

Manipulations of Stocking Magnitude: Addressing Density-Dependence in a Juvenile Cohort of Common Snook (*Centropomus undecimalis*)

NATHAN P. BRENNAN,¹ CARL J. WALTERS,² and KENNETH M. LEBER¹

¹Center for Fisheries Enhancement, Mote Marine Laboratory, Sarasota, Florida, USA

²Fisheries Centre, The University of British Columbia, Vancouver, British Columbia, Canada

We released hatchery-reared juvenile common snook (Centropomus undecimalis) to test the effects of augmenting age-1 abundance by 100% (high augmentation, n D 2) vs 10% (low augmentation, n D 2) in estuarine creeks of southwestern Florida. We monitored in-creek abundance of age-1 snook 1 month before releases in May 2002 to estimate wild snook density and stocking magnitude. All sampling used seining standardized for effort, gear efficiency, and depletion removal. After releases, sampling continued for 1 year. After 1 month, creeks with high augmentation showed a 126% and 74% increase in total age-1 abundance, and low augmentation creeks a 6% increase and an 18% decrease. Total age-1 abundance declined during fall in all creeks, but by winter, abundance increased again, comparable to earlier levels (132% and 67% above the pre-release estimates in high augmented creeks and 8% and 5% in creeks with low augmentation). While overall density was elevated in both high augmentation creeks, hatchery-reared snook in one creek experienced a 64–85% loss within 1 month after release; loss of hatchery-reared or wild snook was negligible in other experimental creeks. Pre-release density was not a good predictor of creek productive capacity, suggesting variation in habitat production and localized recruitment. Further work is needed to understand inter-cohort density-dependent interactions, food chain responses, and variation in habitat productivity.

Keywords coded-wire tag, competition, elastomer, habitat capacity, predation, snook, stock enhancement

INTRODUCTION

Overfishing and habitat alteration are considered to be the primary anthropogenic disturbances to coastal ecosystems (Hallegraeff, 1993; Jackson et al., 2001; Vitousek et al., 1997). Worldwide demands on ocean fishery resources since the early 1990s have exceeded 100 million tons of harvest, and fishery experts predict global marine catch has approached its upper limit (Botsford et al., 1997). Furthermore, historical data indicate that long-term overfishing has been a primary contributor to major structural and functional changes in coastal ecosystems (Jackson et al., 2001). The primary goal of *sustainable* fisheries has evidently not been widely achieved, con-

sidering the number of overfished populations and indirect effects of fisheries on ecosystems (e.g., by catch) (Steele et al., 1992; Botsford et al., 1997; Pauly et al., 1998; Hamilton and Haedrich, 1999). Anthropogenic habitat change and pollution, although difficult to quantify, also pose substantial threats to fishery stocks worldwide. For many marine species, juvenile nursery habitats are associated with coastlines where development and pollution are concentrated, resulting in inherently reduced ability of fish stocks to recover (Bruger and Haddad, 1986; Islam and Haque, 2004; Mumby et al., 2004).

In Florida, common snook (*Centropomus undecimalis*; “snook”) are a coastal, warm-water fish whose populations concern fishery managers because of their ecological and economic value. Snook are valued as one of the top marine sport fishes in Florida and contribute to an annual US\$5.4 billion saltwater recreational fishing industry in Florida alone (American Sport

Address correspondence to Nathan Brennan, Center for Fisheries Enhancement, Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida, 34236 USA. E-mail: nbrennan@mote.org

Fishing Association, 2004). Despite increasingly restrictive fishery regulations on common snook, these populations are considered overfished and below management goals (Muller and Taylor, 2005). Annual fishing mortality rates have steadily increased over the last 20 years, and recruitment has generally declined (Muller and Taylor, 2005). High fishing pressure, coupled with relatively few spawner-sized females in the adult population, has made management of snook stocks difficult (Muller and Taylor, 2005). Furthermore, snook associate with shoreline habitat (Marshall, 1958; Gilmore et al., 1983; McMichael et al., 1989; Peters et al., 1998) and thus depend on coastal waters that may be subjected to intense anthropogenic influences. Collectively, overfishing and habitat loss have caused a general decline in the population, although the relative influence of these is unclear (Muller and Taylor, 2005).

In Florida, snook spawn primarily during summer (June–August) in high salinity (>28 ppt) seawater in the inlets and tidal passes of estuaries, mouths of rivers and canals, and along sandy beaches (Marshall, 1958; Volpe, 1959; Taylor et al., 1998). Post-larval snook recruit to vegetated shallow brackish tidal creeks and canals and lagoons in both low- (riverine) and high-salinity (mangrove swamp and salt marsh) habitats (Peters et al., 1998), with moderately sloping shorelines and basin depths of 1 m or less, with mud or sand substrate. Age-0 cohorts are thought to remain in their rearing habitats through the winter and early spring (Gilmore et al., 1983; McMichael et al., 1989). In Sarasota and Manatee counties, these habitats are tidal creeks and estuarine backwaters, and serve as thermal refuges for snook of all sizes during winter (N. Brennan, unpublished data). Gilmore et al. (1983) hypothesized that after winter, adolescent snook (150–400 mm standard length [SL], mean = 240 mm SL, from east-central Florida populations) undergo an ontogenetic habitat shift to seagrass beds. Adult snook are known to disperse to seagrass beds, estuarine inlets, and beaches by late spring and early summer (Marshall, 1958; Gilmore et al., 1983; Taylor et al., 1998).

Faced with rapid human population growth in Florida and the limitations of traditional management tools, managers have investigated the potential to augment overfished populations with supply-side approaches such as stock enhancement. However, evidence for stock enhancement programs actually accomplishing stock management goals has been sparse, and such programs can be ineffective and even deleterious to wild stocks (Nickelson, 2003; Walters and Martell, 2004; Kostow and Zhou, 2006). Therefore, stock enhancement programs should initially be operated on an experimental basis with rigorous scientific evaluation before full-scale acceptance as a management tool (Blankenship and Leber, 1995; Leber, 1999; Hilborn, 2004; Walters and Martell, 2004). In this context, experiments with stock enhancement can also provide valuable insight into population dynamics, behavior, growth, and survival responses to habitat quality (Miller and Walters, 2004).

The efficacy of stock enhancement should depend on the magnitude of density-dependent processes. With snook, a cannibalis-

tic and piscivorous species, the influence of habitat availability and quality, or recruitment limitation, on stock sizes remains unclear. Many species suffer elevated and density-dependent mortality during specific ontogenetic stages, typically during early life stages (Houde, 1987; Bystrom et al., 2004; Doherty et al., 2004). In fish, highest mortality rates often occur during the larval stages (Houde, 1987; Lorenzen, 1996). Sometimes, however, density-dependent mortality is high in later stages, and overall recruitment rates are restricted by these “survival bottlenecks.” For example, Bystrom et al. (2004) showed that while age-0 char were not affected by density-dependent processes, age-1 char underwent density-dependent ontogenetic feeding shifts and became exposed to high rates of predation. With snook, relative contributions of various life stages to overall survival remain unclear. Loss of habitat can inherently reduce a stock’s production capacity, yet high density-dependent mortality can still occur in remaining habitats from competition and predation. An examination of population responses to manipulative stocking experiments over a variety of habitats would aid in determining the timing and extent of density-dependent effects. Furthermore, if snook are overfished, then experimental and manipulative stocking may be necessary to elicit density-dependent responses in augmented populations.

In this study, we released juvenile (age-1) hatchery reared snook to manipulate localized age-1 recruitment and identify potential resultant density-dependent mortality effects. Mortality responses in the age-0 cohort from age-1 cannibalism or competition were not addressed in this study because primary recruitment pulses of age-0 snook occurred from June–September, well after the experimental releases occurred (in May), and related abundance responses would be confounded with natural variations in creek-specific recruitment. Specifically, we evaluated whether snook nursery habitats are naturally filled to capacity, i.e., if strongly density-dependent survival would preclude increasing the abundance of age-1 snook leading to increased abundances of older snook. To accomplish this we (1) estimated wild age-1 snook abundance in four estuarine tributaries, (2) released hatchery reared age-1 snook to increase the total localized abundance of age-1 snook by either 100% (high augmentation; $n = 2$ creeks) or 10% (low augmentation; $n = 2$ creeks), (3) determined if hatchery-released snook were subjected to higher mortality rates than wild age-1 snook, and (4) determined if overall loss of age-1 snook in creeks with high augmentation was higher than those in creeks with low augmentation.

METHODS

Study Area

Experimental releases were made in four estuarine creeks (Bowlees Creek [BC], Whitaker Bayou [WB], North Creek

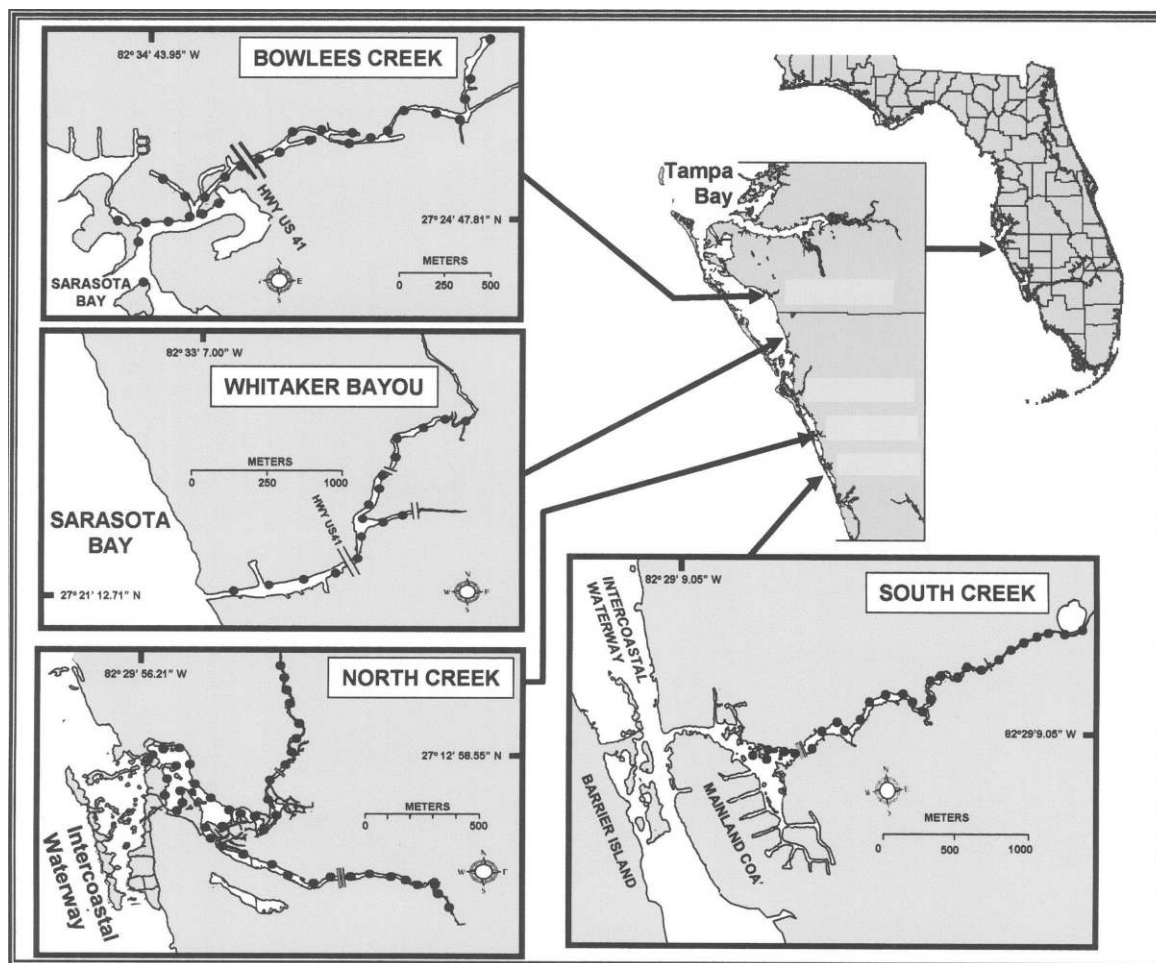


Figure 1 Map of experimental study sites along the coasts of Sarasota and Manatee Counties, Florida. Dots represent locations where collections using the standardized seine occurred. Bowlees Creek and Whitaker Bayou received high augmentation treatments, North Creek and South Creek received low augmentation treatments.

[NC], and South Creek [SC]) in Sarasota and Manatee Counties, on the west coast of Florida, USA (Figure 1). These creeks are tidally influenced and water levels typically fluctuate by about 0.75 m daily. Salinity varies with tides and seasonal rains (wet season during summer). Water temperatures during summer (June–September) typically range from ~28°C–34°C, and winter (December–March) temperatures range from ~12°C–22°C. Dissolved oxygen levels during summer are low compared to

winter (typically <5 mg/l vs >7 mg/l). All creeks are partially influenced by anthropogenic shoreline alterations, and sections of BC, WB, and SC have been dredged to some extent within the last 20 years (Table 1). North Creek remains relatively unaltered, although upstream reaches are surrounded by a golf course and residential properties. Densities of wild age-1 snook (~150–300 mm fork length [FL]) during early summer were about 0.5–3.0 fish/30 m of shoreline (Table 1).

Table 1 Results from standardized sampling in April 2002 and physical attributes of experimental creeks (shoreline distance and percent altered habitat). Population estimates are of age-1 snook found in each creek

Experimental Creek	Number of seine hauls	Number of shores sampled	Total Shoreline (m)	Sampled shoreline (m)	Sampled shoreline (% of total)	% Altered shoreline	Mean CPE	Adjusted Mean CPE	Variance	Calculated age-0 population	Calculated max population
Bowlees Creek	28	38	14051.28	1159	8.25	65%	0.64286	0.814	2.068	375	1715
Whitaker Bayou	18	26	7650.48	793	10.37	14%	1.50000	1.899	9.298	476	1913
North Creek	45	66	25188.672	2013	7.99	<2%	1.93023	2.443	13.825	2018	8003
South Creek	26	34	24262.08	1037	4.27	7%	0.63462	0.803	2.068	639	2904
Totals	117	164	71152.512	5002	7.03					3508	14535

*At the time of study, estimates of percent altered shoreline habitat in Whitaker Bayou were estimated as lower than might be expected due to sedimentation fill along sea walled shorelines, resulting in a more natural bank slope.

Experimental Design and Sampling Methods

We defined “age-1 snook” or “juvenile snook” as offspring from the 2001 spawning year. By April 2002, these snook were approximately 10 (+/-2) months old. Hatchery-reared juveniles were released in May 2002, and our study continued until June 2003, when the juveniles were about 24 months old. We aimed to impose two levels of manipulation: (1) a large addition of hatchery-reared juveniles equal to 100% of the wild juvenile abundance (in creeks BC and WB), and (2) a smaller addition of hatchery-reared fish equal to 10% of the wild stock (in NC and SC).

To estimate in-creek juvenile snook abundance, we used a “leap-frog” systematic sampling design where a standardized bag seine (73 m long \times 3 m deep with 1-cm nylon multifilament mesh) was hauled at roughly every third 30-m section of shoreline throughout each creek (Figure 1, Table 1). Each haul sampled an approximate 30-m \times 21-m rectangle (630 m²). For creek sections less than 21 m wide, we sampled 30 m of creek length but incorporated both shorelines into the sample. The seine, loaded on a 4-m kayak, was deployed by hauling about 21 m of the leading end of the seine towards the shoreline. Once

there, a second person held the outside “corner” of the block, and a third person pulled the kayak parallel to the bank (or against the opposite shoreline) for 30 m, then turned and deployed the remaining 21 m of net towards the shoreline. The seine was then closed and retrieved along the shoreline. To avoid overestimating snook abundance, we divided snook catch by 2 for samples collected from 2-bank sites because of the increased shoreline habitat. Seines were not hauled in narrow areas (i.e., <3 m across) such as mosquito ditches, but these shorelines were assumed to be valid snook habitat and were used to calculate total snook abundance.

Gear Efficiency and Population Estimation

Before abundance estimates, we conducted depletion-removal trials in January and February 2002 to measure gear efficiency. We used a modified depletion-removal population estimate (Hilborn and Walters, 1992) within a defined area to predict single-pass seine efficiency (Figure 2). Three types of depletion-removal methods were used depending on habitat type. In creek

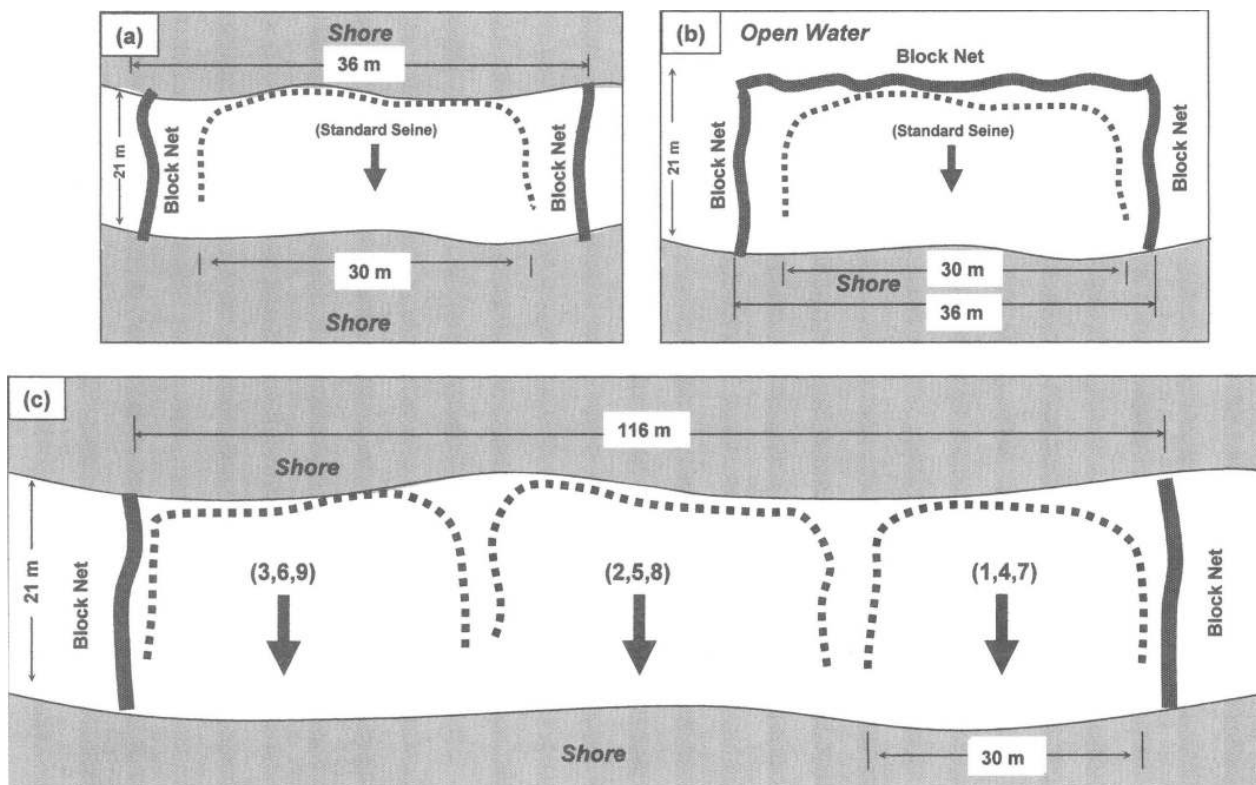


Figure 2 Schematic of depletion-removal methods including (a) “2-bank depletion,” (b) “single-bank depletion,” and (c) “2-bank extended” depletion. Dark lines indicate block nets, lighter dashed lines indicate locations of seine efforts, and arrows indicate the direction of the seine hauls. The numbers in brackets represent the sequence and location of seine hauls (hauls 1 through 9).

areas narrower than 21 m across (i.e., 2 stream banks, “2-bank depletion”), 2 nets (21–24 m long, 0.9 m deep, 1-cm multifilament mesh), about 42 m apart, blocked off upstream and downstream borders of the sampling area (Figure 2a). We used the standard seine described above, to sample ~30 m within this zone, allowing ~6 m from the seine perimeters to the block nets measured along the shoreline to allow for escapement (as might occur in a single pass seine). After this, we seined the entire area 2 more times, for a total of 3 seine hauls (most snook were captured within the first seine, so 3 seine passes sufficiently described the depletion rate, see below). We performed 10 separate “2-bank” depletion experiments.

We also performed “single-bank” depletion along open shorelines (Figure 2b) and used the same method if additional shorelines were farther than 21 m from the sampled shoreline. A 45 m long block net (1-cm multifilament mesh) was deployed parallel to the shoreline, ~21 m away from shore, and 2 21-m seines (same sized mesh, attached at each end of the deployed 45 m long seine) were deployed toward the shore to enclose a rectangular area of ~945 m². Once block nets were in place, a standardized seine was hauled along the inside perimeter of the blocked area. The standard net was stretched 30 m along the inside perimeter of the block net, then each end was pulled toward shore. We allowed ~4 m of space between the ends of the block to allow for escapement (Figure 2b). Again, second and third seine hauls sampled the entirety of the blocked area. For each seine haul, captured snook were counted and measured (FL, mm), then placed in holding containers with aerated creek water until the depletion trial was complete. We performed 8 separate open-bank depletion trials.

We also performed 2-bank extended depletion experiments in 2 areas where we blocked off ~116 m of creek habitat (Figure 2c). We hauled a standard seine sequentially upstream 3 times to the block net. This was repeated for a total of 9 seine hauls.

Using data from the 3-pass depletion removal trials, we calculated the maximum likelihood of the number of snook remaining (N_R) in the net area s after the last depletion pass i (which captured C_{is} juvenile snook) assuming binomially distributed catch for each seine pass, with equal capture probability for each pass. We then estimated the total population of snook in the net area (N_{0s}):

$$N_{0s} = \sum C_{is} + N_{Rs} \quad (1)$$

From this we calculated the number present at the time of each pass ($N_{1s}, N_{2s}, N_{3s} \dots$) and generated an estimate of the capture probability per seine haul (p) as the conditional maximum likelihood estimate for binomial sampling:

$$p = \sum C_{is} / (N_{0s}) \quad (2)$$

We also calculated a p_{common} value for all depletion trials j :

$$p_{\text{common}} = \sum C_{isj} / \sum N_{isj} \quad (3)$$

where i and j index seine hauls and depletion trials, respectively. Estimates of age-1 snook (estimated by length frequency

analysis, see below) abundance in a seined area s at time t (N_{st}) were calculated as:

$$N_{st} = C_{st} / p_{\text{common}} \quad (4)$$

Where C_{st} is the catch of juvenile snook in the seine area s at time t . Adjusted mean catch from all areas s in creek C at time t (\bar{N}_{Ct}) were then extrapolated to total creek shoreline habitat, A_C (obtained from aerial photographs [1cm = 24 m], expressed in 30-m units) to obtain an in-creek population (\hat{N}_{Ct}) of juvenile snook:

$$\hat{N}_{Ct} = \bar{N}_{Ct} * A_C \quad (5)$$

with variance:

$$V(\hat{N}_{Ct}) = A_C^2 * V(\bar{N}_{Ct}) \quad (6)$$

Therefore, the variance estimate uses the maximum likelihood estimate of catch efficiency (without associated variability) but incorporates variation around the mean catch in each creek at time t and assumes creek area A_C is constant.

We used repeated measures analysis to compare pre- and post-release abundance in the creeks. If the April 2002 abundance estimate of wild snook juveniles in a particular creek (pre-release) was less than its early summer (post-release June or July 2002 samples) abundance estimate, we used early summer abundance of age-1 wild snook as our pre-release estimate. We assumed that no new recruitment of wild age-1 snook occurred; age-1 snook typically begin to decline in abundance in creeks by mid-summer (Brennan and Leber, unpublished data; Gilmore et al., 1983). Because large-scale emigration of age-1 snook occurred from mid-summer through fall, we only used early-summer and winter abundance estimates for post-release repeated measures analysis. We also used a linear regression to model augmentation level (expressed as a percentage of standing wild stock), with change in abundance after stocking (also expressed as a percentage), to test if a significant relationship existed between augmentation level and change in abundance.

Density (number per 30 m of shoreline) of juvenile snook in the creeks (D_C) at time t was calculated by dividing total in-creek juvenile snook abundance \hat{N}_{Ct} by total shoreline distance (A_t) as follows:

$$D_{Ct} = \hat{N}_{Ct} / A_t \quad (7)$$

We used data from pre- and post-release sampling to compare observed and expected densities within the creeks. To generate expected density, we assumed that numbers of stocked fish were completely additive to wild juvenile numbers, then used a chi-square test to compare differences in observed and expected age-1 densities after releases occurred. We used an analysis of covariance (ANCOVA) to compare in-creek changes in density (D_{Ct}) of juvenile snook before and after releases (using pre-release density, peak summer density, and peak winter density).

Pre-Release April 2002 Sampling

To estimate pre-release juvenile snook abundance, we performed creek-wide standard seining efforts in each creek before stocking hatchery-reared snook. Captured snook were marked with externally visible implant elastomer (VIE) tags implanted in the caudal fins (see Brennan et al., 2005) with VIE colors specific to creeks to aid in determining site fidelity and inter-creek migration rates, and identify snook recaptured multiple times.

Tagging and Release

Hatchery-reared snook, F1 progeny from wild parental stocks, were hatched in the summer of 2001 and reared until tagging and release in May 2002. Each was tagged with a coded-wire tag (CWT) to identify its associated release information (i.e., release creek, release date, size at release), and two red VIE tags implanted in the caudal fin to externally identify it as a hatchery-reared snook (as in Brennan et al., 2005). Tagged juveniles were returned to their tanks and held for 1 week to recover from the tagging process. Salinities in the rearing tanks ranged from 3–6 ppt and water temperature from 26–30°C.

On the day of release (6 days after tagging), fish from each release group were harvested and checked for tag presence. Snook were transported in tanks with brackish water by truck and boat, and stocked directly into 22-m³ predator-free acclimation enclosures and held for 3 days to improve post-release survival (Brennan et al., 2006). Total transport time to the release sites was ca. 2–5 hr for all release groups, and releases occurred between 1230 and 1900 hr. Enclosures were located along shorelines, mostly vegetated with mangrove (*Rhizophora mangle*), oaks (*Quercus* spp.), palms (*Sabal palmetto*), and Brazilian pepper (*Schinus terebinthifolius*), and at some locations near boat docks and riprap. After 3 days of acclimation, snook were allowed to swim freely from the enclosures. Release numbers were proportional (either 100% or 10%) to pre-release abundance estimates of juvenile snook in each experimental creek.

Post-Release Evaluation

After release, each creek was sampled 6 times (approximately during June, August, October, December 2002, February 2003, and June 2003, Table 2). We identified year classes of wild snook according to length-at-capture based on (1) length frequency distributions of captured snook, (2) corresponding sizes of cultured snook, and (3) tag-recapture data on known

Table 2 Mark-recapture results for the 4 experimental creeks organized according to sample month

Sample Month	Creek	Effort (No. seines)	Captured, tagged, and released		Recaptures			Migrants	
			Wild	Hatchery (recaptures)	Hatchery 2×	Wild	Wild 2×	N	Origin
June 2002	Bowlees Creek	27	16	12	0	1	0	0	
	Whitaker Bayou	16	41	65	0	0	0	0	
	North Creek	45	91	23	0	8	0	0	
	South Creek	26	62	4	0	2	0	0	
July -August 2002	Bowlees Creek	28	22	22	1	3	0	0	
	Whitaker Bayou	16	13	12	0	4	0	0	
	North Creek	46	79	23	1	13	0	0	
	South Creek	26	33	2	0	7	0	0	
Aug.-Sept. 2002	Bowlees Creek	28	20	4	2	0	0	0	
	Whitaker Bayou	16	6	4	0	1	0	0	
	North Creek	45	124	14	1	5	0	0	
	South Creek	29	19	1	0	2	1	0	
Oct.-Dec. 2002	Bowlees Creek	26	72	7	0	4	0	0	
	Whitaker Bayou	16	37	0	0	2	0	0	
	North Creek	34	317	5	1	14	0	0	
	South Creek	0	0	0	0	0	0	0	
Jan.-March 2003	Bowlees Creek	28	4	5	0	7	0	1	Whitaker Bayou
	Whitaker Bayou	16	36	45	4	11	0	0	
	North Creek	46	239	18	1	51	1	0	
	South Creek	26	17	8	0	11	0	0	
June-July 2003	Bowlees Creek	28	14	1	0	1	0	0	
	Whitaker Bayou	16	6	0	0	2	0	0	
	North Creek	45	38	0	0	6	0	0	
	South Creek	27	7	0	0	0	0	0	
Total		656	1313	275	11	155	2	1	

“Hatchery 2×” and “Wild 2×” represent snook that were recaptured in 2 subsequent sampling events. Data are only for the juvenile snook cohort (age-1).

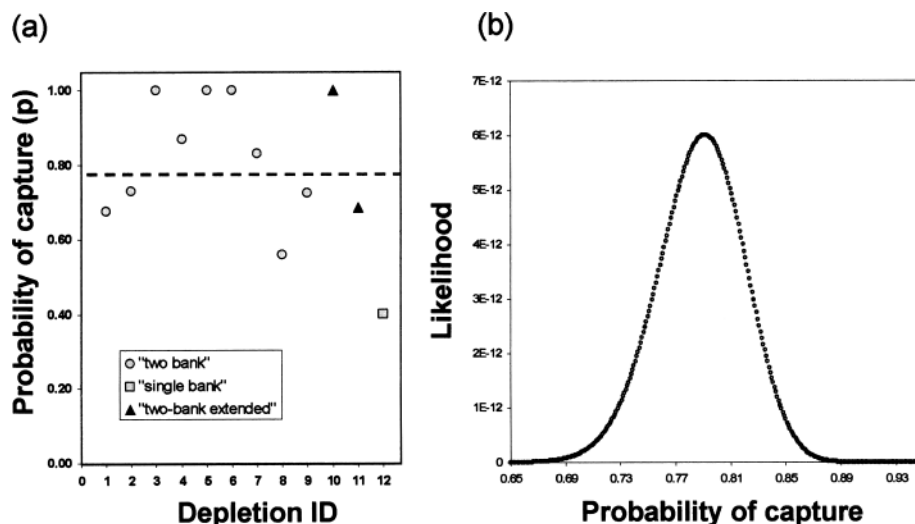


Figure 3 (a) Graphical representation of individual estimates of p values generated from 3 methods of depletion removal trials. The dashed line indicates the mean value of the p estimates. (b) likelihood profile for p_{common} .

young-of-year snook. For hatchery-reared snook, we adjusted catch by accounting for expected tag loss over time (e.g., VIE tag loss after 6 months was 3%; Brennan et al., 2005). All captured snook were counted, measured, and checked for the presence of CWTs with magnetic tag detectors, and visually examined for VIE tags. Untagged wild snook and first-time recaptured hatchery-reared snook were tagged with VIE tags in the caudal fins (using a unique color for each creek) and CWTs. For subsequent recaptures, snook were re-tagged with a VIE of a specific color (BC = orange, WB = green, NC = yellow, SC = pink) and implant location (caudal or anal fin) to identify the creek in which it was captured and the number of times recaptured.

RESULTS

Gear Efficiency

Overall we performed 21 depletion-removal trials. Of these, juvenile snook were captured in 12 trials, and these data were used to generate estimates of seine efficiency. The maximum

likelihood estimate of p_{common} value was 0.79 (90% CI = 0.75 – 0.83; Figure 3 for likelihood profile for the estimate).

In April 2002 our “leap-frog” sampling regime resulted in 117 standardized seine hauls throughout the 4 creeks. Our samples represented about 4–10% of the total shoreline habitat in these creeks (Table 1, Figure 1). We captured 505 snook, of which 183 were estimated to be age-1 juveniles (2001 cohort, ~10 months old). After adjusting for seine efficiency and extrapolating mean CPUE to creek-wide shoreline distance, we estimated in-creek juvenile populations to be 375 juveniles in BC, 476 in WB, 2018 in NC, and 639 in SC (Table 1).

Tagging and Release of Hatchery-reared Snook

Hatchery-reared snook ranged from 84–270 mm FL at tagging (mean length = 177.5 mm FL \pm 2.95 SE), and samples collected in April 2002 of wild juvenile snook of the same age were 79–219 mm FL (mean = 155 \pm 2.43 SE). We tagged and released 2372 hatchery-reared juvenile snook (Table 3), and 6 days after tagging, CWT retention averaged 99.5% (from 14 groups with an average of 84 fish/group), and VIE retention was 100%.

Table 3 Numbers of hatchery reared snook released at 4 experimental release sites

Release Date	Release Group	Size class				Totals	Pre-release wild N	Expected % cultured	Jun-02 % cultured
		small	Medium	Large	Jumbo				
May 20, 2002	Bowlees Creek	106	454	169	160	889	375	70.34	29.03
	Whitaker Bayou	147	514	182	182	1025	476	68.28	53.27
	North Creek	134	178	64	60	436	2018	17.77	23.66
	South Creek	40	52	18	18	128	639	16.69	6.25
Totals		321	1198	433	420	2372	3508		

Snook mean lengths were 138 mm FL for the “small” size class, 160 mm FL for “medium,” 188 mm FL for “large,” and 218 mm FL for “jumbo.” Abundance estimates by creek for the age-1 wild snook before releases (April 2002) are provided with the expected and observed (in June 2002) percentage of hatchery snook in post-release collections.

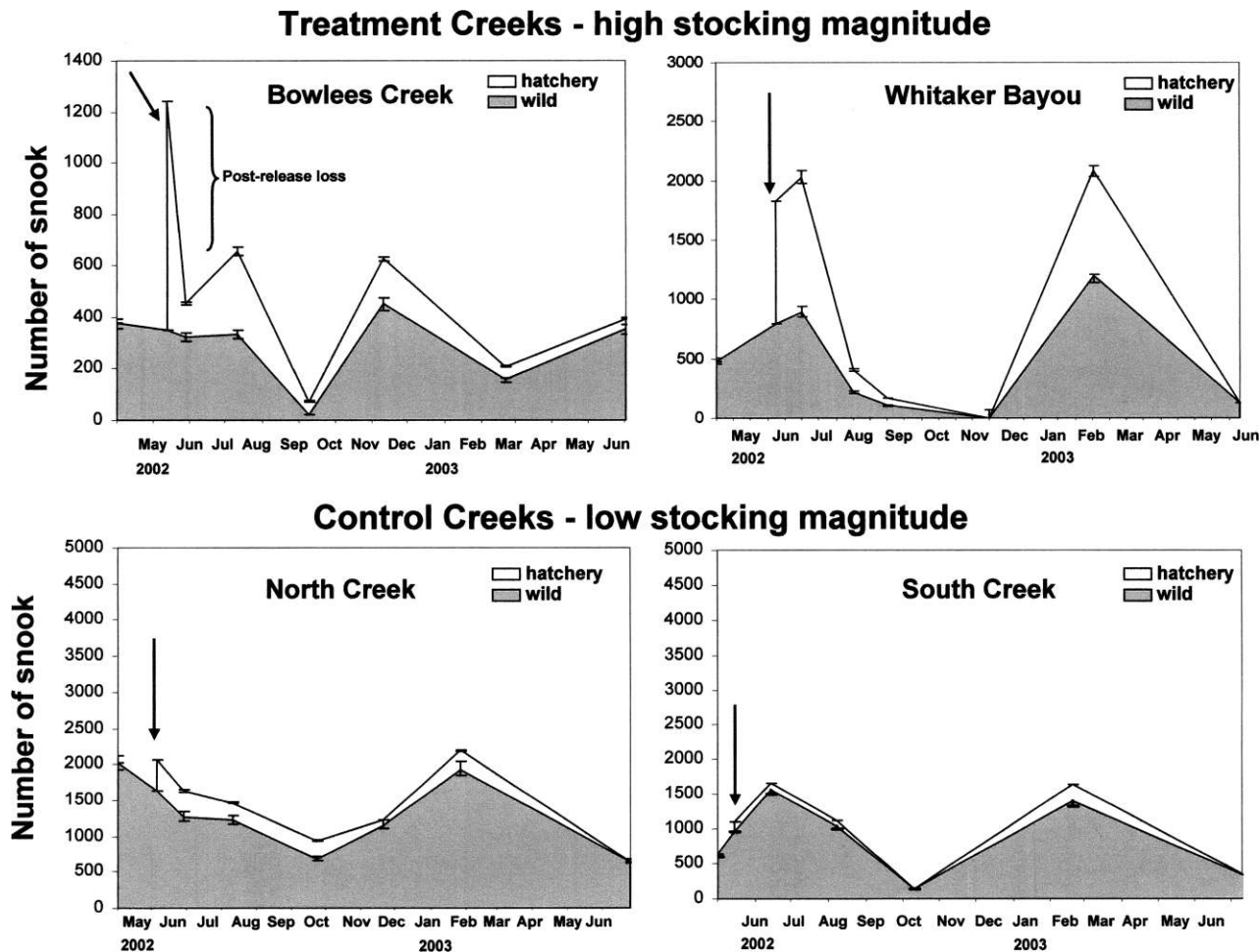


Figure 4 Population estimates of wild and hatchery age-1 snook over time for high augmentation treatment creeks (top) and low augmentation treatment creeks (bottom). Error bars are from abundance estimates obtained from 90% confidence intervals around p_{common} values. Arrows indicate the timing of hatchery-reared snook releases. General increase in wild abundance from summer to winter indicates immigration from other sources.

Post-Release Evaluation

Overall, from 1 June 2002–30 March 2003, we performed 556 standard seine hauls, captured 3261 snook, and captured, tagged, and released 1,588 juvenile snook (Table 2). Of these, 275 were hatchery-reared snook recaptures, and 155 were wild snook recaptures. We found little evidence of inter-creek movement; of 155 color-coded wild snook recaptures, only 1 was recaptured in a creek other than its release creek (about 0.6% found in other creeks) (Table 2). Because all hatchery-reared snook were originally tagged and released with a common VIE color, we were not able to obtain estimates of inter-creek migration from first-time recaptures. Only 11 hatchery-reared snook were recaptured twice, and all of these were captured in the same creek as the first recapture event.

Samples from June 2002 resulted in a total of 410 captured snook, 294 of which were juveniles. Relative abundance of wild juvenile snook in June was 0.86 \times , 1.87 \times , 0.63 \times , and 2.45 \times the April abundance for BC, WB, NC, and SC, respectively (Figure 4). However, when hatchery-reared fish were included, 3 creeks

showed abundance increases compared to April (BC = 1.20 \times , WB = 2.26 \times , NC = 0.81 \times , SC = 2.61 \times that of pre-release estimates). In June abundance estimates of hatchery-reared fish were 120% larger than wild juvenile abundance in WB and 40% of the wild abundance in BC (but 97% in July), 29% of NC wild abundance, and 6% of SC wild abundance (control creeks) (Figure 5a,b).

Juvenile snook generally emigrated from all 4 creeks by fall and then returned in winter (Figure 4). As summer progressed, in-creek abundance of age-1 juveniles steadily declined, and young-of-the-year snook (from 2002 summer spawns, <100 mm FL) numerically dominated snook catches. For example, in early summer, hatchery-reared snook abundance was 37% of the number released in BC, ~100% in WB, 85% in NC, and 75% in SC, respectively. By fall, large declines in hatchery-reared fish were evident in all creeks—6%, 6%, 17%, and 0% of the original numbers released in BC, WB, NC, and SC, respectively (Figure 4). Wild age-1 snook exhibited similar patterns of large late-summer declines in abundance in all creeks. After the first significant drop in temperature (below 22°C), both wild

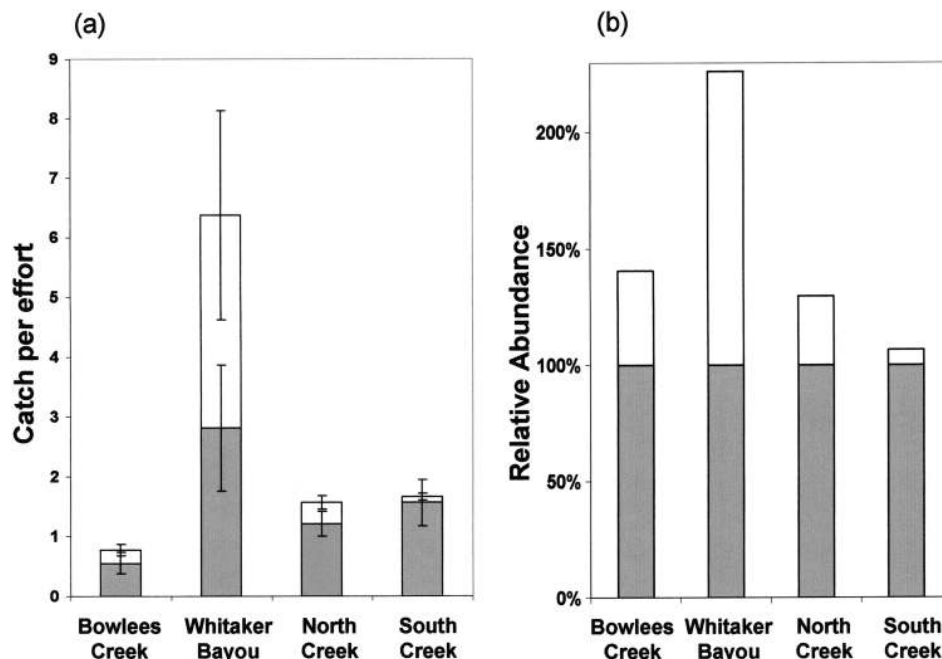


Figure 5 Results from post-release samples taken in June 2002 for (a) catch per effort and (b) relative abundance of hatchery snook (□) to wild juvenile (■) abundance (set at 100%).

and hatchery-reared fish abundance returned to substantial levels comparable to early-summer abundance; winter abundance of wild snook was 120% the peak summer abundance in BC, 134% in WB, 96% in NC, and 89% in SC. Winter abundance of hatchery-reared snook was estimated at 54% of the summer abundance in BC, 78% in WB, 69% in NC, and 258% in SC (Figure 4).

Given the variability in the catch data and the small number of replicates used in the study, our power was low (0.3–0.8) for detecting a 100% difference in population means. Nonetheless, repeated measures analysis showed a significant time and treatment interaction effect for pre- and post-release abundance ($p =$

0.024, $F = 10.78$, $df = 2, 3$). Regression analysis showed no significant relationship between augmentation level and change in abundance from pre- to post-release (using either summer or winter as post-release values; $p = 0.42$, $p = 0.45$, $R^2 = 0.09$ –0.33).

Creek Density

The high augmentation treatment creeks were quite different in their ability to accommodate augmented snook densities. The ANCOVA model showed no significant differences in pre-release snook density ($p = 0.51$, 3 df; Figure 6); however, after

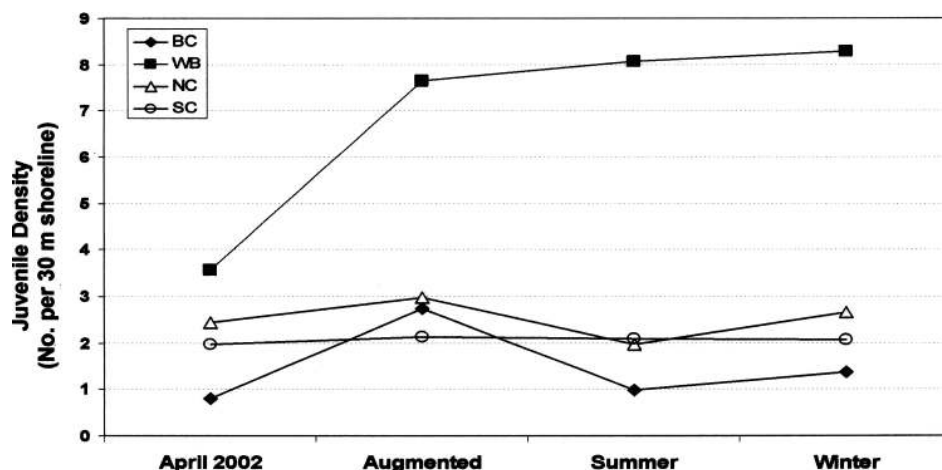


Figure 6 Juvenile snook density responses to augmentation treatments in 4 creeks. Data show densities before releases occurred (April 2002), the expected density given no loss of wild or hatchery-reared snook after a release “augmented,” and actual densities observed in summer (June–July 2002) and winter (November–February) after the releases.

releases, WB showed a significant increase in overall density (over twice the pre-release level) that was maintained through the winter ($p = 0.034$; Figure 6). In BC (also a high augmentation treatment), the expected augmented levels were not sustained (Figure 6), and we estimated that 64–85% of the released cultured fish were lost by the time of the first post-release sample. Loss within wild snook populations was not detected over this period, however. Creeks that received low levels of augmentation showed no significant changes in overall juvenile snook density throughout the study (Figure 6). Chi-square analysis of the observed and expected densities in all four creeks reflected the initial loss of hatchery fish in BC by showing a significant difference between observed and expected post-release densities ($p < 0.001$, chi-square = 306.82, 3 df). Thus, responses of juvenile snook density to various levels of augmentation were creek specific.

DISCUSSION

Experimental releases of high densities of age-1 hatchery-reared snook in two estuarine tributaries elevated total age-1 abundance above pre-release levels throughout the study. At the same time, we found no detectable evidence of suppressed abundance of wild age-1 snook in these habitats. Surplus production capacity for age-1 snook existed at these particular experimental times and locations, although inter-cohort or community-wide responses were unclear. This is not surprising as others have found population sizes below habitat productive capacities (e.g., Orth and Maughan, 1982; Conder and Annear, 1987). Regardless of a habitat's productive capacity, stocks (such as snook) at low levels, with high fecundity, at the edge of their range, and exposed to high environmental variation, typically demonstrate highly variable recruitment (Myers, 2001) and thus can occur at densities below capacity.

This study examines an important assumption about recruitment processes—that density-dependent survival of wild fish may be reduced by the addition of hatchery-reared fish. In salmonid populations, evidence exists for density-dependent responses in wild stocks due to stocking hatchery-reared fish (Nickelson et al., 1986; Nickelson, 2003; Kostow and Zhou, 2006). We found no evidence of high augmentation treatment effects on wild conspecific density, although an effect may have been expressed through initial loss of hatchery-reared fish in BC where the productive capacity may have been substantially exceeded. Abundance patterns of wild age-1 snook throughout the study, however, followed similar patterns in all creeks. Density-dependent growth responses were not measured in this study, but other work in the same creeks (Brennan and Leber, unpublished data), showed suppressed growth in tributaries with high densities of age-1 snook.

After emigration in fall, there was movement back into the creeks of age-1 wild snook in winter, resulting in abundances slightly higher than those in summer. Given the low observed rates of inter-creek movement (0.6% mixing between experi-

mental creeks), the additional abundance in creeks of wild age-1 snook during winter (observed in all creeks) was probably due to immigration of wild snook from other sources, emphasizing their importance as thermal refuge habitat. Furthermore, hatchery-reared snook demonstrated the same seasonal movement pattern and (after initial loss of fish in 1 treatment creek) early-summer abundances were very similar to winter abundance in both treatment and control creeks. Declines in abundance of hatchery-reared snook from summer to winter (after the initial high post-release loss) presumably reflected mortality rates in resident wild age-1 snook.

The use of a fixed-station and systematic sampling program was appropriate in our study because it incorporated a representative spectrum of population and habitat size/quality gradients in the creeks (by attempting to sample every third 30-m section of shoreline habitat, see Hilborn and Walters, 1992). Increases in abundance from April–June (as seen in WB and SC) may reflect improvements in the efficiency and sampling ability of field workers. Such improvements in sampling efficiency or catchability with experience are not uncommon (e.g., Walters and Maguire, 1996). In our experimental creeks, it is doubtful that abundance of wild age-1 snook actually increased (via immigration) before large-scale emigration of juveniles from the creeks in the fall. Furthermore, samples from NC and BC showed expected declines in abundance. Logistical considerations and cost restricted replication and sampling effort for this study. The low experimental power meant that the probability of a Type-II error was high, yet repeated measures detected a significant time/treatment interactive effect on population means and thus treatment-effect size was high. Furthermore, sampling over time showed consistent patterns in all of the creeks (e.g., abundance declines in fall and increases in winter) and further supports our confidence in our estimates of abundance.

Inter-annual variation could have a strong effect on the results of similarly staged release experiments performed at other times (through variations in carrying capacity, recruitment, and subsequent competition and predation; see Walters and Martell, 2004; Brennan, unpublished data). Common snook stocks in Florida have characteristics of high recruitment variability (Myers, 2001), and, even over a 30-km stretch of coastal habitat, evidence exists for high variation in intra-annual recruitment of juveniles (Brennan, unpublished data). As snook are also cannibalistic (Tucker, 2003; Adams and Wolfe, 2006), and age-0 and age-1 snook share nursery habitat for a prolonged period, increases in abundance of age-1 snook may have negative consequences on young-of-year snook populations through cannibalism and competition for refuge and food resources. Cyclic patterns of abundance due to cannibalism are common (Frankiewicz et al., 1999; Sanderson et al., 1999; Fromentin et al., 2000; Claessen et al., 2000; Persson and de Roos, 2006). Snook populations in Florida show strong evidence for patterns of alternating fluctuations of abundance between age-0 and age-1 year classes (Brennan, unpublished data) as do a cousin of snook, barramundi *Lates calCIFer* in Australian estuaries (Walters and Martell, 2004; Griffin, unpublished data) presumably due to intra- and inter-cohort

cannibalism and competition. Release programs that elevate age-1 abundance could intensify such effects, and a cautionary approach is warranted. Nonetheless, the potential for elevating stocks that are below capacity is demonstrated by this study and its potential over the long term must be evaluated.

The presence of small (~60 mm FL) snook in the creeks during fall reflects continued use of creek habitat by young snook throughout the year. Dramatic declines in abundance of age-1 snook in the creeks during late summer–early fall (~200–325 mm FL at this time), probably represent an ontogenetic habitat shift of the age-1 snook. This could possibly be due to (1) a reduction in predation threat as snook attained larger sizes (Koczaja et al., 2005), (2) superior foraging habitat and improved prey availability and preferences outside the creeks (Ruzycki and Wurtsbaugh, 1999), (3) better water quality outside the creeks (Brennan and Leber, unpublished data), or (4) combinations of the above reflecting tradeoffs with size-dependant predation threat and improvements in growth due to better foraging opportunities (e.g., Werner and Gilliam, 1984; Walters and Juanes, 1993; Olson et al., 1995).

Although our results indicated that stocking was additive in both high augmentation treatments (BC and WB), depressed survival of the hatchery-reared fish occurred in one creek (65–85% loss). While density-independent causes cannot be ruled out, it may indicate that the productive capacity in BC was exceeded, and may reflect variation in the productive potential of various juvenile snook habitats. Pre-release density of age-1 snook in BC was lower than in the other creeks, yet density in itself was not predictive of the habitat's potential to accommodate more snook. In BC, shoreline habitat alteration in the form of seawalls and steeply dredged shorelines has been extensive, and ~65% of the total shoreline habitat has been altered (Table 1). Shoreline alteration in the other creeks was much less (about 14% in WB, <2% in NC, and 7% in SC). Age-1 snook densities in NC and SC were similar; however, post-release densities in WB were ~8 times higher than BC densities and 4 times that of NC and SC (Figure 6). While this suggests an effect on a habitat's productive capacity, variation in recruitment, anthropogenic development, and low sample size confound such a comparison.

High juvenile snook abundance was common in habitat characterized by deep mud, overhanging vegetation, gently sloping banks, and low current (<0.1 m/s or stagnant). In our experience, this type of habitat is scarce in highly developed creeks with dredged bottoms and shorelines modified with seawall channelization and boat docks (e.g., BC). These altered habitats often attract predaceous fish possibly due to improved water exchange (from less flow restrictions) or dock lights that attract bait fishes. Such conditions may be costly to snook juveniles through loss of predation refuge and increases in predator abundance. Further research is needed to quantify the influence of anthropogenic alterations on juvenile snook abundance to identify potential loss of production.

In this study, juvenile snook nurseries accommodated abundance increases that persisted over time. Clearly, the use of four experimental tributaries during a particular year to conduct ma-

nipulative tests on recruitment, albeit logistically difficult, is insufficient to capture a broad picture of recruitment dynamics and the long-term productive capacity of various systems. Future studies should also focus on smaller and younger size classes to identify potential survival bottlenecks (e.g., Doherty et al., 2004) and effects of multiple year classes sharing important refugia, where density-dependent growth and mortality may be strongly influential. Understanding community-wide implications and predator-prey interactive effects (e.g., Walters and Kitchell, 2001; Persson et al., 2007), and interannual variation in recruitment and habitat capacity are important considerations that may best be addressed by coupling ecological models with empirical experimentation. Stock enhancement programs should consider strategies that maximize their cost-effectiveness while minimizing threats to wild stocks. Empirical studies such as this, however, are important steps toward understanding these dynamics and can provide baseline information for dynamic age-structured stock recruitment models, often lacking data for juvenile life stages.

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