

Abstract.—We used otolith ageing to describe the population dynamics of black drum, *Pogonias cromis*, collected over a three-year period from the Chesapeake Bay region's commercial and recreational fisheries. Black drum average age, total length, and weight were 26 years, 109.5 cm, and 22.1 kg respectively. The oldest fish was 59 years and fish older than 50 years were present in the catch from 1990 to 1992. Growth in length slowed by age 20, whereas growth in weight did not slow until age 45. A von Bertalanffy growth function was fitted to our data (L_{∞} = 117.3 cm, K = 0.105, t_0 = -2.3 yr) and was similar to that for northeast Florida, but dissimilar to that for the Gulf of Mexico. Fish grow slower but reach larger sizes in the Atlantic than in the Gulf. Estimates of instantaneous total mortality, Z , from maximum age and catch-curve analyses were low, 0.08–0.13, indicating that fishing mortality is also low in the Chesapeake Bay region. Studies to date lend support to the hypothesis that black drum from the east coast of the United States are from a common stock. The fishery of the Chesapeake Bay region is made up of old, large migrants from that larger population and should be managed accordingly.

Age, growth, and mortality of black drum, *Pogonias cromis*, in the Chesapeake Bay region

Cynthia M. Jones

Applied Marine Research Laboratory and Department of Biological Sciences
Old Dominion University, Norfolk, Virginia 23529-0456

E-mail address: jones@estuary.amrl.odu.edu

Brian Wells

Department of Biological Sciences
Old Dominion University, Norfolk, Virginia 23529

Black drum, *Pogonias cromis*, is the largest member of the family Sciaenidae in the western North Atlantic Ocean. Black drum range in U.S. waters from New England south through Florida and across the northern Gulf of Mexico, with Chesapeake Bay being near the northern end of the breeding range (Welsh and Breder, 1923; Hildebrand and Schroeder, 1928). Black drum support important recreational and commercial fisheries throughout their range in the United States. Their population abundance has been historically greater on the Florida coast than northward (Welsh and Breder, 1923), but the degree of stock unity along the east coast of the United States has not yet been determined.

Black drum is migratory in the Chesapeake Bay region. Frisbie (1961) speculated that juveniles move offshore and southward in the fall. Richards (1973) reported that black drum were absent from marine waters off Virginia during winter. Although occasionally caught inshore during winter, black drum generally move inshore to spawn in spring and offshore to overwinter in the fall. The migratory behavior of this fish complicates interpretation of the biological characteristics of the Atlantic coast fishery.

Proper management of the black drum population depends on knowl-

edge of their basic biology throughout their range, particularly their resilience to harvesting. Yet much is unknown about their adult life history and biology in the Chesapeake Bay region where studies have concentrated on early life history. Initial studies of eggs, larvae, and juveniles (Frisbie, 1961; Joseph et al., 1964; Richards and Castagna, 1970) failed to clarify the geographic extent of the spawning and nursery regions. A recent study by Daniel and Graves (1994) concluded that egg production of black drum had been overestimated because of misidentification and that previously reported egg distributions (Joseph et al., 1964) may be incorrect.

Little work has been directed at adult black drum in the Chesapeake Bay region, aside from general faunal studies like that of Hildebrand and Schroeder (1928), and only one study is recent. Studies of early life history by Frisbie (1961) and Joseph et al. (1964) provide little information that can be used in yield modeling to evaluate resilience to harvest. The only studies that provide information specifically useful for modeling include Richards (1973) and Desfosse (1987), both on age and growth. Desfosse (1987) reported ages of 4–15 years with 10-year-olds predominant in the catch, whereas Richards (1973) estimated

maximum age at 35 years. Unfortunately, these studies relied on scales to age black drum. Furthermore, Beamish and McFarlane (1983) reported that scales were not a reliable hard part to age older fish of many species. Hence, the use of scales for ageing black drum in the Chesapeake Bay region may give unreliable results.

Only one recent study of black drum life history has focused on the Chesapeake Bay region; more work has been done in Florida and Gulf of Mexico waters. Pearson (1929) first described the early life stages for black drum in Texas waters. Egg and larval distributions have been reported (Jannke, 1971; Holt et al., 1985; Ditty, 1986), as well as adult distributions (Cody et al., 1978; Ross et al., 1983). Recent studies, based on otolith ageing, report maximum ages of 43 years in the northern Gulf of Mexico (Beckman et al., 1990) and 58 years off the northeast coast of Florida (Murphy and Taylor, 1989). Although Pearson (1929) described spawning migrations of fish over 80 cm, most young fish show little movement between embayments (Osburn and Matlock, 1984).

This paper describes fundamental biological characteristics of black drum in the Chesapeake Bay region that support stock unity of east coast fish. These data can be used as a basis for yield modeling and evaluation of black drum's resilience to harvest. We present the first otolith-based age determination for Chesapeake Bay black drum, which includes characteristics of catch, growth, and mortality. We compare these life history parameters with those derived from other geographic regions.

Methods

Black drum ($n=853$) were collected March through June, 1990–92, from commercial and recreational fisheries on the eastern shore of Virginia where more than 90% of the catch is landed (Jones et al., 1990). Commercial landing sites were located at Willis Wharf, Oyster, and Bayford; recreational sites were at Cape Charles and Cherrystone Point (Fig. 1). Fishermen were asked for the location of their catches. Collection sites were visited daily once the first landings were made. Additionally, in the fall of 1990 and 1992, we obtained juveniles ($n=10$) from special sampling of pound nets near the bay mouth.

Fish were sexed and measured for total length (TL), standard length (SL), total weight (TW), gonad weight (GW), girth at the preopercle (G1), and maximum girth (G2). Sagittal otoliths, dorsal spines, and

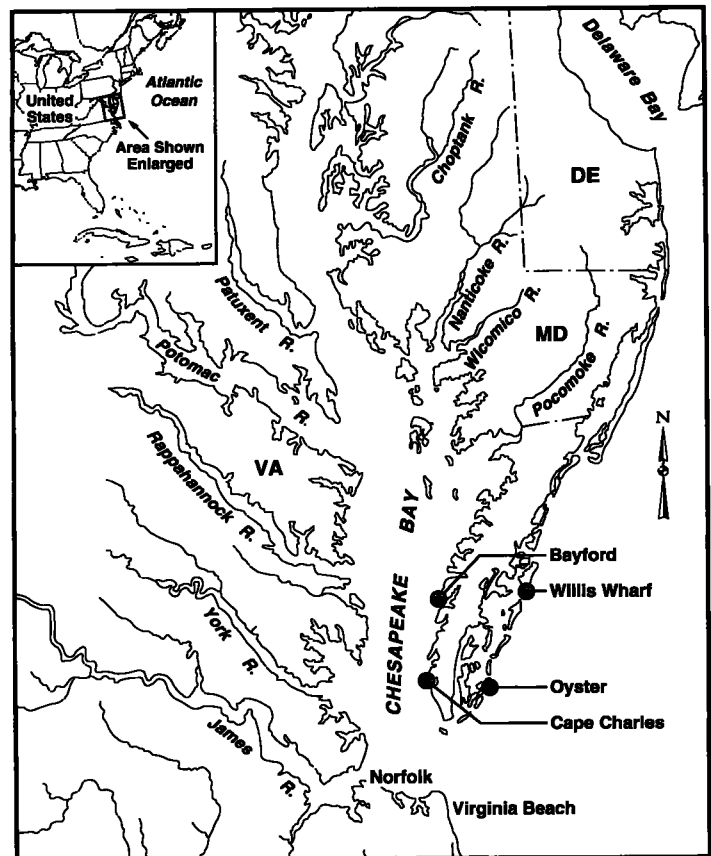


Figure 1

Map of Chesapeake Bay showing Chesapeake Bay region sampling sites.

fin rays were taken from each specimen. One otolith, chosen randomly from each pair, was transversely sectioned through the core on a Beuhler low-speed Isomet saw. Three sections of about 300- μ m thickness were mounted with Flo-texx mounting medium on a slide and read under a dissecting microscope (10 \times) with transmitted light and bright field. Dorsal spines and fin rays were processed similarly (10–40 \times) but sectioned perpendicular to the long axis of the growth plane, close to the base. To compare hard parts, we read random sections without knowledge of length or collection date of specimen.

Ages were assigned on the basis of counts of annuli. We call them presumptive annuli in this paper because we have not completed validation of ages 44–59. However, otolith annuli have been validated to age 43 in the Gulf of Mexico through marginal increment analysis (Beckman et al., 1990; Fitzhugh and Beckman¹), and we have recently shown corre-

¹ Fitzhugh, G. R., and D. W. Beckman. 1987. Age, growth and reproductive biology of black drum in Louisiana waters. Coastal Fisheries Institute, Center for Wetland Resources, Louisiana State University, Final Report of Funded projects FY 1986–1987, 89 p.

spondences between bomb radiocarbon chronologies from the atmosphere and those from otolith cores of black drum (Campana and Jones, 1998). Average birth date was arbitrarily taken to be 1 January (Jearld, 1983). To assess ageing precision, all hard parts ($n=30$) were read twice by each of two readers, and agreement between and within readers was evaluated by percent agreement methods (Beamish and Fournier, 1981; Chang, 1982). Disagreements were resolved by a third reading.

To evaluate changes in otolith size in relation to fish total length and age, otoliths from 300 fish (1990 collections; ages 0–57; 22.9–130.0 cm TL) were measured for maximum length (otolith length [OL] ± 0.01 mm), radius along the sulcal groove (otolith radius [OR] ± 0.001 mm), maximum thickness (otolith width [OWID] ± 0.01 mm), and weight (otolith weight [OWT] ± 0.001 g). Relation between otolith measurements and fish TL and age were evaluated by simple linear regression analysis.

To evaluate growth, observed individual lengths-at-age were fitted to the von Bertalanffy growth function, VBGF (Ricker, 1975), by using nonlinear regression, SAS NLIN procedure DUD method (SAS, 1988). Likewise, individual weights-at-age were fitted to the VBGF. Model parameters were the following: L_{∞} , the mean asymptotic length; W_{∞} , the mean asymptotic weight; K and K' , respectively; the Brody growth coefficient on length and weight; and t_0 and t'_0 , the theoretical age at which the fish would have zero length on length and weight (Ricker, 1975). Growth curve parameters were compared between years and sexes with maximum likelihood ratio tests (Kimura, 1980).

Linear regression was used to determine length-weight relationships for fish ranging from 22.9 to 130.0 cm TL and 0.6 to 49.4 kg TW. Differences between sexes were tested with Rawlings' (1988) tests of homogeneity of slopes and intercepts by using PROC REG in SAS (Littell et al., 1991). The hypothesis of isometric growth (Ricker, 1975) was tested with a t -test.

Instantaneous total annual mortality rates, Z , were estimated from maximum age with Hoenig's pooled regression equation (Hoenig, 1983), by calculating a theoretical total mortality for the entire life span following the reasoning of Royce (1972), and with the regression method, i.e. with a catch curve combining \log_e -transformed recreational and commercial abundance data. In the latter method, mortality estimates were based on data from ages 21–43 and 21–59. Younger ages were truncated because the age group at the apex of the catch curve (age 20) may not have been fully recruited to the fishery (Everhart and Youngs, 1981). Older ages were truncated at the first

age class (age 44) with fewer than five fish following Chapman and Robson (1960). Data from 1990 to 1992 were combined to minimize effects of variation in year-class strength (Robson and Chapman, 1961). The right limb of the catch curve was tested for deviation from linearity by analysis of variance (ANOVA). Estimates of Z were converted to total annual mortality rates ($A=1-e^{-z}$; Ricker, 1975).

All statistical analyses were performed with SAS (SAS, 1988). Rejection of the null hypothesis was based on $\alpha = 0.05$, F -tests in ANCOVA were based on type-III sum of squares (Freund et al., 1986), and assumptions of linearity were checked with residual plots (Draper and Smith, 1981). Data were \log_{10} -transformed to correct for nonlinearity and heterogeneity of variance when necessary. Log-transformed data are presented in graphs and tables in original units, unless otherwise stated. Variables that could not be normalized were compared with Wilcoxon's two-sample test or a Kruskal-Wallis test for more than two samples, and large-sample approximate z -scores or χ^2 were reported.

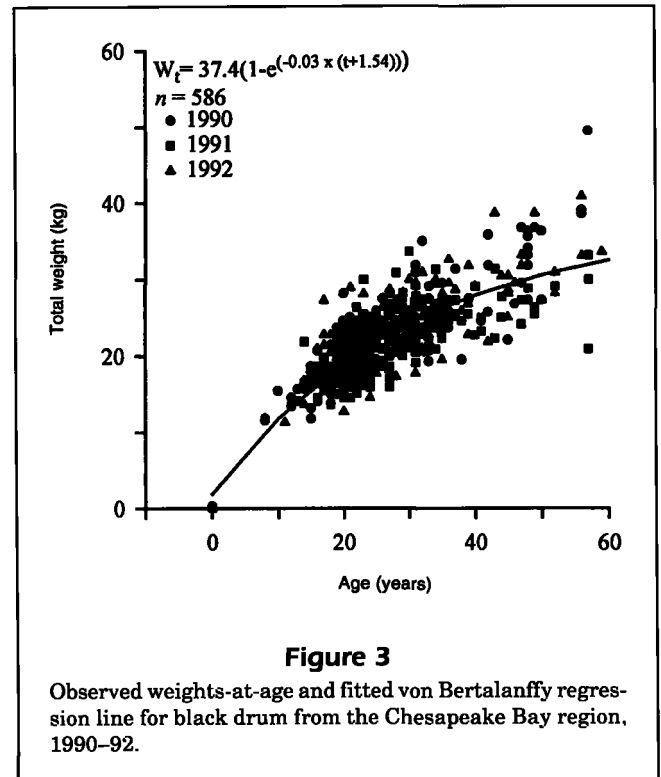
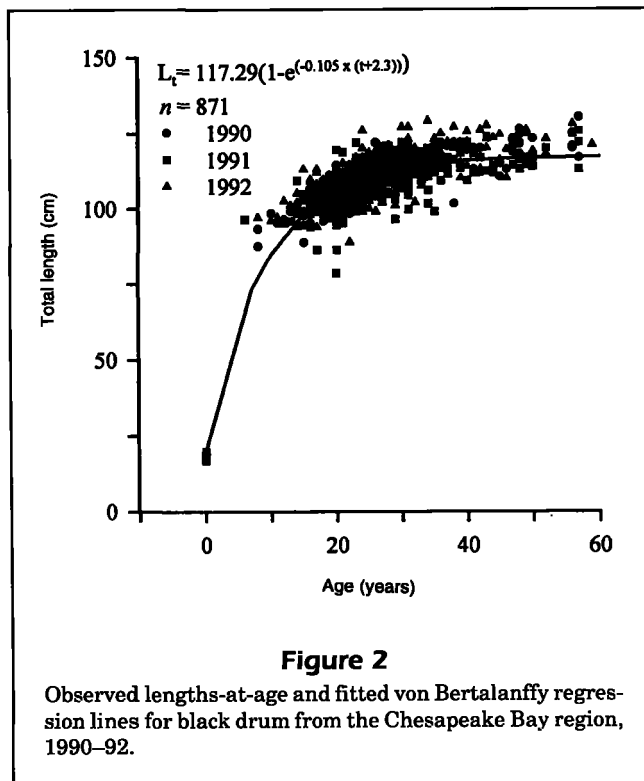
Results

Hard part comparisons

All hardparts showed regular, concentric marks that could be interpreted as annuli. However, marks were not equally clear or consistent between all hard parts. Otoliths were the clearest and most precise of the hard parts to interpret. One hundred percent of otoliths, 36.7% of dorsal spines, and 63.7% of fin rays had marks clear enough to read. Between-reader precision was 100% for otoliths, 27.3% for dorsal spines, and 47.4% for fin rays. Compared with otoliths, dorsal spines and fin rays underestimated age; this underestimation worsened with increasing age (Kruskal-Wallis distribution-free multiple comparison test, MSD=15.81, $P<0.05$). Underageing was especially marked with dorsal spines. On the basis of these results and otolith growth patterns (see next section), we deemed otoliths the clearest, most reliable hard part, and used them for all ageing.

Otolith size relationships to fish size and age

Black drum otoliths continue to increase in size with fish length and age, apparently throughout life. All measures of otolith size—OL, OWT, OR, OWID—were significantly and positively related to fish length and age. Although black drum otoliths continue to increase in size, the relations of various otolith sizes to fish length and age were not consistent. Relations

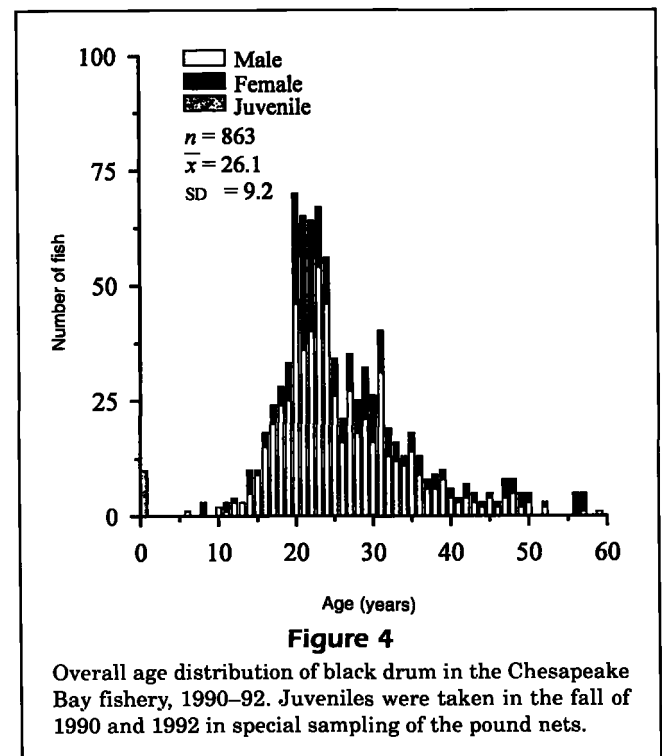


between fish total length and otolith maximum length ($OL=2.69 + 0.20TL$), and otolith maximum width ($OWID=2.69 + 0.14TL$), were isometric, reasonably linear, and therefore were useful for back-calculation of fish lengths. Other relations between total length and all relations on age were exponential functions ($OWT=1.72 \times 10^{-5} TL^{2.66}$; $OR=6.02 \times 10^{-3} TL^{1.46}$; $OL=10.78 Age^{0.256}$; $OWID=8.71 Age^{0.231}$; $OWT=0.231 Age^{0.025}$; $OR=0.964 Age^{0.541}$).

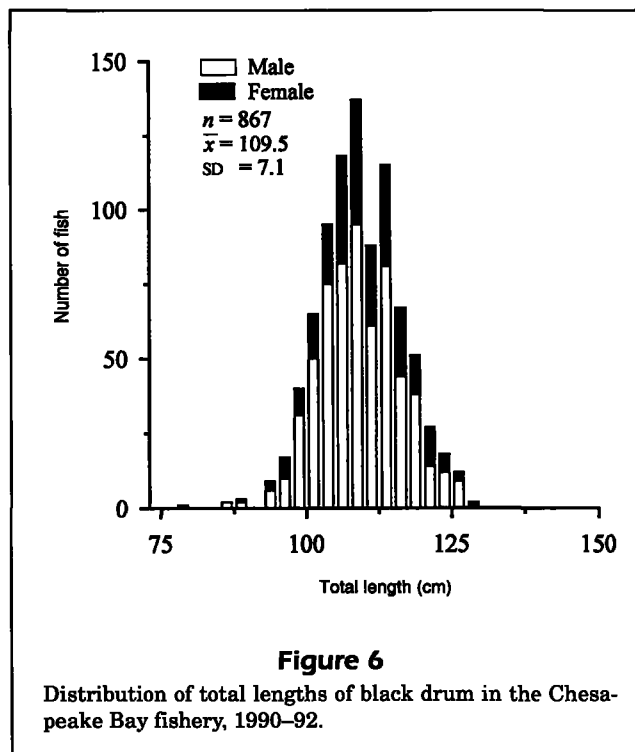
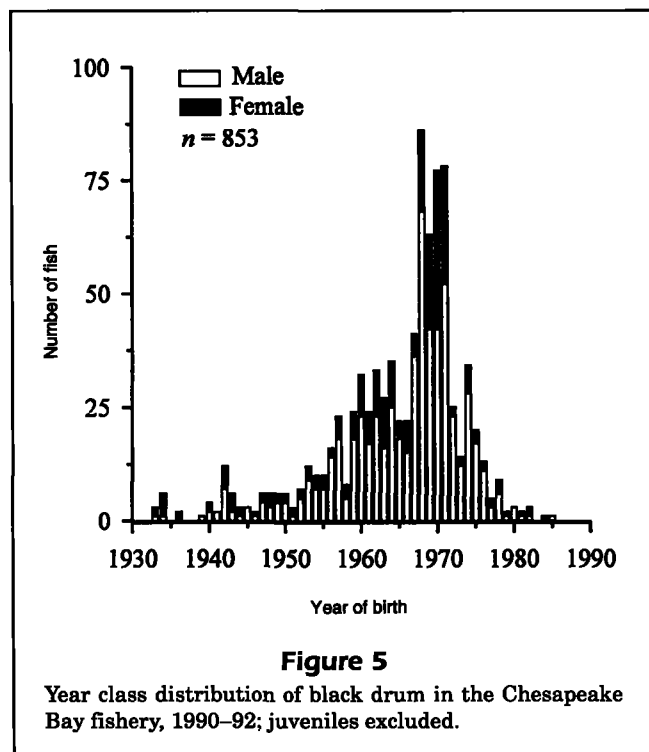
Annuli on black drum otoliths continue to be deposited with increasing fish size. Annuli counts were significantly and positively related to fish length (Fig. 2) and weight (Fig. 3). Fitted regression lines and data plots indicate counts continue to increase most clearly with weight. However, they also increase with length even though there is a leveling off at greater numbers of annuli. Although usually used merely to describe growth patterns, Figures 2 and 3 provide evidence—usually not stated—that otolith age is valid.

Age and size compositions

The Chesapeake Bay fishery generally captures old black drum. Mean age was 26 years (Fig. 4). Ages ranged from 6 to 59 years in the regularly sampled catch, but several juveniles were obtained from sampling pound nets. Median age in the catch was consistent from year to year (1990=25.0, 1991=23.0, 1992=24.0; Kruskal-Wallis $\chi^2=4.53$, $P>0.05$) and be-



tween sexes ($\delta = \text{♀} = 24.0$; Wilcoxon $z=1.01$, $P>0.05$). Age at the 95th percentile was 48 years, indicating that many older fish were landed. The youngest fish

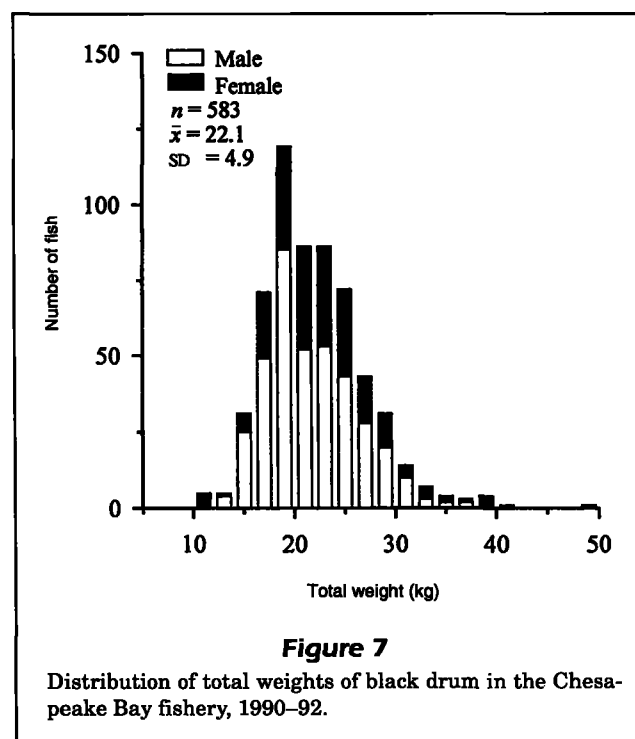


caught, apart from young-of-the-year, was age 6, and age at the 5th percentile was 16 years. No fish between 1 and 5 years were found. Recruitment to the gear appears to be complete by age 20 or 21.

Black drum recruitment in Chesapeake Bay is characterized by occasional, dominant year classes (Fig. 5). Exceptionally large year classes occurred in 1934 and 1942, demonstrated in an abundance that fell above the 95% confidence band of expected year class strength around the catch curve. Abundant, but not exceptional, year classes occurred in 1933, 1943, and 1968. Poor year classes, those that fell below the lower 95% confidence interval, occurred in 1939, 1946, 1951, and 1958. We lack information on recruitment after 1972 because black drum are not fully recruited to the bay fishery until age 21.

Total length of adult black drum in Chesapeake Bay averaged 109.5 cm, ranging from 78.7 to 130.2 cm (Fig. 6). Median length (cm) in the catch was not significantly different from year to year (1990=109.2, 1991=108.0, 1992=110.5; Kruskal-Wallis $\chi^2=4.52$, $P>0.05$), although females were slightly longer than males ($\delta=109.2$, $\text{♀}=109.5$, Wilcoxon $z=2.06$, $P<0.05$). Length at the 95th percentile was 121.9 cm, indicating that many large fish were landed.

Mean total weight of adult black drum in Chesapeake Bay differed slightly between sexes and among years. Total weight of adults averaged 22.1 kg over the period 1990–92 and ranged from 11.3 to 49.4 kg



(Fig. 7). Females were slightly heavier (ANOVA, $F=8.23$, $P<0.05$), probably due to their reproductive product. The difference between sexes, 1.1 kg, amounts to only 5% of average total weight. Fish in

1990 (23.0 kg) were slightly heavier (ANOVA, $F=4.67$, $P<0.05$) than those landed in 1991 (21.4) and 1992 (22.3 kg). Again, the difference among years is only 7% of average total weight.

Comparisons between areas and gears

Black drum collected in Chesapeake Bay and coastal waters did not differ in simple biological attributes. Catches from the two areas showed no significant differences in age (bay=25.8 yr, coastal=26.8 yr, $Z=-1.21$, $P>0.05$), total weight (bay=21.7 kg, coastal=22.4 kg, $Z=-1.32$, $P>0.05$), or total length (bay=109.5 cm, coastal=109.5 cm, $Z=0.09$, $P>0.05$). Hence, data from both areas were pooled in all other analyses.

Recreational and commercial catches showed statistically significant differences in total length ($Z=2.13$, $P<0.05$), but not in total weight (commercial=22.1 kg, recreational=22.2 kg, $Z=0.76$, $P>0.05$), or age (commercial=26.3 yr, recreational=26.9 yr, $Z=1.60$, $P>0.05$). Mean TL of the commercial catch was 109.0 cm ($n=698$, $SE=8.7$ cm), and recreational mean TL was 110.4 cm ($n=166$, $SE=8.6$ cm). Mean, median, ranges, and quantile measures of TL are almost identical for these two fisheries. Although the differences in TL are statistically significant because of large sample size, they are not biologically meaningful. Hence, data from these fisheries were pooled to analyze growth and mortality.

Growth

Observed lengths varied greatly within age (Fig. 2). Growth was rapid before 15 years of age but slowed by age 20. Lengths thereafter varied asymptotically about the mean. Black drum have achieved 58% of L_{∞} by age 6, when fish are first caught in the bay, and have achieved 90% by age 20, after which they are fully recruited to the gears. Apparently growth was very rapid in the first 5 years, ages absent from our collections. The VBGF equation for data pooled over the period 1990–92 is

$$L_t = 117.3 \left(1 - e^{-0.105(t+2.3)} \right).$$

No differences were found in growth curve parameters in length between the sexes ($P>0.05$) or years ($P>0.05$). We observed large numbers of fish at older age, permitting a good estimate for L_{∞} ($n=871$; includes juveniles, $r^2=0.998$). However, because we observed no fish between 1 and 5 years, our estimate of K is not optimum. Parameters estimated and asymptotic standard errors are given in Table 1.

Observed weights of Chesapeake Bay black drum varied greatly within age (Fig. 3). As with age-length

Table 1
Summary of parameter estimates for the von Bertalanffy growth equation on total length (cm) and total weight (kg) of Chesapeake Bay region black drum, *Pogonias cromis* (1990–92).

Parameter	Estimate	SE	95% confidence intervals	
			Lower	Upper
L_{∞}	117.3	0.4	116.5	118.1
K	0.105	0.003	0.099	0.111
t_0	-2.3	0.2	-2.7	-1.9
W_{∞}	37.4	1.7	34.0	40.8
K'	0.033	0.003	0.027	0.039
t'_0	-1.5	0.9	-3.3	0.3

data, growth was rapid for the first 6 years. Although it slowed thereafter, fish still grew appreciably in weight until growth slowed substantially at 45 yr. Black drum have reached 22% of W_{∞} by age 6 when they first appear in the bay as adults, 51% of W_{∞} by age 20, and 78% by age 45. Hence, they grew more slowly in weight than in length. The VBGF equation for data pooled over the period 1990–92 is

$$W_t = 37.4 \left(1 - e^{-0.03(t+1.5)} \right).$$

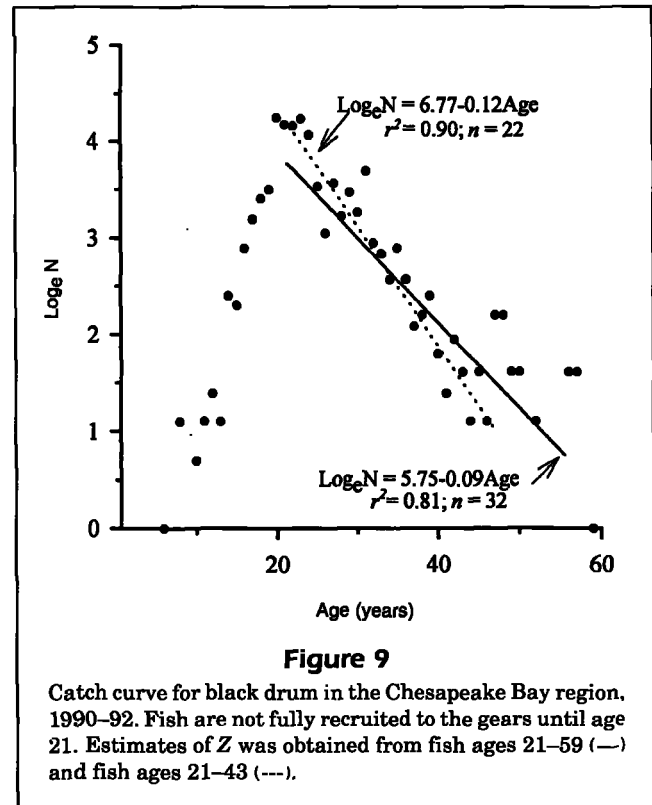
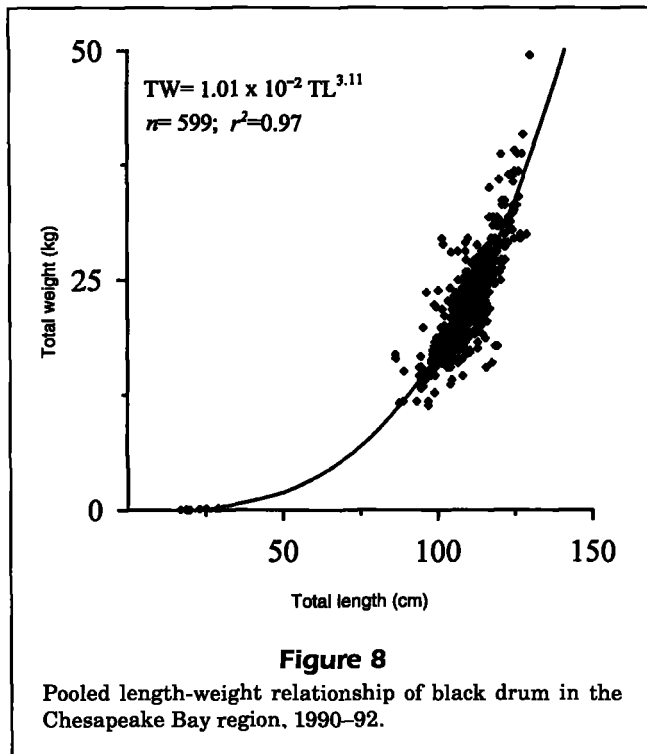
We observed large numbers of older fish, permitting a good estimate for W_{∞} ($n=586$, $r^2=0.977$). However, because we observed no fish between ages 1 and 5, our estimate of K' is not optimum. Parameters estimated, asymptotic standard errors, and 95% confidence intervals are given in Table 1.

No differences were found in weight-growth curve parameters between the sexes ($P>0.05$). However, pairwise comparisons showed parameters differed between the years 1990 and 1991 (1990: $W_{\infty}=57.2$ kg, $K'=0.018$ /yr, $t'_0=-2.24$ yr; 1991: $W_{\infty}=29.8$ kg, $K'=0.052$ /yr, $t'_0=0.06$ yr, likelihood ratio test: $\chi^2=10.54$, $P<0.05$). Fish captured in 1991 weighed less at older ages than in 1990 and 1992. We have no explanation for this; causes could be minor, i.e. sampling error, a slightly greater proportion of older fish that had completed spawning in 1992, or perhaps fish that were in worse condition in 1991.

A pooled length-weight regression was developed (Fig. 8) with the equation

$$TW = 1.01 \times 10^{-2} TL^{3.11} \quad (r^2=0.97; n=599; P<0.01).$$

The slope of the regression line ($b=3.11$; $SE=0.03$) was significantly different from 3.00 (t -test; $t=3.75$; $P<0.05$), indicating allometric growth.



Mortality

Mean instantaneous total mortality rates, Z , ranged from 0.08 to 0.13. Estimates obtained from a maximum observed age of 59 years, and for age truncated at the 95th percentile—48 years, were 0.08 ($A=8\%$) and 0.09 ($A=10\%$) with Hoenig's (1983) method, and 0.08 ($A=8\%$) and 0.10 ($A=10\%$) with Royce's (1972) method. A regression estimate obtained from the slope of a catch curve truncated at older ages (Fig. 9) was 0.12 ($A=13\%$) with 95% confidence intervals of 0.11 ($A=12\%$) and 0.13 ($A=14\%$). This regression line did not deviate significantly from linearity (ANOVA; $F=1.18$; $P>0.05$). A regression estimate obtained from the slope of the full catch curve, i.e. with all older cohorts even when $n<5$, was 0.09 ($A=9\%$) with 95% confidence intervals of 0.08 ($A=8\%$) and 0.09 ($A=10\%$). This regression line, too, did not deviate significantly from linearity (ANOVA; $F=1.29$; $P>0.05$).

Discussion

Age determination methods

We believe otoliths are the preferred, most reliable hard part to use for ageing black drum. Reasons for this include high precision and readability of otoliths, their continued growth with increase in fish size and

age, the increase in the number of annuli with size, and validation over most of the life span. Otolith annuli are extremely clear and easy to read, even out to 59 annuli, and agreement between readings was absolute, 100%. In contrast, fin rays and spines often produced unreadable sections, and fewer bands were counted than on otoliths, especially at older ages.

We have not yet been able to validate black drum otolith ages completely in the Chesapeake Bay region with marginal increments or other analyses. However, evidence from other regions indicate that black drum otoliths are valid throughout much of their life. For example, Fitzhugh and Beckman,¹ and Beckman et al. (1990) used marginal increment analysis to validate otolith annuli formation in black drum to age 43 from Louisiana. However, because most of their fish were age 5 to 27, they had to group the few fish at older ages. Our putative ages extend an additional 15 years beyond the range these authors described. Other evidence indicates members of the family (Sciaenidae) consistently produce annuli throughout life. Beckman et al. (1989) used marginal increment analysis to confirm annulus formation to age 37 in red drum, *Sciaenops ocellatus*. Ross et al. (1995) confirmed annuli formation in two red drum aged 38 and 40 through oxytetracycline marking of otoliths. Although we have not yet fully

validated ages from 44 to 59 years, we have found (see above) that black drum otoliths satisfy the criteria of Van Oosten (1929) for annuli: the number of rings increased with mean size, rings were consistently located on otoliths of different putative ages, and otolith radii correlated highly with putative age.

Although we did not evaluate scales because of their problematic use in ageing, we believe there is direct evidence that they underestimate black drum age in the Chesapeake Bay region. Beamish and McFarlane (1983) documented the tendency of scales to underestimate age, especially at older ages. Richards (1973) and Desfosse (1987) estimated maximum ages for Chesapeake Bay region black drum of only 35 and 10 yr, respectively, using scales. Considering that size composition has not changed over the intervening years (Desfosse, 1987; Hutchinson and Rogers²), these ages are much younger than we observed. Richards should have seen maximum ages of at least 41, Desfosse at least 57. We therefore argue against using scales for ageing black drum.

Implications of age structure

Although we had only three years of data, the long lives of black drum allowed our collections to represent a history of recruitment of over 50 years—as was the case with Pereira et al. (1995) for freshwater drum, *Aplodinotus grunniens*. Our data show that recruitment of black drum from the Chesapeake Bay region generally appears to be low, with only occasional strong year classes that persist for many years, for example the 1934 and 1942 cohorts. Moreover, low average recruitment is anticipated for a species with a long reproductive lifespan (20 years at the age of capture), high batch fecundity (1–14 million eggs), and several batches in a spawning season (Wells, 1994), especially when the population remains at low abundance throughout the years.

Our recruitment history of black drum also showed an absence of fish ages 1 to 5, which is consistent since at least the 1960s. There are several possible causes: 1) low abundance of black drum young that is hard to measure, 2) recent complete recruitment failure, 3) gear specificity, and 4) migration southward during this life stage and later northward migration. We review the evidence in support of these alternatives briefly.

Given its demography, this stock should have a low survival rate during the early life stages that is difficult to distinguish from zero. Black drum's potential lifetime production of 60–840 million eggs requires

mortalities of at least 10^6 or 10^7 during larval and juvenile stages to maintain stable populations. Hence, the high mortality seen in the field (Cowan et al., 1992) is predictable and is difficult, if not impossible, to differentiate from 100% in the field during early life.

The absence of several year classes in the catch of a fishery could also signify complete recruitment failure. Yet indirect evidence does not support this throughout the east coast range. Frisbie (1961) noted the virtual absence of young black drum in the bay and Richards (1973) stated that "black drum of more than 220 to less than 800 mm in length were not readily available . . .". These observations correspond to cohorts from the late 1950s and 1960s which, seen retrospectively in modern catches, showed normal recruitment levels. Even though fish of the expected size of 1–5 year-olds are not typically seen in the bay, these young fish are not missing from the entire geographic range. Fish ages of 1–4 years are found in bycatch from northeast Florida (Murphy and Taylor, 1989). Hence, examination of the catch argues against complete recruitment failure throughout the stock's range.

Fishing gear and practices used for black drum in Chesapeake Bay target large fish and may exclude small fish. The commercial fishery uses anchored and drifted gill nets with 33-cm stretch mesh, which allow smaller fish to escape. Likewise, recreational anglers use hooks that target large fish. Hence, we can explain some of the absence of smaller fish by gear selectivity in the directed fishery. However, if these fish were present in the bay, we would expect to see them in other fisheries, but fishermen have told us that they have never seen these fish in their gear—gear such as pound nets and gill nets of 7.6–15.2 cm (3–6 inch) stretch mesh that would retain these smaller sizes.

Perhaps the strongest alternative explanation for missing 1–5 year-olds lies in the migratory patterns seen in many sciaenids. Specifically, black drum undergo long-range migration along the coasts of the southeast states. Although black drum have been noted as far north as Canada (Welsh and Breder, 1923; Silverman, 1979), they occur more commonly from Delaware south to Florida. Even in the Chesapeake Bay, however, black drum are not resident year round. Frisbie (1961) suggested a southward migration of young fish from Chesapeake Bay in the fall, and the same pattern of fall emigration of juveniles has been shown for Delaware Bay (Thomas and Smith, 1973). Thereafter, only larger and older fish migrate into the bay in the spring—with few younger than six years. In contrast with the Chesapeake Bay pattern, Murphy and Taylor (1989) found that only 20% of their sample from Florida included fish older than age four. Our adult catch data could be ex-

² Hutchinson R., and C. Rogers. 1969. Salt water fishing in Virginia. Dep. Conserv. and Econ. Devel., Richmond, VA, 41 p.

plained by the differential seasonal migration northward of older, larger fish from a population centered farther south, as was first postulated by Welsh and Breder (1923). Finally, two fish tagged in northeast Florida were captured about four months later at the mouth of Chesapeake Bay; thus long-range migrations do occur (Murphy³).

In summary, migration and gear selectivity are likely explanations of the age structure of the Chesapeake Bay fishery and the apparent absence of age 1–5 fish in this region. However, given our data, we cannot rule out local recruitment failure. Movement and exchange is supported by similar sizes-at-age in fish from Florida and Chesapeake Bay (Table 2): mean maximum length is 117.2 cm TL for Florida, 117.3 cm TL for Virginia; maximum ages along the east coast are 58 for Florida (Murphy and Taylor, 1989), 46 for Georgia (Music and Pafford, 1984), and 59 for Virginia (this study).

Stock unity

Several lines of evidence suggest that black drum on the U.S. east coast are from a common stock. Fish throughout the area appear to have similar growth. Von Bertalanffy growth function parameters that we estimated for the Chesapeake Bay region (L_{∞} =117.3 cm; K =0.105/yr; t_0 =-2.3 yr) were similar to those that Murphy and Taylor (1989) found in northeast Florida (L_{∞} =117.2 cm; K =0.124/yr; t_0 =-1.29 yr). In contrast, black drum from the Gulf of Mexico grow more quickly, are smaller at age, and have a smaller maximum size (Table 2). Mitochondrial DNA evidence also suggests a common stock in the western North Atlantic Ocean. No significant differences in frequency

of mtDNA haplotypes were found in fish taken from Virginia and the east coast of Florida (Gold⁴). However, Atlantic east coast fish differed from those sampled in the northern Gulf of Mexico (Gold et al., 1995). Finally, limited tagging data directly suggest black drum move between Chesapeake Bay and Florida (as noted previously).

Implications of mortality estimates

The long life we found in black drum indicates a low mortality rate for larger fish and a stock that cannot support heavy fishing pressure. Our greatest estimate of instantaneous total mortality, Z , converts to an annual total mortality (A) of less than 13%. As $Z = F + M$, natural mortality must also be less than 13%. Because black drum do not completely recruit to the fishery until age 21 in the Chesapeake Bay region, our estimates of total mortality apply to the period of 21 years ago and earlier. For our estimates to be valid today, fishing mortality on young fish must still be low throughout the stock's range. Values of Z have important implications for management. Stocks with high M generally can withstand the highest fishing mortality because fishing simply takes fish that would otherwise die from natural causes. In contrast, stocks with low M (like black drum) do not have a potential for such "excess" natural mortality that can be diverted into fishing mortality (Gulland, 1983; Murphy and Taylor, 1989).

Life history strategy

Black drum have an unusual life history for a long-lived fish. They achieve a large size quickly—84% of

³ Murphy, M. D. 1995. Florida Marine Research Institute, Department of Environmental Protection, 100 Eighth Ave. S.E., St. Petersburg, FL 33701. Personal commun.

⁴ Gold, J. R. 1995. Center for Biosystematics and Biodiversity, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843. Personal commun.

Table 2

Estimates of von Bertalanffy growth function parameters from various studies of black drum. Standard errors in parentheses (when available).

Area and study	Growth parameters			Sample size	Total length range (cm)
	L_{∞} (cm)	K	t_0		
Atlantic coast					
Murphy and Taylor (1989)	117.2 (0.9)	0.124 (0.003)	-1.29 (0.08)	397	20.2–127.5
Northeast Florida					
Present study	117.3 (0.4)	0.105 (0.003)	-2.3 (0.2)	871	22.9–130.2
Gulf of Mexico					
Doerzbacher et al. (1988), Texas	79.8 (4.2)	0.219 (0.027)	—	383	20.3–99.1
Beckman et al. (1990), Louisiana	110.0	0.038	-16.42	1072	—

their total potential growth is accomplished in only 20% of their life span. Moreover, they become sexually mature at age 5–6 years (Murphy and Taylor, 1989) and appear reproductively active over a potential lifespan of some 60 years. Life history theory indicates that species that have an early age at first reproduction and fast growth tend to be short lived (Begon et al., 1990; Charnov, 1993). Typically, long-lived fishes grow slowly and mature late, like sturgeons (Jenkins and Burkhead, 1993) and redfishes, *Sebastes* (Scott and Scott, 1988; Beverton, 1992). Black drum are as long-lived as these fishes but have faster early growth and a relatively early age of first reproduction. This strategy may give black drum a capacity to maintain population stability greater than that seen in similarly long-lived fishes in the presence of heavy fishing.

Acknowledgments

We would like to thank the eastern shore fishermen, and especially the late Clyde Bradford, for helping us to obtain samples. Collections for 1990 and part of 1991 were made by Stephen J. Bobko, and the 1990 data were the basis of his M.S. thesis. The following people assisted in collections: Stephen Nixon, Robert Skinner, Sean Priest, and Bill Sharp. Qing Yang and Tung Quash assisted in otolith processing, and Hassan Lakkis and Qing Yang assisted with statistical analyses. This research was funded by a Wallop/Breaux Program Grant for Sport Fish Restoration from the U.S. Fish and Wildlife Service through the Virginia Marine Resource Commission, Project F-88-R3-7.

Literature cited

- Beamish, R. J., and G. A. McFarlane.**
1983. The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* 112: 35–743.
- Beamish, R. J., and D. A. Fournier.**
1981. A method for comparing the precision of a set of age determination. *Can. J. Fish. Aquat. Sci.* 38:982–983.
- Beckman, D. W., C. A. Wilson, and A. L. Stanley.**
1989. Age and growth of red drum, *Sciaenops ocellatus*, from offshore waters of the northern Gulf of Mexico. *Fish. Bull.* 87:17–28.
1990. Age and growth of black drum in Louisiana waters of the Gulf of Mexico. *Trans. Am. Fish. Soc.* 119:537–544.
- Begon, M., J. L. Harper, and C. R. Townsend.**
1990. *Ecology: individuals, populations and communities*, 2nd ed. Blackwell Scientific Publications, Boston, MA, 945 p.
- Beverton, R. J. H.**
1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *J. Fish. Biol.* 41 (suppl. B):137–160.
- Campana, S. E., and C. M. Jones.**
1998. Radiocarbon from nuclear fallout as applied to the age validation of black drum, *Pogonias cromis*. *Fish. Bull.* 96(2):185–192.
- Chang, W. B.**
1982. A statistical method for evaluating the reproducibility of age determinations. *Can. J. Fish. Aquat. Sci.* 39:1208–1210.
- Chapman, D. G., and D. S. Robson.**
1960. The analysis of a catch curve. *Biometrics* 16:354–368.
- Charnov, E. L.**
1993. *Life history invariants*. Oxford Univ. Press, New York, NY, 167 p.
- Cody, T. J., K. W. Rice, and C. E. Bryan.**
1978. Commercial shrimp and panaeid shrimp studies, northwestern Gulf of Mexico. Texas Parks and Wildlife Dep. Coast. Fish. Proj. Report 2-276-R, 49 p.
- Cowan, J. H. Jr., R. S. Birdsong, E. D. Houde, J. S. Priest, W. C. Sharp, and G. B. Mateja.**
1992. Enclosure experiments on survival and growth of black drum eggs and larvae in lower Chesapeake Bay. *Estuaries* 15:392–402.
- Daniel, L. B., and J. E. Graves.**
1994. Morphometric and genetic identification of eggs of spring-spawning sciaenids in lower Chesapeake Bay. *Fish. Bull.* 92:254–261.
- Desfosse, J. C.**
1987. Preliminary analysis of Virginia's black drum (*Pogonias cromis*) recreational and commercial fisheries. Virginia Marine Resources Commission Report 87-7, Newport News, VA, 27 p.
- Ditty, J. G.**
1986. Ichthyoplankton in neritic waters of the northern Gulf of Mexico off Louisiana: composition, relative abundance, and seasonality. *Fish. Bull.* 84:935–946.
- Doerzbacher, J. F., A. W. Green, and G. C. Matlock.**
1988. A temperature compensated von Bertalanffy growth model for tagged red drum and black drum in Texas bays. *Fish. Res.* 6:135–152.
- Draper, N. R., and H. Smith.**
1981. *Applied regression analysis*, 2nd ed. John Wiley & Sons, New York, NY, 709 p.
- Everhart, W. H., and W. D. Youngs.**
1981. *Principles of fishery science*, 2nd ed. Cornell Univ. Press, Ithaca, NY, 349 p.
- Freund, R. J., R. C. Littell, and P. C. Spector.**
1986. SAS system for linear models, 1986 ed. SAS Institute Incorporated, Cary, NC, 211 p.
- Frisbie, C. M.**
1961. Young black drum, *Pogonias cromis*, in tidal fresh and brackish waters, especially in the Chesapeake and Delaware Bay area. *Chesapeake Sci.* 2:94–100.
- Gold, J. R., L. R. Richardson, C. Furman, and F. Sun.**
1995. Mitochondrial DNA diversity and population structure in marine fish species from the Gulf of Mexico. *Can. J. Fish. Aquat. Sci.* 51 (suppl. 1):205–214.
- Gulland, J. A.**
1983. *Fish stock assessment: a manual of basic methods*. FAO/Wiley series on food and agriculture, vol 1. John Wiley and Sons, New York, NY, 223 p.
- Hildebrand, S. F., and W. C. Schroeder.**
1928. The fishes of Chesapeake Bay. *Bull. U.S. Bur. Fish.* 43:1–388.
- Hoenig, J. M.**
1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.* 82(1):898–903.
- Holt, G. J., S. A. Holt, and C. R. Arnold.**
1985. Diel periodicity of spawning in sciaenids. *Mar. Ecol. Prog. Ser.* 27:1–7.

Jannke, T. E.

1971. Abundance of young sciaenid fishes in Everglades National Park, Florida, in relation to season and other variables. Univ. Miami Sea Grant Program. Sea Grant Fish Bull. 11, 128 p.

Jearld, A., Jr.

1983. Age determination. In L. A. Nielsen and D. L. Johnson (ed.), Fisheries techniques, p 301-324. Am. Fish. Soc., Bethesda, MD.

Jenkins, R. E., and N. M. Burkhead.

1993. Freshwater fishes of Virginia. Am. Fish. Soc., Bethesda, MD, 1079 p.

Jones, C. M., K. H. Pollock, A. Ehtisham, and W. Hinkle.

1990. Assessment of the black drum recreational fishery, 1989, in Virginia. Old Dominion Univ. Res. Found. Tech. Rep. 90-2. Norfolk, VA, 100 p.

Joseph, E. B., W. H. Massmann, and J. J. Norcross.

1964. The pelagic eggs and early larval stages of the black drum from Chesapeake Bay. Copeia 2:425-434.

Kimura, D. K.

1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77:765-776.

Littell, R. C., R. J. Freund, and P. C. Spector.

1991. SAS system for linear models, 3rd ed. SAS Institute, Inc., Cary, NC, 329 p.

Murphy, M. D., and R. G. Taylor.

1989. Reproduction and growth of black drum, *Pogonias cromis*, in northeast Florida. Northeast Gulf Sci. 10:127-137.

Music, J. F., and J. M. Pafford.

1984. Population dynamics and life history aspects of major marine sportfishes in Georgia's coastal waters. Georgia Dep. Natural Resources, Coast. Div. Contrib. Ser. 38: 1-382.

Osburn, H. R., and G. C. Matlock.

1984. Black drum movement in Texas Bays. N. Am. J. Fish. Manage. 4:523-530.

Pearson, J. C.

1929. Natural history and conservation of redfish and other commercial sciaenids on the Texas coast. Bull. U.S. Bur. Fish. 44:129-214.

Pereira, D. L., C. Bingham, G. R. Spangler, D. J. Conner, and P. K. Cunningham.

1995. Construction of a 110-year biochronology from sagittae of freshwater drum (*Aplodinotus grunniens*). In D. H. Secor, J. M. Dean, and S. E. Campana (eds), Recent developments on fish otolith research, p 177-196. Univ. South Carolina Press, Columbia, SC.

Rawlings, J. O.

1988. Applied regression analysis: a research tool. Wadsworth, Inc., Belmont, CA, 553 p.

Richards, W. E.

1973. Age, growth and distribution of black drum (*Pogonias cromis*) in Virginia. Trans. Am. Fish. Soc. 102:584-590.

Richards, C. E., and M. Castagna.

1970. Marine fishes of Virginia's eastern shore (inlet and marsh, seaside waters). Chesapeake Sci. 11:235-248.

Ricker, W. E.

1975. Computations and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Canada 191, 382 p.

Robson, D. S., and D. G. Chapman.

1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181-189.

Ross, J. L., J. S. Pavela, and M. E. Chittenden Jr.

1983. Seasonal occurrence of black drum, *Pogonias cromis*, and red drum, *Sciaenops ocellatus*, off Texas. Northeast Gulf Sci. 6:67-70.

Ross, J. L., T. M. Stevens, and D. S. Vaughan.

1995. Age, growth, mortality, and reproductive biology of red drums in North Carolina waters. Trans. Am. Fish. Soc. 124:37-54.

Royce, W. F.

1972. Introduction to the fisheries sciences. Academic Press. New York, NY, 351 p.

SAS (Statistical Analysis System).

1988. SAS/STAT user's guide, 6.02 ed. SAS Institute Inc., Cary, NC, 1028 p.

Scott, W. B., and M. G. Scott.

1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219, 731 p.

Silverman, M. J.

1979. Biological and fisheries data on black drum, *Pogonias cromis* (Linnaeus). NOAA, Natl. Mar. Fish. Serv. Tech. Rep. 22. Sandy Hook Laboratory, Northeast Fisheries Center. Highlands, NJ, 35 p.

Thomas, D. L., and B. A. Smith.

1973. Studies of young of the black drum, *Pogonias cromis*, in low salinity waters of the Delaware Estuary. Chesapeake Sci. 14:124-130.

Van Oosten, J.

1929. Life history of the lake herring (*Leucichthys artedi* Le Sueur) of Lake Huron as revealed by its scales with a critique of the scale methods. Bull. U.S. Bur. Fish. 44:265-428.

Wells, B. K.

1994. Reproductive biology of Chesapeake Bay black drum, *Pogonias cromis*, with an assessment of fixatives and stains for histological examination of teleost ovaries. M.S. thesis, Old Dominion Univ., Norfolk, VA, 67 p.

Welsh, W. W., and C. M. Breder Jr.

1923. Contributions to the life histories of Sciaenidae of the eastern United States coast. Bull. U.S. Bur. Fish. 39:141-201.