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ARTICLE

Distribution and Habitat Associations of Juvenile Common Snook in the Lower Rio Grande, Texas

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Abstract

Common Snook *Centropomus undecimalis* were once abundant off the Texas coast, but these populations are now characterized by low abundance and erratic recruitment. Most research concerning Common Snook in North America has been conducted in Florida and very little is known about the specific biology and habitat needs of Common Snook in Texas. The primary objective of this study was to describe the habitat use patterns of juvenile Common Snook and their role in the fish assemblage in the lower portion of the Rio Grande, Texas. Secondly, we documented the relationship between age and juvenile reproductive development. Fish were collected during January–March 2006 from the lower 51.5 km of the Rio Grande using a bottom trawl and boat-mounted electrofisher. Measurements of water quality and other habitat traits were recorded at each sampling site. We captured 225 Common Snook exclusively in freshwater habitats above river kilometer 12.9. The distribution of juvenile Common Snook was not random, but influenced primarily by turbidity and dissolved oxygen. Sex differentiation and gonadal development based on histological examination of gonads established that age-1 and age-2 Common Snook were juvenile, prepubertal males. There was no difference between the age groups in their overall distribution in the river. However, age-2 Common Snook were associated with deeper areas with faster currents, higher conductivity, and steeper banks. Overall, Common Snook in the lower Rio Grande show substantial differences in habitat use than their counterparts in other parts of the range of the species, but it is unclear whether this is due to differences in habitat availability, behavioral plasticity, or some combination thereof.

The Common Snook *Centropomus undecimalis* is the most widely distributed and abundant species within the family Centropomidae (Pisces: Perciformes) occupying the western Atlantic Ocean and Gulf of Mexico. The species ranges from about 34°N to about 25°S latitude in the western Atlantic Ocean, which

includes waters off Galveston and the southern tip of Texas, south to Rio de Janeiro (Robins and Ray 1986). Common Snook distribution is primarily restricted by cold weather and freeze events (Storey and Gudger 1936; Shafland and Foote 1983). The lower Laguna Madre and its respective estuaries appear to be

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the northernmost permanent range of the Texas–Mexico snook population (Pope et al. 2006).

Common Snook have been the target of recreational and commercial fisheries along the southern Gulf coast of Texas (Matlock and Osburn 1987). However, it composed less than 0.1% of the sport landings in southern Texas during 1985, and there have been no commercial landings since 1961 (Matlock and Osburn 1987). In 1987, commercial harvest of Common Snook was prohibited in Texas, and the species was designated a sport fish (Pope et al. 2006). Currently, the Texas population of Common Snook is characterized by low abundance and erratic recruitment (Pope et al. 2006). The reason for the historical decline and apparent lack of recovery in the Texas snook population is unclear but may be associated with habitat loss or degradation, extreme cold temperature events, or over fishing (Matlock and Osburn 1987; Pope et al. 2006). Most research concerning Common Snook in North America has been conducted in Florida (e.g., Peters et al. 1998; Taylor et al. 1998; 2000; Stevens et al. 2007; Winner et al. 2010), and very little is known about Common Snook in Texas, particularly their biology, habitat requirements, and interactions or associations with other species.

Common Snook are protandric hermaphrodites that reproduce first as males and then transform into females as they grow and age (Peters et al. 1998; Taylor et al. 1998, 2000). In Florida, Common Snook spawn from April to September with a peak spawning period of July to August (Taylor et al. 1998), although evidence exists to suggest that the spawning season may be more protracted (Gilmore et al. 1983) or even year-round (McMichael et al. 1989). Juvenile Common Snook in Florida seem to prefer estuarine basins of relatively small size (<100,000 m²) with narrow and protected access (Peters et al. 1998). Small juveniles (<100 mm standard length [SL]) prefer habitats located along the shoreline with overhanging vegetation or marsh grasses (Peters et al. 1998), whereas larger juveniles (150–300 mm SL) are found almost exclusively in sea grass habitats in some locations, such as the Indian River Lagoon in Florida (Gilmore et al. 1983). However, larger juveniles occupy a greater range of habitats in other locations along the Gulf coast of Florida (McMichael et al. 1998; Peters et al. 1998).

The lower reach of the Rio Grande along the U.S.–Mexico border is believed to be an important nursery habitat for juvenile Common Snook (Huber 2007). Although habitat use of juvenile Common Snook in the Rio Grande or elsewhere in Texas has not been described, this riverine habitat is clearly different (e.g., few or no mangroves and sea grasses) than the habitat previously described for juvenile Common Snook in Florida (Seaman and Collins 1983; Peters et al. 1998; McMichael et al. 1989). Knowledge of the habitat use and interspecific interactions of juvenile Common Snook in the Rio Grande may provide management agencies opportunities to increase recruitment by manipulating habitat and providing additional nursery areas. Also, because of their size-dependent protandric development, knowledge of the size (age) at sexual differentiation and first reproduction may

be useful to the design of optimal management practices for the recreational fishery. Thus, the primary objective of this study was to describe the habitat use of juvenile Common Snook and its role in the fish assemblage of the lower Rio Grande, and the secondary objective was to document the relationship between age and juvenile reproductive development.

METHODS

Study area.—The Rio Grande is the fourth longest river in North America and forms the border between Texas and Mexico before draining into the Gulf of Mexico. Our study area encompassed the lower portion of the river, beginning at the mouth of the Rio Grande at Boca Chica and extending 51.5 km upstream to just below the cities of Brownsville, Texas, and Matamoros, Mexico (Figure 1). Agriculture is the primary land use in this portion of the Rio Grande watershed and aside from Brownsville and Matamoros, there is relatively little urbanization. However, increased water removals for irrigation and municipal uses have dramatically reduced flows from their historical norm. During drought conditions, flows in the lower Rio Grande have reduced in volume to a level that allowed a sandbar to form at the mouth of the river, which separated the river from the Gulf of Mexico (reviewed in Calamusso et al. 2005).

We divided the river into 16 study reaches of approximately 3.2 river kilometers (rkm) in length (Figure 1). We further grouped the study reaches into upstream (reaches 9–16) and downstream (1–8) to limit daily travel and maximize sampling effort. While this division was made primarily for logistical purposes, there was a distinct shift in habitat along the length of the lower Rio Grande. The riverbanks near Boca Chica were not well defined and in some areas resembled tidal flats and pools with sandy substrates. There was little submerged vegetation and shoreline vegetation consisted primarily of grasses with two small patches of black mangrove *Avicennia germinans*. The substrate gradually transitioned upstream to silt and mud. The banks became steeper and more defined as the river became more channelized in these upstream reaches that included shrubby vegetation, primarily mesquite *Prosopis* spp. and black ebony *Pithecellobium flexicaule*, replacing grasses as the dominant vegetation along the shoreline.

Data collection.—Fish were collected in 2006 from January 1 through March 25, using a trawl to sample channel habitats and a boat-mounted electrofisher to sample habitats along the banks. These months were selected for sampling based on the results of a pilot study conducted in 2005, which indicated both age-1 and age-2 juvenile Common Snook are present in the river during this time (Huber 2007). Samples were collected during the standard work day (0800–1700 hours) during Monday through Friday for safety and logistic reasons and sampling effort was confined to the U.S. side of the river for legal reasons.

Four study reaches, randomly selected from either the upstream or downstream section, were sampled per day. A single trawl haul was performed within each study reach at each

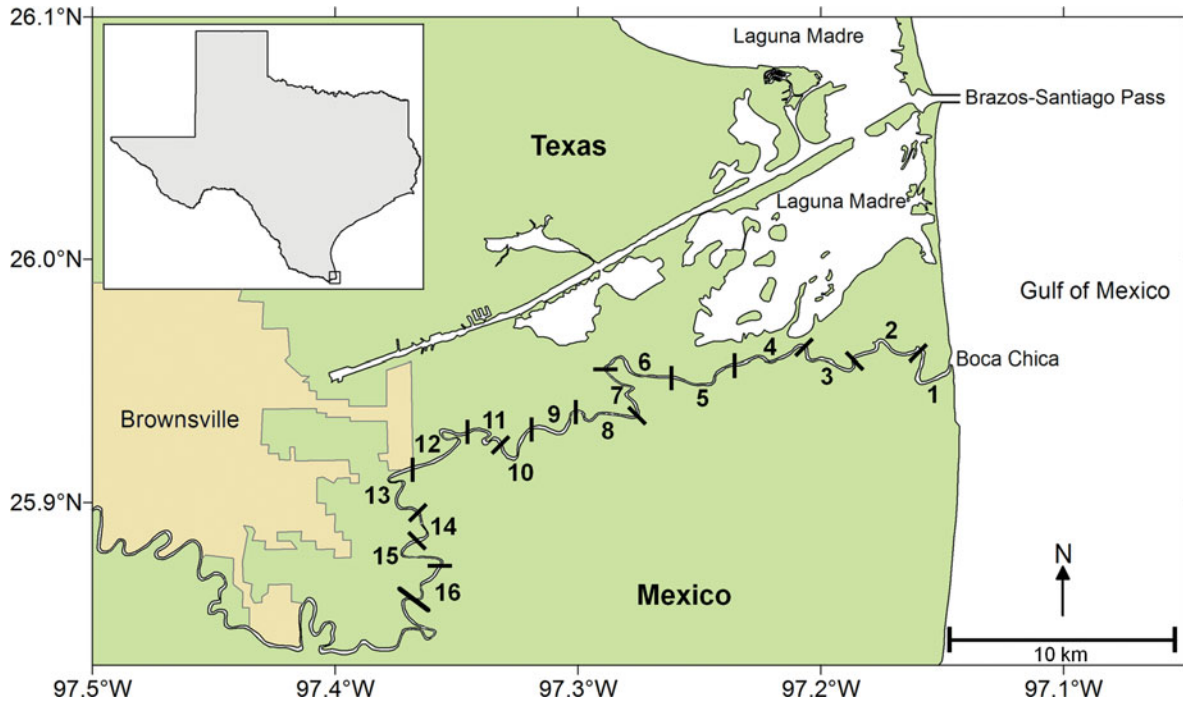


FIGURE 1. The lower Rio Grande and surrounding area in south Texas, showing the 16 study reaches (each 3.2 river kilometers) in which Common Snook were collected.

sampling time using a small otter trawl (3 × 1.5-m mouth and 45.0-mm stretched mesh). Trawls were pulled downstream for 10 min at approximately 1.0 m/s. However, it was not uncommon for a trawl to be stopped before 10 min due to snagging a bottom obstruction. If the trawl was deployed for ≥5 min, the duration was noted and the catch was processed. If the trawl was deployed for <5 min, the trawl was retrieved and emptied immediately and the procedure repeated in another area within the same study reach.

A Smith-Root 5.0 GPP boat-mounted electrofisher with twin booms (Smith-Root Inc, Vancouver, Washington) was used to sample shoreline habitats in the upper 38.6 rkm of our study area above study reach 3 (Figure 1). High conductivity and salinity precluded sampling study reaches 1–3 with this gear type. Within each study reach, we selected four sites by treating the study reach as a transect and randomly generating four numbers between 0 and 3,218 (i.e., the mean length of the study reaches). We then used a handheld GPS unit to navigate to these points along the transect, nosed the boat towards the bank, and activated the electrofisher for approximately 30 s.

The mass (g) and standard length (SL; mm) of all Common Snook caught by trawl or electrofisher were recorded. All other fishes were identified to species, counted, and released. Several Common Snook were euthanized immediately upon capture, and the sagittal otoliths and gonadal tissue were collected from those individuals. Sagittal otoliths were removed and stored in clean, dry vials until read in the laboratory. Gonads were removed and preserved following one of two procedures that

depended on fish size. For smaller fish, the entire carcass was fixed in 10% buffered formalin to maintain integrity of the gonadal tissue. For fish that were too large for whole fixation, the gonadal tissue was removed in the field and fixed in a 10% buffered formalin solution. The tissues were processed in the laboratory for histological examination.

Water-quality measurements were taken at all sampling sites after captured specimens had been processed. Latitude and longitude were determined using a Magellan Navigator 500 handheld GPS receiver (Magellan, San Dimas, California). Current velocity was measured using a Flowmate 2000 flowmeter (Marsh–McBirney, Frederick, Maryland). Turbidity was measured using an Oakton T-100 portable turbidimeter (Oakton Instruments, Vernon Hills, Illinois). Water conductivity, pH, dissolved oxygen, and temperature were measured using an YSI 556 multiparameter meter (YSI Inc., Yellow Springs, Ohio). The YSI-based measurements were collected every 0.3 m down the water column from surface to bottom, and depth was also recorded at each site. All other observations were collected within 1 m of the surface. We recorded several other habitat variables at electrofisher sites describing the physical traits of the shoreline habitat, including substrate type (mud, sand, or mixed) and bank slope (shallow, medium, steep, or cliff), and submerged (emergent grass, cane, woody, mangrove, or none) and terrestrial vegetation type (grass, cane, woody, mangrove, or none).

Otolith and gonad analyses.—Fish age was estimated through microstructure analysis of a representative subsample

of otoliths. Whole otoliths were read using reflected light and a dissecting scope at $10\times$ magnification, as described for Common Snook by Taylor et al. (2000). A January 1 birthdate was used in this study, contrary to the June 1 birthdate used by Taylor et al. (2000). The January 1 birthdate was selected for this study to avoid having a birthdate that would occur in the middle of the protracted spawning season of Common Snook (April–October in Florida; Taylor et al. 1998). Furthermore, the use of a January 1 birthdate is common for fishes in the northern hemisphere because it avoids the confusion associated with a date that divides the summer growing season (see McFarlane et al. 2010). Common Snook collected during this study (January–March) that did not have an annulus present on the edge (annulus formation in Florida occurred during April and May; Taylor et al. 2000) had 1 year added to their annulus count. Otoliths were aged by two independent readers. If the readers disagreed on the age of an otolith, they were reread by both readers. If a consensus could not be reached, a third reader was used, and age was assigned based on agreement of two of the three readers. If a consensus could not be reached by two readers, the sample was eliminated ($n = 6$). We used these data to develop an age–length key to classify juvenile Common Snook into age groups (Isely and Grabowski 2007) that were then used in the analyses described below.

Gonads were processed according to the standard histological procedures described by Luna (1992) for the purpose of assessing the early gonadal development of Common Snook during sex differentiation and before first reproduction. Tissues collected in the field were postfixed in Bouin's fixative for 48 h, rinsed in tap water overnight, dehydrated in a series of ethanol baths, cleared in xylene, and infiltrated with paraffin. Paraffin blocks were sectioned (6–8 μm) using a microtome. Central cross sections of each gonad were placed on precleaned slides and stained using Weigert's hematoxylin and eosin. Gonad sections were viewed with a compound microscope and classified into ad hoc stages according to size and tissue organization and general descriptions of teleost gonadogenesis (Patiño and Takashima 1995; Okuzawa 2002; Alonso-Fernández et al. 2011; Brown-Peterson et al. 2011).

Data analysis.—All statistical analyses were conducted using the SAS 9.2 software package (SAS Institute Inc., Cary, North Carolina) with $\alpha = 0.05$. Catch per unit effort (fish/h) was calculated for both the trawl and electrofisher samples. Mean monthly CPUE were compared using a two-way analysis of variance (ANOVA) with month and study reach as factors. When multiple measurements of water quality were taken at different depths for each site (e.g., conductivity, pH, DO, and temperature) the mean profile value was used for analyses. Bank steepness, substrate, and aquatic and terrestrial vegetation were treated as rank variables. Environmental data were \log_e -transformed to meet parametric assumptions of normality and equality of variance.

We used a modification of the Cramer-von Mises test (see Syrjala 1996) to evaluate whether the spatial distribution of

Common Snook differed month to month. The same test was also used to evaluate the null hypothesis that age-1 and age-2 Common Snook exhibited no differences in monthly distribution. Syrjala's (1996) test for differences in the spatial distributions of two populations normalizes the number of observations for each group, and then computes a test statistic by summing the squares of the differences in abundance of observations between the two groups within rectangular areas of the distribution space. The distribution of test statistics for data that meets the null hypothesis that there is no difference between the groups is obtained by repeatedly and randomly allocating the observations into two groups and computing a test statistic 10,000 times. The P -value testing the null hypothesis is the quantile position of the test statistic computed with the actual data within the set of values for randomized data.

We used canonical correspondence analysis (CCA) to evaluate the relationship between environmental factors and fish assemblage structure (as measured by CPUE) across the study sites. Trawl and electrofisher samples were analyzed separately due to the inability to standardize effort between the two methods and the lack of electrofisher samples from study reaches 1–3. A one-way multivariate ANOVA (MANOVA) was performed on the scores along each significant canonical dimension to test the null hypotheses that there were no differences between sites where snook were present versus where snook were absent; and that habitat use did not differ between age-1 and age-2 Common Snook. We further evaluated whether environmental conditions were different from locations where age-1 and age-2 Common Snook were captured using analysis of covariance (ANCOVA), with age as the independent variable and study reach as a covariate.

RESULTS

Between January and March 2006, 77 trawl and 258 electrofisher samples were taken from the lower Rio Grande. Of the 6,136 fishes and 35 species collected, Common Snook ($n = 214$) was among the 10th most numerically predominant species sampled by both gear types (Table 1), despite being collected only from study reaches 4–16. Mean catch rates of Common Snook varied monthly for trawl ($F_{48, 28} = 3.98$, $P < 0.0001$) and electrofisher ($F_{39, 219} = 3.83$, $P < 0.0001$). The trawl CPUE tended to be higher in January (mean = 9.0/h, SD = 14.6) than in March (mean = 4.6/h, SD = 7.2; $P = 0.05$), but CPUE in February did not differ from the other months (mean = 7.6/h, SD = 13.4; $P \geq 0.47$). Catch rates from the electrofisher followed a similar pattern. Common Snook were captured at a higher rate in January (mean = 111.1/h, SD = 209.4) than in February (mean = 57.8/h, SD = 121.2; $P = 0.02$) and March (mean = 23.7/h, SD = 58.1; $P < 0.0001$). There was no difference in CPUE between February and March ($P = 0.09$).

Length-frequency distributions suggested that at least three age-groups were present in our samples (Figure 2). Examination of otolith microstructure and gonadal histology from a

TABLE 1. Number of individuals (n) and proportion of total catch represented by the 10 most common fish species from trawl samples of channel habitats and electrofishing samples of bank habitats in the lower Rio Grande, Texas, January–March 2006. Letters in parentheses correspond to that species in Figures 4 and 5.

Channel habitat (trawl: 26 species, 2,900 individuals)			Bank habitat (electrofisher: 26 species, 3,236 individuals)		
	n	proportion		n	Proportion
Yellowfin Mojarra <i>Gerres cinereus</i> (A)	1,420	0.490	White Mullet (A)	1,870	0.578
Pinfish <i>Lagodon rhomboides</i> (B)	373	0.129	Striped Mullet (B)	1,119	0.346
Striped Mullet <i>Mugil cephalus</i> (C)	197	0.068	Common Snook	142	0.041
Gafftopsail Catfish <i>Bagre marinus</i> (D)	179	0.062	Age 1	104	
Atlantic Croaker <i>Micropogonias undulatus</i> (E)	164	0.057	Age 2	28	
White Mullet <i>Mugil curema</i> (F)	102	0.035	Age 3 +	10	
Spot <i>Leiostomus xanthurus</i> (G)	92	0.032	Fat Snook <i>Centropomus parallelus</i> (C)	21	0.007
Common Snook <i>Centropomus undecimalis</i>	82	0.028	Gulf Menhaden (D)	20	0.007
Age 1	80		Bigmouth Sleeper <i>Gobiomorus dormitor</i> (E)	17	0.005
Age 2	2		Yellowfin Mojarra (F)	11	0.003
Age 3 +	0		Common Carp <i>Cyprinus carpio</i> (G)	11	0.003
Channel Catfish <i>Ictalurus punctatus</i> (H)	68	0.022	Violet Goby <i>Gobioides broussonetii</i> (H)	9	0.003
Gulf Menhaden <i>Brevoortia patronus</i> (I)	36	0.012	Gizzard Shad <i>Dorosoma cepedianum</i> (I)	3	0.001

representative subset of 40 individuals supported this conclusion (Figure 3). The gonads of the youngest age-group (age 1, 41–156 mm SL) were relatively small and possessed a cavity near the hilar region consistent with the presence of a sperm duct (Figure 3). Age-2 individuals (198–303 mm SL) showed a higher level of gonadal development but were still juvenile males with no signs of spermatogenesis. Distinct germinal ep-

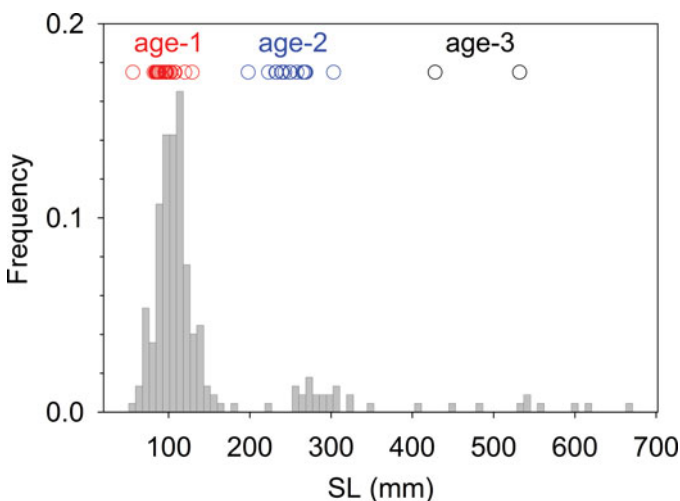


FIGURE 2. Length-frequency histogram of Common Snook captured from the lower Rio Grande, January–March 2006 showing the size distributions of individuals classified as age-1, age-2, and age-3. The lengths and ages of individuals whose ages were estimated from otoliths are represented by the circles plotted against the right y-axis.

ithelium was observed in the gonads of the age-3 and older fish (360–595 mm SL), but active spermatogenesis was seen only in a few of the largest fish captured at the end of March. These 10 older individuals were determined to have reached puberty (Okuzawa 2002) or perhaps adulthood and, thus, were excluded from further analysis because the focus of this study was on juvenile distribution and habitat use. Our data suggest that Common Snook reach a mean length of approximately 95 mm SL in their first year and, on average, add another 154 mm during their second year (Table 2).

Juvenile Common Snook were not randomly distributed across the study reaches ($\chi^2 = 29.83$, $df = 15$, $P = 0.013$) because no Common Snook were captured in the lowermost study reaches (1–3; Table 2). The monthly distributions of Common Snook were consistent along the lower Rio Grande based on the CPUE from trawl-sampled channel habitat ($P \geq 0.054$) and electrofisher-sampled bank habitat ($P \geq 0.65$). The highest CPUE rates of both gear types occurred in the middle and upper study reaches (8–16; Table 3).

TABLE 2. Age (estimated from otolith microstructure analysis) and length data for Common Snook captured from the lower Rio Grande, Texas, January–March 2006.

Age	n	Mean \pm SE length (SL; mm)	Range (SL; mm)
1	23	95 \pm 3	56–129
2	15	249 \pm 6	198–303
3	2	480 \pm 52	428–532

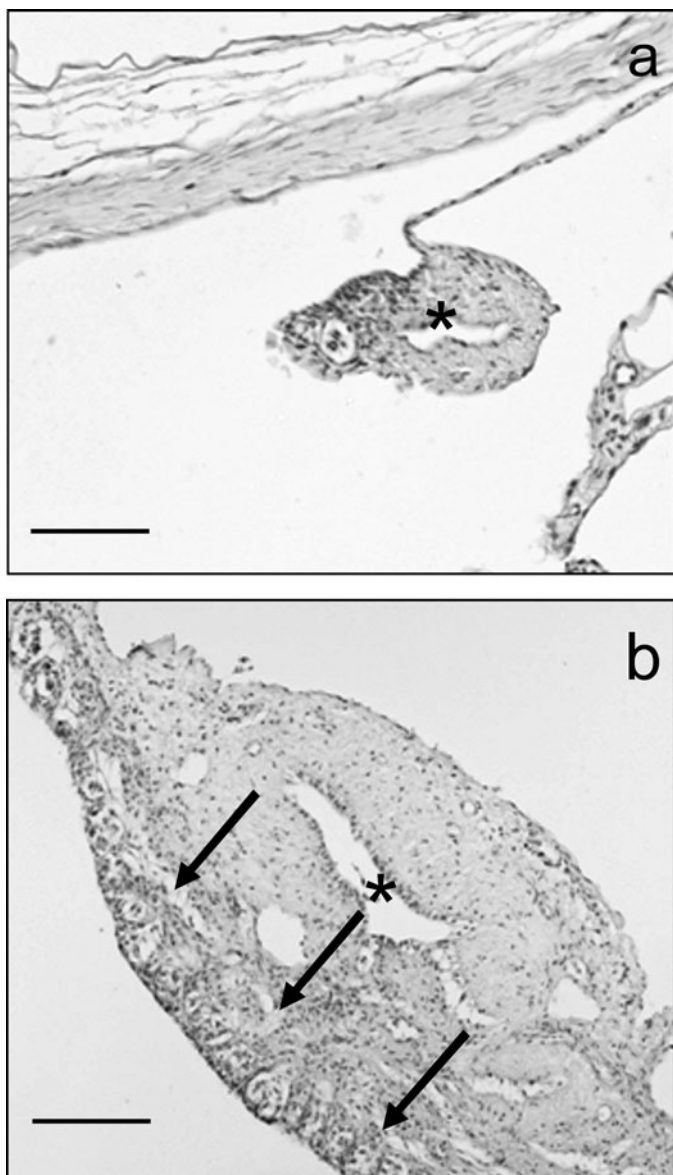


FIGURE 3. Gonadal cross sections from a representative (a) 1-year old and (b) 2-year old Common Snook captured from the lower Rio Grande, January–March 2006. Asterisks indicate sperm ducts and arrows indicate germinal epithelium. Scale bars represent 50 μm in panel (a) and 100 μm in panel (b).

The composition of the fish assemblage in channel habitats was primarily correlated with DO, conductivity, and month in a single canonical dimension (Tables 4, 5). As suggested by their absence from trawl samples taken at the lower study reaches, Common Snook seemed to be loosely associated with a fish assemblage characteristic of lower conductivity such as Yellowfin Mojarra *Gerres cinereus* and Channel Catfish *Ictalurus punctatus* (Figure 4). However, analysis of results from the first canonical dimension suggest that there was no difference in the scores along the first canonical dimension between sample sites where Common Snook were present and those where they were

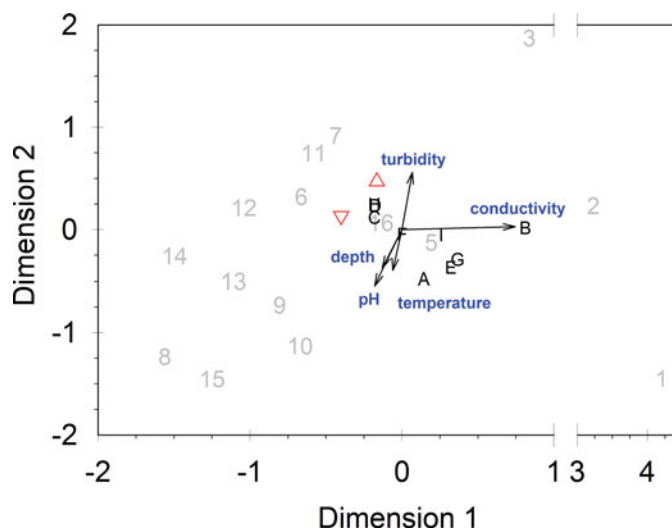


FIGURE 4. Canonical correspondence analysis ordination diagram of the first two canonical dimensions for the 16 stations where channel habitat was sampled by bottom trawl in the lower Rio Grande, January–March 2006. Arrows indicate the environmental variables, and arrowheads indicate the increase in gradient. Numbers represent the study reaches, and letters represent the centroids for the nine most abundant species (see Table 1). The centroids for Common Snook are represented by open triangles with downward pointing triangles representing age-1 fish and upwards pointing triangles representing age-2 fish.

not captured ($F_{1,42} = 3.71$; $P = 0.06$). Furthermore, the study reaches showed a stronger differentiation in physicochemical factors, such as conductivity, than in the composition of their fish assemblages (Figure 4).

In the electrofisher samples, the presence of Common Snook was associated with higher DO and lower conductivity than at sites where they were not collected (Figure 5). Fish assemblage composition in bank habitats was similar in species composition and predominated by Striped Mullet *Mugil cephalus*, White Mullet *Mugil curema*, and Common Snook (Table 1). The fish assemblage was described by three canonical dimensions (Tables 3, 4), but similar to the trawl samples, the study reaches showed greater differentiation in physicochemical factors than in the composition of their fish assemblages (Figure 5). Common Snook presence or absence was most associated with the score along the second canonical dimension (Wilk's $\lambda = 0.91$, $F_{3,130} = 4.11$, $P = 0.003$) and not the first or third canonical dimension ($P \geq 0.43$).

On a coarse study reach level, no differences were detected in the monthly distributions of age-1 and age-2 Common Snook ($P \geq 0.09$). However, the two age-groups seemed to have distinct microhabitat associations along the banks in the first and second canonical dimensions (Wilk's $\lambda = 0.80$, $F_{3,39} = 3.33$, $P \leq 0.048$). Age-2 Common Snook were associated with higher current velocities in areas with deeper water than their younger conspecifics (Figure 5; Table 6). Interestingly, neither age-group seemed to show a strong association with aquatic or terrestrial vegetation. Age-2 Common Snook seemed to have a close association with Smallscale Fat Snook *Centropomus parallelus*

TABLE 3. Mean \pm SD trawl and electrofishing catch per unit effort data and number of sampling events (n) for Common Snook and mean \pm SD water chemistry variables taken from study reaches on the Rio Grande, Texas–Mexico, January–March 2006. Study reach 1 is located at the mouth of the river, while study reach 16 is approximately 51.5 river kilometers upstream.

Study reach	Trawl		Electrofisher		Depth (m)	Current velocity (m/s)	Turbidity (NTU)	Water temperature ($^{\circ}$ C)	Conductivity (μ S/cm)	Dissolved oxygen (mg/L)	pH
	CPUE (fish/h)	n	CPUE (fish/h)	n							
1	0.0 \pm 0.0	5	No effort	0	1.8 \pm 0.7	0.01 \pm 0.17	59.2 \pm 18.4	20.4 \pm 1.4	25963 \pm 17	8.2 \pm 0.9	8.3 \pm 0.3
2	0.0 \pm 0.0	5	No effort	0	2.1 \pm 0.4	0.08 \pm 0.15	39.0 \pm 14.2	20.3 \pm 1.8	17,282 \pm 13,799	9.4 \pm 2.5	8.4 \pm 0.4
3	0.0 \pm 0.0	5	No effort	0	2.2 \pm 0.8	0.13 \pm 0.11	39.1 \pm 14.4	19.8 \pm 2.9	12,083 \pm 13,777	8.8 \pm 1.1	8.3 \pm 0.2
4	6.0 \pm 12.0	4	0.0 \pm 0.0	18	1.1 \pm 0.7	-0.01 \pm 0.08	50.4 \pm 17.3	21.3 \pm 2.1	3,733 \pm 3,628	9.1 \pm 0.7	8.4 \pm 0.2
5	0.0 \pm 0.0	6	111.5 \pm 255.7	20	1.2 \pm 0.7	0.02 \pm 0.11	50.3 \pm 18.5	21.0 \pm 2.4	1,434 \pm 227	9.7 \pm 0.8	8.3 \pm 0.6
6	0.0 \pm 0.0	5	16.2 \pm 55.9	20	1.2 \pm 0.7	0.03 \pm 0.09	58.0 \pm 21.9	21.2 \pm 2.4	1,396 \pm 319.5	9.3 \pm 0.7	8.4 \pm 0.3
7	8.4 \pm 5.4	6	23.3 \pm 54.0	20	1.5 \pm 0.7	-0.03 \pm 0.09	52.1 \pm 19.0	20.3 \pm 2.4	2,730 \pm 5,460	8.6 \pm 1.3	8.2 \pm 0.2
8	16.4 \pm 6.1	4	56.8 \pm 111.7	20	1.4 \pm 0.9	0.00 \pm 0.07	50.0 \pm 18.2	20.1 \pm 2.7	1,278 \pm 172	8.4 \pm 1.3	8.5 \pm 0.5
9	16.5 \pm 21.0	4	63.6 \pm 97.3	20	1.3 \pm 0.7	0.04 \pm 0.09	51.6 \pm 19.1	20.1 \pm 2.6	2,248 \pm 4,256	8.6 \pm 1.1	8.1 \pm 0.8
10	10.5 \pm 5.7	4	52.7 \pm 83.3	20	1.5 \pm 0.9	0.06 \pm 0.07	55.7 \pm 14.8	19.7 \pm 2.4	1,363 \pm 219	8.2 \pm 1.0	8.2 \pm 0.3
11	4.5 \pm 6.2	5	60.9 \pm 80.4	20	1.6 \pm 0.9	0.01 \pm 0.09	50.2 \pm 11.7	21.1 \pm 2.7	4,692 \pm 11,949	8.9 \pm 1.3	8.3 \pm 0.2
12	5.2 \pm 7.1	4	69.9 \pm 120.7	20	1.2 \pm 0.6	0.05 \pm 0.08	49.1 \pm 11.8	20.8 \pm 2.7	1,366 \pm 244	8.8 \pm 1.3	8.1 \pm 0.3
13	8.4 \pm 15.6	5	89.7 \pm 210.9	20	1.3 \pm 0.9	0.06 \pm 0.08	46.4 \pm 17.0	20.1 \pm 2.9	1,350 \pm 247	8.9 \pm 1.7	8.3 \pm 0.3
14	26.4 \pm 26.4	5	24.7 \pm 50.7	20	1.6 \pm 0.5	0.11 \pm 0.08	44.8 \pm 10.6	20.5 \pm 2.7	1,340 \pm 163	7.7 \pm 1.0	8.1 \pm 0.1
15	13.2 \pm 10.7	5	78.1 \pm 115.5	20	1.4 \pm 0.4	0.12 \pm 0.08	43.8 \pm 11.6	20.0 \pm 2.3	1,267 \pm 177	8.4 \pm 0.8	8.1 \pm 0.2
16	2.4 \pm 3.3	5	63.1 \pm 188.0	20	1.7 \pm 0.7	0.13 \pm 0.08	42.3 \pm 14.2	20.4 \pm 2.1	1,269 \pm 185	8.1 \pm 1.1	8.1 \pm 0.3

(Figure 5), but there was no similar association to any particular species for age-1 Common Snook. This distinction was not as clear in channel habitats (Figure 4; Table 6), and statistical comparisons between age groups in channel habitats was not performed due to the low number of age-2 individuals ($n = 2$) captured.

DISCUSSION

Our results, most notably the lack of females among the age-1 and age-2 individuals examined, are consistent with reproductive development of Common Snook in Texas as protandric hermaphrodites, as previously described for Common Snook in Florida (Taylor et al. 2000). Histological examination of their gonads indicated that all age-1 fish were juvenile males and that all age-2 fish also had juvenile testes without any signs of spermatogenesis, albeit at more advanced stages of growth. Differences in size and development within each age-group were presumably due to the protracted spawning period that is typi-

cal for Common Snook (April through September; Taylor et al. 1998). Our observations on the development of juvenile testes are consistent with the results of a laboratory study describing the early gonadal development in Common Snook (Vidal-López et al. 2012). However, it is highly unlikely that any age-2 males examined reached breeding condition during their first potential spawning season as age-1 fish in the preceding year (spring-summer 2005), given the very early developmental stage of age-1 testes. Adult age-1 males (bearing spermatogenic testes) have been collected from Florida populations of Common Snook, but it is unclear if these individuals actively engaged in spawning activity (Taylor et al. 1998, 2000). Common Snook tend to be considerably larger in Florida at the end of their first year (211 mm FL, SD = 3.2) and reach adulthood at 150–200 mm FL (Taylor et al. 2000). These differences persist even when the different birthdates used in this study (January 1) versus Taylor et al. (2000; June 1) are taken into account. Though a more comprehensive age and growth study is needed, our results suggest Common Snook in the lower Rio Grande may grow slower

TABLE 4. Tests of canonical correspondence dimensions for analysis of fish assemblage data from trawl-sampled channel habitats and electrofisher-sampled bank habitat in the lower Rio Grande, January–March 2006.

	Dimension	Canonical correlation	Variance explained	F	df 1	df 2	P
Channel habitat (trawl)	1	0.87	0.36	1.25	270	537	0.02
	2	0.75	0.15	1.01	238	512	0.45
Bank habitat (electrofisher)	1	0.77	0.36	2.34	228	1,518	<0.0001
	2	0.68	0.21	1.84	198	1,412	<0.0001
	3	0.58	0.12	1.51	170	1,303	<0.0001

TABLE 5. Standardized canonical discriminant function coefficients for habitat variables used in canonical correspondence analysis of lower Rio Grande fish assemblages from trawl samples of channel habitats and electrofishing samples of bank habitats, January–March 2006.

Habitat variable	Channel habitat (trawl)		Bank habitat (electrofisher)		
	Dimension 1	Dimension 2	Dimension 1	Dimension 2	Dimension 3
Depth	−0.45	0.04	0.07	−0.15	−0.12
Current velocity	−0.42	0.34	0.85	0.48	0.38
Turbidity	0.36	0.31	−0.33	−0.13	−0.73
Water temperature	−0.09	−0.06	0.22	0.52	0.43
Conductivity	−0.63	0.17	−0.66	1.14	−0.42
DO	−0.71	0.19	−0.19	−0.41	0.89
pH	0.25	−0.23	−0.14	−0.07	0.09
Substrate			0.14	−0.04	0.10
Bank steepness			0.57	0.11	−0.27
Terrestrial vegetation			−0.14	−0.37	−0.15
Aquatic vegetation			−0.19	0.17	−0.08

than their Florida counterparts and, thus, potentially may have a longer reproductive development schedule. For example, only some of the age-2 individuals may have been capable of reaching maturity and spawning during 2006, based on the size and condition of their gonads. The few age-3 and older males (395–595 mm SL) that were examined had considerably larger gonads suggesting that some may have spawned as age-2 fish, but the lack of spermatogenic testes in these age-3 and older individuals is unsurprising because active spermatogenesis is initiated in late winter and spring (Grier and Taylor 1998). It is also important to note the potential implications of a protracted spawning season for our age estimates. The age of individuals spawned at the beginning or end of the season, per our age–length key,

would have a greater chance of being respectively classified to an older or younger age-class, but the distinct separation seen in the age-frequency distribution (Figure 2) suggests that this was not a major factor in our data.

Juvenile Common Snook were not distributed randomly in the lower Rio Grande. Notably, no juvenile Common Snook were captured in the first three study reaches from rkm 0 at Boca Chica to approximately rkm 10, where the water conductivity range was 1,598–54,386 $\mu\text{S}/\text{cm}$ (salinity of 0.8–36.1). In study reaches where Common Snook were captured, their presence was associated with lower water conductivity. This distribution pattern was consistent throughout the study. However, the absence of juvenile Common Snook in the brackish water

TABLE 6. Mean \pm SD habitat variables measured at sites from which age-1 and (or) age-2 Common Snook were sampled in the lower Rio Grande, January–March 2006, and results of ANCOVA evaluating the null hypothesis that there was no difference in these variables between the two age-classes. Sample size (n) represents the number of samples containing individuals of that age-group. Substrate (1 = mud, 2 = mixed, 3 = sand), bank steepness (1 = shallow, 2 = medium, 3 = steep, 4 = cliff), aquatic vegetation (1 = none, 2 = grass, 3 = cane, 4 = tree/woody debris, 5 = mangrove), and terrestrial vegetation (same as aquatic vegetation) are represented by rank variables. No statistical comparisons were performed on the channel habitat due to the small number of age-2 Common Snook captured.

Habitat variable	Channel habitat (trawl)		Bank habitat (electrofisher)			
	Age 1 ($n = 31$)	Age 2 ($n = 2$)	Age 1 ($n = 36$)	Age 2 ($n = 20$)	$F_{1,38}$	P
Depth (m)	1.87 \pm 0.62	1.82 \pm 0.43	1.03 \pm 0.52	1.60 \pm 0.58	7.76	0.01
Current velocity (m/s)	0.06 \pm 0.12	0.06 \pm 0.14	0.03 \pm 0.06	0.08 \pm 0.10	4.88	0.03
Turbidity (NTU)	51.8 \pm 16.8	42.5 \pm 1.9	47.3 \pm 12.7	47.1 \pm 14.0	0.99	0.33
Water temperature ($^{\circ}\text{C}$)	19.5 \pm 3.0	22.6 \pm 2.2	20.5 \pm 1.7	20.4 \pm 2.2	2.09	0.16
Conductivity ($\mu\text{S}/\text{cm}$)	4,657 \pm 10,842	1,270 \pm 37	1,155 \pm 149	1,334 \pm 255	0.89	0.35
Dissolved oxygen (mg/L)	8.8 \pm 1.3	8.2 \pm 1.3	8.1 \pm 0.9	8.3 \pm 1.5	3.56	0.07
pH	8.2 \pm 0.2	8.1 \pm 0.3	8.1 \pm 0.3	8.2 \pm 0.5	5.62	0.02
Substrate			1.0 \pm 0.0	1.0 \pm 0.0	0.45	0.50
Bank steepness			1.9 \pm 1.2	2.8 \pm 1.4	0.78	0.38
Aquatic vegetation			1.1 \pm 1.4	1.3 \pm 1.3	1.66	0.20
Terrestrial vegetation			2.1 \pm 0.9	2.3 \pm 0.9	2.95	0.09

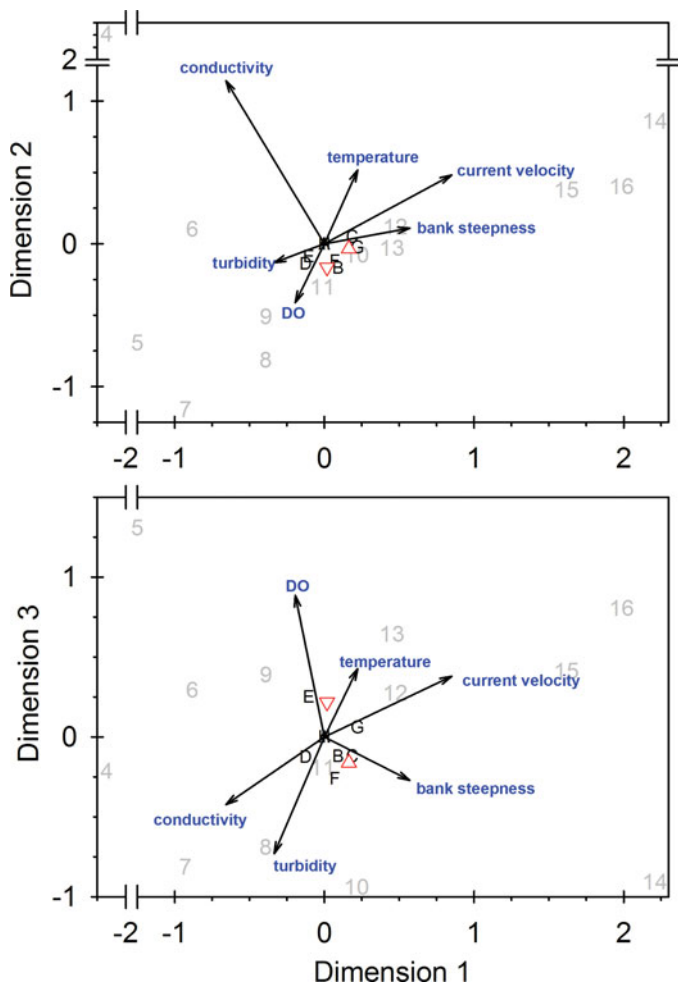


FIGURE 5. Canonical correspondence analysis ordination diagram of the first three canonical dimensions for the 13 stations where bank habitat was sampled by boat-mounted electrofisher in the lower Rio Grande, January-March 2006. Arrows indicate the environmental variables, and arrowheads indicate the increase in gradient. Numbers represent the study reaches, and letters represent the centroids for the nine most abundant species as listed in Table 1. The centroids for Common Snook are represented by open triangles with downward pointing triangles representing age-1 fish and upwards pointing triangles representing age-2 fish.

sections of the river is notable because these fish (200–300 mm SL) are able to tolerate a wide salinity range from freshwater to 35–40 (Peters et al. 1998). Although juvenile Common Snook are thought to return to marine environments to complete their life cycle (Ager et al. 1978; Chapman et al. 1982), our observations suggest that in the Rio Grande this migration may occur primarily outside the sampling period of our study (January-March) or that it might extend over a longer period and thus not detectable with our study design. Alternatively, age-2 and older Common Snook may not have been particularly vulnerable to our bottom trawl, the only sampling gear we could use in these lower reaches, rendering any directed shifts in distribution difficult to detect.

Juvenile Common Snook seemed to exhibit an ontogenetic shift in habitat use in the lower Rio Grande. Age-1 fish were associated with slower currents and shallower water than their age-2 counterparts. The physicochemical habitat conditions where juvenile Common Snook were encountered in the lower Rio Grande were within the ranges reported for populations in Florida (Peters et al. 1998; Winner et al. 2010). However, we found no association between presence and physical habitat, such as submerged or emergent vegetation. Both Peters et al. (1998) and Winner et al. (2010) found that juvenile Common Snook in Florida, particularly smaller individuals, prefer habitats with a predominance of mangroves or sea grasses. Larger individuals may be more flexible in their habitat use (McMichael et al. 1986; Peters et al. 1998). In our study, juvenile Common Snook did not seem to use sites based on either terrestrial or aquatic vegetation and showed no association to mangrove or sea grass habitat. Availability of these habitat types is very limited in the lower Rio Grande. Black mangrove does occur in the lower study reaches, but it is found higher on the shoreline than red mangrove *Rhizophora mangle*, the predominant species in Florida estuaries, and develops a less complex prop root system (Britton and Morton 1989). Sea grasses, such as shoal grass *Halodule wrightii*, are common in southern Texas and form extensive beds in the Laguna Madre system just north of Boca Chica (Britton and Morton 1989; McKee 2008, Figure 1) but seem to be largely absent from the lower Rio Grande. How Common Snook in the lower Rio Grande were able to compose such a large proportion of the fish assemblage without access to these habitats is an interesting question and suggests there may be fundamental differences between Florida and southern Texas populations. Such differences in habitat use are not unheard of, as even local populations in Florida can exhibit substantial plasticity in habitat use (Stevens et al. 2007). Further, it is unclear what influence these differences in habitat availability and use patterns might have on the growth of Common Snook in the lower Rio Grande.

Previous work has indicated that snook are common in the Rio Grande downstream of Brownsville, Texas, but does not note it being such a predominant component of the fish assemblage (Calamusso et al. 2005; Hendrickson et al. 2010). While the high relative occurrence of Common Snook in our samples was unexpected, the fish assemblage approximated what had been previously described for this river segment (Calamusso et al. 2005; Hendrickson et al. 2010). The fish assemblage is typically dominated by euryhaline marine, estuarine resident, and tolerant freshwater fishes. Given the gradient along the river segment, we expected to see a greater amount of differentiation among study reaches in the composition of their fish assemblage. Instead, CPUE for most of the species did not seem to be strongly related to any of the measured environmental variables or tied to any particular study reach. This may be due to a combination of tolerant species, reduced and altered flows in the lower Rio Grande, and resulting changes of the dynamics of the salt wedge in this segment of the river. It is unclear if the reduced diversity

and apparent homogenization of the fish assemblage observed in this study have any influence on the abundance of Common Snook in the lower Rio Grande.

Our data suggest that instream flow is an important component of juvenile Common Snook habitat lower Rio Grande and understanding how it affects habitat quality may be a prerequisite to effective management. Instream flow may also be an important aspect to Common Snook life history as well. Several large males (395–595 mm SL; older than 4 years) and one female (544 mm SL; older than 4 years) were captured at rkm 24.1 by electroshocking the river channel on one occasion outside the study plan (Huber 2007). The presence of these large males and females suggest that adult Common Snook also use the freshwater portion of the lower Rio Grande, at least seasonally. Our sampling period of January–March did not encompass the spawning season, which begins in April and continues through July (Taylor et al. 1998), so it is unclear if these large adults were present in the river in preparation for spawning or if they are present in the river throughout the year. Future research should attempt to determine habitat use patterns of adult Common Snook in the lower Rio Grande and the adjacent Laguna Madre, as well as understand how blockage of the river mouth, as it occurred in 2001 due to low flows (Calamusso et al. 2005), might impact Common Snook populations.

This study is the first examination of the biology of juvenile Common Snook in Texas. Further, this is the first study to examine habitat use by juvenile Common Snook in freshwater habitat that is substantially distant from the adjacent marine environment. However, our study only provides a snapshot and further investigation is necessary to evaluate the annual movements and changes in distribution of Common Snook in the lower Rio Grande and how Common Snook in southern Texas may differ from conspecifics in other parts of its range.

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