Age, growth, maturation, and protandric sex reversal in common snook, *Centropomus undecimalis,* from the east and west coasts of South Florida

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Abstract.–During 1986–91, we examined 2088 common snook, *Centropomus undecimalis*, captured in Jupiter and Lake Worth inlets and adjacent waters on the east coast of Florida and 1784 common snook captured in Tampa Bay on the west coast of Florida. Of fish that were sexed, females ranged in length from 397 to 1105 mm FL, and males ranged from 124 to 925 mm FL. East coast fish were larger overall than west coast fish. Age of common snook was determined from sectioned otoliths. Results from the return of 80 oxytetracycline-marked otoliths combined with analyses of monthly patterns in marginal increments and the percentage of otoliths with an annulus on the edge, demonstrated that a single annulus is formed each year. Common snook can live to 21 years, but most of the fish in our sample were from 1 to 7 years old. The von Bertalanffy growth models were significantly different ($P<0.001$) for each coast and suggested that east coast snook grow faster than west coast snook. Common snook are protandric hermaphrodites. The gonads of 27 transitional specimens contained both degenerating spermatogenic and developing ovarian tissue, and sex reversal was observed in captive common snook. Common snook sex ratios and length-frequency distributions were also consistent with a diagnosis of protandric hermaphroditism. Females smaller than 500 mm FL were uncommon, and only one female less than 400 mm long was captured. The predicted lengths and ages at which 50% of the fish in the population would be females were 767 mm FL and 7.4 years for the east coast and 608 mm FL and 5.1 years for the west coast. Some males on both coasts were sexually mature at lengths less than 200 mm FL and at age 0; most age-1 males were mature on both coasts. All females were considered mature because they were derived from post-spawning males.

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Common snook, *Centropomus undecimalis*, (Perciformes: Centropomidae) are valuable euryhaline fishes that inhabit tropical and subtropical estuarine systems of the western Atlantic. They are abundant off the east coast of Florida from Cape Canaveral southward around the peninsula to Cedar Key off the west coast. They also inhabit waters off Galveston, Texas, south to Rio de Janeiro, Brazil (Gilmore et al., 1983; Rivas, 1986). They are commercially exploited throughout most of their range, except in Texas and Florida where they traditionally have supported large recreational fisheries (Matlock and Osburn, 1987). Snook are stenothermic: their northern range is limited by the winter 15°C isotherm (Shafland and Foote, 1983), similar to the distribution of mangroves which is their principal habitat (Marshall, 1958; Gilmore et al., 1983). Genetic studies of the stock structure suggest that in Florida, east coast and west coast populations are separate stocks (Tringali and Bert, 1996).

Anglers target common snook because of their fighting ability and culinary value (Tucker et al., 1985; Matlock and Osburn, 1987), and concerns about overfishing have resulted in a long history of regulation of the fishery off Florida (Bruger and Haddad, 1986). Size limits were first imposed on the fishery in 1953, and the sale of common snook in Florida has been prohibited since 1956. In 1994, a management goal was established to maintain a minimum spawning potential ratio (SPR) of 40% for common snook stocks (Muller and Murphy[1]). In 1998, the Florida Marine Fisheries Commission enacted the current restrictive regulations to reduce the harvest of snook from Florida waters to maintain a 40% SPR.

Our study examined age, growth, maturation, and sex reversal of common snook which previously had not been diagnosed as being protandrous hermaphrodites. Earlier studies derived ages from either scales or whole otoliths, and ages were poorly validated (Volpe, 1959; Thue et al.[2]). Since these reports, studies on a variety of species have shown that scales are not reliable for aging long-lived fishes and that scale-derived and whole-otolith–derived age estimates are often lower than the validated estimates derived from sectioned otoliths (Beamish and McFarlane, 1983; Casselman, 1983; Lowerre-Barbieri et al., 1994; Crabtree et al., 1996). A validated method for aging snook is necessary to assess previous estimates of growth rates, mortality, and longevity. Our objectives were to describe validated aging techniques, length and age composition, and length and age at maturity of common snook populations from the east and west coasts of Florida. We also diagnosed common snook as protandrous hermaphrodites.

Methods

On the east coast of Florida, common snook were collected with hook-and-line gear during June–August 1987–91 in Sebastian, Jupiter, and Lake Worth Inlets. Young-of-the-year and juvenile common snook were collected on both coasts during April and May in 1989 and 1990 with a 3-m cast net (19-mm stretched mesh) from protected backwaters of coastal rivers. In December 1989, dead or moribund snook that had succumbed to low water temperatures were collected on both coasts. A detailed description of additional collections made with various nets on both coasts may be found in Taylor et al., 1998. Data, otoliths, and gonads collected and used in that study were used in the present study.

In the laboratory, total length (TL), fork length (FL), and standard length (SL) were measured to the nearest mm; all measurements reported in our study are fork lengths. Weights were measured to the nearest gram (g), and gonads were weighed to the nearest 0.01 g. Gonad samples were fixed in 10% buffered formalin for histological processing. Sagittal otoliths were removed and stored dry.

Age and growth

A Buehler Isomet low-speed saw was used to cut four sections approximately 0.5 mm thick that were mounted on a microscope slide (Chilton and Beamish, 1982). Annuli were counted on the section through the core by using compound microscopes and transmitted light. Two independent readers counted annuli on each otolith without knowledge of fish size or capture date. If the two readings disagreed, both readers read the otolith again, for a total of four readings. If three of the four readings agreed, then this reading was accepted as the annulus count; otherwise the otolith was excluded from further analysis.

An annual growth zone in a common snook otolith comprises a narrow, concentric opaque band, formed each winter as growth slows, and a wider, translucent band, formed each summer as growth increases. Opaque winter bands were enumerated as assumed annuli because they were the salient feature in each section. Ages were assigned to each fish on the basis of a 1 June birth date because most snook have completed annulus formation by 1 June and because June corresponds to the approximate beginning of the snook spawning season (Taylor et al., 1998). Annulus counts were adjusted on the basis of an assumed birth date of 1 June. All otoliths that had an annulus on the edge from fish captured between 1 December and 1 June were assigned an age of one less than the annulus count. Fish captured after 1 June and before 1 December were assigned ages equal to the annulus count.

In earlier studies (Volpe, 1959; Thue et al. 1982), whole otoliths or scales were used to estimate ages. To evaluate the validity of using these structures to estimate snook age, we examined whole and sectioned otoliths from 199 fish that included at least five individuals from each abundant age class and the oldest individuals. Whole otoliths were read three times by a single reader. Whole otoliths were submerged in glycerin and read over a dark background with reflected light. Scale impressions from 48 common snook of different ages and lengths were made on acetate slides and read under compound microscopes equipped with transmitted light. Ages from these scales were compared with ages derived from sectioned otoliths of the same fish.

The von Bertalanffy (1957) growth equation $FL_t = L(1 - e^{(-K(t-t_0))})$ was fitted to observed age-length data with nonlinear regressions. These predicted lengths at age were compared with the average observed lengths at age that included some seasonal growth that occurred after the formation of the final annulus. Likelihood-ratio tests were used to compare parameter estimates for males and females (Kimura, 1980). If coast had a significant effect, the equations were calculated for each coast. Length-weight regressions were calculated by linear regression of $\log_{10}$-transformed data. Length-length and length-weight regressions were calculated for common snook of both sexes with pooled data.

Age validation

We captured 754 common snook 327–961 mm and injected them with oxytetracycline (OTC) at a dosage of 25-mg OTC/kg of fish body weight. Fish were then double-tagged with dart and internal-anchor tags and released at the original capture site. We relied on anglers and our own fish-

[1] Muller, R. G., and M. D. Murphy. 1998. A stock assessment of common snook, *Centropomus undecimalis*. Rep. to the Florida Marine Fisheries Commission, Florida Dep. of Environ. Protection. Florida Marine Research Institute, 100 Eighth Ave. SE, St. Petersburg, Florida 33701, 53 p.

[2] Thue, E. B., E. S. Rutherford, and D. E. Buker. 1982. Age, growth and mortality of the common snook, *Centropomus undecimalis* (Bloch), in the Everglades National Park, Florida. U. S. National Park Service South Florida Research Center Report T-683, 32 p.

ery-independent sampling techniques to recapture tagged fish. Otoliths from recaptured OTC-injected common snook were processed, read, and measured according to Chilton and Beamish (1982) and Beamish and McFarlane (1983). The number of annuli formed after the OTC mark was then compared with the number of days since injection.

Measurements from the core to each assumed annulus and to the margin of the otolith were made with a digital image-processing system on an axis extending along the sulcal ridge to the proximal margin of each section. We expressed the distance from the final annulus to the edge of the otolith (the marginal increment) as a percentage of the distance between the last two annuli formed on the otolith, or for fish with only a single annulus, as a percentage of the distance between the otolith core and the first annulus. The monthly percentage of otoliths with an annulus on their margin was plotted by capture month to show when the annuli were formed and to reveal their repetitive seasonal trend in formation. The annularity of the assumed age mark was demonstrated for each age class by plotting monthly mean measurements for all ages pooled into three inclusive groups.

Reproduction

Sections of each gonad were prepared for histological analysis and scored according to the level of reproductive activity, or class. Gonad samples were processed with a modification of the periodic acid Schiff's (PAS) stain for glycol-methacrylate sections, with Weigert's iron-hematoxylin as a nuclear stain and metanil yellow as a counterstain (Quintero-Hunter et al., 1991). Seasonal spawning patterns and spawning frequency of the common snook that we examined were reported by Taylor et al. (1998). We considered common snook in Taylor et al.'s (1998) and Grier and Taylor's (1998) classes 2–5 to be sexually mature. For a more detailed description of common snook testicular maturation see Grier and Taylor (1998). These classes included snook that had testes with evidence of active spermatogenesis and regressed testes with evidence of previous gonadal development.

We diagnosed hermaphroditism in common snook by observing histological sections of transitional-sex-stage individuals and sex-specific age- and length-frequency distributions, according to the criteria of Sadovy and Shapiro (1987). We also conducted an experiment with captive snook to document sex reversal in individual fish. We raised common snook from eggs at the Florida Fish and Wildlife Commission's Stock Enhancement Research Facility. On 6 July 1995, 137 age-4 snook ranging from 445 to 608 mm (mean=534 mm) were identified as males on the basis of presence of flowing milt at the vent and were tagged with passive-integrated transponders (PIT tags). These fish were held for 13 months in a one-quarter acre outdoor pond that had constant exchange of ambient seawater. Water temperature and salinity ranged from 17 to 37°C and from 15 to 34‰, respectively. During December 1995 and January 1996, additional well water (17°C and 3‰) was added to maintain 17°C water temperature and to reduce the salinity to 15‰. Rations consisted of squid, sardines, and dried trout pellets. Fish were fed at the rate of 2% body weight per day.

These fish were examined and sexed on two occasions: after 2 months and after 13 months. Fish that could not be positively identified as males from the presence of flowing milt at the vent were sacrificed and examined by histological analysis.

A logistic function was fitted to the percentage of females in our samples by length and age to estimate the length and age at which 50% of the males in the population transformed into females. Regressions were performed with coast as a categorical effect. If coast was a significant effect, the equations were calculated for each coast. The inflection point of the logistic curves was used as an estimate of the length or age at which 50% of the population had undergone transition from male to female.

Results

The 3872 common snook that were examined ranged in length from 124 to 1105 mm (Fig. 1). Of the fish that we sexed, females ranged in length from 397 to 1105 mm (n=1448) and males ranged from 124 to 925 mm (n=2276; Fig. 2). East coast females were usually larger than west coast females (Fig. 2). East coast females ranged in length from 448 to 1105 mm (n=683), and west coast females ranged from 397 to 1032 mm (n=765; Fig. 2). East coast males ranged in length from 124 to 908 mm (n=1258) and west coast males ranged from 129 to 925 mm (n=1018; Fig. 2). The sex ratio (male to female) of the sample from the east coast (EC) was 1.8:1 and from the west coast (WC) was 1.3:1, significantly skewed towards males on both coasts (EC: χ^2=85, df=1, P<0.01; WC: χ^2=36, df=1, P<0.01). The length-length and length-weight regressions for common snook on each coast were significantly different (P<0.05); the relationship between SL, FL, and TL are presented in Table 1.

Age and growth

Common snook annuli are formed once each year, usually during late winter or spring. We recaptured 80 common snook that had been previously injected with OTC. At recapture, these fish ranged in length from 360 to 960 mm and ranged in age from 2 to 14 years. OTC-injected individuals were at large from 4 to 2505 days. All of the recaptured common snook that were at large long enough to have formed an annulus (n=51) showed the expected pattern of annulus formation: one per year. The fish at large for the longest period was 2 years old when it was injected and was recaptured 2505 days later (Fig. 3). This fish had formed seven annuli after the OTC mark and had been at large for 6 years and 11 months; thus the rate of annulus formation was consistent with our predicted rate of one annulus per year. The oldest fish recaptured was 8 years old when injected and was recaptured 5 years and 10 months later, at age 14. This fish had formed six annuli after the OTC mark.

Monthly patterns in marginal increments were also consistent with the formation of a single annulus each year. We plotted the monthly mean percentage of fish whose oto-

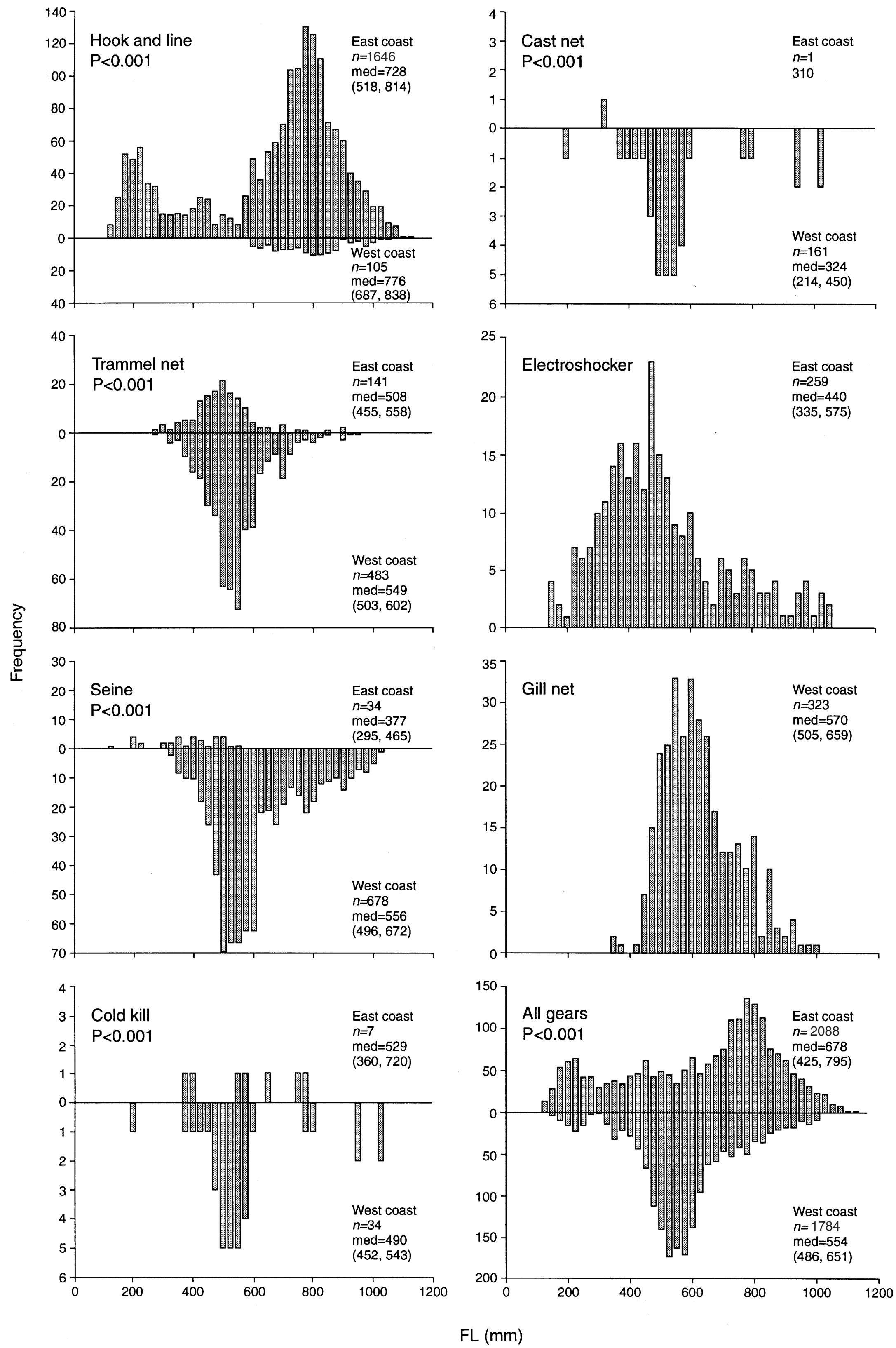

Figure 1

Length distributions, by gear type and coast, of common snook, *Centropomus undecimalis*, collected from South Florida waters during 1986–90. Med = median, numbers in parentheses are the 25th and 75th quartiles, and *P* is the Kolmogorov-Smirnov test value that compares the cumulative distribution of the two samples.

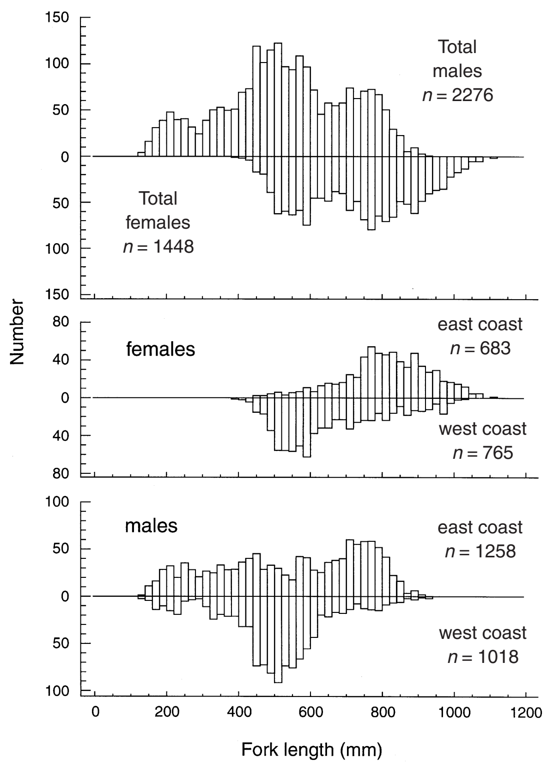

Figure 2

Lengths of male (n=2276) and female (n=1448) common snook, *Centropomus undecimalis*, sampled from South Florida waters.

liths had an annulus on the edge. The greatest percentages occurred during March–May of each year, confirming that annuli are formed then (Fig. 4). A cyclic annual pattern of margin deposition was consistent for common snook of all ages: three inclusive groups, with data pooled sufficient to reveal trends, showed a consistent annual cycle of narrowest margins during March–May and widest margins during late fall and early winter. By June, annulus formation was completed (Fig. 4).

Of the 3883 sectioned otoliths that we examined, 369 (9.5%) were rejected because of disagreements among readings. The length-frequency distribution of fish whose otoliths were rejected because they were unsuitable for age estimation was not significantly different from that of fish whose otoliths were readable (Kolmogorov-Smirnov two-sample test, two-sided test statistic=1.344, P=0.054).

Ages estimated from whole otoliths were significantly less than those estimated from sectioned otoliths (paired t-test, t=4.595, P<0.001). In addition, the slope of the regression of whole-otolith annulus counts on sectioned-otolith annulus counts was 0.873 (SE=0.014), which was significantly less than 1 (t-test=8.75, P<0.001; Fig. 5). Discrepancies between the ages estimated from the two structures were as great as five years, but usually the ages determined from whole otoliths were underestimated by 1–2 years for fish older than 10 years. Ages determined from the two structures agreed for 123 fish, whole-otolith-derived ages were greater for 15 fish, and sectioned-otolith-derived ages were greater for 72 fish. The oldest fish aged from the sectioned otoliths was estimated to be 21 years old and the oldest fish aged from whole otoliths was estimated to be 19 years old.

Table 1

The relationships between standard length, fork length, and total length and between length and weight of common snook, *Centropomus undecimalis*, from South Florida waters off the east and west coasts of Florida. TL = total length (mm), FL = fork length (mm), SL = standard length (mm), WT = whole weight (g). The fork length range for all length-length regressions was 112–1105 mm and for the length-weight regression was 124–1105 mm. Coast was a dummy variable equal to 1 for the east coast and 0 for the west coast used in the original regressions where both coasts were pooled, but only the simplified, two-parameter, coast-specific equations are presented here.

$Y = a + bX$ Y	X	n	Coast	a	b	r^2
SL	FL	2416	east	–5.7186	0.8990	0.998
SL	FL		west	–14.7684	0.9338	
SL	TL	2023	east	–15.4246	0.8564	0.998
SL	TL		west	–21.8457	0.8566	
FL	SL	2416	east	7.1198	1.1109	0.998
FL	SL		west	20.0876	1.0630	
FL	TL	3343	east	–10.8259	0.9526	0.999
FL	TL		west	–14.8606	0.9512	
TL	SL	2023	east	19.3639	1.1652	0.998
TL	SL		west	26.5459	1.1648	
TL	FL	3343	east	11.826	1.0490	0.999
TL	FL		west	16.2241	1.0502	
$\log_{10}WT$	$\log_{10}FL$ 2919		east	–5.0821	3.0434	0.976
$\log_{10}WT$	$log_{10}FL$		west	–5.3564	3.1117	

Because scales were difficult to interpret, we were unable to obtain consistent readings. Ages determined from scales were always younger than ages determined from sectioned otoliths by 1 to 3 years for snook less than 10 years. We were unable to reach agreement for the ages of the ten older snook whose structures were compared. Because of the difficulties in interpreting the banding patterns on scales, we did not attempt to analyze counts derived from scales.

The oldest common snook in our sample was a 21-year-old, unsexed (i.e. sex not determined), east coast fish that was 890 mm long (Table 2). This fish was identified as a male in the field but because no gonad sample was taken, we could not confirm the sex of the fish by histological analysis; consequently, we considered the fish to be of undetermined sex in all analyses. The oldest east coast male, other than the unconfirmed 21-year-old fish, was 15 years old (865 mm); the largest east coast male was 908 mm long and 11 years old. The oldest east coast female was 18 years old (1025 mm), and the largest east coast female was 1105 mm long and 16 years old (Table 2). The oldest west coast male was 12 years old (810 mm), and the largest west coast male was 925 mm long and 4 years old. The oldest west coast female was 15 years old (982 mm), and the largest west coast female was 1032 mm long and 10 years old (Table 3).

Common snook grew rapidly until age 5–7 years after which growth slowed considerably (Fig. 6). The most abundant age classes of males were from 2 to 7 years old and those of females were from 3 to 8 years old (Tables 2 and 3). Only 10 east coast specimens were estimated to be older than 16 years, and no west coast fish were older than 16 years. The smallest and youngest female was a 397-mm west coast fish estimated to be 1 year old (Table 3). On the east coast, the smallest and youngest female was a 448-mm fish estimated to be 2 years old (Table 2). The sex-specific age-frequency distributions for the two coasts were significantly different, and east coast fish were older overall than west coast fish (Kolmogorov-Smirnov two-sample, $P<0.05$). The coast-specific differences in age were more pronounced for females than for males (Table 2, Fig. 2).

The von Bertalanffy growth models suggest that east coast fish grow more rapidly than do west coast common snook (Fig. 6, Table 4). Results of likelihood-ratio tests showed a significant difference in the overall von Bertalanffy growth models for east coast and west coast snook (χ^2=284.90, df=3, $P<0.001$). East coast estimates of K = 0.24, (95% confidence interval=0.22–0.25) and t_0 = –0.10 (95%CI=–0.01–(–0.19)) were significantly different from west coast estimates of K=0.18 (95% CI=0.14–0.21) and t_0 = –1.35 (95% CI=–1.68–(–1.01)), ($P<0.005$, $P<0.001$, respectively). The east coast estimate of L, 989 mm (95% CI=966–1012) and 947 mm (95% CI=884–1010) for west coast fish were similar (P=0.342). For fish ages 1–2, the observed lengths at age of west coast fish were greater than those of east coast fish, but for fish in most of the older age classes, lengths of east coast fish were greater (Tables 2 and 3). Lengths at age predicted from the von Bertalanffy growth model for ages 0–2 were greater for west coast fish than for east coast fish, but those for all older age classes were greater for east coast fish than for west coast fish.

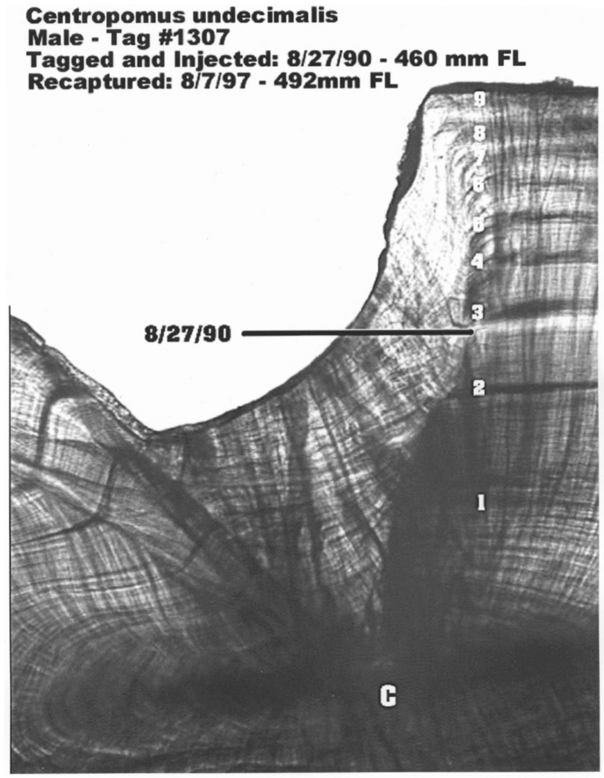

Figure 3

A transverse section of an otolith from an age-9 common snook, *Centropomus undecimalis*, that was injected with oxytetracycline (OTC) on 27 August 1990 and released at the entrance to Bishop's Harbor in lower Tampa Bay, Florida. The fish was recaptured 6 years and 11 months later at the same location and had formed seven annuli between the OTC mark and the otolith's edge.

Maturation and sex transition

Common snook present biological characteristics that are consistent with protandric hermaphroditism. We examined 27 wild-caught specimens that we considered were at the transitional-sex stage on the basis of simultaneous presence in the gonad of ovigerous lamellae and remnants of the dorsal sperm ducts that contained sperm. The mean length and age of these transitional-sex-stage common snook were 515 mm and 3.4 years. They ranged in length from a 240-mm, 1-year-old male specimen that had a prodigious number of ova in the peripheral portions of the testis, to an 824-mm, 7-year-old female with residual sperm in remnant sperm ducts. All ovaries, transitional and otherwise, contained remnants of the major dorsal sperm ducts, regardless of season or reproductive condition (Fig. 7). In addition, transitional gonads contained degenerating spermatogenic and developing ovarian tissue

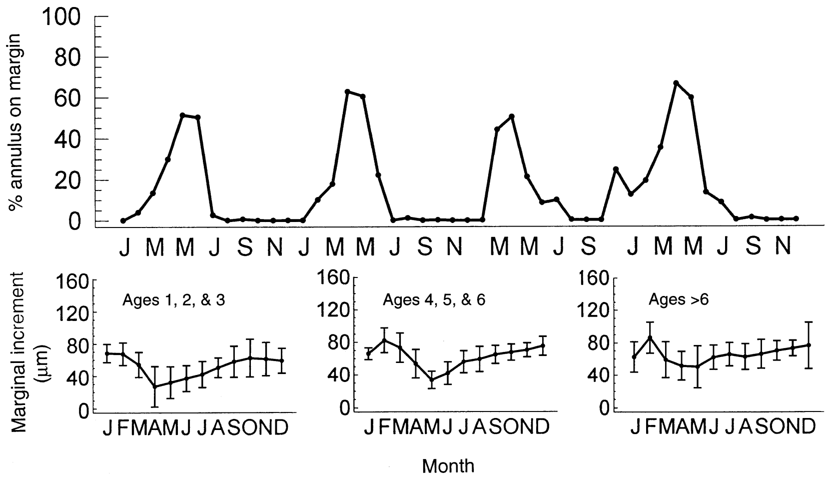

Figure 4

Percentage, by month, of otoliths with an annulus on the edge and mean monthly marginal increments with standard errors for all age classes pooled into three groups for common snook, *Centropomus undecimalis,* from south Florida waters.

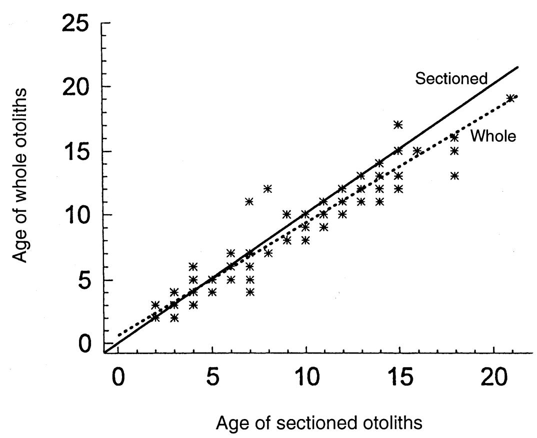

Figure 5

The relationship between annulus counts determined from sectioned and whole otoliths. The regression equation is $WO = 0.499 + SO \times 0.874$, where WO is the annulus count from whole otoliths and SO is the annulus count from sectioned otoliths (r^2=0.949, n=199).

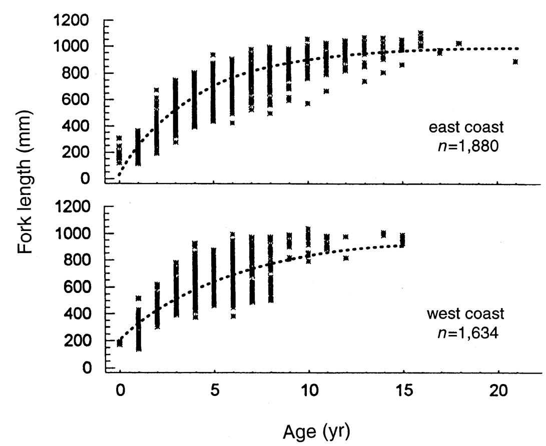

Figure 6

The von Bertalanffy growth curves for common snook, *Centropomus undecimalis*, from the east and west coasts of Florida. Parameter estimates are given in Table 4.

(Fig. 8). Most (74%) transitional-sex-stage fish were captured during September–November, shortly after the end of the spawning season, suggesting that sex reversal of postspawning males takes place shortly after spawning. The small number of transitional-sex-stage fish in our sample suggests that sex reversal occurs quickly.

During the 13-month experiment designed to document sex reversal, three males changed into females. The 137 four-year-old fish whose sex we monitored were initially sexed in July 1995 and ranged in length from 445 to 608 mm (mean=508 mm). In September 1995, we sexed the fish again and found that the largest individual (tag no. 96-344C, 617 mm) had completed sex reversal and that its ovary contained early vitellogenic oocytes. We examined these fish a final time on 17 August 1996 and found that they ranged in length from 467 mm to 649 mm (mean=534 mm). Two additional fish that were 622 mm (tag no. 10685C) and 584 mm (tag no. 13CB03) long had reversed sex, and their ovaries contained nonvitellogenic oocytes. The largest fish, a male, (tag no. 13BC2E) was

Table 2

Average observed and predicted (von Bertalanffy) fork lengths (mm) of east coast sexed and unsexed common snook, *Centropomus undecimalis*, and average observed lengths of females and males. The average observed length at age includes some seasonal growth that occurred after the formation of the final annulus. Values in parentheses are standard error and sample size.

Age (yr)	All snook		Females	Males
	Average observed	Predicted	Average observed	Average observed
0	185 (10.1;17)	22		228 (21.8;5)
1	211 (3.2;266)	225		231 (3.9;166)
2	359 (7.7;131)	385	580 (46.6;4)	357 (6.9;122)
3	514 (7.7;230)	511	644 (10.5;44)	484 (7.6;186)
4	629 (7.0;268)	611	695 (9.2;85)	597 (8.5;179)
5	698 (6.1;310)	690	760 (7.5;114)	661 (7.5;194)
6	755 (6.4;209)	753	809 (5.9;95)	711 (8.8;114)
7	792 (7.3;127)	802	841 (7.5;58)	748 (9.3;68)
8	820 (9.5;104)	841	874 (8.0;60)	747 (13.4;44)
9	849 (10.1;71)	872	902 (8.7;37)	782 (11.7;31)
10	903 (12.5;42)	897	936 (8.5;29)	807 (26.1;11)
11	911 (13.5;30)	916	943 (9.8;20)	832 (23.8;9)
12	948 (15.6;19)	932	973 (13.0;15)	854 (16.8;4)
13	959 (18.3;20)	944	989 (13.0:15)	832 (30.5;4)
14	960 (28.5;8)	953	994 (20.3;6)	857 (48.5;2)
15	987 (22.6;7)	961	1007 (11.8;6)	865 (1)
16	1048 (19.2;5)	967	1048 (19.2;5)	
17	961 (10.0;2)	971	961 (10.0;2)	
18	1024 (1.5;2)	975	1024 (1.5;2)	
19	978			
20	980			
21	890 (1)	982		

608 mm in 1995 and grew to be the largest fish in the study in 1996 (649 mm) but did not reverse sex. At the end of the experiment, the two fish that had reversed sex were the second-and third-largest snook.

Common snook sex ratios and length-frequency distributions were consistent with a diagnosis of protandric hermaphroditism. The overall sex ratio (male to female) for fish on both coasts, over the entire size range, was 1.6:1.0, significantly different from the expected 1:1 (χ^2=184, df=1, P<0.001). Females smaller than 500 mm were uncommon (4.63% of total observed), and only one female smaller than 400 mm was captured. Logistic curves were used to describe length- and age-related shifts in the common snook sex ratio. The predicted length at which 50% of the fish in the population were females was 767 mm on the east coast and 608 mm on the west coast (Fig. 9, Table 5). The predicted age at which 50% of the fish in the population were females was 7.4 years on the east coast and 5.1 years on the west coast (Fig. 9, Table 5).

Males reached sexual maturity at 150–200 mm on both coasts. The smallest mature east coast male was 175 mm long and the smallest mature west coast male was 152 mm long. The youngest mature male on both coasts was age 0. Our sample contained only 13 immature east coast males and 60 immature west coast males.

Discussion

We sampled common snook from a variety of fishery-independent and fishery-dependent sources. Some specimens were donated by recreational anglers, and others were caught by biologists using hook-and-line gear. We also used trammel and gill nets and haul seines to capture fish. On the east coast, most of the large common snook we sampled were caught by hook and line during the spawning season from spawning aggregations. In contrast, most west coast samples were collected with seines and trammel nets, and we did not regularly sample west coast spawning aggregations. We cannot quantify the potential biases resulting from the use of these different types of gears and sample sources, but our east coast material may have been biased towards larger fish because larger more aggressive individuals were harvested with hook and line. Our finding on the east coast of larger and older common snook and of larger observed and predicted lengths at age for most age classes

Table 3

Average observed and predicted (von Bertalanffy) fork lengths (mm) of west coast sexed and unsexed common snook, *Centropomus undecimalis*, and average observed lengths of females and males. The average observed length at age includes some seasonal growth that occurred after the formation of the final annulus. Values in parentheses are standard error and sample size.

Age (yr)	All snook: Average observed	All snook: Predicted	Females: Average observed	Males: Average observed
0	179 (7.0;2)	200		179 (7.0;2)
1	272 (8.0;106)	320	460 (32.5;4)	264 (7.4;102)
2	442 (4.3;186)	421	487 (6.4;44)	428 (4.6;142)
3	521 (3.4;359)	505	548 (4.6;177)	494 (4.2;182)
4	587 (5.0;332)	576	623 (7.2;157)	555 (6.1;175)
5	625 (6.2;220)	636	664 (8.8;106)	589 (7.1;114)
6	651 (7.9;226)	686	720 (10.6;102)	594 (8.5;124)
7	719 (12.6;125)	728	796 (14.2;64)	637 (15.2;61)
8	751 (23.4;40)	763	827 (25.5;23)	647 (27.6;17)
9	928 (18.1;9)	793	928 (18.1;9)	
10	926 (24.7;10)	818	969 (15.1;7)	826 (19.1;3)
11	927 (12.0;10)	838	931 (12.6;9)	891 (1)
12	891 (81.0;2)	856	972 (1)	810 (1)
13	871			
14	995 (7.7;3)	883	995 (7.7;3)	
15	953 (12.6;4)	893	953 (12.6;4)	

Table 4

Parameter estimates of the von Bertalanffy growth model for common snook, *Centropomus undecimalis*, collected from the waters of South Florida. Values in parentheses are standard errors.

	n	L (mm FL)	K	t_0	Adjusted r^2
East coast	1880	989.3 (11.64)	0.235 (0.0076)	–0.0976 (0.04447)	0.835
West coast	1634	947.3 (32.15)	0.175 (0.0155)	–1.352 (0.1714)	0.610

Table 5

Relationships of percent female to fork length (mm) and age (years) for common snook, *Centropomus undecimalis*, from South Florida waters. *FL* = fork length (mm) and *Age* = age (years). P_{50} = the absolute value of $(a+b)/c$, which is the inflection point of the curve and is the length or age predicted by the logistic regression at which 50% of the common snook in our sample were females. Coast is a dummy variable equal to 1 for the east coast and 0 for the west coast. PD is the adjusted percentage of deviance explained by the model.

	Percent female = $e^{(a+b(coast)+cX)}/(1 + e^{(a+b(coast)+cX)})$					
X	n	a	b	c	PD	P_{50}
FL	3723	–5.713 (0.2114)	–1.495 (0.1006)	0.0094 (0.00035)	0.269	767 mm east coast 608 mm west coast
Age	3380	–1.578 (0.0900)	–0.705 (0.0778)	0.307 (0.0171)	0.093	7.4 years east coast 5.1 years west coast

may reflect sampling bias rather than a true difference in the maximum fish sizes reached on the two coasts.

Other comparative studies on two inshore (Florida) Sciaenidae species also have found that east coast fishes attain greater sizes or grow at faster rates than do west coast fishes (Murphy and Taylor, 1990; Murphy and Taylor, 1994). Although gear biases may have confounded growth differences in these comparative studies, there is some basis for physiological differences in common snook. Tringali and Bert (1996) have provided evidence that common snook in Florida comprise two genetically different populations: one population in Atlantic waters and one in Gulf waters. They have reported that mtDNA divergence, both in haplotype diversity and in nucleotide sequence, supports the hypothesis that the two populations are reproductively isolated, which may account for a portion of the observed differences in biological parameters.

Age and growth

Our findings suggest that scales and whole otoliths may not be suitable for aging common snook older than 6–9 years, the point at which our length-at-age data began to reach an asymptote. Ages derived from whole otoliths were reasonably accurate for snook younger than about 10 years, but ages of older snook were consistently underestimated. Furthermore, whole otoliths were more difficult to read than sectioned otoliths and therefore readers' counts from whole otoliths often varied, principally because the closely spaced annuli on the edge of whole otoliths were difficult to differentiate. Our observations of common snook scales led us to conclude that they were not suitable for use in age estimation. Whole-otolith–derived estimates of longevity reported by Volpe (1959) and scale-derived estimates by Thue et al. (1982) of 7–8 years are considerably less than our sectioned-otolith–derived estimate of 21 years. Both Volpe (1959) and Thue et al. (1982) examined fewer fish than we did; therefore their samples would be expected to contain fewer old individuals than ours did. Their samples were also collected many years before ours, and additional regulations have been imposed on the fishery since their studies; however, the magnitude of the discrepancies in ages between our study and theirs is so great that we suspect they underestimated the ages of many fish. Thue et al. (1982) reported von Bertalanffy growth parameters for common snook, but their growth model did not reach an asymptote; consequently, their estimate of $L = 1615$ mm for combined sexes is much greater than our estimate for either coast and is far larger than the length reported for any common snook. We suspect that their growth curve did not reach an asymptote because they consistently underestimated the ages of old common snook.

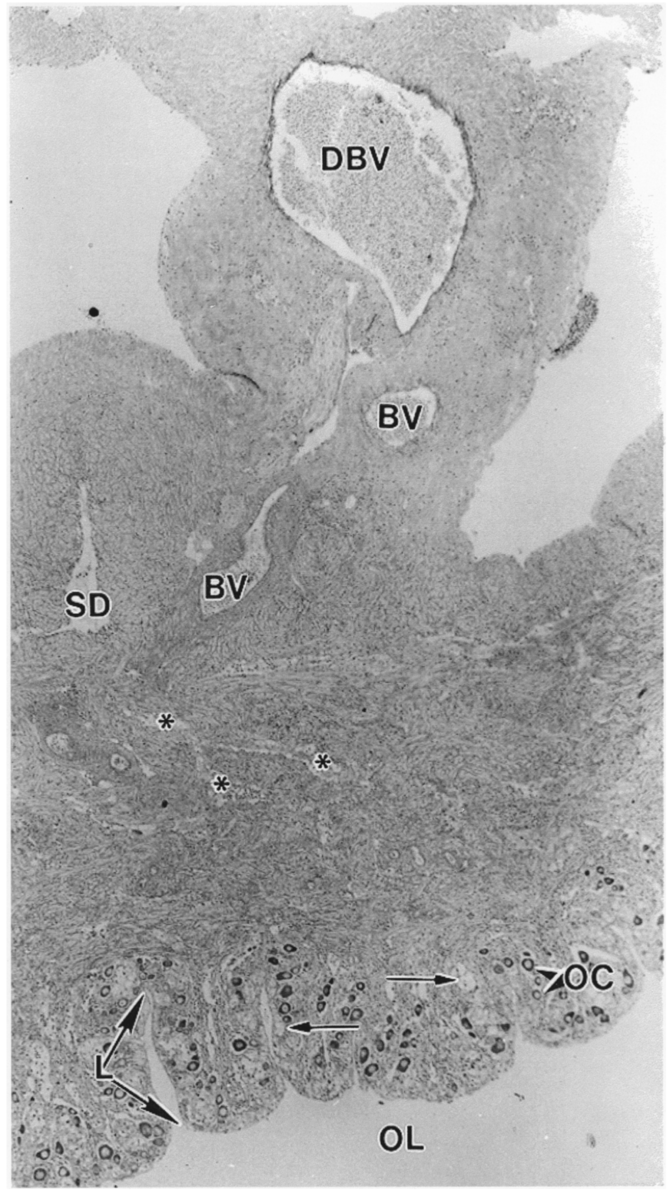

Figure 7

A histological section from a transitional-sex-stage common snook, *Centropomus undecimalis* (632 mm FL), captured in lower Tampa Bay in July 1989. Remnants of the major sperm duct (SD) and collecting tubules (*) are present in the dorsal matrix. Located throughout the peripheral ovigerous lamellae (L) are female germ cells that are either primary growth oocytes (OC) or meiotic and interphase oogonia (arrows). The dorsal (DBV) and lateral (BV) blood vessels are distinguished from the sperm ducts by the presence of red blood cells. OL = ovarian lumen.

Growth data for common snook in our study fitted the von Bertalanffy model well. The poor fit at age 0 for the east coast is explained by the collection of young-of-the-year fish in April and May, just prior to their first birthday when they were longest at age. The asymptotic values of

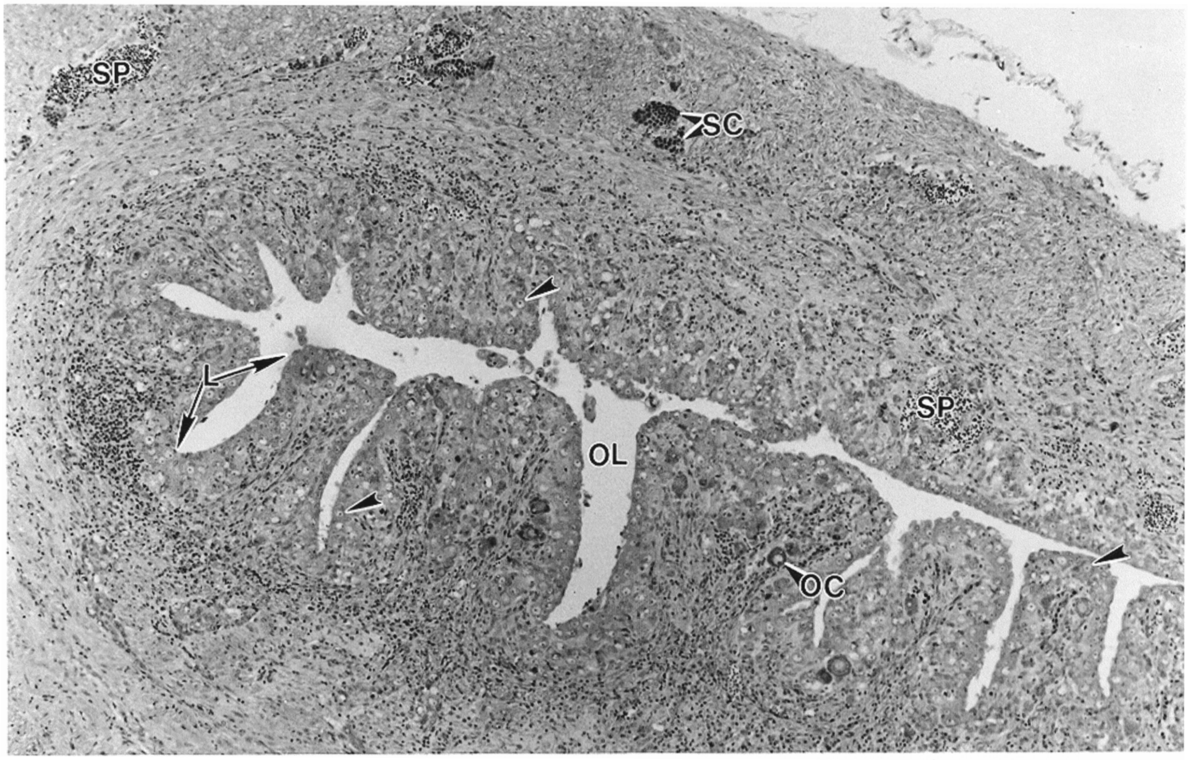

Figure 8

A histological section from a transitional common snook, *Centropomus undecimalis* (474 mm FL), captured in lower Tampa Bay in September 1989. Cysts that contain sperm (SP) and spermatocytes (SC) are visible in the peripheral wall of the gonad. Central lamellae (L) contain primary growth oocytes (OC) in addition to clusters of meiotic and interphase oogonia (arrow). OL = ovarian lumen.

approximately one meter may be a result of the difficulty of sampling large robust snook; trophy-size individuals are not uncommon in Florida and snook 1155–1194 mm are recorded (IGFA, 1998).

Maturation and sex transition

We based our determination that common snook are protandrous hermaphrodites on the following criteria presented by Sadovy and Shapiro (1987): 1) sex ratios shifted from exclusively male to predominantly female with increasing size and age, 2) transitional-sex-stage individuals were observed whose gonads contained both degenerating spermatogenic and developing ovarian tissue, and 3) sex change was documented in captive fish. Common snook have not previously been diagnosed as protandrous hermaphrodites, but another centropomid, the barramundi *Lates calcarifer*, has been diagnosed as a protandric hermaphrodite (Moore, 1979; Davis, 1982).

The male-to-female sex ratios previously reported for southwest Florida common snook (e.g. Volpe 1959, Thue et al.,1982), are similar to ours, with the exception of those reported by Marshall (1958). Thue et al. (1982) reported a 3:1 sex ratio for common snook smaller than about 500 mm and younger than age 2 in the Everglades National Park and a sex ratio 1:11 for common snook larger than 800 mm and older than age 8. Volpe (1959) reported a similarly skewed sex ratio of 1:3 for fish larger than 800 mm from southwest Florida. These shifts in the common snook sex ratio with increasing length and age are consistent with our diagnosis of protandrous hermaphroditism. In contrast, Marshall (1958) found that there were more females than males smaller than 500 mm (1.0:1.1) and that the overall sex ratio for common snook in southwest Florida was not significantly different from 1:1. It is possible that Marshall (1958) did not observe the actual sex ratio of the population he studied because 288 of the 531 total specimens in his sample had been gutted and were not included in the analysis.

Male common snook reach sexual maturity at surprisingly small lengths and ages, some at lengths less than 200 mm. We considered a fish to be sexually mature if mature sperm were present in the testis. According to this criterion, immature males made up <2% of our sample. Furthermore, most of the males we classified as immature were caught outside of the spawning season, and we may have misclassified some regressed mature fish as immature. Because our sample contained so few males that we could be certain were immature, we did not attempt to fit a logistic function to male maturity. The small mature

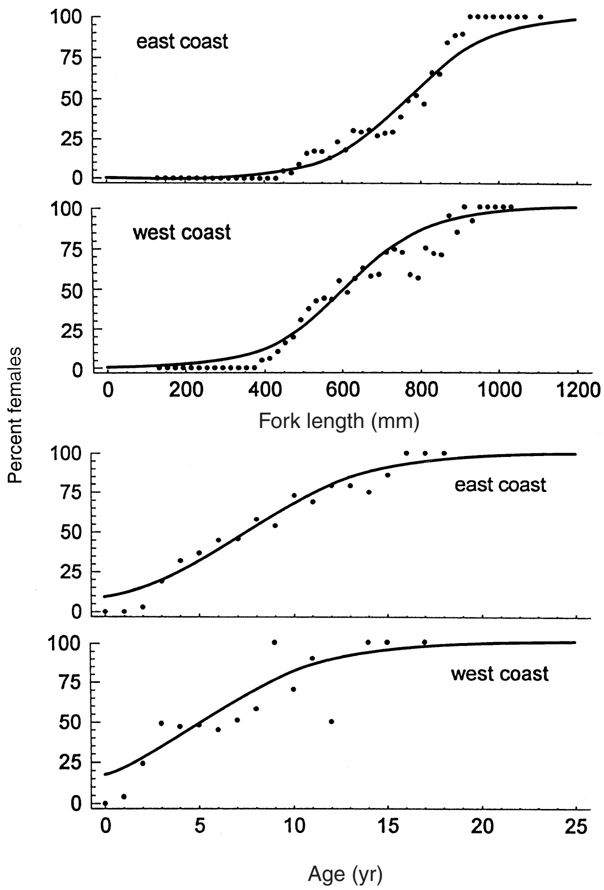

Figure 9

Logistic curves describing the percentage of females of common snook, *Centropomus undecimalis*, as a function of fork length (east coast n=1940, west coast n=1783) and age (east coast n=1742, west coast n=1638).

males we observed were smaller than those observed by previous workers; however, previous studies of maturation were based only on a macroscopic examination of gonads. Marshall (1958) examined 239 common snook from southwest Florida and concluded that 50% of the specimens of both sexes were mature at 400 mm and that all common snook, with few exceptions, were mature at 500 mm. Volpe (1959) used Marshall's lengths-at-maturity data to estimate the age at first maturity to be 3 years. It is unclear whether the small males we observed were spawning males, but they appeared to be capable of spawning; therefore we considered them to be sexually mature. Common snook typically spawn in large aggregations near passes and inlets (Taylor et al., 1998). We did not observe males smaller than 350 mm in spawning aggregations, and most spawning males were longer than 400 mm; however, we can not eliminate the possibility that some spawning involved smaller males outside these large aggregations. Additional research is needed to determine whether or not these small, precocious males are active members of the spawning population.

We considered all female common snook to be sexually mature on the assumptions that they develop directly from males that had previously spawned, that sex transition occurs shortly after spawning, and that they would be capable of spawning as females during the next spawning season. Among other centropomids, *L. calcarifer* also undergoes sex change near the end of the spawning season (Davis, 1982; Guiguen et al., 1994). Davis (1982) found that in *L. calcarifer,* oocytes first appear as the testes ripen for the final time and that sex reversal is completed shortly after spawning. This finding is consistent with our observations of common snook. Most transitional-sex-stage individuals were captured during September–November; we did not observe any transitional fish from April to June and only one transitional fish in February and one in March. Sex reversal appears to occur quickly and shortly after spawning, and we found no evidence to suggest that females do not spawn during their first spawning season after transition from male to female. This conclusion is supported by the captive fish that completed sex reversal and developed vitellogenic oocytes in only two months. Management decisions based on length and age at maturity of females should more appropriately focus on the size and age at sex transition, and all females should be included in estimates of spawning stock biomass.

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