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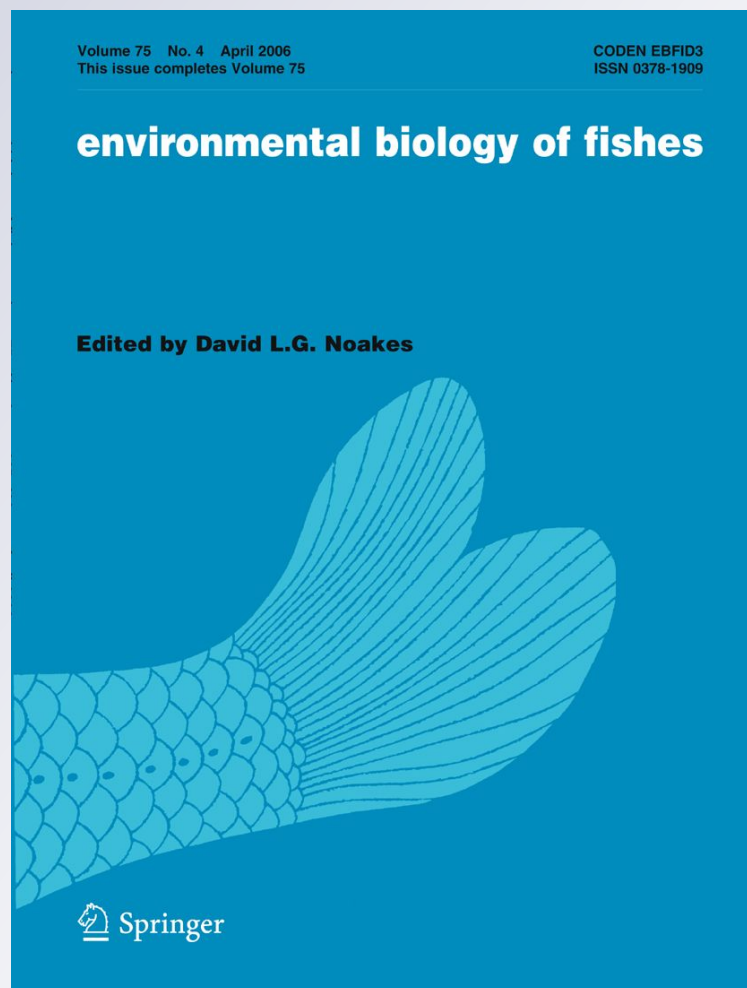
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Characteristics of spawning ground fidelity by a diadromous fish: a multi-year perspective

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Abstract Spawning site fidelity has long been documented for anadromous salmonids, and more recently in estuarine and marine fish. The level of fidelity has implications for population dynamics, conservation, and management. This study extended a previous examination of spawning ground fidelity for common snook, *Centropomus undecimalis*. We used seines to sample 28 km of Gulf of Mexico beaches, spawning grounds for snook, during spawning season (May through September) from 2007 through 2010. Of 3,304 snook tagged, 171 unique fish were recaptured a total of 186 times and, of those, 166 fish (97.08%) (181 recaptures=97.31%) were recaptured on the same island where they were tagged. One hundred seven of the recaptures occurred in the same year they were tagged, and 79 occurred one or more years after they were tagged, indicating fidelity was expressed within and across years. Distance between tag and recapture locations within and among years demon-

strated fidelity at a spatial scale much smaller than barrier island (mean distance between tag and recapture = 1.59 ± 0.12 km; island lengths 6.8, 8.9 and 12.4 km). Furthermore, mapping of capture locations revealed clumped distribution of snook on spawning grounds, further suggesting snook propensity for specific locations. Fish size had no effect on fidelity. We conclude that common snook show a high level of spawning site fidelity in southwest Florida, which may result in spawning group segregation, may influence the response of snook to disturbances, and may have implications for adult-to-nursery ontogenetic connections.

Keywords Site fidelity · Spawning · *Centropomus undecimalis* · Tag-recapture

Introduction

Fidelity to spawning grounds have long been documented for anadromous salmonids (e.g. Groot and Margolis 1991), and only more recently for marine and estuarine species. The level of fidelity exhibited by some marine fishes has implications for population dynamics, conservation, and management. For example, Robichaud and Rose (2001) discovered that Atlantic cod (*Gadus morhua*) exhibited fidelity to spawning grounds, and suggested that this fidelity may partly explain the lack of recovery of the Atlantic

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cod stocks in the New England and Nova Scotia region of North America. Colin (1992) determined that Nassau grouper (*Epinephelus striatus*) traveled up to 100 km to reach a spawning site, which helps explain the large spatial scale decline of Nassau grouper when spawning sites are targeted by fishing. Similarly, 60–81% of weakfish (*Cynoscion regalis*) (Thorrold et al. 2001) return to their natal estuary to spawn, and 59–99% of adult red drum (*Sciaenops ocellatus*) were found within or near their natal estuary (Rooper et al. 2010).

If exhibited at sufficient levels, spawning site fidelity may induce spawning segregation, thus inducing a metapopulation structure (Hanski and Gilpin 1997; Smedbol and Stephenson 2001) in what otherwise appears to be a single population. This can be true even if this segregation is not evident through genetic testing. Since the larvae from broadcast spawning that occurs in a location will, on average, be subject to similar current dynamics each year, a spawning area may contribute disproportionate numbers of recruits to one or more locations. Swearer et al. (1999), for example, found that most recruits to the north shore of St. Croix, U.S. Virgin Islands, originated on the north side of St. Croix, whereas most recruits along the south shore originated in locations that were upstream of the island.

Even in situations where it is not possible to address metapopulation structure resulting from spawning segregation, understanding that the segregation exists helps improve population models and increase understanding of ecosystem dynamics. Recognition of spawning segregation can be incorporated into spatial models of actual and anticipated natural and anthropogenic stressors. In addition, such knowledge may help frame research on connectivity between adult spawning locations and important juvenile habitats.

In previous research, Adams et al. (2009) used tag-recapture methods to document fidelity to spawning grounds by common snook, *Centropomus undecimalis*, over a two-year period. Fidelity was demonstrated at the scale of the individual barrier islands (6.8 km to 12.4 km in length) along which snook spawn in summer. This study extends the examination to 4 years, and documents the spatial and temporal components of fidelity for this species, focusing on the degree of fidelity over time, and locations and movements on spawning grounds.

Materials and methods

Study location

Charlotte Harbor is a 700 km² coastal plain estuarine system in southwest Florida (USA) (Hammett 1990; Fig. 1). The Peace, Myakka, and Caloosahatchee rivers, as well as many smaller creeks throughout the drainage, transport large amounts of fresh water into the harbor. The climate is subtropical; mean seasonal water temperatures range from 12° to 36°C, and freezes are infrequent (Poulakis et al. 2003). The estuary is separated from the Gulf of Mexico by a string of barrier islands, with tidal exchange through four inlets that separate the barrier islands – Boca Grande Pass, Captiva Pass, Redfish Pass, and San Carlos Pass. The Gulf-side shorelines of the islands are entirely sandy beaches. The passes are a mixture of natural sand and anthropogenically-hardened shorelines. Common snook spawn in proximity to the passes and at a few locations along the barrier island beaches during summer (Taylor et al. 1998; AJA pers. obs.).

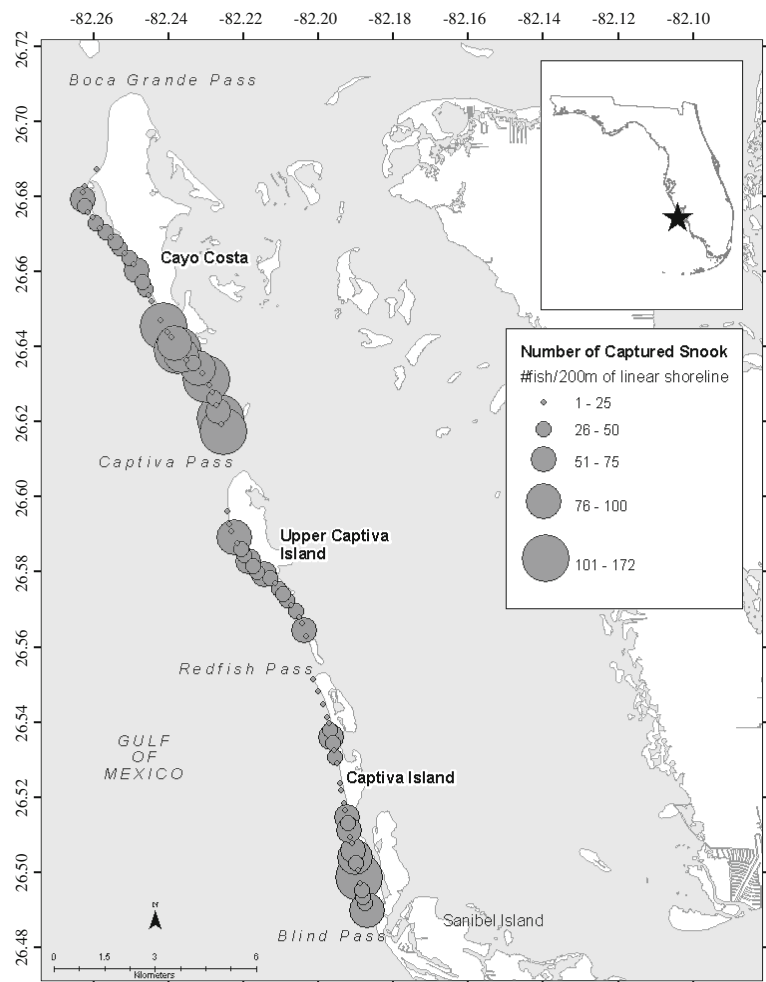
Focal species

Common snook, *Centropomus undecimalis*, is an estuarine-dependent catadromous fish present throughout the Caribbean Sea, and as far north as central Florida (USA) in the Gulf of Mexico and Atlantic Ocean (Taylor et al. 1998). In Florida, common snook is an economically important recreational species that receives intensive fishing pressure and is under strict management regulation (Taylor et al. 1998). The juvenile stage is dependent upon oligo- and meso-haline wetland habitats, whereas adults forage throughout the estuary but are dependent upon warm, saline coastal waters for spawning (Taylor et al. 1998). Snook spawning season in Florida extends from May through September (Taylor et al. 1998), though spawning in the Charlotte Harbor region has been observed in October (AJA pers. obs.).

Capture protocol

Sampling protocol was conducted according to Adams et al. (2009). From May through September of 2007, and May through August of 2008 through 2010, snook were captured along Gulf beaches of

Fig. 1 Locations and abundance of tagged and recaptured snook within study area in southwestern Florida, USA



three barrier islands – Cayo Costa (12.4 km long), Upper Captiva (6.8 km), and Lower Captiva (8.9 km) – between Boca Grande Pass and Blind Pass using seine nets (Fig. 1). Sampling effort was similar by island and year, though the number of samples per day ranged from one to seven and depended on the number of snook spotted and captured. For example, if a large number of snook were captured in a sample, the time to measure and tag the fish reduced the amount of time available for more samples on that day. On days in which few snook were spotted, the net was set ‘blind’ (e.g. set without seeing fish) to ensure samples were obtained on that day. Snook were captured in blind sets, especially on days with low water visibility.

Sampling occurred between 07:00 h (onset of suitable sunlight for sighting fish) and 12:00 h (increase in volume of human activity on beaches, water temperatures reached stressful levels for snook).

Sampling occurred as conditions allowed – onshore winds and/or high surf prevented sampling, as did proximity of hurricanes – and did not focus on a particular lunar phase. On each sample day, the entire length of beach that could be sampled on each island (e.g. free of trees and other debris) was searched if time allowed. A shallow-draft net boat was used to set seine nets around groups of common snook that were spotted along the beach. The procedure was to steer the boat along the beach and, when snook were spotted, one end of the net was deployed off the back of the boat and the boat was used to set the net around the school. During summer, snook typically hold within 2 m of shore, so this method is very effective. The nets were hauled onto shore, and the fish captured in the center bag. Three center-bag seine nets (91.44 m×2.44 m with 19.05 mm mesh, 182.88 m×2.44 m with 15.00 mm mesh, 152.40 m×

2.44 m with 19.05 mm mesh) were used during this study. Once captured, the snook were placed in mesh holding pens until tagging.

Tag-recapture

Tagging

Snook were tagged internally with 23 mm HDX Passive Integrated Transponder (PIT) tags (TIRFID 2000, Texas Instruments). Prior to tagging, snook were removed from the holding pens, and placed in a cooler with a seawater and Alka-Seltzer mix (1–1.5 tabs per 4 L seawater) to immobilize the fish. Once immobilized, a PIT tag with a unique 16-digit identification number was inserted into the abdominal cavity through a 3 mm incision (Adams et al. 2006). Standard length (SL), PIT tag number, and latitude-longitude were recorded for each fish. After tagging, fish were placed in a recovery pen for approximately 5 min and released at the site of capture. Since tagging experiments with juvenile snook reported no mortality (Adams et al. 2006) and there was only one mortality out of 3,304 fish tagged in this study, post-tagging mortality was assumed to be minor. A necropsy was conducted on the post-tagging mortality and no injury from the tagging procedure, parasites, or any other obvious causes for the mortality were found.

Recapture

Recapture occurred by seine along the Gulf of Mexico beaches of the barrier islands during spawning season (May through September). During seine sampling and prior to tagging, all snook were scanned with an Allflex ISO compatible RFID portable reader (model number RS601, Allflex) for PIT tags. In addition, on numerous sampling days, snook were not tagged – all captured snook were scanned for tags and released. For recaptures, PIT tag number, SL and latitude-longitude were recorded and the fish were released.

Analysis

Latitude and longitude were used to calculate the shortest distance along the shoreline between tag and recapture. Distances (m) were pooled across years for

each island, square-root transformed and analyzed with a one-way ANOVA supported by a Tukey post-hoc test to determine whether distance between tag and recapture locations differed among islands. Separately, distance data were analyzed to determine if there was a difference related to whether the fish was recaptured in the same year it was tagged or one or more years later. Distance data for fish that were recaptured more than once were examined with a paired *t*-test (with Bonferroni adjusted probability of 0.05) to determine if distances differed between the tagging location and the first and second recapture locations. The locations of all snook (tagged and recaptured) were plotted per 200 m of linear shoreline using ESRI ArcGIS to determine whether snook showed a clumped distribution on each barrier island.

To determine whether snook stayed on spawning grounds for different durations in each year, days at large (number of days between tagging date and recapture date) were calculated for each snook recaptured in the same season it was tagged, log transformed and examined with a two-way ANOVA with Island and Year as factors. A linear least squares regression was used to determine whether snook size influenced distance between tag and recapture locations.

Results

A total of 3,304 snook was tagged during this study: 754 in 2007, 1043 in 2008, 833 in 2009, and 674 in 2010. Tagged snook ranged from 307 mm to 851 mm standard length. Although sampling effort was similar on all islands, more snook were tagged on Cayo Costa than Upper or Lower Captiva (Table 1). There were 186 total recaptures during the study (5.63%), and sizes of tagged and recaptured fish were similar (Table 1). Of the 186 total recaptures, 171 were unique fish, and 11 fish were recaptured more than once. The capture and recapture rate decreased markedly in 2010 (Table 1) due to a severe cold disturbance in January 2010 that caused high levels of mortality in the regional snook population (AJA, unpublished data). However, this disturbance did not influence site fidelity; tag-recapture patterns remained the same.

Over the four-year study, 166 of the 171 unique fish recaptured (97.08%) were recaptured on the same island where they were tagged, indicating that site fidelity to

Table 1 Number of snook tagged and number of recaptures on Gulf of Mexico beaches during spawning season (May through September) by year and island. Total number tagged =3,304. Total number of recaptures=186 (of 171 unique fish, 11 were recaptured more than once)

Year	Island						
	Cayo Costa		Upper Captiva		Lower Captiva		
	Tag	Recap	Tag	Recap	Tag	Recap	
2007	291	14	164	6	299	0	
2008	475	14	266	12	302	2	
2009	395	59	134	34	304	9	
2010	476	26	104	7	94	3	
Total	1637	113	668	59	999	14	
Standard Length (mm)							
Median	412	420	422	418	404.5	422	
Mean	418	417.78	429.66	432.4	413.96	425.73	
Standard Error	1.18	7.12	1.88	13.3	2.18	11.84	

spawning locations is the predominant pattern for snook. One hundred seven of the recaptures occurred in the same year as tagging, and 79 occurred 1 or 2 years after tagging. When examined by island, site fidelity occurred at an even smaller spatial scale than island-level: distance between tag and recapture differed by island (ANOVA $p < 0.01$, $df = 170$, $F = 6.993$): mean = 1773.71 ± 160.96 m (median = 1290.59 m) for Cayo Costa; 871.90 ± 75.31 m (758.48 m) for Upper Captiva; and 1377.62 ± 334.53 m (1039.81 m) for Lower Captiva. Distance between tag and recapture locations did not differ for snook captured in the same year they were tagged or one or more years later (Fig. 2a). However, fish that were recaptured twice were recaptured at a greater distance from the tagging location the second time ($t = -3.558$, Bonferroni adjusted $p < 0.05$, $df = 10$; Fig. 2b), though there was no clear trend in distance within or among years.

Four of the five snook that were recaptured on an island different from where they were tagged were originally tagged on Upper Captiva, the shortest barrier island. Two of the fish recaptured on a different island were recaptured in the same year of tagging, and three were recaptured one or more years after tagging.

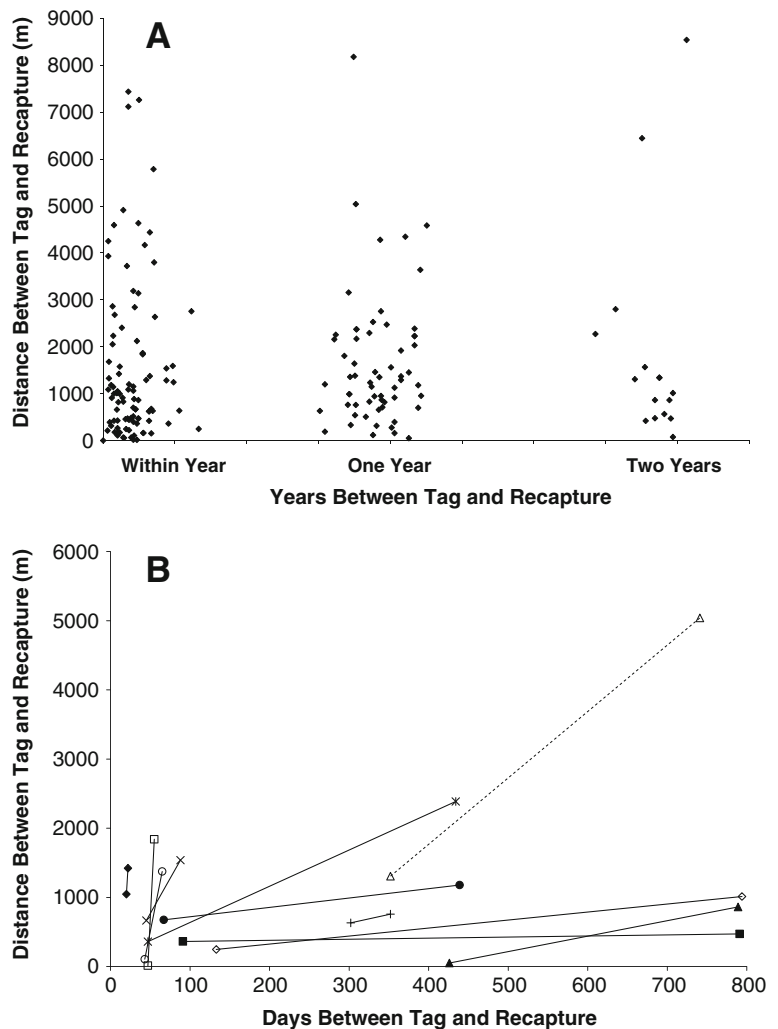
Graphical examination of snook capture locations revealed clumped distributions (Fig. 1), further indicating propensity of snook to aggregate at particular locations and further supporting a pattern of strong site fidelity. Days-at-large did not differ by year or island (ANOVA $p > 0.05$, $df = 105$, $F = 1.610$). Standard length did not affect the distance between tag and recapture locations ($R^2 = 0.001$, $p > 0.1$).

Discussion

This study demonstrates an extremely high level of spawning site fidelity over multiple years over an extensive area of spawning ground shoreline. Moreover, this study demonstrates that adult snook on spawning grounds show site fidelity at a spatial scale much smaller than barrier island length, which increases the likelihood of spawning segregation for the snook population in Florida. This has numerous ecological and management implications.

The recapture strategy used in this study ensured that an accurate depiction of snook movements on spawning grounds was obtained. Although the recapture rate in this study was not high, it was similar to other studies that used internal tags and required physical recapture of marine fishes (e.g., Leber et al. 1995; Willis et al. 1995) as well some using external tags (e.g., Fowler and Stobo 1999). Furthermore, it is common knowledge that snook move between estuarine habitats and spawning grounds during spawning season, which likely contributed to the relatively low overall recapture rate in that this study sampled only a portion of the overall local population. The extensive length of coastal beach habitat sampled during this study would have detected long-distance, inter-island movement as well as any tendency toward increased dispersal over time or with fish size. Even if snook dispersed to other spawning locations outside the study area, for example, if such behavior was common it would have also resulted in movements among islands sampled in this study, but such movement was rare. Interestingly, a single barrier

Fig. 2 Relationship between distance moved between tag and recapture locations over time. **a** Distance between tag and recapture locations for snook that were recaptured within the same year they were tagged, and recaptured 1 or 2 years after tagging. Data points are shifted horizontally within each year to reduce overlap and more clearly present the data. **b** Distances between tag and recapture locations for fish that were recaptured more than once. The two recapture locations for each fish share the same symbol and are connected by a line. The fish connected by the dashed line was recaptured on an island different than where it was tagged on the second recapture. All other fish were recaptured on the same island on which they were tagged



island – Upper Captiva – was involved in all of the snook that did not show fidelity: four moved away and one moved to the island.

Despite individual differences in the degree of movement, the overall pattern for snook on spawning grounds is one of fidelity. At the population level, the lack of inter-annual difference in distance between tag and recapture locations indicates that the population as a whole shows fidelity. Although there was a trend of increasing distance from tagging location with the second recapture, for all but one individual both recaptures were on the same island, and for many individuals the increase in distance was <1 km.

This study sampled the size classes that dominate the snook population along the Gulf of Mexico coast during spawning season, so results are applicable to

the spawning population present on these grounds. Snook are protandrous hermaphrodites, with a population-level sex ratio skewed toward males (male:female=1.6:1.0) (Taylor et al. 2000). Moreover, females smaller than 452 mm SL are rare (Taylor et al. 2000), and the predicted length at which the sex ratio is 1.0:1.0 is 553 mm SL on the Gulf of Mexico coast (Taylor et al. 2000). In this study, large (assumed to be female) snook were only observed occasionally in the spawning grounds. The mean standard length of tagged snook was 422 mm, notably less than the size at which sex change appears to first occur (452 mm), and considerably less than the size (553 mm) at which the expected sex ratio is 1:1. However, since snook length was not a factor in distance between tag and recapture locations, and

only one of the snook that showed inter-island movement was greater than 450 mm, the results of this study are valid for the snook population present on spawning grounds.

It is also possible that adult snook reach a threshold size at which they are less likely to exhibit site fidelity. In this scenario, once they reach a threshold size, large females may use multiple spawning sites along a coastline as a bet-hedging strategy for successful reproduction, which would result in more genetic mixing. This would be in contrast to males and small females that show fidelity to locations where spawning is known to occur, thus ensuring participation in reproduction. If there is a threshold size at which behavior changes, it is greater than what was sampled in this study. This is clearly an area which requires additional examination.

There are numerous implications for such a high level of spawning site fidelity. Fidelity to spawning grounds may make snook more susceptible to natural or anthropogenic disturbances. Damage from hurricanes, for example, can cause fish displacement (Letourneur 1996; Paerl et al. 2001). Waves and currents from hurricanes can move large amounts of sediment, changing beach and barrier island topography such that inlets may be filled or new inlets opened. This may in turn cause hydrographic changes that affect larval transport from spawning locations, and thus affect spawning success. Similarly, red tide, caused by the toxic dinoflagellate *Karenia brevis*, is a patchy disturbance that causes extensive fish mortalities. Anthropogenic disturbances can have equally damaging results. Coastal beaches are subject to beach nourishment programs to combat natural erosion processes. Effects of beach nourishment include an increase in suspended sediment throughout the water column, decrease in water clarity, and the loss of invertebrate assemblages, which are integral sources of sustenance for fish and many other organisms (Peterson and Bishop 2005). Loss of prey for larger predators may force fish to migrate in search of more suitable habitat with a larger prey selection or result in poor condition of fish that remain in the affected location. Dredging and shoreline hardening may produce similar impacts on snook and other species that use beach habitats.

Depending on how snook find spawning locations, both anthropogenic and natural disturbances can be problematic. If the mechanism for forming fidelity in

snook is *spawning-group fidelity* (Robichaud and Rose 2001), newly mature individuals may congregate at a location that provides suitable spawning conditions, regardless of whether fish have previously spawned there. This allows for colonization of new spawning locations without prior experience, making the spawning population more adaptable to disturbances. If snook find spawning sites via *social learning* (Colin 1996), newly mature fish will follow surviving adults to traditional spawning sites, thus increasing local abundance of spawners at these sites (as long as sufficient older fish remain after a disturbance). As long as the traditional site remains a viable spawning habitat, this will result in a strong response to a disturbance. If, however, a traditional location is badly impacted by a disturbance, fish that continue to spawn or newly spawn in this location may experience reduced fitness. In contrast, if *philopatry* (Robichaud and Rose 2001) is the mechanism by which snook find spawning locations, loss of multiple year classes of the site's lineage would result in loss of spawning individuals at that site, and slow the rate of response to a disturbance.

Spawning site fidelity also implies a consistent spatial structure of connectivity between spawning locations, larval transport, and nursery habitats. One would expect a spawning site to, on average, provide larvae to a particular area, thus connecting specific spawning and nursery habitats. If this area contains suitable nursery habitat, then that spawning location can expect some reproductive success. On the other hand, if the larval settlement area contains no or poor quality nursery habitat, then reproductive success of that spawning site will be low. In the case of snook, a relatively short larval duration (~ 2 weeks) and proximity of spawning grounds and juvenile habitats may enhance the spatial ontogenetic connectivity because the larvae travel shorter distances so are subject to less spatial complexity of currents.

The extent to which spawning site fidelity influences genetic structure of the population depends on the mechanism by which fidelity is established, whether its duration is lifelong, and spatial considerations. In the case of spawning-group and socially learned fidelity, the connection breaks down as juveniles leave nursery habitats, grow into adults, and find spawning locations. This is because their spawning site selection is based on factors exclusive to sexual

maturation and the adult life stage, so are not necessarily connected to the juvenile life stage and habitat location. This may make it difficult to detect spawning segregation in the population genetic structure, especially at the within-estuary scale, where spawning locations are within relatively close proximity. However, if spawning site selection is limited to locations near the natal estuary, among-estuary segregation may be detectable. In contrast, if site fidelity results from philopatry, then the link between spawning sites and juvenile habitats may be strong because juveniles that survive to maturity will spawn at their natal spawning location. In this scenario, a distinct sub-population genetic structure should be evident among estuaries, and perhaps even with an estuary.

Future research efforts should be three-fold. First, research should examine the mechanism for snook spawning site fidelity because each mechanism has different implications for how snook populations will respond to both natural and anthropogenic disturbances. Second, whether snook reach a size threshold at which they lose spawning site fidelity should be examined, because of significant population-level implications resulting from different spatial genetic input from small and large snook. Third, genetic analysis may help determine the relationship between spawning sites and juvenile habitats at multiple scales. This research would determine the extent of genetic structure among spawning sites within and among estuaries, the level of genetic similarity between spawning sites and juvenile habitats within estuaries, the extent to which portions of the population can be identified with a specific spawning location (i.e., at the site, island, or estuary level) and the strength of any connections across successive generations. Since snook are already managed in Florida as two regional stocks due to genetic differences (Atlantic Ocean and Gulf of Mexico stocks) (Tringali and Bert 1996), it is likely that some level of within-region genetic structure exists. This information would be useful for prioritizing habitat conservation as well as gaining a better understanding of ecological factors influencing ontogenetic connectivity. Finally, information on spawning site fidelity and connectivity to juvenile habitats would be useful for adaptive management strategies that can respond to events such as natural and anthropogenic disturbances and habitat loss.

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