Abstract-We examined 536 permit (Trachinotus falcatus, 65-916 mm FL) collected from the waters of Florida Keys and from the Tampa Bay area on Florida's Gulf coast to describe their growth and reproduction. Among permit that we sexed, females ranged from 266 to 916 mm in length (mean=617) and males ranged from 274 to 855 mm (mean=601). Ages of 297 permit ranging from 102 to 900 mm FL were estimated from thin-sectioned otoliths (sagittae). The large proportion of otoliths with an annulus on the margin and an otolith from an OTC-injected fish suggested that a single annulus was formed each year during late spring or early summer. Permit reach a maximum age of at least 23 years. Permit grew rapidly until an age of about five years, and then growth slowed considerably. Male and female von Bertalanffy growth models were not significantly different, and the sexes-combined growth model was $FL=753.1(1-e^{-0.348(Age+0.585)})$. Gonad development was seasonal, and spawning occurred during late spring and summer over artificial and natural reefs at depths of 10-30 m. Ovaries that contained oocytes in the final stages of oocyte maturation or postovulatory follicles were found during May-July. We estimated that 50% of the females in the population had reached sexual maturity by 547 mm and an age of 3.1 years and that 50% of the males in the population had reached sexual maturity by 486 mm and an age of 2.3 years. Because Florida regulations restrict the maximum size of permit caught in recreational and commercial fisheries to 20-inch (508-mm), most fish harvested are sexually immature. With the current size selectivity of the fishery, the spawning stock biomass of permit could decrease quickly in response to moderate levels of fishing mortality; thus, the regulations in place in Florida to restrict harvest levels appear to be justified.

Manuscript accepted 19 July 2001. Fish. Bull. 100:26–34 (2002).

Age, growth, and reproduction of permit (*Trachinotus falcatus*) in Florida waters

Roy E. Crabtree Peter B. Hood Derke Snodgrass

Florida Marine Research Institute Florida Fish and Wildlife Conservation Commission 100 Eighth Avenue SE St. Petersburg, Florida 33701-5095 Present address (for R. E. Crabtree): Division of Marine Fisheries Florida Fish and Wildlife Conservation Commission 620 Meridian St. Tallahassee, Florida 32399-1600

E mail address (for R. E. Crabtree): crabtrr@gfc.state.fl.us

The family Carangidae supports a diverse array of economically important fisheries in tropical and subtropical waters worldwide. In the southeastern United States, many carangid stocks are managed at both the state and Federal level. Recently, the National Marine Fisheries Service determined that the Gulf of Mexico greater amberjack stock is overfished, but the status of most carangid stocks is unknown (Anonymous¹). For most carangid stocks, no quantitative stock assessments have been completed, in part, because little biological information exists regarding carangid growth rates and reproduction. As a result, the adequacy of current management measures to prevent overfishing of many carangid stocks is unclear.

Permit, Trachinotus falcatus, are the basis of an important recreational fishery and a small commercial fishery in Florida. Estimates of Florida recreational landings are unreliable but may exceed 100,000 fish per year (Armstrong et al.²). Commercial landings of permit peaked in 1991 at 200,000 pounds and then decreased to 50,000 pounds in 1995 (Armstrong et al.²). Current regulations in Florida include a 10-inch (254-mm FL) minimum size limit and a 20-inch (508-mm FL) maximum size limit on both the recreational and commercial harvest. In addition, recreational anglers are permitted daily to take 10 permit per bag of combined permit and Florida pompano (Trachinotus car-

olinus). Many anglers pursuing permit do so with professional guides on a charter vessel. In addition to being popular in South Florida, permit are targeted by numerous fishing tourists and recreational anglers in the Bahamas and at locations throughout the Caribbean. Despite the economic importance of permit in these regions, there are no published reports describing growth, longevity, or length and age at sexual maturity. Such information is needed to evaluate the effects of fishing mortality on permit populations. Previous studies of permit life history by Fields (1962) and Finucane (1969) were based only on an examination of larvae and young-of-the year permit. Our study describes growth, longevity, and the length and age at which fish become sexually mature. In addition, we document spawning of permit in South Florida waters based upon a histological examination of ovaries and seasonal patterns in the abundance of juveniles.

¹ Anonymous. 2001. Report to Congress: status of fisheries of the United States, 122 p. National Marine Fisheries Service, 1315 East-west Highway, Silver Spring, MD, 20910.

² Armstrong, M. P., P. B. Hood, M. D. Murphy, and R. G. Muller. 1996. A stock assessment of permit, *Trachinotus falcatus*, in Florida waters. Unpubl. rep. to the Florida Marine Fisheries Commission. Florida Marine Research Institute, 100 Eighth Avenue SE, St. Petersburg, Florida 33701-5095.

Methods

Collections

Permit that we examined were collected from the Florida Keys (n=308; between 25°40′N, 80°10′W and 24°30′N, 82°20′W) during 1995–97 and the Tampa Bay area (n=228; 27°40′N, 82°45′W) during 1990–95. Most Florida Keys permit were caught with hook-and-line gear (n=215) or speared (n=58) over artificial and natural reefs in the waters off the lower and middle Keys in depths ranging from 10 to 30 m. Other, usually smaller, permit were captured with gill nets (n=16), seines (n=18), and bottom trawls (n=1) over or near shallow banks adjacent to the Keys. Most of the permit sampled in the Tampa Bay area were small (<400 mm FL) and were captured with seines along sandy beaches; some larger Tampa Bay permit were captured with gill nets (n=53) or trammel nets (n=14).

Standard length (SL), fork length (FL), and total length (TL) were measured to the nearest millimeter (mm) and weight was measured to the nearest gram. Unless otherwise indicated, all lengths reported in our study are fork lengths. Otoliths (sagittae) were removed, rinsed in water, and stored dry until sectioned; they were later weighed to the nearest 0.01 mg. Gonad weight was recorded to the nearest gram (g), and gonad samples were removed from the fish and preserved in 10% buffered formalin; they were later soaked in water for 24 hours and stored in 70% ethanol.

Collections of juvenile permit from sandy beaches off Tampa Bay and the Florida Keys were made with a 21.3 imes1.8-m bag seine (6.4-mm mesh in the wings and 3.2-mm mesh in the bag). Seine hauls were made perpendicular to the beach for distances up to 50 m, depending on water depth. Lengths of up to 50 fish from each sample collection were measured to the nearest millimeter. Near Tampa Bay, we collected fish at the Gulf of Mexico beaches of Treasure Island (November 1992 –October 1994; 27°46'N, 82°46.5'W) and Indian Shores (August 1993-November 1994; 27°50'N, 82°50'W). Sampling at each site consisted of five seine hauls every two weeks. Six sandy beaches were sampled monthly in the Florida Keys from July 1994 to July 1997: Lower Matecumbe Beach (July 1994-April 1996; 24°50.95'N, 80°4415'W), Coco Plum Beach (July 1994-April 1996; 24°43.65'N, 81°00.10'W), Clarence P. Higgs Beach, Key West (July 1994–July 1997; 24°32.79'N, 81°47.26'W), Bahia Honda State Park (October 1994-May 1997; 24°39.81'N, 81°15.44'W), Boca Chica Beach (October 1994-April 1996; 24°33.60'N, 81°41.65'W), and Sugarloaf Beach (January 1995–May 1996; 24°36.57'N, 81°33.49'W).

Age and growth

The left sagitta was usually used for age estimation; however, if the left otolith was broken, lost, or destroyed during processing, the right otolith was substituted. We prepared otoliths for age estimation by embedding them in Spurr, a high-density plastic medium (Secor et al., 1992). A 1-mm to 2-mm-thick transverse section containing the otolith core was cut with a Buehler Isomet low-speed saw with a diamond blade. The section was mounted on a microscope slide with thermoplastic glue (CrystalBond 509 adhesive) and was polished with wet or dry sandpaper (grit sizes ranging from 220-2000) until annuli were visible. Sections were then polished on a Buehler polishing cloth with 0.05-gamma alumina powder to remove scratches. Without knowledge of fish size or capture date and using a compound microscope equipped with transmitted light, two readers independently counted annuli on each otolith twice. If three of the four readings agreed, then this mode was accepted as the annulus count. If three of the four readings did not agree, each reader again counted annuli independently and without knowledge of previous counts. If three of the resulting six readings agreed, then this mode was accepted as the annulus count. If there were not three readings that agreed, the otolith was excluded from further analysis. In six cases, two sets of three readings that were in agreement occurred. For these six otoliths the two sets of readings differed by only one annulus; therefore the mean was accepted as the annulus count.

The percentage of otoliths with an annulus on the edge was then plotted by month so that we could look for a seasonal pattern in annulus formation. We did not attempt to measure marginal increments because the margin of permit otoliths is highly sculptured and easily broken; however, we did believe that we could discern the presence of an annulus on the otolith's edge.

The von Bertalanffy (1957) growth equation $FL_t = L_{\infty}$ $(1-e^{-K(t-t_0)})$ was fitted to observed age-length data with nonlinear regression procedures. Age was esimated as the annulus count because permit both spawn and form annuli at about the same time of year. Our estimates of length at age include some seasonal growth that occurred after the formation of the final annulus. Length-weight regressions were calculated by linear regression of \log_{10} -transformed data.

Sex-specific growth models were compared with an approximate randomization test described by Helser (1996). This test is based on the premise that when the null hypothesis of no sex-specific differences in growth is true, a test statistic derived by random assignment of fish to one of two populations will not be different from that observed between sexes. The test statistic is calculated as the residual sums of squares for the sexes-combined von Berta-lanffy growth model minus the residual sums of squares for the two sex-specific models. A probability distribution of the test statistic was generated by a randomization routine with 1000 iterations of the nonlinear models. Only sexed fish were included in the statistical comparison.

Age validation

Permit used in the age-validation experiments were captured in waters off the Florida Keys with hook-and-line gear. After capture, permit were tagged with dart-type tags and injected with Liquamycin LA-200 (200-mg oxytetracycline [OTC]/mL) in the dorsal musculature at a dosage of about 100-mg OTC per kg fish weight. Permit were then held in a 33.5-m-long by 5.5-m-wide by 0.75-mdeep pond at the Florida Fish and Wildlife Conservation Commission's Keys Marine Laboratory in Long Key. Fish were held at ambient temperatures and were fed frozen shrimp and fish until satiated at least three times a week. Although several permit were injected and held for various periods, only one fish survived long enough to have formed an annulus after the OTC injection. The otolith section from this fish was examined with a compound microscope (40–100×) equipped with ultraviolet light so that the fluorescent OTC mark could be detected.

Reproduction

Histological sections of gonads were prepared and assessed for reproductive state. Gonad samples were prepared for histological examination with a modification of the periodic acid Schiff's (PAS) stain for glycol-methacrylate sections and with Weigert's iron-hematoxylin as a nuclear stain and metanil yellow as a counterstain (Quintero-Hunter et al., 1991).

Developmental stages of oocytes were determined and oocytes were counted from histological preparations at 100× with a compound microscope attached to a digital image-processing system. Four oocyte stages were recognized in permit ovaries: primary growth, cortical alveolar, vitellogenic, and oocytes in the final stages of maturation (Wallace and Selman, 1981). The final stages of oocyte maturation (FOM) included yolk coalescence, germinal vesicle migration, germinal vesicle breakdown, and hydration. We also counted postovulatory follicles (POFs) and PAS-positive melanomacrophage centers (Ravaglia and Maggese, 1995; Crabtree et al., 1997), which were present in many ovaries. When stained with the PAS stain, these PAS-positive structures are brilliant purple. Melanomacrophage centers are thought to be active in degrading atretic oocytes, postovulatory follicles, and residual cells of the spermatogenic cycle (Chan et al., 1967; Ravaglia and Maggese, 1995). The developmental stage of at least 300 oocytes and other structures on each slide was determined and counted in arbitrarily chosen fields, and frequencies were expressed as a percentage of the total count. We counted all oocytes that had at least 50% of their area visible in a field before moving to the next field.

We examined seasonal reproductive patterns by plotting monthly juvenile length frequencies and monthly mean gonadosomatic indices (GSIs). Gonadosomatic indices were calculated for 129 sexually mature female permit ranging in length from 476 to 916 mm and for 122 sexually mature male permit ranging in length from 449 to 855 mm as

GSI = (GW / (TW - GW))100,

where GW = total gonad weight (g); and TW = total fish weight (g).

Length and age at sexual maturity

Females were considered sexually mature if vitellogenic oocytes were present or if the histological sections appeared disorganized, highly vascularized, and contained widespread evidence of atresia. We followed the classification of Hunter and Macewicz (1985) in recognizing atresia. Most immature females had small well-organized gonads that contained little evidence of atresia. We interpreted the widespread occurrence of PAS-positive melanomacrophage centers in inactive ovaries as evidence of past gonadal development, and we considered permit with regressed (no vitellogenic oocytes present) ovaries that contained many of these structures to be sexually mature. Males were considered sexually mature if testes contained evidence of ongoing spermatogenesis, residual sperm, or widespread PAS-positive melanomacrophage centers associated with gonadal recrudescence. We estimated the length and age at which 50% of the fish in the population reached sexual maturity by fitting a logistic function to the percentage of fish that were sexually mature and to their respective lengths and ages. Regressions were performed with sex as a categorical effect. If sex was a significant effect, the equations were then reduced to separate sex-specific equations. The inflection point of the logistic curves was used as an estimate of the length or age at which 50% of the population had reached sexual maturity.

Results

Permit that we collected from waters off the Florida Keys ranged from 258 to 916 mm in length (*n*=308), and the permit collected from the Tampa Bay area ranged from 65 to 812 mm in length (*n*=228). Among permit that we sexed, females ranged from 266 to 916 mm in length (mean=617, SD=155.7, *n*=187) and males ranged from 274 to 855 mm (mean=601, SD=145.8, *n*=166; Fig. 1). The sex ratio of our sample was 1:1.1 (male:female) and was not significantly different from 1:1 (χ^2 test, *P*>0.05). Neither the slopes (*P*=0.464) nor the elevations (*P*=0.063) of the length-weight equations for male and female permit were significantly different. The pooled length-weight equation for sexed and unsexed fish was

 $\log_{10} WT = 2.803 \log_{10} FL - 4.078,$ (*n*=488, *r*²=0.996)

where WT = weight in grams; and FL = fork length in mm.

Age and growth

When viewed with transmitted light, permit otoliths have opaque (dark) annuli that alternate with translucent (light) zones (Fig. 2). Proceeding from the otolith's core towards the otolith's proximal margin, annuli are regularly spaced along the sulcal ridge. In some individuals, the annuli are indistinct and irregular in appearance, which made age estimation difficult. We considered 51 otoliths (17.3%) from permit ranging in length from 243 to 916 mm to be unreadable. The length-frequency distribution of fish whose otoliths were considered unreadable was not significantly different from that of fish whose otoliths were considered readable (Kolmogorov-Smirnov twosample test, D=0.144, P=0.32); thus, no particular length



group of fish was systematically excluded from the ageand-growth analysis.

Annulus formation in permit occurs during spring and early summer. The percentage of permit with an annulus on the otolith's margin was greatest during summer and least during October-March, suggesting that annulus formation is seasonal and that annuli first become visible during late spring or early summer (Fig. 3). A single OTC-injected permit was successfully held for a sufficient length of time to be useful in age validation. This fish was captured and injected with OTC on 17 June 1993. The fish was sacrificed on 30 January 1996 and measured 600 mm in length. After 31 months in captivity, which included two spring-summer periods, the fish had formed two annuli, a number that is consistent with our hypothesis that a single annual mark forms annually during late spring or early summer. Also visible immediately before the OTC mark was an annulus that was probably formed during late spring of 1993, just prior to capture and OTC injection. Moreover, there was a wide margin subsequent to the last annulus that is consistent with the six or more months of otolith growth after formation of the final annulus in late spring or early summer of 1995.

Estimated ages of 298 permit ranged from 0 to 23 years for fish 102 to 900 mm long. Permit grew rapidly until about age five, and then growth slowed considerably (Table 1, Fig. 4). Most of the fish in our sample were less than 10 years old, although fish 10–15 years old were common. The oldest permit examined was a 23-year-old (781-mm) male (Table 1). Estimates of von Bertalanffy growth model parameters are presented in Table 2. The growth models for male and female permit were not significantly different (approximate randomization test, P=0.059).

Sexual maturation

We estimated that 50% of the males in the population reached sexual maturity by 486 mm and an age of 2.3 years, and 50% of the females in the population reached sexual maturity by 547 mm and an age of 3.1 years (Table 3). The smallest sexually mature male in our sample was 449 mm long, and the youngest sexually mature male was 3 years old. Our estimate of the age at 50% maturity for males was less than the age of the youngest mature male observed. This knife-edge maturity curve could be an artifact of our small sample size. The smallest sexually mature female in our sample was 476 mm long, and the youngest sexually mature female was 3 years old. All of the ovaries we examined contained primary-growth-stage oocytes. Cortical alveolar-stage oocytes occurred only in ovaries from permit larger than 450 mm and older than 2 years and were common only among permit larger than 500 mm and older than 3 years. Vitellogenic oocytes were found only in ovaries from fish larger than 550 mm and older than 3 years and were common only among permit larger than 600 mm. The length and age at which vitellogenic oocytes were commonly found agrees well with our estimate of the length and age at which 50% maturity was



reached, suggesting that we misclassified few gonads with regression.

Spawning seasonality

Permit spawning appeared to be seasonal in the areas we sampled and occurred at least during May-July. We

examined 15 permit ovaries that contained either oocytes in the final stages of maturation or POFs, structures indicative of imminent or recent (<24 h) spawning. We usually did not know the time of day when fish were caught, but all fish were captured during daylight hours (0700–1700 h). Oocytes in the final stages of maturation were found during June and July, and POFs were found

Table 1

Average observed and predicted fork lengths (mm) of permit, *Trachinotus falcatus*. 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)	Sexes combined		Females		Males	
	Average observed	Predicted	Average observed	Predicted	Average observed	Predicted
0	160 (12.7;17)	139	277 (1)	212		149
1	301 (5.9;56)	319	310 (14.5;8)	353	334 (12.5;17)	337
2	476 (7.6;10)	447	479 (6.8; 8)	458	465 (33.5:2)	464
3	564 (10.1;27)	537	555 (12.1;13)	538	572 (15.9;14)	550
4	612 (6.3;28)	601	620 (9.8;14)	599	604 (7.6;14)	608
5	643 (8.7;29)	645	664 (13.8;10)	644	632 (10.5;19)	647
6	663 (8.7;26)	677	658 (10.7;20)	679	680 (9.3;6)	673
7	687 (12.0;17)	699	687 (10.8;9)	704	687 (23.6;8)	691
8	703 (16.9;12)	715	695 (22.7;7)	724	715 (27.4;5)	703
9	713 (15.1;21)	726	710 (26.8,11)	743	717 (13.3;10)	711
10	743 (30.0;6)	734	754 (34.2;5)	750	688 (1)	717
11	746 (21.8;12)	740	811 (25.3;4)	758	714 (23.2;8)	721
12	738 (35.3;5)	744	797 (0.5;2)	765	698 (46.9;3)	723
13	787 (19.4;9)	746	803 (26.2;6)	769	754 (15.7;3)	725
14	762 (19.5;13)	748	783 (12.8;7)	773	737 (38.9;6)	726
15	753 (13.4;4)	750	737 (1)	776	759 (17.3;3)	727
16		751		778		727
17		751		779		727
18	745 (48.5:2)	752	793 (1)	781	696 (1)	728
19		752		781		728
20	667 (1)	753	782		667 (1)	728
21	687 (1)	753	916 (1)	783	687 (1)	728
22		753		783		728
23	781 (1)	753	783		781 (1)	728

Table 2

Parameter estimates of the von Bertalanffy growth model for permit, *Trachinotus falcatus*, from South Florida waters. Values in parentheses are standard errors. FL = fork length.

Sex	n	<i>L</i> (mm FL)	K	t ₀	adjusted <i>r</i> ²
Females	127	784.2 (13.79)	0.28 (0.027)	-1.12 (0.249)	0.833
Males	123	728.2 (9.52)	0.39 (0.034)	-0.58 (0.168)	0.855
Combined	297	753.1 (7.12)	0.35 (0.015)	-0.59 (0.065)	0.921

during May–July (Fig 5). Vitellogenic oocytes were most plentiful during March–July and were absent during October–December. No samples were available for histological examination in January or February, but it seems



Mean percentage and standard error of permit (*Trachinotus falcatus*) otoliths with an annulus on the margin plotted by month. Numbers above the lines are the monthly sample sizes.

unlikely that spawning occurred during these months. Females with the greatest GSIs (>4%) were captured during March–August, and GSIs were least (<1.5%) during October–December (Fig. 6). Male GSIs were generally similar in magnitude to female GSIs and followed the same pattern.



In the Tampa Bay area, small permit (<40 mm) were present from June to November, suggesting that spawning extends into the fall. In the Florida Keys, small fish (<40 mm) were present all year, suggesting an extended spawning season, recruitment from other areas with different seasonal spawning patterns, or variable juvenile growth rates.

Discussion

We obtained permit from a variety of fishery-dependent and fishery-independent sources; consequently, our sample is biased towards certain size classes, and the bimodal size-frequency distribution of our sample probably does not reflect that of the population or the Florida harvest. All the small fish (<300 mm) we examined were from fishery-independent sources; most large fish were from fishery-depen-



Table 3

The relationship of percentage mature and fork length (mm) and the relationship of percentage mature and age (years) for permit, *Trachinotus falcatus*, from South Florida waters. FL = fork length (mm) and AGE = age (years). P₅₀ is the absolute value of ((a+b)/c), is the inflection point of the curve, and is the length or age predicted by the logistic regression at which 50% of the permit in our sample were sexually mature. Sex is a dummy variable equal to 1 for males and 0 for females. PD is the adjusted percentage of deviance explained by the model.

			Percent female = $e^{(a+b(sex)+cX)}/(1+e^{(a+b(sex)+cX)})$					
X	п	а	Ь	С	PD	P ₅₀		
FL	314	-30.41 (6.336)	3.34 (1.087)	0.056 (0.0114)	0.84	486 mm (males) 547 mm (females)		
AGE	233	-6.71 (0.878)	1.71 (0.576)	2.14 (0.238)	0.09	2.3 years (males) 3.1 years (females)		

dent sources, such as charterboats. We did not sample any permit from the commercial fishery, which principally targets smaller fish as a result of the maximum size limit of 20 inches (508 mm FL) for permit caught by commercial vessels. Armstrong et al.² reported that most harvested permit in Florida were <440 mm. In contrast, our sample contained many fish larger than 600 mm. The high proportion of large permit in our sample could reflect a tendency for charterboats in the Florida Keys to select larger permit than those selected by more typical anglers statewide. Armstrong et al.'s² assessment was based on more systematic and statewide sampling than ours, and the differences between their sample and ours probably reflects our attempt to obtain a sample of all available size classes rather than a representative sample of the Florida harvest.

Age and growth

The oldest permit in our sample was estimated to be 23 years old. Although we examined many relatively large permit, larger fish than those we examined have been caught. Robins (1992) reported that permit can reach 1100 mm FL and a weight of 23 kg; consequently, permit longevity probably exceeds our estimate of 23 years. There are no other estimates of age and growth of permit for comparison, but our longevity estimates are similar to those determined from sectioned otoliths for other carangids. Manooch and Potts (1997) aged greater amberjack and found fish as old as 17 years. The oldest carangid yet studied is the trevally, *Caranx georgianus*, reported to reach an age of 46 years (James, 1984). The much smaller Florida pompano has been reported to reach an age of 7 years (Hood et al.³).



Gonadosomatic indices (GSI, \star) and means (+) for sexually mature female and male permit, *Trachinotus falcatus*, plotted by month.

Our estimates of the von Bertalanffy growth model parameters are within the range of those reported for other carangids (James, 1984; Sudekum et al., 1991; Manooch and Potts, 1997). We found no significant differences between male and female von Bertalanffy growth models, but the significance level (P=0.059) was close enough to 0.05 to cause us to suspect that a difference might exist. Hood et al.³ also found no sex-specific differences in growth models for pompano.

Sexual maturation

We sampled relatively few permit between 300 and 500 mm long, the size at which sexual maturity is reached. The lack of fish in this critical size range resulted in the knifeedge maturity curves. Larger sample sizes are needed to derive more precise estimates of age and size at sexual maturity. In an assessment of the status of permit stocks in Florida, Armstrong et al.² assumed that permit mature at about 440 mm FL on the basis of limited biological data available at the time. Our estimates of length at 50% maturity are larger: 486 mm for males and 547 mm for females. As a consequence of Florida's 20-inch (508-mm) recreational and commercial maximum size limit, most of the permit harvested are sexually immature (Armstrong et al.²).

Spawning

We believe that permit spawn over artificial and natural reefs in the waters of the middle and lower Florida Keys because ovaries of fish caught over these structures contained oocytes in the final stages of maturation and POFs. Other researchers have inferred that permit spawn in nearshore waters from the capture of early-stage larvae (Fields, 1962; Finucane, 1969). Permit ovaries that contained fresh POFs and oocytes in the final stages of maturation also contained clutches of early- and mid-stage vitellogenic oocytes, suggesting that permit are multiplebatch spawners.

Spawning occurred at least during May–June in the Florida Keys during 1995–97. Juvenile length frequencies in the Keys suggest a more prolonged spawning season—perhaps even year-round spawning; however, the prolonged presence of small juveniles could also be attributed to variable juvenile growth rates rather than extended spawning. This question could be resolved by direct aging of juveniles to evaluate growth rates. Our sample of adult permit may have been too small to reveal low levels of spawning outside of spring and early summer, and no mature permit were collected during January or February. On the basis of seasonal occurrence of juveniles, Finucane (1969) suggested that permit spawn during April–June in the Tampa Bay area, but Fields (1962) found juveniles

³ Hood, P. B., D. T. Merryman, and D. J. Harshany. 1999. Age, growth, mortality, and reproduction of the Florida pompano, *Trachinotus carolinus*, from Florida waters. Unpubl. manuscript. Florida Marine Research Institute, 100 Eighth Avenue SE, St. Petersburg, FL.

year round suggesting a prolonged spawning period. Other carangids spawn during spring and summer: Caranx

ignobilis and Caranx melampygus spawn during May-August in Hawaii (Sudekum et al., 1991) and T. carolinus spawns during January-August in Florida (Hood et al.³).

Our data suggest that maturation occurs at greater lengths than assumed by Armstrong et al.²; however, even using our maturation data, their observation that most permit landed are sexually immature remains true. With the current selectivity of the fishery, permit spawning stock biomass could decrease quickly in response to moderate levels of fishing mortality; thus, the regulations in place in Florida to restrict harvest levels appear to be justified. Significantly better estimates of the magnitude and age structure of the catch would be required to complete a comprehensive age-structured stock assessment.

Acknowledgments

We thank Capt. J. C. Wells, who provided us with most of the permit examined in this study and whose efforts made this work possible, and Don DeMaria, who also provided specimens. We thank John Swanson, Bill Gibbs, and the staff at the Keys Marine Laboratory for their assistance; Jim Colvocoresses, John Hunt, and others at the South Florida Regional Laboratory for their cooperation; and David Harshany, Heather Patterson, Dan Merryman, Graham Gerdeman, and Connie Stevens for their assistance. We also thank Jim Colvocoresses, Rich McBride, Jim Quinn, Judy Leiby, and Llyn French for helpful comments on the manuscript. This work was supported in part under funding from the Department of the Interior, U.S. Fish and Wildlife Service, Federal Aid for Sportfish Restoration F-59.

Literature cited

- Chan, S. T. H., A. Wright, and J. G. Phillips.
 - 1967. The atretic structures in the gonads of the rice-field eel (Monopterus albus) during natural sex-reversal. J. Zool. (Lond.) 153:527-539.
- Crabtree, R. E., D. Snodgrass, C. W. Harnden.
 - 1997. Maturation and reproductive seasonality in bonefish, Albula vulpes, from the waters of the Florida Keys. Fish. Bull. 95:456-465.

- 1962. Pompanos (Trachinotus spp.) of south Atlantic coast of the United States. Fish. Bull. 62:189-222.
- Finucane, J. H.
 - 1969. Ecology of the pompano (Trachinotus carolinus) and the permit (Trachinotus falcatus) in Florida. Trans. Am. Fish. Soc. 95:478-486.

Helser, T. E.

1996. Growth of silver hake within the U.S. continental shelf ecosystem of the northwest Atlantic Ocean. J. Fish. Biol. 48:1059-1073.

Hunter, J. R., and B. J. Macewicz

1985. Measurement of spawning frequency in multiple spawning fishes. In An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, Engraulis mordax (R. Lasker, ed.), p. 79-94. NOAA Tech. Rep. NMFS 36.

James, G. D.

- 1984. Trevally, Caranx georgianus Cuvier: age determination, population biology, and the fishery. N. Z. Ministry Agr. Fish. Fish. Res. Bull. 25, 50 p.
- Manooch, C. S., III, and J. C. Potts.

1997. Age, growth and mortality of greater amberjack from the southeastern United States. Fish. Res. 30:229-240.

Quintero-Hunter, I., H. Grier, and M. Muscato.

1991. Enhancement of histological detail using metanil yellow as counterstain in periodic acid Schiff's hematoxylin staining of glycol methacrylate tissue sections. Biotechnol. Histochem. 66:169-172.

Ravaglia, M. A., and M. C. Maggese.

1995. Melano-macrophage centers in the gonads of the swamp eel, Synbranchus marmoratus Bloch, (Pisces, Synbranchidae): histological and histochemical characterization. J. Fish Dis. 18:117-125.

Robins, C. R.

1992. American nature guides to saltwater fish. Smithmark Publ., Inc., New York, NY, 192 p.

Secor, D. H., J. M. Dean, and E. L. Laban.

- 1992. Otolith removal and preparation for microstructural examination. In Otolith microstructure examination and analysis (D. K. Stevenson and S. E. Campana, eds.), p. 19-57. Can. Spec. Publ. Fish. Aquat. Sci. 117.
- Sudekum, A. E., J. D. Parrish, R. L. Radtke, and S. Ralston
- 1991. Life history and ecology of large jacks in undisturbed, shallow, oceanic communities. Fish. Bull. 89:493-513.

von Bertalanffy, L. 1957. Quantitative laws in metabolism and growth. Q. Rev. Biol. 2:217-231.

Wallace, R. A., and K. Selman.

Fields. H. M.

^{1981.} Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325-343.