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POPULATION CHARACTERISTICS OF THE BLACK SEA BASS *CENTROPRISTIS STRIATA* FROM THE SOUTHEASTERN U.S.

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ABSTRACT

We examined the age structure and status of the southeastern U.S. stock of black sea bass, using recorded and estimated landings and size frequencies of fish from commercial, recreational, and headboat fisheries from 1979–1990. Annual landings in numbers at age were estimated by application of separable virtual population analysis (VPA), which was used to estimate annual, age-specific fishing mortality for different levels of natural mortality (M = 0.2, 0.3, 0.4 and 0.5 yr^{-1}). Mortality levels (F) ranged from 0.54 to 1.59 between 1979 and 1990 for fully recruited ages (4–7) (M = 0.3). Maximum spawning potential ranged from 42% to 50% based on mature female biomass, from 49% to 56% based on egg production, and from 22% to 30% based on total mature (male and female) biomass. Because black sea bass are protogynous hermaphrodites (transforming from females to males) and the effect of changes in population abundance on sex transformations is unknown, the percent reduction in males to females was estimated solely on increased mortality by fishing (ranging from 50% to 60% of the unfished proportion). Thus, the use of maximum spawning potential based on total mature biomass should also be considered for comparison to a biological reference point used in defining overfishing.

Black sea bass, *Centropristis striata*, also called blackfish, is a member of the family Serranidae and inhabits continental shelf waters, predominantly between Cape Canaveral, Florida, and Cape Cod, Massachusetts (Mercer, 1989). Two populations are thought to occur along the Atlantic coast, separated by Cape Hatteras, North Carolina (Mercer, 1989; Shepherd, 1991). Black sea bass occur in depths of 2–120 m, but most adults are found in 20 to 60 m (Mercer, 1989). Although black sea bass north of Cape Hatteras are migratory, movements of those south of Cape Hatteras are limited and less well-defined (Ansley and Davis, 1981; Collins et al., in press).

Spawning for black sea bass occurs from January through June along the southeastern U.S. coast, peaking from March to May (Mercer, 1989). Wenner et al. (1986) also found ovarian activity in September and suggested a small fall spawn probably extending into October. They found mature gonads in none of the females at age 0, 48.4% at age 1, 90.3% at age 2, 99.1% at age 3, and 100% at all older ages. Black sea bass are protogynous hermaphrodites, but mature males occur in all age groups (Table 1). Wenner et al. (1986) provided several relationships for estimating fecundity from length, weight, or age.

In this paper we compute and document changes in age structure and population size of black sea bass found off the eastern Atlantic Coast of the United States south of Cape Hatteras, North Carolina. Specifically, given age-specific estimates of instantaneous fishing mortality rates and information on growth, sex ratios, maturity and fecundity, analyses of yield per recruit and spawning stock biomass per recruit (percent maximum spawning potential) were used to determine status of the southeastern U.S. black sea bass stock.

METHODS

There are three fisheries for black sea bass: commercial, recreational, and headboat. The commercial fishery is principally prosecuted by blackfish traps and by hook and line, with some landings by trawl.

Table 1. Southeastern U.S. black sea bass sex composition by age, 1978–1982

Age (yr)	Proportion Female	Transition	Male
0	0.849	0.015	0.136
1	0.829	0.072	0.099
2	0.686	0.166	0.148
3	0.571	0.227	0.202
4	0.369	0.241	0.390
5	0.187	0.193	0.620
6	0.119	0.117	0.764
7+	0.093	0.103	0.804

The recreational fishery includes fishing from shore, and from private and charter boats. For sampling purposes, the headboat fishery (charter-type operations that charge recreational fishermen per person or "head") is considered separate from the recreational fishery. Annual catch (number and weight) and length data from these three fisheries, together with length at age information, permitted development of a catch-in-numbers-at-age matrix for 1979–1990.

Estimates of instantaneous total mortality (Z) are initially obtained by length-based analysis using length frequency distributions of fishery and gear (Hoenig et al., 1987). Development of the catch-in-numbers-at-age matrix allows application of catch curve approaches either by year class or fishing year for estimation of Z. Independent estimates of instantaneous natural mortality (M) based on life history relationships (Pauly, 1979; Hoenig, 1983), permit estimation of instantaneous fishing mortality rates (F = Z − M). Separable virtual population analysis (Doubleday, 1976) is used to reconstruct the age-specific population and estimates of age- and year-specific instantaneous fishing mortality rates for 1979–1990.

Development of Catch-in-Numbers-at-Age Matrix.—Data for development of the catch-in-numbers-at-age matrix for the study area of the southeastern U.S. (Miami, Florida, to Cape Hatteras, North Carolina) came from numerous sources. Commercial fishery data were obtained from NMFS (Southeast Fisheries Science Center, Beaufort, North Carolina, and Miami, Florida) from the General Canvas data base (for catch statistics, 1972–1990) and from the Trip Interview Program (TIP) data base (for length and weight statistics, 1983–1990). Recreational catch estimates and length and weight information were obtained through the Marine Recreational Fisheries Statistics Survey (MRFSS) data base (NMFS, Washington, D.C.) for 1979–1990. Headboat catch estimates and length and weight sampling data were obtained from NMFS (Southeast Fisheries Science Center, Beaufort, North Carolina) for 1974–1990. Fishery independent length and weight data from commercial gears (hook and line and traps, 1979–1988) were made available from the MARMAP (Marine Resources Monitoring, Assessment, and Prediction) Program (South Carolina Marine Resources Research Institute, Charleston).

Estimation of the catch-in-numbers-at-age matrix is described in Vaughan et al. (1991, 1992). The basic approach consists of multiplying the catch in numbers (n, scalar) by an age–length key (A, matrix) by a length-frequency distribution (L, vector) to obtain catch in numbers at age (N, vector):

$$N_{a\times 1} = n \cdot A_{a\times b} \cdot L_{b\times 1} \quad (1)$$

where a is the number of ages (e.g., ages 0 to 8+ years) and b is the number of length intervals (e.g., 1-in increments from 2 in to 20+ in). If catch is available only in weight (as is the case with commercial landings), then catch is converted to numbers by dividing catch in weight by mean weight per fish landed for the same fishery/gear, time period (annual), and geographic region (southeastern U.S.). Length data for a given fishery/gear is converted to weight by a weight–length relationship and the average mean weight per fish for that fishery is calculated annually.

HISTORICAL LANDINGS. Adjustments were necessary to obtain commercial landings for the southeastern U.S. (Cape Hatteras, North Carolina to Miami, Florida). Because all black sea bass caught north of Cape Hatteras, North Carolina, are assumed to belong to a separate stock from that under analysis, North Carolina commercial landings needed to be divided at Cape Hatteras. All reported fish trawl landings (NMFS gear code 210, General Canvas data) from North Carolina were assumed to have taken place north of Cape Hatteras (although some catches from north of Cape Hatteras were landed south of Cape Hatteras), while reported landings from all other commercial gears (mostly traps and hook and line) were assumed to take place south of Cape Hatteras (Nelson Johnson, NMFS Beaufort Laboratory, Beaufort, North Carolina, pers. comm.). To obtain annual landings in numbers by gear from annual catch in weight by gear, landings in weight by gear (General Canvas data) were divided by mean weight of fish landed by that gear (TIP data).

Recreational catch statistics in weight and numbers were estimated from the Marine Recreational Fishery Statistics Survey conducted from 1979 through 1990 (Essig et al., 1991). Three catch types are defined for the recreational fishery: Type A refers to catches that are available for identification and measurements; and Type B refers to catches that are not available for identification or measurement. The latter category is subdivided into: Type B1 catches, used for bait, filleted, discarded dead, etc.; and Type B2 catches, released alive. Compared to other fisheries, such as red drum (Vaughan, 1992) and weakfish (Vaughan et al., 1991), a large percentage of the catch was type B (81%: 45% Type B1 and 36% Type B2) for black sea bass. We used a 5% post-release mortality (Bugley and Shepherd, 1991) to include a portion of the type B2 fish in the landings, although Collins (in press) concluded that post-release mortality varied with depth and could be much greater than 5%.

Two adjustments were required before the recreational catch data could be incorporated into the catch-at-age matrix. Recreational catch estimates needed to be subtracted for headboat catch estimates from 1979 through 1985 (duplicated with a separate headboat sampling program), and North Carolina recreational catch estimates for the area north of Cape Hatteras. In both cases intercept sampling for length was assumed proportional to catch.

Headboat landings for the period 1979–1985 were adjusted by state. About 1,289 of the 1,302 intercept samples (e.g., length measurements) in Florida identified under the combined charter/headboat mode were from headboats, so about 99% of the landings for this mode were estimated as from headboats, and the remaining 1% from charterboats. Similarly, an estimate of about 50% of the charter/headboat mode landings in Georgia were from charterboats, and 20% in South Carolina based on intercept samples.

Adjustments for North Carolina recreational catch were similar, but more complex. For the charter/headboat intercept samples in this state during 1979–1985, 18% were charterboat south of Cape Hatteras. During this same period, 63% of the shore mode intercept samples and 80% of the private boat mode intercept samples were from south of Cape Hatteras. For the recent period (1986–1990), the percent of intercept samples from south of Cape Hatteras was 60% for shore mode, 91% for charterboat mode, and 85% for private boat mode. Estimated recreational landings for North Carolina were divided by mode and year according to the above estimated proportions.

Headboat landings were estimated from the NMFS Beaufort Laboratory sampling program (Dixon and Huntsman, in press). To aid in distinguishing from charter boats (sampled by MRFSS), which ordinarily charge by the trip, the working definition for headboat is any vessel that usually carries 15 or more passengers regardless of manner of payment. Headboat landings in weight and numbers were available for North and South Carolina from 1975 through 1990. All North Carolina headboat landings were from south of Cape Hatteras, so no adjustments were needed. Estimated landings for northeast Florida (from Georgia through Sebastian, Florida) were available from 1976 through 1990, and for southeast Florida (from Fort Pierce through Miami, Florida) from 1981 through 1990.

Total headboat effort in angler days and catch of black sea bass in weight per unit effort were available for the same time period (1975–1990 for North and South Carolina, 1976–1990 for northeast Florida, and 1981–1990 for southeast Florida). Catch per unit effort (CPUE) was calculated by dividing catch in pounds by effort in angler days.

Weight was related by power function to total length for southeastern U.S. black sea bass collected from the three fisheries. Fishery-specific relationships, combined with the appropriate length frequency data, were used to estimate mean weight for a given fishery/gear/year. An overall weight–length relationship was used in population-level models.

Length Frequency Distributions. Commercial length and weight data were available from sampling of commercial landings through the NMFS Trip Interview Program (TIP) database between 1984 through 1990 from North Carolina through the east coast of Florida. Only North Carolina data were available for 1983. North Carolina fish trawl data were eliminated from consideration because we assumed they came from catches made north of Cape Hatteras.

Annual length frequency distributions for commercial hook and line, traps and trawls (from other than North Carolina) were available from 1983–1990. With trawl landings being minuscule and few fish sampled (54), one overall length frequency distribution was used for all years 1979–1990. Because of low sample size (41) for commercial trap lengths in 1986, the mean length frequency distribution for the bracketing years (1985 and 1987) was used in its place.

To increase the number of years available for analysis, a method was sought to extend commercial length frequency distributions back to 1979 (when the MRFSS began). Scientific sampling by commercial gear (hook and line and blackfish traps) were available from MARMAP for 1979–1988. Because scientific sampling and commercial fishing serve different purposes, the MARMAP length frequency distributions for 1979–1983 could not be directly substituted for the corresponding missing commercial length frequency distributions.

To remedy this problem, median lengths calculated from the commercial and scientific hook and line data sets were compared. A no-intercept regression was performed to develop a scaling factor (1.28 ± 0.01) by which to multiply the overall length frequency distribution for hook and line. The length frequency distributions for 1979–1983 were generated from this scaling factor. Hence, the shape of the commercial hook and line length frequency distributions were maintained, while using the MARMAP hook and line data simply for scaling.

Similarly, median lengths calculated from the two trap data sets were compared. In an approach comparable to that for hook and line, a no-intercept regression was performed to develop a scaling factor (1.15 ± 0.03) to obtain trap length frequency distributions for 1979–1983. The relationship between median lengths from commercial and MARMAP data was quite good for hook and line, and not as good for traps. Although the majority of commercial landings are by traps, commercial landings generally make up less than a third of total landings, so potential bias is minimal. Hence, annual length frequency distributions for the period 1979–1990 were available for each of the three gears to use in developing the catch-in-numbers-at-age matrix.

Recreational length frequency distributions from the MRFSS data base were available by fishing mode from 1979–1990. Headboat length frequency distributions from the MRFSS (1979–1985) were not used in the development of the catch-in-numbers-at-age matrix. However, annual headboat length frequency distributions from NMFS Beaufort Laboratory were available for the period 1974–1991. Only those from 1979–1990 were used in developing the catch-in-numbers-at-age matrix. Annual median total lengths were obtained by fishery and gear to examine for trends in size of fish landed.

Age–Length Keys. Age–length data were based on MARMAP program samples taken from the South Atlantic Bight during 1978–1990. Black sea bass were collected with a variety of gears, but primarily with blackfish traps, Florida snapper traps (Collins, 1990), and hook-and-line. Weights (nearest g) and lengths (total and standard, nearest mm) were recorded, and otoliths (sagittae) were removed and stored dry. Otoliths were examined whole under reflected light with a dissecting microscope, and age estimates were based on the number of opaque zones visible. Good evidence for the annual nature of these opaque zones (marginal increment analysis) was derived from a subset (1978–1981) of these specimens (Wenner et al., 1986).

Growth in total length as a function of age was fit to the von Bertalanffy (1938) growth equation using nonlinear regression with the Marquardt option (SAS Institute Inc., 1987). Initial estimates of the parameters were done using all available measurements from 1978 through 1990 with equal weights. Total length rather than standard, and inches rather than centimeters were used in the analyses because management measures such as minimum or maximum size limits are all based on total length in inches.

Estimation becomes a problem when large numbers of young fish and few old fish are available for fitting parameters (Vaughan and Kanciruk, 1982). Only one black sea bass out of 15,992 was 20-in or longer in total length. Hence, a weighting by the inverse of the number of fish of each age was used to reduce the effect of the large numbers of younger fish and increase the relative weight of the few, older fish. This approach was applied to all data from the MARMAP sampling program (1978–1990).

Age–length keys (matrices) are needed to convert length frequency distributions to age frequency distributions. These keys were developed from the same MARMAP data used in estimating von Bertalanffy growth parameters (N = 15,992). The keys consist of the proportion of fish of each age sampled from a given length interval. For development of the catch-in-numbers-at-age matrices that follow, we used annual age–length keys from 1979 through 1990 with total length divided into 1 inch increments from 2 in to 20+ in and ages 0 through 8+ years. Total lengths greater than 20 in (one individual) and ages greater than 8 (16 individuals) years are pooled with lengths of 20 in and 8 years, respectively.

Catch-in-Numbers-at-Age Matrix. Annual application of Eq. (1) to each fishery/gear (commercial hook and line, commercial traps, commercial trawls, recreational, and headboat) were performed separately and accumulated for each year to obtain annual estimates of catch in numbers at age for 1979–1990.

Mortality and Population Dynamics.—Hoenig et al. (1987, Eq. 5) suggested a simple means of quickly estimating instantaneous total mortality rate (Z) from length frequency distributions of a fishery and independent estimates of L_∞ and k from the von Bertalanffy growth equation (unweighted and weighted approaches). The median, instead of mean, of the lengths greater or equal to the modal length interval forms the basis of the calculation. The median was selected because it is invariant under nonlinear transformations (e.g., logarithm) (as suggested in application to weakfish in Appendix II of Seagraves, 1992).

Instantaneous total mortality rate (Z) was also estimated from catch curve analysis (Ricker, 1975) by year class (cohort) and fishing year from the catch-in-numbers-at-age matrix. Estimates were obtained by regressing the natural logarithm of catch in numbers against age for fully recruited ages (descending right-hand limb, ages 4 through 7).

Natural Mortality. Pauly (1979) obtained the following relationship for estimating M based on growth parameters and mean environmental temperature:

$$\log_{10}M = 0.0066 - 0.279 \cdot \log_{10}L_{inf} + 0.6543 \cdot \log_{10}k + 0.4634 \cdot \log_{10}T \quad (2)$$

where M equals instantaneous natural mortality rate, L_{inf} (cm) and k (yr^{-1}) are parameters from the von Bertalanffy growth equation, and T (°C) is mean environmental temperature. A temperature of 20°C (Charles Wenner, South Carolina Marine Resources Research Institute, Charleston, pers. comm.) was used to represent mean nearshore temperature off of Charleston, South Carolina. Estimates of M based on Pauly's (1979) approach ranged from 0.2 to 0.6. Lower estimates of M are associated with higher estimates of L_{inf} and lower estimates of k.

Another life history approach suggested by Hoenig (1983) is based on the maximum age observed in the population. Because the relationship he developed is based on Z, instead of M, the maximum age in the unfished population (F = 0; M = Z − F) would provide an estimate of M. The oldest fish in the MARMAP data set was age 10, yielding an estimate of M equal to 0.4 . Higher ages provide lower estimates of M, suggesting that 0.4 should be viewed as a maximum. Reports of black sea bass as old as age 20 (SEFSC, 1992) suggest a minimum estimate of M equal to 0.2. Recent status reports by NEFSC (1991) and SEFSC (1992) suggest M of 0.3 for black sea bass, and this value was used by Low (1981). Most of our analyses are based on M equal to 0.3, with additional analyses for M equal to 0.2, 0.4 and 0.5.

Fishing Mortality. The catch-in-numbers-at-age matrix was interpreted using virtual population analysis (VPA) techniques to obtain age-specific estimates of population size and fishing mortality rates. Virtual population analysis sequentially estimates population size and fishing mortality rates for younger ages of a cohort from a starting value of fishing mortality for the oldest age (Murphy, 1965). An estimate of natural mortality, usually assumed constant across years and ages, was also required. The separable method of Doubleday (1976), which was used in this analysis, assumes that age- and year-specific estimates of F can be separated into products of age and year components. We used the FORTRAN program developed by Clay (1990), based on Pope and Shepherd (1982).

The catch-in-numbers-at-age matrix analyzed consisted of catch in numbers for ages 0 through 7 and fishing years 1979 through 1990. Starting values for F were based on the mean of the final two year class estimates of Z (0.95 yr^{-1}) and final F obtained by subtracting M from Z. Sensitivity of estimated F to uncertainty in M was investigated by varying M from 0.2 to 0.5 by 0.1, and potential bias in F in the most recent years by varying the final year used in the analysis from 1986 and 1990 (initial year was 1979 throughout).

Yield per Recruit. Yield per recruit analysis was conducted based on the method of Ricker (1975), who subdivided the exploited phase into a number of segments (e.g., years) during which mortality and growth rates are assumed constant. This approach permits instantaneous natural and fishing mortality rates to vary during the fishable life span and permits a general growth pattern to be used. Total equilibrium yield per recruit is obtained by summing the catches in each segment over the total number of segments. Input data were based on both sexes combined.

Spawning Stock Biomass per Recruit. Gabriel et al. (1989) developed maximum spawning potential (%MSP) as a biological reference point. It was calculated as a ratio of spawning stock size when fishing mortality was equal to observed or estimated F divided by the spawning stock size calculated when F equaled zero. All other life history parameters were held constant (e.g., maturity schedule and age-specific sex ratios). Hence, the estimate of %MSP was increased when fishing mortality was decreased.

Comparisons of age-specific spawning stock biomass were based on mature female biomass, egg production, or even on total mature biomass (both males and females). To address the change in male to female ratio with increasing mortality, we estimate the reduction in the proportion of mature males to mature males and females in numbers compared to what that proportion would be when F equals zero.

We used the relationship between fecundity (E, number of eggs) and total length (TL, mm) based on the least-squares linear-regression equation (r^2 = 0.62, N = 115):

$$\log_{10}E = -0.605 + 2.335(\log_{10}TL), \quad (3)$$

to provide an alternative to female spawning stock biomass as a measure of spawning potential expressed as percent maximum spawning potential (Wenner et al., 1986). Separate sex-based growth relationships were used for males and females in these calculations.

Results

Historical Data.—Adjusted reported southeastern U.S. commercial landings in weight of black sea bass peaked in 1974 at 1.5 million pounds and dropped to a low of 0.3 million pounds in 1978. Since then, landings have ranged between 0.6 and 1.2 million pounds (Table 2). For the period 1972–1990, 78% of reported black sea bass commercial landings were by traps and 21% by hook and line, with the remaining 1% by gill nets, haul seines, pound nets, and trawls. About 60% of the reported commercially caught black sea bass were landed in North Carolina, 30% in South Carolina, 2% in Georgia, and 8% in Florida.

Table 2. Southeastern U.S. black sea bass landings in weight and numbers by fishery caught between Cape Hatteras, NC, and Miami, FL, 1979–1990

Year	Commercial	Recreational	Headboat	Total
		Thousands of pounds		
1979	859.1	920.5	586.7	2,366.3
1980	1,050.4	1,855.6	643.6	3,549.6
1981	1,240.1	681.1	711.3	3,632.5
1982	974.3	1,816.0	735.5	3,525.8
1983	664.8	617.0	723.9	2,005.7
1984	645.3	2,310.9	693.2	3,649.4
1985	599.8	1,044.8	595.7	2,240.3
1986	710.0	442.6	562.9	1,715.5
1987	597.3	745.1	646.5	1,988.9
1988	815.4	1,345.7	635.2	2,796.3
1989	825.1	816.1	478.0	2,119.2
1990	1,011.0	250.3	379.6	1,640.9
		Thousands of fish		
1979	803.0	2,274.2	920.8	3,998.0
1980	1,035.5	1,955.2	1,177.7	4,168.4
1981	1,355.6	1,270.5	710.6	3,336.7
1982	1,126.6	2,316.0	1,238.9	4,681.5
1983	765.9	1,456.0	723.3	2,945.2
1984	730.5	2,925.4	692.6	4,348.5
1985	676.9	2,058.7	595.2	3,330.8
1986	665.3	995.4	562.4	2,223.1
1987	618.0	1,176.1	673.7	2,467.8
1988	919.4	1,539.3	1,028.0	3,486.7
1989	1,057.4	1,090.2	765.1	2,912.7
1990	1,080.6	551.1	658.6	2,290.3

Recreational landings in numbers during the period 1979–1990 were highly variable, ranging from about 0.6 million fish (A + B1 + 5%B2) in 1990 to 2.3 million fish in 1982 (Table 2). Proportion of landings by state average about 30% landed in Florida, 5% in Georgia, 31% in South Carolina, and 34% in North Carolina. For mode of fishing, proportion of landings were about 4% for shore based, 22% for charterboats, and 74% for private boats.

Headboat landings ranged from 0.6 million fish (weighing 0.6 million pounds) in 1986 to 1.2 million fish (weighing 0.7 million pounds) in 1982 (Table 2). The majority of landings were in South Carolina (56% by weight and 58% by number), with northeast Florida next (27% by weight and 26% by number), followed by North Carolina (16% by weight and 15% by number) and southeast Florida (1% both by weight and number).

Total headboat effort in angler days was highest in southeast Florida, followed by northeast Florida, South Carolina, and North Carolina. Landings in pounds of black sea bass per angler day (CPUE) were greatest for South Carolina and North Carolina (Fig. 1). Declining trends in CPUE appear to be present for North and South Carolina, which together represent a majority of headboat landings (72% by weight and 73% by number), especially since 1981. No apparent trends were noted for northeast or southeast Florida.

In general, estimated recreational landings dominated (43% by weight and 49% by numbers), followed by reported commercial landings (33% and 27%, respec-

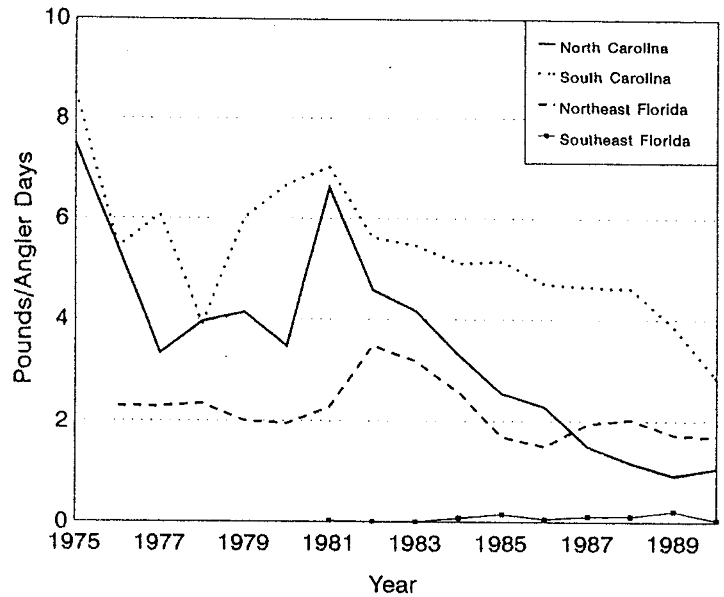

Figure 1. Southeastern U.S. Black sea bass catch per unit effort (pounds per angler day) by headboat area, 1975–1990.

tively) and then estimated headboat landings (24% by weight and numbers) for the 1979–1990 period. However, the relative contribution varied annually. In 1990, for example, reported commercial landings dominated (62% by weight and 49% by numbers) with recreational landings coming in last (15% by weight and 24% by numbers).

High annual variability in recreational catch estimates raised the question as to whether there were difficulties in expanding the catch estimate from the intercepts and telephone survey or whether the observed variability resulted from underlying biological processes (e.g., as a result of annual variability in recruitment). A limited analysis based on 3-year moving averages of the catch and landings data for 1979–1990 was conducted to assess the effect of smoothing this annual variability on population level results and conclusions.

Growth in Weight and Length.—The estimated relationship for weight (pounds, W) as a function of total length (in, L) was based on all fisheries-dependent data (N = 77,638):

$$\ln W = -6.90 + 2.71 \ln L, \qquad (4)$$

where r^2 = 0.88 and mean squared error is 0.042.

Parameter estimates for the von Bertalanffy growth equation are summarized in Table 3. Different estimates of von Bertalanffy parameters for the three sex categories (female, transition, and male) do not necessarily reflect differences in growth. Because there were few old females relative to males (due to protogyny),

Table 3. Estimated parameters for von Bertalanffy growth equation with southeastern U.S. black sea bass data from 1978–1990. Standard error given parenthetically below estimate [TL (in) = $L_{inf}(1 - \exp(-k(age - t_0)))$]. Sex-based growth equations based on data from 1978–1982 inclusive.

Type	N	L_{inf}	k	t_0
		Unweighted data		
All	15,992	31.5	0.082	−1.23
		(1.3)	(0.005)	(0.06)
		Weighted data*		
All	15,990	18.51	0.212	−0.48
		(0.08)	(0.003)	(0.02)
Female	5,575	24.3	0.096	−1.63
		(0.5)	(0.004)	(0.05)
Trans	2,165	18.0	0.185	−1.29
		(0.3)	(0.008)	(0.08)
Male	3,214	17.7	0.252	−0.36
		(0.1)	(0.006)	(0.03)

* Weighted by inverse of number of fish at each age.

greater difficulties in parameter estimation arose. However, sizes for the ages available for inclusion in regression adequately reflect those observed in the data, and were useful for representing the observed (though small) differences in size at age for the sexes in calculating yield per recruit and spawning stock biomass per recruit.

No significant temporal trends were noted in total median length, other than a

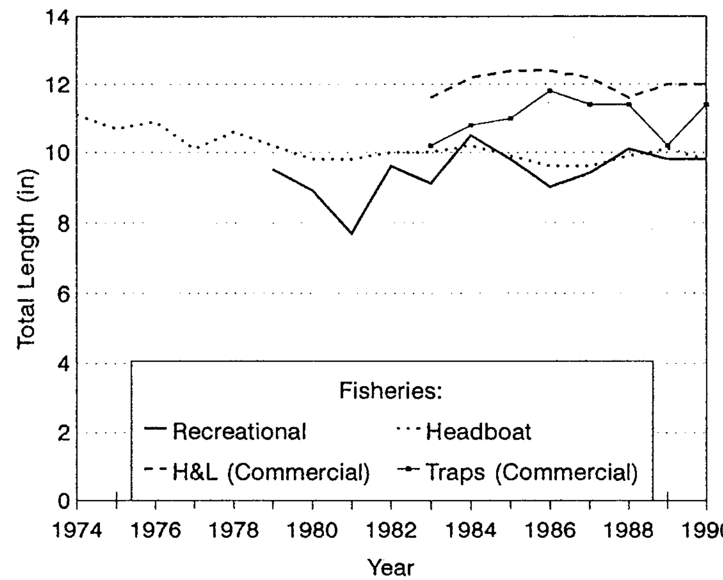

Figure 2. Annual median total length of southeastern U.S. black sea bass by fishery and gear.

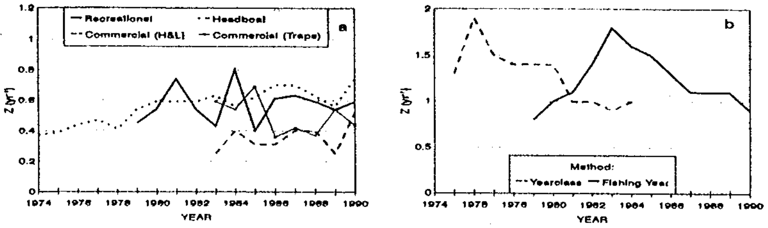

Figure 3. Annual estimates of instantaneous total mortality rate (Z) for southeastern U.S. black sea bass for a) method of Hoenig et al. (1987) using length distributions from fisheries, and b) catch curve analysis.

consistent, gradual decline in headboat median lengths from about 11" to 10" TL (Fig. 2).

Trends in Mortality.—Annual estimates of total mortality (Z) based on median lengths and weighted growth parameters (sexes combined) from headboat landings generally increased from a low in 1974 of 0.37 to a high in 1990 of 0.74 (Fig. 3a). Temporal trends were not as evident in the annual estimates of Z from the other fisheries/gears. Estimates of Z from commercial gears tended to be lowest (means of 0.36 for hook and line and 0.49 for traps and trawl). Mean estimated Z for recreational (0.58) and headboat (0.57) were very similar.

Instantaneous total mortality rate (Z) by year class (cohort) were greater for earlier cohorts (1.9 for 1976 cohort) than more recent cohorts (0.9 for 1983 cohort) (Fig. 3b). Estimates of Z were initially low for the early fishing years in this analysis (0.8 in 1979), then high (1.8 in 1983), and then low again (0.9 in 1990).

Annual age-specific estimates of F were obtained from the separable VPA applied to the original catch-in-numbers-at-age matrix (Fig. 4a) and to the 3-yr moving average (Fig. 4b). Estimates of F for age 0 were always less than or equal to 0.001, while ages 4 through 7 were assumed fully recruited and F was averaged. For M of 0.3, annual estimates of F (ages 1, 2, 3, 4+) tended to be higher for the period 1979 through 1985 compared to 1986 through 1990 for both the original and 3-yr moving average analyses. Estimates of fishing mortality were very

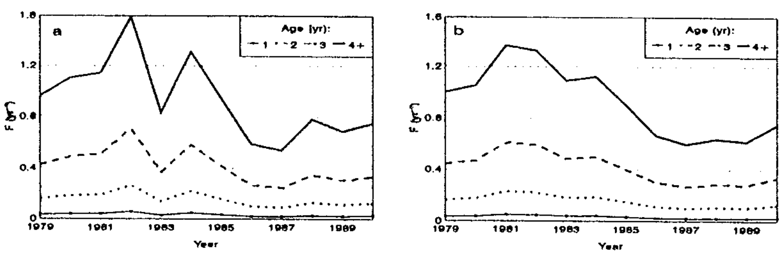

Figure 4. Annual estimates of instantaneous fishing mortality rate (F) for southeastern U.S. black sea bass by separable virtual population analysis using a) original catch-in-numbers-at-age matrix, and b) 3-yr moving average of catch estimates.

Table 4. Southeastern U.S. black sea bass catch-in-numbers-at-age (in thousands) matrix for ages 1 through 8+ (and total numbers) and years 1979 through 1990. Total catch in weight (thousands of pounds) are also presented. Note that 5% of catch-release recreationally caught fish (type B2 fish from MRFSS) are included in estimates by number (modal age underlined).

Year	Age (yr) 0	1	2	3	4	5	6	7	8+	Number (1,000)	Weight (1,000 lbs)
1979	7.6	255.6	1,052.7	1,162.1	787.5	389.9	256.1	68.4	23.3	3,998.0	2,366.3
1980	8.2	198.4	743.3	1,543.2	1,060.8	367.7	172.7	41.3	33.0	4,168.5	3,549.6
1981	6.6	272.4	750.7	981.5	855.3	314.2	96.0	37.8	22.1	3,336.7	2,632.5
1982	25.7	422.4	1,285.1	1,449.3	1,155.0	245.2	80.3	14.2	4.4	4,681.5	3,525.8
1983	7.5	360.8	796.5	923.0	599.8	229.5	22.8	3.3	1.9	2,945.2	2,005.7
1984	4.2	530.7	412.3	1,328.7	1,430.7	479.6	148.3	11.8	2.1	4,348.5	3,649.4
1985	20.6	318.7	578.6	1,087.0	948.7	293.3	68.6	11.3	4.0	3,330.8	2,240.3
1986	0.6	112.8	687.5	523.4	516.2	300.1	68.3	10.0	4.2	2,223.1	1,715.5
1987	0.6	180.4	543.1	919.6	476.2	241.1	80.3	19.4	7.2	2,467.8	1,988.9
1988	2.8	79.5	713.6	1,010.0	1,110.0	388.4	120.5	49.4	12.6	3,486.7	2,796.3
1989	0.4	63.9	418.2	1,037.3	929.3	335.3	94.3	20.2	14.0	2,912.7	2,119.2
1990	0.2	33.1	363.5	810.8	559.1	320.9	156.7	33.3	12.6	2,290.3	1,640.9

similar based on the two catch-in-numbers-at-age matrices, although as expected there is some smoothing of the peaks and valleys for the 3-yr moving average.

Separable VPA was conducted using the original catch-in-numbers-at-age matrix (Table 4) with M varying from 0.2 to 0.5 by 0.1 (Fig. 5a). Estimates of fishing mortality on fully recruited ages, shows a small and consistent bias. Full F is underestimated if M is overestimated (e.g., if M = 0.2), and full F is overestimated if M is underestimated (e.g., if M = 0.4 or 0.5).

Because virtual population analyses works backwards from an assumed or starting F for the oldest age of a cohort to the youngest age, confidence in estimated F (or population size) was least for the most recent estimate and converges towards "truth" for the youngest ages. Estimates generally converged within about 2 to 3 years. Fully recruited fishing mortality rates (age 4+) were compared where the most recent year of data for analysis was varied from 1986 to 1990 to determine whether there was any consistent bias (Fig. 5b). There was a tendency to overestimate F in the most recent years. Subsequent population-level analyses were based on averaging instantaneous fishing mortality rates for two time periods: 1979–1985 and 1986–1990 (Table 5). Fishing mortality was higher and more variable during the earlier period.

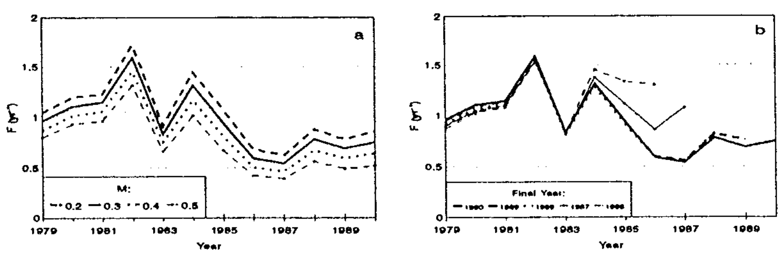

Figure 5. Sensitivity of annual estimated instantaneous fishing mortality rates (F) from separable virtual population analysis applied to southeastern U.S. black sea bass to a) varying range of instantaneous natural mortality rate (M), and b) varying final year used in the analysis.

Table 5. Mean estimates of age-specific instantaneous fishing mortality rate (F) on southeastern U.S. black sea bass for two time periods using separable virtual population analysis. Corresponding exploitation rates given in parentheses [u = F(1 − e^−Z)/Z]. Estimates given for different assumed levels of natural mortality.

Natural mortality M	Age (yr) 0	1	2	3	4+
			1979–1985		
0.2	0.0 (0.0)	0.05 (0.05)	0.22 (0.20)	0.57 (0.40)	1.23 (0.65)
0.3	0.0 (0.0)	0.04 (0.04)	0.19 (0.15)	0.50 (0.34)	1.12 (0.60)
0.4	0.0 (0.0)	0.03 (0.03)	0.15 (0.12)	0.44 (0.30)	1.01 (0.54)
0.5	0.0 (0.0)	0.02 (0.02)	0.12 (0.09)	0.37 (0.25)	0.91 (0.49)
			1986–1990		
0.2	0.0 (0.0)	0.03 (0.03)	0.14 (0.12)	0.35 (0.27)	0.76 (0.49)
0.3	0.0 (0.0)	0.03 (0.02)	0.11 (0.09)	0.30 (0.23)	0.67 (0.43)
0.4	0.0 (0.0)	0.02 (0.01)	0.09 (0.07)	0.25 (0.18)	0.57 (0.36)
0.5	0.0 (0.0)	0.01 (0.01)	0.06 (0.05)	0.20 (0.14)	0.48 (0.31)

Yield per Recruit.—Estimates of yield per recruit were summarized in Table 6 for different levels of M and two time periods (1979–1985 and 1986–1990). Increasing natural mortality led to decreasing yield per recruit. A comparison of yield per recruit plotted against full fishing mortality (ages 4–7) for different ages at entry showed only slight differences between the two time periods (Fig. 6). Two traditional biological reference points obtained from the yield per recruit approach are F_{max} and $F_{0.1}$ (Sissenwine and Shepherd, 1987). Based on the separable VPA estimates of F (with M = 0.3) from the recent time period (1986–1990), these are estimated as $F_{max} = 0.9$ and $F_{0.1} = 0.4$ for fully recruited ages.

Spawning Stock Biomass per Recruit.—Relative mature female biomass, egg production, and mature male biomass computed for F = 0 was compared to that calculated for mean age-specific F estimated from separable VPA (M = 0.3) (Fig. 7). In all cases, modal value was shifted to younger age, with decrease in overall numbers with higher F represented by reduced area under curves. Small differences were noted between female biomass and egg production (Fig. 7a, b). Great-

Table 6. Yield per recruit (Y/R) and percent maximum spawning potential of southeastern U.S. black sea bass based on mean age-specific fishing mortality rates for two periods (1979–1985 and 1986–1990). Estimated based on separate Von Bertalanffy growth parameters for females and males, females includes all transitional fish, and original catch-in-numbers-at-age matrix used to estimate F.

Natural mortality	Y/R (lbs)	% Maximum spawning potential: Total	Female	Eggs	Male	Percent male*
			Fishing years: 1979–1985			
0.2	0.36	12	26	33	6	45
0.3	0.27	22	42	49	12	54
0.4	0.20	34	56	62	19	63
0.5	0.15	46	67	72	28	71
			Fishing years: 1986–1990			
0.2	0.39	17	32	39	10	51
0.3	0.27	30	50	56	19	61
0.4	0.19	44	64	69	30	70
0.5	0.12	58	76	80	42	78

* Percent relative reduction in numbers of mature males between fished and unfished conditions.

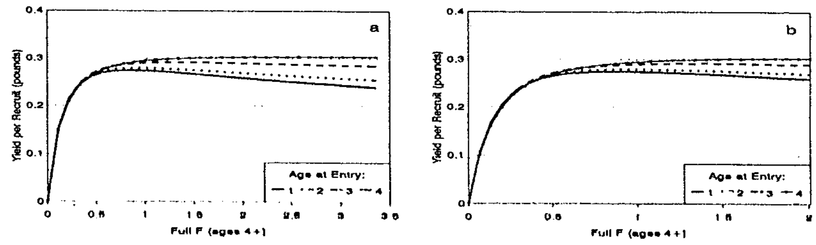

Figure 6. Yield per recruit from southeastern U.S. black sea bass for increasing instantaneous fishing mortality rate (F) and age at entry to fishery for two temporal periods: a) 1979–1985, and b) 1986–1990.

est effect of F was on males, because fewer older fish remain with higher F, and most older fish were males (Fig. 7c).

Estimates of percent maximum spawning potential were developed from estimated F (Table 5) for two time periods based on total mature biomass, female biomass, and male biomass (Figs. 8, 9). Based on the separable VPA estimates of F (with M = 0.3) from the recent time period (1986–1990), full F yielding 30% MSP was greater than 2.0 for mature female biomass and egg production, 0.64 for total mature biomass, and 0.37 for mature male biomass.

Corresponding estimates were made of the reduced proportion of males in the population for these two time periods (Figs. 8d and 9d). For example, a value of 60% under "Percent Male" implies that if the proportion of males in the unfished population (all mature ages) were 50%, then the introduction of fishing mortality would reduce this proportion to 30% (60% to 50%).

Discussion and Management Implications

Compared to several recent assessments [e.g., red drum (Vaughan, 1992), weakfish (Vaughan et al., 1991), and red porgy (Vaughan et al., 1992)], the data for southeastern U.S. black sea bass were quite good. Only estimation of commercial length frequency distributions for hook and line and traps for 1979–1983 from MARMAP data were necessary to fill a data gap.

The use of 5% post-release mortality may be low (Collins, in press). The type B2 recreational catches represented about 36% of the recreational landings in numbers. With the use of 5% post-release mortality the type B2 catches represent only about 3% of the recreational landings. If post-release mortality were as high as 25%, then the type B2 catches would increase to 12% of the recreational landings. Without the type B2, recreational landings in numbers represent about 48% of the total landings. Thus, increasing the post-release mortality from 5% to 25% would increase their contribution to the total landings from 1% to 6%. Error of this magnitude is not likely to change the results significantly.

A major problem for many stock assessments is obtaining good estimates of natural mortality (M). The estimate of 0.3 used for black sea bass was based on life history analogy (Pauly, 1979; Hoenig, 1983) and agreed with the value used for the stock north of Cape Hatteras. Sensitivity of F to M (Fig. 5a) did not suggest any large bias for small errors in M.

Although declining rends in headboat CPUE and median total lengths reflected the impact of fishing on the U.S. south Atlantic black sea bass stock, these trends

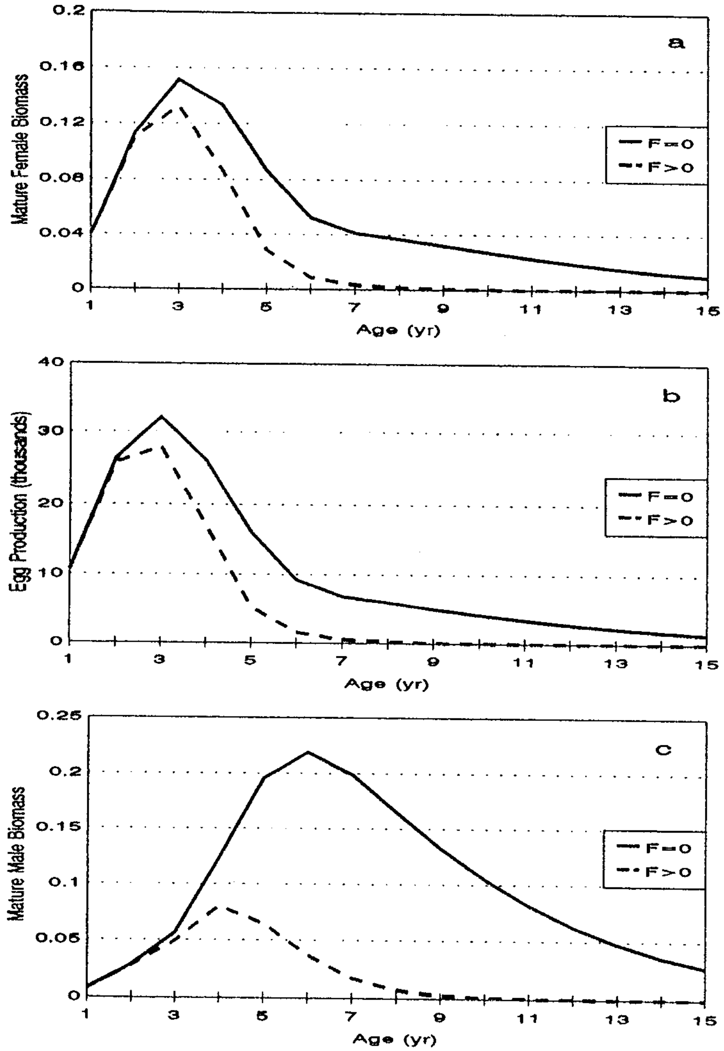

Figure 7. (a) Relative mature female biomass, (b) egg production, and (c) mature male biomass of southeastern U.S. black sea bass obtained with instantaneous fishing mortality rate (F) set to 0 compared to that obtained from estimated value (F > 0).

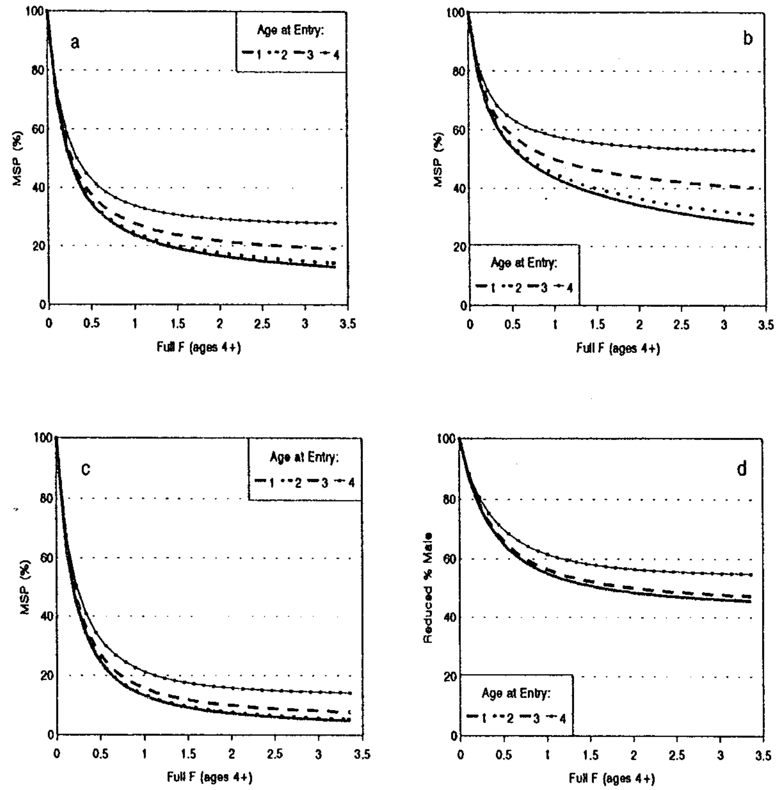

Figure 8. Percent maximum spawning potential for southeastern U.S. black sea bass calculated from a) total mature biomass, b) female biomass, and c) male biomass for increasing instantaneous fishing mortality rate (F) and age at entry to fishery for 1979–1985 time period. Also shown is (d) percent reduction in ratio of males to females for same time period.

were relatively shallow and did not suggest any immediate concern with overfishing.

Low (1981) obtained estimates of F ranging from 0.30 to 0.53 (or Z ranging from 0.60 to 0.83 with an M of 0.3) from data collected with traps off South Carolina in 1978 and 1979. Wenner et al. (1986) obtained higher estimates of Z, based on trap catch curve analysis, ranging from 0.72 in 1978 to 1.32 in 1981, and for hook and line ranging from 0.73 in 1979 to 1.43 in 1981.

Our estimates of Z from a simple length-based approach were generally lower although they overlapped, ranging between 0.4 and 0.7 (Fig. 4a). Annual estimates of Z from catch curve analysis on fishing years agreed more closely with estimates obtained by Low (1981) and Wenner et al. (1986); e.g., 0.8 in 1979 and 1.4 in 1981. Estimates of Z (full F + M) from separable VPA were higher (1.26 in 1979 and 1.44 in 1981 with M = 0.3).

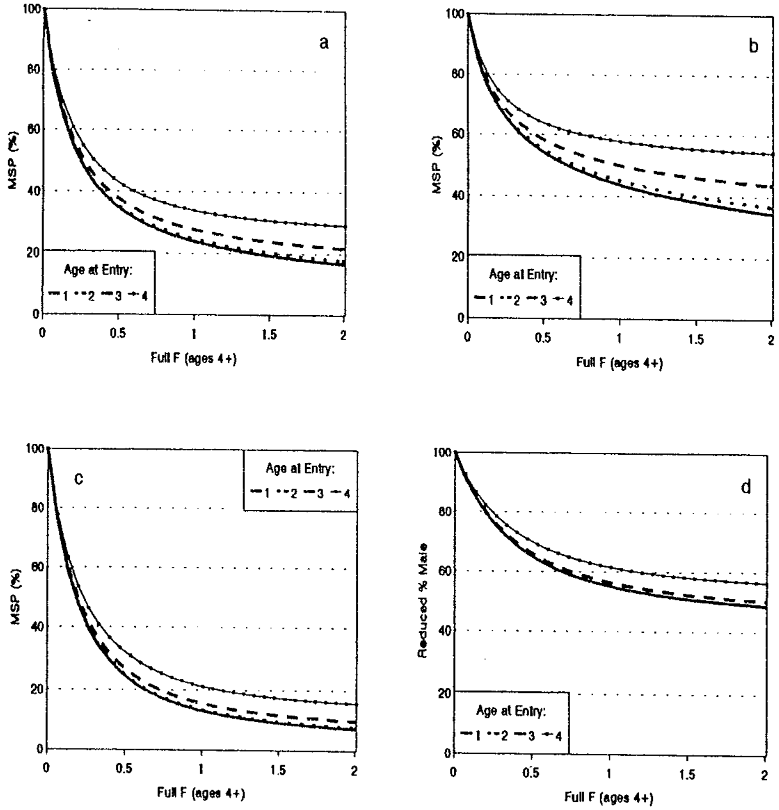

Figure 9. Percent maximum spanning potential for southeastern U.S. black sea bass calculated from a) total mature biomass, b) female biomass, and c) male biomass for increasing instantaneous fishing mortality rate (F) and age at entry to fishery for 1986–1990 time period. Also shown is (d) percent reduction in ratio of males to females for same time period.

Discrepancies were found between the instantaneous total mortality rates obtained from the length-based analysis on headboat data which suggested an increasing trend in overall mortality in recent years (increasing from 0.37 to 0.74 between 1975 and 1990, Fig. 4a), compared to instantaneous fishing mortality rates from the separable VPA which suggested a decrease in fishing (and overall) mortality in recent years (1986–1990) (Fig. 4a). However, the magnitude of estimated fishing mortality on fully recruited ages was higher in the most recent years (full F averages about 0.74 for the period 1986–1990, so Z would be about 1.04). Further, bias in recent year estimates of fishing mortality estimates from VPA would suggest that they might be slightly overestimated (Fig. 5b). Estimates from the VPA are probably more accurate, because they combine information across fishing years and are not based on an equilibrium assumption inherent in the annual length-based method.

Typically, yield per recruit analysis is conducted to relate harvest to two factors controllable by the fishery manager. First, the age at entry to the fishery may be controlled through mesh size regulations or minimum size limits. The other factor is fishing mortality, which can be controlled through quotas, seasonal closures, or bag limits. In addition, two traditional biological reference points are obtained from this approach, F_{max} and $F_{0.1}$. Estimates for these two values (0.9 and 0.4, respectively for M = 0.3) bracket the mean full F (0.67) for the most recent time period (1986–1990), giving an equivocal signal of stock status during this recent time period based on these two biological reference points. Estimated full F for the earlier time period (1979–1985) was higher (1.12) and may have been indicative of overfishing based on these two biological reference points.

Estimates of %MSP based on female biomass and egg production are generally higher than the 30% biological reference point used by the South Atlantic Fishery Management Council (Table 6). Estimates of %MSP for males are generally small with the proportion of mature males expected to be reduced to about 60% from fishing mortality associated with the recent time period for M = 0.3. A slightly greater reduction in males would be expected for the earlier time period when fishing mortality was higher. With total mature biomass, %MSP was estimated to be 30% with full F of 0.67. Full F for the earlier time period (1.12), which produces an estimate of %MSP of 22, is about 67% greater than the full F for the more recent time period which produced an estimate of 30% MSP.

Because black sea bass are protogynous hermaphrodites with most sea bass functioning initially as females and then as males, increasing fishing mortality on all ages reduced the proportion of mature males to mature females. Whether this will alter the age of transition is not known, and it was not possible to account for the effect of population density on transformation rate in population models. It has been suggested that males are currently not limiting, but the degree to which increasing fishing mortality can cause them to become limiting is unknown. Increased rate of transformation from females to males due to reduced abundance of males, which has been reported in other protogynous reef fish (Shapiro, 1979), would lead to additional declines in mature female biomass. If females do not transform at a greater rate when the population is depressed, then the complementary concern may arise as to whether sufficient numbers of mature males will be present during spawning.

Other than smoothing out the peaks and valleys in estimates of fishing mortality (Fig. 4), applying a 3-yr moving average to the landing data (by fishery) did not lead to significantly different estimates of F. Hence, the general conclusions drawn in this paper are not particularly sensitive to potential problems in estimating recreational catches that may be causing the observed variability.

For red porgy, Vaughan et al. (1992) suggested using total mature population biomass as a measure of spawning potential, which for black sea bass produces an estimate of 22% for the 1979–1985 period and 30% for the 1986–1990 period (Table 6). The former value is below and the latter value is equal to the value 30% typically used by the South Atlantic Fishery Management Council to define overfishing for the snapper-grouper complex of species (SAFMC, 1990). Whether the value of 30% remains the relevant biological reference point when %MSP is estimated from total mature biomass is a separate issue.

It appears that the southeastern U.S. stock of black sea bass is in better condition than those of many sympatric reef species despite heavy fishing pressure [probably because of earlier age of maturity (about 50% at age 1) compared to later age of full recruitment to the combined fisheries (at about age 4)]. Higher %MSP and lower Z in recent years may be due to the minimum legal size (8 in

TL) established in 1983 (SAFMC, 1983). The %MSP estimate of 30% for 1986–1990 suggests that more stringent regulation of the fisheries may not be necessary. However, continued monitoring of the status of the stock is recommended.

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