Abstract–Status of the southeastern U.S. stock of red porgy (*Pagrus pagrus*) was estimated from fishery-dependent and fishery-independent data, 1972–97. Annual population numbers and fishing mortality rates at age were estimated from virtual population analysis (VPA) calibrated with fishery-independent data. For the VPA, a primary matrix of catch at age was based on age-length keys from fishery-independent samples; an alternate matrix was based on fishery-dependent keys. Additional estimates of stock status were obtained from a surplus-production model, also calibrated with fishery-independent indices of abundance.

Results describe a dramatic increase in exploitation of this stock and concomitant decline in abundance. Estimated fully recruited fishing mortality rate (*F*) from the primary catch matrix increased from 0.10/yr in 1975 to 0.88/yr in 1997, and estimated static spawning potential ratio (SPR) declined from about 67% to about 18%. Estimated recruitment to age 1 declined from a peak of 3.0 million fish in 1973–74 to 94,000 fish in 1997, a decline of 96.9%. Estimated spawning-stock biomass declined from a peak of 3530 t in 1979 to 397 t in 1997, a decline of 88.8%. Results from the alternate catch matrix were similar. Retrospective patterns in the VPA suggest that the future estimates of this population decline will be severe, but may be less than present estimates.

Long-term and marked declines in recruitment, spawning stock, and catch per unit of effort (both fishery-derived and fishery-independent) are consistent with severe overexploitation during a period of reduced recruitment. Although *F* prior to 1995 has generally been estimated at or below the current management criterion for overfishing (*F* equivalent to SPR=35%), the recent spawning-stock biomass is well below the biomass that could support maximum sustainable yield. Significant reductions in fishing mortality will be needed for rebuilding the southeastern U.S. stock.

Severe decline in abundance of the red porgy (*Pagrus pagrus*) population off the southeastern United States

Douglas S. Vaughan

Michael H. Prager

Center for Coastal Fisheries and Habitat Research
National Oceanic and Atmospheric Administration
101 Pivers Island Road
Beaufort, North Carolina 28516
E-mail address (for D. S. Vaughan): Doug.Vaughan@noaa.gov

New analyses of the red porgy (*Pagrus pagrus*) stock off the southeastern U.S. coast indicate that dramatic changes in age structure and population abundance have occurred over the last 25 years. The red porgy, a protogynous sparid also known as silver snapper and pink snapper, associates with reefs and is commonly found over irregular and low-profile hard bottoms at depths between about 20 and 200 m (Manooch and Hassler, 1978). The species has been an important component of the snapper-grouper complex in the coastal Atlantic Ocean off the southeastern United States, particularly off North and South Carolina.

This study is the first complete assessment of red porgy in this region since 1986 (Vaughan et al., 1992). We introduce methodological improvements that strengthen analyses considerably, including fishery-independent data to calibrate the virtual population analysis (VPA), as recommended in a recent review of marine stock assessments (NRC, 1998). Extensive analyses were made of the sensitivity of major results (estimates of abundance and fishing mortality rate) to assumptions. Sensitivity analyses (in the broad sense) included separate VPAs on two catch matrices, one based on fishery-independent age-length keys and the second on fishery-derived keys; estimation with different assumptions about natural mortality rate; a retrospective analysis; alternate treatments of zeroes in an abundance index; and the use of a surplus-production model to provide complementary estimates of stock abundance and management benchmarks.

Robustness of major conclusions to these factors and relatively close agreement between estimates from catch-at-age models and production models strengthen the finding that the red porgy stock was severely depleted at the close of 1997.

Range, stock structure, and reproductive biology

Red porgy have an extensive range—they are found off the southeastern U.S. Atlantic coast; in the Gulf of Mexico; off the South American Atlantic coast from Brazil to Argentina; off Portugal and Spain; in the Mediterranean Sea; off west Africa south to the Cape Verde Islands; and around the Azores, Madeira, and Canary Islands. The stock unit analyzed in our study includes fish from U.S. Atlantic waters off North Carolina (NC) south of Cape Hatteras; South Carolina (SC); Georgia (GA); and the east coast of Florida (FL). This range expands that previously defined for the stock, which (Vaughan et al., 1992; Huntsman et al.[1]) included fish only from waters off NC and SC. Within the current stock definition, red porgy have been most abundant from NC and SC waters. Tagging studies

[1] 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 Southpark Circle, Charleston, SC 29407. [Available from Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC, 28516.]

have shown neither long-range migrations nor extensive local movements of adult red porgy (Manooch and Hassler, 1978), nor has circumstantial or anecdotal information suggested such movements. Peak spawning occurs from March through April (Manooch, 1976). Red porgy eggs and larvae are pelagic, hatch 28 to 38 h after fertilization, and can survive transport by ocean currents for 30 days or more (Manooch et al., 1981). Thus, the population off the U.S. Atlantic coast could in theory receive eggs or larvae from the Gulf of Mexico stock. However, because of the distances involved and the variability of ocean currents, the likelihood of significant population mixing in this way seems small, and we adopted the stock boundaries described above.

Red porgy attain maximum size slowly and live relatively long (an 18-year-old specimen is the oldest on record), but maturity occurs far younger. Roumillat and Waltz[2] collected red porgy between 1979 and 1987 along the continental shelf between Cape Fear, NC, and Cape Canaveral, FL, using trawl nets, traps, and hook-and-line gear. Life history information was obtained from 7104 red porgy; 5820 otoliths were examined (including 134 from historical or port samples), of which 5491 had discernable rings; estimation of sex composition was based on 6044 red porgy. Mature gonads were found in 18.8% of females at age 1, 85.2% at age 2, 99.7% at age 3, and 100% at older ages.

Red porgy are protogynous hermaphrodites. Thus, females predominate at smaller size intervals, but males occur in all age groups. Age-specific sex ratios reported by Roumillat and Waltz[2] (their Table 6) were used in our analyses: 89% female at age 1, 91% at age 2, 77% at age 3, 67% at age 4, 59% at age 5 , 51% at age 6, 25% at age 7, and 21% at age 8.

Methods

Fishery-dependent data sources and adjustments

In the study area (Cape Hatteras, NC, through the east coast of FL), three fisheries take red porgy: commercial, recreational, and headboat. Hook-and-line has been the most common commercial gear, but occasional significant landings are taken with trawls and traps. Trawling for red porgy has been banned since 1989 (Amendment 12 [SAFMC[3]]) The recreational fishery includes all recreational fishing from shore, from private boats and from charter boats (for-hire vessels that usually accommodate six or fewer anglers as a group). The headboat fishery (larger for-hire vessels that charge per angler) is sampled

separately, and for that reason is distinguished here from other recreational fisheries. Recreational and headboat fisheries, like the commercial fishery, use hook-and-line gear almost exclusively. Data sources for all three fisheries are described in our study and summarized in Table 1.

Commercial fishery Landings statistics in weight for the commercial fishery, 1972–97, were obtained from the NMFS general canvass database (NMFS, Southeast Fisheries Science Center, Beaufort, NC, and Miami, FL). In addition, North Carolina commercial landing statistics by gear for red porgy were provided by NC Division of Marine Fisheries (NCDMF). Fishery-based length and weight statistics, 1983–97, were obtained from the NMFS Trip Interview Program (TIP) database. Length frequencies from SC commercial landings, 1976–80, were taken from Vaughan et al. (1992).

Commercial landings statistics, 1972–84, are recorded as "porgies," but include some other species. Following Vaughan et al. (1992), we multiplied such non-North-Carolina landings by 0.9 to approximate landings of red porgy only; North Carolina data were corrected by NCDMF before we received them. Commercial landings were available only in weight and were converted to counts by dividing catch in weight by mean weight per fish for the same gear and year. To compute annual mean weights, fish lengths from the TIP database were converted to weight with estimated weight–length relationships, described below.

Annual length-frequency distributions L were developed for commercial hook-and-line gear for each area (Carolinas vs. Florida), 1983–97. Commercial length frequencies for 1972–82 were taken from Vaughan et al. (1992). Because trap and trawl landings have been quite small since the mid–1980s and few fish have been sampled (1611 [trap]; 1455 [trawl], mostly between 1986 and 1988), two overall length-frequency distributions for each gear were used, one for 1972–89 and the other for 1990–97. Gear-specific commercial length-frequency distributions were weighted by catch in number by state to obtain catch at length by gear and state.

Recreational fishery Recreational catch and effort estimates and data on length and weight composition, 1979–97, were obtained from the NMFS Marine Recreational Fisheries Statistics Survey (MRFSS) database (Gray et al., 1994; Marine Recreational Fisheries Statistics, 1999). Fishing modes used by MRFSS include shore-based, private-boat-based, and charter-boat based fishing. Within each mode, three catch types are defined: "A" catches were available to sampling personnel for identification and measurement; "B1" catches were unavailable because they had been used for bait, filleted, discarded dead, etc.; and "B2" catches were unavailable because they had been released. Postrelease mortality of B2 catches was assumed to be 18% (Dixon and Huntsman[4]). Following

---

[2] Roumillat, W. A., and C. W. Waltz. 1993. Biology of the red porgy *Pagrus pagrus* from the southeastern United States. Data report 1993 MARMAP, South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29422-2559.

[3] SAFMC (South Atlantic Fishery Management Council. 2000. Final, amendment number 12 to the fishery management plan for the snapper grouper fishery of the South Atlantic region. South Atlantic Fishery Management Council, Charleston, SC, 159 p. + appendices.

[4] Dixon, R. L. and G. R. Huntsman. 1993. Survival rates of released undersized fishes (abstract). Sixth Annual MARFIN Conference, Atlanta, GA, 12–13 October 1993. [Available from Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC, 28516.]

Table 1

Data sources for analysis of red porgy off the southeastern United States. Sample size *n* is number of fish lengths measured. Aging data sources are given in Table 2. Symbol *N* is number of fish, *W,* weight of fish caught.

Data source	Years	Database	Type	*n*
Commercial fishery	1972–97	NMFS, general canvass	Landings (*W*)	—
	1972–97	NC Div. Mar. Fish.	NC landings (*W*)	—
	1983–97	NMFS trip interview	Lengths and weights	62,042
	1976–80	SCDNR (Vaughan et al., 1992)	Lengths	8855
Recreational fishery (private and charter boats)	1979–97	NMFS MRFSS	Catch (*N* and *W*) Lengths and weights	— 945
Headboat fishery	1972–97	NMFS headboat survey (NC, SC)	Catch (*N* and *W*) Lengths and weights	— 44,131
	1976–97	NMFS headboat survey (GA-N.E. FL)	Catch (*N* and *W*) Lengths and weights	— 1454
	1981–97	NMFS headboat survey (S.E. FL)	Catch (*N* and *W*) Lengths and weights	— 1166
Fishery-independent	1979–97	MARMAP hook and line	CPE (*N*) and lengths	2085
	1980–97	MARMAP traps (FL snapper and chevron)	CPE (*N*) and lengths	10,784

Vaughan et al. (1992), we adjusted the data to avoid duplication from inclusion of headboat landings in charter-boat landings reported by MRFSS, 1979–85.

Mean recreational landings by mode were calculated for 1979–97 and used for 1972–78, a period of minimal exploitation before MRFSS data were collected. Because recreational landings are a small fraction of the total, this procedure, while approximate, was better than assuming landings of zero in that period.

Recreational length-frequency distributions from MRFSS, 1979–97, were weighted by catch (A+B1) in number by mode, wave (2-month interval), and state. The minimal catch associated with shore-based fishing was pooled with the private-boat mode. Headboat length-frequency distributions from MRFSS (1979–85) were not used in development of catch matrices for the recreational fishery because more complete data were available from the headboat sampling program.

Headboat fishery Estimates of headboat catch in numbers and weight and fishing effort in angler-days (Table 1) were obtained from the NMFS (Beaufort, NC) headboat sampling program (Huntsman, 1976; Huntsman et al., 1978). Zero-intercept linear regression analyses on NC and SC data were used to estimate landings from GA to northeast FL and landings from southeast FL, and fishing effort back to 1972. Catch per effort (CPE) in numbers was calculated by dividing annual catch in numbers by annual effort.

Length samples from headboats were not available from GA or FL before 1976, nor from southeast FL before 1981. We used mean length-frequency distributions for 1976–80 to fill in for GA and FL, 1972–75, and length-frequency distributions from GA to northeast FL to fill in for southeast FL, 1976–80. Annual headboat length-frequency distributions from the headboat sampling program, 1972–97, were weighted by catch in numbers caught during that season (January–May, June–August, September–December), and geographic area (NC, SC, GA to northeast FL, southeast FL) to obtain catch in length by season and area.

Development of catch-at-age matrices

Estimates of catch at age in numbers were made by using an approach similar to that of Vaughan et al. (1992). Total catch in numbers (*n*, scalar) for each combination of time, gear, and area was multiplied by an age-length key (A, matrix of dimension $a \times b$); the product was multiplied by the corresponding length-frequency distribution (L, vector of length *b*) to obtain catch in numbers at age (N, vector of length *a*):

$$\mathbf{N} = n \cdot \mathbf{A} \cdot \mathbf{L}. \qquad (1)$$

Here, *a* is the number of ages (for this study, ages 0 to 8⁺) and *b* is the number of length intervals (for this study, 15 intervals of 25 mm each from 200 mm to 550⁺ mm).

Age-length keys Separate age-length keys were developed from fishery-dependent and fishery-independent data. Fishery-dependent keys for 1972–74 were those of Manooch and Huntsman (1977); for 1986, those of Vaughan et al. (1992); for 1996–97, those of Potts and Manooch (2002). Keys for 1975–85 and 1987–95 were approximated by linear interpolation from available keys (method of Vaughan et al., 1992).

We constructed fishery-independent keys from samples taken in 1979–94 (Harris and McGovern, 1997) by the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, a fishery-independent sampling program of the SC Department of Natural Resources. In that study, 8660 red porgy were collected, primarily with hook and line and various traps, and preserved sagittae were used for age estimation. As a compromise between estimating annual keys based on smaller sample sizes and an overall key, which would disguise growth variability over time, we grouped MARMAP aging data into 3-yr periods, with the last four years divided instead into two 2-yr periods: 1979–81, 1982–84, 1985–87, 1988–90, 1991–92, 1993–94. Potts and Manooch (2002) aged 111 red porgy collected during 1996–97 by the MARMAP program (predominantly younger fish, maximum age of 6). We used an age-length key from those data for 1995–97. Where fewer than 10 fish occurred in a 25-mm total-length interval, we pooled the data over longer time periods.

No aging data are available from fishery-independent sources before 1979. We constructed a key, used for 1972–74, from fishery samples taken in those years (Manooch and Huntsman, 1977). For 1975–78, we interpolated linearly between that key and the earliest key derived from fishery-independent data (1979–81). Thus, the fishery-independent (primary) catch matrix described below reflects some fishery-dependent data in the earliest years.

Catch-at-age matrices Equation 1 was applied to each fishery-gear combination and catch-at-age estimates were accumulated for each year to obtain estimates of annual catch in numbers at age (the catch matrix), 1972–97. This was done twice, first by using the fishery-independent age-length keys to obtain the primary catch matrix, and then by using fishery-derived age-length keys to obtain the alternate catch matrix. (Although the designation of "primary" and "alternate" matrices is somewhat subjective, it was based on the more extensive and continuous quality of fishery-independent data, as discussed later. Despite the designation, most analyses were conducted twice, once with each matrix.) Final catch matrices each contained numbers of fish caught at ages 1 through 8+ in fishing years 1972 through 1997; partial recruitment for age-0 red porgy was essentially zero.

We judged coherence of catch matrices by examining pairwise correlations between ages as a cohort progressed through the fishery. For fully recruited ages and with F varying only moderately from year to year, we expected to be able to follow a strong or weak cohort through the catch matrices. Both matrices generally showed significant correlations ($P<0.1$) between lagged catches at adjacent ages. A few significant correlations were found among lagged catches for nonadjacent ages.

Growth in length and weight

Von Bertalanffy (1938) growth models were fitted from data on total length (mm) and age obtained from fishery-independent and fishery-dependent sources (Table 2). Disaggre-gated aging data could not be located for fishery-dependent data from 1972 to 1974 and from 1986; therefore observed midinterval lengths at age from keys were used for those years. For fishery-dependent data for 1989–98 and fishery-independent data for 1996–97, back-calculated length at oldest age was used, a procedure that avoids potential bias by the use of multiple measurements per fish (Vaughan and Burton, 1994). For fishery-independent data, 1979–94, observed length at age was used, adjusted for month of collection. The particularly high standard error associated with the estimate of L_∞ for fishery-independent data, 1996–97, was associated with a lack of fish older than 6 years of age in the sample (Table 2).

We estimated weight W (in kg) from total length L (in mm) by using the relationship $W = aL^b$. Parameter estimates were as follows: for fishery-dependent modeling, we used values from Manooch and Huntsman (1977) ($a = 2.524 \times 10^{-5}$ and $b=2.894$) for the 1970s and 1980s; and from Potts and Manooch (2002; $a=8.85 \times 10^{-6}$ and $b=3.060$) for the 1990s. For fishery-independent modeling, we used values for 1972–78 from Manooch and Huntsman (1977), and we estimated values for 1979–97 from MARMAP data, 1979–94, ($a=3.064 \times 10^{-5}$ and $b=2.865$).

Abundance indices

Fishery-independent data on length, weight, age, and CPE, 1979–97 (Table 1) were obtained through the MARMAP program (Collins and Sedberry, 1991; Harris and McGovern, 1997). In computing fishery-independent indices of abundance from those data, we used CPE from hook-and-line and trap gears only. We extended data from chevron trap, 1988–97, back to 1980 with data on Florida snapper trap, using a conversion factor determined by MARMAP (Collins, 1990; Vaughan et al., 1998); we refer to the resulting series as "extended" chevron trap. To obtain age-specific indices of abundance for hook-and-line, 1979–97, and extended chevron trap, 1980–97, we applied Equation 1, using CPE in place of n, and using annual MARMAP estimates of CPE, age-length keys, and length-frequency data for each gear.

Like the catch matrices, matrices of fishery-independent CPE estimates were examined for coherence through correlations among lagged CPE. The hook-and-line index showed greatest coherence among ages 1 through 4, whereas the extended chevron-trap index appeared quite coherent over a wider range of older ages (3 through 7).

Mortality estimation

Instantaneous total mortality rates (Z) were estimated from cohort-specific catch-curve analyses (Ricker, 1975) of the two catch matrices by using only ages that appeared fully recruited (4 through 7). Empirical approaches were also used to estimate total mortality rate (Z). The more complex of two methods presented by Hoenig (1983) is based on age of the oldest fish observed, sample size, and age of recruitment to the sampling procedure. Assuming those quantities to be 18 yr, 10,000 fish, and 1 yr, we estimated $Z = 0.58$/yr, a likely upper bound on M.

Table 2

Parameters of von Bertalanffy growth models for red porgy off southeastern United States. Maximum age in the sample is labeled t_{max}; sample size is n. Parameters estimated from observed mid-interval length at age in fishery-dependent data for 1972–74 and 1986; from back-calculated length at oldest age in fishery-dependent data for 1989–1998 and fishery-independent data for 1996–97; and from observed length at age adjusted for month of collection in fishery-independent data for 1979–94. Asymptotic standard error is in parentheses below corresponding parameter estimate.

Type of data and year	n	L_∞ (mm)	k	t_0	$t_{max\,(yr)}$	Range (mm)
Fishery-dependent data						
1972–74	1685	575.8	0.16	−1.88	15	185–640
		(2.5)	(0.002)	(0.03)		
1986	535	1252.9	0.40	−4.05	12	213–615
		(28.7)	(0.001)	(0.04)		
1989–98	492	796.6	0.09	−2.34	18	247–723
		(43.9)	(0.009)	(0.23)		
Fishery-independent (MARMAP) data						
1979–94	8601	485.5	0.23	−1.48	14	142–568
		(5.3)	(0.01)	(0.06)		
1979–81	1171	501.3	0.34	−0.15	13	142–557
		(5.4)	(0.01)	(0.06)		
1982–84	2159	626.1	0.15	−1.61	14	145–568
		(24.6)	(0.01)	(0.14)		
1985–87	2332	542.5	0.16	−2.24	12	176–523
		(20.4)	(0.01)	(0.16)		
1988–90	1268	424.2	0.31	−1.06	12	176–487
		(8.6)	(0.02)	(0.14)		
1991–92	842	425.1	0.25	−1.62	13	179–456
		(10.1)	(0.02)	(0.20)		
1993–94	829	375.7	0.43	−0.78	12	183–501
		(5.5)	(0.04)	(0.18)		
1996–97[1]	111	754.7	0.10	−1.27	6	151–384
		(246.3)	(0.05)	(0.38)		

[1] Otoliths from fish collected during 1996–97 by MARMAP but aged by C. Manooch and J. Potts (NOAA Beaufort Laboratory).

We estimated natural mortality rate empirically (Pauly, 1979) from parameters L_∞ and K of the von Bertalanffy growth function and mean environmental temperature. Estimates ranged from $M = 0.27$/yr to $M = 0.57$/yr, based on mean sea temperature of 22°C (Manooch et al., 1998) and the range of growth parameters estimated in our study (Table 2). A similar method, that of Ralston (1987) and based solely on growth parameter K, provided estimates from $M = 0.22$/yr to $M = 0.64$/yr. Given the uncertainty in M, we chose a base $M = 0.28$/yr (Vaughan et al., 1992). We also performed bracketing estimates of most quantities using $M = 0.20$/yr and $M = 0.35$/yr.

Fishing mortality rate F was estimated by subtracting the assumed natural mortality rate from the total mortality rate. These estimates of F were used only as terminal-year values in the separable VPA.

Virtual population analyses

Primary and alternate catch matrices were analyzed by using virtual population analysis (VPA) to obtain annual age-specific estimates of F and population size. First, a separable VPA (Doubleday, 1976; Pope and Shepherd, 1982), as implemented by Clay (1990), was used to estimate partial recruitment by age for later use in calibrated VPA. Data from 1992–97 were used for this purpose because a 12-inch minimum size limit was introduced in 1992 (amendment 4[SAFMC[5]]), and using data from both before and after imposition of the size regulation would likely violate the separability assumption. The starting value of F for the separable VPA was the mean of three final year-class estimates of Z (~0.78/yr), less M.; i.e. $F \sim 0.50$/yr.

A calibrated VPA (Pope and Shepherd, 1985; Gavaris, 1988) was then applied, as implemented in the FADAPT

computer program,[6] by using the two fishery-independent abundance indices (hook-and-line and extended chevron trap). Most calibrated VPA runs were made with both indices, but a few were made with individual indices to assess sensitivity. The hook-and-line index included estimates of zero in 1992 and 1996, to which a small value (0.0001) was added before log transformation, a technique often used in statistical ANOVA models (e.g. Snedecor and Cochran, 1980). Effects of that approach were explored by assuming missing values in place of zeroes in an additional calibrated VPA run.

Several additional techniques were used to examine sensitivity to assumptions. Sensitivity of estimated F and recruitment to age 1 to uncertainty in M was investigated by conducting the separable and calibrated VPAs with alternate values of M (0.20/yr and 0.35/yr). Retrospective analyses of the calibrated VPA were conducted to investigate the possibility of systematic deviations ("retrospective patterns") in estimates of F and recruitment in most recent years, in comparison to estimates obtained for the same years from later analyses. In the retrospective analyses, we varied the final year of data used from 1992 to 1997; the initial year was 1972 throughout.

For presentation of results, we averaged estimated quantities within three time periods: 1972–78, representing a lightly fished stock; 1982–86, representing the stock after increasing exploitation during the early 1980s; and 1992–96, representing conditions since the last major change in management (amendment 4[SAFMC[5]]), but omitting the terminal year (1997) to reduce retrospective effects (discussed below). We refer to these as early, middle, and recent periods. Recruitment was defined as the number of fish at age 1 on January 1.

Yield per recruit

Equilibrium yield per recruit (YPR) was estimated by the method of Ricker (1975), which divides the exploited life span into phases of constant mortality and growth rates; total YPR is obtained by summing yield across phases. Parameter estimates from YPR analysis were for both sexes and across the three time periods described above. It has long been recognized that fishing at F_{max} (F that maximizes YPR) can cause recruitment failure (Gulland and Boerema, 1973; Clarke, 1991; Caddy and Mahon, 1995), and the reference point $F_{0.1}$ was introduced as a more conservative alternative (Gulland and Boerema, 1973). Using most recent growth and selectivity, we computed both F_{max} and $F_{0.1}$.

Spawning potential ratio

Static spawning potential ratio (static SPR)—also known as equilibrium SPR or maximum spawning potential (Gabriel et al., 1989)—is a measure of fishing mortality rate scaled to a species' biology. Static SPR for a given

fishing mortality rate F^* is computed as the ratio SPR = SS(F^*) / SS(0), where SS(F^*) is the spawning-stock size (lifetime cohort spawning contribution) expected under F^*, and SS(0) is the corresponding spawning-stock size expected under $F = 0$. Other life history parameters are assumed constant at most recent values. Increases in F reduce static SPR.

In species that do not change sex, spawning-stock biomass is usually computed as total mature female biomass or total egg production (Prager et al., 1987), quantities that are highly correlated. Because red porgy change sex, we used four representations of spawning-stock biomass: female mature biomass, male mature biomass, total (male + female) mature biomass, and total egg production, each assuming the sex ratios at age given above (Roumillat and Waltz[2]).

To compute total egg production, we used the relationship between fecundity (E, number of eggs) and total length (TL, mm) of Manooch (1976):

$$\ln E = -14.1325 + 4.3598 \,(\ln TL), \tag{2}$$

Sex ratio in the mature population can be changed by fishing. We estimated reduction in the proportion of males among mature fish from the proportion expected with no fishing and assuming that the rate of sex transformation is not affected by changes in population structure.

Spawner-recruit relationships

The relationship between spawning-stock biomass and resulting recruitment to age 1 was modeled by using the Beverton-Holt spawner–recruit function (Ricker, 1975):

$$R = \text{SSB}/(b_0 \times \text{SSB} + b_1), \tag{3}$$

where R = recruitment;
　　SSB = spawning-stock biomass, and
　　b_0, b_1 = fitted parameters.

To reduce the influence of retrospective patterns, SSB and R series (estimated from VPA) used in recruitment modeling were terminated at 1992. We used total mature biomass, rather than the more usual female mature biomass, to represent SSB in recruitment modeling.

With the estimated stock-recruitment relationship, 500-year simulations of the stock were made to estimate equilibrium yield and spawning-stock biomass as functions of fishing mortality rate. The simulations used mean population numbers, 1992–96, as starting values. Age-specific selectivity for the same period and the most recent growth patterns were used throughout. We thus estimated MSY, B_{MSY}, and F_{MSY} for each catch matrix.

Surplus-production model

A surplus-production model was fitted to obtain additional estimates of management benchmarks and stock status. We used the Prager (1994, 1995) formulation and implementation of the continuous-time Graham-Schaefer (logis-

---

[6] FADAPT by V. R. Restrepo (International Commission for the Conservation of Atlantic Tunas, Calle Corazón de María, 8, Sixth Floor, 28002 Madrid, Spain).

tic) model (Schaefer, 1954, 1957; Pella, 1967; Schnute, 1977; Prager, 1994). The approach is an observation-error estimator assuming proportional error variance and conditioned on observed landings. We attempted to fit the generalized production model (Pella and Tomlinson, 1969; Fletcher, 1978) by similar methods. Data were total landings in weight, 1972–97, and CPE indices derived separately from fishery-independent hook-and-line and trap data, 1979–97.

Initial difficulty in obtaining estimates was traced to two years of zero CPE in the fishery-independent hook-and-line index. Because the fitting was conducted in logarithmic transform, zeroes could not be accommodated; our initial, unsuccessful approach was to substitute very small values. We obtained estimates through the alternate procedure of considering those values missing, which is statistically equivalent to setting the observation weights to zero.

Because some estimates were moderately sensitive to assumptions about the starting stock biomass, B_1, in relation to carrying capacity, K, we obtained estimates at a range of values, namely $B_1/K = \{0.55, 0.65, 0.75, 0.85, 0.95\}$, a range chosen to reflect the stock's lightly fished status before the first year (1972). Fixing the starting value of relative biomass can reduce variance of estimates considerably (Punt, 1990). Bootstrapping with 700 repetitions was used to estimate 80% bias-corrected confidence intervals (Efron and Tibshirani, 1986) on the central set of estimates ($B_1/K=0.75$).
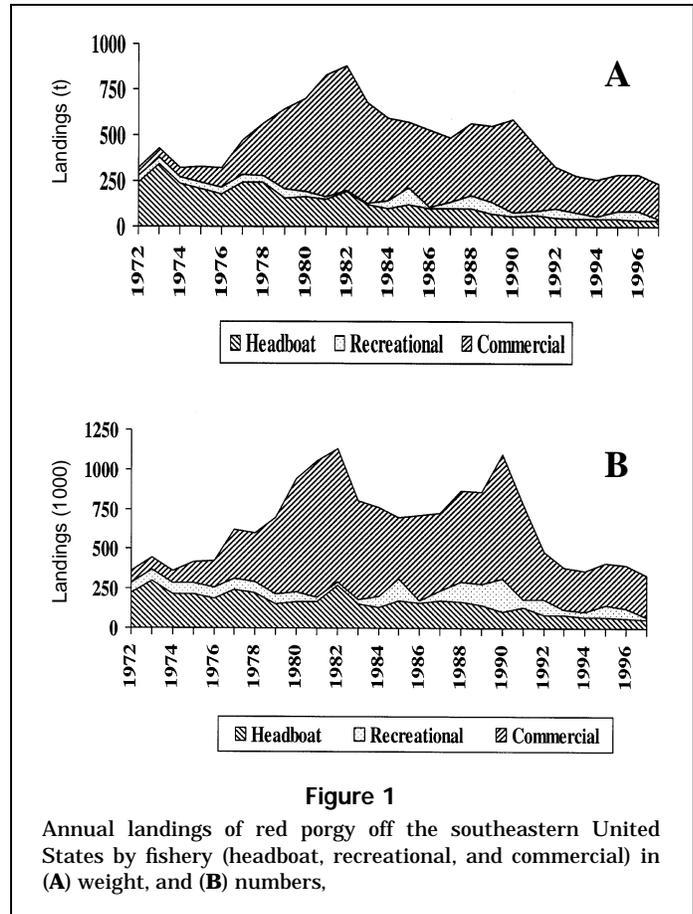
Results

In this section, all results are reported for the base value of M = 0.28/yr unless otherwise stated. Results reflect analysis of the primary catch matrix unless use of the alternate matrix is specifically mentioned.

Summary of landings and CPE

During the study period (1972–97), total landings in weight rose from about 325 t in 1972 to a maximum of 880 t in 1982 (Fig. 1A). Landings have been at or below 300 t since 1992, with 234 t in 1997. The headboat fishery accounted for about 52%–80% of total landings through 1977; commercial landings have been most prevalent since (Fig. 1B, Table 3). Maximum landings in numbers were about 1.13 million fish in 1982 (Table 4).

Commercial landings in weight rose from 45 t in 1972 to 678 t in 1982 and declined to 200 t/yr or less since 1992 (Fig. 1A); landings in numbers had a similar pattern (Fig. 1B). Commercial trawl landings averaged about 14% of commercial landings, 1972–84 but were quite small by 1985, and trawl gear was prohibited as of 12 January 1989 by amendment 1 to the Fishery Management Plan (amendment 12 [SAFMC[3]]). Hook-and-line landings have been about 95% of commercial landings by weight since 1985.

Recreational landings in numbers have shown no consistent trend, averaging about 70,000 fish per year, with

Figure 1

Annual landings of red porgy off the southeastern United States by fishery (headboat, recreational, and commercial) in (**A**) weight, and (**B**) numbers,

some outstanding years of more than 100,000 fish between 1985 and 1990 (Fig. 1B). Catch by mode of fishing has been highly variable, but recreational landings have mainly been taken by charter boat (43% by number during the 1990s) and private boat (55%). Although remaining landings (<3%) are attributed to fishing for red porgy from shore, this amount is unlikely to be correct. These records may result from errors in recorded fishing mode or from erroneous species identification, but in either case would have negligible effect on our analyses.

Headboat landings have declined from 200,000 fish/yr during the 1970s to around 100,000–200,000 fish/yr in the 1980s and fewer than 100,000 fish/yr since (Fig. 1B). Most landings have come from NC and SC.

Mean weight in the commercial hook-and-line and headboat fisheries in the Carolinas has decreased, especially since about 1978 (Fig. 2). Mean weight in all fisheries combined has shown a general decline from 1972 to 1991 (Fig. 2) but has since increased somewhat.

All data on catch per effort (CPE) exhibited long-term decline. Declining headboat CPE was apparent from both NC and SC (Fig. 3). The fishery-independent abundance indices, also based on CPE, showed corresponding declines (Fig. 3): the extended chevron-trap index decline was precipitous; that in the hook-and-line index was similar, but somewhat less dramatic. (The CPE series derived from

Table 3

Red porgy landings in numbers (1000) by fishery, area, and gear or mode. Listed recreational landings from private boats include minor landings from shore.

| | Commercial | | | | | | Recreational and headboat | | | | | | | |
| | NC + SC | | | GA + FL | | | NC + SC | | | GA + FL | | | | |
Year	Trawl	Traps	Lines	Trawl	Traps	Lines	Private	Charter	Headboat	Private	Charter	Headboat	Commercial	Recreational and headboat
1972	0.6	22.9	0.9	0.2	1.3	45.4	31.7	27.1	201.4	9.9	1.0	18.6	71.1	289.7
1973	13.5	9.8	2.1	0.0	0.2	50.9	31.7	27.1	274.4	9.9	1.0	25.3	76.4	369.4
1974	0.0	20.3	3.5	0.0	0.5	47.5	31.7	27.1	201.3	9.9	1.0	18.6	71.8	289.5
1975	1.2	31.5	3.0	0.0	0.5	95.7	31.7	27.1	197.3	9.9	1.0	18.2	131.9	285.2
1976	9.0	28.9	24.4	36.2	0.4	67.9	31.7	27.1	173.8	9.9	1.0	12.9	166.7	256.4
1977	55.2	12.9	33.3	112.9	3.2	92.3	31.7	27.1	218.9	9.9	1.0	24.7	309.8	313.3
1978	6.9	0.2	136.2	1.0	0.0	163.6	31.7	27.1	176.4	9.9	1.0	47.4	307.9	293.4
1979	87.0	3.3	253.0	0.0	0.0	140.8	37.5	2.0	128.8	14.8	3.0	27.8	484.0	213.9
1980	271.3	7.9	211.7	52.4	0.0	166.4	8.7	7.8	148.7	40.5	4.2	19.8	709.7	229.7
1981	276.4	16.4	342.2	50.9	0.0	174.0	8.1	15.1	156.9	3.9	0.1	11.1	859.9	195.2
1982	212.3	8.6	450.1	30.1	0.0	139.5	5.1	10.0	265.0	6.3	0.0	7.9	840.6	294.2
1983	114.0	17.4	378.1	6.9	0.0	104.5	18.3	9.7	152.7	0.9	0.1	3.1	621.0	184.7
1984	60.7	17.6	301.5	17.6	0.2	158.5	5.7	67.4	124.4	0.0	1.0	5.6	556.0	204.1
1985	0.0	2.6	231.5	6.8	0.2	142.4	45.4	1.9	167.1	89.9	0.8	9.4	383.5	314.5
1986	8.2	25.8	285.8	6.6	0.0	208.1	13.4	2.6	140.8	0.1	0.0	20.3	534.6	177.1
1987	6.9	19.1	308.3	0.0	0.0	156.5	44.2	16.1	151.0	1.9	0.0	22.6	490.9	235.7
1988	28.2	19.3	369.3	0.2	4.0	146.6	57.8	66.9	157.9	3.3	0.0	10.6	567.5	296.5
1989	0.0	21.1	389.2	0.0	4.9	164.6	37.4	95.1	137.4	0.0	0.0	9.1	579.8	279.0
1990	0.0	80.5	436.8	0.0	16.5	248.4	197.7	13.8	97.5	0.9	0.0	7.3	782.2	317.1
1991	0.0	93.7	324.3	3.3	5.5	173.7	25.6	12.9	122.7	14.5	0.0	7.1	600.6	182.8
1992	0.0	4.4	211.0	2.0	0.2	82.6	29.3	61.3	81.1	3.0	0.0	4.8	300.2	179.6
1993	0.0	14.9	175.0	2.9	8.7	65.6	10.8	18.6	78.5	1.4	4.8	3.2	267.1	117.4
1994	0.0	11.1	189.3	2.2	0.3	53.9	14.7	17.8	67.7	2.5	0.0	2.7	256.8	105.4
1995	0.0	8.4	177.1	4.5	1.4	72.0	3.4	70.0	66.8	1.8	0.4	4.0	263.4	146.2
1996	0.0	6.4	188.4	0.3	0.0	79.8	36.3	17.5	61.2	0.3	5.0	3.7	274.8	124.0
1997	0.0	4.1	172.9	1.1	0.0	90.8	3.6	7.8	49.8	1.3	0.0	4.1	268.8	66.5

Table 4

Primary and alternate catch-in-numbers-at-age matrix for red porgy off the southeastern United States. Matrix is in thousands of fish, is based on fishery-independent age-length keys, and includes 18% (by number) of released recreationally caught fish. Each year's modal age is underlined.

Year	1	2	3	4	5	6	7	8+	Total (1000)
Primary catch-in-numbers-at-age matrix									
1972	13.2	60.7	56.2	55.9	<u>87.3</u>	44.1	23.5	19.0	359.9
1973	13.7	63.0	62.8	64.6	<u>102.4</u>	55.3	36.8	46.3	444.9
1974	13.7	64.8	63.1	58.8	<u>76.9</u>	35.5	21.7	26.0	360.5
1975	16.7	<u>116.5</u>	96.3	51.3	37.4	38.9	28.2	30.3	415.6
1976	13.8	<u>88.3</u>	87.5	60.4	56.4	46.1	32.5	36.7	421.7
1977	12.9	92.7	102.4	88.9	<u>106.0</u>	78.2	60.2	80.5	621.9
1978	15.3	101.0	106.2	88.2	<u>115.6</u>	69.1	46.9	58.0	600.3
1979	13.9	134.4	<u>145.5</u>	90.6	57.9	95.5	78.4	81.0	697.2
1980	14.6	153.9	<u>212.2</u>	128.6	76.6	121.6	100.2	130.9	938.6
1981	16.3	206.5	<u>218.3</u>	215.6	156.6	86.8	55.7	99.2	1055.1
1982	24.7	<u>289.8</u>	246.1	218.6	147.7	76.5	47.3	83.9	1134.8
1983	35.6	128.2	184.0	<u>185.5</u>	98.2	65.6	45.5	63.0	805.7
1984	31.1	137.7	<u>202.5</u>	186.6	85.5	50.8	28.3	37.5	760.0
1985	34.1	116.4	118.1	<u>155.6</u>	127.6	84.3	38.0	24.0	698.0
1986	29.0	143.4	134.9	<u>160.6</u>	118.6	71.3	32.5	22.3	712.7
1987	71.8	<u>227.2</u>	176.9	95.9	38.3	44.4	32.4	39.0	725.8
1988	87.9	<u>288.7</u>	219.0	109.0	42.2	46.8	30.5	38.2	862.4
1989	40.0	232.9	<u>247.2</u>	122.9	92.5	37.5	36.6	46.8	856.3
1990	66.2	<u>325.1</u>	322.5	146.1	105.2	40.2	40.3	49.9	1095.4
1991	46.7	160.4	162.9	<u>181.1</u>	97.5	54.9	29.6	49.9	783.0
1992	19.6	63.7	95.7	<u>124.2</u>	73.3	42.1	22.0	38.9	479.4
1993	3.9	38.9	53.2	<u>95.7</u>	94.7	51.0	24.0	23.2	384.5
1994	3.3	32.5	47.7	89.2	<u>91.0</u>	50.4	24.7	23.5	362.2
1995	5.2	39.9	54.7	<u>98.0</u>	97.2	52.6	23.8	24.1	395.5
1996	4.9	44.9	57.9	<u>99.9</u>	95.6	50.6	21.5	21.1	396.3
1997	2.3	31.9	46.2	<u>85.3</u>	85.2	45.2	20.2	18.8	335.2

continued

headboat catches are shown for comparison, but were not used in calibrating VPAs.)

In the primary catch matrix, modal age (underlined in Table 4) varied between 2 and 5; age 4 has been most common in recent years. Modal age in the alternate catch matrix (Table 4) was similar, but showed less annual variation, probably because of interpolation across years of the age-length keys. A few strong year classes have moved through the population, most notably those that were age 2 in 1987–90, but no strong year classes have followed. The modal age has increased since 1992, the year in which a 12-inch minimum size limit was imposed (amendment 4 [SAFMC[5]]).

Trends in mortality and recruitment

In our calibrated VPAs, ages 4 through 7 were always considered fully recruited, and estimates of F were typically averaged over those ages, weighted by population numbers at age. Those weighted averages are referred to here as full F.

In analysis of the primary catch matrix, estimates of F for all ages were lowest in the early years (Table 5). Fishing mortality on ages 1–3 increased between the early and middle periods and then declined, but full F (ages 4+) increased and remained high. This pattern probably reflects the imposition of the 12-inch TL minimum size limit in 1992 with amendment 4 (SAFMC[5]). Estimates of F from the alternate catch matrix in the recent period were generally higher for ages 3+ than estimates from the primary catch matrix. Slightly lower estimates of F in the recent time period were obtained from the primary catch matrix when missing values, rather than small numbers, replaced zeroes in computing the hook-and-line index.

Estimates of full F from both catch matrices started low, rose abruptly from the late 1970s to 1982, decreased some-

Table 4 (continued)

| Year	1	2	3	4	5	6	7	8+	Total (1000)
Alternate catch-in-numbers-at-age matrix									
1972	13.2	60.7	56.2	55.9	<u>87.3</u>	44.1	23.5	19.0	359.9
1973	13.7	63.0	62.8	64.6	<u>102.4</u>	55.3	36.8	46.3	444.9
1974	13.7	64.8	63.1	58.8	<u>76.9</u>	35.5	21.7	26.0	360.5
1975	18.7	71.0	<u>79.4</u>	78.7	74.7	40.6	21.5	31.7	416.2
1976	15.2	57.6	69.1	79.7	<u>85.8</u>	49.2	26.6	39.0	422.2
1977	14.2	65.6	83.3	105.3	<u>128.4</u>	82.8	52.8	89.9	622.3
1978	16.6	78.5	99.0	102.4	<u>121.2</u>	75.2	43.9	63.7	600.5
1979	15.2	78.2	98.4	116.6	<u>150.7</u>	99.9	59.3	79.7	697.9
1980	15.8	86.0	129.2	171.7	<u>213.4</u>	116.6	70.1	136.6	939.3
1981	12.6	93.9	149.2	197.9	<u>247.8</u>	136.6	86.2	131.2	1055.1
1982	18.7	150.5	191.4	216.7	<u>252.0</u>	122.2	73.9	109.5	1134.8
1983	41.5	132.9	135.4	146.2	<u>162.0</u>	70.3	48.7	69.0	805.8
1984	36.4	145.9	<u>154.0</u>	151.0	153.5	54.5	27.9	36.8	760.1
1985	27.5	120.7	142.0	140.3	<u>156.6</u>	56.3	25.8	28.9	698.0
1986	25.2	120.5	159.5	<u>169.0</u>	131.4	52.3	23.0	31.7	712.7
1987	6.9	88.3	<u>204.0</u>	180.5	129.8	56.4	26.1	34.6	726.6
1988	15.4	111.7	<u>262.3</u>	224.5	141.3	53.8	23.8	31.3	864.0
1989	15.1	132.5	<u>255.2</u>	199.0	140.6	58.5	25.2	32.7	858.8
1990	32.5	216.4	<u>330.7</u>	247.5	158.7	57.7	23.0	32.9	1099.4
1991	22.5	165.6	<u>238.3</u>	180.9	104.5	34.4	14.7	22.6	783.4
1992	10.5	65.6	<u>138.4</u>	129.1	86.9	28.8	9.6	11.0	479.8
1993	1.9	29.8	104.6	<u>125.7</u>	80.5	24.6	8.4	9.1	384.5
1994	1.8	27.2	91.9	<u>119.7</u>	79.7	24.1	9.0	9.0	362.3
1995	3.6	37.7	108.4	<u>128.4</u>	81.1	21.6	6.8	7.9	395.5
1996	0.3	9.1	104.6	<u>142.5</u>	89.8	30.4	9.2	10.6	396.3
1997	0.1	3.3	76.9	<u>125.8</u>	83.9	28.4	8.1	8.8	335.2
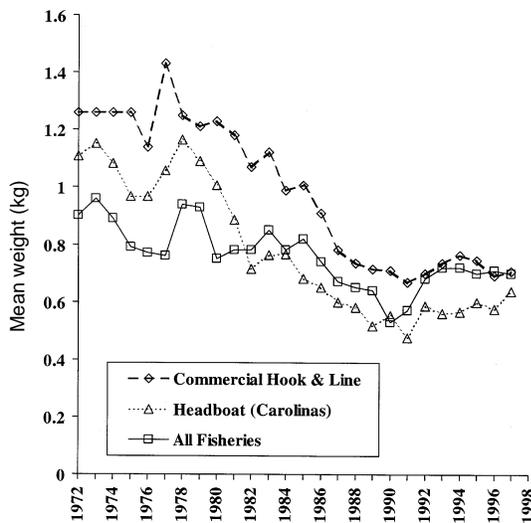
Figure 2

Annual mean weight of red porgy off the southeastern United States in landings from commercial hook-and-line, headboats from the Carolinas, and from all fisheries. Minimum size limit was introduced in 1992.
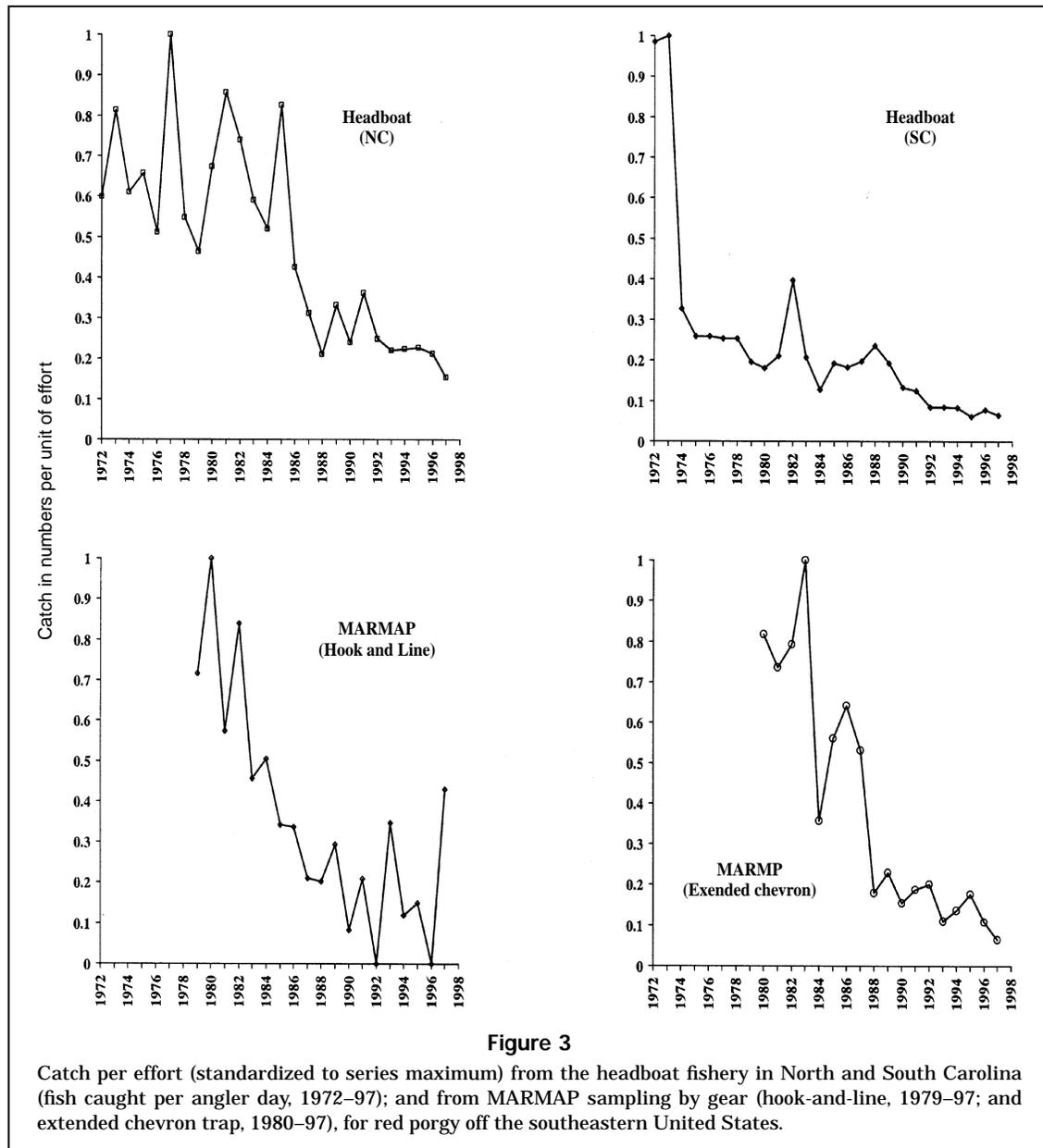
what, and gradually increased through the present (Fig. 4A). Of the two matrices, the primary matrix provided lower estimates of full F in the recent period, particularly with zeroes replaced by missing values.

Estimates of recruitment were not particularly sensitive to estimation procedure. A general decline in recruitment, 1973–97, was estimated from both catch matrices and with either treatment of zeroes (Fig. 4B).

Sensitivity runs on the primary catch matrix, but with M = 0.20/yr or M = 0.35/yr, estimated that patterns in F and recruitment were similar to those with the base value of M = 0.28/yr (Fig. 5). Under the assumption M = 0.20/yr, estimated values of F were higher than the base assessment; whereas under the assumption M = 0.35/yr, estimated values of F were lower (Fig. 5A). Effect of the value of M on recruitment increased with each year backwards in time. Regardless of the value of M, the pattern of estimates was of initially high recruitment, followed by a long period of severe decline (Fig. 5B).

For comparative purposes, VPA fits were also made by using only the hook-and-line index or only the extended chevron-trap index. Essentially no differences were noted in estimates of full F or recruitment to age 1.

In our VPAs, we estimated statistical weights for the two calibration indices. Estimated weights varied only slightly

Figure 3

Catch per effort (standardized to series maximum) from the headboat fishery in North and South Carolina (fish caught per angler day, 1972–97); and from MARMAP sampling by gear (hook-and-line, 1979–97; and extended chevron trap, 1980–97), for red porgy off the southeastern United States.

with different assumptions about M. Base analysis of the primary catch matrix estimated weights of 0.08 for hook-and-line CPE and 0.92 for extended chevron-trap CPE; analysis of the alternate catch matrix estimated weights of 0.05 and 0.95. When missing values were used in place of zeroes in the hook-and-line index, estimated weights were 0.50 for hook-and-line CPE and 0.50 for extended chevron trap CPE, demonstrating that treatment of zeroes is an important consideration. The main change in results from using missing values was decreased estimates of F in recent years (Fig. 4A).

In the retrospective analysis, estimates of F generally converged in about 3 to 4 years; convergence in estimates of recruitment took a year or two longer (Fig. 6). A large positive retrospective pattern was evident in full F in the

most recent year, and a corresponding negative pattern in estimates of recruitment (Fig. 6). The retrospective pattern was similar when using missing values for zeroes.

Yield per recruit and related benchmarks

Estimates of equilibrium YPR were somewhat sensitive to the value of M assumed, with larger assumed values of M corresponding to smaller estimates of YPR. The highest YPR was obtained during the middle time period (Table 6); however, high theoretical values of yield per recruit can result from fishing mortality rates that are not sustainable.

The two biological reference points F_{max} and $F_{0.1}$ (Beverton and Holt, 1957; Sissenwine and Shepherd, 1987) were estimated from the yield-per-recruit analysis. Assuming

partial recruitment based on average F at age, these reference points were estimated for the recent time period from the primary and alternate catch matrices as F_{max} = 0.5/yr and 0.7/yr, respectively; and $F_{0.1}$ = 0.23/yr and 0.25/yr, respectively (Table 7).

Spawning potential ratio, spawning-stock biomass, and stock-recruitment model

Estimates of static SPR were calculated by catch matrix, time period, and assumed value of M and for four measures of spawning biomass (total mature biomass, mature female biomass, mature male biomass, and egg production) (Table 6; Fig. 7). Static SPR based on mature female biomass was less affected by increases in F than static SPR based on mature male biomass because younger fish are predominantly female and older fish, male. For example, full F that produced 59% SPR in mature female biomass produced 49% SPR in egg production, 42% SPR in total mature biomass, and 27% SPR in mature male biomass (Table 6).

Corresponding estimates were made of reduction in the proportion of males due to fishing in the three periods. For example, a value of 69% in the last column of Table 6 means that if the proportion of males in the mature unfished population had been 50%, introduction of fishing mortality would reduce this proportion to 34.5% of the population (69% × 50%). These estimates were made on the basis of observed sex ratios at size and assuming that the rate of transformation from female to male does not increase as the population is fished down.

Total spawning stock biomass (SSB) was estimated from the primary catch matrix to have reached its peak in about 1979 at 3530 t, declining to 397 t in 1997 (Fig. 8A). When missing values were substituted for zeroes in computing the CPE index, estimates of SSB near the end of the series were slightly higher (Fig. 8A). Estimates from the alternate matrix were similar, with the largest differences occurring before 1983 (Fig. 8A).

Static SPR estimated from the primary catch matrix was high during the 1970s, reached 67% in 1975, and declined to a minimum of 33% in 1982, increased again to 55% in 1993, and declined to about 18% in 1997 (Fig. 8B). Estimates from the alternate catch matrix were similar, but markedly lower from 1983 to 1994 (Fig. 8B). Values of full F providing spe cified values of static SPR (based on female egg production and total spawning stock biomass) are summarized in Table 7, along with values of full F averaged by period, for comparative purposes.

The recent management definition of overfishing is static SPR <35% (amendment 12 [SAFMC[3]]). Our primary estimates are of static SPR >35% from 1972 to 1994 (except for 1982), lower thereafter. Estimates from the alternate catch matrix show static SPR >35% from 1972 to 1980, lower thereafter.

During the early to mid 1970s, a large spawning stock produced high recruitment. Despite a high spawning-stock size estimated through about 1983, SPR and recruitment declined, and the unsustainable landings of the late 1970s and 1980s reduced the spawning stock to levels
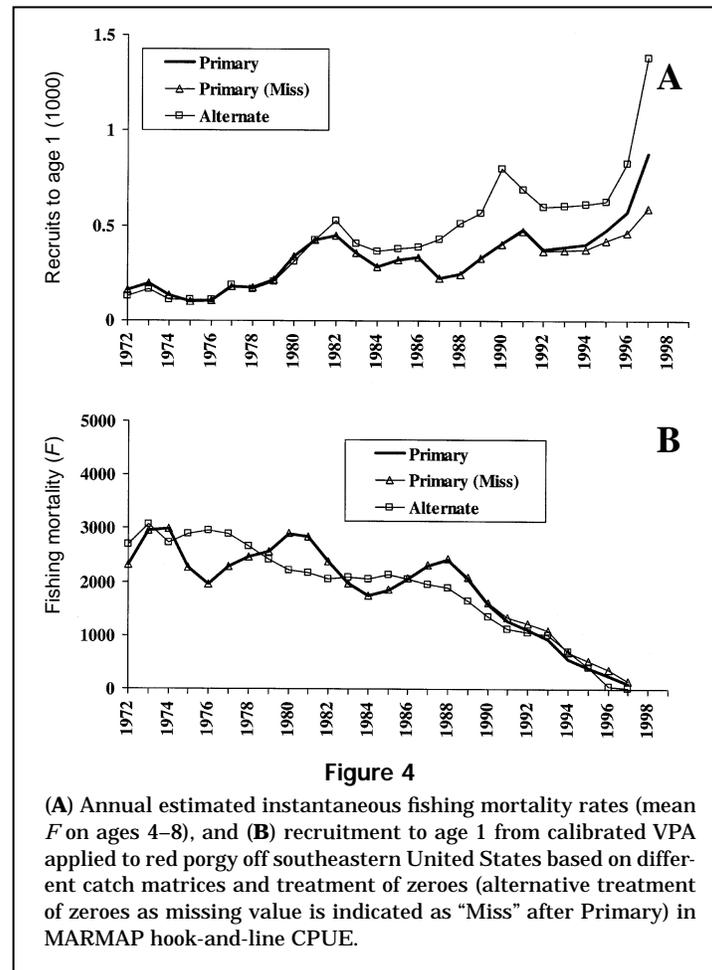
Table 5

Mean estimates (from calibrated virtual population analyses) of age-specific instantaneous fishing mortality rate (F) on red porgy off southeastern U. S. during three time periods. Estimates from primary catch matrix (see text) are given for three levels of natural mortality rate M, two treatments of missing values for M=0.28. Estimates from alternate catch matrix given for M = 0.28 only. Exploitation rate in final column is based on catch of ages 1–8 divided by estimated population number of same ages.

	Age (yr)				Exploitation rate
Analysis	1	2	3	4+	(ages 1–8)
Primary (MARMAP) catch matrix					
(M=0.28)					
1972–78	0.007	0.06	0.08	0.15	0.06
1982–86	0.018	0.12	0.19	0.35	0.12
1992–96	0.014	0.10	0.15	0.44	0.16
(M=0.28, zeroes in index treated as missing)					
1972–78	0.007	0.06	0.08	0.15	0.06
1982–86	0.018	0.12	0.19	0.35	0.12
1992–96	0.011	0.08	0.13	0.40	0.14
(M=0.20)					
1972–78	0.010	0.08	0.11	0.20	0.08
1982–86	0.025	0.16	0.24	0.43	0.16
1992–96	0.017	0.12	0.17	0.49	0.19
(M=0.35)					
1972–78	0.005	0.04	0.06	0.11	0.04
1982–86	0.013	0.09	0.14	0.28	0.09
1992–96	0.012	0.09	0.14	0.40	0.14
Alternate catch matrix					
(M=0.28)					
1972–78	0.006	0.04	0.06	0.14	0.05
1982–86	0.017	0.10	0.18	0.42	0.13
1992–96	0.007	0.06	0.27	0.66	0.18

not expected (under the stock–recruitment model) to provide good recruitment. Similar patterns were apparent in stock-recruitment curves derived from both catch matrices (Fig. 9).

Estimates of benchmarks from simulations

Estimates of MSY, B_{MSY} and F_{MSY} were made from the stock–recruitment model and age-structured simulations (Table 8; Fig. 10). In addition, minimum stock size threshold (MSST), a benchmark recently introduced into U.S. Federal fishery management, was calculated from B_{MSY} as suggested in Restrepo et al. (1998), namely as MSST = $(1-M)$ B_{MSY}, with M = 0.28/yr. Although benchmarks are somewhat sensitive to assumptions examined, sensitivity was small compared with the difference between estimated benchmarks and current status of the stock and fishery (Table 8). For example, estimates of MSY obtained in this way (240–280 t/yr) were similar to recent landings (about

Figure 4

(**A**) Annual estimated instantaneous fishing mortality rates (mean *F* on ages 4–8), and (**B**) recruitment to age 1 from calibrated VPA applied to red porgy off southeastern United States based on different catch matrices and treatment of zeroes (alternative treatment of zeroes as missing value is indicated as "Miss" after Primary) in MARMAP hook-and-line CPUE.

200–300 t/yr), but well below landings taken earlier (e.g. >800 t in 1981 and 1982). Estimates of fishing mortality rates in the recent period are about 2.7 to 3.6 times those that could produce MSY (Table 8). Because benchmark estimates are based on selectivity patterns estimated for 1992–96, their values are expected to change with the recent introduction of higher minimum size limits. However, the general picture is unlikely to change.
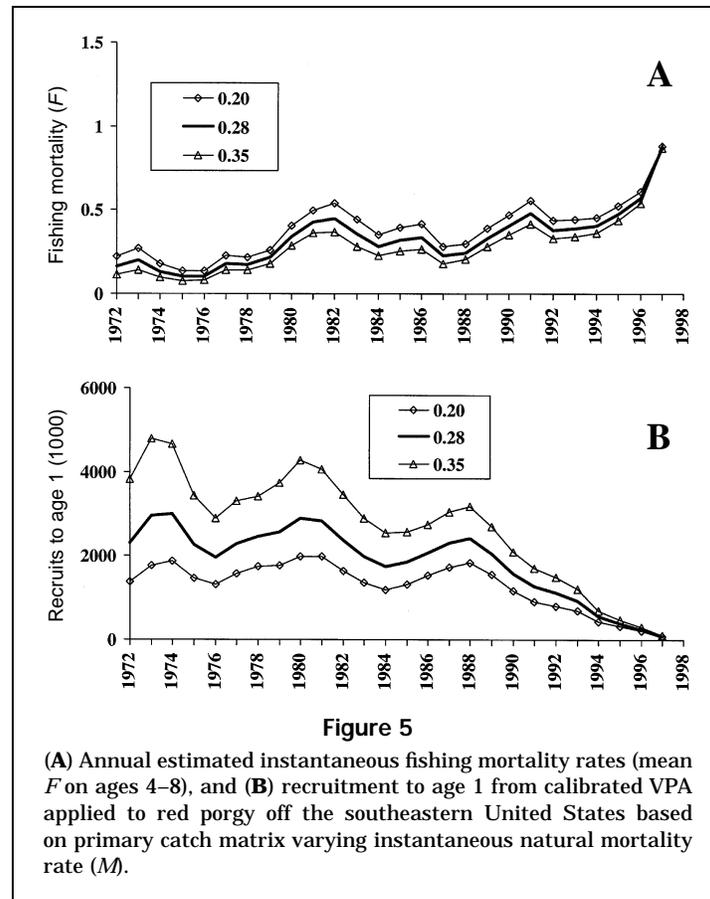
Surplus-production model

It was not possible to estimate the shape parameter of the generalized production model from these data; therefore, we present results only for the logistic model. Fits of that model with various assumptions about B_1/K were statistically equivalent (log likelihoods from –2.29 to –2.25), indicating that the data–model combination is not informative about relative biomass level at the start of the time series. We present results under a range of assumptions centered on $B_1/K = 0.75$ (Table 9). The estimate of MSY was moderately sensitive to the assumption on B_1/K, varying about 18.5% around the central estimate (Table 9); it was also higher than our estimates from age-structured methods (Table 8). Nonetheless, the bias-corrected 80% confidence

interval on the central MSY estimate (Table 9) and the corresponding 50% interval (not shown) included the age-structured estimates of MSY; therefore there was some agreement between methods.

Estimates of stock and fishery status expressed in relative terms (Table 9) were similar to those from the age-structured analysis (Table 8) and like those estimates depicted a heavily overexploited stock. Stock biomass at the start of 1998 was estimated as about 25% of the biomass that can support MSY (B_{MSY}), a result that was remarkably insensitive to the assumption on B_1/K. Fishing mortality rate in 1997 was estimated as about twice the fishing mortality rate associated with MSY (F_{MSY}), a result only slightly sensitive to the assumption on B_1/K. Equilibrium yield available in 1998 was estimated as about 44% of MSY; this reduction was due to the stock's reduction well below B_{MSY}.

Estimates of relative stock and fishery status over time displayed a pattern of increasing fishing mortality rate and decreasing abundance over time (Fig. 11). It appears that the biomass moved below B_{MSY} in about 1982 and that the fishing mortality rate has been above F_{MSY} since about 1978. Estimated confidence intervals on F/F_{MSY} are remarkable in encompassing a wide range that since

Figure 5

(**A**) Annual estimated instantaneous fishing mortality rates (mean *F* on ages 4–8), and (**B**) recruitment to age 1 from calibrated VPA applied to red porgy off the southeastern United States based on primary catch matrix varying instantaneous natural mortality rate (*M*).

about 1980 has included only values greater than unity (Fig. 11B).

Discussion

This work includes numerous advances from previous assessments (Vaughan et al., 1992; Huntsman et al.[1]). The major improvements are availability of additional fishery-dependent and fishery-independent aging data and of fishery-independent indices for calibrating VPAs. Other changes include expanded geographic range, new estimates of sex ratios and maturity schedules, new growth parameters, application of a more modern algorithm for calibrated VPA, and application of a nonequilibrium surplus-production model. Our conclusions agree with both earlier assessments in finding a population in decline.

Because unbiased sampling of wild fish stocks is extremely difficult and fishery data sets are small (in number of years of data), fish population models are not precise approximations of reality. Accurately characterizing uncertainty in assessment results is difficult or impossible: although statistical estimates of uncertainty can be obtained, it is not known how to balance them against factors that tend to increase certainty, such as agreement among data sources or methods and among assessments conducted over time. Any formal estimate of uncertainty

in the present assessment results would be large. Nonetheless, in light of our use of complementary models, several independent data sources, and two largely independent sets of age-length keys, and based on agreement with past assessments, we believe that the present results are unequivocal in their major finding of a severely depleted population.

By using two treatments of observed zeroes in CPE series, we illustrated that some results can be sensitive to the method used to treat zeroes. Although addition of a constant before logarithmic transformation is a widely used practice and has been a common statistical recommendation (e.g. Snedecor and Cochran, 1980; Berry, 1987), it is becoming evident that the practice can be problematic in estimation of abundance indices. Logarithmic transformation is made under the assumption of lognormally distributed data, and presence of zeroes in itself violates that assumption. Moreover, results can depend strongly on the additive constant chosen (Porch and Scott, 1994; Ortiz et al., 2000). The root of the problem is that transformed zeroes are usually extreme values in the data set and thus highly influential. Several other statistical models have been proposed, of which the most promising in this application may be the delta–lognormal model (Lo et al., 1992; Ortiz et al., 2000). However, this is still an active area of methodological research, and the matter remains unresolved. We thus used two treatments of zeroes and have

Table 6

Static yield per recruit (YPR) and spawning potential ratio (SPR) of red porgy off southeastern United States. Estimates are based on mean age-specific fishing mortality rates from calibrated VPA on primary or alternative catch matrices (see text), are made under several assumptions about natural mortality rate, *M,* and treatment of missing values in hook-and-line abundance index, and use selectivity for most recent time period, (1992–96).

| Analysis | YPR (g) | Spawning potential ratio | | | | Percentage of males in relation to no fishing[1] |
		Total	Female	Eggs	Male	
Primary (MARMAP) catch matrix						
(*M*=0.28)						
1972–78	152.3	61	74	67	49	83
1982–86	214.3	40	58	47	26	71
1992–96	162.2	42	59	49	27	69
(*M*=0.28, zeroes in index treated as missing)						
1972–78	152.3	61	74	67	49	83
1982–86	214.2	40	58	47	26	71
1992–96	160.9	44	61	51	29	70
(*M*=0.20)						
1972–78	263.5	43	60	49	33	74
1982–86	306.6	25	43	31	15	61
1992–96	229.5	29	47	37	17	60
(*M*=0.35)						
1972–78	89.8	74	84	78	63	89
1982–86	149.5	54	69	60	39	78
1992–96	118.7	52	67	58	36	75
Alternate catch matrix						
(*M*=0.28)						
1972–78	145.1	64	77	70	53	84
1982–86	261.4	33	53	37	20	69
1992–96	198.2	27	46	33	14	64

[1] Percent relative reduction in numbers of mature males between fished and unfished conditions; i.e. proportion of males under fished conditions is *x*% of proportion of males under unfished conditions.

presented both sets of results, which are different, but not remarkably so.

Several issues arise from choosing as "primary" the catch matrix developed from fishery-independent age data and as "alternate" the matrix from fishery-dependent data. The choice was by necessity somewhat subjective, but was based on the long-term (1979–94), continuous nature of the fishery-independent data on age at size and its larger sample sizes, in contrast to the intermittent age sampling in the fishery, which required frequent interpolation of age-length keys to construct the alternate catch matrix. The different selectivity of the fishery-independent gear should not significantly bias the primary catch matrix, but fishery-independent samples at larger sizes were sometimes very small, making it necessary to pool data across longer periods for the largest sizes. Parallel analyses were conducted with the two catch matrices to determine sensitivity of major results to the choice of matrices as primary and alternate.

Size selectivity of the gear can have much greater effect in fitting growth models. Fishery-dependent sampling, by selecting larger fish, may overestimate mean size at younger ages, but estimate L_∞ more accurately, whereas fishery-independent sampling, by selecting smaller fish, may underestimate L_∞. In a simulation study, Goodyear (1995) noted: ". . . samples drawn from size-selective gears or fisheries yield biased estimates of mean length at age. . . . Even slight changes in sampling protocol can result in misleading temporal shifts of estimates of size at age." This aspect of the differing selectivity between gears seems important to us, and it can bias estimation of growth models. As a result, we cannot say whether estimated temporal differences in size at older ages result from changes in growth patterns in response to long-term overexploitation (Harris and McGovern, 1997) or from a change in sampling-gear selectivity in the fishery-independent sampling gear (Potts et al., 1998).

Despite questions about size at age over time, patterns of population benchmarks and stock status estimated from
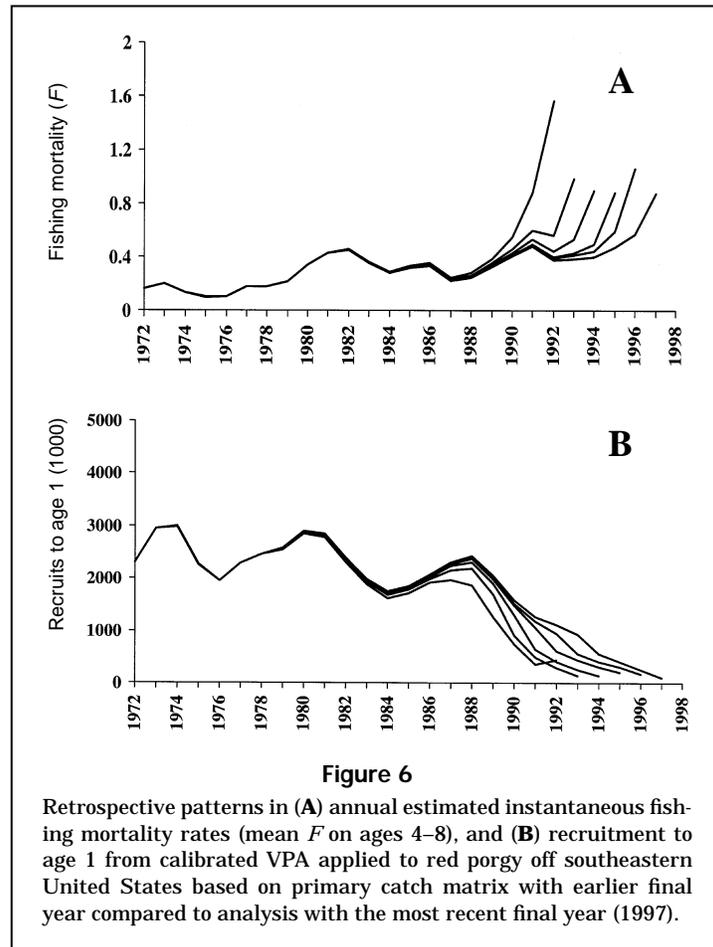
Table 7

Potential biological reference points developed from static yield per recruit (YPR) and spawning potential ratio (SPR) analyses for red porgy off southeastern United States estimated from output from calibrated VPA using selectivity for most recent time period (1992–96), and based on primary catch matrix (three levels of M, and run with missing value for 0.0 in parentheses) or alternate catch matrix (M=0.28). See text for derivation of catch matrices.

	Primary catch matrix				Alternate catch matrix
	M=0.20	M=0.28	M=0.28 (missing)	M=0.35	M=0.28
Yield per recruit (YPR) analysis					
$F_{0.1}$	0.15	0.23	(0.23)	0.31	0.25
F_{max}	0.25	0.53	(0.56)	0.84	0.72
Static spawning potential ratio analysis (static SPR)					
Female (eggs)					
F_{30}	0.25	0.49	(0.50)	0.79	0.77
F_{35}	0.20	0.37	(0.38)	0.60	0.55
F_{40}	0.17	0.29	(0.30)	0.46	0.41
Total spawning-stock biomass					
F_{30}	0.25	0.42	(0.43)	0.69	0.51
F_{35}	0.20	0.33	(0.34)	0.52	0.38
F_{40}	0.17	0.26	(0.27)	0.40	0.30
Observed full F by period					
1972–78	0.20	0.15	(0.15)	0.11	0.14
1982–86	0.43	0.35	(0.35)	0.28	0.42
1992–96	0.49	0.44	(0.40)	0.40	0.66

Table 8

Parameters and potential biological reference points developed for Beverton-Holt spawner-recruit model of red porgy off southeastern United States. Estimates are based on calibrated VPA by using selectivity for most recent time period (1992–96), and based on primary catch matrix (fishery-independent keys; includes separate run with missing value for zeroes in hook-and-line index) or alternate catch matrix (fishery-dependent keys).

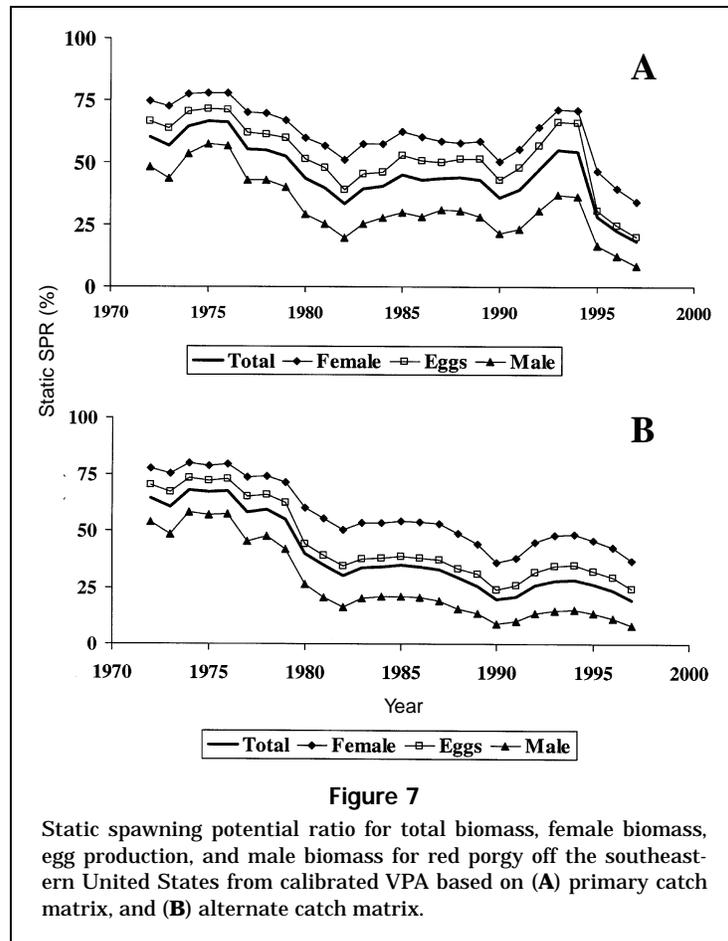| Parameter estimate or reference point	Primary catch matrix	Primary CM (missing)	Alternate catch matrix
Parameter estimates (standard error in parentheses)			
b_0	1.83×10^{-4}	2.01×10^{-4}	2.32×10^{-4}
	(7.0×10^{-5})	(6.7×10^{-5})	(5.3×10^{-5})
b_1	0.669	0.617	0.605
	(0.185)	(0.175)	(0.157)
$\max\{R_1\} = 1/b_0$	5.46×10^6	4.98×10^6	4.31×10^6
Reference points			
MSY	242	248	277
F_{MSY}	0.14	0.15	0.18
B_{MSY}	2564	2425	2387
MSST	1846	1746	1719
Estimates of SSB (spawning stock biomass) by period			
1972–78	2884	2885	3367
1982–86	2326	2330	2651
1992–96	876	953	669
Estimates of stock status			
$F_{92\text{-}96}/F_{MSY}$	3.2	2.7	3.6
$B_{92\text{-}96}/B_{MSY}$	0.34	0.39	0.28

Figure 6

Retrospective patterns in (**A**) annual estimated instantaneous fishing mortality rates (mean F on ages 4–8), and (**B**) recruitment to age 1 from calibrated VPA applied to red porgy off southeastern United States based on primary catch matrix with earlier final year compared to analysis with the most recent final year (1997).

Table 9

Estimates of biological benchmarks and stock status from application of logistic surplus-production model to red porgy off the southeastern United States. Symbols are B_1 = biomass in first year; K = carrying capacity; MSY = maximum sustainable yield; B_{98}/B_{MSY} = biomass at start of 1998 (year following analysis) relative to biomass at MSY; F_{97}/F_{MSY} = fishing mortality rate in 1997 compared with F at MSY; Ye_{98} = equilibrium yield available in 1998. Because B_1 could not be estimated with any precision, the model was fitted under a range of assumptions on its value in relation to that of K. For central case, 80% confidence intervals are shown in parentheses.

Benchmark or status indicator	Assumed value of B_1/K				
	0.55	0.65	0.75	0.85	0.95
MSY (t/yr)	506	482	459 (98–555)	437	416
B_{98}/B_{MSY}	0.247	0.247	0.248 (0.116–0.373)	0.250	0.252
F_{97}/F_{MSY}	1.85	1.93	2.01 (1.36–5.08)	2.09	2.17
Ye_{98} (t)	219	209	199 (69.0–304)	191	183
Ye_{98}/MSY	0.434	0.433	0.434 (0.219–0.607)	0.437	0.440

Figure 7

Static spawning potential ratio for total biomass, female biomass, egg production, and male biomass for red porgy off the southeastern United States from calibrated VPA based on (**A**) primary catch matrix, and (**B**) alternate catch matrix.
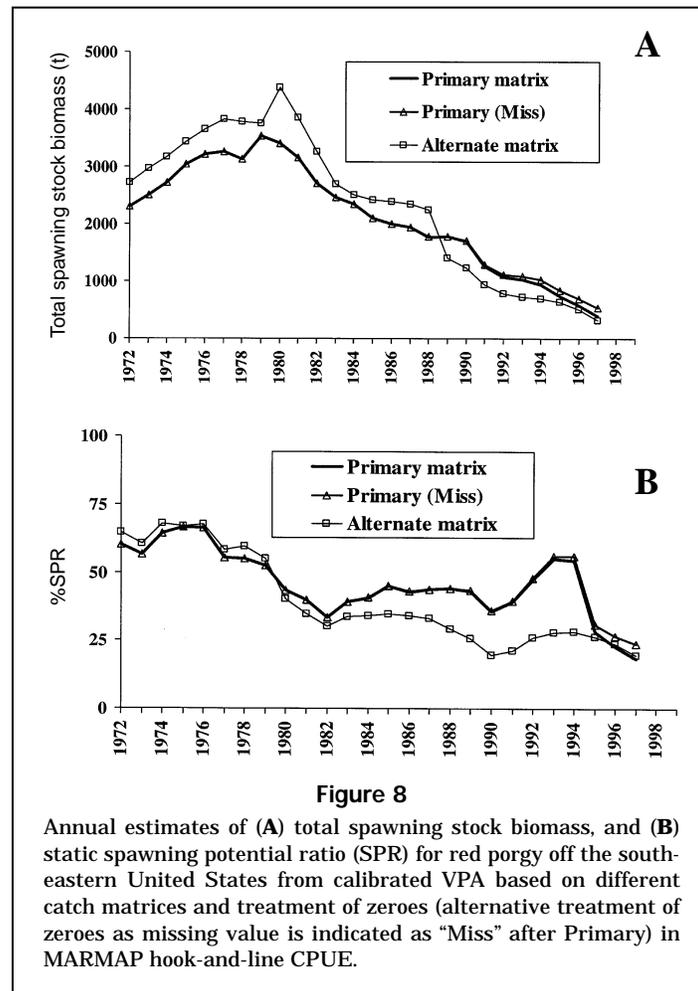
the two matrices (and, indeed, in all sensitivity runs) were similar, depicting much higher population size and spawning biomass during the 1970s and severe decline through the 1980s and 1990s. This pattern was independent of the large retrospective pattern in the terminal year. Declining trends in CPE from headboats and in fishery-independent sampling (Fig. 3), combined with the observed decline in recruitment (Fig. 4B), also depict an increasingly depleted population. Additional evidence is provided by the surplus-production model, which estimated that the population was at high levels during the 1970s, but that since the mid 1980s it has been far below the level capable of producing MSY (Fig. 11). Implementation of a 12-inch minimum size limit in 1992 (amendment 4 [SAFMC[5]]) appears to have reduced F only on ages 1–3, but F on fully recruited ages (4+) has increased (Table 5).

Static SPR (in total mature biomass) is estimated for the recent period at 42% and 27% from the primary and alternate catch matrices, respectively (Table 6). Mean SPR estimated from the primary catch matrix for all three periods is above SPR=35%, the value used by the South Atlantic Fishery Management Council to define overfishing for red porgy (amendment 12 [SAFMC[3]]). Estimated SPR from the alternate catch matrix is below 35% in the recent period (Table 6).

Coleman et al. (1999), in a discussion of reef fish management, pointed out that SPR as usually estimated from female biomass or egg production has proven less effective for protogynous reef fishes than for fishes that do not change sex. With the loss of the largest size classes, predominantly male, remaining males may not be able to increase harem size sufficiently to fertilize all available females. Thus, determining SPR solely on female reproductive contribution may not capture the true decline in reproduction caused by fishing. For that reason, Vaughan et al. (1992, 1995) recommended calculating static SPR from total mature biomass, broadening the concept of static SPR for protogynous species. Vaughan et al. (1995) calculated reduction in the proportion of males for black sea bass due to changes in fishing mortality and under the assumption that transition rate does not change with population abundance. They estimated a reduction of about 40% due to recent fishing mortality, a reduction similar to the ~30% we estimated for red porgy.

Whether males are currently limiting, or the degree to which increased fishing mortality can cause them to become limiting, is unknown. Regardless, increased fishing mortality on all ages would be expected to reduce the proportion of males in the mature population. The rate at which the imposition of fishing mortality may alter the av-

Figure 8

Annual estimates of (**A**) total spawning stock biomass, and (**B**) static spawning potential ratio (SPR) for red porgy off the southeastern United States from calibrated VPA based on different catch matrices and treatment of zeroes (alternative treatment of zeroes as missing value is indicated as "Miss" after Primary) in MARMAP hook-and-line CPUE.

erage age of transition to male is unknown, as is the effect of population density on transformation rate.

Increased sex transformation due to reduced abundance of males, as reported in other protogynous reef fish (Shapiro, 1979), would cause declines in mature female biomass and egg production beyond those expected from fishing alone. McGovern[7] found a greater percentage of males in smaller size classes in 1991–99 than in 1979–81 and suggested that red porgy have compensated for the loss of large individuals by becoming male at smaller sizes. If so, a smaller change in sex ratio, but a greater reduction in egg production, would be expected than implied by increasing fishing mortality alone.

New evidence suggests that red porgy are indeterminate, serial spawners (Daniel[8]). That is, the size and number of batches of eggs are not fixed at the start of the spawning season, but older, larger females spawn in larger

batches, more frequently, and possibly over a longer season than younger, smaller females. If so, SPR based on egg production estimated from a fixed weight–fecundity relationship would be unrealistic, and SPR based on total mature biomass would underestimate the contribution of older fish, and thus underestimate the effects of fishing.

Huntsman and Schaaf (1994) proposed accounting for sex-composition changes by multiplying total egg production by a factor representing the probability of successful fertilization. They calculated that probability (Q) for a given fishing mortality rate F^* from the relative change in male contribution of spawning products under fishing:
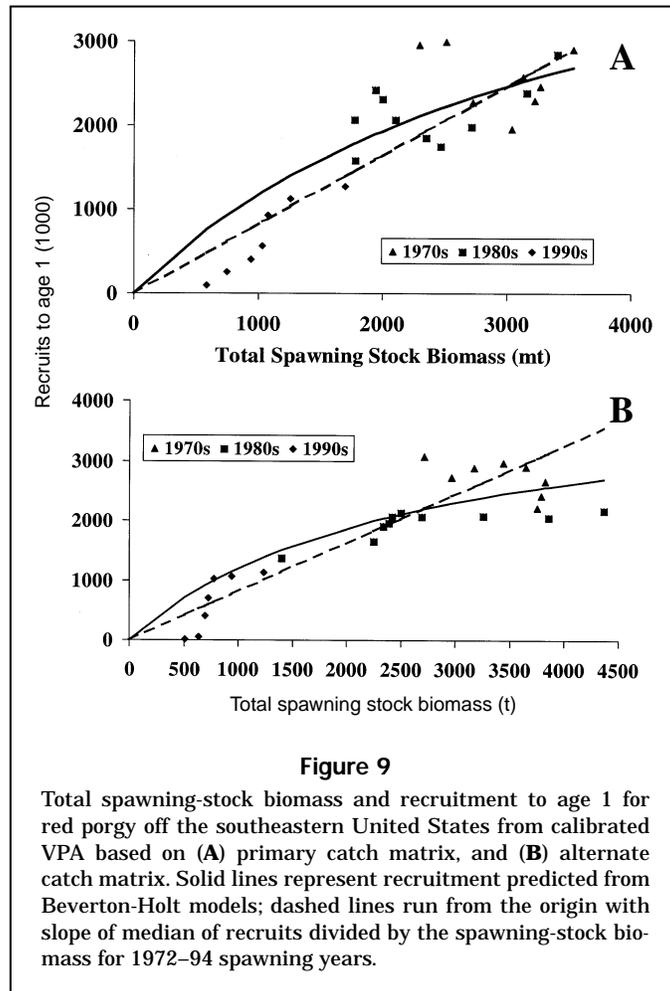
$$Q = \frac{(G_m / G_f) \mid F = F^*}{(G_m / G_f) \mid F = 0},$$

where G_m and G_f = the gamete contributions of males and females, respectively.

Huntsman and Schaaf (1994) computed G_m as total male biomass and G_f as total female egg production. When new information on red porgy batch spawning becomes avail-

---

[7] McGovern, J. C. 2001. Personal commun. South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422.

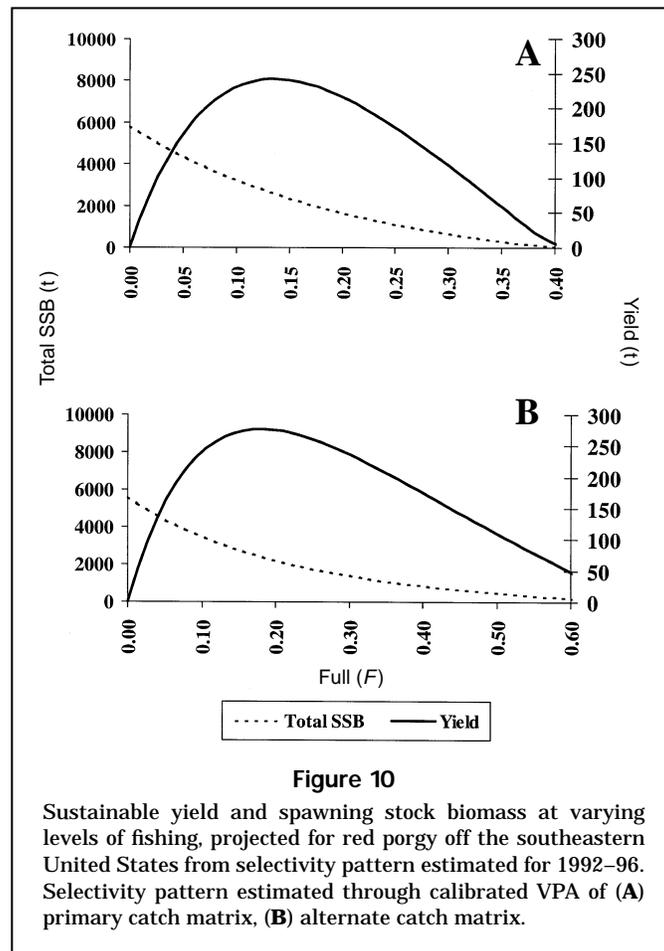[8] Daniel, E. A. 2001. Personal commun. University of Charleston, Charleston, SC 29424.

Figure 9

Total spawning-stock biomass and recruitment to age 1 for red porgy off the southeastern United States from calibrated VPA based on (**A**) primary catch matrix, and (**B**) alternate catch matrix. Solid lines represent recruitment predicted from Beverton-Holt models; dashed lines run from the origin with slope of median of recruits divided by the spawning-stock biomass for 1972–94 spawning years.

able and allows calculation of total population fecundity at Z and M, we recommend exploring that approach. Population simulations for a protogynous grouper (Huntsman and Schaaf, 1994) suggest greater vulnerability to fishing than for a comparable gonochoristic stock. It appears that the questions of what SPR measure is most appropriate and how it should be computed cannot be answered until the overall reproductive biology of the species is far better understood.

As usual for fish populations, the spawner–recruit relationship is only roughly defined by the data (Fig. 9), and the years in which the model does not fit raise interesting questions. In the fit based on the primary catch matrix (Fig. 9A), the two large residuals at the start might be taken as suggestive of a dome-shaped recruitment curve, they simply might reflect random error, or they might result from the additional computations needed to extend the catch matrix back to 1972. The analysis based on the alternate catch matrix (Fig. 9B) shows a more pronounced pattern, in which data from the 1970s demonstrate higher recruitment for a given level of spawning-stock size than later data. This pattern might be taken as evidence of a regime shift (change in underlying ecological conditions, from natural or anthropogenic causes), or it might be an artifact of the smaller data sets of age-length data used in this approach. Other explanations are equally possible for residual patterns in Figure 9, A and B. These observed data suggest "depensation" (reverse compensation; decreased, rather than increased, recruitment per spawner at lower population sizes) at very low spawning biomasses, but this suggestion is uncertain because of high retrospective error in estimating recruitment in the most recent years.

Growth overfishing was not estimated to be severe. Mean full F in the early period was estimated well below both F_{max} and $F_{0.1}$. Mean full F in the middle period was estimated as about 152% of $F_{0.1}$, and mean full F for the recent period was estimated as about 191% of $F_{0.1}$, both below F_{max} (Table 7). This stock appears to be one in which recruitment overfishing can be induced before growth overfishing, and for that reason reference points such as F_{max} and even $F_{0.1}$ would be insufficiently conservative for its management.

The estimate of B_{MSY} computed from the recruitment model and selectivity vector can be an appropriate target biomass for management and the corresponding MSST can be a threshold to define overfished status (Restrepo et al., 1998). Estimates of spawning-stock biomass were well above MSST, 1972–78; approached MSST, 1982–86; and were well

Figure 10

Sustainable yield and spawning stock biomass at varying levels of fishing, projected for red porgy off the southeastern United States from selectivity pattern estimated for 1992–96. Selectivity pattern estimated through calibrated VPA of (**A**) primary catch matrix, (**B**) alternate catch matrix.
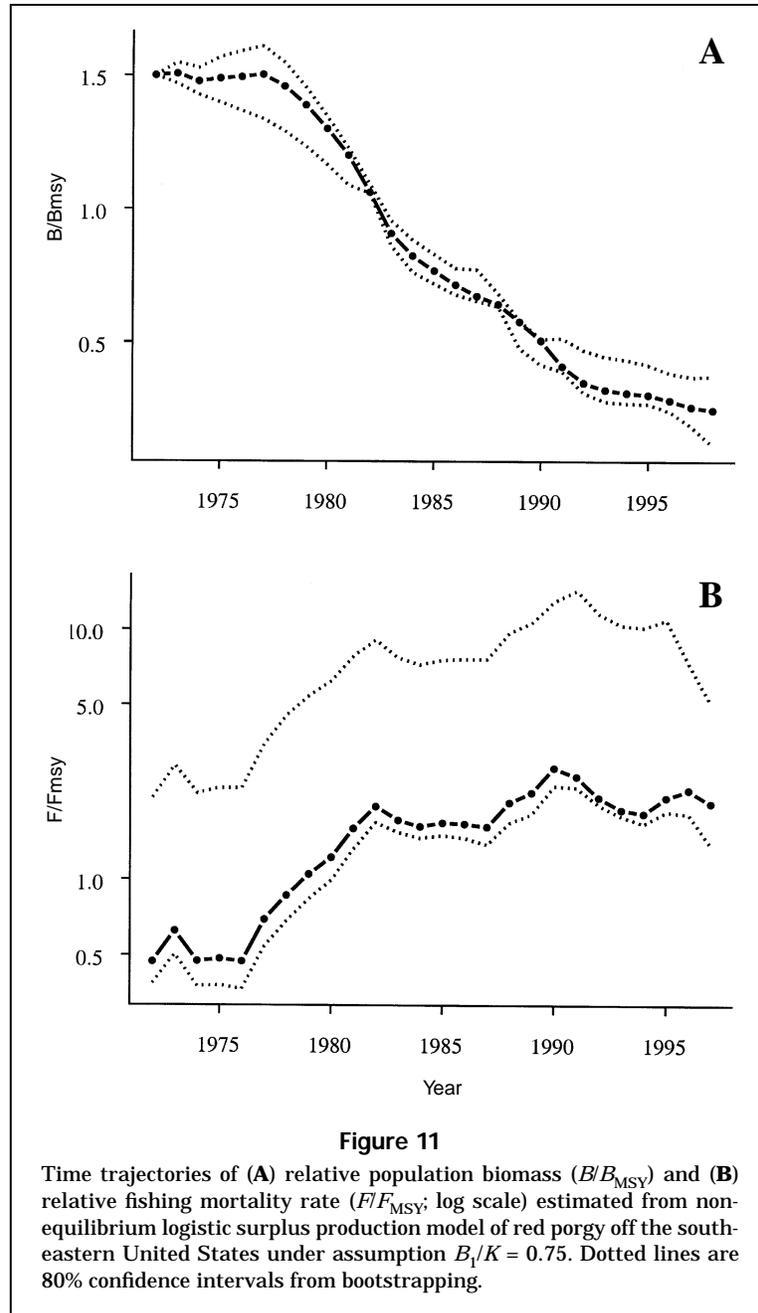
below MSST, 1992–96 (Table 8). Still lower estimates of spawning-stock biomass were obtained for the terminal year, although we view terminal-year estimates with scepticism because of retrospective patterns. The production model, not commonly subject to such retrospective patterns, also estimates current biomass as well below MSST (Table 9).

Current estimates of full F (Table 5 for 1992–96) are considerably higher than estimates of F_{MSY} (Tables 8 and 9). In addition, estimates of F_{MSY} are considerably lower than F values corresponding to static SPR of 30% to 40%. If static SPR is used as a reference point, a value higher than SPR = 40% will be necessary to maintain the stock at reasonably productive levels.

It seems inescapable that heavy fishing mortality has been a major cause of the decline in recruitment (Fig. 4B), particularly in the late 1970s and 1980s. Although fishing mortality was lower in the mid-1980s, it increased again in the 1990s for fully-recruited ages (Fig. 4A), and thus static SPR has also declined (Fig. 7). Patterns of increasing F and declining SPR are even more pronounced in estimates from the alternate catch matrix (Figs. 4A, 7). Even though spawning-stock biomass remained high in the late 1970s, recruitment began to decline (Fig. 9). This finding suggests that the usual effects of heavy fishing pressure

may have been compounded by other population-specific factors (e.g. those relating to sex structure) or extrinsic factors (e.g. unfavorable environmental conditions) affecting the reproductive success of the population.

Management of hermaphroditic reef fishes is difficult, and it has had few successes (Coleman et al., 1999). As we have shown, interaction of a population's size and sex structures complicates the attempt to model reproductive capacity (e.g. SPR) as a function of fishing mortality rate. Size limits can have subtle side effects if they result in a deficit of males and if larger females in the population consequently change sex at a higher rate. Use of bag limits and size limits in management makes it likely that fish will be caught and released, imposing discard mortality that is incompletely observable. Discard mortality has been found an important factor in collapse of at least one fish stock (Myers et al., 1997). Fish that aggregate become more catchable (increased catchability coefficient $q = F/f$) as abundance declines, another phenomenon associated with risk of collapse (Clark, 1974; Gulland, 1975). Ludwig (1998) has suggested on theoretical grounds that the best management strategy for stocks that may collapse is rapid adjustment of harvest size in response to changes in stock abundance. Ludwig noted: "It is noteworthy that the com-

Figure 11

Time trajectories of (**A**) relative population biomass (B/B_{MSY}) and (**B**) relative fishing mortality rate (F/F_{MSY}; log scale) estimated from non-equilibrium logistic surplus production model of red porgy off the southeastern United States under assumption $B_1/K = 0.75$. Dotted lines are 80% confidence intervals from bootstrapping.

plications in stock dynamics all have the same effect upon performance of [management] strategies: they all may cause drastic increases in the probability of extinction and decreases in the expected discounted total yield." It was in the face of such difficulties and uncertainties that the concept of precautionary management was developed (FAO, 1995).

In conclusion, as of 1997 the stock of red porgy off the southeastern United States appears to be in poor condition and getting worse. Even after allowing for retrospective patterns and regardless of catch matrix, estimates are of long-term declines in spawning-stock biomass, recruitment, and catch per effort in the headboat fishery and in fishery-independent surveys. Such estimates strongly suggest overexploitation—overexploitation at an unsustainable rate. Static SPR since 1985 has generally been above the present criterion for overfishing (SPR > 35%), based on estimates from our primary catch matrix. (Estimates from the alternate catch matrix are lower, and estimates from that matrix are generally even more pessimistic about stock status.) During that period, recruitment and spawning stock have continued to decline. Given the present low population level and poor recruitment, we believe that substantial reductions in fishing mortality rate will be necessary to re-

build the stock, whether or not factors other than fishing have contributed to the decline. The situation may be analogous to that of striped bass (*Morone saxatilis*) off the U.S. Atlantic coast in the 1980s, a population that was extremely depressed, with landings reduced by about 75% from their peak. Models of that decline suggested that sharp reductions in fishing mortality would increase the population's growth rate, regardless of the relative importance of fishing and environmental conditions in the preceding decline. Under vigorous management (with sharp reductions in fishing mortality) the population has made a remarkable recovery (Richards and Rago, 1999).

Since completion of this assessment, the South Atlantic Fishery Management Council has taken several actions to promote recovery. As noted in amendment 12 (SAFMC[3]), amendment 9 to the FMP increased the red porgy minimum size limit to 14-inch total length, established a bag limit of 5 fish per person per day, prohibited purchase or sale of red porgy during March and April, and restricted commercial harvest to the recreational bag limit during those months. Subsequently, a prohibition on landing red porgy (moratorium) was enacted for the period 8 September 1999 through 28 August 2000. Amendment 12 (SAFMC[3]) to the FMP, which became effective on 29 August 2000, reduces the recreational bag limit to 1 fish per person per day, extends the closed season to 4 months (January–April), and allows a 50-pound trip limit for commercial landings during the remaining 8 months of each year. Furthermore, the maximum fishing mortality threshold (MFMT) was increased from SPR = 30% (amendment 4 [SAFMC[5]]) to SPR = 35% (amendment 12 [SAFMC[3]]). It remains to be seen whether these actions will be sufficient to achieve the recovery of red porgy.

Acknowledgments

Literature cited

Berry, D. A.
  1987. Logarithmic transformations in ANOVA. Biometrics 43:439–456.
Beverton, R. J. H., and S. J. Holt.
  1957. On the dynamics of exploited fish populations. Reprinted 1993 by Chapman and Hall, New York, NY, 533 p.
Caddy, J. F., and R. Mahon.
  1995. Reference points for fisheries management. FAO Fish. Tech. Pap. 347. FAO, Rome, 83 p.
Clark, C. W.
  1974. Possible effects of schooling on the dynamics of exploited fish populations. J. Cons. Int. Explor. Mer 36:7–14.

Clarke, W. G.
  1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat. Sci. 48:734–750.
Clay, D.
  1990. TUNE: a series of fish stock assessment computer programs written in FORTRAN for microcomputers (MS DOS). Int. Comm. Conserv. Atl. Tunas, Coll. Vol. Sci. Pap. 32:443–460.
Coleman, F. C., C. C. Koenig, A.-M. Eklund, and C. B. Grimes
  1999. Management and conservation of temperate reef fishes in the grouper-snapper complex of the southeastern United States. Am. Fish. Soc. Symp. 23:233–242.
Collins, M. R.
  1990. A comparison of three fish trap designs. Fish. Res. 9:325–332.
Collins, M. R., and G. R. Sedberry.
  1991. Status of vermilion snapper and red porgy stocks off South Carolina. Trans. Am. Fish. Soc. 120:116–120.
Doubleday, W. G.
  1976. A least squares approach to analyzing catch at age data. Res. Bull., Int. Comm. Northwest Atl. Fish. 12:69–81.
Efron, B., and R. Tibshirani.
  1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Stat. Sci. 1:54–75.
FAO (Food and Agriculture Organization of the United Nations).
  1995. Precautionary approach to fisheries. Part 1: Guidelines on the precautionary approach to capture fisheries and species introductions. FAO Fish. Tech. Rep. 350. FAO, Rome, 52 p.
Fletcher, R. I.
  1978. On the restructuring of the Pella-Tomlinson system. Fish. Bull.76:515–521.
Gabriel, W. L., M. P. Sissenwine, and W. J. Overholtz.
  1989. Analysis of spawning stock biomass per recruit: an example for Georges Bank haddock. N. Am. J. Fish. Manag. 9:383–391.
Gavaris, S.
  1988. An adaptive framework for the estimation of population size. Canadian Atl. Fish. Sci. Adv. Comm. Res. Doc. 88/29, St. Andrews, New Brunswick, Canada, 12 p.
Goodyear, C. P.
  1995. Mean size at age: an evaluation of sampling strategies with simulated red grouper data. Trans. Am. Fish. Soc. 124:746–755.
Gray, G. W., L. L. Kline, M. F. Osburn, R. J. Salz, D. A. Van Vorhees, and J. F. Witzig.
  1994. MRFSS user's manual: a guide to the National Marine Fisheries Service marine recreational fisheries statistics survey database. Special report 37, Atlantic States Marine Fisheries Commission, Washington, DC.
Gulland, J. A.
  1975. The stability of fish stocks. J. Cons. Int. Explor. Mer 37:199–204.
Gulland, J. A., and L. K. Boerema.
  1973. Scientific advice on catch levels. Fish. Bull. 71:325–335.
Harris, P. J., and J. C. McGovern.
  1997. Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972–1994. Fish. Bull. 95:732–747.
Hoenig, J. M.
  1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82:898–903.
Huntsman, G. R.
  1976. Offshore headboat fishing in North Carolina and South Carolina. Mar. Fish. Rev. 38(3):13–23.

Huntsman, G. R., D. R. Colby, and R. L. Dixon.
    1978.   Measuring catches in the Carolina headboat fishery. Trans. Am. Fish. Soc. 107:241–245.
Huntsman, G. R., and W. E. Schaaf.
    1994.   Simulation of the impact of fishing on reproduction of a protogynous grouper, the graysby.   N. Am. J. Fish. Manag. 14:41–52.
Lo, N. C., L. D. Jacobson, and J. L. Squire.
    1992.   Indices of relative abundance from fish spotter data based on delta-lognormal models.   Can. J. Fish. Aquat. Sci. 49:2525–2526.
Ludwig, D.
    1998.   Management of stocks that may collapse.   Oikos 83: 397–402.
Manooch, C. S., III.
    1976.   Reproductive cycle, fecundity, and sex ratios of the red porgy, *Pagrus pagrus* (Pisces: Sparidae) in North Carolina. Fish. Bull. 74:775–781.
Manooch, C. S., III, L. E. Abbas, and J. L. Ross.
    1981.   A biological and economic analysis of the North Carolina charter boat fishery.   Mar. Fish. Rev. 43(8):1–11.
Manooch, C. S., III, and W. W. Hassler.
    1978.   Synopsis of biological data on the red porgy, *Pagrus pagrus* (Linnaeus).   U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 412, 19 p.
Manooch, C. S., III, and G. R. Huntsman.
    1977.   Age, growth, and mortality of the red porgy, *Pagrus pagrus*.   Trans. Am. Fish. Soc. 106:26–33.
Manooch, C. S., III, J. C. Potts, D. S. Vaughan, and M. L. Burton.
    1998.   Population assessment of the red snapper from the southeastern United States.   Fish. Res. 38:19–32.
Marine Recreational Fisheries Statistics.
    1999.   Marine recreational fisheries statistics survey data. NMFS/Office of Science & Technology/Fisheries Statistics & Economics Division, September 10, 1999.   [Available from http://www.st.nmfs.gov/st1/recreational/database/index. html.] 14 August 2000.
Myers, R. A., Hutchings, J. A., and N. J. Barrowman.
    1997.   Why do fish stocks collapse? The example of cod in Atlantic Canada.   Ecol. Appl. 7:91–106.
NRC (National Research Council).
    1998.   Improving fish stock assessments.   National Academy Press, Washington, D.C., 177 p.
Ortiz. M., C. M. Legault, and N. M Ehrhardt.
    2000.   An alternative method for estimating bycatch from the U.S. shrimp trawl fishery in the Gulf of Mexico, 1972–1995.   Fish. Bull. 98:583–599.
Pauly, D.
    1979.   On the inter-relationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks.   J. Cons. Int. Explor. Mer 39:175–192.
Pella, J. J.
    1967.   A study of methods to estimate the Schaefer model parameters with special reference to the yellowfin tuna fishery in the eastern tropical Pacific ocean.   Ph.D. diss., Univ. Washington, Seattle, WA, 156 p.
Pella, J. J., and P. K. Tomlinson.
    1969.   A generalized stock production model.   Bull. Inter-Am. Trop. Tuna Comm. 13:419–496.
Pope, J. G., and J. G. Shepherd.
    1982.   A simple method for the consistent interpretation of catch-at-age data.   J. Cons. int. Explor. Mer 40:176–184.
    1985.   A comparison of the performance of various methods for tuning VPAs using effort data.   J. Cons. Int. Explor. Mer 42:129–151.

Porch, C. E., and G. P. Scott.
    1994.   A numerical evaluation of GLM methods for estimating indices of abundance from west Atlantic bluefin tuna catch per trip data when a high proportion of the trips are unsuccessful.   Int. Comm. Cons. Atl. Tunas (Madrid), Coll. Vol. Sci. Pap. 42(1):240–245.
Potts, J. C., and C. S. Manooch, III.
    2002.   Estimated ages of red porgy from fishery-dependent and fishery-independent data and comparison of growth parameters.   Fish. Bull. 100(1):81–89.
Potts, J. C., C. S. Manooch III, and D. S. Vaughan.
    1998.   Age and growth of vermilion snapper from the southeastern United States.   Trans. Am. Fish. Soc. 127:787–795.
Prager, M. H., J. F. O'Brien, and S. B. Saila.
    1987.   Using lifetime fecundity to compare management strategies: a case history for striped bass.   N. Am. J. Fish. Manag. 7:403–409.
Prager, M. H.
    1994.   A suite of extensions to a nonequilibrium surplus-production model.   Fish. Bull. 92:374–389.
    1995.   User's manual for ASPIC: a stock-production model incorporating covariates, program version 3.6x.   NMFS Southeast Fisheries Science Center, Miami Laboratory Document MIA–2/93–55, 4th ed., 29 p.   [Available from author.]
Punt, A. E.
    1990.   Is $B_1 = K$ an appropriate assumption when applying an observation error production-model estimator to catch-effort data?   S. Afr. J. Mar. Sci. 9:249–259.
Ralston, S.
    1987.   Mortality rates of snappers and groupers.   *In* Tropical snappers and groupers: biology and fisheries management (J. J. Polovina and S. Ralston, eds.), p. 375–404. Westview Press, Boulder, CO.
Restrepo, V. R., and ten coauthors.
    1998.   Technical guidance on the use of precautionary approaches to implementing national standard 1 of the Magnuson-Stevens Fishery Conservation and Management Act.   U.S. Dep. Commer., NOAA Tech. Memo. NMFS–F/SPO–31.
Richards, R. A., and P. J. Rago.
    1999.   A case history of effective fishery management: Chesapeake Bay striped bass.   N. Am. J. Fish. Manag. 19:356–375.
Ricker, W. E.
    1975.   Computation and interpretation of biological statistics of fish populations.   Bull. Fish. Res. Board Can. 191:1–382.
Schaefer, M. B.
    1954.   Some aspects of the dynamics of populations important to the management of the commercial marine fisheries.   Bull. Inter-Am. Trop. Tuna Comm. 1(2):27–56.
    1957.   A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean.   Bull. Inter-Am. Trop. Tuna Comm. 2:247–268.
Schnute, J.
    1977.   Improved estimates from the Schaefer production model: theoretical considerations.   J. Fish. Res. Board Can. 34:583–603.
Shapiro, D. Y.
    1979.   Social behavior, group structure, and the control of sex reversal in hermaphroditic fish.   Adv. Stud. Behav. 10: 43–102.
Sissenwine, M. P., and J. G. Shepherd.
    1987.   An alternative perspective on recruitment overfishing and biological reference points.   Can. J. Fish. Aquat. Sci. 44:913–918.

Snedecor, G. W., and W. G. Cochran
    1980. Statistical methods, seventh edition. Iowa State Univ. Press, Ames, IA, 507 p.
Vaughan, D. S., and M. L. Burton.
    1994. Estimation of von Bertalanffy growth parameters in the presence of size-selective mortality: A simulated example with red grouper. Trans. Am. Fish. Soc. 123:1–8.
Vaughan, D. S., M. R. Collins, and D. J. Schmidt.
    1995. Population characteristics of the black sea bass *Centropristis striata* from the southeastern U.S. Bull. Mar. Sci. 56:250–267.
Vaughan, D. S., G. R. Huntsman, C. S. Manooch III, F. C. Rohde and G. F. Ulrich.
    1992. Population characteristics of the red porgy, *Pagrus pagrus*, stock off the Carolinas. Bull. Mar. Sci. 50:1–20.

Vaughan, D. S., B. Zhao, M. R. Collins, J. C. McGovern, and H. S. Meister.
    1998. Evaluation of multiple survey indices in assessment of black sea bass from the U.S. south Atlantic coast. *In* Fishery stock assessment models (F. Funk, T. J. Quinn II, J. Heifetz, J. N. Ianelli, J. E. Powers, J. F. Schweigert, P. J. Sullivan, and C. -I. Zhang, eds.), p. 121–136. Lowell Wakefield Fisheries Symposium, Univ. Alaska Sea Grant College Program, Report 98-01.
von Bertalanffy, L.
    1938. A quantitative theory of organic growth. Hum. Biol. 10:181–213.