

Site fidelity and condition metrics suggest sequential habitat use by juvenile common snook

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ABSTRACT: The common snook *Centropomus undecimalis* is an estuarine-dependent fish that relies on landward wetlands as nursery habitat. Despite its economic importance, portions of the snook's early life history are poorly understood. We compared habitat use of young-of-the-year (YOY) snook in 2 geomorphic mesohabitats (tidal pond and tidal creek) along an estuarine gradient (upstream vs. downstream) within a single wetland during fall recruitment. We used abundance, length, condition indices, and stable isotopes to assess ontogenetic mesohabitat use and site fidelity. We found that (1) YOY snook were more abundant within the upstream creek and ponds; (2) the smallest snook were found only in ponds; (3) snook from ponds had lower condition (Fulton's *K* and hepatosomatic index); (4) snook began moving from ponds to the creek at ~40 mm standard length; and (5) snook from the 2 mesohabitats were isotopically distinct, indicating high site fidelity at rather small spatial scales. Collectively, these data identified sequential use of mesohabitats, wherein seaward-spawned YOY snook moved landward and recruited to pond habitats, where they dedicated energy to growth (as length) before making an ontogenetic habitat shift to the creek. Once in the creek, YOY snook condition improved as they approached maturity and started the downstream return towards seaward locations. The wetland network that was previously viewed as generalized nursery habitat instead consists of mesohabitats that support different life stages in sequence. This represents ontogenetic habitat complementation, in which lower availability of a required mesohabitat type may limit the entire wetland's contribution to the adult population.

KEY WORDS: *Centropomus undecimalis* · Habitat complexity · Mesohabitat · Nursery habitat · Stable isotopes · Tidal creek · Estuarine pond · Ontogenetic shifts · Landscape ecology

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INTRODUCTION

In freshwater and coastal ecosystems, it is understood that different geomorphic habitat types ('mesohabitats') may impart different growth and mortality rates to fish, thus affecting fitness (Rosenfeld & Boss 2001, Sheaves 2005). The relative availability of 2 or more required (high fitness) mesohabitats can be viewed either from the perspective of changing needs during life history (Rosenfeld & Boss 2001) or from the perspective of a single life stage that requires more than 1 type of mesohabitat over shorter time scales (e.g. a mesohabitat for foraging and an-

other for refuge; McIvor & Odum 1988). In either case, differences in availability among required mesohabitats determine the extent of 'habitat complementation' (Dunning et al. 1992, Schlosser 1995). Landscapes with high levels of habitat complementation are thought to support larger populations. In this paper, we document complementary mesohabitat use by an estuarine-dependent fish within a wetland that was formerly believed to serve as generalized habitat.

Many estuarine-dependent fish species follow a similar life-history strategy involving the use of multiple habitats. Thus, in testing life-history hypotheses,

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researchers must often explore large spatial scales to gather information from each of the many habitats that a species may use during different life stages. Spatial scale has a well known influence on the results obtained from habitat-use analyses (Levin 1992, Hawkins et al. 1993, Crook et al. 2001). In the case of fishes, most habitat analyses are based on site-level information, and thus patterns that occur at other scales are often overlooked (Dunham & Vinyard 1997). Studies of habitat use can be improved by recognizing the inherent limits of spatial resolution, by choosing the appropriate scale for specific hypotheses, and by nesting scales of study where possible (Levin 1992).

The concept of nursery habitat has been viewed very broadly in terms of both life history and the spatial scale of its designation. All life stages from post-settlement through subadults may be considered to use 'nursery' habitat. However, for species that are long-lived and attain large adult sizes, there are often sequential ontogenetic habitat changes within the pre-reproductive period that require consideration and further definition. Nursery habitats are often comprised of a variety of smaller mesohabitats that may play specific roles in juvenile fish development. Mesohabitats are visibly distinguishable features that differ in hydrologic or geomorphologic parameters, (e.g. geomorphic shape, flow velocity, volume, and sediment type; Kehmeier et al. 2007). Studies designed to compare differences in species distribution data or community metrics (i.e. predation risk, diet, density) among various mesohabitats can be useful for testing hypotheses and refining life-history models (McIvor & Odum 1988, Kehmeier et al. 2007, Stevens et al. 2010). Further, studies along estuarine gradients provide a strong study design that accommodates the well-demonstrated response of fishes to the complex gradients of tidal range, salinity, and wetland type within estuaries (e.g. Deegan & Garritt 1997, Ley et al. 1999).

Although various abundance metrics are routinely measured in fish ecology, sole dependence on abundance or density can be misleading when assessing the importance of specific habitats because these metrics fail to show the relative contribution of different habitats to adult stocks (Beck et al. 2001, Dahlgren et al. 2006). Collection of additional metrics such as condition, growth, and site fidelity can add meaningful insight into the ecological processes underlying habitat use. For example, measuring condition addresses concerns that habitat quality, when considered in a fitness-based context, is not adequately addressed by estimates of organism density

alone (Dahlgren et al. 2006). It is believed that higher-quality habitats result in improved fish condition (Ricker 1975) and thus greater future reproductive potential (Marshall et al. 1999, McBride et al. 2013).

Fishes that use multiple habitats prior to maturation often proceed through a more or less predictable ontogenetic sequence of habitat use. Knowing the degree of individual commitment to these habitats (i.e. knowing site fidelity) helps determine whether the habitat use is facultative, wherein individual fish search for better habitat within short time frames (e.g. hours to days), or obligatory, wherein the fish remain in 1 small area for weeks or months at a time. Understanding this aspect of habitat use is important to species management (Able 2005). Researchers have traditionally measured site fidelity and sequential movements using artificial tagging techniques. However, high mortality rates during early life history often make it impracticable to tag enough individuals to allow recapture of a sufficient number for analysis. Thus, researchers have recently begun to use natural chemical tags to track residency, movements, and general habitat-use patterns (reviewed by Gillanders 2009). Fodrie & Herzka (2013) compared the relative merits of 2 natural tags (otolith microchemistry and stable isotope ratios) in tracking ingress of ocean-spawned California halibut *Paralichthys californicus* into a Pacific coast estuary. Skinner et al. (2012) validated use of stable isotope analysis vs. traditional mark-recapture (external tagging) for mummichogs *Fundulus heteroclitus* and found very similar results (i.e. high site fidelity).

Centropomid fishes (snooks and *Lates* perches) are distributed throughout the coastal and freshwater regions of the world's tropics and warm-temperate zones, where they are often dominant predators that support important fisheries. The common snook *Centropomus undecimalis* (hereafter 'snook') is locally abundant from the Florida (USA) peninsula through the southern Gulf of Mexico and the Caribbean Sea to Brazil (Rivas 1986). Within this general range, adults are particularly known for close associations with mangrove-dominated estuarine shorelines (e.g. Winner et al. 2010), yet they also frequent a diversity of non-mangrove habitats in freshwater (Trotter et al. 2012, Blewett & Stevens 2013), estuarine (e.g. Gilmore et al. 1983, McMichael et al. 1989), and marine settings (R. Taylor unpubl. data).

According to the prevailing life-history model for snook, young juveniles recruit to shallow, quiescent habitats near the border between mangrove-dominated wetlands and terrestrial uplands (Fore &

Schmidt 1973, Gilmore et al. 1983, McMichael et al. 1989, Peters et al. 1998, Stevens et al. 2007). Researchers hypothesize that these landward wetland habitats serve as snook nursery grounds based on the abundance of very small juveniles in these habitats compared to other habitats within the estuary (i.e. Stevens et al. 2007). These habitats are often inaccessible by power boat, causing juvenile snook to be strongly under-represented in fisheries-independent monitoring data (Stevens et al. 2007). Snook nursery habitats are geographically small and have low hydrodynamic connectivities as a result of diminished tidal range. These habitats are also in proximity to developed uplands and are therefore often influenced by upland drainage and associated pollutants (Malkin 2010). Snook are protandrous hermaphrodites; emigration from landward nurseries is dominated by mature or maturing males that are roughly 1 yr old and average approximately 180 mm in standard length, SL (Taylor et al. 2000). A more recent telemetry study of larger juvenile snook (120–320 mm SL) determined that some snook remain within their juvenile habitats for an additional year (Barbour & Adams 2012).

In the present study, we sought to test the early life-history model for juvenile snook that has been hypothesized in the literature (i.e. Stevens et al. 2007). Rather than sampling a large area to locate nursery habitats, we targeted a wetland area that had been identified as snook nursery habitat during previous fish surveys (McMichael et al. 1989, Peters et al. 1998, Taylor et al. 1998). We used multiple metrics over a smaller spatial scale to examine the early-life-history model that had been described in the literature. We further hypothesized that early juvenile snook use specific mesohabitats within what was believed to be generalized nursery habitat. Specific objectives were (1) to determine whether there were differences in snook abundance, size, or condition among different locations (upstream vs. downstream) and mesohabitat types (tidal creek vs. tidal pond) within the wetland; and (2) to use isotopic composition to determine the degree of site fidelity within the wetland.

MATERIALS AND METHODS

Study area

The study area was lower Frog Creek, a tidal tributary of southeastern Tampa Bay, Florida, USA. Frog Creek is a relatively large coastal creek (11.3 km

long) that originates near Parrish, Florida (27.5890° N, 82.3341° W) and drains into Terra Ceia Bay (27.5785° N, 82.5631° W; Fig. 1; DEP 2009). Based on geospatial information system data layers from the Southwest Florida Water Management District, the immediate watershed of the creek is about 12.6 km², although Cabbage Slough and Buffalo Creek watersheds also drain into Frog Creek within its freshwater reaches, creating a total watershed area of about 52.2 km² (www.swfwmd.state.fl.us/data/gis/layer_library/category/physical_sparse). Direct anthropogenic impacts to the tidal portion of this creek system have been minimal, as downstream creek banks are undeveloped and occur within the state-managed Terra Ceia Aquatic Preserve. However, residential development and agricultural uses in the upper watershed have resulted in increased nutrient loads to the system (TBRPC 1986). In relation to other Tampa Bay tidal creeks, Frog Creek is among the least impacted (TBRPC 1986).

A variety of mesohabitats within the Frog Creek wetland network are determined by tidal influence and geomorphology. In addition to the tidal creek, there are several karst ponds within the wetland, several of which connect directly to the creek. Tides in Tampa Bay proper are a mixture of diurnal and mixed semidiurnal tides (Goodwin & Michaelis 1976), with an average tidal range of 0.67 m (Lewis & Estevez 1988). In Frog Creek, streamside vegetation marks a distinctive change in salinity upstream of the northern-most pond (Fig. 1), where there is an abrupt transition from brackish tidal waters to tidal fresh waters (TBRPC 1986). The tidal freshwater reach is narrow, deep, and sinuous, and its shorelines are dominated by low-salinity or freshwater vegetation, including live oak *Quercus virginiana*, cattails (*Typha* spp.), sabal palm *Sabal palmetto*, giant leather ferns (*Acrostichum* spp.), and various grasses. In contrast, the 3.2 km long downstream tidal portion is more geomorphologically variable, as it alternates between wide shallow areas and deep narrow runs; it is overwhelmingly dominated by mangroves, and becomes bayou-like as it widens towards its mouth at Terra Ceia Bay. In this tidal portion of the creek are several small karst dissolution ponds (surface area approximately 1800–7500 m²) directly connected to the mainstem creek that provide a contrasting, more quiescent type of estuarine habitat.

Generally, these ponds are shallow with slow-moving water and relatively deep, soft, muddy substrates (Table 1). The 2 upstream ponds contain a mixture of shoreline vegetation including cattails, *Rhizophora mangle* (red mangrove), and *Laguncularia racemosa*

(white mangrove). Floating *Eichhornia crassipes* (water hyacinth) is also seasonally abundant. The 2 downstream pond shorelines are dominated by red and white mangroves. In contrast, creek sites are characterized by more variable water depths, stronger currents, firmer substrates (more sand), and fringing

mangroves (Table 1). Preserve managers eradicated cattails from the 2 upstream ponds between the 2 juvenile recruitment seasons in this study. Thus during Year 2, shorelines in upstream ponds contained only scattered mangroves, decaying cattail rhizomes, and dead vegetation.

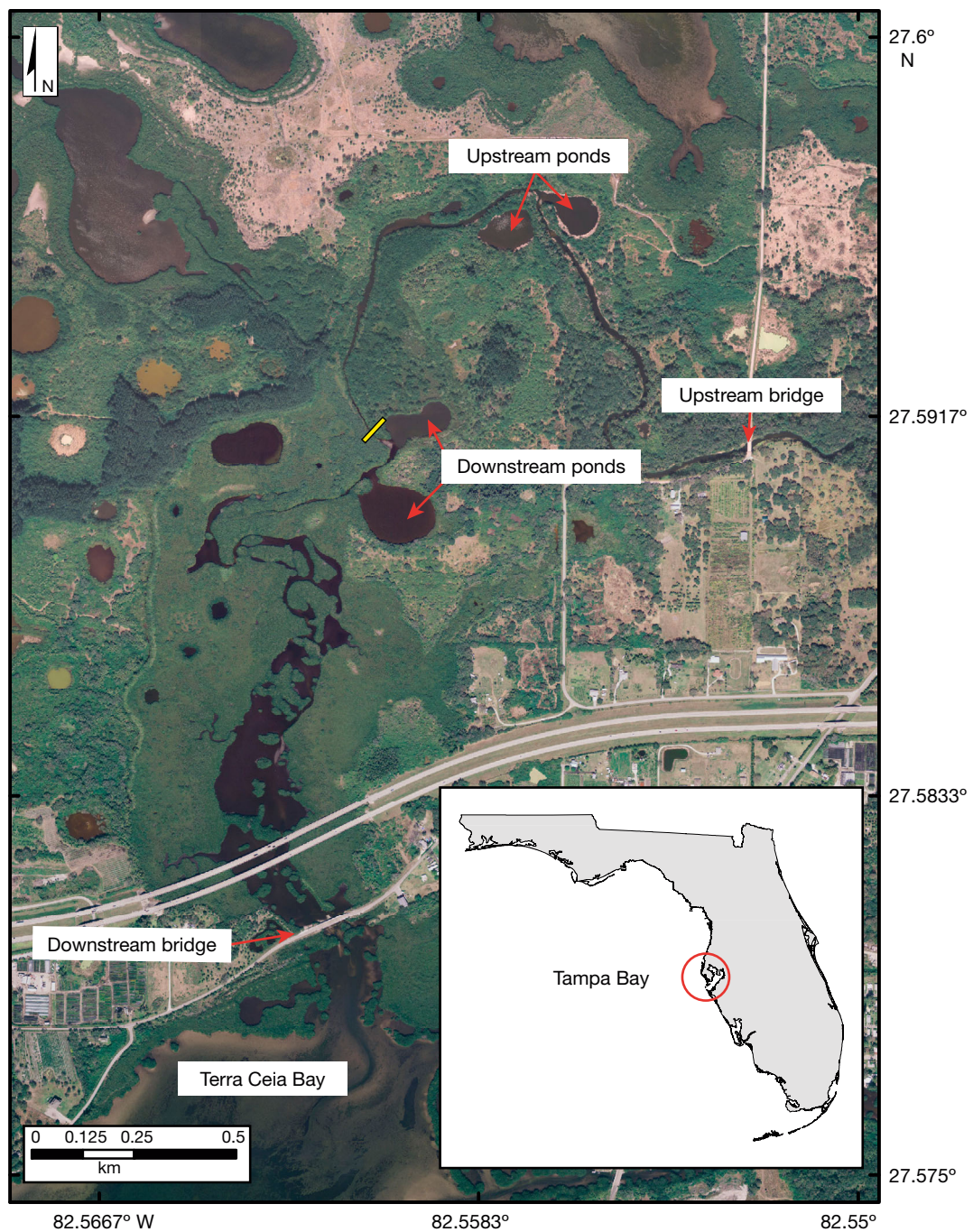


Fig. 1. Frog Creek in 2006. The yellow line intersecting the creek indicates the point separating the upstream and downstream portions of the creek for the purpose of this study. The inset shows the location of Tampa Bay within Florida, USA

Table 1. Summary of environmental and physicochemical variables (means \pm SE) collected by location and habitat type; N = 36 samples per habitat type and location for Year 1 and N = 12 samples per habitat type and location for Year 2. Current velocity was calculated by timing floating debris over a distance of 1 m. Inundation was measured as the distance between the end of the seine and the water line. Slope was calculated as rise/run (change in depth between 2 poles divided by the distance between the poles). DO: dissolved oxygen; NA: not applicable; mangr: mangroves

Habitat	Shoreline vegetation Dominant	Shoreline vegetation Secondary	Substrate Type	Substrate Depth (m)	Current (m s ⁻¹)	Water depth (m)	Inundation (m)	Slope	Temp. (°C)	Salinity (psu)	pH	DO (mg l ⁻¹)
Year 1 (Sep 2006–Feb 2007)												
Upstream												
Pond	Cattails	White mangr	Mud	0.24 \pm 0.01	NA	0.43 \pm 0.02	3.84 \pm 0.42	0.02 \pm 0.00	21.1 \pm 0.7	6.4 \pm 0.8	8.0 \pm 0.1	7.8 \pm 0.6
Creek	White mangr	Red mangr	Sand	0.04 \pm 0.01	0.09 \pm 0.01	0.63 \pm 0.04	2.75 \pm 0.38	0.04 \pm 0.01	22.0 \pm 0.7	6.0 \pm 0.9	7.8 \pm 0.1	7.2 \pm 0.7
Downstream												
Pond	White mangr	Red mangr	Mud/sand	0.14 \pm 0.01	NA	0.40 \pm 0.02	3.34 \pm 0.31	0.02 \pm 0.00	23.4 \pm 0.7	12.3 \pm 1.1	7.9 \pm 0.1	7.7 \pm 0.4
Creek	Red mangr	White mangr	Sand	0.04 \pm 0.00	0.14 \pm 0.02	0.46 \pm 0.03	2.87 \pm 0.38	0.02 \pm 0.00	21.8 \pm 0.7	13 \pm 1.2	7.6 \pm 0.1	6.8 \pm 0.4
Year 2 (Nov 2007 and Feb 2008)												
Upstream												
Pond	None ^a	White mangr	Mud	0.28 \pm 0.01	NA	0.34 \pm 0.02	3.37 \pm 0.77	0.02 \pm 0.01	23.6 \pm 0.4	11.6 \pm 0.7	8.3 \pm 0.0	8.6 \pm 0.4
Creek	White mangr	Red mangr	Sand	0.07 \pm 0.01	0.08 \pm 0.01	0.63 \pm 0.05	2.39 \pm 0.5	0.07 \pm 0.01	22.8 \pm 0.2	13.2 \pm 1.5	8.1 \pm 0.0	6.1 \pm 0.6
Downstream												
Pond	White mangr	Red mangr	Mud	0.13 \pm 0.02	NA	0.36 \pm 0.02	3.98 \pm 0.39	0.02 \pm 0.00	23.3 \pm 0.2	18.2 \pm 0.2	8.1 \pm 0.0	6.7 \pm 0.6
Creek	Red mangr	White mangr	Sand	0.09 \pm 0.02	0.09 \pm 0.02	0.41 \pm 0.02	2.33 \pm 0.38	0.02 \pm 0.01	22.2 \pm 0.3	18.9 \pm 0.5	7.9 \pm 0.0	4.7 \pm 0.4

^aCattail eradication took place between the 2 study years, leaving the upstream pond shorelines devoid of vegetation

Sample collection

We sampled the 3.2 km long reach of tidal creek and 4 adjacent pond habitats, as a previous study showed that this geographic area supported a high density of young-of-the-year (YOY) snook (Krebs et al. 2005). This reach was divided into upstream and downstream components at a point where the creek narrows: each reach thus contained a mainstem creek section and 2 estuarine ponds (Fig. 1). Each month we used seines to collect 6 pond samples (3 pond⁻¹) and 6 creek samples within each reach, for a total of 24 samples mo⁻¹. All collections were made at shoreline sites that were randomly located. During the first recruitment year, we sampled monthly from September 2006 through February 2007, resulting in 144 seine deployments. For an interannual comparison, we sampled 2 additional months (November 2007 and February 2008) during the subsequent recruitment year.

Because of the low numbers of snook captured in the downstream tidal creek and ponds, additional samples were collected to augment the number of YOY snook available for non-density analyses. Supplemental seine deployments were made in the downstream creek (n = 3) and ponds (n = 3) in October 2006, resulting in the collection of an additional 7 YOY snook from the downstream creek and 15 YOY snook from the ponds. These supplemental samples were only used for length, condition, and stable isotope analyses.

Seine deployments used a 9.14 m, 3.2 mm delta mesh, center-bag haul seine pulled immediately adjacent to the shoreline vegetation. Each haul was pulled parallel to shore a distance of 9 m, sampling an area of ~61 m². Upon collection, snook were enumerated. Larger snook (>180 mm SL) were measured to the nearest mm SL and released. YOY snook, defined as those <180 mm SL (Taylor et al. 2000), were immediately placed on ice in the field and then frozen upon return to the laboratory.

Sample processing

Each YOY snook was processed in the laboratory. Standard, fork, and total lengths were measured to the nearest mm. Blotted whole-body (somatic) wet weight and blotted liver wet weight were measured to the nearest 0.1 mg using a Mettler Toledo top-loading balance. Length and weight measurements were used to calculate Fulton-type condition factor (*K*) and hepatosomatic index (HSI) for each individ-

ual snook (Anderson & Gutreuter 1983). Growth was estimated as the slopes of log-transformed length–weight curves and analyzed by both habitat type and location.

$$K = (W/SL^3) \times 10^4 \quad (1)$$

where W = somatic weight in grams, and SL = standard length in mm.

$$HSI = (W_l/W) \times 100 \quad (2)$$

where W_l = liver weight in grams, and W = somatic weight in grams.

Snook muscle tissue for isotopic analysis was filleted from the body and skinned. Muscle samples were rinsed with deionized water, dried in an oven at 55°C for 48 h, ground to a powder using a mortar and pestle, and stored in sealed glass vials. Individual samples were later weighed on a microbalance and placed in tin capsules for analysis. We used a Carlo Erba 2500 Series I elemental analyzer to combust the samples at 1050°C, and the isotopic ratios of the gas products were measured using a continuous-flow inlet system on a Finnigan Mat Delta Plus XL stable-isotope ratio mass spectrometer. All samples were run in duplicate or triplicate and compared to both internal and international standards (Pee Dee Belemnite for carbon and air for nitrogen). Results are displayed in delta (δ) notation and reported as parts per mil (‰), calculated as:

$$\delta = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1000 \quad (3)$$

where R is the ratio of the heavy to the light isotopes. Stable carbon and nitrogen isotopic ratios of YOY snook were analyzed by habitat type, location, and length to examine patterns in habitat use. For length analyses, YOY snook were separated into 10 mm size increments, and the isotopic ratios were examined by habitat type and location.

Statistical analysis

Traditional estimates of species-specific density are calculated as the mean number of target taxa per area sampled, including 0 occurrences. Whereas this approach is conceptually straightforward, many datasets contain abundant 0s, a condition leading to positively skewed distributions that are not normally distributed (Fletcher et al. 2005). Further, routine transformations may fail to bring about normalization to these 0-inflated distributions. A recommended solution to this problem is to split conventional density into its component parts, i.e. frequency of occurrence

(% of samples containing target taxa) and concentration (number per area sampled when present, exclusive of 0 values; Serafy et al. 2007). We adopted the approach of using concentration (0 values excluded) while also reporting conventional density estimates (0 values included) to permit comparison with previous studies.

Two-way crossed parametric analysis of variance (ANOVA) was conducted using the general linear model in SAS version 9.1 (SAS Institute 2003). The data did not always meet assumptions of normality; therefore, we used the Box-Cox method to determine and apply the most appropriate transformation for normalizing the data. Location (upstream, downstream) and mesohabitat type (creek, pond) served as independent factors for examining differences in the dependent variables (snook concentration, SL , K , HSI , and isotopic composition). Note that time was not considered as a factor in the analysis, as no statistical tests were performed between recruitment years.

ANOVA results are presented graphically (Box et al. 2005) to allow visual comparison of location and habitat effects and to depict the normalization results of Box-Cox transformation. All observations were converted to residuals by subtracting the grand mean. Mean residuals for each effect were then multiplied by the square root of $(n - 3)$, where $(n - 3)$ is the ratio of residual degrees of freedom to factor (habitat, location) degrees of freedom.

Condition indices such as K are subject to misinterpretation caused by non-isometric (allometric) variation in the weight-at-length relationship during growth. In such cases, either a restriction of comparisons to same-size fish or statistical removal of allometric trends prior to comparison is required (Clark 1928, Froese 2006). Juvenile snook become more elongate with growth, creating the false impression that K was decreasing. This trend was removed using a nonlinear regression model that produced symmetrical residuals across the examined range (20–150 mm SL). Note that the alternative approach of treating length as a covariate would not accommodate nonlinearity.

RESULTS

Year-class composition

We collected 480 snook over the 2 yr of the project (Table 2). The majority of snook were collected during the first recruitment year (2006–2007), as we cap-

Table 2. Abundance, density (mean \pm SE) and frequency of common snook *Centropomus undecimalis* collected with a 9.1 m center-bag haul seine by month and year. YOY: young of the year; SL: standard length

Month	No. of samples	All snook			YOY snook only (<150 mm SL)		
		Count	Density (100 m ⁻²)	% frequency	Count	Density (100 m ⁻²)	% frequency
Year 1 (2006–2007)							
Sep	24	24	1.6 ± 0.6	41.7	18	1.2 ± 0.5	25.0
Oct	24	71	4.9 ± 1.5	62.5	69	4.7 ± 1.5	62.5
Nov	24	115	7.9 ± 2.9	54.2	115	7.9 ± 2.9	54.2
Dec	24	72	4.9 ± 1.6	66.7	67	4.6 ± 1.6	62.5
Jan ^a	24	48	3.3 ± 1.1	50.0	48	3.3 ± 1.1	50.0
Feb	24	102	7.0 ± 2.4	75.0	99	6.8 ± 2.4	66.7
Mean per month	24	72	4.9 ± 0.8	58.3	69	4.7 ± 0.8	53.5
Total	144	432			416		
Year 2 (2007–2008)							
Nov	24	26	1.8 ± 0.5	50.0	8	0.5 ± 0.2	25.0
Feb	24	22	1.5 ± 0.4	50.0	6	0.4 ± 0.2	16.7
Mean per month	24	24	1.6 ± 0.3	50.0	7	0.5 ± 0.2	20.8
Total	48	48			14		
^a A strong cold front may have affected the number of snook captured during this month							

Table 3. Mean \pm SE variables related to the collection of young-of-the-year common snook *Centropomus undecimalis* in Frog Creek, Florida, USA (fish density includes 0 count values, fish concentration excludes 0 values). Condition factor (*K*) residuals were multiplied by 100. HSI: hepatosomatic index

Variable	Fish 100 m ⁻²		Frequency of capture (%)	Length (mm)	Condition factor (<i>K</i>) residuals	HSI	δ ¹³ C (‰)	δ ¹⁵ N (‰)
	Density	Concentration						
Habitat type								
Pond	6.8 ± 1.4	10.1 ± 1.9	67	53.4 ± 1.4	-1.24 ± 0.69	0.87 ± 0.01	-25.5 ± 0.1	12.3 ± 0.1
Creek	2.7 ± 0.6	6.8 ± 1.2	40	64.5 ± 0.9	1.06 ± 0.88	0.98 ± 0.02	-24.9 ± 0.1	11.4 ± 0.1
Location								
Upstream	6.9 ± 1.4	12.4 ± 2.2	56	55.8 ± 1.4	0.02 ± 0.69	0.89 ± 0.01	-25.3 ± 0.1	12.0 ± 0.1
Downstream	2.6 ± 0.4	5.0 ± 0.6	51	59.1 ± 1.0	-1.45 ± 0.90	0.94 ± 0.02	-25.2 ± 0.1	11.8 ± 0.1

tured 432 snook in 84 of the 144 seine hauls (58%). During the first recruitment year, snook were collected at a mean (\pm SE) density of 4.9 \pm 0.8 fish 100 m⁻². In comparison, only 48 snook were captured in 24 of the 48 seine hauls during the second year (1.6 \pm 0.3 fish 100 m⁻²). Of the 480 snook captured, 436 were YOY, measuring <180 mm SL, and were retained for further analyses. However, upon review of length-frequency histograms, we determined that 6 YOY snook caught in September, measuring between 151 and 180 mm SL, were slow-growing members of the previous year's cohort and were thus omitted from further analyses. The first year yielded a higher percentage of YOY snook (96% of all snook captured) in contrast to the second year (29%). YOY snook were also collected at a higher frequency (percentage of samples containing the target species) during the first year (53%) compared to the second

year (21%). Since so few YOY snook were collected during the second recruitment year, further statistical analysis was restricted to snook collected during the first recruitment year.

YOY abundance by mesohabitat and location

Both the density and concentration of YOY snook varied by mesohabitat type and location (Table 3). YOY snook were captured at higher densities in ponds (6.8 \pm 1.4 fish 100 m⁻²) and upstream (6.9 \pm 1.4 fish 100 m⁻²) as opposed to creek (2.7 \pm 0.6) or downstream (2.6 \pm 0.4 fish 100 m⁻²). The concentration of YOY snook followed a similar pattern, although the difference by location was more pronounced. Results of the 2-way crossed ANOVA on transformed data identified a statistical difference in YOY snook con-

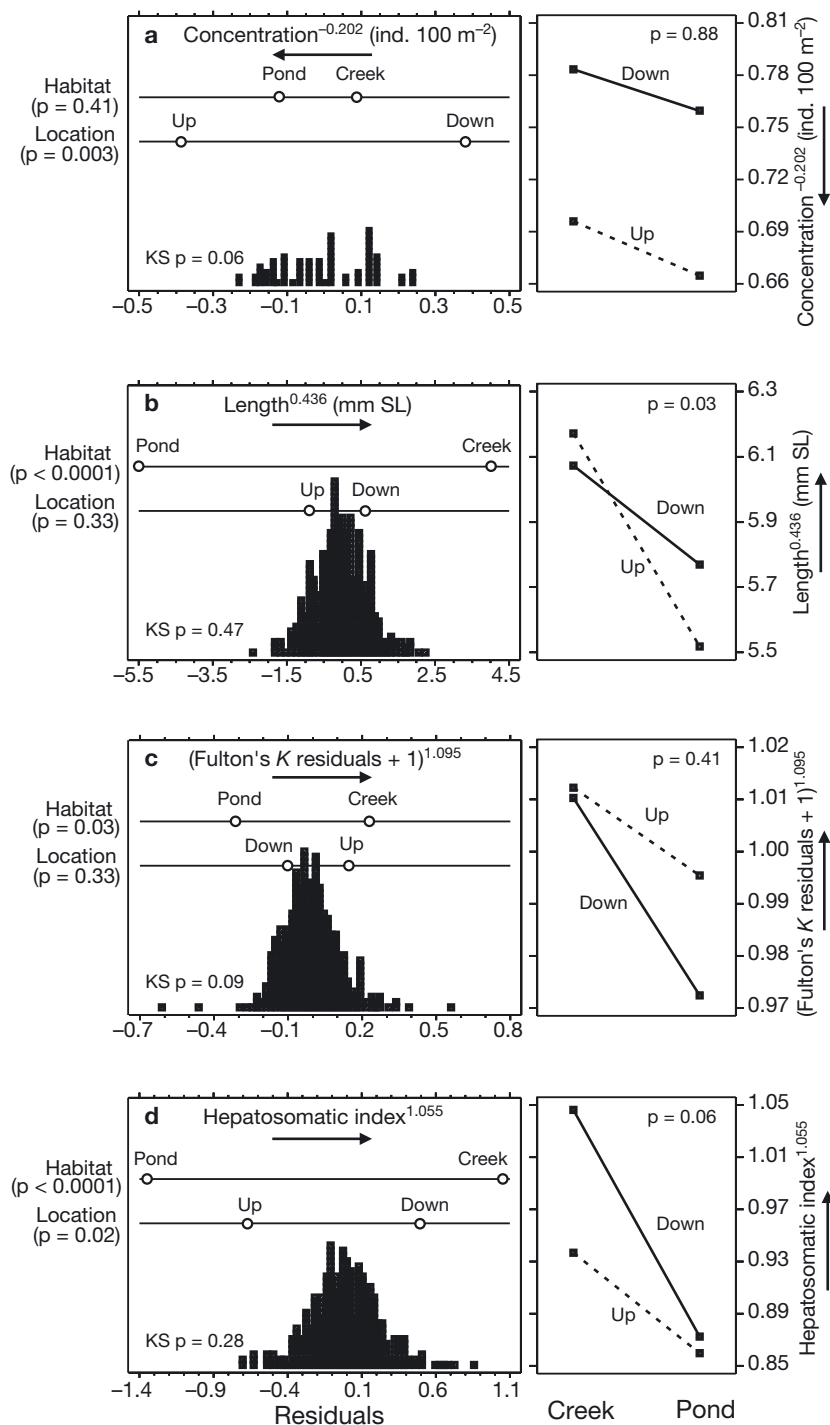


Fig. 2. Graphical ANOVAs for (a) concentration, (b) standard length, (c) residual *K*, and (d) hepatosomatic index of young-of-the-year (YOY) common snook *Centropomus undecimalis*. Histograms present results of Box-Cox power transformations to improve normality, with p-values from Kolmogorov-Smirnov tests (KS) indicated in lower left corners of plots. Magnitude of differences by habitat type and location are plotted above histograms, with ANOVA p-values reported to the left of these. Interaction effects and associated p-values appear in the right-hand panels

centration by location ($p < 0.01$), indicating that YOY snook were more concentrated in upstream habitats (Fig. 2a). Despite the apparent difference in concentration by mesohabitat type, no statistical differences were observed by mesohabitat or the interaction between mesohabitat and location. Although the analysis did not reveal a significant interaction variable, the strong effects of location were likely influenced by the type of mesohabitat within the estuarine gradient, as upstream ponds yielded the highest densities of YOY snook.

Length analysis

The 2006 snook year class was observed throughout the 6 mo sampling period for trends in length and growth. YOY snook ranged from 16 to 119 mm in SL ($n = 428$). We examined snook length by month to estimate cohort growth over time (Fig. 3). The number of individuals collected from the downstream creek and pond mesohabitats was insufficient for comparing apparent growth by mesohabitat type or location. Average snook length increased from 30 ± 2.10 mm SL in September to 67 ± 2.63 mm SL in January before stabilizing in February (66 ± 1.50 mm SL). The lack of increase during February was the result of a small influx of new recruits that were first observed in January and continued recruiting into February (Brame 2012). Growth rates estimated from modal progression ranged from 0.17 to 0.90 mm d⁻¹ and averaged 0.36 mm d⁻¹ over the 2006–2007 recruitment period. Highest growth rates were measured in September when the juveniles were smallest and the weather was warmest. It should be noted that length-frequency distributions combine the interactions of recruitment, growth, mortality, and emigration (Anderson & Gutreuter 1983). Therefore, our calculation of growth rate may be strongly affected by the rates of mortality and emigration, which were not measured in this study.

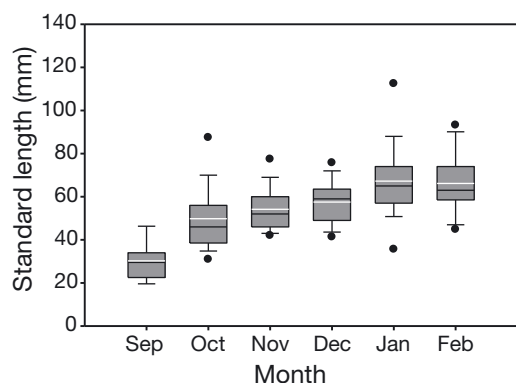


Fig. 3. Mean (white line) and median (black line) standard lengths of young-of-the-year (YOY) common snook *Centropomus undecimalis* by month, September 2006 to February 2007. Boxes: 25th–75th percentiles; whiskers: 5th–95th percentiles; dots: outliers

Snook collected from ponds were smaller than those collected from the creek (2-way crossed ANOVA, $p < 0.01$; Fig. 2b). However, a statistical difference in the interaction variable (location by mesohabitat type) suggests that the difference in length by mesohabitat type was largely influenced by the location of that mesohabitat within the estuarine gradient. Snook from upstream ponds were the smallest while snook collected in the downstream creek were the largest.

K and HSI

Fish with higher K are assumed to be healthier as they weigh more per unit length. Mean K among all YOY snook ($n = 394$) was 1.48 ± 0.01 and ranged from 0.94 to 2.06. As a general trend, smaller snook had higher condition than larger snook, which is likely attributable to allometric growth. After removing this trend using regression, a difference in residual K by mesohabitat type was observed ($p = 0.03$), wherein creek snook had higher residual K than pond snook (Fig. 2c).

HSI ranged from 0.17 to 1.74 and averaged 0.91 ± 0.01 ($n = 376$). Snook in ponds had a lower mean HSI (0.87 ± 0.01) than those collected from the creek (0.98 ± 0.02), and snook from the upstream portion of the creek had a lower mean HSI (0.89 ± 0.01) than those from the downstream section (0.94 ± 0.02). The 2-way crossed

ANOVA identified statistical differences in HSI by both mesohabitat type ($p < 0.01$) and location ($p = 0.02$; Fig. 2d). The interaction variable was also marginally significant ($p = 0.06$), suggesting that the factors were not independent, wherein snook from the downstream creek had the highest HSI and snook from the upstream ponds had the lowest HSI.

Stable isotope analysis

We analyzed 294 YOY snook for stable carbon and nitrogen isotopes. YOY snook $\delta^{13}\text{C}$ ranged from -28.05 to -21.33 and averaged $-25.23 \pm 0.06\text{‰}$. Values for $\delta^{15}\text{N}$ ranged from 8.02 to 14.23 and averaged $11.94 \pm 0.08\text{‰}$. Statistical differences were observed in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ when analyzed by mesohabitat type ($p < 0.01$; Fig. 4). Snook collected from ponds had higher $\delta^{15}\text{N}$ and lower $\delta^{13}\text{C}$ in comparison to snook captured from the creek (Fig. 5). We observed no statistical differences in the isotopic composition of snook when examined by location along the estuarine gradient or by the interaction of mesohabitat and location.

Comparison of isotopic ratios of YOY snook by size class and mesohabitat type indicated that (1) pond and creek fish were generally well-separated in iso-

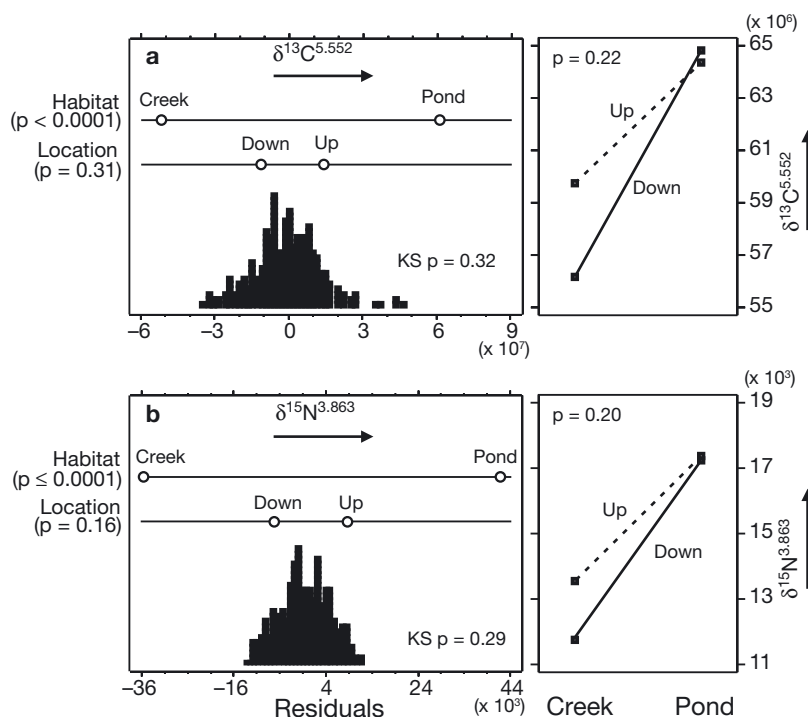


Fig. 4. Graphical ANOVAs for (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ of young-of-the-year (YOY) common snook *Centropomus undecimalis* (presentation as in Fig. 2)

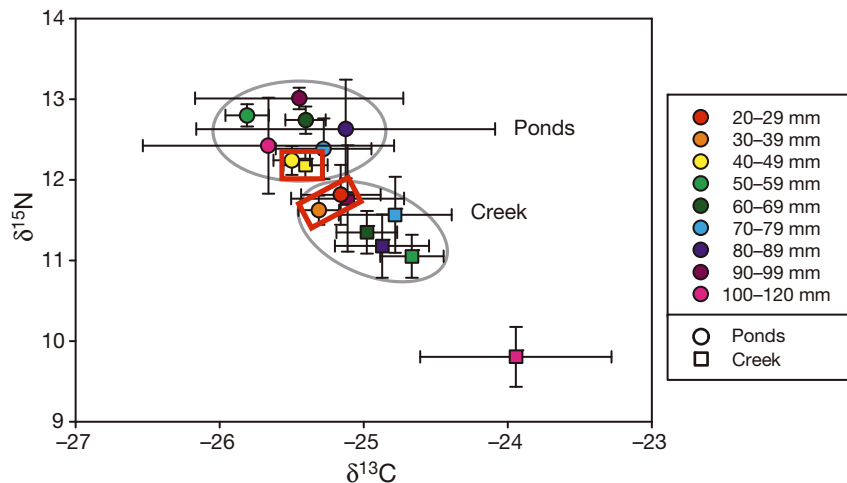


Fig. 5. Average isotopic composition of young-of-the-year (YOY) common snook *Centropomus undecimalis* by size class and habitat type (pond vs. creek). Large circles group observations by habitat type. Red boxes identify the smallest size classes of snook from each habitat type

topic space; and (2) where the same size class occurred in both mesohabitats, their isotopic ratios were non-overlapping and thus distinctive (Fig. 5). The 3 instances where overlap occurred corresponded to the smallest size classes of snook from each of the mesohabitats. This indicated that the smallest individuals from each mesohabitat had yet to assimilate an isotopic signature associated with the mesohabitat where they were captured. It further suggests that they had very recently recruited to the mesohabitats where they were captured, as isotopic turnover rates in small, fast-growing individuals are expected to be high (Herzka 2005). For example, the 2 smallest size classes of snook collected in ponds (20–39 mm SL) had isotopic signatures more indicative of those snook collected in the creek, suggesting they had just moved from the creek into the pond and had yet to assimilate the pond's isotopic signature. In general, the isotopic distinctiveness provides strong support for high site fidelity.

DISCUSSION

Habitat shifts during the juvenile stage

Although YOY snook are most abundant (i.e. highest densities) in backwater wetlands that border uplands, the bodies of water in which they occur have been described using various geomorphic designations such as river, tidal creek, canal, lagoon, oxbow, embayment, pond, impoundment, and mosquito-control ditch (Fore & Schmidt 1973, Gilmore et

al. 1983, McMichael et al. 1989, Ali-aume et al. 2000, Stevens et al. 2007, Greenwood et al. 2008). Early juvenile snook generally occur in higher abundance along quiet, lentic shorelines (regardless of gross geomorphic characterization) than in lotic or high-energy shorelines (Stevens et al. 2007, 2010, Greenwood et al. 2008). In the current study, YOY snook were more abundant (based on concentration) in the upstream portion of the study site, suggesting that YOY snook move upstream as far as possible before establishing site fidelity. Spawning occurs at seaward locations, including Terra Ceia Bay, which is the receiving basin for Frog Creek (Burghart et al. 2014). In the process of moving from seaward spawning grounds to upstream habitats, the smallest size classes of snook (i.e. those <40 mm SL) recruited specifically to pond mesohabitat. The finding that snook collected from ponds were, on average, smaller than those collected from the adjacent creek (Fig. 2, Table 3) indicates that recruiting juveniles used the creek only as a corridor for moving upstream and settling in pond mesohabitats. This is further supported by the absence of the smallest size classes of YOY snook (<40 mm SL) from creek collections. Beginning at a length of approximately 40 mm SL, YOY snook underwent another ontogenetic mesohabitat shift as they began to move from ponds into the creek.

The smaller size class of YOY snook that occupied the ponds coincided with the early juvenile stage (<45 mm SL) described by Peters et al. (1998), where these smaller juveniles loosely schooled among mangrove prop roots and other shoreline structure in shallow protected basins with restricted openings. A tendency to aggregate, coupled with reduced cumulative effects of natural mortality, would account for the high densities of snook within the ponds. Gilmore et al. (1983) reported that snook move out of the creeks towards mangrove coastlines and seagrass beds in the larger estuary at about 150 mm SL. The very low abundance of snook >150 mm SL in the present study supports these observations, although larger snook may have also been more successful in avoiding our gear, as Barbour & Adams (2012) showed that some snook remained in juvenile habitats until reaching lengths of approximately 320 mm SL.

Several factors could influence the distribution and survival of YOY snook within the pond mesohabitat, including reduced predation, higher density of food, and bioenergetics (Major 1978). Although the present study was not designed to collect larger predatory fish, we were able to quantify the abundance of prey fishes and larger invertebrates collected as seine by-catch. Poeciliid fishes, a primary prey item for YOY snook (Harrington & Harrington 1961, Fore & Schmidt 1973, Gilmore et al. 1983, McMichael et al. 1989), were 6 times more abundant in ponds than in the creek (A. B. Brame unpubl. data). There was also a lack of visible currents in the ponds, a factor which would contribute to the conservation of energy, as the smallest size classes of snook were not forced to swim against currents once they became established in ponds. Lower energetic costs in ponds would allow YOY snook to allocate more energy to growth (length increase), perhaps leading to higher survival rates. Stevens et al. (2010) similarly identified prey availability and current velocity as possible factors contributing to differences in fish community structure between mainstem and backwater habitats in a nearby Florida estuary. Thus, lentic tidal habitats may provide superior conditions for the smallest snook.

Isotopic distinctions

The isotopic distinctiveness of snook between the 2 mesohabitat types supports the hypothesis that YOY snook select specific mesohabitats within the nursery and show fidelity to those habitats for extended periods of time. The isotopic differences observed in creek- versus pond-captured YOY snook can be explained by habitat-related differences in nitrogen or carbon sources, coupled with differences in the relative importance of particular biogeochemical processes. Snook were clearly not moving with any regularity between creek and ponds or else they would have had similar carbon and nitrogen isotopic values. Although others have similarly used stable isotopes to infer site fidelity in fishes in both freshwater (Gray et al. 2004) and estuarine settings (Green et al. 2012, Skinner et al. 2012), ours is the first to successfully apply these techniques to such a small spatial scale. Our results suggest that the young snook are maintaining home ranges that measure hundreds of meters or less, which is consistent with observations of passive telemetry in Charlotte Harbor, Florida, where juvenile snook home ranges and emigration rates increased with fish length (Barbour & Adams 2012).

Distinctions in the isotopic composition of snook between mesohabitats likely reflect differences in biogeochemical sources and processes. Pond snook had lower $\delta^{13}\text{C}$ than creek snook (Fig. 5), which is consistent with carbon recycling within quiescent habitats (Keough et al. 1998, Yakir & Sternberg 2000). The ponds had low flows and were highly depositional, resulting in the accumulation of depleted (more negative) C3-based organic matter as detritus (C4 plants had very low biomass in the study area). Remineralization of this depleted C3 organic matter by detritivores introduces depleted DIC into the water column (Bouillon et al. 2008). Longer residence times for water and lower turbulent mixing support accumulation of depleted DIC within the quiescent pond settings, increasing the likelihood that depleted DIC will be recycled for use in new photosynthesis. This process leads to further fractionation (depletion) of the carbon as it passes through the C3 photosynthetic pathway again (Keough et al. 1998, Aspetsberger et al. 2002, Bouillon et al. 2011). In contrast, the creek had stronger currents that originated from both tidal exchange and freshwater inflows from the watershed. This more turbulent setting is more likely to exchange DIC with the atmosphere, reducing the likelihood of DIC recycling and resulting in more enriched (higher) $\delta^{13}\text{C}$ values (Keough et al. 1998).

In a geomorphic setting that was somewhat similar to Frog Creek, Roach et al. (2009) reported depleted carbon values in seston and benthic algae from lagoonal habitats in comparison to a tropical mainstem floodplain river. Fish collected from the lagoonal habitats in their study did not have reduced $\delta^{13}\text{C}$ levels, which they attributed to extensive movement and feeding between the 2 mesohabitats. In contrast, YOY snook collected from ponds during our study had reduced $\delta^{13}\text{C}$ values, indicating that individual fish had high site fidelity and were not occupying the 2 mesohabitat types interchangeably.

Differences in snook nitrogen isotopic composition between the 2 mesohabitat types in the present study are likely the result of both within-habitat and watershed processes. Under anoxic conditions in the sediments, porewater, or water column, denitrification leads to production of isotopically depleted (more negative) nitrogen that is exported to the atmosphere as nitrogen gas (N_2), while isotopically enriched (more positive) nitrogen remains as waste (Altabet et al. 1999, Montoya et al. 2002). Lentic habitats are more likely to experience anoxic conditions than lotic ones, thus possibly contributing to the difference in

snook $\delta^{15}\text{N}$ between the 2 mesohabitats in our study. In addition, Aspetsberger et al. (2002) noted that poorly connected floodplains along an Austrian river generally had high levels of bacteria that utilized excess organic material, leading to higher isotopic values for nitrogen (and lower values for carbon) in samples of particulate organic matter. Nitrogen from floodplains was also affected over longer time frames as organic matter was progressively metabolized through ammonification and denitrification (Vander Zanden & Rasmussen 1999, Aspetsberger et al. 2002). Such microbial processing leads to nitrogen in resources within lentic, denitrifying environments being isotopically enriched (more positive) as residence times increase.

The watershed is likely a source of depleted (negative) nitrogen for Frog Creek because of use of synthetic fertilizers within the catchment. Most synthetic fertilizers consist of ammonia created by the Haber-Bosch process, which uses atmospheric N_2 ($\delta^{15}\text{N} = 0\text{‰}$) to produce fertilizer in the -4.0 to 4.0‰ range (McClelland et al. 1997, Kendall 1998). Rainfall tends to wash inorganic fertilizers from the watershed into streams where they are incorporated into primary producers and the food web, lowering consumer $\delta^{15}\text{N}$. In the present study, synthetic fertilizers used in upstream orange groves likely entered Frog Creek, thus resulting in relatively lower $\delta^{15}\text{N}$ values for snook captured there. This difference in source may be coupled with higher total denitrification in the ponds, creating the observed differences in snook nitrogen isotopes.

Condition

We hypothesized that condition, measured as K and HSI, would vary by mesohabitat, whereby the most optimal habitats would contain snook with higher condition indices. Before comparing K by mesohabitat type, K was regressed on fish length to identify allometric effects. The regression detected a size-related difference, wherein smaller snook had higher condition (as K) than larger snook (>60 mm SL). Allometric growth was not considered in previous studies of juvenile snook condition (Fore & Schmidt 1973, Gilmore et al. 1983). K (using fork length) in the present study ($n = 394$, mean $K = 0.98 \pm 0.005$) was similar to that of other studies in Florida (Fore & Schmidt 1973: $n = 193$, mean $K = 1.05$; Gilmore et al. 1983: $n = 194$, mean $K = 0.93$).

Based on distribution data, the ponds seemed to be the preferred mesohabitat for the smaller snook

(<40 mm SL), yet these smaller snook had lower K and HSI values. It appears that smaller snook within ponds were dedicating more energy to increasing body length rather than adding mass in the form of body weight or liver weight. This strategy would cause smaller snook to have lower condition regardless of mesohabitat type or location. Additionally, a marginally significant interaction within the ANOVA for HSI indicated that snook from the upstream ponds had the lowest HSI and snook from the downstream creek had the highest. As YOY snook grew and moved into the downstream creek, HSI increased. This occurred as these snook continued to mature and were preparing to move from the nursery to larger estuarine habitats (e.g. rivers, barrier islands, bays).

Synthesis

Results of this study indicate small-scale differences in habitat use that affect juvenile snook autecology. Data from the present study reveal a new type of ontogenetic mesohabitat partitioning for snook (Fig. 6), wherein the smallest fish recruit initially from seaward spawning locations to tidal ponds, where they dedicate energy to growth (increased length) instead of storage, resulting in initially low apparent condition. At approximately 40 mm SL, snook start an ontogenetic shift to creek mesohabitats, where condition increases prior to maturation and emigration to seaward locations. The pond-to-creek mesohabitat shift is evident in both the length data and the isotope data, which indicate that the smallest snook collected from the creek (40–49 mm SL) were isotopically similar to snook collected from the ponds. This indicates that these small snook had recently moved from the pond to the creek and had yet to assimilate the creek's isotopic signature. Our results also identify high site fidelity for juvenile snook, as significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were observed among snook in mesohabitats that were only a few hundred meters apart.

Condition-based metrics are indicators of nursery mesohabitat performance that relate directly to fitness, as the delivery of robust individuals to the spawning stock translates into increased reproductive potential (Marshall et al. 1999, McBride et al. 2013).

The collective findings of this study modify the existing paradigm for YOY snook habitat use, and have implications for resource managers who are charged with either preserving productive wetland

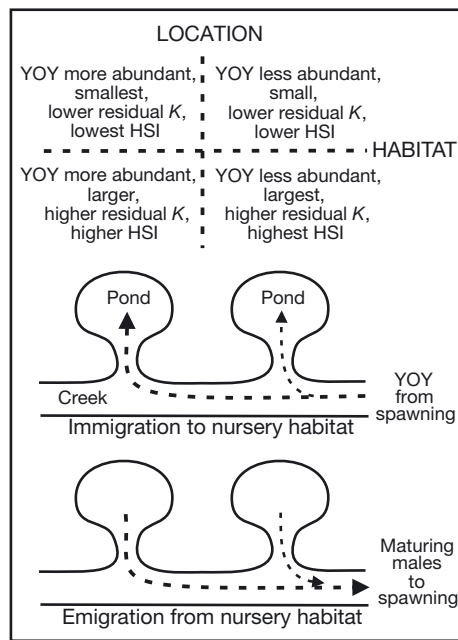


Fig. 6. Diagram summarizing the recruitment and use of the habitat by young-of-the-year (YOY) common snook *Centropomus undecimalis*, based on data collected during the fall recruitment of 2006. HSI: hepatosomatic index

networks or restoring less-than-optimal habitats. Geographic areas that were once viewed as generalized nursery habitat may instead consist of mesohabitats that are used sequentially (Fig. 6). This creates the possibility that some mesohabitats within the nursery-habitat landscape are more limiting than others. When density dependence affects survival, and when the relative availability of required mesohabitats is unbalanced (i.e. low habitat complementation), then the less available mesohabitat could limit the nursery habitat's overall contribution to the adult population.

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