

Size-based, seasonal, and multidirectional movements of an estuarine fish species in a habitat mosaic

Andrew B. Barbour^{1,*}, Aaron J. Adams^{2,*}, Kai Lorenzen¹

¹School of Forest Resources and Conservation, Program of Fisheries and Aquatic Sciences, 7922 NW 71st St, University of Florida, Gainesville, Florida 32653, USA

²Florida Institute of Technology, Biological Sciences, Vero Beach Marine Laboratory, 150 W. University Blvd, Melbourne, Florida 32901, USA

ABSTRACT: To improve understanding of uni- versus multidirectional movement, seasonal dynamics, and the role of body size in tropical and sub-tropical nursery habitat, we conducted a 4 yr study on 1917 tagged juvenile common snook *Centropomus undecimalis* in 4 mangrove creeks. We detected 86% of individuals marked with autonomous passive integrated transponder (PIT) tag antennae. Marked fish were divided into 2 size classes (SC) for analysis: SC1 (approximately age-0) and SC2 (approximately age-1). A higher percentage of SC2 than SC1 snook migrated, SC2 made longer movements, and the 10 d probability of migration was 2.4-fold higher in SC2 than SC1. For both size classes, migration probabilities varied seasonally, with lowest rates in the coldest months. Furthermore, migration events during fall and winter tended to be temporary movements, while migration in spring and summer was more often permanent. Increased catch proportion of late-stage SC1 and early-stage SC2 individuals outside the creeks in spring/summer temporally aligns with increased permanent migration, suggesting a large-scale seasonal movement away from the study creeks. During this potential seasonal transition to alternative habitats, increased mortality at the end of the first year, as implied by proportionally fewer SC1 than SC2 individuals returning to the creeks in the following year, may act as an early population bottleneck. Alternatively, some individuals may lack fidelity and instead move to habitat not studied here. This work suggests that movement from nursery habitat can be bidirectional, size dependent, and seasonally dependent, and that the studied habitat functions as part of a habitat mosaic.

KEY WORDS: PIT · Telemetry · Nursery · Snook · Mangrove · Charlotte Harbor

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Movement among habitats is a vital ecological process often used to maximize individual fitness. Incentives for movement are varied, but are often provided by spatial and temporal heterogeneity in habitats resulting in differential growth and predation rates (Sogard 1997). For example, juvenile fish make movements to successive habitats as their ontogenetic requirements change (Werner & Gilliam 1984). This size-based juvenile habitat selection can be driven by the growth to mortality ratio offered by

each habitat at the given body size (Dahlgren & Eggleston 2000). As a result of inter-habitat movement, fitness can be maximized, predator-prey dynamics are altered, and nutrients are translocated (Winemiller & Jepsen 1998, Boucek & Rehage 2013). Implications of connectivity are ever-present in complex ecological systems, as is exhibited through the deleterious effects of habitat fragmentation (Kruess & Tschardtke 1994), in the definition of habitat mosaics (Sheaves 2009), or in marine reserve functionality (Olds et al. 2012). The design of effective conservation and management strategies relies upon proper

identification of habitats important to each life stage (Levin & Stunz 2005), and this is directly affected by inter-habitat connectivity. Despite the importance of connectivity to ecology, inter-habitat movement patterns are poorly understood in sub-tropical and tropical fish, thus limiting the understanding of population dynamics (Gillanders 2005).

Connectivity, i.e. the ability to transition between habitat patches, is especially important in our understanding of nursery habitats, which are defined as juvenile habitats that make a disproportionate contribution to the adult population (Beck et al. 2001, Dahlgren et al. 2006). Nursery habitats offer a favorable combination of growth, survival, juvenile density, and connectivity to adult habitats (Beck et al. 2001). Connectivity is an important characteristic since a habitat high in value for growth, survival, and density would not be considered a successful nursery if juveniles were unable to transition to sub-adult and adult habitats. Connectivity can be limited by processes like habitat fragmentation (Kruess & Tscharrntke 1994), high current velocities (Rosenfeld & Boss 2001), or the degradation of habitat corridors (Barrett & Bohlen 1991). Few studies have directly measured movement patterns from juvenile habitats in sub-tropical and tropical fish, making this a vital missing link in our understanding of nurseries for such species (Beck et al. 2001, Adams et al. 2006a). Under the classical definition of nursery habitat, transitions from nurseries are unidirectional (Beck et al. 2001). However, movement from nursery habitat may not be discrete and unidirectional, which would make quantification of juvenile habitat contribution to adult populations more difficult (Nagelkerken 2009). For example, some species undertake regular movements between habitats, such as tidal and diurnal migrations (reviewed by Sheaves 2005, Krumme 2009). Additional work is needed to understand whether nursery habitats function as a singular habitat type, or as habitat mosaics with multidirectional connectivity (Sheaves 2009, Fulford et al. 2011).

The lack of information on movement patterns from nursery habitats is generally due to the difficulty of tracking individuals from transient aquatic populations. Mark–recapture/resighting methods often result in too few individuals marked (e.g. acoustic telemetry) or recaptured (e.g. physical recapture methods) to draw meaningful conclusions on connectivity. Newer laboratory techniques, such as otolith microchemistry (Gillanders 2005), provide general information useful for identifying nurseries, but have limited utility in identifying the transitional patterns between nursery and adult habitats. As no

ideal method for studying nursery habitat connectivity exists, advances in our understanding rely upon novel methodological applications, the combination of multiple data sources, and quantitative modeling.

To advance our understanding of movement patterns in nursery habitat, we conducted a 4 yr mark–recapture/resighting study with a novel methodological application. Our objectives were: (1) to understand how seasonality and body size affected juvenile movement, in particular the incidence of temporary and permanent migration events; (2) to determine whether individual mangrove creeks functioned as the nursery unit or as part of a broader mosaic; and (3) to determine whether movement away from mangrove creeks was uni- or multidirectional (temporary versus permanent migration). We also examined potential causal drivers of observed movement patterns by analyzing our data with respect to temperature, prey abundance, and fisheries-independent monitoring (fish abundance data collected by a state agency).

MATERIALS AND METHODS

Study area

Charlotte Harbor is a 700 km² coastal plain estuarine system in southwest Florida (USA) (Hammett 1990; see Fig. 1 in Barbour & Adams 2012). The climate is sub-tropical, with mean seasonal water temperatures ranging from 12 to 36°C and infrequent freezing air temperatures (Poulakis et al. 2003). Seagrass flats (262 km²; Sargent et al. 1995) dominate the benthic habitat and mangroves dominate the shorelines (143 km²; L. Kish unpublished data).

This study was conducted in 4 red mangrove *Rhizophora mangle* fringed, tidal, estuarine creeks, each approximately 1.6 km long, on the eastern shoreline of Charlotte Harbor. The creeks varied in width from 2 m passes to >60 m bays, and average depths ranged from 0.5 to 2.0 m with the deepest occurring in the narrow passes. The mouths of the 2 northern creeks (South Silcox [SS] and North Silcox [NS]) were separated from Charlotte Harbor by 0.5 to 0.75 km of flooded mangroves and by 0.2 km of flooded mangroves between the mouths (Fig. 1A). The 2 southern creeks (Yucca Pen [YP] and Culvert Creek [CC]) were 10 to 12 km south of the northern creeks (see Fig. 1 in Barbour & Adams 2012). The mouths of the southern creeks were separated by 1.4 km and drained directly into Charlotte Harbor (Fig. 1B).

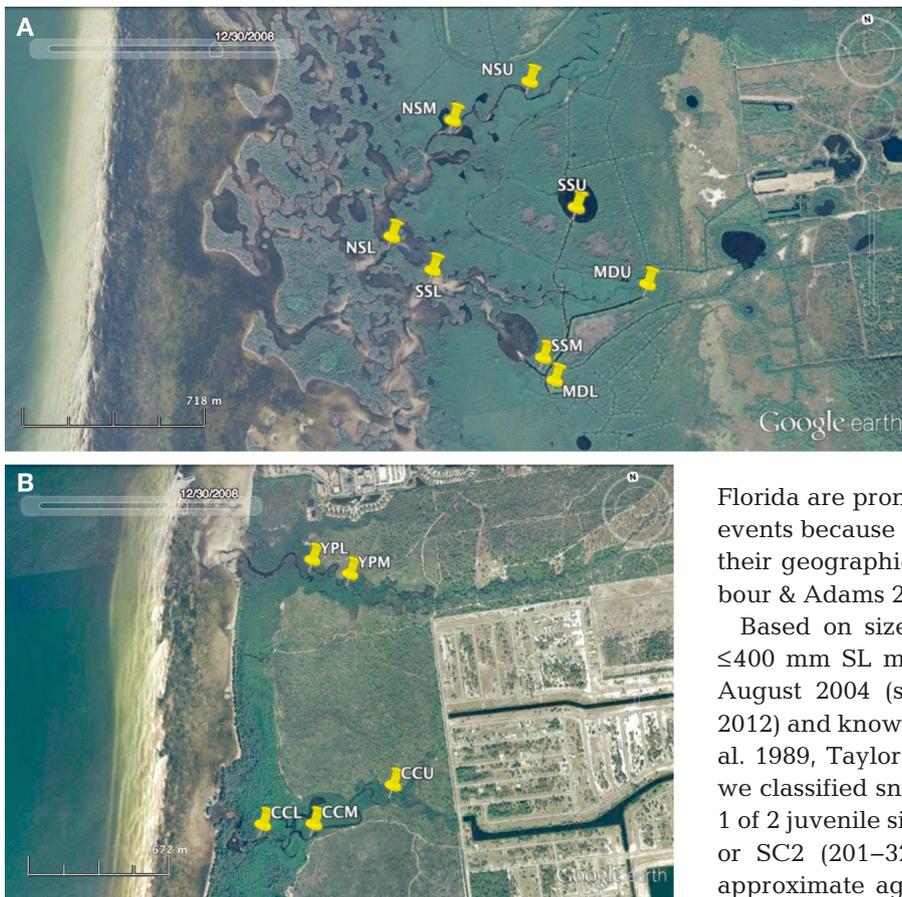


Fig. 1. Google Earth images of the 4 study creeks in Charlotte Harbor, Florida, USA. (A) The northern creeks are 10 to 12 km north of (B) the southern creeks. Lower (L), middle (M), and upper (U) PIT tag antennae locations are indicated by pins for North Silcox (NS), South Silcox (SS), Yucca Pen (YP), and Culvert Creek (CC). Lower (MDL) and upper (MDU) sections of a mosquito ditch are marked

Focal species

Common snook *Centropomus undecimalis* (hereafter referred to as 'snook') is a sub-tropical/tropical, estuarine-dependent, euryhaline species that is ecologically and economically important throughout its range, especially in Florida (Taylor et al. 2000). Adult snook spawn in passes and inlets at the mouths of estuaries from April through September (Taylor et al. 1998). The nearshore planktonic larval stage lasts approximately 2.5 wk (Peters et al. 1998), and juveniles settle into spatially complex, shallow, mesohaline to oligohaline habitats (Peters et al. 1998). Juvenile snook are common in or near mangrove creeks year-round, with highest densities in the fall and winter, until they reach approximately 300 mm standard length (SL) after 2 yr and enter the adult

population (Taylor et al. 2000). Snook larger than 300 mm SL use open estuarine and nearshore habitats (e.g. mangrove shorelines, artificial structures) from spring through fall, and may overwinter in riverine or creek habitats (Blewett et al. 2009). Larger snook opportunistically cannibalize juveniles, especially during winter periods of mangrove creek co-habitation (Adams & Wolfe 2006). Snook in

Florida are prone to mortality during severe cold events because they exist at the northern edge of their geographic range (Adams et al. 2012, Barbour & Adams 2012).

Based on size-frequency plots of 3757 snook ≤ 400 mm SL marked in the study creeks since August 2004 (see Fig. 2 in Barbour & Adams 2012) and known life-history traits (McMichael et al. 1989, Taylor et al. 2000, Stevens et al. 2007), we classified snook ≤ 320 mm SL as belonging to 1 of 2 juvenile size classes: SC1 (120–200 mm SL) or SC2 (201–320 mm SL). These size classes approximate age-0 (SC1) and age-1 (SC2) individuals based on Taylor et al. (2000), but this has not been confirmed through aging of fish within our study system. SC1 begins at the minimum tagging size of 120 mm SL.

Marking, recapturing, and resighting

Using a center bag seine (21 \times 1.2 m, 3.1 mm mesh) and hook-and-line, we captured and recaptured juvenile snook within the study creeks from November 2008 to June 2009 (marking year 1), November 2009 to February 2010 (marking year 2), and October 2010 to January 2011 (marking year 3). We scanned all fish with a handheld passive integrated transponder (PIT) tag reader (model no. RS601, Allflex®) after capture, documented physical recaptures, and measured SL to the nearest millimeter. We marked new individuals with uniquely coded half-duplex PIT tags (23 mm length \times 3.4 mm diameter, 0.6 g in air; Texas Instruments TIRFID S-2000). We inserted tags into the abdominal cavity through a 3 mm incision posterior and ventral to the pectoral fin. For this mark, a controlled study found 100% tag retention with no mortality for juvenile snook ≥ 120 mm SL, and no

need for sutures to close the incision (Adams et al. 2006b). All fish were released within 100 m of their capture location.

To increase our probability of detecting marked fish, we deployed an array of autonomous PIT tag antennae (Barbour et al. 2011, 2012). Antennae resighted marked individuals by reading and storing a PIT tag's unique number as a marked fish entered an antenna's magnetic field. We constructed 11 PIT tag antennae, placing an antenna in the lower, middle, and upper stratum (0.5 km per stratum) of each creek with the exception of YP upper (due to financial constraints; Fig. 1). Thus, if an individual was detected on 2 antennae, it would have had an approximate minimum movement of 0.5 km. Few antennae covered 100% of creek width, but all covered >75%. Antennae resighted fish continuously from November 2008 to January 2012. A complete description of the antenna array is provided by Barbour et al. (2011, 2012). During this study, sedimentation from a mangrove restoration project at the head of NS drastically reduced abundance of snook, making sampling in NS inefficient. Thus, we only marked fish in CC, YP, and SS, but resighted fish in all 4 creeks.

Quantifying migration

We defined migration as the recapture or resighting of a fish outside of its marking creek within its marking year. Marking years began in October or November (see Appendix B in Barbour 2013) to allow the new summer-spawned cohort sufficient time to grow to marking size, and ended on 31 July to avoid marking new individuals from the next cohort. We collected migration information within the creeks (i.e. a snook tagged in one creek and recaptured/resighted in a different creek), both with the seine net during marking events and with PIT tag antennae. We identified all individuals that migrated within their marking year and limited further analysis to these individuals.

Modeling seasonal and size-based migration

We created a model to determine whether within-year migration probabilities changed with season and/or fish length. After combining marking and recapture/resighting data for all marking years from 11 October to 30 June, we divided the timeframe into 10-d bins ($q = 26$ bins). Ten-day bins were selected

due to the compromise between the temporal resolution needed for exploring seasonality and a limited sample size of migrants. We quantified the number of migrants that were marked (M_t) and that migrated (E_t) per 10-d bin (t), modeling only the first instance of migration for each individual. We excluded marked individuals that we did not detect as migrants because inclusion would require an assumed survival rate to be incorporated into the model. We calculated the total number of marked fish present per 10-d bin (N_t) as:

$$N_t = N_{t-1} + M_t - E_t \quad (1)$$

We estimated the number of migrants per 10-d bin by multiplying the estimated total number of marked fish present by the 10-d rate, or probability, at which migration occurred (r):

$$\hat{E}_t = \hat{N}_{t-1} \times \hat{r} \quad (2)$$

We initialized $\hat{N}_1 = M_1$, and thereafter estimated the total number of marked fish as:

$$\hat{N}_t = \hat{N}_{t-1} + M_t - (\hat{N}_{t-1} \times \hat{r}) \quad (3)$$

We calculated the likelihood of \hat{E}_t using a Poisson distribution, and summed the natural log-likelihoods over t . We maximized the total log-likelihood value by varying r .

Migration change points

We conducted a change-point analysis to determine whether the migration probability changed seasonally. If a time τ ($1 < \tau < q$) is a change point, then the dynamics from times 1 to q can be modeled with 2 separate processes ($(N)_t^{(1)}$ and $(N)_t^{(2)}$, the first operating from times 1 to $\tau - 1$ and the latter from τ to q (Chen & Gupta 2012). In our model, we included a change-point in the migration probability (r) to investigate movement seasonality:

$$\hat{N}_t = \begin{cases} \hat{N}_{t-1} + M_t - \hat{N}_{t-1} \times \hat{r}_1 \\ \hat{N}_{t-1} + M_t - \hat{N}_{t-1} \times \hat{r}_2 \end{cases} \quad (4)$$

When observations arise under multiple processes — in this instance, $(N)_t^{(1)}$ and $(N)_t^{(2)}$ — the likelihood function of the time series is the product of the likelihood function for the observations coming from both processes. We maximized this joint likelihood at each potential change point and calculated the relative likelihood value for each change point as compared to the most likely value for τ . We used the 14.7% likelihood interval (Kalbfleisch 1985) to construct a 95% confidence interval for the relative likelihoods.

Using change points within this confidence interval, we compared model parsimony with Akaike's information criterion (Akaike 1973) adjusted for small sample size (AIC_c) (Burnham & Anderson 2002) to evaluate seasonality and size-based differences in migration. We defined models with ΔAIC_c ($\Delta AIC_c = AIC_c$ value of given model minus minimum AIC_c of the models run) values < 2 as being equivalent and $\Delta AIC_c > 10$ as having no support (Burnham & Anderson 2004). When comparing models with different combinations of change points, we made an *a priori* decision to not test models that had temporally close change points since we pooled data from multiple years. Thus, we limited our analysis to seasonal, as opposed to weekly/monthly, fluctuations in movement probability.

Temporal trends in migration type

To investigate temporal trends in migration type (temporary versus permanent), we examined the monthly ratio of permanent to temporary migrants. A permanent migration event occurred when the individual did not return to its marking creek within its marking year following detection outside its marking creek. Temporary migration occurred when a migrant returned to its marking creek within its marking year after being detected as a migrant. Each month, we determined whether each migrant temporarily or permanently migrated, and assigned a value of '1' to the appropriate migration type per individual. The permanent to temporary migration ratio simply compares the number of individuals that permanently versus temporarily migrated in a given month.

Since we examined monthly trends in migration for this analysis, an individual could migrate multiple times in a single marking year. For example, in November we marked Fish 5162 in CC and then detected it in YP; it returned to CC in December and was last detected in January when it moved to YP. Thus, Fish 5162 received a '1' for temporary migration in November and a '1' for permanent migration in January. In the instances when a fish temporarily and then permanently migrated in a single month, we assigned a value of '0.5' to both the temporary and permanent migration categories. We summed the totals for temporary and permanent migrants separately by month and size class, and used the monthly ratio of permanent to temporary migration to describe temporal trends in migration type.

Drivers of movement

We conducted additional analyses to explore 5 potential mechanisms responsible for the observed movement patterns: (1) seasonal activity rates; (2) year-after returns; (3) catches of juveniles in adult habitat; (4) prey availability; and (5) abiotic factors (water temperature and salinity). First, we determined the number of antennae each individual was detected at per month as a proxy for seasonal activity rates. The underlying assumption in this analysis was that snook would be detected by fewer antennae in the winter as a result of lower water temperatures inducing lethargy (Shaffland & Foote 1983).

Second, we quantified individuals detected in the year after marking. Comparing the proportion of larger fish to smaller fish that returned to the study creeks in the subsequent year provided a metric to infer the role of mortality in the observed migration patterns. We hypothesized that larger fish (SC2) would lose their dependency on the study creeks with increasing size (Taylor et al. 2000, Stevens et al. 2007), while smaller fish (SC1) would return to form a new SC2. Additionally, this analysis provided insight into whether an increase in permanent migration in the spring was an artifact of sampling ceasing in the late summer, thereby reducing resighting opportunities for spring migrants.

Third, we compared the timing of observed movement patterns with catches of juvenile snook in adult habitats. From January 1997 to December 2010, the Florida Fish and Wildlife Conservation Commission fisheries-independent monitoring (FIM) program conducted seine netting at multiple locations in Charlotte Harbor (Winner et al. 2010). We plotted a histogram of the FIM monthly, length-based catches to determine when juvenile snook utilized non-creek habitats in Charlotte Harbor.

Fourth, from November 2002 to September 2007 (not overlapping mark-recapture of juvenile snook), Adams et al. (2009a) collected prey items from the 4 study creeks every other month with a center bag seine (22 × 1.2 m, 3.2 mm mesh) at the spring low tides. To determine whether fluctuations in prey density or size drove creek-use patterns, we plotted monthly prey density (all years combined) and size each month for each creek. Finally, we measured water temperature and salinity (ppt) during all snook and prey-species sampling events using a YSI 556MPS.

RESULTS

Our resighting methodology detected a majority of individuals and revealed juvenile snook migration in all size and creek combinations. We marked 851 juvenile snook in marking year 1 (712 SC1 and 139 SC2), 593 in marking year 2 (469 SC1 and 124 SC2), and 473 in marking year 3 (241 SC1 and 232 SC2; see Appendix B in Barbour 2013). Using PIT tag antennae resightings, we detected 80.7% of snook marked in year 1, 88.2% in year 2, and 91.5% in year 3. Within their marking year, we documented 7 SC1 (0.5%) and 9 SC2 (1.8%) fish as moving between the northern and southern creeks, a distance exceeding 10 km. We documented migrants in all size class, creek, and year combinations (Table 1). More individuals exhibited site fidelity (defined here as being detected only in their marking creek) than migration, and migration was most pronounced in South Silcox creek (Table 1). We only sampled inside and 1 to 2 km² outside of the study creeks within a 700 km² estuary; therefore, our migration estimates are very conservative due to our spatially limited sampling and the demonstrated movement abilities of juveniles (Table 2).

Movement differed by size class, with more SC2 than SC1 individuals detected as migrants in every creek and year combination (Table 1). In total, antennae detected 9.5% of SC1 and 34.5% of SC2 individuals as migrants. Additionally, SC2 made larger movements, as determined through resightings on multiple antennae as a proxy for minimum distance traveled (Table 2). When estimating the 10 d migration probability (r) with values of $M_{SC1} = 135$ and $M_{SC2} = 171$ (Eq. 3), AIC strongly supported models with distinct migration probability for each size class (Table 3). Migration probabilities for SC2 were higher than SC1 in all models, and when directly compared without a change point for either size class, r for SC2 was 2.4-fold higher than for SC1 (Table 3).

Migration was seasonal, with highest probabilities in the fall and spring. Relative-likelihood determination of potential change points for r (Eq. 4) delineated 2 potential change points for SC2 individuals (21

Table 1. Percentage of marked *Centropomus undecimalis* detected as migrating (Mig.) within their marking year by creek and size class (SC1: 120–200 mm, SC2: 201–320 mm standard length). We classified individuals that were detected only in their marking creek as ‘non-migrants’ (Non.)

		Year 1		Year 2		Year 3	
		Mig.	Non.	Mig.	Non.	Mig.	Non.
Culvert Creek	SC1	5.2	84.3	12.2	71.5	9.1	77.9
	SC2	54.3	43.5	21.2	54.5	28.4	64.2
Yucca Pen	SC1	12.3	84.4	4.7	83.5	4.5	89.8
	SC2	18.4	81.6	20.4	77.8	26.7	70.0
South Silcox	SC1	15.1	48.1	39.9	54.0	23.7	64.5
	SC2	50.1	27.3	75.0	25.0	47.1	26.4

Table 2. Cumulative number and percentage of marked *Centropomus undecimalis* by size class (SC) resighted by at least the given number of antennae within their marking year. Antennae were separated by ≥ 0.5 km; therefore, detection by 3 antennae represents a minimum movement of 1.0 km. Detection by >6 antennae required movement between the northern and southern creeks, resulting in a minimum movement of 10 km. We used the cumulative number of fish detected by at least the given number of antennae. SC1: 120–200 mm, SC2: 201–320 mm standard length

No. of antennae	Min. distance moved (km)	SC1		SC2	
		No. of fish	% of marked	No. of fish	% of marked
2	0.5	839	59.0	381	77.0
3	1.0	310	21.8	222	44.8
4	1.5	69	4.9	90	18.2
5	2.0	28	2.0	52	10.5
6	2.5	1	0.1	6	1.2
7	>10.0	0	0.0	3	0.6
8	>10.0	0	0.0	1	0.2

December and 1 January) and 4 for SC1 individuals (1 and 21 December, 1 and 10 May; Fig. 2). Using these change points, AIC selection criteria could not differentiate the top 6 models, which were composed of different combinations of temporally close change points (Table 3). These models all had 3 change points: change points for the start of winter and end of spring for SC1 and in winter for SC2 (Table 3). The models identified a decrease in migration during the winter for both size classes, concurrent with the lowest seasonal water temperatures (Blewett et al. 2009, see Fig. 4-4 in Barbour 2013). However, it was more common for individuals to be detected by multiple antennae in the winter than in the warmer months (Fig. 3). This could be interpreted as decreased movement or as an artifact of reduced use of the creeks in the summer.

Seasonal movement patterns suggested a potential migration from the creeks in late spring (April/May) for SC1. Migration increased in the spring concurrent

Table 3. Results from migration model (Eq. 4) with change points for the migration probability (r) determined through relative likelihoods (Fig. 3). For each size class (SC), the timing (τ) of the change point(s) are given in the first column, followed by the number of parameters (k) in the given model, Akaike's information criterion corrected for small sample sizes (AIC_c) score of the model, and the k parameter values. We considered models with $\Delta AIC_c < 2$ as equivalent. SC1: 120–200 mm, SC2: 201–320 mm standard length

Change-point timing (τ)		k	AIC_c	ΔAIC_c	SC1			SC2	
SC1	SC2				r_1	r_2	r_3	r_1	r_2
21 Dec and 1 May	1 Jan	5	254.12	0.00	0.18	0.091	0.19	0.34	0.20
21 Dec and 10 May	21 Dec	5	254.19	0.07	0.18	0.091	0.19	0.34	0.20
1 Dec and 1 May	1 Jan	5	254.43	0.31	0.31	0.10	0.20	0.34	0.20
1 Dec and 10 May	1 Jan	5	254.60	0.48	0.31	0.10	0.20	0.34	0.20
21 Dec and 10 May	1 Jan	5	254.64	0.52	0.19	0.095	0.21	0.34	0.20
21 Dec and 10 May	21 Dec	5	254.72	0.60	0.19	0.095	0.21	0.34	0.20
1 Dec	1 Jan	4	259.41	5.29	0.29	0.096		0.34	0.20
21 Dec	1 Jan	4	259.89	5.77	0.17	0.089		0.34	0.20
21 Dec and 1 May	None	4	264.16	10.04	0.18	0.091	0.19	0.24	
1 Dec and 1 May	None	4	264.47	10.35	0.31	0.10	0.20	0.24	
None	1 Jan	3	266.27	11.84	0.10			0.34	0.20
1 Dec	None	3	269.46	15.03	0.29	0.096		0.24	
None	None	2	276.33	21.90	0.10			0.24	
SC1 = SC2		1	303.18	48.75	0.16			0.16	

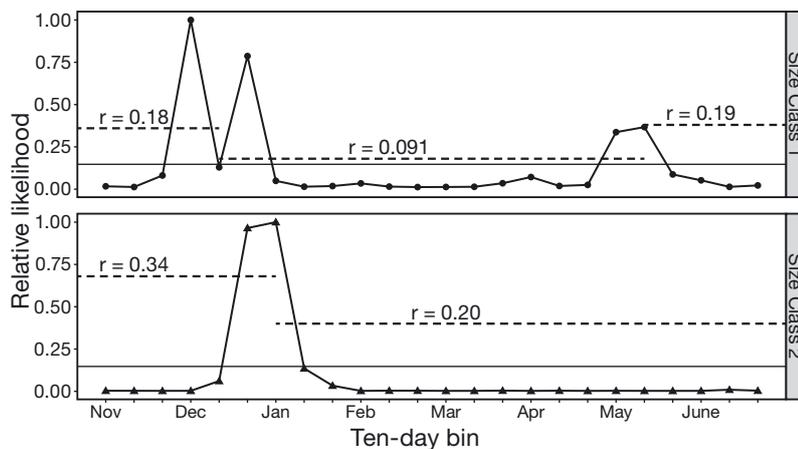


Fig. 2. Relative likelihood for each potential change point (τ) placement (Eq. 4) for juvenile *Centropomus undecimalis* migration probabilities (Size Class 1: 120–200 mm, Size Class 2: 201–320 mm standard length). The solid horizontal lines represent the 95% confidence intervals determined by the 14.7% relative likelihood interval. Also plotted are the migration probabilities (r) from the lowest Akaike's information criterion model (Table 3)

with water temperatures increasing above 25°C, and concurrently with a wet season (summer) decrease in salinity (see Fig. 4-6 in Barbour 2013). In each marking year, the number of marked fish detected per day substantially decreased by late-spring/early-summer (Fig. 4). This decline in detections was concurrent with an increase in the SC1 migration probability (Table 3), an increase in the permanent to temporary migration ratio (Fig. 5), and an increase in the catches of SC1 and SC2 snook in the FIM data from June through September (Fig. 6). An increased migration probability suggests increased movement,

the increase in the permanent to temporary migration ratio suggests an increased incidence of permanent migration, and FIM catches suggest that SC1 individuals entered areas typically used by adults concurrently with these changes. Although a higher percentage of SC2 than SC1 snook migrated in every creek and year combination (Table 1) and SC2 snook made larger movements (Table 2), the spring increase in the permanent to temporary migration ratio was most pronounced in SC1 (Fig. 5). Despite an expectation that SC2 individuals would lose their fidelity to the study creeks with increasing size, a higher percentage of SC2 than SC1 fish returned to the creeks in the subsequent marking year in almost all

year and marking creek combinations (Fig. 7). This suggests either a higher site fidelity or over-summer survival for SC2 individuals.

There was no obvious association between prey availability and snook presence in creeks. Plots of monthly prey density from 1237 seine net samples over 6 yr did not reveal a clear seasonal pattern in prey availability (Fig. 8). In fact, prey density in NS and SS appeared to increase in the summer, when juvenile snook abundance was lowest. Additionally, the size of 70563 captured prey items remained relatively constant throughout the year (see Fig. 4–12 in

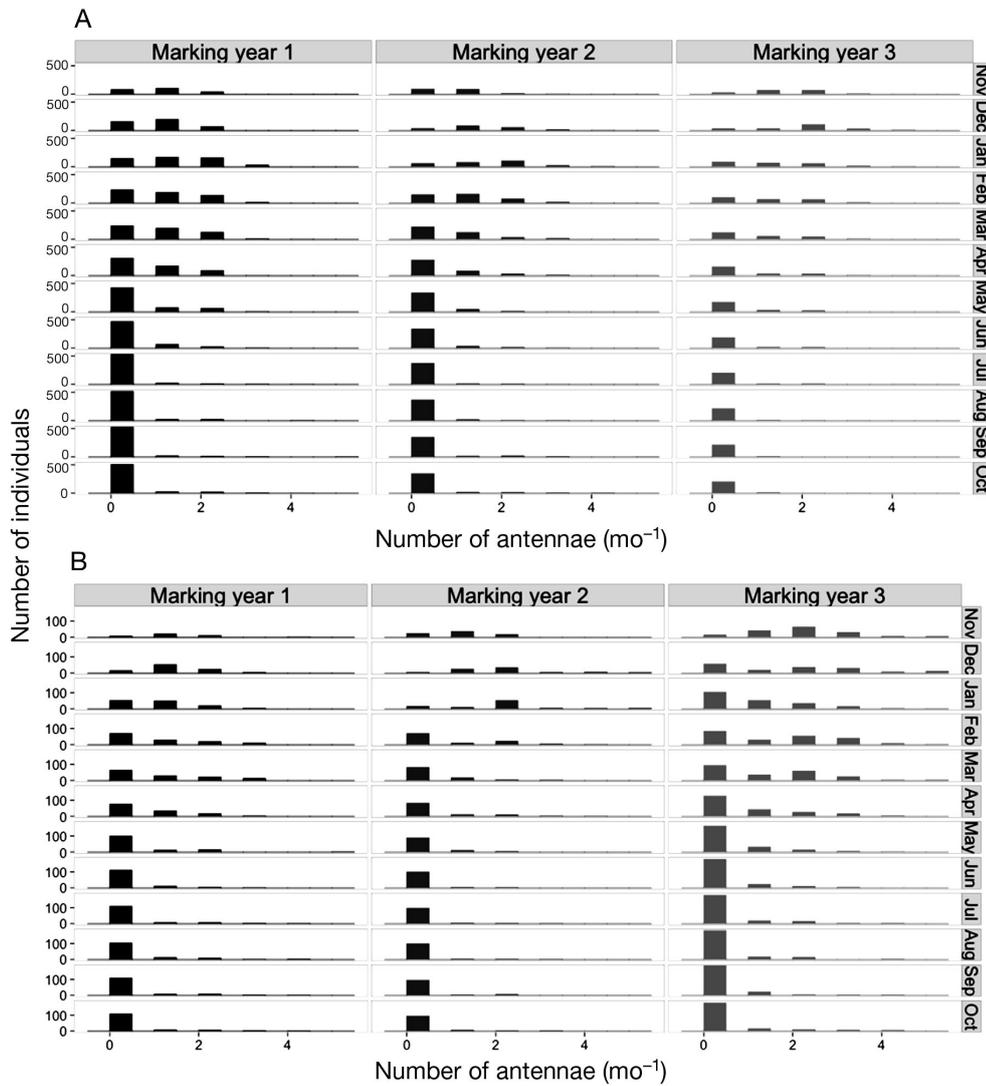


Fig. 3. Number of passive integrated transponder tag antennae at which each marked *Centropomus undecimalis* was detected per month for: (A) size class (SC) 1 (120–200 mm standard length, SL), and (B) SC2 (201–320 mm SL). ‘Antennae detected at’ per month serves as a proxy for movement due to spatial separation. Analysis was only performed on individuals within their marking year. The sum of bar-graph values in a single facet represents the cumulative number of marked snook by the end of the month

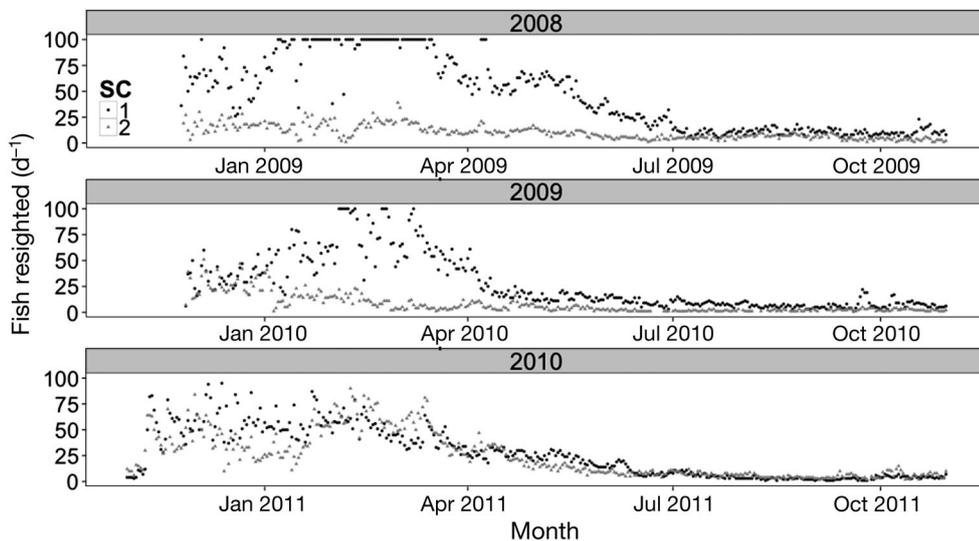


Fig. 4. Number of marked *Centropomus undecimalis* detected within the marking creeks each day for size classes (SC) 1 and 2. SC1: 120–200 mm, SC2: 201–320 mm standard length. Detections are separated by marking year, and only include individuals marked in the given year. For visual clarity, the maximum y-axis value was limited to 100 fish resighted d^{-1}

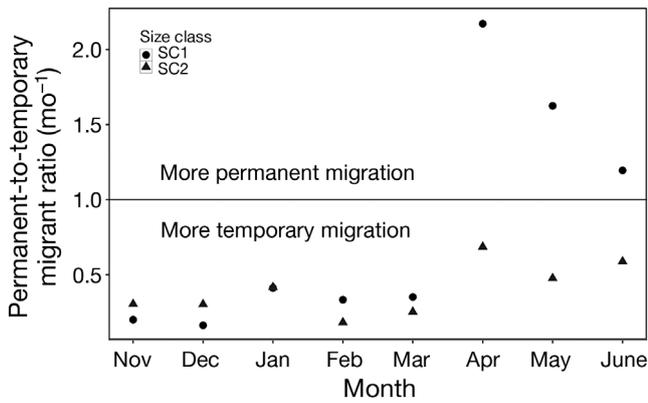


Fig. 5. Monthly ratio of permanent to temporary migration for both size classes (SC) of *Centropomus undecimalis* during the 3 yr study. SC1: 120–200 mm, SC2: 201–320 mm standard length. Horizontal line represents a 1:1 permanent to temporary migration ratio

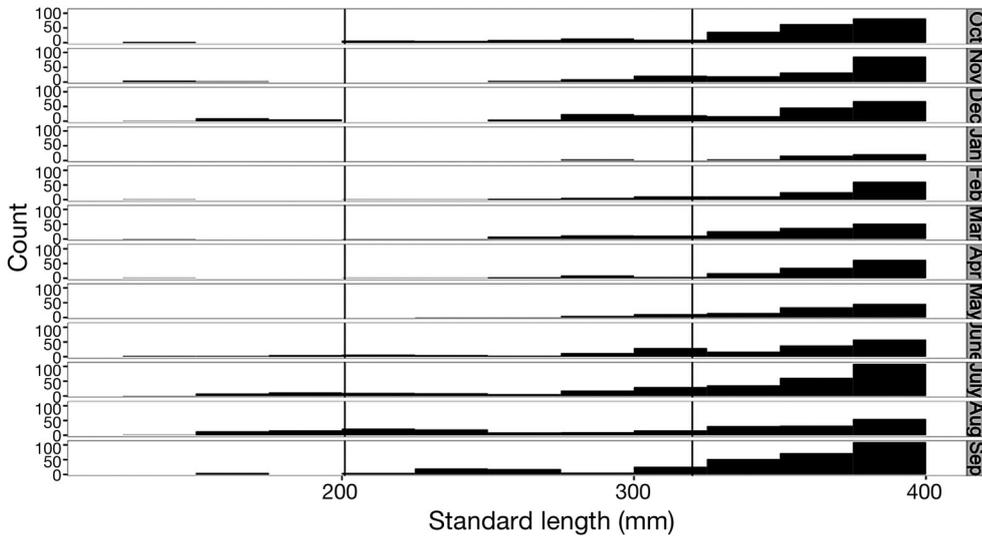


Fig. 6. Florida Fish and Wildlife Conservation Commission fisheries-independent monitoring *Centropomus undecimalis* catch data from Charlotte Harbor, Florida, USA. Monthly data combined from January 1997 to December 2010 and plotted by number of fish caught per 25 mm standard length bin. Maximum size plotted is limited to 400 mm due to a focus on juveniles. Figure includes 100 size class (SC) 1, 465 SC2, and 1800 larger snook. SC1: 120–200 mm, SC2: 201–320 mm standard length. Vertical lines represent lower and upper limits for SC2

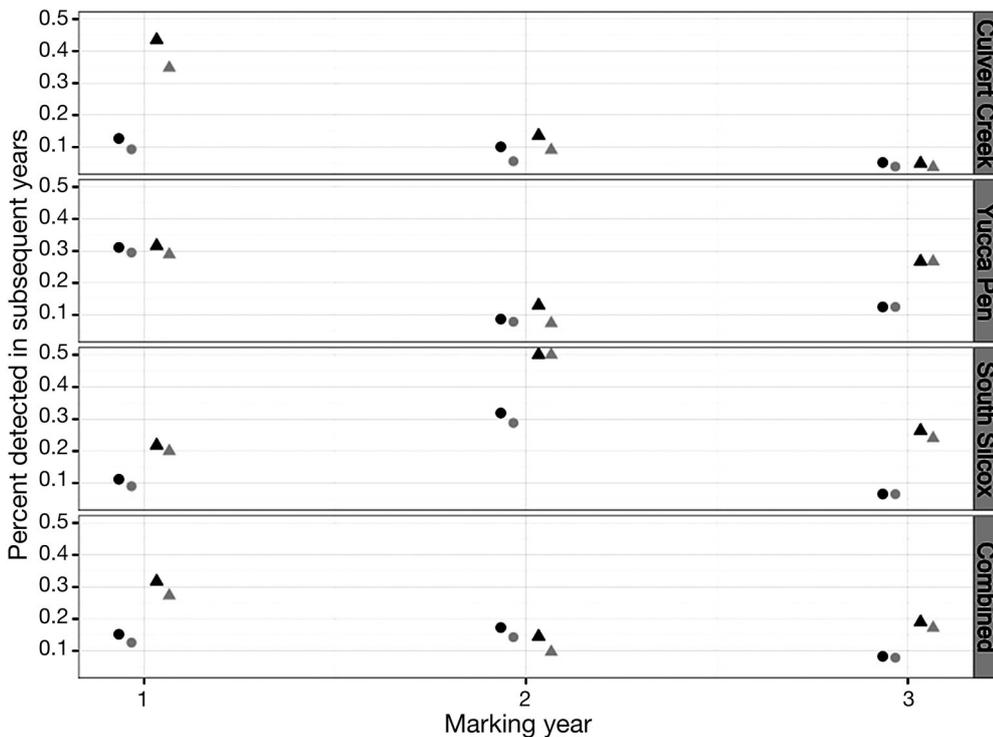


Fig. 7. Percent of marked *Centropomus undecimalis* by size class (SC) detected in any study creek (Any) or at least in their marking creek (Marking) in the marking year subsequent to their own. SC1: 120–200 mm, SC2: 201–320 mm standard length. Detections are separated by marking creek and marking year

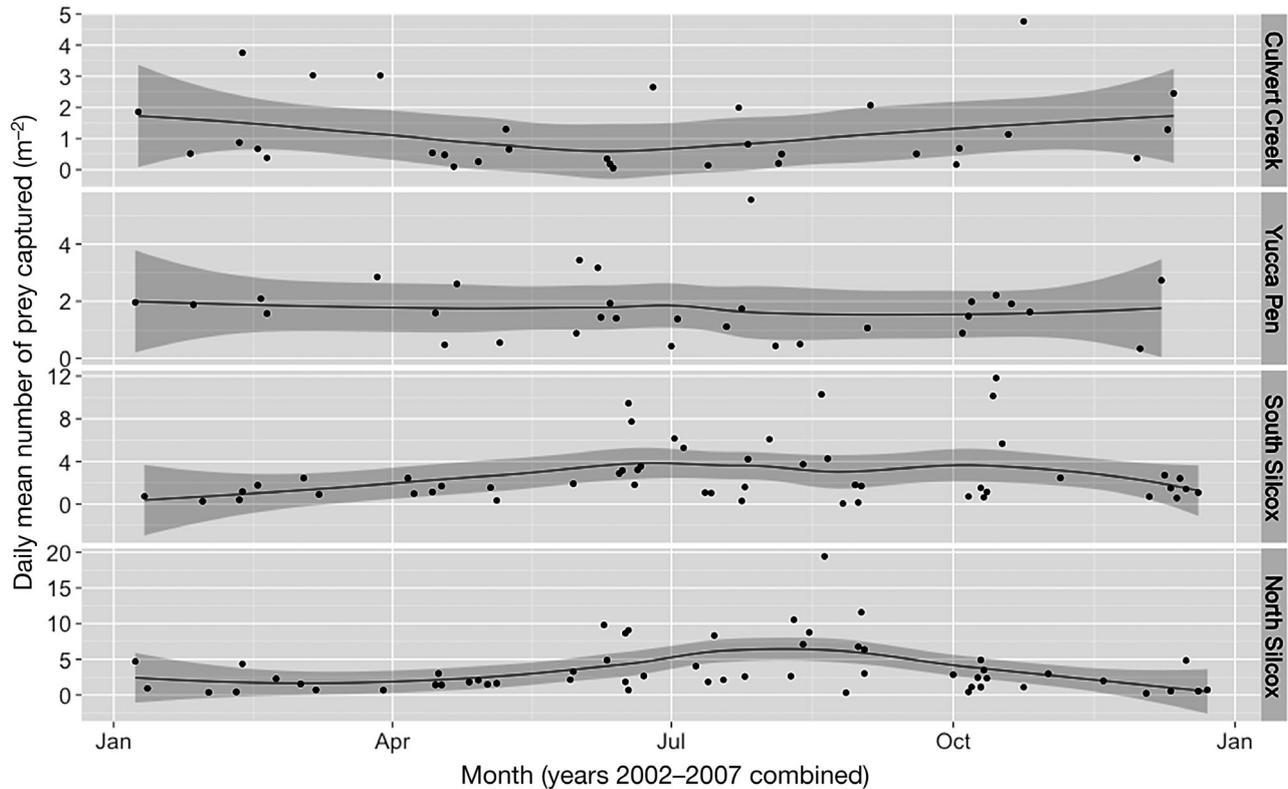


Fig. 8. Loess curve with 95% CI fitted to mean daily value of sampled prey density during targeted prey species collection via seine net. The scale of the y-axis has been varied for visual clarity

Barbour 2013), which suggests that a shift in prey size did not limit juvenile snook foraging opportunities.

DISCUSSION

Seasonal differences in juvenile snook migration and survival revealed a complex early life history habitat use pattern. The study creeks appeared to serve as a seasonal nursery habitat with high use during the winter followed by a spring migration away from the creeks to an as yet to be determined habitat. This seasonality defined the study creeks' role as part of a habitat mosaic that included multi-directional movements (e.g. temporary migration) between habitats. Moreover, this inter-habitat use pattern differed among age classes, challenging the notion of a discrete nursery habitat. This not only furthers the understanding of snook life history for management purposes, but also raises important questions for studies of nursery habitat use and ontogenetic connectivity. Now that patterns have been discerned, drivers of these characteristics need to be determined.

Seasonality in habitat use: migration or mortality

Low detections of marked fish in the summer can be explained as either migration or mortality. Prior studies assumed that documented declines in juvenile fish abundance were evidence of mortality (Carr & Hixon 1995, Watson et al. 2002) considering that habitat fidelity is a common trait among juvenile fishes (Rountree & Able 1992, Ross & Lancaster 2002). This assumption may be reasonable for species with Type I life histories that are habitat specialists, but for Types II and III, viz. habitat generalists and ontogenetic shifters, respectively, movement is likely to be a substantial factor (Adams et al. 2006a). Snook appear to fall between Type II and III strategies due to their ontogenetic changes in habitat use, but with brief periods of habitat overlap. Our data imply that movement was at least the initial driver of abundance declines, due to the increased migration probability and increased permanent to temporary migration ratio in the spring. This is supported by the extensive >10 km movement undertaken by some first-year individuals, a presumably high risk and generally unexpected behavior for juveniles (Doherty 1987, Carr & Hixon 1995, Watson et al.

2002), and by the high incidence of migration despite only sampling inside the study creeks within a 700 km² estuary.

Changing abiotic conditions may have driven seasonal migration. Seasonal changes in freshwater inflow and other environmental conditions can induce changes in density and species composition of mangrove fishes along estuarine gradients (Ley et al. 1999). Temperature increased and salinity decreased during the same time period as snook reduced use of creek habitat. Meanwhile, prey density and size remained largely unaltered. In fact, in South and North Silcox, which more closely resemble unaltered systems than the southern creeks (Adams et al. 2009a), prey density increased during the summer. This suggests a possible predatory release from juvenile snook, thereby creating an abundant food source for returning snook and for new post-settlement individuals in the subsequent season. However, this interpretation does not explain why SC2 snook return at a higher rate than SC1 unless SC1 shift to a new habitat and remain there or succumb to high over-summer mortality.

Alternatively, interactions with adult snook may drive juvenile movement. Juvenile snook are cannibalized by adults (Adams & Wolfe 2006) and spatially segregate by body size in mangrove creeks as demonstrated by Barbour (2013). In the early summer, adult snook leave the estuary to spawn near barrier islands (Adams et al. 2009b). This may allow juveniles to move into habitats previously occupied by cannibalistic adults, which presumably offer more favorable growth conditions. This interpretation is supported by increased summer detections of juvenile snook in FIM data, but the high incidence of skip spawning may leave some of these habitats occupied by adults (Trotter et al. 2012).

The seasonal dynamics of snook growth rates and spawning offers a more thorough interpretation for spring declines in habitat use and lack of SC1 returns. In Charlotte Harbor, snook spawn from April through September, followed by larval settlement in creek habitats approximately 2.5 wk later (Peters et al. 1998, Taylor et al. 1998, Adams et al. 2009b). It has been suggested that early- and late-summer cohorts form during this spawning period (McMichael et al. 1989). In order to reach SC1 by November at a maximum growth rate of 0.9 to 1.2 mm d⁻¹ (McMichael et al. 1989), an individual must have been spawned in early summer. Winter growth rates slow to a minimum of 0.5 mm d⁻¹ (McMichael et al. 1989), meaning that early summer-spawned individuals would enter SC2 in the spring/summer after their initial recruit-

ment. These individuals would then enter a second period of high growth, allowing them to outgrow SC2 and fully transition to adult habitat by the end of their second summer. In contrast, late-summer spawned snook would be smaller than our minimum tagging size of 120 mm SL during their first winter and would grow to SC2 over their second summer. These individuals would be marked as SC2 in their second year of life. This increased time spent in creek habitat may lead to formation of a stronger natal-creek imprint (Dittman & Quinn 1996, Lohmann et al. 2008), thereby explaining why SC2 fish, which should shift to adult habitats as they grow, return to the study creeks more frequently than SC1 fish. Such a mechanism would also allow for at least 2 cohorts of snook to be created each summer, bolstering replenishment of the adult stock.

Mortality may explain spring declines in habitat use, an increasing permanent to temporary migration ratio, and lack of SC1 fidelity. Mortality could function through 2 mechanisms: (1) increased predator exposure mediated by temperature-induced snook movement, or (2) seasonal predator presence within the creeks. Increasing water temperatures in the spring increase snook activity rates (Shafland & Foote 1983, Howells & Sonski 1990), leading to increased movement between creeks. This increased movement may inherently increase predation risk (McNay & Voller 1995, Limburg 2001), or there may be a spring influx of transient predators (Carr & Hixon 1995). The first scenario is supported by increased catches of SC2 individuals in Charlotte Harbor FIM data over the summer, where a diversity of large-bodied predators are commonly targeted by the recreational fishery. In reference to the second explanation, although Carangidae have occasionally been spotted entering the creeks, the main predators are adult snook and wading birds (Frederick & Loftus 1993, Adams & Wolfe 2006), which are mainly present in the winter (Barbour 2013). Thus, the second scenario, while possible, appears unlikely. Regardless, if the summer between SC1 and SC2 is indeed a high-mortality period as compared to low within-creek mortality (Barbour & Adams 2012) documented by Barbour (2013), this may serve as a population bottleneck (Doherty et al. 2004) that shapes year-class strength through a second recruitment gauntlet (Limburg 2001).

Irrespective of the mechanism of observed declines, the low density of cannibalistic snook (Adams & Wolfe 2006) inhabiting mangrove creeks during the summer has substantial population-level implications. Low densities of juvenile snook in the summer

would reduce cannibalization of the summer spawn, ensuring creation of a new year class through spatial segregation of cannibals and their potential prey (Barbour 2013). This contrasts the proposed mechanism for a saw-toothed recruitment pattern in other species, wherein a strong age-0 population suppresses the establishment of the next year's age-0 cohort through cannibalism of new recruits (Walters & Martell 2004).

Defining the nursery habitat unit

Considering that migration depends upon the definition of a study system's boundaries, interpretation of our results relies upon our subjective delineation of the nursery habitat unit (Kendall et al. 2003, Ross 2003). Here, we assumed individual mangrove creeks acted as the nursery unit for juvenile snook in Charlotte Harbor. This assumption stemmed from finding juvenile snook primarily in mangrove creeks (Stevens et al. 2007, Winner et al. 2010, Barbour & Adams 2012), logistical pragmatism, and the belief that movement outside the creek unit would be prohibitively high risk, as others have assumed (Doherty 1987, Carr & Hixon 1995, Watson et al. 2002). Instead, if we had defined creek pairs as the nursery unit, our estimates of migration would have been substantially lower. However, the spring declines in creek use and concurrent increase in SC2 snook outside the creeks in FIM data would still serve as evidence of a seasonal migration or mortality bottleneck.

Delineating an appropriate study unit for juvenile fish is particularly difficult, as individuals may expand into additional habitats with increasing body size (Serafy et al. 2003). In this scenario, individuals essentially incorporate more and more habitats in their repertoire as they grow, thereby producing substantial size-structure overlap among habitats (Serafy et al. 2003). This aligns with the size distributions of our catches of snook, which show that adult snook seasonally inhabit what are otherwise nursery habitats (Barbour & Adams 2012), and with the observation that SC2 individuals made more frequent movements between creek units than smaller individuals. Thus, SC2 would require a broader definition of the nursery unit that includes fringing mangrove shorelines adjoining creeks and the neighboring seagrass and oyster beds. Such a broad definition of the nursery unit would further highlight the potential negative impacts of habitat fragmentation (Kruess & Tschardtke 1994) and the importance of

the coastal ecosystem habitat mosaic, including transit corridors between habitats (Sheaves 2009).

In addition to the effect of increasing juvenile body size on the scale of nursery habitat, seasonality may affect its relative valuation. Mangrove creeks in Charlotte Harbor offer a favorable settlement habitat for larvae (Peters et al. 1998, Stevens et al. 2007), higher summer than winter growth rates (McMichael et al. 1989), and lower summer than winter densities of cannibalistic snook (Barbour 2013). While growth rates in winter are substantially lower than in the summer (McMichael et al. 1989), survival is high during this period (Barbour 2013), presumably allowing a favorable growth to mortality ratio (Dahlgren & Eggleston 2000). Following age-0 use of mangrove creeks from summer settlement through the first winter, the spring/summer decrease in habitat use documented here would typically be interpreted as an ontogenetic shift. However, because 10 to 20% of SC1 individuals return in the subsequent fall/winter and SC2 snook are caught in substantial numbers within the creeks, this putative spring migration appears to be part of a habitat expansion or multidirectional movement. Thus, although the mangrove creeks are largely abandoned by SC1/SC2 during the summer, the creeks appear to be a valuable part of SC2 nursery habitat during their second winter. This seasonal value may be due to the use of the creeks as a thermal refuge during the winter (Blewett et al. 2009, Barbour & Adams 2012, Barbour 2013) in order to avoid mortality associated with extreme low water temperatures (Shafland & Foote 1983, Howells & Sonski 1990, Adams et al. 2012).

CONCLUSIONS

This study highlights the difficulties of untangling the processes contributing to utility of a nursery habitat, an important step in habitat-based management (Stoner 2003). It is likely that the processes affecting juvenile habitat use in sub-tropical and tropical estuarine ecosystems are too complex to be reduced to a singular paradigm. Whereas the classical definition of nursery habitat defined it as an initial habitat in a series of distinct ontogenetic shifts towards adult habitat, our data support the notion that some juveniles expand their habitat use with increasing body size and alter their habitat valuation seasonally. Such multidirectional movement in the use of a nursery mosaic increases the difficulty of quantifying the contribution of juvenile habitat to adult populations (Nagelkerken 2009). That we studied a highly mobile

organism, as opposed to a species that is relatively stationary during given life stages, likely contributed to the conclusions reached on multidirectional movement (Adams et al. 2006a). As with most juvenile fish studies, we found correlation, not causation, leaving the causal drivers for observed trends open to interpretation. However, the information gained from this work will help focus future studies, including the identification of tradeoffs associated with movement to new habitats (Dahlgren & Eggleston 2000) and work done to further our general understanding of nursery habitat.

Acknowledgements. Funding was provided by a National Science Foundation Graduate Research Fellowship under Grant No. DGE-0802270, the National Sea Grant College Program of the U.S. Department of Commerce's National Oceanic and Atmospheric Administration under Grant No. NA06OAR4170014, Florida Fish and Wildlife Conservation Commission Project No. 11409, and by the Southwest Florida Water Management District. We thank the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute for access to their Fisheries Independent Monitoring data. Thanks to D. Behringer, M. All, and J. M. Ponciano for comments on the manuscript, and to T. Yess, R. Boucek, J. Adams, and numerous volunteers for assistance in the field.

LITERATURE CITED

- Adams AJ, Wolfe RK (2006) Cannibalism of juveniles by adult common snook (*Centropomus undecimalis*). *Gulf Mex Sci* 24:11–13
- Adams AJ, Dahlgren CP, Kellison GT, Kendall MS and others (2006a) Nursery function of tropical back-reef systems. *Mar Ecol Prog Ser* 318:287–301
- Adams AJ, Wolfe RK, Pine WE, Thornton BL (2006b) Efficacy of PIT tags and an autonomous antenna system to study the juvenile life stage of an estuarine-dependent fish. *Estuar Coasts* 29:311–317
- Adams AJ, Wolfe RK, Layman CA (2009a) Preliminary examination of how human-driven freshwater flow alteration affects trophic ecology of juvenile snook (*Centropomus undecimalis*) in estuarine creeks. *Estuar Coasts* 32:819–828
- Adams AJ, Wolfe RK, Barkowski N, Overcash D (2009b) Fidelity to spawning grounds by a catadromous fish, *Centropomus undecimalis*. *Mar Ecol Prog Ser* 389: 213–222
- Adams AJ, Hill JE, Kurth BN, Barbour AB (2012) Effects of a severe cold event on the subtropical, estuarine-dependent common snook, *Centropomus undecimalis*. *Gulf Caribb Res* 24:13–21
- Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) Second International Symposium on Information Theory. Akademiai Kiado, Budapest, p 267–281
- Barbour AB (2013) Processes affecting nursery habitat value of an estuarine-dependent fish. PhD dissertation, University of Florida, Gainesville, FL
- Barbour AB, Adams AJ (2012) Biologging to examine multiple life stages of an estuarine-dependent fish. *Mar Ecol Prog Ser* 457:241–250
- Barbour AB, Adams AJ, Behringer DC, Yess T and others (2011) PIT tag antennae arrays as fishery monitoring tools in tropical environments. Proceedings of the 63rd Gulf and Caribbean Fisheries Institute, San Juan, Puerto Rico, p 118–124
- Barbour AB, Adams AJ, Yess T, Behringer DC, Wolfe RK (2012) Comparison and cost-benefit analysis of PIT tag antennae resighting and seine-net recapture techniques for survival analysis of an estuarine-dependent fish. *Fish Res* 121-122:153–160
- Barrett GW, Bohlen PJ (1991) Landscape ecology. In: Hudson WE (ed) Landscape linkages and biodiversity. *Defenders of Wildlife*, Island Press, Washington DC, p 49–161
- Beck MW, Heck KL, Able KW, Childers DL and others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641
- Blewett DA, Stevens PW, Champeau TR, Taylor RG (2009) Use of rivers by common snook *Centropomus undecimalis* in Southwest Florida: a first step in addressing the overwintering paradigm. *Fla Sci* 72:310–324
- Boucek RE, Rehage JS (2013) No free lunch: displaced marsh consumers regulate a prey subsidy to an estuarine consumer. *Oikos* 122:1453–1464
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY
- Burnham KP, Anderson DR (2004) Multimodal inference: understanding AIC and BIC in model selection. *Sociol Methods Res* 33:261–304
- Carr MH, Hixon MA (1995) Predation effects on early post-settlement survivorship of coral-reef fishes. *Mar Ecol Prog Ser* 124:31–42
- Chen J, Gupta AK (2012) Parametric statistical change point analysis: with applications to genetics, medicine, and finance. Springer, New York, NY
- Dahlgren CP, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81:2227–2240
- Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM and others (2006) Marine nurseries and effective juvenile habitats: concepts and applications. *Mar Ecol Prog Ser* 312:291–295
- Dittman AH, Quinn TP (1996) Homing in Pacific salmon: mechanisms and ecological basis. *J Exp Biol* 199:83–91
- Doherty PJ (1987) The replenishment of populations of coral reef fishes, recruitment surveys, and the problems of variability manifest on multiple scales. *Bull Mar Sci* 41: 411–422
- Doherty PJ, Dufour V, Galzin R, Hixon MA, Meekan MG, Planes S (2004) High mortality during settlement is a population bottleneck for a tropical surgeonfish. *Ecology* 85:2422–2428
- Frederick PC, Loftus WF (1993) Responses of marsh fishes and breeding wading birds to low temperatures: a possible behavioral link between predator and prey. *Estuaries* 16:216–222
- Fulford RS, Peterson MS, Grammer PO (2011) An ecological model of the habitat mosaic in estuarine nursery areas. Part I: interaction of dispersal theory and habitat variability in describing juvenile fish distributions. *Ecol Model* 222:3203–3215
- Gillanders BM (2005) Using elemental chemistry of fish

- otoliths to determine connectivity between estuarine and coastal habitats. *Estuar Coast Shelf Sci* 64:47–57
- Hammett KM (1990) Land use, water use, streamflow, and water quality characteristics of the Charlotte Harbor inflow area, FL. USGS Water Supply Paper 2359-A. US Geological Survey, St. Petersburg, FL
- Howells RG, Sonski AJ (1990) Lower temperature tolerance of snook, *Centropomus undecimalis*. *Northeast Gulf Sci* 11:155–158
- Kalbfleisch JG (1985) Probability and statistical inference. Springer-Verlag, New York, NY
- Kendall MS, Christensen JD, Hillis-Starr Z (2003) Multi-scale data used to analyze the spatial distribution of French grunts, *Haemulon flavolineatum*, relative to hard and soft bottom in a benthic landscape. *Environ Biol Fishes* 66:19–26
- Kruess A, Tscharrntke T (1994) Habitat fragmentation, species loss, and biological control. *Science* 264:1581–1584
- Krumme U (2009) Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. In: Nagelkerken I (ed) Ecological connectivity among tropical coastal ecosystems. Springer, Dordrecht, p 271–324
- Levin PS, Stunz GW (2005) Habitat triage for exploited fishes: Can we identify essential 'Essential Fish Habitat?' *Estuar Coast Shelf Sci* 64:70–78
- Ley JA, McIvor CC, Montague CL (1999) Fishes in mangrove prop-root habitats of Northeastern Florida Bay: distinct assemblages across an estuarine gradient. *Estuar Coast Shelf Sci* 48:701–723
- Limburg KE (2001) Through the gauntlet again: demographic restructuring of American shad by migration. *Ecology* 82:1584–1596
- Lohmann KJ, Putman NF, Lohmann CMF (2008) Geomagnetic imprinting: a unifying hypothesis of long-distance natal homing in salmon and sea turtles. *Proc Natl Acad Sci USA* 105:19096–19101
- McMichael RH, Peters KM, Parsons GR (1989) Early life history of the snook *Centropomus undecimalis*, in Tampa Bay, Florida. *Northeast Gulf Sci* 10:113–125
- McNay RS, Voller JM (1995) Mortality causes and survival estimates for adult female Columbian black-tailed deer. *J Wildl Manag* 59:138–146
- Nagelkerken I (2009) Evaluation of nursery function of mangroves and seagrass beds for tropical decapods and reef fishes: patterns and underlying mechanisms. In: Nagelkerken I (ed) Ecological connectivity among tropical coastal ecosystems. Springer, Dordrecht
- Olds AD, Connolly RM, Pitt KA, Maxwell PS (2012) Habitat connectivity improves reserve performance. *Conserv Lett* 5:56–63
- Peters KM, Matheson RE, Taylor RG (1998) Reproduction and early life history of common snook, *Centropomus undecimalis* (Bloch), in Florida. *Bull Mar Sci* 62:509–529
- Poulakis GR, Blewett DA, Mitchell ME (2003) The effects of season and proximity to fringing mangroves on seagrass-associated fish communities in Charlotte Harbor, Florida. *Gulf Mex Sci* 21:171–184
- Rosenfeld JS, Boss S (2001) Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. *Can J Fish Aquat Sci* 58:585–593
- Ross SW (2003) The relative value of different estuarine nursery areas in North Carolina for transient juvenile marine fishes. *Fish Bull* 101:384–404
- Ross SW, Lancaster JE (2002) Movements and site fidelity of two juvenile fish species using surf zone nursery habitats along the southeastern North Carolina coast. *Environ Biol Fishes* 63:161–172
- Rountree RA, Able KW (1992) Fauna of polyhaline subtidal marsh creeks in southern New Jersey: composition, abundance and biomass. *Estuar Coasts* 15:171–185
- Sargent FJ, Leary TJ, Crewz DW, Kruer CR (1995) Scarring of Florida's seagrasses: assessment and management options. Tech Rep TR-1. Florida Marine Research Institute, St Petersburg, FL
- Serafy JE, Faunce CH, Lorenz JJ (2003) Mangrove shoreline fishes of Biscayne Bay, Florida. *Bull Mar Sci* 72:161–180
- Shafland PL, Foote KJ (1983) A lower lethal temperature for fingerling snook (*Centropomus undecimalis*). *Northeast Gulf Sci* 6:175–177
- Sheaves M (2005) Nature and consequences of biological connectivity in mangrove systems. *Mar Ecol Prog Ser* 302:293–305
- Sheaves M (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic. *Mar Ecol Prog Ser* 391: 107–115
- Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull Mar Sci* 60: 1129–1157
- Stevens PW, Blewett DA, Poulakis GR (2007) Variable habitat use by juvenile common snook, *Centropomus undecimalis* (Pisces: Centropomidae): applying a life-history model in a southwest Florida estuary. *Bull Mar Sci* 80:83–108
- Stoner AW (2003) What constitutes essential nursery habitat for a marine species? A case study of habitat form and function for queen conch. *Mar Ecol Prog Ser* 257: 275–289
- Taylor RG, Grier HJ, Whittington JA (1998) Spawning rhythms of common snook in Florida. *J Fish Biol* 53: 502–520
- Taylor RG, Whittington JA, Grier HJ, Crabtree RE (2000) Age, growth, maturation, and protandric sex reversal in common snook, *Centropomus undecimalis*, from the east and west coasts of South Florida. *Fish Bull* 98:612–624
- Trotter AA, Blewett DA, Taylor RG, Stevens PW (2012) Migrations of common snook from a tidal river with implications for skipped spawning. *Trans Am Fish Soc* 141:1016–1025
- Walters CJ, Martell SJD (2004) Fisheries ecology and management. Princeton University Press, Princeton, NJ
- Watson M, Munro JL, Gell FR (2002) Settlement, movement and early juvenile mortality of the yellowtail snapper *Ocyurus chrysurus*. *Mar Ecol Prog Ser* 237:247–256
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Annu Rev Ecol Syst* 15:393–425
- Winemiller KO, Jepsen DB (1998) Effects of seasonality and fish movement on tropical river food webs. *J Fish Biol* 53: 267–296
- Winner BL, Blewett DA, McMichael RH, Guenther CB (2010) Relative abundance and distribution of common snook along shoreline habitats of Florida estuaries. *Trans Am Fish Soc* 139:62–79