of nearshore. The study area included 8 geographic regions: Volusia, Canaveral, Sebastian, Fort Pierce, St. Lucie, Jupiter, Palm Beach and Delray; 7 major inlets: Ponce (PONI), Port Canaveral (CANI), Sebastian (SEBI), Fort Pierce (FTPI), St. Lucie (STLI), Jupiter (JUPI), and Palm Beach (PABI); and 3 coastal rivers: St. Sebastian, St. Lucie, and Loxahatchee, joined by the Indian River Lagoon (IRL) (Fig. 1).

Acoustic array

Tagged fish were monitored within a collaborative array of over 200 receivers spanning >300 km from PONI to Delray (Fig. 1). Within the array, Fish and Wildlife Research Institute (FWRI) staff deployed and maintained 62 automated Vemco acoustic receivers in rivers, estuaries, inlets, nearshore and offshore environments. Additional receivers were

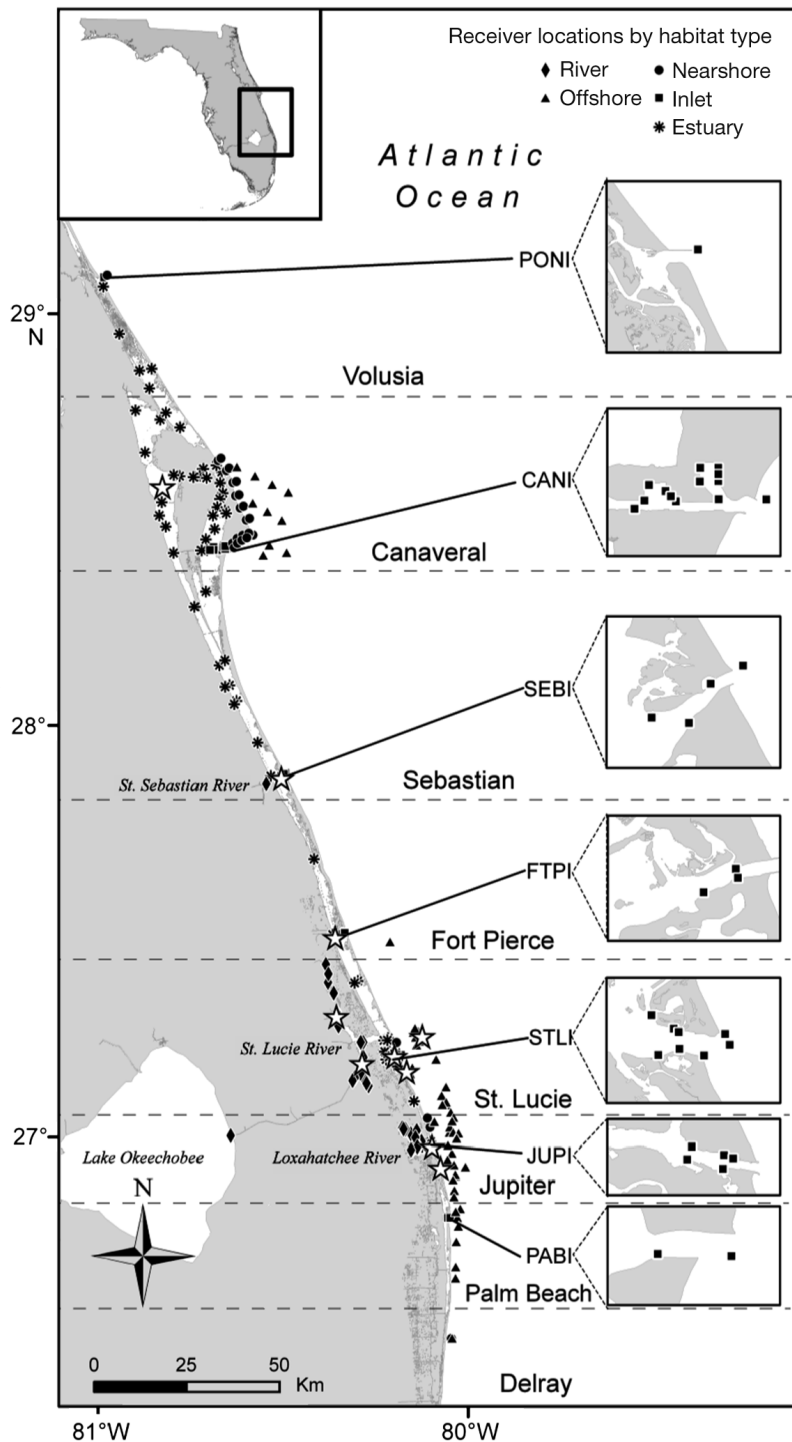


Fig. 1. East coast of Florida with Fish and Wildlife Research Institute receivers and Florida Atlantic Coast Telemetry Group receivers by habitat type (see figure key), and (☆) tagging locations of common snook. Insets on the right are close-ups of receiver coverage in the 7 inlets: Ponce (PONI), Port Canaveral (CANI), Sebastian (SEBI), Fort Pierce (FTPI), St. Lucie (STLI), Jupiter (JUPI), and Palm Beach (PABI). Regions are delineated with horizontal dashed lines

maintained by several organizations in the Florida Atlantic Coast Telemetry (FACT) group (see 'Acknowledgements'). In 2008, inlet receiver coverage only included PABI, JUPI and STLI. Receivers were placed in 4 additional inlets (FTPI, SEBI, CANI, and PONI) before the spawning season in 2009. Receiver data collection and maintenance were conducted every other month.

Capture and tagging

During sampling from February 2008 to August 2011, adult-sized common snook were caught using (1) rod and reel gear in inlets, nearshore and offshore areas ($n = 180$); (2) a Smith-Root 9.0 GPP Electrofisher in rivers ($n = 45$); (3) a 183 m haul seine in rivers and estuaries ($n = 35$); (4) a cast net in estuaries ($n = 8$); or (5) a trammel net in estuaries ($n = 3$). Fish were implanted with Vemco V-16 transmitters having an expected battery life of 4 yr. After collection, fish were measured (TL) to the nearest millimeter and marked with an external dart tag. Sex was determined by external examination of the vent area, a protocol having 96% accuracy for common snook (Lowerre-Barbieri et al. 2003). Females exhibited an oviduct opening directly posterior to the anal slit and ripe males extruded milt under pressure applied to the abdomen (Neidig et al. 2000). Sex determination was more difficult during the winter months when gonads were in regressing and recovering states. When sex could not be determined, the sex of the individual was not assigned. Methods for transmitter implantation were identical to those outlined in a previous study on common snook (Lowerre-Barbieri et al. 2003) with the addition of 1 or 2 Vicryl™ sutures to close the incision line. After surgery (total time <5 min), fish were held in an aerated holding tank for 5 to 10 min for assessment of their condition, to allow full recovery, and for verification of transmitter functionality before release. Fish were released at the side of the boat as close as possible to the point of capture. Fish caught offshore were examined for signs of barotrauma (protruding eyes and stomach). No fish caught showed signs of extended eyes and 4 had protruding stomachs. In those rare cases, fish were vented following an adapted protocol from Roach et al. (2011) where the air bladder was punctured through the surgical incision instead of the body wall. Fish caught at a depth greater than 18 m were recompressed by returning them to depth with a weighted line otherwise known as a drop-down rig (e.g. Hochhalter & Reed 2011, Butcher et al.

2012). Once the fish reached the bottom, a quick pull on the line causes the hook to slip out of the mouth.

Telemetry data and spawning variables

Telemetry data normally contain a certain amount of erroneous detections which can increase in number due to code collisions from the detection of other tags, and abiotic (e.g. boat) and biotic (e.g. snapping shrimp) noise (Heupel et al. 2006, Pincock 2012). Prior to analyses, 'false' detections and single detections were removed from the dataset (see Clements et al. 2005). Exclusion of tagged fish from analysis based on low detection duration (i.e. the number of days between first and last detection) and/or suspect detection data (i.e. continuous detection on a single receiver) has become more common in telemetry based studies (e.g. Danylchuk et al. 2011, Walsh et al. 2012, Wood et al. 2012, Bijoux et al. 2013). For this study, detection duration was calculated by season per fish. We defined the spawning season as extending from 15 April through 15 October based on Taylor et al. (1998). Tagged fish with <10 d detection duration in a spawning season were removed from analysis for that season.

We calculated a predicted length for each fish at the beginning of every spawning season by estimating age at capture and adding a computed growth based on age and time. Initial age was estimated using the von Bertalanffy growth function solved for age (t). Additional parameters include growth coefficient (K), asymptotic length (L), hypothetical age at which fish would have zero length (t_0), and length at time of capture (L_t). Parameter estimates $K = 0.23$, $L = 989.30$ and $t_0 = 0.0976$ are specific to the Atlantic stock of common snook and were updated from Taylor et al. (2000) (R. Taylor pers. comm.).

$$t = \frac{1}{K} \ln \left(\frac{L - L_t}{L} \right) + t_0 \quad (1)$$

The rate of change (growth) as a function of age was calculated using a Von Bertalanffy growth curve. L_t was differentiated with respect to t as follows:

$$\frac{dL}{dt} = t_0 - \left(\frac{1}{K} \right) \ln \left(\frac{L - L_t}{L} \right) \quad (2)$$

The potential for asynchronous hermaphrodites to change sex during the course of a longterm study increases when the sample population approaches or exceeds the known size at sex transition. In our study, common snook originally sexed as male ($n = 97$, range 538 to 952 mm TL) met and exceeded the

size range associated with sex transition (263.58 to 876.20 mm TL; Taylor et al. 2000). We acknowledge that common snook originally sexed as male during surgery may have changed sex at any point in the study, but most likely during the fall after any spawning season (Taylor et al. 2000). For this reason, male sex assignment was only used in the first spawning season after tagging. If a male had more than one year of data, the sex variable was treated as missing data, the same as individuals that were not assigned sex in the field. There is no evidence that female snook revert back to males, so females were modeled as such for the entirety of the study (Taylor et al. 2000).

Spawning aggregation sites were defined as 'any temporary aggregations formed by fishes that have migrated for the specific purpose of spawning' (Claydon 2004, p. 266). Based on previous studies that have shown histological evidence that common snook spawn in inlets (Taylor et al. 1998), we preselected all inlets in the study area as potential aggregation sites. A spawning aggregation was determined by the detection of multiple tagged individuals in an inlet on the same day. Aggregation and individual spawning traits were quantified by several measures including density, arrival, spawning period, number of trips to an inlet, event length, hiatus length, and spawning status (for definitions see Table 1).

Data analysis

Generalized linear mixed-effects models (GLMM) were used to model aggregation and individual spawning traits as a function of abiotic and biotic factors. GLMM are particularly suited for analyses of detection data and have been employed successfully in other studies using this type of data (e.g. Rogers &

White 2007). Aggregation spawning traits were modeled as a function of time (month, day and year), space (inlet), water temperature and lunar cycle. Individual spawning traits were modeled as a function of time (year), space (area of residence), sex and total length. Area of residence was defined as the most common region/habitat system an individual was detected in prior to the start of the spawning season. For individual spawning trait models, tag ID was entered as a random effect (Table 2). When the main effects were significant, least squares mean (LSM) post hoc tests were used to compare differences between groups. Best-fit models for aggregation and spawning traits were selected using the second order adjustment of the Akaike Information Criterion (AICc).

Table 2. Predictors used in the generalized linear mixed-effects models (GLMM) for aggregation and individual spawning traits. (c): categorical variable

Spawning dynamics (response variables)	Biotic and abiotic factors (predictor variables)
	Aggregation
Density	Inlet (c) Water temperature Lunar phase (c) Month (c) Year (c) Day
	Individual
Arrival date	Year (c)
Spawning period	Area of residence (c)
Number of trips	Sex (c)
Event length	Total length
Hiatus length	Tag ID (c) (<i>random effect</i>)
Number of inlets	
Spawning status	

Table 1. Definition of aggregation and individual spawning traits

Trait	Definition
Aggregation	
Density	The number of tagged fish detected per day by inlet
Individual	
Arrival date	The first day (1 to 366) an individual was detected in an inlet
Spawning period	The period (in days) between the first and last day, inclusive, an individual was detected in an inlet
Number of trips	The number of trips an individual made to an inlet
Event length	The time (in days) an individual is continuously detected in an inlet followed by an absence of at least 24 h
Hiatus length	The time between spawning events when an individual was not detected in an inlet (i.e. spawning interval)
Spawning status	An individual was detected in an inlet (1) or not detected in an inlet (0) during the spawning season

Table 3. Summary statistics (mean \pm SE and range) of common snook tagged with V-16 acoustic transmitters, by year (271 individuals). TL: total length; nd: no data. TL and sex were recorded at the time of original capture. An 'unknown' category was created because it was difficult to determine sex in the winter (non-spawning) period

Year	Female		Male		Unknown	
	n	TL (mm)	n	TL (mm)	n	TL (mm)
2008	80	898.93 \pm 9.41 (685–1109)	30	774.46 \pm 15.10 (602–891)	22	814.04 \pm 15.39 (629–999)
2009	40	869.80 \pm 18.97 (630–1065)	45	768.40 \pm 17.57 (538–952)	7	669.71 \pm 22.50 (590–742)
2010	8	916 \pm 16.90 (820–999)	9	843.88 \pm 26.79 (690–930)	4	877.75 \pm 22.13 (833–938)
2011	13	894.15 \pm 15.23 (825–990)	13	833.69 \pm 23.09 (620–950)	nd	nd

For all analyses, data transformations to meet assumptions of normality and homoscedasticity were calculated using a natural log transformation. Analyses were conducted using SAS[®] 9.2 software.

RESULTS

A total of 271 sexually mature common snook were implanted with V-16 acoustic transmitters (Table 3). Our high survival rate (95%) and examination of a completely closed incision line in a recaptured fish 2 wk after tag implantation confirmed that our surgery technique was successful. Fish were tagged in all 5 systems (number tagged per system: river 55, estuary 56, inlet 74, nearshore 23, offshore 63) in 5 regions (number tagged per region: Canaveral 34, Sebastian 15, Fort Pierce 36, St. Lucie 152, Jupiter 34). Fifteen fish were never detected post release and 19 fish were never detected during a spawning season. The remaining 237 tagged fish had detection data during 1 or more spawning seasons and logged >3.1 million valid detections (Table 4).

Of the 237 fish with detection data during the spawning season, we omitted 34 tagged individuals (total 34 seasons) completely and 1 season from 15 tagged individuals (total 15 seasons) from further analysis due to low detection duration (<10 d). As a result, our dataset comprised 203 tagged fish with a combined 359 seasons of data. The majority of tagged snook (n = 105) had 1 spawning season of detection data. However, 51 individuals were monitored over 2 spawning seasons, 36 over 3 spawning seasons, and 11 over 4 spawning seasons.

Tagged fish fell into one of 3 categories: (1) tagged fish that were detected in an inlet every spawning season they were tracked (n = 136, 243 seasons), (2) tagged fish that were never detected in an inlet during the spawning season (n = 47, 61

seasons), and (3) tagged fish that were detected in an inlet during some spawning seasons but not every season they were tracked (n = 20, 55 seasons).

Models with lowest AICc are reported in Table 5; however not all best fit models contained significant main effects.

Aggregation spawning traits

Over the course of the study, tagged individuals were detected in CANI, SEBI, FTPI, STLI, JUPI and PABI. No tags were detected in PONI. After completion of the array (February 2009), tagged individuals were detected in the 6 inlets during every spawning season. The GLMM revealed that inlet, water temperature, month, and year (each $p < 0.0001$) had significant effects on aggregation density (Table 5). In general, an increase in aggregation density corresponded with temperatures rising above 23.66°C (SD = 1.75) in April. Water temperature during peak aggregation in July averaged 27.25°C (SD = 2.77), below the mean maximum summer water temperature of 28.82°C (SD = 0.81) in September (Fig. 2). The highest modeled aggregation densities were seen in SEBI, STLI, and

Table 4. Summary of acoustic receiver detections of common snook implanted with acoustic transmitters, during the spawning season (15 April to 15 October) in each year

Year	Number of tags with valid detections	Total number of valid detections	Number of valid detections per tagged fish (mean \pm SE) (range)	Total number of stations with detections
2008	99	619401	6194 \pm 830 0–47819	71
2009	136	870687	6175 \pm 1070 0–80259	78
2010	95	685474	6854 \pm 1082 0–55581	77
2011	81	931708	11225 \pm 1901 0–100520	83

Table 5. Best fit models based on lowest corrected Akaike information criterion (AICc) values and significance of main effects specified in the GLMM model for aggregation and individual spawning traits of common snook

Trait	Effect	df	F	p	AICc
Aggregation					
Density	Inlet	6,4897	39.50	<0.0001	22448.0
	Water temperature	1,4897	32.52	<0.0001	
	Month	11,4897	81.56	<0.0001	
	Year	3,4897	42.51	<0.0001	
	Lunar phase	7,4897	0.75	0.6282	
Individual					
Arrival date	Year	3,67	7.47	0.0002	-90.9
	Sex	1,67	10.03	0.0023	
Spawning period	Sex	1,27	1.54	0.2249	331.4
	Area of residence	11,27	0.99	0.4772	
Number of trips	Sex	1,27	5.35	0.0286	213.7
	Area of residence	11,27	1.47	0.2016	
Event length	Sex	1,27	0.23	0.6347	365.5
	Area of residence	11,27	0.96	0.4998	
Hiatus length	Sex	1,27	17.23	0.0003	226.7
	Area of residence	11,27	2.07	0.0608	
Number of inlets	Sex	1,26	4.09	0.0536	110.9
	Area of residence	1,26	0.70	0.4098	
	Total length	11,26	2.80	0.0150	
Spawning status	Year	3,29	8.64	0.0003	93.4
	Sex	1,29	3.22	0.0833	
	Area of residence	12,29	4.51	0.0004	
	Total length	1,29	4.71	0.0383	

JUPI, while PABI and PONI had the lowest (Fig. 3). The model also predicted that density significantly increases from May to June (LSM: $t_{4897} = -7.97$, $p < 0.0001$), peaks in July, and rapidly drops off between August and September (LSM: $t_{4897} = 12.90$, $p < 0.0001$; Fig. 4). Aggregation density was highest in 2008 (estimated marginal mean [EMM] = 1.9141, SE = 0.1475), and decreased every year during the study.

Individual spawning traits

Traits were calculated for the 156 individuals that were detected in an inlet for at least 1 season from 2008 through 2011 (Table 6). GLMM revealed varying influences of year, sex, area of residence, and total length, on spawning traits (Table 5).

Initial migrations to spawning sites were staggered throughout the summer (arrival date: 105 to 288, i.e. April 15 to October 15), but were concentrated in the middle of the spawning season (mean \pm SE: 194.02 ± 2.74 , i.e. July 13) (Table 6). The model indicated that females migrated to spawning sites (191.24 ± 2.69 , i.e. July 10) earlier in the season than males (220.09 ± 8.24 , i.e. August 8; LSM: $t_{76} =$

0.03864 , $p = 0.0023$). Year was a significant predictor in the GLMM ($p = 0.0002$) and in 2008, fish migrated to spawning sites later than all other years (LSM 2009: $t_{67} = 2.64$, $p = 0.0498$; 2010: $t_{67} = 4.56$, $p = 0.0001$; 2011: $t_{67} = 3.30$, $p = 0.0083$).

Although tagged fish were constantly present in inlets throughout the spawning season, composition of the aggregation changed daily; common snook migrated in and out of 1 or more spawning aggregations throughout the summer. Tagged fish made (mean \pm SE) 7.70 ± 0.44 trips to an inlet and were detected for 3.28 ± 0.43 d (event length) before leaving for 10.19 ± 1.45 d (hiatus) (Table 6). Females made more trips (8.47 ± 0.47) compared to males (4.72 ± 0.83 ; LSM: $t_{27} = 2.31$, $p = 0.0286$). Females also had a shorter hiatus (8.90 ± 1.01 d) between trips than males (15.96 ± 7.32 d; LSM: $t_{27} = -4.15$, $p = 0.0003$). Individual spawning period ranged from 1 to 181 d but did not encompass the entire spawning season (38.57 ± 2.50 d) (Table 6).

Tagged fish were detected in one or more inlets (range 1 to 5) during the spawning season (mean \pm SE: 1.50 ± 0.05) (Table 6). Of the 156 tagged fish detected in an inlet, 47% ($n = 74$) were detected in >1 inlet in a single season. TL ($p = 0.0150$) was a significant predictor of the number of inlets in which a tagged fish was detected (Table 5). TL varied among individuals that used multiple inlets, but in general larger fish were detected in fewer inlets compared to smaller tagged fish (Fig. 5).

Spawning status

Spawning status was significantly affected by year ($p = 0.0003$), area of residence ($p = 0.0004$), and TL ($p = 0.0383$) (Table 5). A greater number of tagged fish were not detected in an inlet during 2008 compared to all other years (LSM 2009: $t_{29} = -4.93$, $p = 0.0002$; 2010: $t_{29} = -4.16$, $p = 0.0014$; 2011: $t_{29} = -3.94$, $p = 0.0025$). TL was a significant predictor of spawning status but the relationship of size and probability of spawning was not clear. Mean size of 'non-spawning' fish residing in the St. Lucie River and Canaveral estuary was smaller than 'spawning' fish that reside in

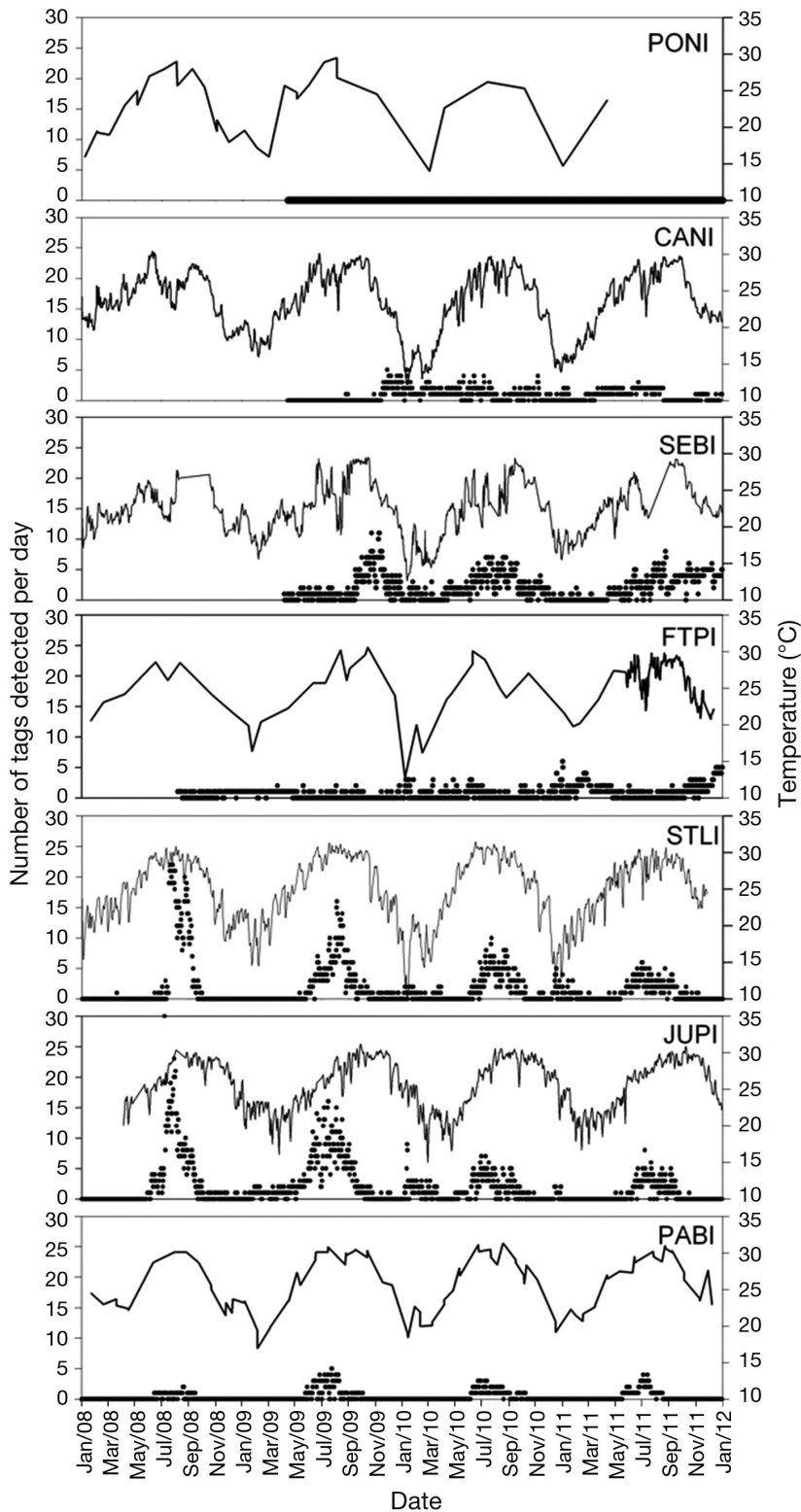


Fig. 2. Number of tagged common snook detected per day (dots) and temperature (lines) at 7 tagging locations (for locations and abbreviations see Fig. 1) from 2008 to 2011. Daily, weekly, or monthly temperature data was provided by the Florida Institute of Technology, National Oceanic and Atmospheric Administration, and the South Florida Water Management District

the same areas. However, mean size of 'non-spawning' fish in the Fort Pierce and St. Lucie estuary was greater than their 'spawning' cohabitants (Fig. 6). Some tagged fish residing in the St. Lucie River, St. Lucie estuary, Fort Pierce estuary, and Canaveral estuary (total $n = 50$, 95 seasons) and all fish residing offshore of St. Lucie and Ft. Pierce ($n = 17$, 21 seasons) skipped spawning for at least 1 season.

DISCUSSION

Aggregation spawning traits

Common snook were shown to spawn in 6 inlets from CANI to PABI during the summer months with peak densities within a 2 mo period between July and August. Aggregations formed after April when water temperatures exceeded 23°C. These observations paralleled those of Tucker & Campbell (1988), who found the temperature at which common snook commenced spawning ranged from 22 to 23°C. Abiotic factors including water temperature provide important cues for the formation of aggregations. For catadromous fishes, a change in water temperature triggers the downstream migration to spawning sites (*Alosa alosa*, Acolas et al. 2004; *Salmo trutta*, Bendall et al. 2005; *Pseudaphritis urvillii*, Crook et al. 2010; *Macquaria colonorum*, Walsh et al. 2013).

A consistent pattern of aggregation formation was documented in 6 inlets since the completion of the array in 2009, which expands the range of known common snook spawning sites (FTPI, Tucker & Campbell 1988; JUPI and PABI, Taylor et al. 1998). The lowest aggregation densities were observed in inlets at the periphery of the study site, PABI and PONI. No tags were deployed in PONI, PABI or their immediate areas. However, we did detect a low number of tagged fish in PABI every year. Spawning site selection based on balancing the energetic

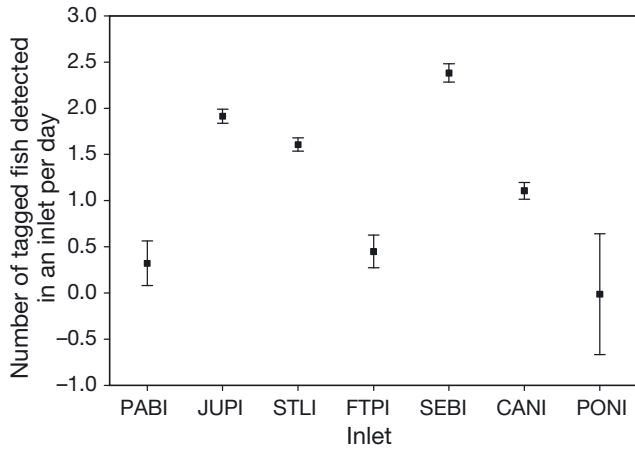


Fig. 3. Number of tagged common snook detected per day (density) in each inlet from 2008 to 2011 (for locations and abbreviations of tagging locations see Fig. 1). Density is presented as the mean response (estimated marginal mean [EMM] ± SE) for each inlet adjusted for all other variables in the model

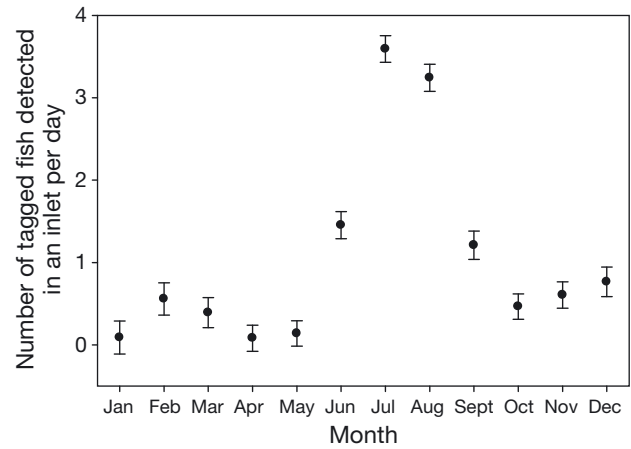


Fig. 4. Number of tagged common snook detected per day in inlets (density) by month from 2008 to 2011. Density is presented as the mean response (EMM ± SE) for each month adjusted for all other variables in the model

Table 6. Summary statistics (mean ± SE and range) of spawning traits of common snook with >10 d of detection duration. M: male; F: female; U: unassigned sex. Arrival date are shown as day of the year (doy), with days numbered from 1 to 366

Sex	No. of individuals	No. of seasons	Arrival date (doy)	Spawning period (d)	No. of trips to an inlet	Event length (d)	Hiatus length (d)	No. of inlets
F	89	158	191.24 ± 2.69 105–273	43.82 ± 2.83 1–181	8.47 ± 0.47 1–38	2.31 ± 0.33 0.01–32.83	8.90 ± 1.01 1.18–98.05	1.42 ± 0.05 1–5
M	33 ^a	33	220.09 ± 8.2 105–288	20.12 ± 5.93 1–150	4.72 ± 0.83 1–21	3.92 ± 0.99 0.01–22.49	15.96 ± 7.32 1.41–148.19	1.33 ± 0.11 1–3
U	50 ^a	81	175.85 ± 4.31 105–265	50.87 ± 4.80 1–173	9.85 ± 0.81 1–31	4.18 ± 0.78 0.01–36.02	8.92 ± 1.21 0.86–62.73	1.72 ± 0.10 1–5
All	156	272	194.02 ± 2.74 105–288	38.57 ± 2.50 1–181	7.70 ± 0.44 1–38	3.28 ± 0.43 0.01–36.02	10.19 ± 1.14 0.86–148.19	1.50 ± 0.05 1–5

^aIncludes 15 tagged fish that were assigned to male sex in the first season of spawning after tagging, and in subsequent seasons were considered as unassigned sex

cost of migrating verses site-specific benefits (cost-benefit optimization; Dodson 1997, Gladstone 2007) could lead to a strong delineation of catchment areas where animals that reside and feed within a certain radius of a spawning site would migrate to that spawning site (Claydon et al. 2012). Catchment and migration distance widely varies among species and can range from a few meters to hundreds of kilometers (Zeller 1998, Bolden 2000, Sala et al. 2003, Meyer et al. 2007). It is possible that densities were lowest or non-existent for PONI and PABI because tags were not deployed within catchment areas. In addition, PONI may represent the northern boundary of spawning sites on the Eastern Seaboard. PONI lies just above 29°N, the northern limit for mangrove distribution (Kangas & Lugo 1990), which is also thought to mirror the distribution of common snook (Gilmore et al. 1983).

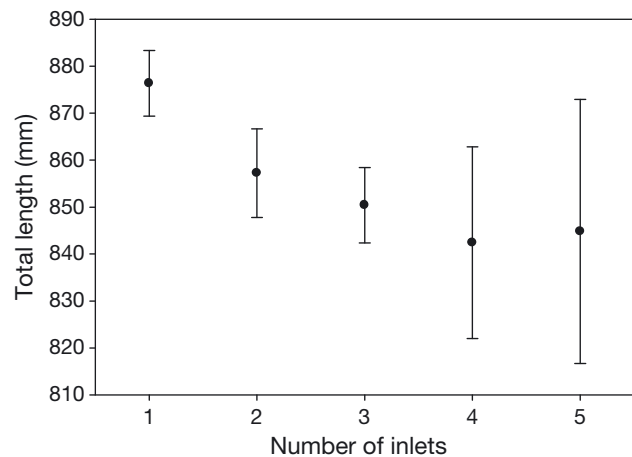


Fig. 5. Total length (mean ± SE) of tagged common snook, grouped into the number of inlets they were detected in from 2008 to 2011

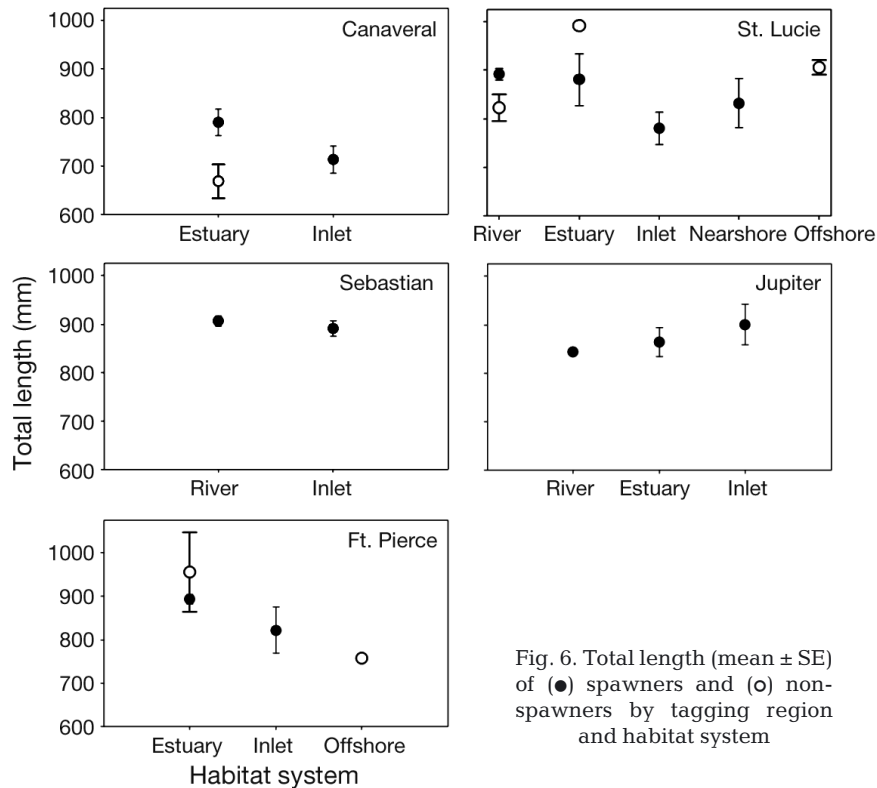


Fig. 6. Total length (mean \pm SE) of (●) spawners and (○) non-spawners by tagging region and habitat system

Temporal variation in aggregation density was only observed during the first year of the study and may be an artifact of the study design. Higher aggregation densities and later arrival dates may be explained by the number and timing of tag deployments. In 2008, only 30 tags were deployed before the start of the spawning season and additional tag deployments did not occur until the end of April that same year resulting in later arrival dates. Also in 2008, more tags were deployed in inlets ($n = 72$) compared to all other years (total 35 tags deployed in inlets between 2009 and 2011) increasing the chance of fish being detected in an inlet. This could have resulted in an artificially high density for that year.

Individual spawning traits

This study confirms that a number of factors drive variation in spawning traits of common snook. An individual's sex, area of residence and to a lesser extent size appeared to potentially affect the patterns of migration and spawning status of common snook to varying degrees, but not necessarily as predicted.

Common snook aggregations showed high turnover rates; fish made an average of 8 migrations to an aggregation site, stayed in the aggregation for only

3 d and left for 10 d. Repeated migrations away from aggregation sites have been observed for common snook (Lowerre-Barbieri et al. 2003) and other aggregate-forming catadromous fishes (Walsh et al. 2012) where number of intra-seasonal migrations ranged up to 5 per individual. Since migrations away from the spawning aggregation were ubiquitous among the study population, we propose that common snook disperse to feed. Feeding studies have shown a 3-fold increase in the incidence of prey in the stomachs of common snook in rivers during the summer compared to the winter (Blewett et al. 2013) and in tropical latitudes freshwater productivity exceeds marine productivity, suggesting a benefit in dispersing to feed inshore (Gross et al. 1988).

Furthermore, common snook did not spawn over the entire summer, initial migrations were asynchronous, and the individual spawning period was relatively short, similar to the spawning behavior of the closely related barramundi (Moore 1982). In our study, 47% ($n = 74$) of tagged common snook detected in inlets were observed at multiple spawning sites (2 to 5) during a single season, which differs from a previous telemetry study on common snook on the west coast, where only 2 tagged fish (sample size 19) were detected in >1 spawning site (Adams et al. 2009).

Studies on sexual differentiation in spawning behavior have shown that for many species, males make more trips (*Salvelinus confluentus*: Barnett & Paige 2013), arrive earlier at spawning sites (*Gadus morhua*, Windle & Rose 2007) and spend more time on spawning grounds (*Alosa alosa*, Acolas et al. 2004; *Epinephelus fuscoguttatus*, Rhodes et al. 2012). In contrast, our study showed female common snook arrived earlier, made more trips and had a shorter hiatus length compared to males, resulting in more time spent at an aggregation site. It is postulated that female fitness is more dependent on body size than males and thus females migrate more often to seek feeding grounds to gain energy for continual egg production throughout the spawning season (Jonsson & Jonsson 1993, Domínguez-Petit & Saborido-Rey 2010, Somarakis et al. 2012). This is supported by the presence of several stages of developing oocytes simultaneously occurring in female common snook (Taylor et al. 1998).

We have shown size-associated differences in levels of site fidelity, a concept postulated but not proven in previous studies on common snook (Adams et al. 2011). In contrast to what was predicted, we found that larger fish showed greater site fidelity to a single spawning site compared to smaller fish that used more spawning sites within a season. Traditionally, size is considered a strong determinant of reproductive success in teleosts; older, larger fishes are the first to spawn (*Scomber scombrus*, Dawson 1986), spawn more frequently (*Danio rerio*, Uusi-Heikkilä et al. 2010), produce offspring with increased survival rates and growth (Kamler 2005) and are more often selected as mates (*Oncorhynchus nerka*, Quinn & Foote 1994). Even among broadcast spawners, such as common snook, mate choice is an integral component of the reproductive strategy (Engen & Folstad 1999, Hutchings et al. 1999). Site selection and fidelity are partially attributed to learned behavior among fishes (Colin 1996), and are potentially influenced by levels of reproductive success. In birds, individuals that achieve high reproductive success are more likely to breed in the same area, while individuals that experience low reproductive success are less likely to return to the same nesting site (Haas 1998). Therefore, a large fish would show greater homophily to a spawning site where their size provided an advantage in mating, while a small fish might visit multiple spawning sites to seek additional mating opportunities.

The interpretation of data from multiple-year studies on asynchronous hermaphroditic species is challenging. However, understanding how differences in size and sex affect spawning behavior of these species is of key importance. We acknowledge that (1) tagged fish grew during this 4-yr study and (2) it is likely that at least a portion of the animals originally sexed as male transitioned to female at some point during the study. We have attempted to compensate for those influential features (see 'Materials and methods'). While we feel our approach was conservative, it could be a factor in the magnitude of the effect of sex and size on spawning behavior observed during this study.

Spawning status

Not all tagged fish were detected in an inlet during the spawning season, confirming the results of previous studies on common snook and closely related species that a portion of population does not spawn on an annual basis (Milton & Chenery 2005, Crook et

al. 2010, Trotter et al. 2012). The aforementioned studies found nearly half of the population did not spawn every year, while our study suggests that only an average of 24% (range 23 to 26%) of common snook skipped spawning. In 2008, when a greater number of tagged fish skipped spawning, the array was not complete. It is possible that the 23 tagged fish that were not detected in an inlet in 2008 spawned in an inlet that did not have receivers. Variation in spawning status of common snook was attributed to the effects of size and area of residence. Segments of the population residing inshore in the St. Lucie River, and the St. Lucie, Fort Pierce, and Canaveral estuaries were not detected in an inlet for 1 or more spawning seasons while all fish residing offshore were never detected in an inlet. Studies have suggested that common snook may use estuaries, nearshore and offshore waters as spawning grounds (Marshall 1958, Taylor et al. 1998, Alvarez-Lajonchère & Tsuzuki 2008). Histological evidence of spawning in these habitats on the east coast is lacking; but they are environmentally suitable for spawning (Gilmore et al. 1983). At least 1 species from the same geographic range with similar salinity requirements for reproduction has been found to spawn in the estuary as well as in inlets and nearshore water (*Sciaenops ocellatus*, Reyier et al. 2011).

A size differential among spawners and skip-spawners was not immediately apparent in our study. Size related factors found to contribute to skip spawning have included gonadal or pituitary immaturity in small fish and delayed maturity in larger fish (Lowerre-Barbieri et al. 2011). When comparing conspecifics from the same area of residence, skip-spawners were smaller than spawners in the St. Lucie River and Canaveral estuary, but were larger than spawners in the St. Lucie estuary and Fort Pierce estuary. More detailed gonad sampling of fish in these areas during the spawning season as well as studies on size at maturity is needed to fully understand potential skip-spawning. However, the number of tagged fish not detected in an inlet during the spawning season illustrates that all sexually mature common snook may not spawn every year.

Fisheries management

From a fisheries management perspective, it is clear the spatial and temporal predictability of common snook spawning aggregations makes them potentially vulnerable to overfishing. On the east coast of Florida, common snook have been targeted

annually during the period of regulated harvest that overlaps the spawning season (approximately 3 mo). Of 9 tagged fish harvested during the study, 5 were taken during the spawning season. An additional 22 tagged fish were recaptured and released during the study, of which 21 were recaptured during the spawning season. In other fisheries, data indicate that aggregations have diminished or ceased to exist after extensive fishing pressure (Craig 1969, Sadovy & Eklund 1999, Sala et al. 2001, Ames 2004).

The existence of a considerable and apparently non-declining recreational fishery of common snook on the east coast (Muller & Taylor 2012) supports the notion that common snook may be resilient to fishing pressure. Studies have shown that catch and release mortality is low (2.13%, Taylor et al. 2001) and fishing does not seem to interfere with spawning behavior (Lowerre-Barbieri et al. 2003). However, our understanding of compensatory mechanisms is still poor. For common snook, the observed sex-specific differences and susceptibility of larger individuals to hook and line gear (Welch et al. 2010) elevate the probability of sexual selection (large females) of aggregation-based fisheries. In sequential hermaphrodites, such as common snook, overfishing skews the sex ratio of the population to the side of the original sex, in this case male, and causes sexual transition to occur at smaller sizes (Allsop & West 2004, Hamilton et al. 2007). This measure of flexibility governing sex allocation allows the population to maintain high reproductive output; however under heavy pressure it breaks down as the gametes of the terminal sex become limited (Vincent & Sadovy 1998).

Despite the spatial and temporal predictability of common snook spawning aggregations, complex spawning behavior influenced by sex, size and regional differences creates a dynamic environment in which the composition of an aggregation fluctuates daily. Future research into environmental parameters, disturbance events, and migratory corridors linked to reproduction are encouraged, as their effects on spawning aggregations may impact the design of monitoring programs and management decisions.

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