

# Emigration-corrected seasonal survival of a size-structured fish population in a nursery habitat

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**ABSTRACT:** We studied how emigration and seasonal dynamics affect apparent survival estimates in a nursery habitat, thereby altering habitat valuation. During a 3 yr study, we marked 1917 juvenile common snook *Centropomus undecimalis* and resighted 85.7% with a telemetry array in 4 mangrove creeks. We grouped individuals by size class, marking year, and creek, and estimated survival ( $\phi$ ) using the Barker joint-data model. Using telemetry data, we estimated seasonal emigration probabilities and simulated the effect of emigration on  $\phi$  estimates. We found a minimal effect of emigration on  $\phi$  estimates, the magnitude of which may be explained by emigration underestimates due to telemetry coverage or high resighting rates reducing bias. We found seasonal and size-based variation in  $\phi$  estimates. Our approach allowed survival estimation during a severe thermal-disturbance event that reduced survival in 2 creeks and may have had its impact mitigated in a third creek by an anthropogenic habitat alteration serving as a thermal refuge. Significant fine-scale spatial segregation of size classes likely acted to reduce intercohort cannibalism, thereby maintaining the high survival rates. We recommend caution when estimating apparent survival, since the lack of estimated survival bias was likely due to our extensive telemetry data, which buffered against the effects of emigration. We conclude that temporal variability in juvenile habitat use and survival requires seasonal classification of nursery habitat value, the consideration of multi-habitat nursery mosaics, and an exploration of the role of predation on habitat use.

**KEY WORDS:** Mark–resighting · PIT tags · PIT tag antenna · Charlotte Harbor

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## INTRODUCTION

Fish use a diverse set of life-history strategies to maximize their reproductive potential (Winemiller & Rose 1992), some of which involve the decoupling of adult and juvenile forms through distinct ontogenetic stages (e.g. Werner & Gilliam 1984, Osenberg et al. 1992, Pittman & McAlpine 2003). The ontogenetic shift is often defined by spatial separation between adults and juveniles, such that different life stages use different habitats. Juvenile habitats are considered nursery habitats if they contribute recruits to the

adult population at a disproportionately high rate (Beck et al. 2001, Dahlgren et al. 2006). For many species, nursery habitats are nearshore (Beck et al. 2001), and are increasingly important to identify in an era of coastal development and habitat degradation (Beach 2002). As it is difficult to identify nurseries by directly quantifying their contribution to adult habitats, 4 factors are often used to infer nursery habitat value: (1) density, (2) growth, (3) survival, and (4) movement to adult habitats (i.e. connectivity) (Beck et al. 2001). Due to methodological and financial constraints, nursery habitat research typically

focuses on 1 or 2 of the first 3 factors (density, growth, or survival) (Adams et al. 2006a).

The survival of juveniles is often compared between habitats to identify nurseries (e.g. Koenig & Coleman 1998, Ross 2003, Koenig et al. 2007), because there are multiple methods available to quantify survival and due to survival's overall significance in population dynamics (e.g. high juvenile mortality modifying recruitment patterns: Shulman & Ogden 1987, Robertson 1988). However, ecological and methodological issues exist with the survival metric, and these factors are rarely sufficiently addressed. Ecologically, instantaneous survival is unlikely to be temporally static, which complicates the use of overall survival estimates to compare potential nursery habitats. The movement of transient predators (Hixon & Carr 1997), fluctuations in abiotic characteristics including temperature and salinity (Ley et al. 1999), variable food availability (Boucek & Rehage 2013), and changing predation vulnerability with increasing body size (Werner & Gilliam 1984, Dahlgren & Eggleston 2000) are a few of the factors that may alter survival during a study. Further, seasonal dynamics (Ley et al. 1999, Boucek & Rehage 2013) may result in a variable valuation of a given habitat as a nursery, with the habitat being highly valuable as a nursery during certain months and not valuable during others. Thus, there is a need to understand temporal variability in survival in juvenile habitats to properly understand their nursery function.

Methodologically, the use of mathematically derived survival probabilities can prove problematic as the true estimate is typically of apparent survival ( $\phi$ ), which does not differentiate between emigration and mortality. This issue is rarely sufficiently addressed in studies of juvenile survival, leading to potential misestimates of survivorship. To the extent that observed losses are due to movement, survival in another habitat is possible and would have population consequences entirely different from mortality (Frederick 1997, Overholtzer-McLeod 2005). This is especially true for nursery habitat, because, by definition, juvenile fish using nursery habitat must eventually move to non-juvenile habitats (Beck et al. 2001), and may use nursery mosaics resulting in multidirectional movement between habitat units (Sheaves 2005). Additionally, juvenile movements in nursery habitat may vary seasonally (Barbour et al. 2014), further confounding survival estimates. Therefore, when using survival to evaluate nursery habitat value, special care must be taken to understand whether losses are due to mortality, seasonal emigration to different juvenile habitats, within-life stage

movements in a mosaic, or an ontogenetic shift to adult habitat.

Declines in abundance caused by movement are commonly attributed to mortality due to the difficulty of directly identifying emigrants. To address this issue, past researchers have used multiple methods, such as (1) using immigration rates as an estimate of emigration rates (Connell & Jones 1991, Watson et al. 2002); (2) assuming that if a system were sufficiently isolated, emigration would not occur due to the high risk of mortality during movement (Doherty 1987, Carr & Hixon 1995); or (3) assuming the distance of movements were negligible compared with the size of the sample area (Watson et al. 2002). When studying juvenile survival in nursery habitat, these assumptions are often easily challenged. For example, as juveniles grow and their predation risk decreases, individuals may undertake an ontogenetic shift, moving from habitats with a lower growth-to-mortality ratio to those with a higher growth-to-mortality ratio (Dahlgren & Eggleston 2000). The possibility of accessing higher-quality habitat due to decreased mortality risk with increasing size could provide incentive for higher-risk movement over long distances (Barbour 2013). Furthermore, if movement is from low- to high-quality habitat, movement rates would not be randomly and equally distributed, causing movement to be unidirectional and resulting in unequal immigration and emigration rates. As juvenile movement is an inherent ecological process shaping observed patterns of abundance (Shulman 1985, Robertson 1988) and an essential aspect of nursery habitat (e.g. connectivity), emigration is likely to have a significant influence on survival-based nursery habitat studies. However, the influence of emigration is dependent on life-history strategies, as some species are site attached while others make frequent movements to distinct habitat units for each life stage (Doherty 1987, Carr & Hixon 1995, Dahlgren & Eggleston 2000, Barbour & Adams 2012), as has been conceptually modeled elsewhere (Fig. 1 in Adams et al. 2006a)

To determine how temporal variability in juvenile survival influences nursery habitat value and how emigration biases survival estimates, we conducted a 3 yr telemetry study on juvenile common snook *Centropomus undecimalis* in 4 tidal mangrove creeks (putative nursery habitat in Charlotte Harbor, Florida, USA). Our objectives were to (1) identify seasonal and size-based differences in apparent survival; (2) determine how known emigration rates of our study species affected apparent survival estimation; and (3) correct apparent survival estimates for

emigration. After correcting apparent survival estimates for emigration bias, we investigated 2 likely drivers of mortality: temperature-driven disturbances and the spatial distribution of intercohort cannibals. The results of this study highlight the importance of considering the temporal context of survival estimates when evaluating juvenile habitats as potential nurseries.

## MATERIALS AND METHODS

### Study area

Charlotte Harbor is a 700 km<sup>2</sup> coastal plain estuarine system in southwest Florida (USA) (Hammett 1990). The climate is subtropical with mean seasonal water temperatures ranging from 12 to 36°C and infrequent freezing air temperatures (Poulakis et al. 2003). Seagrass flats (262 km<sup>2</sup>; Sargent et al. 1995) dominate the benthic habitat and mangroves dominate the shorelines (143 km<sup>2</sup>; L. Kish unpubl. 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 (Fig. 1 in Barbour & Adams 2012). 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 and North Silcox) 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. The 2 southern creeks (Yucca Pen and Culvert Creek) were 10 to 12 km south of the northern creeks, drained directly into Charlotte Harbor, and were separated by 1.4 km of mangrove shoreline and seagrass beds.

### Focal species

Common snook *Centropomus undecimalis* (hereafter referred to as 'snook') is a subtropical and 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 ~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 com-

mon in or near mangrove creeks year round, with highest densities in the fall and winter, until they reach ~300 mm standard length (SL) after 2 yr and enter the adult population (Taylor et al. 2000, Adams et al. 2006). Snook >300 mm SL use open estuarine and nearshore habitats (e.g. mangrove shorelines, artificial structure) from spring through fall, and presumably overwinter in riverine or creek habitats (Blewett et al. 2009, Barbour et al. 2014), although some snook reside in deeper estuarine habitats in winter (A. J. Adams unpubl. data). Larger snook cannibalize juveniles, especially during winter periods of mangrove creek co-inhabitation (Adams & Wolfe 2006). Snook in Florida exist at the northern edge of their geographic range (Adams et al. 2012, Barbour & Adams 2012) and are prone to mortality during severe cold events in which water temperatures reach their lethal thermal minimum of 12.5°C (Shafland & Foote 1983).

### Marking, recapture, and resighting

Using a center bag seine (21 m × 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 April 2009 (marking year 1), November 2009 to February 2010 (marking year 2), and October 2010 to February 2011 (marking year 3) (Table 1). 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. All unmarked fish were tagged with uniquely coded half-duplex PIT tags (23 mm length × 3.4 mm diameter, 0.6 g in air; Texas Instruments TIR-FID 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. 2006). 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, 2012a). 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 antenna, placing an antenna in the lower, middle, and upper stratum (0.5 km per stratum) of each creek with the exception of Yucca Pen upper (due to financial constraints) (Fig. 1). Few antennae covered 100% of

Table 1. Survival estimation primary period start date, type, and interval length for capture histories. Marking year 1 is 29 November 2008 to 31 July 2009; year 2 is 30 November 2009 to 31 July 2010; and year 3 is 15 October 2010 to 31 July 2011. Primary period type refers to whether marking occurred during the primary event (capture) or if the primary period was artificially created (dummy). Intervals were calculated in relation to a 31 d period equaling length 1

Marking year 1			Marking year 2			Marking year 3		
Primary start date	Type	Interval length	Primary start date	Type	Interval length	Primary start date	Type	Interval length
29 Nov	Capture	0.48	30 Nov	Capture	1.10	15 Oct	Capture	0.84
14 Dec	Capture	0.45	3 Jan	Capture	1.0	10 Nov	Capture	0.61
28 Dec	Capture	0.65	3 Feb	Capture	1.0	29 Nov	Capture	0.23
17 Jan	Capture	0.90	6 Mar	Dummy	1.0	6 Dec	Capture	1.39
14 Feb	Capture	1.0	6 Apr	Dummy	1.0	18 Jan	Capture	0.42
17 Mar	Dummy	1.13	7 May	Dummy	1.0	31 Jan	Capture	0.19
21 Apr	Capture	1.0	7 Jun	Dummy	1.0	6 Feb	Capture	1.0
22 May	Dummy	1.0	8 Jul	Dummy	0.74	9 Mar	Dummy	1.0
22 Jun	Dummy	1.26				9 Apr	Dummy	1.0
						10 May	Dummy	1.0
						10 Jun	Dummy	1.0
						11 Jul	Dummy	0.65

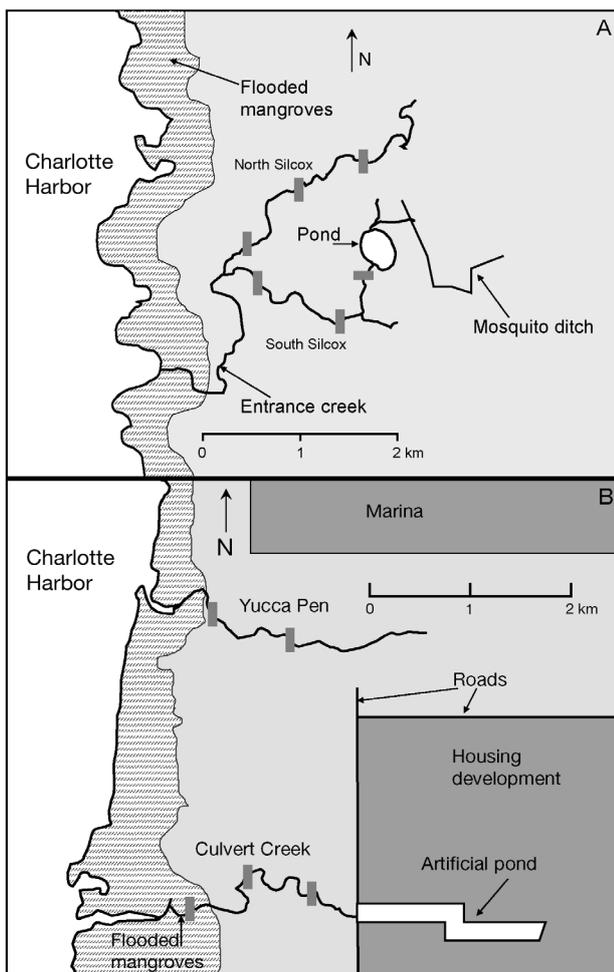


Fig. 1. The 4 study creeks in Charlotte Harbor, Florida, USA. (A) The northern creeks are 10 to 12 km north of (B) the southern creeks. Small gray oblongs: lower, middle, upper PIT-tag antenna locations

creek width, but all covered >75%. Antennae resighted fish continuously from November 2008 through July 2011. A complete description of the antenna array is provided in Barbour et al. (2011, 2012a).

During this study, sedimentation from a mangrove restoration project at the head of North Silcox drastically reduced the abundance of snook, making sampling in North Silcox inefficient. Thus, we only marked fish in Culvert Creek, Yucca Pen, and South Silcox, but resighted fish in all 4 creeks. Additionally, a concurrent study employed pulsed gastric lavage on some marked individuals in year 3, which increased lethal and sublethal handling effects (Barbour et al. 2012b).

### Survival estimation

We estimated survival using the Barker survival model (Barker 1997, 1999) within Program MARK (White & Burnham 1999). This model allows for incorporation of information from physical capture during discrete primary periods and continuous resighting from all antennae during secondary periods (the intervals between primary periods) (Fig. 1 in Barbour et al. 2013). We defined capture–recapture events as the primary periods, and coded for uneven time intervals by scaling 31 d to equal an interval of length 1 (Table 1). We added artificial (dummy) primary periods at 31 d intervals after the completion of physical capture (tagging events) to continue monthly estimation of survival until 31 July of each marking year (Table 1). We divided marked fish into 2 size classes: SC1 (120–200 mm SL) and SC2 (201–320 mm SL), which approximated to age 0 (SC1) and age 1

(SC2) individuals (Taylor et al. 2000, Barbour & Adams 2012). We created capture histories for each individual, and grouped individuals by marking creek, marking year, and size class.

For the Barker model, Program MARK estimates 7 parameters (Table 2) (White & Burnham 1999). Since physical recaptures were minimal compared with antennae resightings (Barbour et al. 2012a, 2014), we only included marking information and antennae resightings in the capture histories. This allowed us to fix the parameters recapture ( $p = 0$ ), dead recovery ( $r = 0$ ), and fidelity ( $F = 1$  and  $F' = 0$ ), thereby reducing the Barker model to 3 parameters (Barbour et al. 2013). Since resightings did not occur over the entire geographic range of our study species and since we fixed the site fidelity parameters ( $F$  and  $F'$ ), we hereafter refer to survival ( $s$ ) as apparent survival ( $\phi$ ), which incorporates the effects of mortality and emigration.

We allowed  $\phi$ ,  $R$ , and  $R'$  to vary seasonally (see Table 2 for definitions). We defined fall as occurring prior to January, winter as occurring January through March, and spring and summer as April through July (hereafter referred to as 'spring'). We based this seasonality on seasonal change points in an emigration rate estimated from movement data during the 3 yr survival study (Barbour et al. 2014). Additionally, due to the mobile nature of our study species (Barbour et al. 2014), it is likely that we marked several transient individuals not resident to the study creeks. To minimize the influence of these transients on  $\phi$  and reduce the influence of handling effects (Barbour et al. 2012b), we estimated the first  $\phi$  interval for all newly marked individuals separately from the 3 seasonal estimates. We hereafter refer to this estimate as 'first capture'. Due to concerns over potential convergence issues with the Barker model at certain parameter values (Barbour et al. 2013), we used simulated annealing for numerical optimization within MARK (White & Burnham 1999).

### Simulating the effect of emigration on survival estimates

The Barker joint-data model is structured to account for emigration through the site fidelity ( $F$  and  $F'$ ) parameters. Since we fixed these parameters and estimated apparent as opposed to true survival, emigration could have biased our estimates. To determine the effect of emigration on  $\phi$ , we extended a previous simulation model (Barbour et al. 2013) to include known movement rates (Barbour et al. 2014). We classified emigrants as individuals detected on a PIT tag antenna outside of their marking creek within their marking year (Barbour et al. 2014).

The simulation model is described thoroughly elsewhere (Barbour et al. 2013), but is summarized as follows. We simulated a population in which mortality and detection occurred as daily processes during  $d = 180$  d. Beginning with a population of  $n = 200$  individuals marked on day one, we set both true monthly survival ( $s_m$ ) and capture probability ( $p_m$ ) to 0.9. Conversions to daily probabilities ( $s_d$  and  $p_d$ ) are Eqs. (1) and (2) in Barbour et al. (2013). Each day we conducted a Bernoulli trial for each individual with probability  $s_d$  to determine whether the individual survived or died, followed by a Bernoulli trial of probability  $p_d$  to determine whether surviving individuals were detected. At the end of the simulation, we collapsed daily detections into  $m = 6$  monthly sampling periods and estimated survival using the Barker model. The marking event on Day 1 was the only primary period with capture information, and detections informed monthly secondary periods.

As a departure from this initial simulation, we added biological complexity in the form of monthly emigration. Using site-specific movement rates from previous work (Barbour et al. 2014), we conducted another Bernoulli trial for each individual

Table 2. Barker joint-data model parameter definitions

Parameter	Definition
$s_i$	Probability that an animal alive at $i$ is alive at $i + 1$
$p_i$	Probability that an animal at risk of capture at $i$ is captured at $i$
$r_i$	Probability that an animal that dies in $i$ , $i + 1$ is found dead
$R_i$	Probability that an animal that survives from $i$ to $i + 1$ is resighted (alive) sometime between $i$ and $i + 1$
$R'_i$	Probability that an animal that dies in $i$ , $i + 1$ without being found dead is resighted alive in $i$ , $i + 1$ before it died
$F_i$	Probability that an animal at risk of capture at $i$ is at risk of capture at $i + 1$
$F'_i$	Probability that an animal not at risk of capture at $i$ is at risk of capture at $i + 1$ (this definition, as used in Program MARK, differs from the definition in Barker (1997) to force probability-driven internal constraints) (White & Burnham 1999)

at the start of each month. This Bernoulli trial determined whether the individual emigrated or remained in the study area for the month based on a monthly emigration probability ( $e_m$ ). Regardless of the outcome of this trial,  $s_m$  did not change. If the individual emigrated, we conducted another Bernoulli trial to determine whether the individual temporarily or permanently emigrated based on the probability of permanent emigration ( $e_{m,perm}$ ). Temporary emigrants returned in the subsequent month and were subject to a new emigration Bernoulli trial, while permanent emigrants did not return in any subsequent month.

We informed the seasonal monthly emigration probability ( $e_m$ ) and the probability of an emigration event being permanent ( $e_{m,perm}$ ) with previous data from our study system (Barbour et al. 2014) (Table 3). We calculated  $e_{m,perm}$  by averaging the monthly permanent-to-temporary emigration ratios (Figs. 4 & 5 in Barbour et al. 2014) for each season, and converting these ratios to probabilities. To calculate  $e_m$ , we reran the seasonal emigration model for each size class (Eqs. 4-1 to 4-4 in Barbour et al. 2014) with 2 changes. First, we mirrored our method of apparent survival estimation by setting change points ( $\tau$ ) in the emigration rate ( $w$ ) for SC1 and SC2 as 1 January and 1 April (Eq. 4-4 in Barbour et al. 2014). At these change points, the value of  $w$  changed to a season-specific rate. Second, we included marked individuals that did not emigrate, which redefined  $w$  as the probability of emigrating. To adjust for declines due to mortality, we altered the model to include an assumed monthly mortality rate of 10%.

We applied these rates on a seasonal basis (fall = Months 1 and 2, winter = Months 3 and 4, spring = Months 5 and 6) within the previously described simulation (Barbour et al. 2013). We conducted a parallel simulation with no emigration to compare  $\hat{\phi}$  estimates in the presence and absence of emigration. We estimated  $\phi$ ,  $R$ , and  $R'$  as seasonal parameters, and fixed

Table 3. Emigration data (Barbour et al. 2014) used to inform emigration rates for apparent survival bias simulation. The emigration parameters included the monthly emigration probability ( $e_m$ ) and the probability of an emigration event being a permanent emigration ( $e_{m,perm}$ ). Size class 1: 120–200 mm standard length (SL); size class 2: 201–320 mm SL

Size class	Parameter	Fall	Winter	Spring
1	$e_m$	0.044	0.019	0.020
1	$e_{m,perm}$	0.15	0.27	0.63
2	$e_m$	0.26	0.096	0.026
2	$e_{m,perm}$	0.23	0.22	0.37

$p = 0$ ,  $r = 0$ ,  $F = 1$ , and  $F' = 0$ . This directly mirrored our method of apparent survival estimation for the true mark–resighting data, except that we did not model an effect of transient individuals. We built the simulation in program R (R Development Core Team 2013) and estimated survival with the RMark package (Laake & Rexstad 2008).

We used simulated annealing for optimization and iterated the simulation 10 000 times. For each iteration, we computed the relative departure of the estimated survival from the true survival as follows:

$$\text{relative departure} = (\hat{s}_m - s_m) \times s_m^{-1} \tag{1}$$

We then estimated relative bias as the average, over all iterations, of these relative departures. Additionally, we quantified percent coverage by counting the number of successful iterations per parameter set in which the true value for  $s_m$  was included in an estimation model's 95% confidence interval of  $\hat{s}_m$  for each seasonal estimate.

### Correcting survival estimates for emigration

We corrected our telemetry derived apparent survival estimates with the relative bias from our emigration simulation. We rearranged:

$$s - s \times (\text{bias}) = \hat{\phi} \tag{2}$$

to estimate the true survival value ( $s$ ) for each seasonal maximum likelihood apparent survival estimate as:

$$s = \frac{\hat{\phi}}{1 - \text{bias}} \tag{3}$$

We did not bias-correct confidence intervals and removed uninformative parameter estimates (parameters with a standard error equal to 0 or >1).

### Explaining survival patterns

We collected 2 forms of auxiliary data to investigate observed patterns in survival. First, a severe cold event affected the study area during the second marking year (Adams et al. 2012). Snook are prone to mortality at water temperatures <12.5°C (Shafland & Foote 1983), and snook in Charlotte Harbor likely suffered high mortality from the January 2010 cold event (Adams et al. 2012, Barbour & Adams 2012). A manmade mosquito ditch (Resh & Balling 1983, Brockmeyer et al. 1997) exists in South Silcox (Fig. 1), which has no parallels in

Yucca Pen or Culvert Creek. Past catches of densely aggregated juvenile snook in this mosquito ditch during cold weather suggest that the ditch acts as a thermal refuge (A. J. Adams & A. B. Barbour pers. obs.). After completion of the survival study, we placed HOBO pendant underwater temperature loggers at the lower and upper antenna of each creek and within the mosquito ditch to evaluate its potential as a thermal refuge relative to other portions of the creeks.

Second, adult snook cannibalize juveniles within our study system (Adams & Wolfe 2006). Since it is believed that intercohort competition and cannibalism can regulate populations (Walters & Martell 2004), we investigated the effect of intercohort movement on spatial distribution. We conducted 2 analyses. For the first analysis we included 7686 snook marked within and outside of the study creeks since 2004 (full details in Barbour & Adams 2012). We separated snook into 5 size bins: (1) 120–200 mm SL, (2) 201–300 mm SL, (3) 301–400 mm SL, (4) 401–500 mm, and (5) >500 mm. We advanced marked individuals by one size bin every August, which conservatively estimated snook growth rates (Taylor et al. 2000). Using antennae resightings, we plotted the daily number of snook detected from each size bin per antenna. We also performed a Pearson's chi-squared test with Yates' continuity correction on the co-occurrence of different size bins in 462 seine-net pulls from June 2004 through February 2011. The null hypothesis was that the presence of a given size bin of snook (1, 2, 3, or 4) in a single seine-net capture event would be independent of the presence of snook >500 mm (size bin 5).

## RESULTS

We marked and detected a high number of juvenile snook. 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) (Appendix B in Barbour 2013). Within their marking year, we detected 80.7% of snook marked in year 1, 88.2% marked in year 2, and 91.5% marked in year 3 (Barbour et al. 2012a).

## Apparent survival

There were multiple month and size-class combinations for which apparent survival could not be estimated. Due to the low number of marked SC2 individuals, many SC2  $\phi$  estimates were unidentifiable (estimates with no confidence intervals, or intervals ranging from 0 to 1), except for year 2 winter and year 3 (Fig. 2). No year 2 estimates existed for South Silcox SC2 due to a low number of marked individuals (Appendix B in Barbour 2013). In year 2, there were no fall  $\phi$  estimates for either size class since only one fall interval existed (Table 2) and this interval was assigned to the 'first capture' estimate. First-capture  $\phi$  estimates tended to be substantially lower than seasonal estimates for SC1 (Fig. 2).

Apparent survival estimates varied seasonally and were affected by a thermal-disturbance event in year 2. Seasonal  $\phi$  estimates typically declined in the spring. Year 2 winter  $\phi$  estimates were significantly lower than winter estimates from other years with the exception of year 3 South Silcox SC1. The year 2 decrease in winter  $\phi$  was concurrent with a decrease in regional water temperatures below snook's thermal lethal tolerance in January 2010, which resulted in a mass mortality event of adults (Adams et al. 2012).

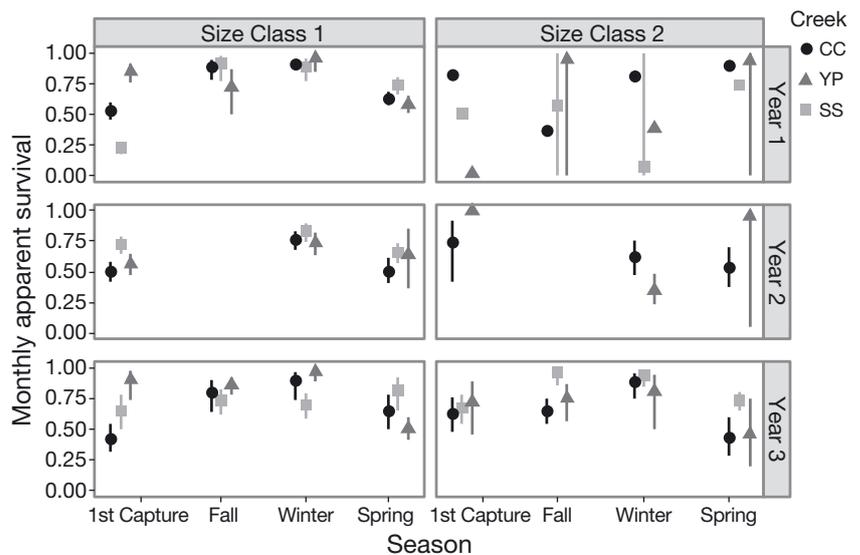


Fig. 2. Barker joint-data model apparent survival estimates and 95% confidence intervals from 3 yr of juvenile common snook PIT tag telemetry in Charlotte Harbor, Florida, USA. Marking occurred in the mangrove-lined creeks Culvert Creek (CC), Yucca Pen (YP), and South Silcox (SS) in 2008–2009 (year 1), 2009–2010 (year 2), and 2010–2011 (year 3). The 'first capture' estimate refers to the apparent survival of marked fish in the interval after they were marked. Size class 1: 120–200 mm standard length (SL); size class 2: 201–320 mm SL

During this apparent thermal-disturbance event, SC1  $\phi$  was highest in South Silcox. In 2012, within-creek temperature loggers documented 2 cold events (Fig. 3), during which water temperatures remained above the thermal lethal level of snook in the South Silcox mosquito ditch (Fig. 1A) and dipped below the lethal level in all but one other location.

### Emigration

We documented substantial movement between creeks and found that movement rates were seasonally dependent and highest for SC2. Of 1422 marked SC1 and 495 marked SC2 snook, we detected 135 SC1 and 171 SC2 individuals as emigrating during

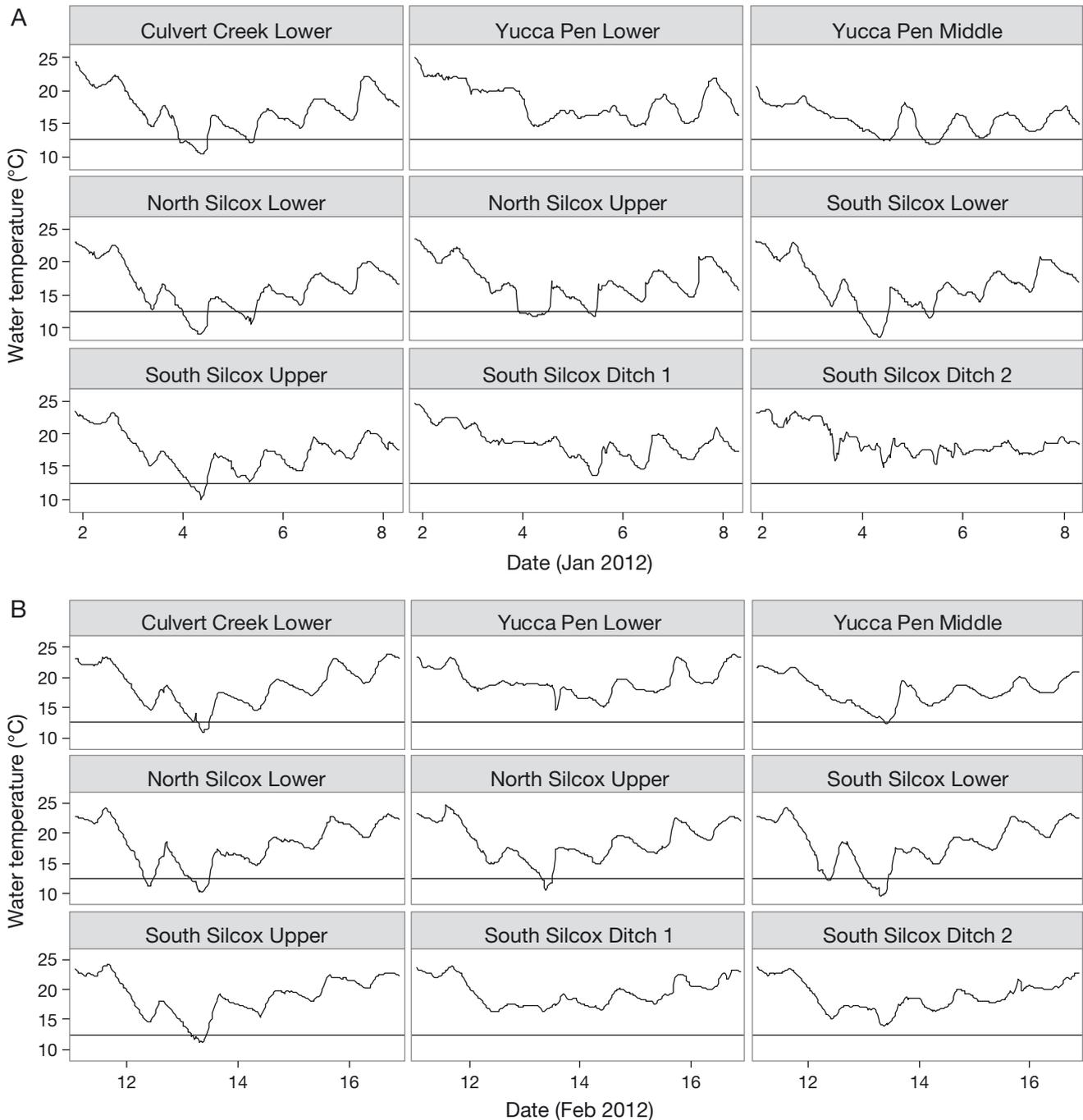


Fig. 3. HOBO Pendant® water temperature data from 2 cold fronts in (A) January and (B) February 2012. Solid horizontal line represents the thermal lethal minimum temperature for common snook of 12.5°C

the study (further details in Barbour et al. 2014). The fall monthly emigration probability ( $e_m$ ) for SC2 was 6 times higher than for SC1 (Table 3). For both size classes,  $e_m$  was highest in the fall, decreased in winter, and did not increase in the spring. The seasonal probabilities of an emigration event being permanent ( $e_{m,perm}$ ) were generally similar between size classes. Seasonally,  $e_{m,perm}$  was highest in the spring and was almost twice as high in SC1 than SC2 during this season.

Simulated apparent survival estimates were not substantially affected by estimated emigration rates. Incorporating emigration (Table 3) into a population simulation revealed little effect on the mean relative bias or coverage of SC1  $\phi$  estimates (Fig. 4). However, SC2  $\phi$  estimates were biased by a mean of  $\pm 5\%$  in the fall and spring and exhibited poor coverage in the fall when  $e_m$  was highest. Variability in relative bias increased slightly when permanent emigration rates were highest (spring SC1). Correcting maximum likelihood estimates of  $\phi$  for the simulated emigration bias (Fig. 4) did not markedly affect estimates (Fig. 5). In particular,  $\phi$  estimates did not substantially change during the winter disturbance event in year 2, and adjusting for emigration did not explain the consistent spring declines in  $\phi$ .

**Intercohort cannibalism**

Daily plots of snook detections revealed multiple antennae failures and seasonal abundance trends, but did not show spatial segregation by size class. Plots of daily detections revealed multiple PIT tag antennae failures in year 1 (Fig. 6A), 3 antennae failures in year 2 (Fig. 6B), and near perfect antennae function in year 3 (Fig. 6C) (failures are characterized by week to multi-month periods of no detections). Detections show a similar seasonal pattern to  $\phi$  estimates, with the number of individuals detected decreasing in the spring. Despite an assumption that SC1 individuals would leave an area when larger size classes were present, the Yucca Pen lower, Culvert Creek middle, and South Silcox middle antennae showed concurrent daily use by a high number of individuals from multiple size classes. However, within Culvert Creek and South Silcox

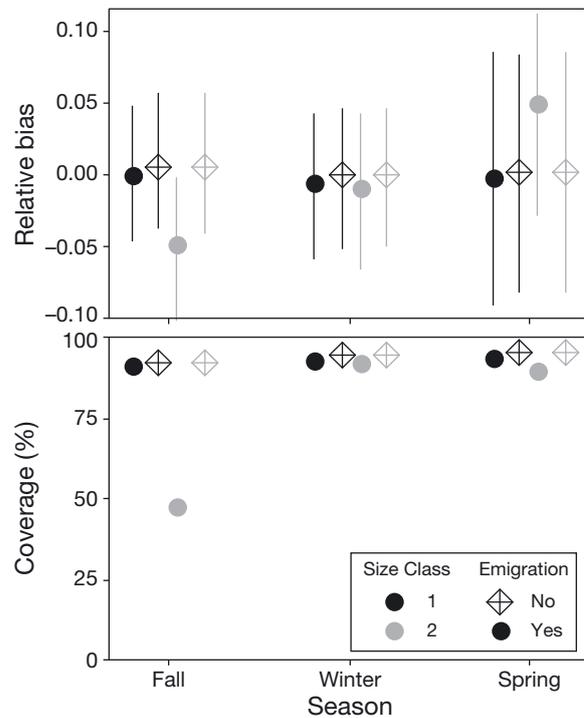


Fig. 4. Relative bias and percent coverage of monthly Barker joint-data survival estimates from a simulation including estimated emigration probabilities (Table 3). Simulation partitioned by size class 1 (120–200 mm standard length, SL) and 2 (201–320 mm SL), and compared with a simulation in which no emigration occurred

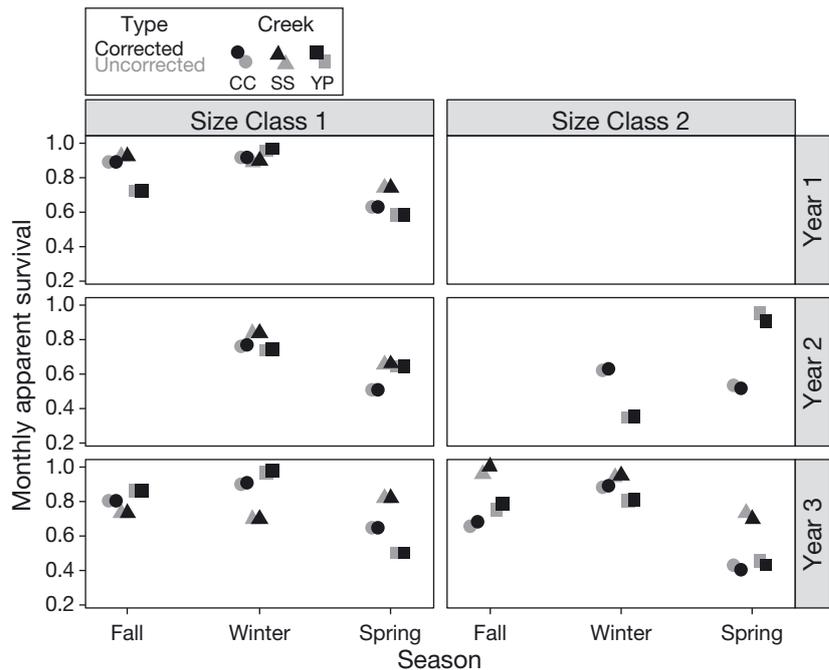


Fig. 5. Uncorrected (values from Fig. 2) and emigration bias (values from Fig. 4) corrected maximum likelihood apparent survival estimates for Culvert Creek (CC), Yucca Pen (YP), and South Silcox (SS) in the 3 study years. Unidentifiable parameters censored from figure

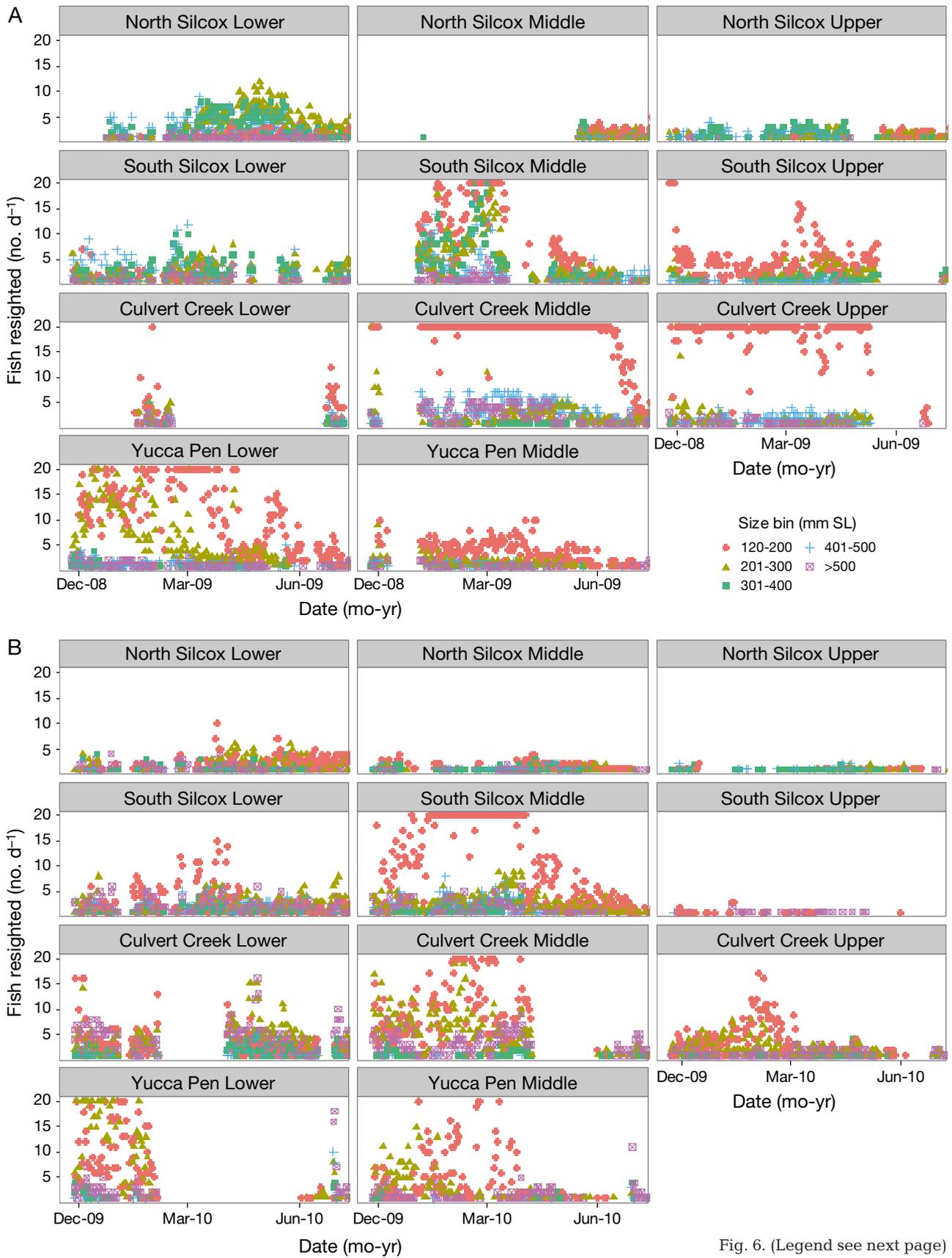


Fig. 6. (Legend see next page)

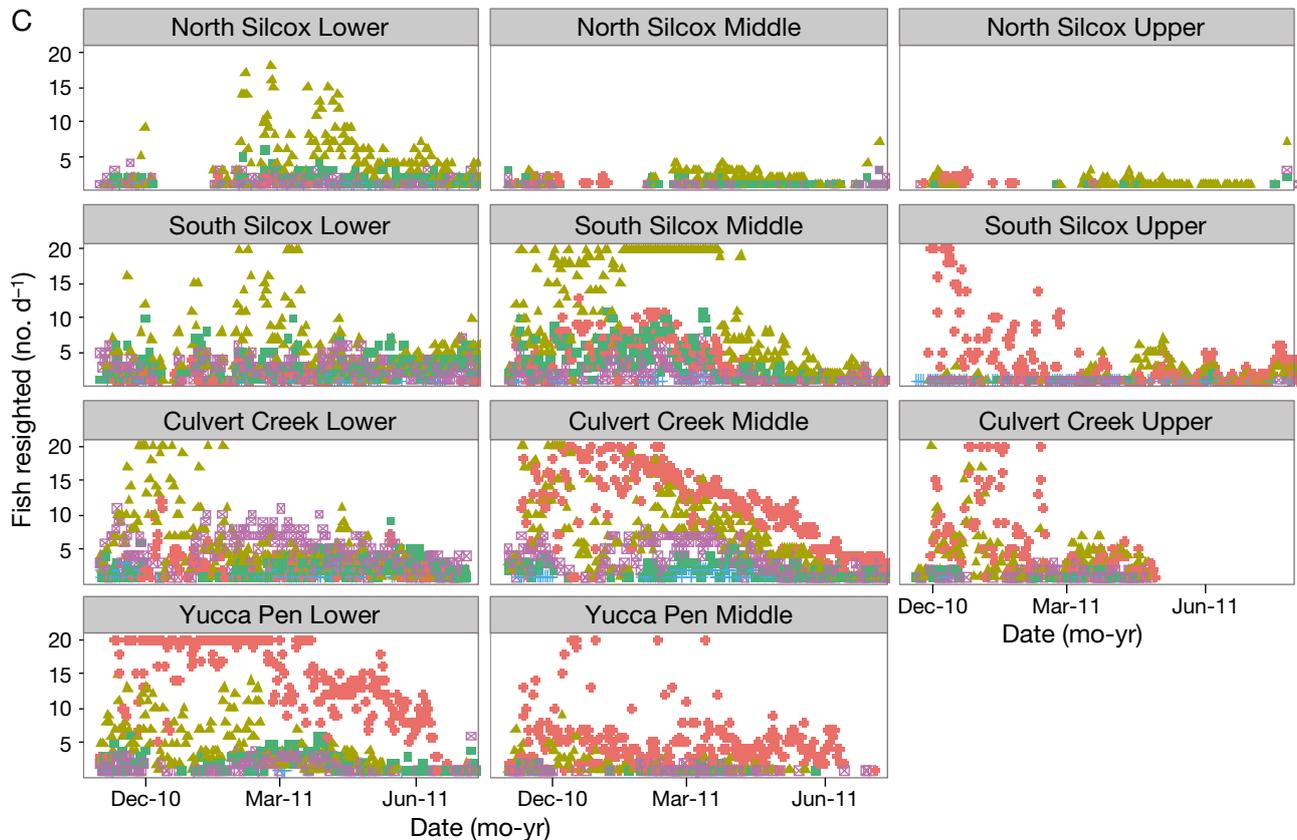


Fig. 6. Number of common snook *Centropomus undecimalis* detected at each PIT tag antenna each day during (A) year 1, (B) year 2, and (C) year 3. For visual clarity, daily detections were limited to a maximum of 20 fish per day per antenna per size class and zero detections were not plotted. Periods of no detections generally represent an antenna malfunction

(the 2 marking creeks with a lower, middle, and upper antenna), there appeared to be a distinct spatial pattern of size-based creek use. Larger individuals constituted the majority of detections at the lower antennae and smaller individuals dominated detections at the upper antennae. The middle antennae served as mixing zones between size classes (Fig. 6).

Seine-net catches showed significant spatial segregation by size class. Chi-squared analysis revealed a significant negative relationship between the presence of snook >500 mm SL (size bin 5) and SC1 snook ( $\chi^2 = 12.1923$ ,  $df = 1$ ,  $p = 0.0004799$ ) in seine-net catches. The presence of snook 200–300 mm SL was independent of snook >500 mm ( $\chi^2 = 0$ ,  $df = 1$ ,  $p = 1.0$ ), while 400–500 mm SL presence was strongly positively correlated ( $\chi^2 = 11.95335$ ,  $df = 1$ ,  $p = 0.0005513$ ).

## DISCUSSION

Our approach revealed seasonal trends in emigration and apparent survival. Spring declines and the

winter disturbance event highlighted apparent survival seasonality. Although emigration patterns were seasonal, estimated emigration rates only affected apparent survival estimates for larger juveniles. However, while observed emigration did not explain spring declines in apparent survival, it is possible that movement to areas we did not survey, such as other mangrove creeks or habitat types used as part of a nursery mosaic (Barbour et al. 2014), drove these declines. While the use of apparent survival may be an acceptable proxy for survival of smaller juveniles over short periods, seasonal survival patterns reveal a need for temporal valuation of nursery habitat.

## Emigration

Many studies of juvenile survival assume that observed losses are due entirely to mortality (reviewed in Frederick 1997). While this may hold true for species with site-attached life histories, it is becoming recognized that emigration influences

survival estimates for species with Type III life strategies (Frederick 1997, Overholtzer-McLeod 2005), wherein adults and juveniles use distinct habitats (Adams et al. 2006a). Ignoring the role of emigration could lead to misidentification of nursery habitats by underestimating survival and thereby undervaluing habitat importance. Moreover, incorporating emigration into studies of juvenile fishes will lead to a better understanding of the potential importance of juvenile habitat mosaics (Sheaves 2005, 2009, Adams et al. 2006a, Barbour et al. 2014).

Despite the risks associated with juvenile fish movement, emigration is likely a ubiquitous ecological process important for maximizing fitness, particularly with regard to seasonal fluctuations in habitat value. Care must be taken to determine whether individuals move due to increased body size and/or ontogenetic shifts (Dahlgren & Eggleston 2000, Faunce & Serafy 2007), are using a complex juvenile habitat mosaic with seasonal variations in habitat value (Sheaves 2009, Barbour et al. 2014), or move due to another reason, such as a priority effect (Almany 2003, 2004). This is reflected in our use of  $e_{m,perm}$ , which measured the relative probability of temporary against permanent movements, and determined a seasonal trend where permanent movements (potential ontogenetic shifts) occurred disproportionately in the spring (Barbour et al. 2014), just prior to new larval recruitment. Our data suggest that juvenile common snook use mangrove creeks primarily in the fall and winter and shift habitats in the summer. This would improve survival of the new recruitment class settling in the creeks over the summer (Peters et al. 1998, Taylor et al. 1998, Barbour et al. 2014) by reducing the potential for inter-cohort cannibalism and competition during the typically high-mortality settlement period (Shulman & Ogden 1987).

In addition to seasonality, emigration rates changed with juvenile body size. The observed difference in documented emigration (9.5% of SC1 vs. 34.5% of SC2) was likely driven by SC2 individuals having a larger home range size and undertaking more frequent movements, while SC1 exhibited deliberately timed movements (Barbour et al. 2014) to maximize their growth-to-mortality ratio as has been demonstrated in other fish (Dahlgren & Eggleston 2000). If the main emigration event for SC1 individuals was a movement to a non-creek habitat in the spring through the expanding use of a nursery mosaic (Barbour et al. 2014), we would have been unable to detect and subsequently correct for this in our apparent survival estimates. This scenario may be

likely since the probability of a SC1 emigration event being permanent (Barbour et al. 2014) increased concurrently with a spring decline in apparent survival.

### **Incorporating emigration and apparent survival**

Our emigration modeling and simulation approach did not reveal substantial apparent survival bias. Emigration did substantially bias SC2 apparent survival in the fall, but little movement was detected after this season. While a decline in winter emigration was expected due to cold-induced lethargy (Shafland & Foote 1983), we expected a spring increase in movement concurrent with increasing temperatures. The lack of this increase is likely an artifact of our emigration quantification method. We modeled  $e_m$  using only an individual's first instance of emigration. Therefore, a temporary emigrant in the fall could not be counted again in the winter or spring when estimating  $e_m$ . Due to the high rate of movement in the fall, <10% of the 171 SC2 emigrants remained for calculation of the spring rate. Thus, our spring  $e_m$  value for SC2 was likely an underestimate, and we suggest true emigration rates may substantially bias apparent survival estimates for larger, more mobile juveniles.

The lack of simulated apparent survival bias may also be due to the type of emigration and the high capture probability. In addition to permanent emigration confounding the calculation of apparent survival, temporary emigration violates the assumptions that all marked animals remain for the study duration, or if they migrate out of the population, they do so permanently (Schwarz & Stobo 1997). However, the degree of bias may be related to the capture probability (Zehfuss et al. 1999) and the form (Markovian or completely random) of temporary emigration (Kendall et al. 1997). Further, temporary emigration may only bias capture probability as opposed to survival (Kendall & Nichols 1995). Here, potentially due to our high capture probabilities (85.7% of 1917 marked individuals detected), random temporary emigration is unlikely to have substantially biased our estimates (Zehfuss et al. 1999). Although seasonal estimates were biased in the fall and spring in our emigration simulation, the overall survival was estimated accurately since the biases were of equal and opposite magnitude. Thus, while permanent emigration biased individual estimates, the Barker joint-data model proved to be robust at estimating total survival within our simulation.

Although we did not find substantial mathematical bias in apparent survival, we still urge future studies to consider the effects of emigration. Being limited in spatial scale, our study generated conservative estimates of emigration. Thus, it is possible that our apparent survival estimates were indeed biased by higher rates of true emigration. Additionally, even if emigration does not bias apparent survival, knowledge of juvenile movements, which were more common than expected here, further understanding of habitat-use patterns.

### Drivers of mortality

Extreme low winter temperatures limit the distribution of snook and affect juvenile survival. Severe thermal-disturbance events occur almost once per decade and affect adult snook in Florida (Storey & Gudger 1936, Gilmore et al. 1978, Adams et al. 2012), but the effects on juveniles are less studied due to the difficulty of accessing juvenile habitats. In the southern creeks, maximum likelihood estimates of winter apparent survival decreased from  $\sim 0.9 \text{ mo}^{-1}$  in non-disturbance years to 0.7 during winter 2010. These estimates represent the entire winter season (January through March), so survival during the thermal disturbance was likely much lower than 0.7. Thus, recurring winter disturbance events are a major influence on juvenile common snook population dynamics in Florida. This is not surprising since snook live at the northern end of their geographic range in Florida. Snook have their population distribution limited by the  $15^{\circ}\text{C}$  winter isotherm, below which the water temperatures have a high probability of breaching the  $12.5^{\circ}\text{C}$  lethal limit (Shafland & Foote 1983, Adams et al. 2012). The identification of potential thermal refuges where water temperatures remain above the lower lethal limit during extreme cold events (e.g. manmade mosquito ditches) represents a potential opportunity for enhancement of an economically important fishery at the northern end of its range.

Within-creek juvenile spatial distribution and survival were strongly influenced by the presence of adults. Antennae resightings showed frequent use of the study creeks by cannibalistic adult snook, and size distributions revealed a slight spatial segregation wherein adults disproportionately used the lower versus the upper creek strata. This visual analysis relied on continuous data (antennae resightings) discretized to daily bins, thus potentially masking fine-scale or intraday patterns (e.g. tidal) in spa-

tial distribution. For example, the South Silcox middle antenna frequently detected adult and SC1 snook on the same day. However, analysis of discrete seine-net pulls revealed a significant negative relationship between large adult and SC1 presence. This not only supports the importance of cannibalism in driving juvenile use of mangrove creeks (Adams & Wolfe 2006), but also highlights the disadvantages of discretizing continuous data (Barbour et al. 2013).

Creating a 'first capture' survival estimate allowed us to disentangle the effects of handling stress (Barbour et al. 2012b) and transient individuals on apparent survival estimates. Given that mortality from PIT tagging is negligible (Adams et al. 2006) and we only employed gastric lavage in year 3, the low 'first capture' survival estimates indicate a high incidence of non-lethal handling effects (Barbour et al. 2012b) or a high population of transient individuals. Transient individuals can invalidate traditional capture-recapture survival estimates that rely on the study of residents only, and we suggest future studies consider their influence (Pradel et al. 1997). Despite this 'first capture' estimate, year 3 apparent survival in South Silcox was lower than expected. We believe that disproportionate use of pulsed gastric lavage in South Silcox in year 3 contributed to higher than average initial mortality and emigration (Barbour et al. 2012b), which reduced an already small marking cohort (76 individuals). This may have led to a parameter identifiability issue or an increase in emigration bias due to low sample size available for resighting.

### Study limitations

It is important to note that we would have been unable to draw the aforementioned inferences on emigration and apparent survival without the high efficiency of our mark-recapture methodology. An inability to efficiently track a high number of individuals through mark-recapture is the major limitation of most marine fish studies. For example, we physically recaptured  $\sim 1\%$  of the nearly 4500 juveniles marked in our study creeks in the past 8 yr (Barbour & Adams 2012). Using physical recapture only, we would not have documented the observed rates of emigration, would have presumed high site fidelity to individual creeks despite a long-term physical recapture dataset, and our estimates may not have been robust to emigration bias. Although future studies cannot be expected to repeat the combination of sample size and recapture rate of our study, future

studies must be careful in their conclusions about juvenile movements due to the ease with which movements are missed.

Although our methodology led to multiple new insights, it also limited our inferences. Emigration information was collected with PIT tag antennae within creeks. Thus, emigration was only detected when an individual entered a different study creek. Since we relied on within-creek detections as a proxy for true emigration, our estimates of emigration were extremely conservative. For example, if an individual marked in South Silcox moved within the contiguous and continuous shallow mangrove-and-creek mosaic, we would have been unable to detect its movement. Future work should be conducted to determine the seasonal role of inter-creek movement versus movements to other habitats not studied here.

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