

Abstract.—Aspects of the life history of red porgy from the South Atlantic Bight (SAB) were examined for four periods (1972–74, 1979–81, 1988–90, and 1991–94), and annual changes in the age and growth of red porgy were described for data collected during 1988–94. The life history of red porgy during 1972–74 was assumed to represent that of an unfished population, although this population had been subject to light fishing pressure. From 1972–74 to 1979–81, the back-calculated size-at-age increased slightly for ages 2–8. By 1988–90 and 1991–94, however, the back-calculated size-at-age for the same age classes was significantly smaller than that in 1979–81. In addition, size-at-maturity and size-at-sexual-transition occurred at progressively smaller sizes for 1988–90 and 1991–94. The mean size-at-age (observed and back-calculated) declined for most ages between 1988 and 1994. Von Bertalanffy growth curves fitted to the mean back-calculated size-at-age for each year showed similar decreasing trends. Changes in life history may be a response to sustained 20-year overexploitation that has selectively removed individuals predisposed towards rapid growth and larger size.

Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972–1994*

Patrick J. Harris

John C. McGovern

South Carolina Department of Natural Resources
PO Box 12559, Charleston, South Carolina 29422

E-mail address (for P. Harris): harrisp@mrd.dnr.state.sc.us

The red porgy, *Pagrus pagrus*, is a protogynous sparid distributed throughout the Atlantic Ocean and Mediterranean Sea at depths of 18 to 280 m (Manooch and Hassler, 1978; Vassilopoulou and Papaconstantinou, 1992). In the South Atlantic Bight (SAB) off the southeastern coast of the United States, red porgy are commonly associated with sponge or coral habitat (or both) with rocky outcrops and rocky ledges (Grimes et al., 1982), frequently referred to as "live bottom." Areas of live bottom are distributed patchily throughout the SAB, and patch size can range from square meters to square kilometers (Powles and Barans, 1980). Nevertheless, red porgy in the SAB are thought to constitute a single stock (Manooch and Huntsman, 1977).

Red porgy are an important segment of the commercial fisheries of the SAB, averaging 6% of the snapper-grouper landings since 1978 (SAFMC¹). Similarly, red porgy make up a considerable portion of the recreational harvest of reef fishes in the SAB (Huntsman et al.²). The fishery for red porgy in the SAB has, however, experienced a serious decline in landings since 1982 (Vaughan et al., 1992; Huntsman et al.²), as well as a decline in fishery-independent catch per unit of effort (CPUE) (Fig. 1). Estimates of stock size derived from virtual

population analysis (VPA) showed a peak population size in 1975 and a steady decline through 1992 (Vaughan et al., 1992; Huntsman et al.²). Although estimates of stock size derived from fishery-independent CPUE for 1993–1995 suggest a slight population recovery (Harris, personal obs.), the spawning stock ratio, estimated at 18% in 1993, is still considerably below the 30% level used by the South Atlantic Fishery Management Council to define when a species is overfished (Huntsman et al.²).

Apart from a size limit instituted in 1992, management of the fishery has remained essentially unchanged, in spite of an apparent continual decline of the resource. The ability of fishermen to locate good fishing areas (i.e. patches of live bottom) precisely using LORAN-C and Global Positioning Systems technology and

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¹ SAFMC. 1991. Amendment 4, regulatory impact review and final environmental impact statement for the snapper grouper fishery of the South Atlantic Region. South Atlantic Fishery Management Council, 1 South Park Circle, Charleston, SC, 225 p.

² Huntsman, G. R., D. S. Vaughan, and J. C. Potts. 1993. Trends in population status of the red porgy *Pagrus pagrus* in the Atlantic Ocean of North Carolina and South Carolina, USA, 1971–1992. South Atlantic Fishery Management Council, 1 South Park Circle, Charleston, SC 29422.

an increase in the number of vessels participating in the snapper-grouper fishery in the SAB resulted in a steadily increasing fishing mortality from 1972 through 1993 (Huntsman et al.²). For new management regulations to be considered, current life history data need to be made available. The most recent published discussion of SAB red porgy life history was based on data collected between 1972 and 1974 (Manooch, 1976; Manooch and Huntsman, 1977).

It has been shown that age structure, size-at-age, and reproductive strategies of a population will change in a predictable fashion that responds to declining abundance (Lack, 1968; Rothschild, 1986). There is, however, concern over the extent and permanence of these changes (Edley and Law, 1988; Bohnsack, 1990). The effect of sustained heavy exploitation, combined with current management strategies in regard to particular size restrictions and quotas or bag limits on the life history of a fished stock, is poorly documented. Staff of the Marine Resources Monitoring, Assessment, and Prediction Program (MARMAP), a federally funded program based at the South Carolina Department of Natural Resources in Charleston, SC, have collected life history data on red porgy since 1979. When combined with data collected from 1972 through 1974 (Manooch, 1976; Manooch and Huntsman, 1977), data spanning 24 years were available to determine if the life history of the red porgy population in the SAB had changed.

Long-term life history data and the increase in fishing pressure provide a mechanism to test the impact of sustained exploitation on the life history of a reef fish species in the SAB. Therefore, the objectives of this paper were to describe temporal changes in the age, growth, and reproduction of red porgy for four periods during 1972–94 and to identify annual changes in age and growth that occurred during 1988–94.

Methods

Red porgy were collected from 1979 to 1994 during standard MARMAP sampling with chevron traps, hook-and-line gear, Florida traps, and blackfish traps (Collins, 1990; Collins and Sedberry, 1991) in the SAB from Cape Fear, North Carolina, to Cape Canaveral, Florida. Specimens were collected during daylight

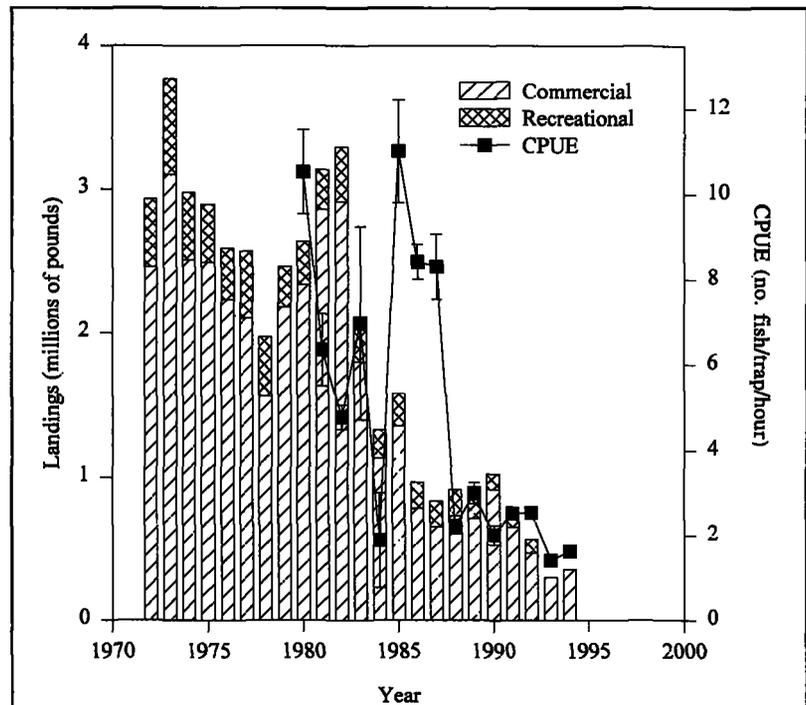


Figure 1

Commercial and recreational landings of red porgy since 1972. Recreational landings are from headboat surveys conducted by the Beaufort Laboratory of the National Marine Fisheries Service (70%), and the Marine Recreational Fisheries Statistics Survey (30%). CPUE = MARMAP trap catch per unit of effort.

hours primarily between May and August of each year.

MARMAP sampling strategies changed slightly between 1979 and 1994. From 1979 to 1987, samples were collected randomly from four large areas of live bottom (identified by using underwater television) with hook-and-line gear, blackfish traps, and Florida traps to follow trends in the abundance of the various species. Additional sites outside these areas were sampled as time and weather conditions allowed (see Collins and Sedberry, 1991). Traps were baited with cut clupeids, buoyed off the research vessel, and soaked for one to four hours. Hook-and-line gear consisted of bandit reels (commercial bottom-fishing hook-and-line gear) or rod and reel with 6/0 Penn Senator high-speed reels and Electramate electric motors. Terminal gear always consisted of three hooks fished vertically and baited with cut squid or cigar minnow (*Decapterus* sp.). All fishes caught were measured (mm fork length [FL]), and the total weight for each species, from each collection, was recorded (g). All red porgy collected during these years were kept for life history studies.

In 1988 and 1989, a chevron trap was added to the gear used to sample reef fishes. During these years, the research vessel was anchored over a known live

bottom area that was verified with underwater television. Each of the three trap types (blackfish, Florida, and chevron) was deployed either from the bow, stern, or midships of the research vessel (see Collins, 1990). Hook-and-line collections were taken with rod and reel and with the three-hook terminal rig. Fishes were processed as described for 1979–87. All red porgy collected in 1988 and 1989 were kept for life history studies.

Based on the data collected during 1988 and 1989, a decision was made to discontinue the use of blackfish and Florida traps in 1990 because chevron traps sampled a greater species diversity (Collins, 1990). During the late 1980's, all live bottom locations identified during underwater television surveys and from sampling in previous years were plotted with LORAN-C coordinates to the nearest 0.1 μ s and included in a sample site database. Currently, there are over 2,500 live bottom sites in the MARMAP database, from which 300–600 randomly chosen sites have been sampled each year since 1989. In addition, since 1989, the SAB has been stratified on the basis of latitude. Zone 1 includes all sites sampled south of 32°N, zone 2 all sites between 32°N and 33°N, and zone 3 all sites north of 33°N. Buoyed chevron traps were deployed from the research vessel and soaked for approximately 90 minutes. Hook-and-line (rod-and-reel) collections were made for 30 minutes at dawn or dusk. All fishes sampled were processed as in previous years. Because of concerns about potential gear selectivity, the length frequency of all red porgy caught by all four gear types during 1988 and 1989 was compared.

Since 1989, fork lengths (cm) and total weight (10 g) were recorded for all red porgy sampled in each zone for each year with a Limnoterra FMB-IV electronic fish measuring board and a Toledo electronic scale interfaced with a XT-type personal computer. In 1990 and 1994, all red porgy collected during sampling were used for life history studies. In 1991–93, up to 15 fish from each 1-cm size class and all fish larger than 350 mm FL were kept from each zone for life history studies. Red porgy used for life history studies were measured to the nearest mm (total length [TL], FL, and standard length [SL]) with a Limnoterra FMB-IV electronic fish measuring board interfaced with a XT-type personal computer. Individual weights were measured to the nearest gram with a triple beam balance.

Age and growth

Sagittae were removed at sea and stored dry. In the laboratory, the whole right otolith was immersed in cedar wood oil and examined for annuli (one translucent and one opaque zone) (Manooch and Hunts-

man, 1977) with a dissecting microscope with incandescent reflecting light and an ocular micrometer (1979–87) or with a dissecting microscope and reflected light from a fiber-optic light source (1988–94). The latter microscope had an attached Hitachi KP-C550 video camera connected to a personal computer equipped with a MATROX frame grabber and OPTIMAS image analysis software. The digitized image was viewed on a television monitor, and annuli were measured with OPTIMAS software. For both systems, measurements were taken from the core of each otolith to the outer edge of each opaque zone and to the edge of the otolith on a straight line midway between the posterodorsal dome and the most posterior point on the otolith (Frizzel and Dante, 1965). Annuli on this plane were consistently clearer and easier to enumerate, especially for older fish. For years where large numbers of red porgy were collected, a minimum of 350 randomly chosen fish were aged per year. All fish larger than 350 mm (FL) were aged for all years. The first reader collected measurements from all otoliths, whereas the second reader counted increments from a randomly chosen 35% of otoliths for each year. If agreement between the two counts was less than 90% for any year, the second reader read all otoliths for that year. When counts differed, otoliths were reread by both readers and discarded from further analyses if a difference in readings persisted.

Back-calculated lengths-at-age were computed by using the scale proportional hypothesis (Francis, 1990):

$$L_i = - (a/b) + (L_c + a/b) (O_i / O_c),$$

where L_i = length at the formation of the i th increment;

O_i = otolith radius at the formation of the i th increment;

O_c = otolith radius at the time of capture;

L_c = fish length at the time of capture;

a = intercept of otolith radius on fish length regression;

b = slope of the otolith radius on fish length regression.

Lengths were backcalculated to the most recently formed increment for comparisons of annual growth (1988–94) and to all increments for comparisons between periods (1979–81, 1988–90, and 1991–94). The SigmaPlot curve-fitting module with the Marquardt-Levenburg algorithm was used to fit von Bertalanffy growth curves to the mean back-calculated length-at-age for each year or period (SigmaPlot, 1994).

Because red porgy are protogynous sparids, and undergo a size- and behavior-related transition from

females to males, no comparison of size-at-age or growth rates were undertaken for the sexes separately. Life history data collected during four periods (1972–74, 1979–81, 1988–90, and 1991–94) were compared. The first study (1972–74) used red porgy sampled from headboats operating from North and South Carolina (see Manooch, 1976; Manooch and Huntsman, 1977). Specimens were collected throughout the year and gonads from 736 fish were examined macroscopically to assess sex and stage of maturity (Manooch, 1976). Scales from 3,278 individuals were examined to determine ages, and 222 fish were aged from whole otoliths (Manooch and Huntsman, 1977).

Red porgy collected during 1979–81, 1988–91, and 1991–94 were grouped by period. Otolith radius to fork length least-squares regressions were fitted separately for each period (except that of 1972–74) owing to concerns about temporal changes in somatic growth. Von Bertalanffy growth curves (von Bertalanffy, 1938) were fitted to the mean back-calculated size-at-age for each of the four study periods. Size-at-age was backcalculated for all increments measured. Mean observed and back-calculated sizes-at-age were compared between periods for each age with a single-factor ANOVA. Size and age distributions and size-at-age were compared between the three latitudinal zones sampled with single factor and two-way ANOVA's. It appeared from observations during sampling that larger fish may be associated with the shelf break; therefore size and age distributions, and size-at-age were also compared for different depths. Because the shelf break is located at about 48 m, two depth zones—0 to 45 m and 46 to 90 m—were compared. The same tests were performed in comparing annual data collected between 1988–94.

Reproduction

The posterior portion of the gonads of red porgy from 1979 to 1994 was removed from the fish and fixed in 10% seawater formalin for 1–2 weeks, then transferred to 50% isopropanol for 1–2 weeks. Gonad samples were processed with an Auto-Technicon 2A Tissue Processor, vacuum infiltrated, and blocked in paraffin. Three transverse sections (6–8 μm thick) were cut from each sample with a rotary microtome, mounted on glass slides, stained with double-strength Gill haematoxylin, and counter-stained with eosin y. Sex and reproductive state were assessed by one reader according to histological criteria (Table 1). Specimens with developing, ripe, spent, or resting gonads were considered sexually mature. For females, this definition of sexual maturity included specimens with oocyte development at or beyond the

yolk vesicle stage and specimens with beta, gamma, or delta stages of atresia. Sex ratios, size-at-first-maturity, and the percent of mature females by 20-cm size class were calculated for all functional males and females, 1989–94. Sex ratio, size-at-first-maturity, and the percent of mature females were determined by size class for 1979–81, 1988–90, and 1991–94, and chi-square (χ^2) analysis was used to determine if there were significant differences in the proportion of males to all fish collected during the three periods and if there were differences in size-at-maturity between periods.

Results

1979–1994

A total of 20,756 (13,120 during 1972–74) red porgy were sampled during the four periods, of which 4,503 were aged and 4,293 sexed and staged (Table 2). The mean FL of fish collected from 1979 to 1994 showed a declining trend; however, there was no trend in mean age (Table 2). Increment formation was assumed to be annual (Collins et al., 1996; Manooch and Huntsman, 1977).

Age and growth

The mean observed size-at-age declined markedly from 1972–94 through 1991–94. Except for fishes aged 2–8 yr collected during 1979–81, the mean sizes-at-age for all ages for the three periods between 1979 and 1994 were smaller than those during 1972–94 (Fig. 2). The observed sizes-at-age in 1988–90 and 1991–94 were significantly smaller than those during 1979–81 ($P < 0.01$) for ages 2 through 8. Red porgy aged 3 through 5 collected during 1991–94 were also significantly smaller than fish of the same age collected during 1988–90 ($P < 0.01$). We were unable to include data collected by Manooch and Huntsman (1977) in our statistical analyses. The mean back-calculated size-at-age showed trends similar to the mean observed size-at-age (Fig. 3). Fish aged 2–8 were significantly smaller during 1988–90 and 1991–94 than during 1979–81, and fish aged 2–5 significantly smaller in 1991–94 than in 1979–81 and 1988–90.

The von Bertalanffy growth curves derived from mean back-calculated lengths for each period (Fig. 4) showed similar trends. The theoretical mean maximum fork length (L_∞) declined by 100 mm from 1972–74 to 1991–94 (Table 3). The theoretical growth rate (k) was higher between 1991 and 1994 than between 1972 and 1974. This difference is a reflection of the large decline in L_∞ , rather than an increase in growth

Table 1

Histological criteria developed by MARMAP (Charleston, SC) to determine reproductive stage in red porgy, *Pagrus pagrus* (see D'Ancona, 1949, 1950; Wallace and Selman, 1981; Alekseev, 1982, 1983; Hunter et al., 1986; Sadovy and Shapiro, 1987; Matsuyama et al., 1988; West, 1990; Roumillat and Waltz¹).

Reproductive state	Male	Female
Immature (virgin)	No primary males found. Juveniles were either females or, infrequently, simultaneous or transitional (see below).	Previtellogenic oocytes only; no evidence of atresia. In comparison with resting female, most previtellogenic oocytes <80 μm , area of transverse section of ovary is smaller, lamellae lack muscle and connective tissue bundles and are not as elongate, germinal epithelium along margin of lamellae is thicker, ovarian wall is thinner.
Developing	Development of cysts containing primary and secondary spermatocytes through some accumulation of spermatozoa in lobular lumina and dorsomedial sinuses.	Oocytes undergoing cortical granule (alveoli) formation through nucleus migration and partial coalescence of yolk globules.
Running and ripe	Predominance of spermatozoa in lobules and dorsomedial sinuses; little or no occurrence of spermatogenesis.	Completion of yolk coalescence and hydration in most advanced oocytes. Zona radiata becomes thin. Postovulatory follicles sometimes present.
Developing, recent spawn	Not assessed.	Developing stage as described above as well as presence of postovulatory follicles.
Spent	No spermatogenesis; some residual spermatozoa in lobules and sinuses.	More than 50% of vitellogenic oocytes with alpha- or beta-stage atresia.
Resting	Little or no spermatocyte development; empty lobules and sinuses.	Previtellogenic oocytes only; traces of atresia. In comparison with immature female, most previtellogenic oocytes >80 μm , area of transverse section of ovary is larger, lamellae have muscle and connective tissue bundles, lamellae are more elongate and convoluted, germinal epithelium along margin of lamellae is thinner, ovarian wall is thicker.
Mature specimen, stage unknown	Mature, but inadequate quantity of tissue or post-mortem histolysis prevent further assessment of reproductive stage.	Mature, but inadequate quantity of tissue or post-mortem histolysis prevent further assessment of reproductive stage.
Simultaneous (bisexual)	Presence of distinct ovarian and testicular regions in approximately equal amounts and of the same reproductive state. This gonad structure was infrequently observed in both juvenile and adult fish.	
Transitional	Ventrolateral proliferation of active testicular tissue (spermatogonia through spermatozoa) along the outer surface of the ovarian wall in spent or resting ovary (functional protogyny) or immature ovary (juvenile protogyny). As testicular tissue envelopes regressing ovary, ovary collapses laterally and sperm sinuses form within former ovarian wall.	

¹ Roumillat, W. A., and C. W. Waltz. 1993. Biology of the red porgy, *Pagrus pagrus*, from the southeastern United States. MARMAP Final Data Report, South Carolina Department of Natural Resources, Charleston, SC. 38 p.

rate (i.e. the negative relation between L_{∞} and k). However, k was highest for the 1979–81 period, when L_{∞} was also still relatively high.

Reproduction

Our examination of 4,293 gonads ($n=1,397$, 1979–81; $n=727$, 1988–90; $n=2,169$, 1991–94) revealed that

sexual transition was occurring at smaller sizes in the later periods. There was a significant increase ($P<0.001$) in the number of males with time (Table 4). However, in 1988–90 and in 1991–94, the proportion of males to the total number of fish sexed was significantly greater at smaller sizes than during 1979–81 (Table 4). At 301–350 mm TL, male red porgy made up 24% of the fish that were sexed dur-

Table 2

Sampling data for the four study periods 1972–74, 1979–81, 1988–90, and 1991–94.

Year	Fish sampled	No. aged	Mean fork length (mm)	Mean age (years)	No. sexed
1972–74	13,120	222	—	—	—
1979–81	1,933	1,177	293	3.07	1,397
1988–90	1,853	1,261	254	2.44	727
1991–94	3,850	1,843	257	3.062	2,169
Total	20,756	4,503	268	2.86	4,293

ing 1991–94, in contrast with 7% at the same size interval during 1979–81 ($P < 0.001$; Table 4). In 1979–81, male red porgy constituted 12% of the fish examined at 351–400 mm TL compared with 32% in 1988–90 ($P < 0.01$) and 49% in 1991–94 ($P < 0.001$; Table 4).

Size-at-maturity of female red porgy has also changed. Female red porgy became sexually mature at smaller sizes in 1991–94 than in 1979–81. During 1991–94, female red porgy first became sexually mature at 176–200 mm TL (mean age=0.9). In 1979–81, the first mature female was at 201–225 mm TL (mean age=0.9) (Table 5). There were significantly more mature females (54%; $P < 0.001$) at 251–275 mm TL (mean age=1.9) in 1991–94 than during 1979–81 (27%; mean age=1.7).

1988–1994

A total of 2,629 live bottom stations and 5,265 red porgy were sampled May through August 1988–94, of which 4,349 specimens were kept for life history studies (Table 6). The majority of the samples were collected with chevron traps. During 1988 and 1989, there was no difference between the size range of red porgy collected in chevron traps and the size range of red porgy collected in blackfish traps, Florida traps, hook-and-line gear, or all three of these gear types combined (Fig. 5). Similarly, there was no difference in the size range of red porgy sampled by hook-and-line gear and chevron traps between 1990 and 1994 (Fig. 5). Between 1988 and 1991, however, the mean size of red porgy captured with hook and line was significantly larger each year than the mean size of porgy taken with the remaining gear types ($P < 0.05$), although there was no significant difference between mean size of fish captured with the gear types used in 1993 and mean size of fish captured with the gear types used in 1994. The size of red porgy sampled during 1988–94 ranged from 90 to 501 mm

Table 3

Von Bertalanffy growth equation parameters derived from the mean back-calculated fork length for each time period.

Parameter	1972–74	1979–81	1988–90	1991–94
k	0.226	0.343	0.273	0.281
L_{∞}	459.3	391.4	382.7	356.4

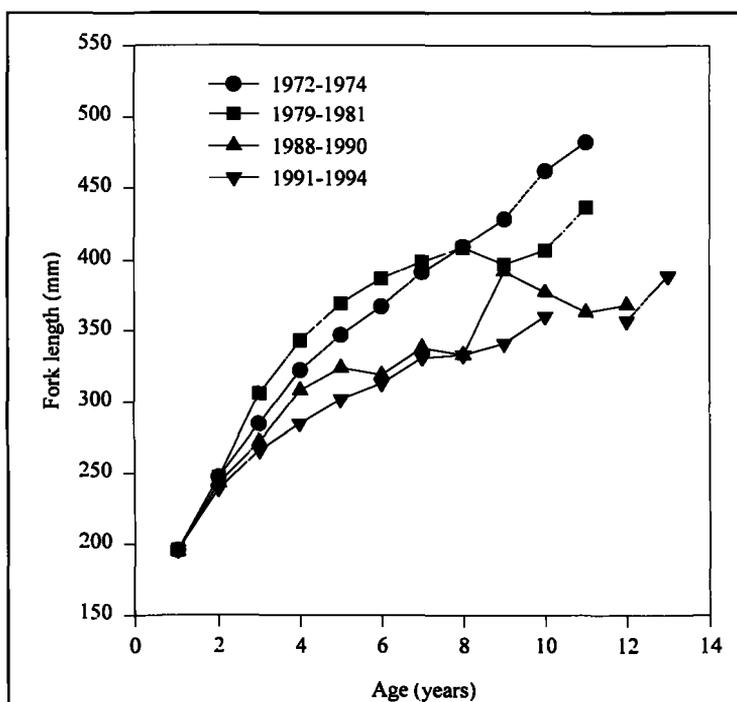


Figure 2

The mean size at capture for red porgy collected in 1972–74, 1979–81, 1988–90, and 1991–94. Ages for red porgy collected between 1972 and 1974 were taken from Manooch and Huntsman (1977).

FL. The mean size was 256 mm FL, with the highest frequency occurring at 240 mm FL. The length frequency of aged red porgy was very similar to the length frequency of all red porgy sampled.

Age and growth

Ages were obtained for 2,935 (67%) of the red porgy otoliths collected (Table 6). Agreement between the first and second reader averaged 93%, and was never less than 90% for any year. The mean observed size-at-age declined for most ages between 1988 and 1994 (Table 7), although there was a significant increase in the mean age of red porgy over the study period (Fig. 6; $P < 0.01$; $r^2 = 0.94$). The mean observed size-at-age for red porgy 2 years and older sampled during 1988 and 1989 was significantly larger than all other years, with the mean observed size-at-age in 1992 and 1993 consistently the smallest (Table 7; Fig. 7). Above age 6, growth rates appeared to taper off sharply for all years (Fig. 7). Age-6 red porgy collected during 1988 had the third highest mean length recorded for all age classes in any year. Similar to the mean observed size at age, mean back-calculated size at the most recent annulus was significantly larger for 1988 and 1989 compared with other years for ages 2 and greater and also appeared to reach asymptotic size at age 6 for each year (Table 8; Fig. 8).

The von Bertalanffy growth curves fitted to the mean back-calculated growth size at most recent age (ages 1–10) for each year demonstrated some differences between years (Fig. 9), with growth curves from 1988 and 1989 showing larger fish at age, and higher L_{∞} and k . Both k and L_{∞} tended to decrease dur-

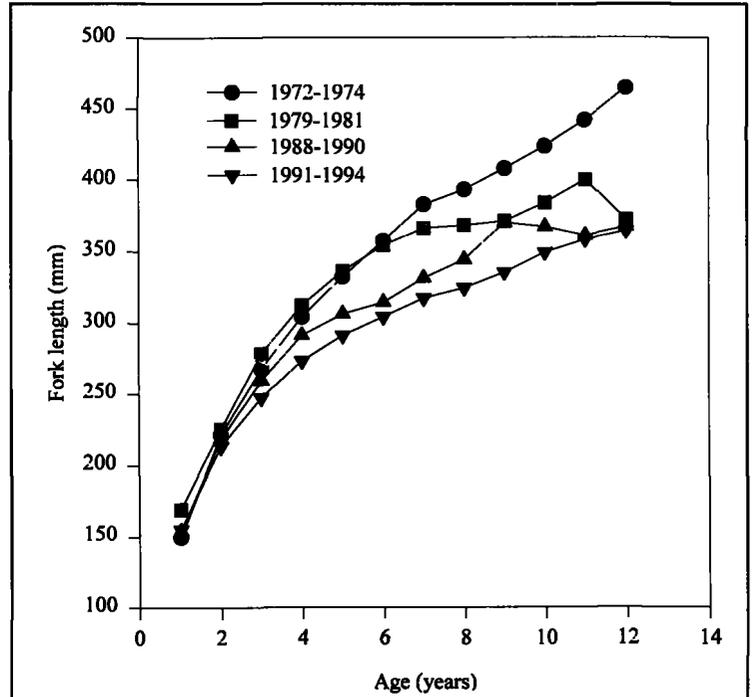


Figure 3

The mean back-calculated size at age for red porgy collected in 1972–74, 1979–81, 1988–90, and 1991–94. Back-calculated lengths for red porgy collected between 1972 and 1974 were derived from scale ages.

ing the study period, although neither of these trends were significant (linear regression; $P > 0.05$; Fig. 10).

No significant differences were apparent in size distribution, age distribution, or size-at-age between

Table 4

Percentage of male red porgy relative to the total number of individuals sexed during 1979–81, 1988–90, and 1991–94. A significant difference (χ^2 ; $P < 0.01$) in the proportion of males for a particular size class collected during 1979–81 is denoted by "A". A significant difference (χ^2 ; $P < 0.01$) in the proportion of males that were collected during 1988–90 is denoted by "B".

Size (mm TL)	1979–81			1988–90			1991–94		
	Total	Males	%Males	Total	Males	%Males	Total	Males	%Males
<200	19	—	—	16	—	—	57	—	—
200–250	216	—	—	140	2	1.43	372	4	1.08
251–300	271	10	3.69	163	5	3.07	491	33	6.72 ^B
301–350	313	21	6.71	226	25	11.06	814	194	23.83 ^{AB}
351–400	239	29	12.13	136	44	32.35 ^A	371	183	49.33 ^{AB}
401–450	160	38	23.75	38	17	44.74 ^A	57	25	43.86 ^A
451–500	158	108	68.35	8	4	50.00	6	4	66.67
501–550	18	12	66.67	—	—	—	1	—	—
551–600	2	1	50.00	—	—	—	—	—	—
Total	1,397	220		727	97		2,169	443	

the three latitudinal zones. However, significant differences were apparent in the size and age distribution between the two depth zones ($P < 0.05$), with larger and older fish occurring in the deeper zone. There were no significant differences in the size-at-age between these two zones ($P > 0.05$).

Discussion

Samples were collected from throughout the SAB during 1988–94. However, 69% of the collections and 73% of the aged red porgy were taken from zone 2 (32°N–33°N). Zone 2 was sampled most frequently because it was most accessible from Charleston, South Carolina, the base of operations (latitude 32° 45'N). Once settled, red porgy do not appear to move very much (Parker, 1990) and could experience differential growth rates because of differing environments. Therefore the concentration of sampling in zone 2 could have resulted in biased estimates of size-at-age. However, the comparison of size-at-age of red porgy showed no significant differences between latitudinal or depth zones; therefore, although there may be localized differences in growth rates, perhaps associated with different patches of live bottom, the mean growth rate appears to be similar throughout the region. The mean depth and temperature of areas sampled in the MARMAP surveys have not changed significantly since 1987; thus these environmental variables, at least, have not caused the life history changes in red porgy (Fig. 11).

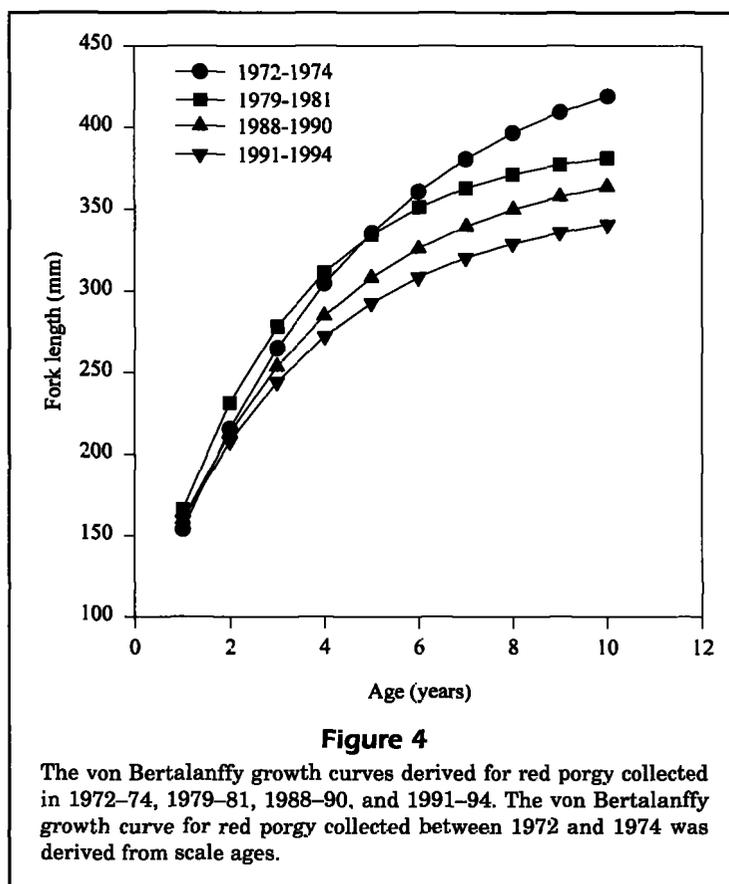


Figure 4

The von Bertalanffy growth curves derived for red porgy collected in 1972–74, 1979–81, 1988–90, and 1991–94. The von Bertalanffy growth curve for red porgy collected between 1972 and 1974 was derived from scale ages.

There were significant differences in size and age by depth, with larger and older fish occurring in deeper water. This difference may be due to fishermen operating in deeper water with larger hooks and baits to target groupers, thus reducing the availability of this gear to red porgy, particularly to smaller

Table 5

Percentage of red porgy females that were sexually mature relative to all females collected during 1979–81 and 1991–94. A significant difference (χ^2 ; $P < 0.01$) in the proportion of mature females is denoted by "A".

Size (mm TL)	1979–81			1991–94		
	Total females	Number mature females	Percent mature females	Total females	Number mature females	Percent mature females
<200	16	—	—	55	2	3.64
200–225	91	1	1.10	182	4	2.20
226–250	85	11	12.94	156	26	16.67
251–275	103	28	27.18	157	85	54.14 ^A
276–300	78	77	98.72	211	189	89.57
>300	512	512	100.00	615	606	98.54
Total	885	62	1,376	912		

individuals. Therefore, red porgy in deeper water may experience reduced fishing mortality in comparison with those in shallower waters. In shallower water,

fishermen reduce hook and bait size to catch smaller fishes, and more red porgy of all sizes are landed. Alternatively, the increase in size and age with depth

Table 6

Sampling data for 1988–94, collected from the RV *Oregon* (1988–89) and the RV *Palmetto* (1990–94).

Year	Trap collections	No. porgy	Hook-and-line collections	No. porgy	No. processed	No. aged
1988	84	294	261	170	427	371
1989	65	248	198	174	388	345
1990	348	957	111	44	997	545
1991	306	830	33	25	519	426
1992	324	1,107	25	1	494	419
1993	414	722	52	45	538	385
1994	370	1,107	38	11	986	444
Total	1,911	5,265	718	470	4,349	2,935

Table 7

Mean observed fork length (mm) at age for red porgy (standard error in parenthesis).

Age (yr)	1988	1989	1990	1991	1992	1993	1994
1	191 (2) n=124	203 (3) n=70	197 (3) n=78	200 (2) n=126	190 (2) n=78	206 (3) n=70	186 (1) n=53
2	256 (2) n=107	248 (2) n=149	234 (2) n=218	237 (2) n=110	228 (2) n=119	245 (3) n=78	253 (2) n=101
3	284 (3) n=95	284 (4) n=54	264 (2) n=180	274 (3) n=71	261 (3) n=72	267 (3) n=104	264 (3) n=50
4	328 (7) n=26	305 (5) n=39	295 (5) n=26	282 (4) n=70	287 (3) n=64	290 (4) n=59	283 (3) n=106
5	386 (34) n=2	328 (6) n=18	314 (10) n=16	303 (8) n=17	305 (4) n=43	308 (5) n=35	297 (3) n=86
6	334 (7) n=4	305 (34) n=3	317 (13) n=5	335 (7) n=13	310 (7) n=14	305 (5) n=25	313 (5) n=32
7	374 (10) n=5	340 (35) n=3	308 (7) n=6	339 (20) n=5	321 (7) n=8	359 n=1	334 (5) n=9
8	352 (3) n=4	335 n=1	307 (9) n=3	322 (5) n=4	328 (5) n=2	348 (25) n=6	324 (6) n=4
9	389 n=1	394 (42) n=2	384 (17) n=2	362 n=1	344 (8) n=6	322 (18) n=2	
10		372 (28) n=2		361 (16) n=4		344 (7) n=2	390 n=1
11		363 n=1					
12		368 n=1			360 n=1	354 n=1	
13					390 (9) n=2		

could reflect a gradual movement of red porgy towards deeper water as they age. Grimes et al. (1982) suggested that red porgy associated with shallow reefs may temporarily move to deep water in response to unusually cold water temperatures. However, tagging studies have shown that settled red porgy undertake very little long-term movement (Grimes et al., 1982; Parker, 1990). Another reef species, black sea bass (*Centropristis striata*), has shown limited movement of larger fish to deeper water (Ulrich and Low³; Harris and McGovern, personal obs.).

Fishing mortality (F) of red porgy has increased since 1972, although between 1972 and 1975 it showed a slight decline (Vaughan et al., 1992). The

F for fully recruited ages (5–9) increased from 0.2 in 1976 to 1.3 in 1991 (Huntsman et al.², Murphy VPA, $M=0.28$). The F for ages 1–4 showed similar trends, although the magnitude of the increase was less (Huntsman et al.², Murphy VPA, $M=0.28$). Owing to the changes in the life history of red porgy since 1972, these estimates of fishing mortality are probably high; yet, the increasing trend in fishing pressure is evident. Except for an increase during 1981–83, landings of red porgy have been declining since 1973 (Fig. 1). Similarly, the number of recruits to age 1 have declined steadily since 1974 (Huntsman et al.², Murphy VPA, $M=0.28$). An estimate of SSR in 1993 was only 18% (Huntsman et al.², Murphy VPA, $M=0.28$). Again, the changes in the life history of red porgy since 1972 indicate that Huntsman et al.² may have underestimated the decline in the abundance of age-1 fish.

Concurrent with the fishery becoming increasingly overexploited, there has been corresponding change

³ Ulrich, G. F., and R. A. Low. 1992. Movement and utilization of black sea bass, *Centropristis striata*, in South Carolina. Final Unpubl. Rep. NOAA Award No. NA90AA-D-FM656, 11 p.

Table 8
Mean back-calculated fork length (mm) at age for red porgy (most recent annulus; standard error in parenthesis).

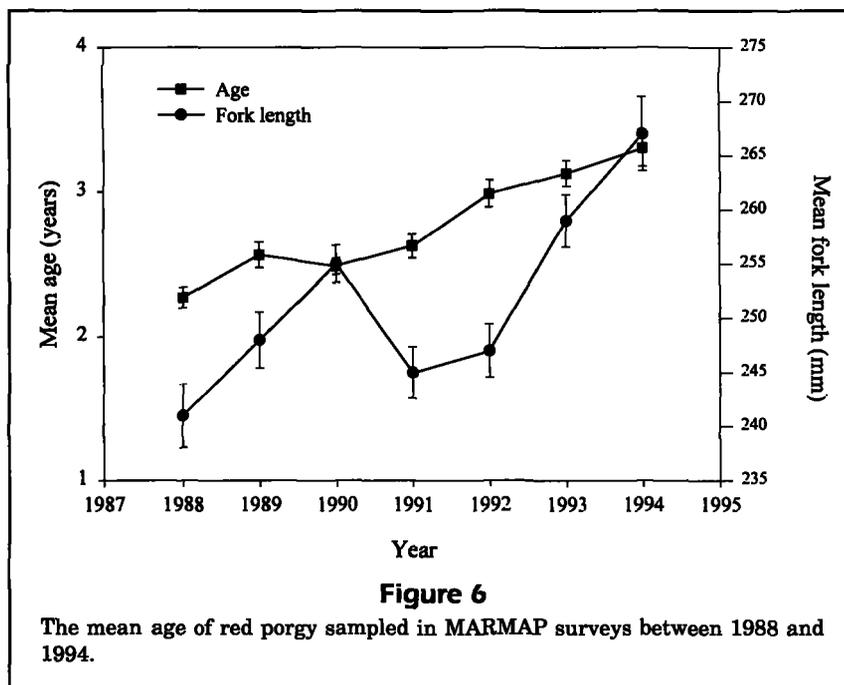
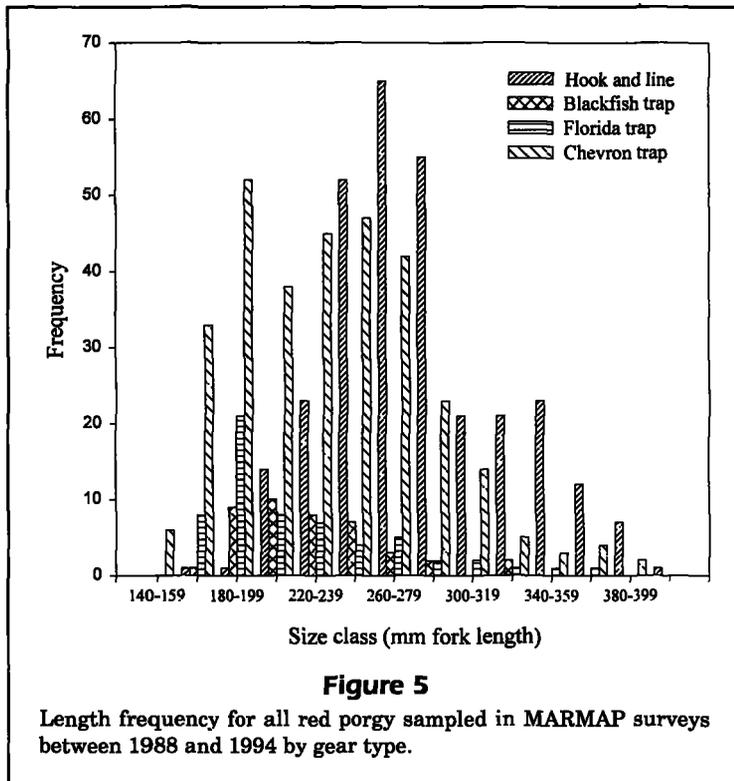
Age (yr)	1988	1989	1990	1991	1992	1993	1994
1	163 (2) <i>n</i> =124	180 (3) <i>n</i> =70	173 (4) <i>n</i> =78	166 (2) <i>n</i> =126	159 (2) <i>n</i> =78	171 (2) <i>n</i> =70	161 (2) <i>n</i> =53
2	230 (2) <i>n</i> =107	233 (2) <i>n</i> =148	218 (2) <i>n</i> =218	219 (2) <i>n</i> =110	210 (2) <i>n</i> =119	227 (3) <i>n</i> =78	237 (2) <i>n</i> =101
3	266 (3) <i>n</i> =95	273 (3) <i>n</i> =54	252 (2) <i>n</i> =180	259 (3) <i>n</i> =71	246 (3) <i>n</i> =72	257 (3) <i>n</i> =104	253 (3) <i>n</i> =50
4	316 (6) <i>n</i> =26	300 (6) <i>n</i> =38	286 (5) <i>n</i> =26	271 (3) <i>n</i> =70	274 (3) <i>n</i> =64	281 (4) <i>n</i> =59	275 (3) <i>n</i> =106
5	382 (31) <i>n</i> =2	325 (7) <i>n</i> =18	304 (11) <i>n</i> =16	292 (8) <i>n</i> =17	298 (4) <i>n</i> =43	301 (5) <i>n</i> =35	291 (3) <i>n</i> =86
6	328 (7) <i>n</i> =4	301 (32) <i>n</i> =3	311 (13) <i>n</i> =5	326 (6) <i>n</i> =13	299 (7) <i>n</i> =14	298 (6) <i>n</i> =25	307 (5) <i>n</i> =32
7	369 (10) <i>n</i> =5	339 (34) <i>n</i> =3	294 (7) <i>n</i> =6	331 (18) <i>n</i> =5	313 (6) <i>n</i> =8	354 <i>n</i> =1	329 (5) <i>n</i> =9
8	347 (3) <i>n</i> =4	335 <i>n</i> =1	300 (10) <i>n</i> =3	314 (5) <i>n</i> =4	320 (4) <i>n</i> =2	351 (20) <i>n</i> =7	320 (6) <i>n</i> =4
9	389 <i>n</i> =1	392 (40) <i>n</i> =2		354 <i>n</i> =1	335 (8) <i>n</i> =6	292 <i>n</i> =1	
10		371 (27) <i>n</i> =2	378 (17) <i>n</i> =2	350 (16) <i>n</i> =4		336 (4) <i>n</i> =2	382 <i>n</i> =1
11		362 <i>n</i> =1					
12		367 <i>n</i> =1			356 <i>n</i> =1	349 <i>n</i> =1	
13					382 (8) <i>n</i> =2		

in the life history of red porgy during a 22-year period (1972 to 1994). The first study of age and growth on red porgy (1972–74) (Manooch and Huntsman, 1977) was assumed to describe a stock with the same life history as the virgin population, even though it

was subject to light fishing pressure. By the late 1970's and early 1980's, the growth pattern of the stock had changed. The mean observed and back-calculated lengths-at-age as well as the von Bertalanffy growth curve for the 1979–81 period showed a larger size at age for ages 2–6 but a lower theoretical maximum size. The increase in growth rate, and resultant increase in size-at-age observed during this period, is considered a typical density-dependent response to an increase in mortality as the depressed population responds to an increased availability of resources (Pitcher and Hart, 1982; Rothschild, 1986). The decrease in theoretical maximum size between 1979 and 1981 may have resulted from the selective removal of larger individuals from the population by fishermen and not from a biological change in the theoretical maximum size that the fish could attain.

During the mid 1980's through the early 1990's, increasing fishing pressure apparently continued the selective removal of larger, faster growing individuals from the population, further exacerbating the changes in the life history of red porgy. By 1988–90, mean back-calculated sizes-at-age were significantly smaller for all ages except age 1 in comparison with 1979–81. In 1988–90, the values of k and L_{∞} were smaller than during 1979–81 and 1972–74, indicating a reduced growth rate and a lower theoretical maximum attainable size. Mean back-calculated size-at-age for specimens collected between 1991 and 1994 were significantly smaller than those collected in 1988–90, except for ages 1, 7, and 10. These temporal reductions in the size-at-age and growth rates suggest that many individuals genetically predisposed towards rapid growth and larger size may have been selectively removed from the population, leaving behind individuals that tend to be slower growing and smaller.

Red porgy also responded to the continued removal of larger individuals from the population over many generations by females becoming sexually mature at smaller sizes during 1991–94 than during 1979–81. Manooch (1976) reported that female red porgy became mature at much larger sizes than those



found in the present study. Furthermore, the red porgy population has responded to increased fishing pressure by undergoing sexual transition and by producing significantly more males at smaller sizes in recent years than during 1979–81. Koenig et al. (1996) reported that gag, *Mycteroperca microlepis*, a protogynous grouper, was undergoing sexual transition at much smaller sizes during 1991–93 in the Gulf of Mexico than were reported by Hood and Schlieder (1992) for the same region, during 1977–80. Changes in life history aspects of gag from the Gulf of Mexico were attributed to steadily increasing fishing pressure.

The decrease in mean size-at-age, growth rates, and size-at-maturity during 1988–1994 is probably a continuation of the changing life history pattern of the population that has resulted from sustained fishing pressure and indicates the degree of change that can occur over relatively short periods of time. These relatively rapid changes in size-at-age may reflect the inability of an overfished or depressed population to absorb or respond to further decreases in population size. Apart from the decreases in size-at-age apparent from recent years, the mean age and fork length of the population has increased since 1988. These increases may be due to a decline in the number of younger fish recruiting to the population. The net effect of fewer young fish in the population (and therefore samples) would be an increase in the mean age and size of the sampled fish. Length-frequency data collected in MARMAP surveys since 1988 indicates no strong recruiting year class (age-1) since 1990. Huntsman et al.² found that the estimated number of 1-year-old red porgy had declined steadily since 1973 (Murphy VPA, $M=0.28$); their results also indicate that the population may be experiencing a decline in recruitment.

A decline in recruitment may be attributed to several factors that are the result of sustained overfishing. First, as the number of fish in the population declines, fewer and fewer females are available to spawn, resulting in a decline of total potential egg production (Vaughan et al., 1992; Huntsman et al.²). Second, decreases in size-at-maturity and size-at-age result

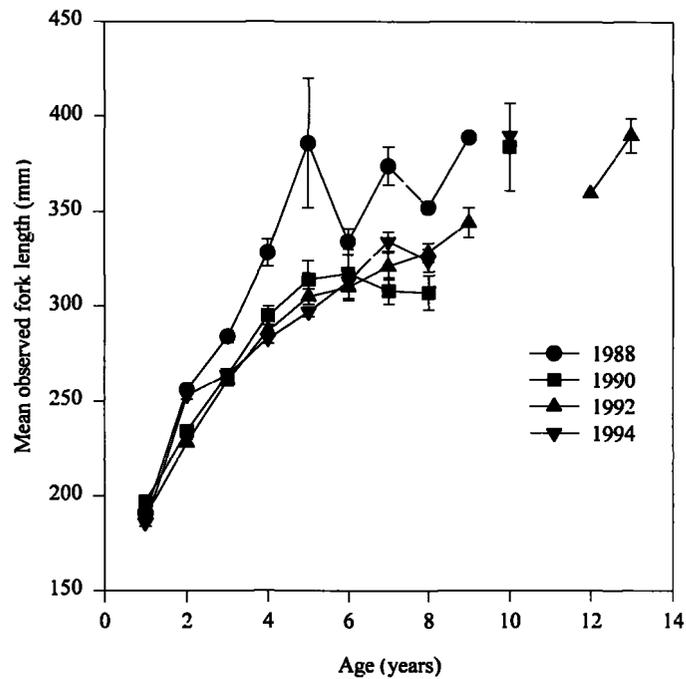


Figure 7
The mean observed size-at-age of red porgy for every second year between 1988 and 1994.

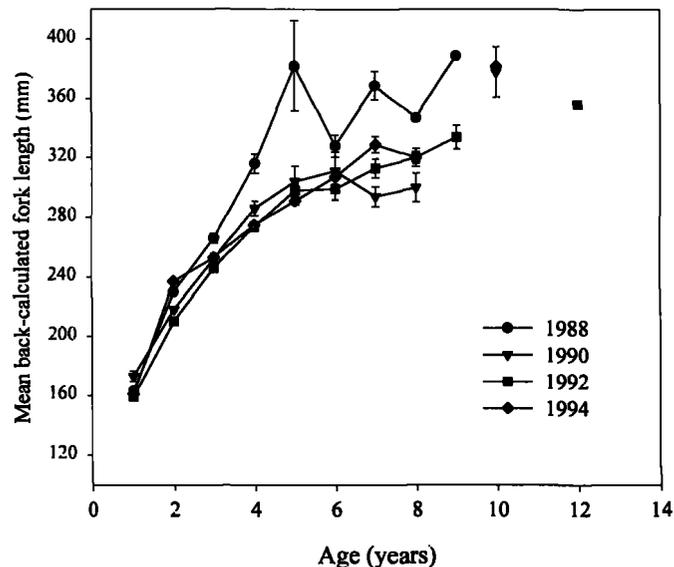


Figure 8
The mean back-calculated size-at-age for every second year between 1988 and 1994.

in fish that are less fecund than larger fish (Manooch, 1976). Finally, smaller females may produce eggs that are poorer in quality than those produced by larger

females because smaller individuals put more energy into somatic growth rather than into reproductive tissue (Rothschild, 1986). Zhao and McGovern⁴ found that an apparent population size threshold at 30% of the virgin spawning biomass existed for vermilion snapper (*Rhomboplites aurorubens*) in the SAB, below which recruitment failure was almost inevitable. A similar situation may exist for red porgy in the SAB, with recruitment failure exacerbated by the reduction in size of mature females.

Reproductive (i.e. recruitment) failure may also be affected by the change in size of male red porgy, as well as the changes in sex ratio that have occurred since 1972–74. Currently, some red porgy undergo transition at 200–250 mm FL. The sex ratio in 1991–94 at 352–400 mm FL was 1.3 males for each female. In 1972–74, the sex ratio for this size class was 0.06 males per female (Manooch, 1976, macroscopic sexing). Males began to outnumber females only above 451 mm FL. Koenig et al. (1996) have hypothesized that sperm limitation may be a factor in the decline of gag, *Mycteroperca microlepis*, in the northern Gulf of Mexico as the number of males in the population has declined. The size and number of male red porgy

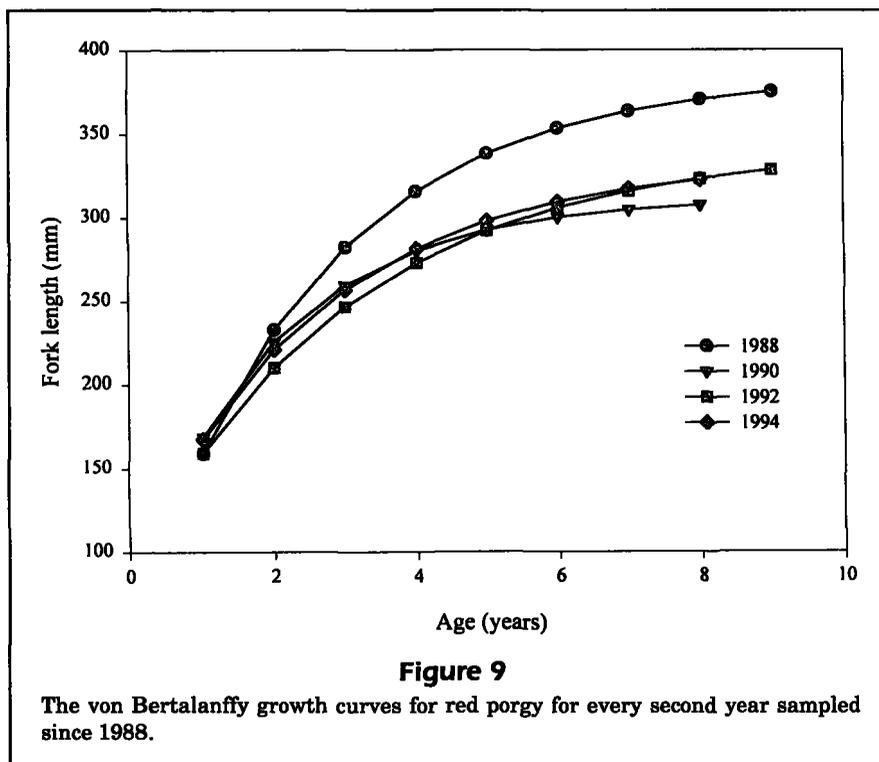
in the population have similarly been greatly reduced. The reduction in size and number of males may also be a significant factor in the decline in the number of 1-year-old red porgy recruiting to the SAB population.

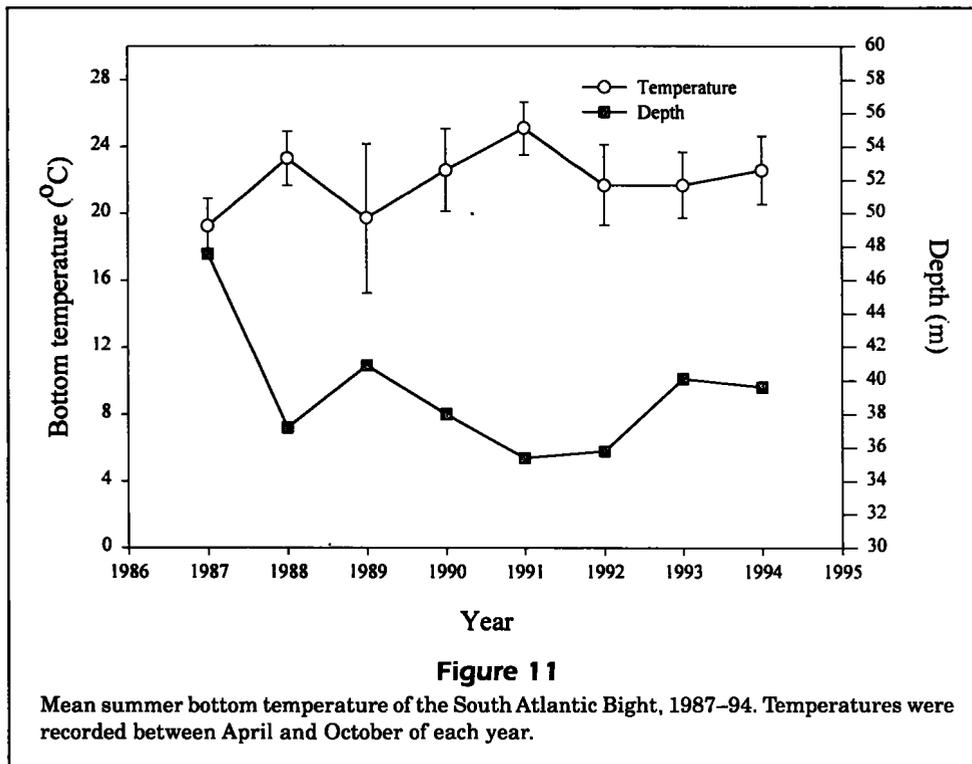
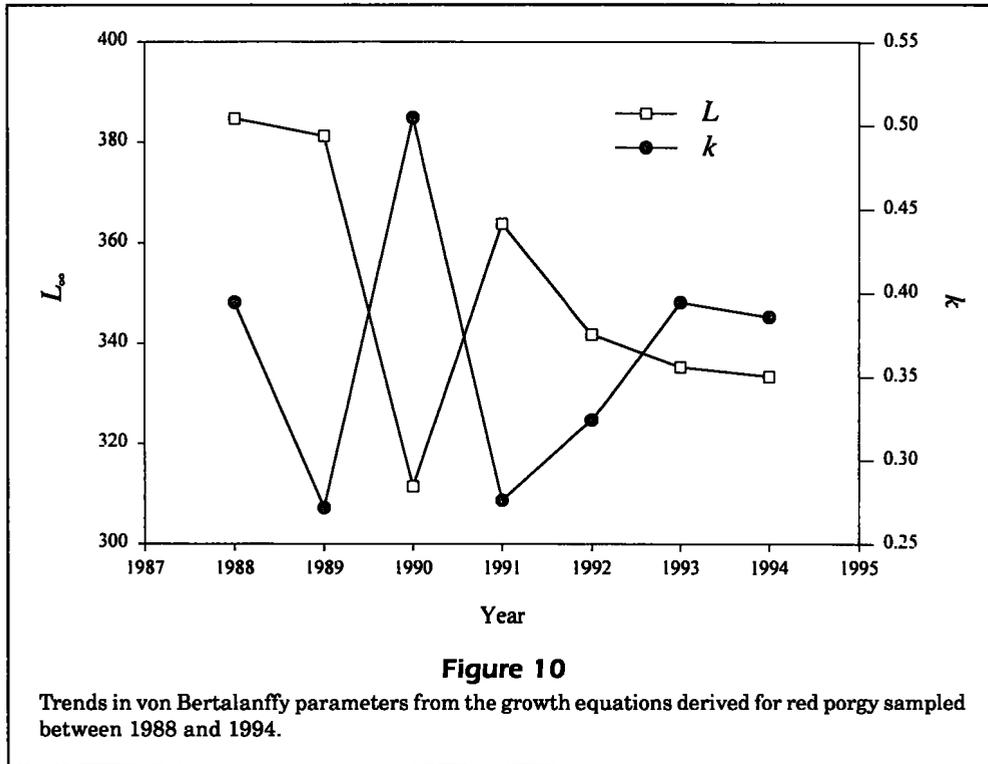
Huntsman et al.² concluded that the red porgy population of the SAB was overfished and that the population was severely depressed. These conclusions were based on the results of Murphy and separable VPA's that used only two age length keys—one from 1972–74 and one from 1986—and that used von Bertalanffy parameters and a length-weight relation from 1972–74. The life history of red porgy has changed markedly since 1986. In fact, as this study shows, significant decreases in size-at-age have occurred within a matter of years in this heavily fished population. The dramatic changes in the life history of red porgy and the resultant changes in parameters used for stock assessment suggest the status of the population in the SAB needs to be reassessed.

Protogynous fishes may be particularly vulnerable to sustained heavy fishing pressure and size selective mortality (Huntsman and Schaaf, 1994), particularly if sex reversal occurs primarily in response to exogenous controls (sociodemographic factors) (Koenig et al., 1996). The decline in size at sex transition since 1979 suggests that the timing of transition in red porgy is not determined by size, but rather by some social or behavioral stimulus.

Red porgy probably do not aggregate to spawn; instead they appear to be permanently schooled on the available areas of live bottom in the SAB. Koenig et al. (1996) suggested that if a population of protogynous fish remained aggregated throughout the year, transition could occur year-round and thus the normal male to female ratio could be maintained. If the numerical sex ratio is maintained, the impact of overfishing on a protogynous species is reduced (Huntsman and Schaaf, 1994). The increase in the sex ratio seen from 1979–81 to 1988–90 may represent overcompensation for the depletion of males from the population. The males of many reef-associated protogynous sparids show strong territoriality (van der Elst, 1988). If these males are more aggressive and are more likely to be caught by fishermen (Koenig et al.,

⁴ Zhao, B., and J. C. McGovern. 1995. Population characteristics of the vermilion snapper, *Rhomboplites aurorubens*, from the southeastern United States. Report to the South Atlantic Fishery Management Council, 1 South Park Circle, Charleston, SC 29422, 35 p.





1996; Gilmore and Jones, 1992), then another fish, presumably the largest (=dominant) female would take over that territory and begin to undergo transition (Shapiro, 1981). As modern technology allows

fishermen to locate good fishing sites precisely, all large fish could be removed from an area. The increase in the number of males seen during 1988–90 may also be a function of fish size. As large males

were removed from the population, smaller fish could occupy the now vacant territory and undergo transition. As new males became increasingly smaller, the size of the territory they could successfully hold might also become smaller, freeing territory for additional males. However, as the size of the fish declined even further, it is possible that the males would be unable to compete against other species, thereby further reducing the available habitat for red porgy males and reducing the sex ratio to the same level as that found in 1979–81.

It has been hypothesized that the selective removal of individuals predisposed to rapid growth and greater size may cause a genetic shift resulting in a population of slower growing, smaller individuals than those found in the unfished population (Bohnsack, 1990; Sutherland, 1990). Edley and Law (1988) found that individuals of a population of *Daphnia magna* subjected to size-selective mortality of its large individuals for 10 generations did not return to the size and growth rates of a control population, even after the size selective pressure was removed. Changes in the life history of red porgy over the last two decades strongly confirm the hypothesis of Bohnsack (1990) and Sutherland (1990). Although exploitation may not last long enough to result in a permanent genetic shift to slower growing, smaller individuals, phenotypic changes have already occurred. Failure to consider the potential evolutionary changes that could be induced in a population through fishing mortality could result in a reduction of the maximum potential yield of that stock (Law and Grey, 1989). In addition, a reduced population of smaller red porgy could have implications in reef fish community structure, i.e. the role of smaller red porgy in a reef habitat may be different, or smaller red porgy may be less able to compete for more desirable habitat.

Current management strategies only enhance the impact of the size selective mortality associated with fisheries. In 1992, Amendment 4 of the SAFMC snapper-grouper management plan was enacted, requiring a minimum size of 12 inches (305 mm TL) for red porgy in catches (SAFMC¹). Fishermen tend to target larger fish because these bring the largest return (economic for commercial fishermen, aesthetic for recreational fishermen). Size-at-maturity for red porgy females was 270 mm TL in 1972–74; 200–225 mm TL in 1979–81; and 175–200 mm TL in 1991–94. However, 100% maturity occurred at 350 mm TL during 1972–74 and >300 mm TL in 1991–94. Thus, many faster growing individuals may reach legal size before they are sexually mature or when they have only had the opportunity to spawn once or twice. Slower growing individuals would take longer to reach the size limit and have a greater chance to spawn be-

fore becoming available to the fishery, thus further exacerbating the effect of size-selective mortality.

The SAB population of red porgy has undergone significant changes in life history, presumably in response to sustained, long-term size-selective overexploitation. Individuals in the population are smaller, have reduced growth rates, a reduced theoretical maximum size, and undergo sexual maturity and transition at smaller sizes now than 20 years ago. The selective pressure of fishing mortality may be causing a genetic shift towards a slower growing, smaller population. Unless appropriate management measures are taken, sustained overfishing could result in a permanent genetic shift in the fish or a total collapse of the stock (or both).

Acknowledgments

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