Age, Growth, and Reproduction of Scamp, Mycteroperca Phenax, in the Southwestern North Atlantic, 1979 – 1997

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AGE, GROWTH, AND REPRODUCTION OF SCAMP, *MYCTEROPERCA PHENAX*, IN THE SOUTHWESTERN NORTH ATLANTIC, 1979–1997

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ABSTRACT

Scamp (*Mycteroperca phenax*) is a protogynous grouper that is a popular commercial and recreational species along the Atlantic coast of the southeastern United States. Scamp were sampled from the commercial and recreational fishery (1979–1996), and from the Marine Resource Monitoring Assessment and Prediction (MARMAP) program, a fishery-independent sampling program (1979–1997). Ages were determined from transverse sections for 2573 of the 3142 scamp for which we had otoliths (82%), and 2470 gonads were examined histologically. Data from all data sources were pooled, and trends between two periods, 1979–89 and 1990–97, were examined. Median length decreased significantly from 610 mm TL in 1979–89 to 570 mm TL in 1990–97, although there were no significant differences in the median age, size at maturity, and age at maturity between periods. The percentage of males declined from 34% to 21% for specimens >500 mm TL, although the sample size was much smaller during the earlier period (336 vs 1645). The percentage of scamp age 10 and older declined from 17% in 1979–89 to 7% in 1990–97. Females spawned from late February through mid-July, with a peak during March through May. Fishery-independent sampling revealed that: (1) spawning probably occurred during the late afternoon and evening, and (2) higher proportions of scamp spawned around new moon and full moon. The relationships between batch fecundity and TL, FL, ovary-free body weight, and whole body weight were highly significant. Potential annual fecundity is indeterminate and was estimated to range from 1,313,000 to 10,503,200 oocytes in specimens 445–712 mm TL. The wide ranges of size and age at sex transition and the temporal distribution of transitionals suggest that sex transition is socially mediated. The decrease in the percentage of males, and reduction of egg production caused by the loss of older, larger females from the population suggests scamp may be increasingly vulnerable to continued overexploitation. A spawning season closure on the fishery for gag may result in a further increase of the exploitation of scamp, requiring close monitoring of the population for the foreseeable future.

Scamp (*Mycteroperca phenax*) is a protogynous grouper that is a popular commercial and recreational species along the Atlantic coast of the southeastern United States. It ranges from North Carolina to Key West, the Gulf of Mexico, and along the southern shore of the Caribbean (Heemstra and Randall, 1993). Scamp are found in areas of living *Oculina* coral off the east coast of Florida (Gilmore and Jones, 1992) and over ledges and high-relief rocky bottoms in the eastern Gulf of Mexico (Bullock and Smith, 1991). Although the overall total commercial landings of species from the snapper-grouper complex declined from a high of 5445 mt in 1982 to a low of 2877 in 1996, commercial landings of scamp increased from 54 mt in 1982 to a high of 225 mt in 1990. Between 1992 and 1997, commercial landings of scamp were relatively stable, averaging 135 mt per year.

A recent stock assessment found the scamp population in the southeastern US to be in good condition and not overfished (M = 0.15; Manooch et al., 1998). Coleman et al.

(1996) reported that a decline in the proportion of male scamp in the northeastern Gulf of Mexico from 38% to ~21% between the 1970s and the early 1990s may have been due to increased fishing pressure, particularly when scamp are aggregated for spawning.

Investigations of a congener, gag (*M. microlepis*), showed that the sex ratio of gag declined from 20% to 6% males in the Atlantic off the southeastern US coast (Cape Hatteras, North Carolina to Fort Lauderdale, Florida; McGovern et al., 1998), although a recent stock assessment found the gag population not to be overfished (M = 0.15; Potts and Manooch 1998). However, stock assessments using models designed for gonochoristic species may not be applicable to protogynous species and the reduction in the percentage of males may be a more relevant indicator of the status of the population (Huntsman and Schaaf, 1994).

Recent changes to the snapper/grouper management plan (Amendment 9—closure of the fishery for gag during March and April) may further increase fishing pressure on scamp—particularly during the spawning season. The only previous investigation of scamp life history off the southeastern US coast was based on data collected during 1972–79 that described age, growth, mortality, food habits, and spawning season of scamp off the Carolinas (Matheson et al., 1986). Reproductive stage was assessed in females only using macroscopic techniques, thus no information on sex ratio was presented. Due to changes seen in the life history patterns of gag, and concerns that a similar situation may be occurring with scamp, as evidenced in the Gulf of Mexico, we investigated scamp collected from the southeastern US between 1979 and 1997 to determine if any changes in life history parameters were apparent and to describe the reproductive biology of scamp using histological techniques.

Methods

Sample Acquisition.—Scamp were sampled from the commercial and recreational fishery from 1979–1996, and by the Marine Resource Monitoring Assessment and Prediction (MARMAP) program, a fishery-independent sampling program, from 1979–1997. Some additional female scamp were sampled during 1998 for fecundity analyses. A concerted effort was made to collect scamp from the commercial fishery during January through December, 1996.

Scamp were collected throughout the South Atlantic Bight (SAB; Cape Hatteras, North Carolina to Cape Canaveral, Florida) on MARMAP research cruises aboard the RV Dolphin, RV Oregon, RV Lady Lisa and RV Palmetto using hook and line and three types of traps (Fig. 1; see Harris and McGovern, (1997) for a complete description of MARMAP sampling methodology). All scamp captured were measured (mm, total and fork length (TL, FL)), and weighed (g, whole). Both sagittae were removed and stored dry in coin envelopes. A section from the posterior portion of the gonad was removed, placed in a Tissue-Tek® and preserved in 10% formalin buffered with seawater. During 1996–98, the ovaries of developing and running ripe females were removed, weighed (±0.1 g) and preserved in 10% formalin buffered with seawater for fecundity analyses.

Scamp sampled from the commercial fishery between 1979–1982 were sampled by biologists onboard commercial vessels, while those sampled during 1996 were intercepted at South Carolina fish houses. All scamp sampled from commercial vessels were captured with snapper reels. Whenever possible, the entire catch of a single boat was sampled, otherwise boxes of fish that had already been weighed (≈50 kg each) by the fish house were randomly chosen for sampling. The fish house did not sort scamp in each box; rather each box was filled with fish until the total weight of the box was around 50 kg. We therefore felt a random selection of boxes to be processed provided as close to a random sample of the catch as possible. Each fish sampled was measured (mm, TL and FL), and weighed (g, whole or gutted). If the fish was sampled whole, the gonad was removed and

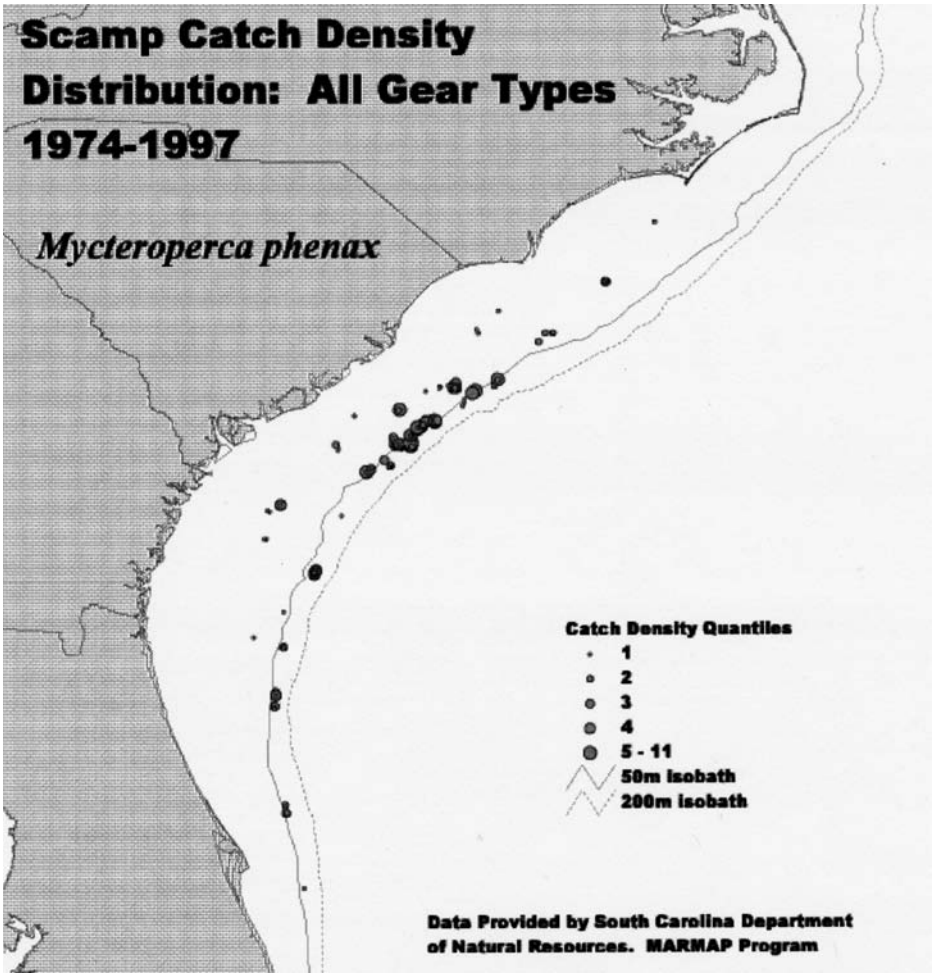

Figure 1. Locations of MARMAP scamp catches, 1974–97.

placed on ice for processing, as described above, in the laboratory. The left sagitta was removed from each fish and stored dry in a coin envelope. If the left otolith was lost or damaged, the right otolith was taken.

Additional scamp samples were obtained by the National Marine Fisheries Service from headboat catches. Samples were obtained from Cape Lookout, North Carolina, to the Dry Tortugas, Florida from 1979–1996. The left sagitta and total or fork length (mm) were provided to the authors.

Age and Growth.—Otoliths were embedded in epoxy resin and a thin transverse section (≈0.5 mm thick) was cut through the core of the otolith using a Mark V MC600 variable-speed saw. The section was rinsed in warm water, and placed on a drop of Baxter Accu-Mount 60 mounting medium. A second drop of Accu-Mount was placed on top of the section. The section was then examined for increments using a Nikon SMZ-U dissecting microscope and transmitted light. The microscope had an attached Hitachi KP-C550 video camera that was connected to a personal computer equipped with a Matrox frame grabber and Optimas image analysis software. Otolith radius was measured from the core to edge directly adjacent to the sulcal groove on the ventral portion of the otolith. Increments (one translucent and one opaque zone) were measured from the core to the distal edge of each opaque zone on the same axis. Two readers, with no knowledge of fish size or

date of capture, counted increments independently, and a single reader measured increments. If counts differed between readers, the otoliths were reexamined simultaneously by both readers, and discarded from further analyses if differences could not be resolved. Back-calculated lengths at age were calculated using the body proportional hypothesis (Francis, 1990).

Mean lengths, ages, and lengths at age (observed and back-calculated) of scamp collected during 1979–89 and 1990–97 were compared between data sources (commercial, headboat, or MARMAP) and time periods using ANOVA. The NLIN procedure using the Marquardt algorithm was used to fit the von Bertalanffy growth curve to the observed and back-calculated lengths at age for each period (SAS Institute, Inc., 1989). All statistical tests were conducted using SAS, and the results were considered significant if P was <0.05 (SAS Institute, Inc., 1989).

Reproduction.—To assess sex and reproductive stage, all gonads collected were prepared for histological examination. The posterior portion of the gonad was transferred to 50% isopropanol after a 2–6 wk fixation in 10% formalin, processed and vacuum infiltrated in a Modular Vacuum Tissue Processor, and blocked in paraffin. The imbedded samples were sectioned at 7 mm, stained with double-strength Gill hematoxylin, and counter-stained with eosin-y. Sex and reproductive stage were assigned independently by two readers using histological criteria defined by McGovern et al. (1998); a minor modification was that most primary growth oocytes in immature females were less than 60 μm in diameter. If assessments differed between readers, samples were examined simultaneously by both readers, and discarded if differences could not be resolved. Specimens with developing, ripe, spent, or resting gonads were considered to be sexually mature. For females, this definition of sexual maturity included specimens with oocyte development at or beyond the cortical alveoli stage and specimens with beta, gamma, or delta stages of atresia. Females that possessed hydrated oocytes or postovulatory follicles ≤24 h old were considered to be in spawning condition. Postovulatory follicles ages were estimated using criteria from Hunter et al. (1986). To ensure that females were correctly assigned to the immature and resting categories, the length-frequency histogram for immature females was compared to the histograms for resting females and females with evidence of certain maturity (e.g., developing , ripe, or spent). If there was little or no overlap between the two histograms representing mature individuals and the histogram for immature females, we concluded that immature and resting stages had been correctly assigned.

Size at 50% maturity (L_{50}, female) and age at 50% maturity (A_{50}, female) were determined with the PROBIT procedure (SAS Institute, Inc., 1989). The LOGISTIC procedure was used to determine which model (gompit, logit, or probit) to use in the PROBIT procedure.

Fecundity.—Definitions of potential annual fecundity, determinate fecundity, and indeterminate fecundity follow Hunter et al. (1992). Three stages of yolked oocytes, migratory nucleus oocytes, hydrated oocytes, and atretic oocytes were identified in samples from formalin-preserved gonads (sensu Hunter et al., 1992).

Densities of hydrated oocytes from five random locations in the ovaries of seven fish were compared to determine if oocyte stages were randomly distributed. Samples weighed approximately 35 mg and consisted of 25–50 hydrated oocytes. The effects of location and individual fish on density were assessed with a repeated measures ANOVA.

To estimate total fecundity, two 15–25 mg samples were taken from random locations in the ovaries, and stage-3 yolked oocytes were counted. Monthly regression equations were computed to describe the relationship between total fecundity and fish length. An ANCOVA was performed to examine the effect of month on total fecundity. As scamp exhibited indeterminate fecundity, estimates of batch fecundity and spawning frequency were used to calculate annual fecundity. To estimate batch fecundity, two 25–35 mg samples were taken from random locations in the ovaries of 63 commercial and 13 fishery-independent specimens, and hydrated oocytes or migratory nucleus oocytes (n = 1 specimen) were counted. The estimate of spawning frequency was based on the occurrence of hydrated oocytes. All statistical tests were conducted using SAS, and the results were considered significant if P was <0.05 (SAS Institute, Inc., 1989).

RESULTS

SAMPLE AQUISITION.—A total of 3175 scamp were collected between 1979–97 of which 33 specimens had no length data. Of those scamp remaining, 1,002 were collected during MARMAP (fishery-independent) research cruises (May–October), 1723 were sampled at commercial fish houses, and 417 were sampled from headboats (Table 1). Although more than 50 scamp were sampled every month from the commercial fishery except January (n = 18), the bulk of the scamp were collected between February and September. As lengths were not normally distributed (Kolmogorov-Smirnov test; $P < 0.001$; Fig. 2), median rather than mean lengths are reported. The median length of all fish sampled was 577 mm TL (n = 3142). Although scamp sampled from headboats were smaller than scamp sampled by MARMAP (520 mm TL vs 523 mm TL), this difference was not significant (Kruskal-Wallace (K-W)). The median length of scamp sampled from the commercial fishery (610 mm TL) was significantly larger than both fishery-independent and headboat samples (K-W). The median lengths showed a significant decrease from 610 mm TL in 1979–89 to 570 mm TL in 1990–97.

AGE AND GROWTH.—Ages were determined for 2573 of the 3142 scamp for which we had otoliths (82%). Marginal increment analysis indicated that one increment is formed in scamp otoliths each year, generally during December and January (Fig. 3). We therefore assumed a birth date of January 1 for all aged fish, and advanced the ages of scamp with a wide translucent marginal increment captured in January, February or March by 1 yr. Scamp ranged in age from 1 to 30 yrs old, and the median age was 5 yrs old. Scamp sampled from the commercial fishery were significantly older (median 5 yrs, range 1–30, n = 1380) than scamp sampled by MARMAP (median age 4 yrs, range 1–25, n = 819) and from headboats (median age 4 yrs, range 1–23, n = 374, K-W with Dunn's comparison). Scamp sampled from the commercial fishery were significantly older than scamp from headboat and fishery-independent samples within each time period (Table 1). Furthermore, the median age of scamp from within each data source showed significant declines between the two time periods (Mann-Whitney, Table 1), and the percentage of sampled scamp age 10 and older decreased from 17.2% during 1979–89, to 7.3% during 1990–97.

Table 1. Catch statistics for each time period and data source sampled between 1979–89, 1990–97, and an overall total for all scamp sampled between 1979–97. Lengths are mm TL, ages are years. A denotes a significant difference between periods ($P < 0.05$); B denotes a significant difference between data sources ($P < 0.05$).

	MARMAP				Headboat			
	No. sampled	Median length	No. aged	Median age	No. sampled	Median length	No. aged	Median age
1979–1989	132	685	92	5	299	601	269	4
1990–1997	870	516	727	4 [A]	118	453	105	3 [A]
Total	1,002	522	819	4	417	502	374	4
	Commercial				Combined			
	No. sampled	Median length	No. aged	Median age	No. sampled	Median length	No. aged	Median age
1979–1989	364	668	216	6.5 [B]	795	610	577	5
1990–1997	1,359	600	1,164	5 [A,B]	2,347	570	1,996	5
Total	1,723	610	1,380	5	3,142	577	2,573	5

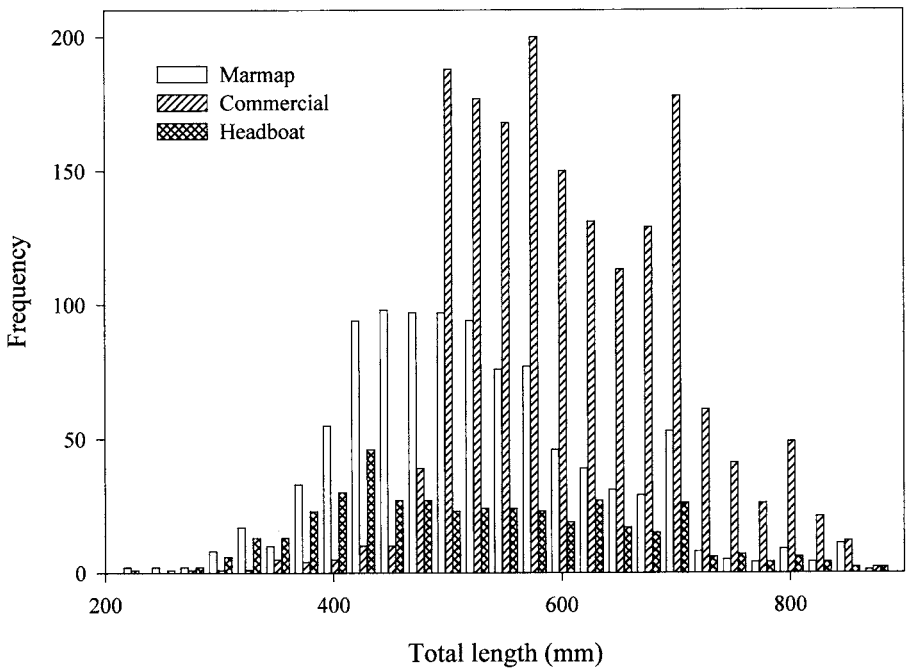

Figure 2. Length frequency distribution of scamp sampled from three fisheries, 1979–97.

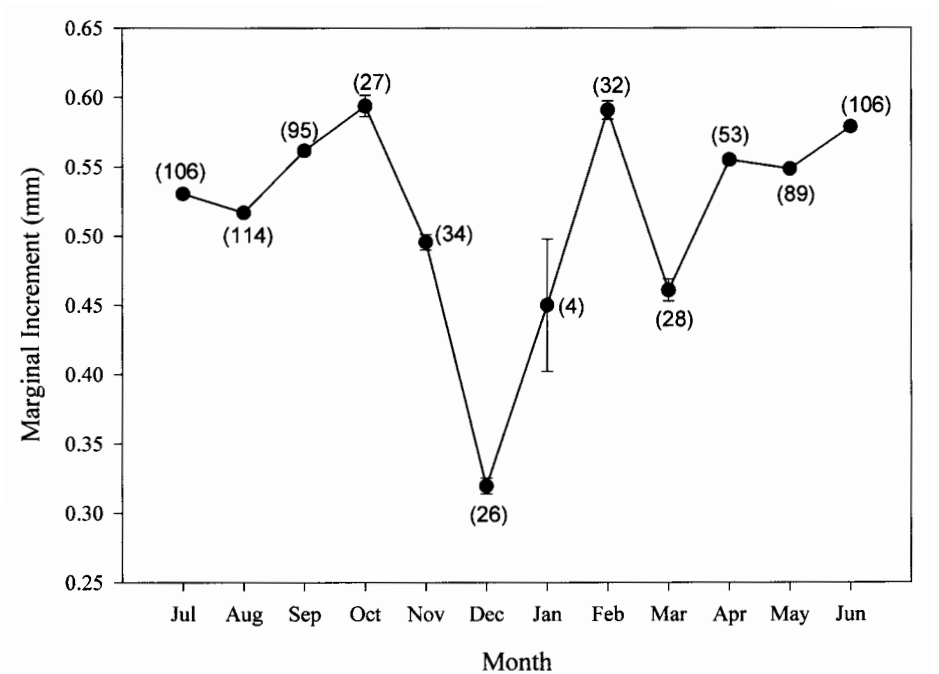

Figure 3. Mean monthly standardized marginal increment for scamp from all fisheries. Number in parentheses is the number of scamp for each month. Error bars are ±1 SE.

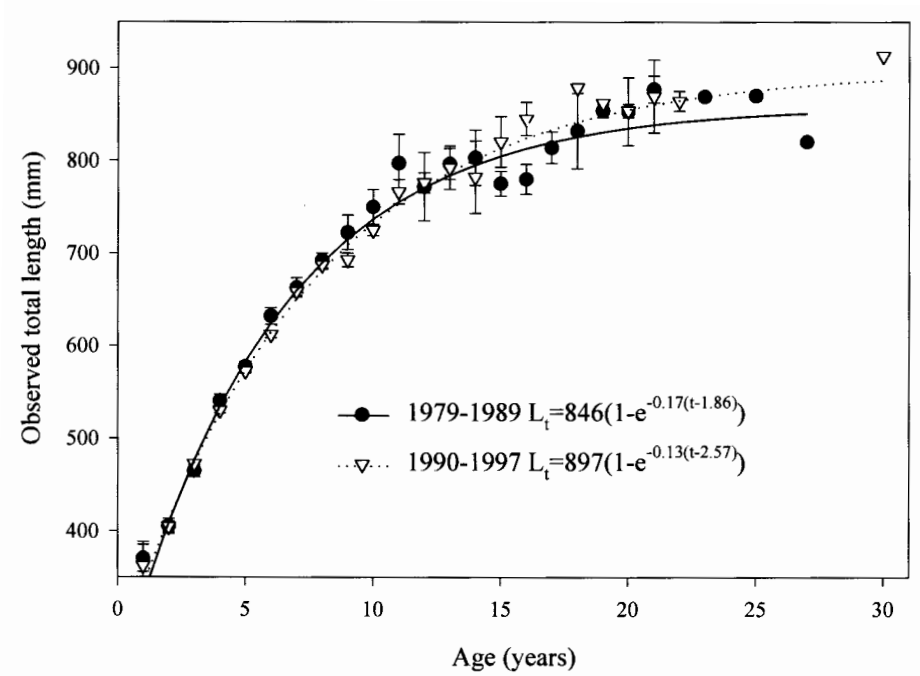

Figure 4. Mean observed lengths at age and fitted von Bertalanffy growth curves of scamp from all data sources for 1979–89 and 1990–97.

The median age for pooled data was the same for both periods, and was not significantly different. The mean age of scamp sampled decreased from 6.5 yrs old in 1979–89 to 5.5 yrs old in 1990–97.

During 1979–89, scamp from the headboat fishery were larger than those from the commercial fishery or MARMAP for ages 5 and 9, whereas age-17 scamp were significantly larger in MARMAP samples than the other two data sources (K-W with Dunn's comparison). No other significant differences in length at age were evident. During 1990–97, the commercial fishery caught significantly larger fish at ages 3 and 4, and significantly smaller fish than MARMAP at age 7 and than headboats at age 9 (K-W with Dunn's comparison). However, no temporal trends were evident, either within any data source or for all data combined. As there were few significant differences in the observed mean length at age between gear types during 1979–89 and 1990–97, data from all data sources were pooled for each period (Fig. 4).

Mean back-calculated lengths at age showed slightly different trends. Scamp sampled from headboats were significantly larger than scamp from MARMAP at ages 1 and 2, and significantly larger than scamp from the commercial fishery at ages 4 and 11–13 for 1979–89. However, during 1990–97, scamp from the commercial fishery were significantly larger than those from headboats and MARMAP for ages 1–3, and MARMAP for age 4. There was no evidence of Lee's phenomenon in the back-calculated lengths at age. Based on the results of comparisons on mean back-calculated lengths at age, these data were also pooled for each period. The mean back-calculated lengths at age of scamp sampled in 1979–89 were significantly larger than those from 1990–97 for ages 1–4, whereas scamp aged 9 and 10 from 1979–89 were significantly smaller than those from

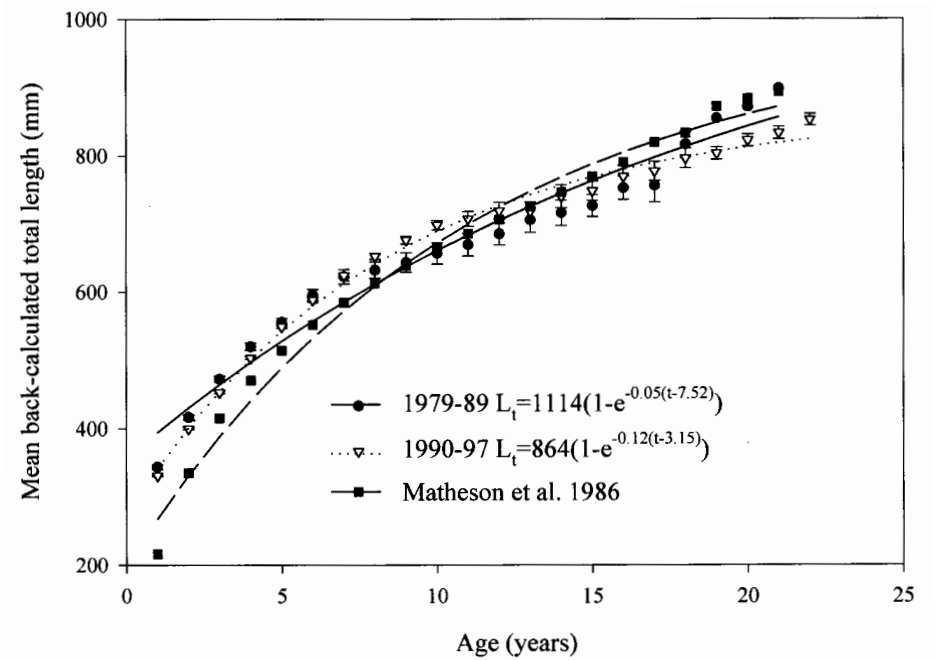

Figure 5. Mean back-calculated lengths at age and fitted von Bertalanffy growth curves of scamp from all data sources for 1979–89 and 1990–97.

1990–97 (K-W with Dunn's comparison). Von Bertalanffy growth curves were fitted to un-weighted back-calculated mean lengths at age as convergence criteria could not be met for fitting to weighted mean back-calculated lengths from 1979–89 (Fig. 5).

REPRODUCTION.—Based on the results of the length at age analyses, reproductive data were pooled by time period (1979–89; 1990–97) for all data sources. Histological examination of 2372 sexually mature scamp sampled during 1979–89 and 1990–97 revealed that males represented a significantly smaller proportion of the catch during 1990–97 (χ^2 = 28.537; $P < 0.001$; Table 2). Comparisons between periods were restricted to specimens >500 mm TL because a 20 in TL (508 mm TL) minimum size limit was implemented in 1992 for commercial and recreational fisheries. The percentage of males declined from 34% to 21% for specimens >500 mm TL, although the sample size was much smaller during the earlier period (336 vs 1645). Most of the decline occurred after the late 1980s, as the percentage of males was unchanged (19%) in fishery-independent collections made with chevron traps during 1988–92 and 1993–97, the subset of our data set representing the longest period of sampling with one gear type. Median length of specimens >500 mm TL was significantly larger during 1979–89 than 1990–97 (610 vs 570; Mann-Whitney; $P < 0.0001$).

The near overlap in the length histograms of female scamp that were definitely mature and females that were resting and the minimal overlap in the histograms for immature and resting scamp indicated that reproductive tissue was correctly assigned to the immature and resting categories (Fig. 6). Female scamp reached sexual maturity at 351–400 mm TL and age 2 during 1979–89, whereas the length and age at first maturity were 301–350 mm TL and age 1 during 1990–97 (Tables 3,4). Length and age at 50% maturity were

Table 2. Sex by length interval of sexually mature scamp collected off Cape Canaveral (Florida) through South Carolina (>80% off South Carolina). Sex ratio is reported for specimens >500 mm because a 20 in (508 mm) minimum size limit was implemented in 1992. F = female; M = male; T = transitional.

	1979–1989			1990–1997		
mm TL	F	M	T	F	M	T
301–350	–	–	–	6	–	–
351–400	4	–	–	28	–	–
401–450	5	–	–	120	–	1
451–500	21	–	1	205	–	–
501–550	27	–	1	424	16	20
551–600	45	1	1	341	37	22
601–650	32	2	1	228	32	16
651–700	25	8	1	122	82	34
701–750	11	9	8	47	94	16
751–800	10	13	–	16	46	7
801–850	3	28	2	4	24	3
851–900	1	33	–	1	12	–
901–950	–	–	–	–	1	–
No length	–	–	–	12	9	2
Total	250	102	15	1,542	344	119
% (all fish)	68.1	27.38	4.1	76.9	17.2	5.9
% (>500 mm)	61.7	33.7	4.7	71.9	20.9	7.2

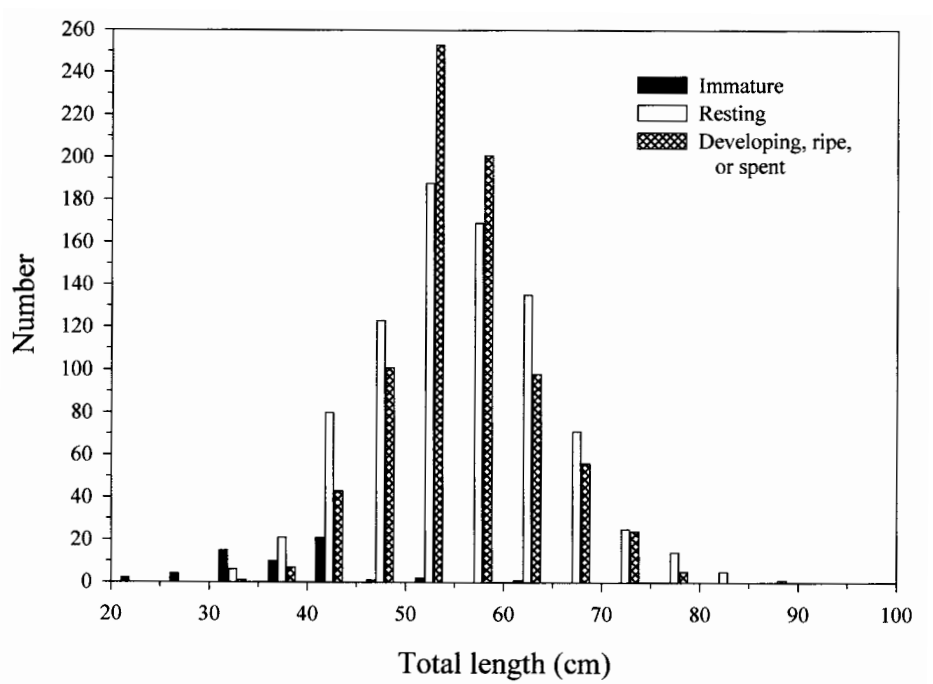

Figure 6. Comparison of length frequencies of female scamp collected during 1979–97 that were categorized as immature (n = 56), definitely mature (n = 790), or resting (n = 837). Definitely mature specimens were developing, ripe, or spent.

Table 3. Percentage of mature specimens by length interval for female scamp collected primarily off South Carolina. Specimens in the developing, spawning, spent, or resting stages were considered mature. n = number of specimens.

mm TL	1979–1989 n = 131		1990–1997 n = 1180	
	%	n	%	n
201–250			0	(2)
251–300	0	(1)	0	(3)
301–350	0	(3)	33	(18)
351–400	67	(3)	73	(33)
401–450	75	(4)	83	(118)
451–500	100	(15)	99	(169)
501–550	100	(15)	99	(284)
551–600	100	(35)	100	(234)
601–650	96	(23)	100	(177)
651–700	100	(17)	100	(91)
701–900	100	(19)	100	(51)

374 mm TL (Normit; 95% CI = 312–405) and 1.72 yr (Gompit; 95% CI = -3.65–2.41) for 1979–89, and 353 mm TL (Normit; 95% CI = 331–369) and 1.28 yr (Logit; 95% CI = 0.81–1.60) for 1990–97. There were no significant differences in either L_{50} (Gompit, P = 0.61) or A_{50} (Gompit; P = 0.35) between periods. Nearly all females were mature at 451–500 mm TL and age 4 (Tables 3,4). The size ranges for immature and mature females were 240–542 mm TL (n = 55; median = 386) and 313–875 mm TL (n = 1,758; median = 555). While there were no differences in the mean lengths or ages of immature scamp between 1979–89 and 1990–97, mature scamp were significantly smaller (594 vs 557 mm TL) and younger (5.6 vs 4.9 yrs) during the later period.

Females were in spawning condition from late February through mid-July based on the occurrence of hydrated oocytes or postovulatory follicles (Fig. 7A). Peak spawning occurred from March through May. Hydration occurred primarily during the morning and

Table 4. Percentage of mature specimens by age interval for female scamp collected primarily off South Carolina. Specimens in the developing, spawning, spent, or resting stages were considered mature. n = number of specimens.

Age (yr)	1979–1989 n = 94		1990–1997 n = 1006	
	%	n	%	n
1	0	(1)	50	(14)
2	50	(4)	66	(61)
3	78	(9)	94	(174)
4	100	(20)	98	(219)
5	100	(32)	99	(269)
6	100	(9)	100	(114)
7	100	(5)	100	(60)
8	100	(4)	100	(49)
9	100	(2)	100	(22)
10	100	(3)	100	(20)
11–16	100	(5)	100	(4)

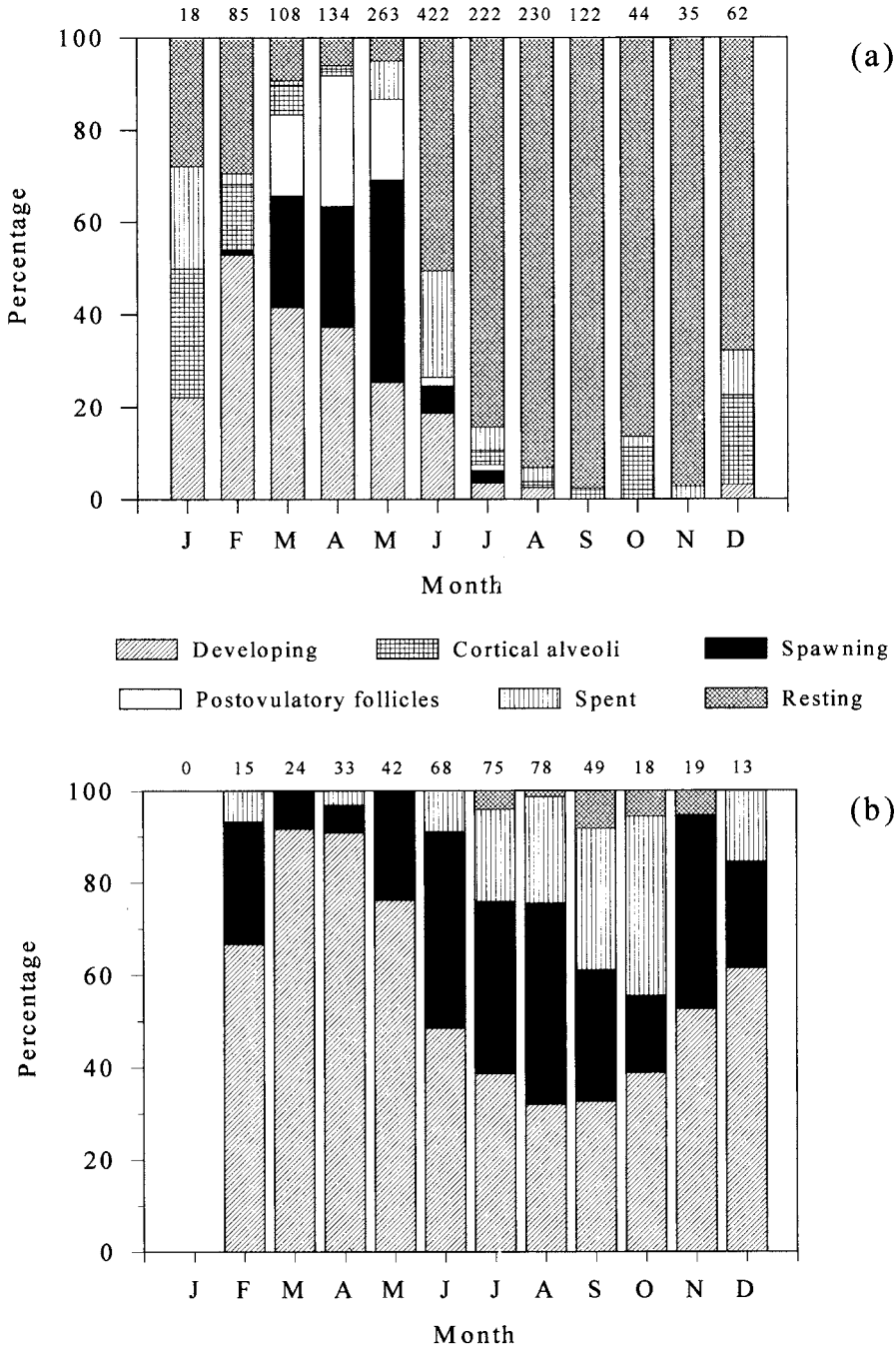

Figure 7. Reproductive seasonality of female (A) and male (B) scamp collected during 1979–97. All specimens were examined histologically. Number of specimens examined by month is above each bar.

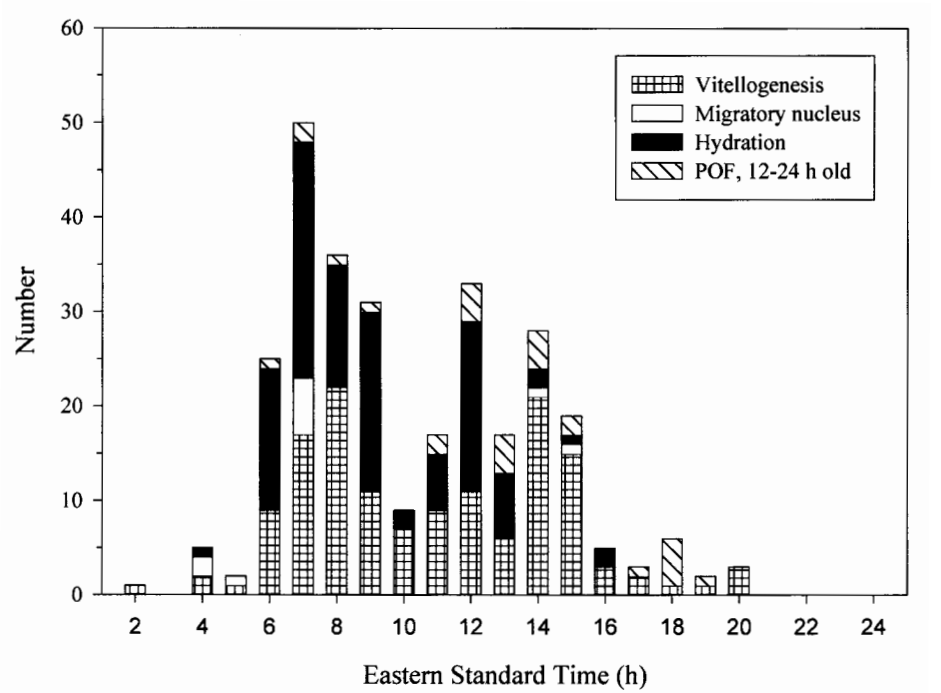

Figure 8. Time of spawning in scamp collected during fishery-independent sampling in 1980–97. All specimens (n = 292) had oocytes undergoing vitellogenesis and were categorized according to the most advanced stage of oogenesis. POF = postovulatory follicle. 2:00 EST = 1:00–1:59.

early afternoon (Fig. 8), which means that scamp probably spawned in the late afternoon and evening. The extent of spawning during evening hours could not be determined because <10 scamp were collected between hour 21 and hour 5 of the next day. However, the occurrence of only one scamp with <12 h old postovulatory follices was additional evidence that spawning occurs in the evening. Spawning individuals (n = 140) were captured on research cruises off South Carolina (32°04′ to 32°52′N) and east of St. Augustine (29°57′N), Florida, at depths 33 to 93 m. Approximate fishing locations provided by fishermen showed that spawning scamp sampled from the commercial fishery (n = 51) were captured off South Carolina and Georgia (31°53′ to 32° 57′N) at depths of 30–80 m. Male scamp in spawning condition were collected throughout the year (Fig. 7B). The highest combined percentage of spent and resting individuals occurred during July through October, which coincided with the end of the female spawning season.

There was also evidence in fishery-independent samples that spawning was correlated with the lunar cycle. Higher proportions of scamp with oocytes undergoing vitellogenesis had migratory nucleus oocytes, hydrated oocytes, or 12–24 h old postovulatory follicles around new moon and full moon (Fig. 9).

Sex transition occurred throughout the year, but the primary period of transition was August through November (Fig. 10). Transition occurred over wide size and age ranges (401–850 mm TL and ages 2–16), however, 89% of the 131 specimens with a length measurement were 502–750 mm TL and 77% of the 106 specimens aged were 5–9 yrs old.

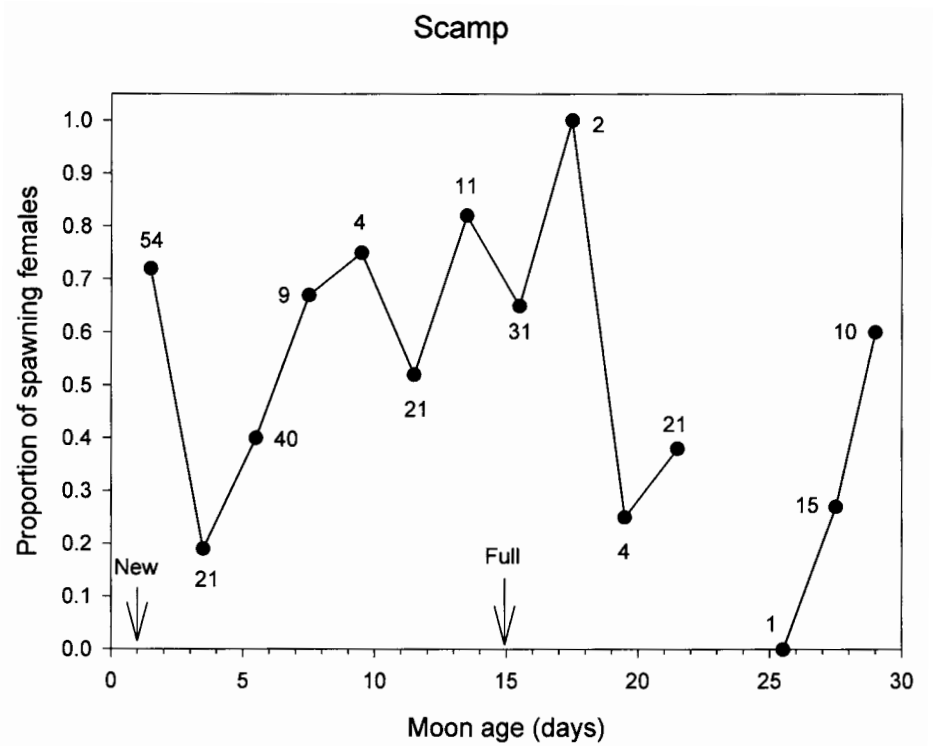

Figure 9. Relationship between lunar cycle and the proportion of spawning females among scamp with oocytes undergoing vitellogenesis. Specimens with migratory nucleus oocytes, hydrated oocytes, or postovulatory follicles 12–24 h old were considered to be in spawning condition. The number of specimens examined is above each point.

FECUNDITY.—Hydrated oocytes were randomly distributed within the ovary. There was no difference in oocyte density between five randomly selected locations ($F = 1.34$, $P > 0.25$, $df = 4$) in seven scamp, which indicated that samples for estimating total fecundity and batch fecundity could be taken from any location without bias. Total fecundity as a function of total length was essentially constant during the spawning peak, March through May, but decreased in June and July as indicated by the decrease in the elevation of monthly regression equations (Fig. 11). The interaction term ($P = 0.0863$) in an ANCOVA showed that the slopes of the monthly equations were not significantly different (Table 5); however, the elevation of the July equation was lower ($P < 0.0001$) than those from March through June. Additionally, total fecundity was greater in April than in May ($P = 0.0013$) and June ($P = 0.0043$). The relation between total fecundity and total length was highly significant in March through May, but not during June and July (Table 5). Atretic oocytes were not very abundant in the samples. They were present in the samples from 33% of 79 specimens and the monthly mean proportion of atretic oocytes per sample from March through July was 0.04–0.025, with the highest proportion occurring in July at the end of the spawning season.

Although total fecundity decreased during June and July, the last 2 mo of the spawning season, frequency distributions of oocyte diameter showed that the relative percentage and size of stage-3 vitellogenic oocytes varied little between March and June (Fig. 12).

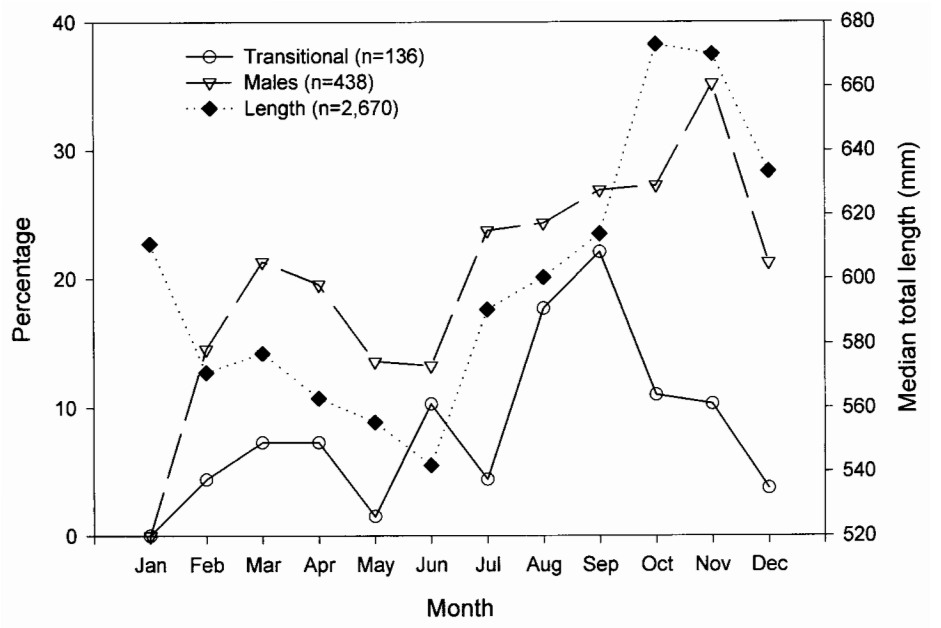

Figure 10. Temporal distributions of transitional and male scamp, and median length of all mature scamp collected during 1979–97.

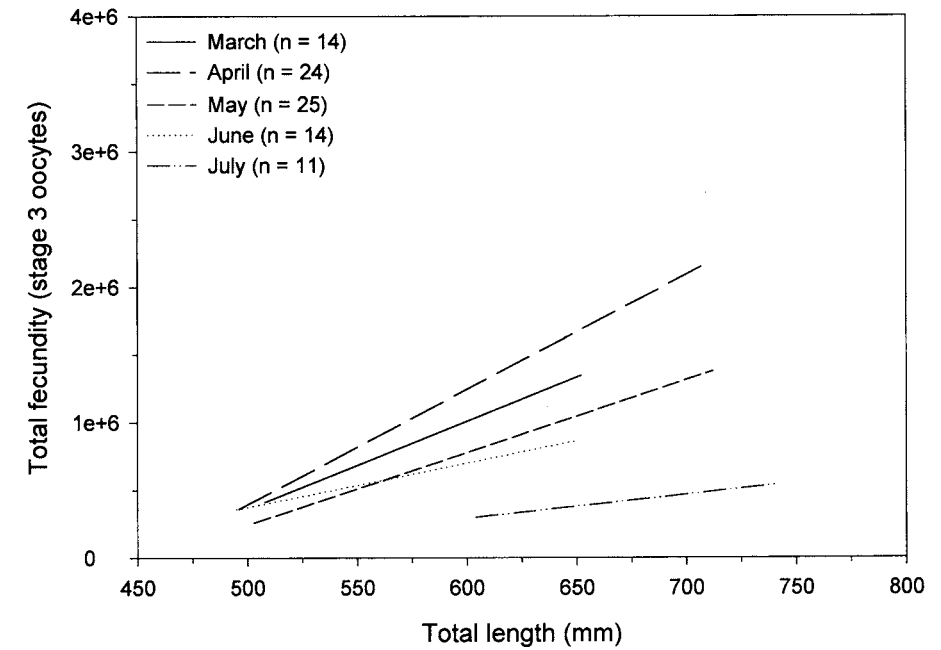

Figure 11. Estimates of total fecundity in scamp as a function of total length based on specimens collected with hook and line on commercial vessels and headboats during 1996. Coefficients of regression equations are listed in Table 5.

Table 5. Linear regression coefficients for the relationship between total length (TL in mm) and total fecundity (TF) of scamp, *Mycteroperca phenax*. The effect of month on this relationship was evaluated with analysis of covariance. * P < 0.001, ** P > 0.05.

	Linear equation TF = a + bTL					Analysis of covariance			
Month	a	b	r^2	F	n	Variables	df	F	P
March	–2.88e6	6479.7	0.68	29.21*	14	Month	4	1.33	0.2649
April	–3.84e6	8473.3	0.45	19.50*	24	TL	1	32.66	<0.0001
May	–2.43e6	5342.9	0.50	24.95*	25	Month * TL	4	2.12	0.0863
June	–1.26e6	3274.2	0.18	3.77**	14	Error	79		
July	–0.76e6	1749.6	0.17	2.98**	11	Total	88		

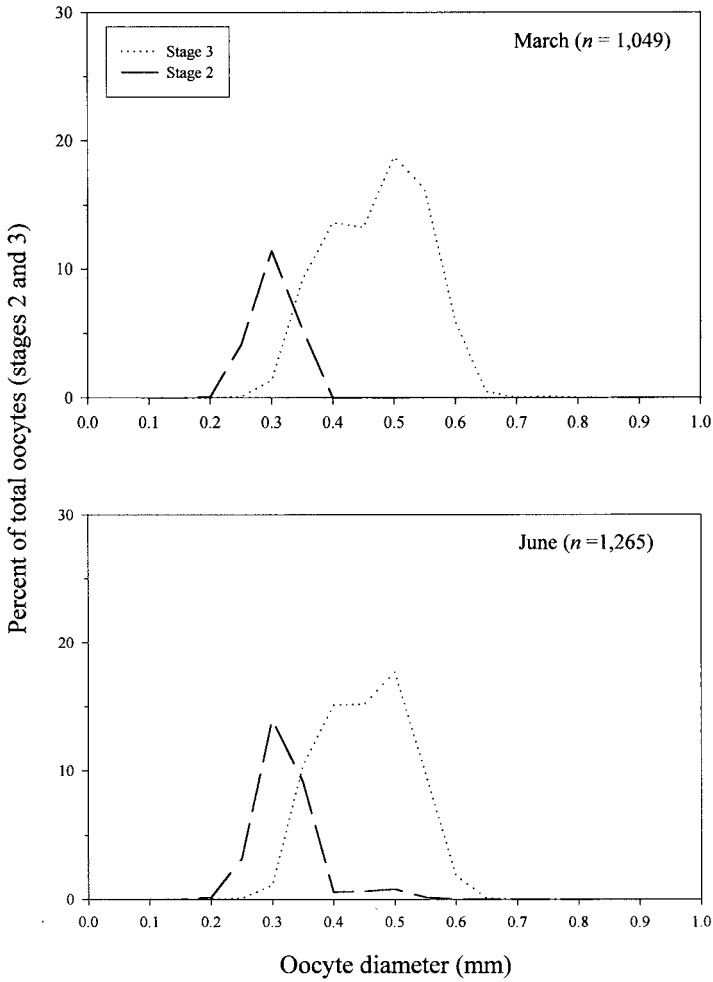

Figure 12. Frequency distribution of oocyte diameter for vitellogenic oocytes (stages 2 and 3; see Hunter et al. 1992) in scamp collected with hook and line on commercial vessels and headboats during 1996. Four specimens were randomly selected for each month. Sample size (n) represents the total number of oocytes measured.

Table 6. Number of female scamp with hydrated oocytes (HO) and total number of mature females with vitellogenic oocytes in samples caught with: 1) hook and line on commercial vessels and headboats during 1996, and 2) chevron traps during fishery-independent sampling in 1988–97. The proportions of specimens with hydrated oocytes were used to determine spawning frequency.

Month	Fishery-dependent		Fishery-independent	
	No. with HO	No. mature females	No. with HO	No. mature females
March	4	6	14	25
April	24	94	11	27
May	50	77	57	124
June	2	24	19	67
July	6	16		
Total	86	217	101	243
Proportion of total	0.396		0.416	
Average proportion	0.406			

The lack of a progressive decline in total fecundity during the spawning peak (March through May; Fig. 11) and the lack of a gap between stage-2 and stage-3 vitellogenic oocytes (Fig. 12) indicated that annual fecundity is indeterminate in scamp.

Given that fecundity is indeterminate, it was necessary to estimate batch fecundity and spawning frequency to produce estimates of potential annual fecundity. These estimates were based on hydrated oocytes because most sampling occurred during daylight, the time of hydration (Fig. 8). Postovulatory follicles were not used to estimate spawning frequency because they were probably more abundant at night, when very little sampling was done. Additionally, follicle degeneration was rapid, as indicated by the low frequency (<0.1) of 12–24 h old follicles. The proportion of specimens with hydrated oocytes was very similar in fishery-dependent and fishery-independent collections (Table 6). A proportion of 0.4 corresponded to a spawning periodicity of 2.5 d. With a spawning season of 106 d (mid March through June), an individual female could spawn 42 times.

The relation between batch fecundity and TL, FL, ovary-free body weight, and whole body weight was highly significant, whereas the relation with age was not significant (Table 7). Batch fecundity as a function of total length did not differ between March and June, as indicated by the lack of differences in slopes ($F = 0.14$, $P = 0.936$, $df = 3$) and intercepts ($F = 0.80$, $P = 0.500$, $df = 3$) between months. Specimens collected in July were excluded from analyses of batch fecundity because July spawning was noted during only 1 yr between 1988 and 1997. Given the similarity of the monthly equations, data from

Table 7. Linear regression coefficients for the relationship between batch fecundity (BF; number of hydrated eggs) and total length (mm), fork length (mm), whole and ovary-free body weight (g), and age (yr) in scamp. Specimens were collected during March–June. *P < 0.0001.

X	Linear equation BF = a + bX						
	a	95% CI	b	95% CI	Adjusted r^2	F	n
Total length	–333,408	107,070.8	819.5	189.4	0.496	74.88*	76
Fork length	–346,746	107,172.2	909.9	204.3	0.511	79.38*	76
Ovary-free weight	–9,651	35,564.8	62.6	14.6	0.540	73.79*	63
Whole weight	–11,673	33,991.4	60.5	13.2	0.572	83.90*	63
Age	74,635	82,406.1	10,999	15,758.0	0.015	1.95	63

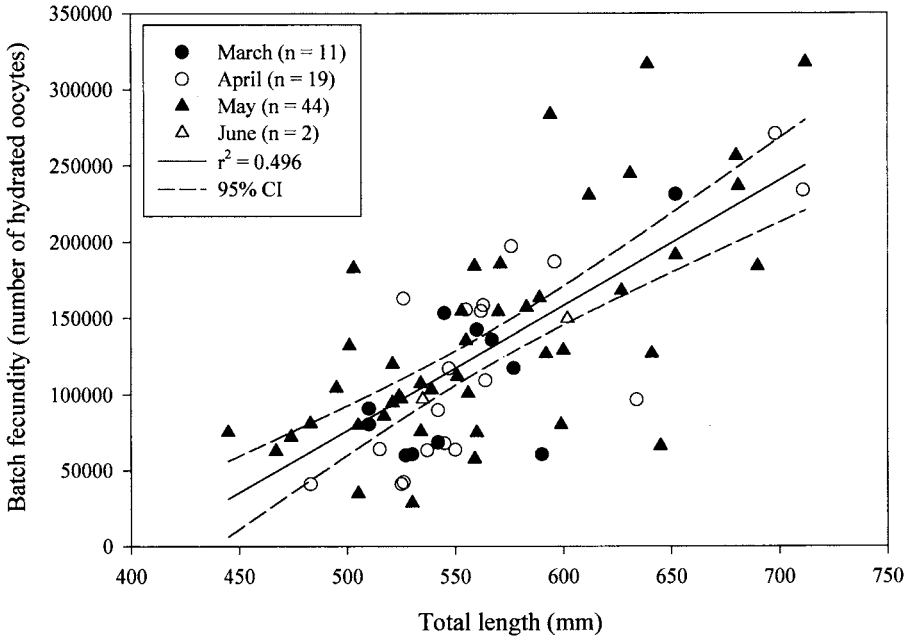

Figure 13. Batch fecundity as a function of total length in scamp collected during March through June. Specimens from the commercial fishery (n = 63) and fishery-independent sampling (n = 13) were examined. Coefficients of the regression equation are listed in Table 7.

March through June were combined to estimate the relationship between batch fecundity and total length (Fig. 13). Multiplying the estimated spawning frequency (42) by batch fecundity estimates for scamp 445–712 mm TL (Fig. 13) produced estimates of potential annual fecundity that ranged from 1,313,300 to 10,503,200 oocytes.

Discussion

Our data confirm that scamp in the SAB are long-lived and slow growing. Due to the variety of gear types used to collect scamp for this study (recreational, commercial, fishery-independent hook and line, and black sea bass, Florida, and Chevron traps) and large sample size, we posit that our study accurately presents the current age, length, and reproductive structure of the population in the SAB.

The size at age of scamp in the SAB has shown little change since 1979. There are no significant temporal differences in the mean observed lengths at age from the different data sources or for the pooled data between periods, suggesting that scamp have not encountered sustained high fishing mortalities. The most recent stock assessment estimated F = 0.18 for 1992–1996 and concluded that management actions taken by the South Atlantic Fisheries Management Council (SAFMC) have been instrumental in beginning the rebuilding the stock of scamp off the southeastern United States, from a spawning potential ratio (SPR) of 0.19 during 1989–1991 to 0.35 during 1992–1996 (M = 0.15; Manooch et al., 1998). As the SAFMC considers a species severely overfished at an SPR < 20%, and overfished at an SPR < 40%, scamp is still in overfished status.

Furthermore, as there is now a spawning season closure in place for gag in the SAB, it is probable that fishing pressure on scamp will increase. Scamp have constituted an increasing percentage of the snapper/grouper landings in recent years, and this trend could be accelerated in the future. Therefore, scamp should be closely monitored to detect if any temporal changes in length at age, which may indicate severe overfishing, become evident in the population.

The growth curves fitted to the observed sizes at age for both periods, and to back-calculated sizes at age for 1990–97 are similar to each other, whereas the curve fitted to the back-calculated sizes at age for 1979–89 is quite different. This curve had to be fitted to un-weighted mean sizes at age to achieve convergence, further demonstrating the necessity of a sufficiently large sample to describe the growth of long-lived species such as scamp. Additionally, incorporation of inaccurate growth parameters into yield-per-recruit and stock assessment procedures would further exacerbate any errors associated with the small sample size.

Our results for female scamp show that spawning begins as early as late February and usually ends in June. Spawning females were collected from the commercial fishery in July 1996, but this is probably atypical because no spawning females were captured after June in 10 yrs of fishery-independent sampling with Chevron traps. These results differ slightly from those of Matheson et al. (1986), who examined scamp that were collected off South Carolina primarily during May through August. They determined macroscopically that scamp spawn during April through August, with a peak in May and June; however, the sample size in April was six and no fish were collected during January through March.

The decline in the median age and length of scamp due to the removal of larger and older individuals may affect the population in ways that are not accounted for in the SPR. The larger and older fish are almost exclusively male. The percentage of male scamp in our samples, which we have suggested provides a good representation of the population in the SAB, has decreased from 34% during 1979–89 to 21% in 1990–97—similar to the depressed levels reported for the Gulf of Mexico in the 1990s (Coleman et al., 1996). During 1972–79, Matheson et al. (1986) aged 503 scamp from the same region as in our study with sectioned otoliths. The median age of those scamp was 8 (range 1–21; calculated from their Table 1), considerably greater than the median age of scamp sampled during either period of our study. Of these, 33% were age 10 and older, contrasted to 17% for 1979–89 and 7% for 1990–97 in the present study, suggesting that the percentage of males may have been even higher during 1972–79 than we recorded for 1979–89. The selective removal of males may affect reproductive output by limiting sperm production, thereby limiting recruitment and population growth. Even if the percentage of males was similar between the 1970s and 1980s, the loss of the largest females could significantly reduce reproductive output through the removal of the most fecund fish, thereby adversely affecting the ability of the population to recover from overfishing.

The wide range of lengths and ages of transitional fish argues against size mediation of transition. Gilmore and Jones (1992) provide evidence that scamp are found in aggregations for an extended period after the spawning season. From a submersible, they frequently observed aggregations of up to 20 individuals at one site off the southeast coast of Florida, and even larger aggregations, approximately 100 individuals, at a second site. The larger aggregations were seen twice during mid to late September, at least 2 mo after the end of spawning. The percentage of transitionals in our study began to increase in

August and increased steadily through November, consistent with the timing of aggregation formation as observed by Gilmore and Jones (1992). Although there was an increase in median length of 60–90 mm from July through September, initiation of transition appeared to lag the increase in length by one month, further suggesting transition is not size mediated. Although it seems probable that socially mediated transition is initiated in post-spawning aggregations, the social controls that are involved have yet to be described for scamp.

The 508 mm TL (age 3–4) size limit for scamp appears to be large enough to allow almost all scamp to spawn at least once as females before recruitment to the fishery. Scamp are relatively small and young at first maturity, and the L_{50} is considerably less than the size limit. Nevertheless, we have found that total and batch fecundity of scamp are strongly correlated to size. Presumably, as larger scamp (predominately males) are removed from the population, smaller fish initiate transition to replace them, and are therefore lost to the population as egg producers. The overall effect of increased fishing mortality is therefore not only to reduce the number of males in the population, but also to reduce the total potential egg production of the population. Recruitment is thus further limited by the shift in egg production to smaller, less fecund, fish, even though maturity is usually attained well before recruitment to the fishery.

Our data to date suggest that although scamp is overfished in the SAB, no changes in sizes at age are apparent. The decrease in the percentage of males is a cause for serious concern and should be closely monitored. The reduction in population fecundity due to the decline in mean size and age of the population render the population more vulnerable to recruitment failure, thereby inhibiting the ability of the population to recover from overfishing. With the potential for further increases in fishing pressure on scamp as the fishery for gag is restricted, the population of the SAB could quickly be pushed into severely overfished status.

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ADDRESS: *South Carolina Marine Resources Research Institute, South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, South Carolina 29422*. (P.J.H.) *E-mail:* <*harrip@mrd.dnr.state.sc.us*>.