# Age, Growth, Mortality, and Reproductive Biology of Red Drums in North Carolina Waters

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Abstract.--Red drums Sciaenops ocellatus were sampled in North Carolina waters from October 1987 through December 1990. Ages determined from sectioned otoliths were validated by lengthfrequency and marginal-increment analyses, and the recapture of oxytetracycline-marked fish. Fish growth was rapid during the first 5 years, after which annual growth increments were much smaller. Growth was best described by a continuous double von Bertalanffy growth curve, with a transition age of 4.4 years;  $K_1$ , the growth coefficient for fish younger than the transition age, was 0.30/year and  $K_2$ , the growth coefficient for fish older than the transition age, was 0.07/year. Maximum observed age and size were 56 years and 1,250 mm fork length (FL) for males and 52 years and 1,346 mm FL for females. Fifty-percent maturity was attained among males by age 2 at 621-640 mm FL and among females by age 3 at 801-820 mm FL. Spawning occurred from August through early October in estuarine waters of Pamlico Sound and nearshore ocean waters close to barrier island inlets. Commercial and recreational landings increased during the 1980s, with most of the harvest composed of immature, age-1 fish caught during the fall. Unadjusted annual return rates (18-25%) for tagged juveniles were high. Annual survival rates based on tag-recapture data were only 6-24%, and estimates of instantaneous total mortality rates (Z) from cohort-based catch curves were 1.56-2.88 for the 1985-1988 year-classes. The relative abundance of 20-55-year-old red drums has declined 90% since 1968-1972.

The red drum Sciaenops ocellatus is an estuarine-dependent species, occurring from Massachusetts to Key West, Florida, on the U.S. Atlantic coast and from southwest Florida to northern Mexico in the Gulf of Mexico (Lux and Mahoney 1969; Mercer 1984). Red drums supported a commercial fishery during the 1930s as far north as New Jersey, but since 1950 annual landings north of Virginia have been less than 1 metric ton (Mercer 1984). Currently, commercial fisheries along the Atlantic coast are virtually nonexistent, except in North Carolina. Florida has prohibited the sale of red drum, South Carolina recently established it as a game fish, and Georgia regulations prohibit the taking of red drum with nets (SAFMC 1990). Strict regulatory measures have been enacted throughout the Gulf of Mexico to reduce the likelihood of overfishing (Murphy and Taylor 1990).

Red drums are sought by recreational anglers throughout North Carolina's coastal waters. The surf and inlets from Oregon Inlet to Cape Lookout and the shoals and river mouths in Pamlico Sound support a trophy fishery that has produced 10 of the 16 current world records; 8 of the 10 record fish exceeded 25 kg. The current all-tackle record red drum (43 kg) was caught from the Hatteras Island surf (IGFA 1992).

Red drums attain their largest reported sizes in North Carolina, but we found no published age and growth research for these waters. Similarly, collections of juvenile red drums in North Carolina indicated that spawning occurs during summer and early fall (Weinstein 1979; Mercer 1984), but detailed information on reproductive biology is unavailable. Along the Atlantic coast, red drum growth has been described in Georgia (Pafford et al. 1990), South Carolina (Wenner et al. 1990), and Florida (Murphy and Taylor 1990); spawning seasonality and maturity have been described for South Carolina (Wenner et al. 1990) and the east coast of Florida (Murphy and Taylor 1990). In this paper, we validate an aging procedure and describe age and growth, maturity schedules, and spawning seasonality for red drum in North Carolina waters.

High mortality and tag-return rates have been reported for Georgia, Florida, and South Carolina (Music and Pafford 1984; Murphy and Taylor 1990; Wenner et al. 1990). Stock assessments for the southern Atlantic coast have indicated that subadult red drums are overfished (Vaughan and Hel-



FIGURE 1.—Locations in coastal North Carolina where red drums were collected or tagged and released during 1986–1990 (DMF is Division of Marine Fisheries).

ser 1990; Vaughan 1992). Therefore, in this paper we also address the size and age composition and exploitation patterns of the recreational and commercial fisheries, and describe mortality rates of red drums in North Carolina waters.

#### Methods

Age and growth.—Red drums were collected from October 1987 through December 1990 throughout North Carolina coastal waters. Most collections were from Pamlico Sound and its tributaries, and from the surf and inlets of the Outer Banks between Oregon Inlet and Cape Lookout (Figure 1). Red drums were captured by hook and line, gill nets, pound nets, commercial trawls, and long haul seines. Fork length (FL, mm) was recorded for all fish and is used for all lengths mentioned in text unless otherwise noted. Total length (TL) was recorded in 1989 and 1990, and whole weight (W) to the nearest 0.1 kg was obtained when possible.

Otoliths (sagittae) were excised and stored dry. A Buehler Isomet low-speed saw with diamond wafering blades was used to cut 0.4-0.7-mm-thick transverse sections of the sagittae through the core. Sections were mounted on a microscope slide with Accu\*mount mounting medium. Sections were read by two authors independently by means of a dissecting microscope ( $20 \times$  magnification) with reflected light; a common reading was conducted to resolve differences.

Validation of ages from otoliths followed three criteria provided by Bagenal (1978). The percent occurrence of opaque margins on otoliths was plotted by month to determine the timing of annulus formation (Beckman et al. 1989). Red drums (N= 118) captured with hook and line were injected with oxytetracycline (OTC; 25 mg/kg body weight), tagged, and released from 1988 through 1990. Sections of the sagittae from recaptured OTC-marked fish were viewed under ultraviolet light to determine how many opaque zones were deposited since the time of release. Finally, monthly length-frequency modes were compared to lengths of otolith-determined age-groups.

The ages of red drums were adjusted because the first annulus formed 19–21 months after the actual hatching date. September 1 was used as a biologically realistic birthdate because it was the midpoint of the peak-spawning period. Ages were incremented 1 year on this date.

Growth of red drums was described by fitting a continuous double von Bertalanffy growth curve to data by a nonlinear, iterative, least-squares approach (Vaughan and Helser 1990). The model was fit to observed lengths at age for 839 red drums by means of the PROC NLIN procedure with Marquardt option (SAS Institute 1987). Each age was adjusted to account for the month of capture based on a September 1 birthdate; for example, fish captured in October were considered 1/12 year older than their assigned otolith age. A weighting scheme, based on the inverse of sample size for each age, was used to decrease the impact of large sample sizes of young fish.

Reproductive biology.-Gonads from 805 red drums were excised and stored in 10% buffered formalin from 1988 through 1990. Before examination, gonads were removed from the preservative, washed, and blotted dry. Sex was determined and gonads were weighed to the nearest 0.1 g. Ovaries and testes were staged macroscopically, and stage confirmation was made by histological examination of 29% of the gonads. Medial sections of preserved gonadal tissue were transferred to 50% isopropyl alcohol, processed through a Technicon Duo II tissue processor, and blocked in paraffin. Sections (7  $\mu$ m thick) were cut from each gonad with a rotary microtome, stained with Harris's hematoxylin, and counter-stained with eosin Y.

Characteristics of the developmental stages were based on the macroscopic and histological features described by Murphy and Taylor (1990), but modified by merging their "immature" and "resting virgin" stages into a stage called "immature," and their "spent" and "recovering" stages into a stage called "spent." The developmental stages are thus: (1) immature, (2) maturing, (3) well developed (mature), (4) ripe (gravid), (5) partially spent, (6) spent, and (7) resting. Mature fish were those in stages 3–7.

Gonadosomatic index (GSI) was calculated by using the formula: GSI =  $(GW/FL^3)100$ , where GW = preserved gonad weight (g) and FL = fork length (cm). Because many of the samples were obtained from filleted carcasses, fork length was used instead of body weight to develop a GSI. The Statistical Analysis System (SAS Institute 1985) was used for maximum-likelihood analysis (PROBIT) to generate 50% maturity schedules.

Tag-recapture data.—In all, 3,002 red drums were tagged and released in estuarine waters from 1986 to 1990. Fish were captured in commercial pound nets, anchored gill nets, and runaround gill nets set in Pamlico Sound grass flats adjacent to Hatteras and Ocracoke islands and in the Pamlico, North, and New rivers (Figure 1). All healthy red drums were measured, tagged, and released. Fish ranged from 223 to 880 mm, but 98% were 220– 500 mm (10–15 months old). In 1986, Floy cinchup tags and Floy internal anchor tags were used. after which only Floy internal anchor tags were used. Tags were uniquely numbered and included a legend indicating that a reward would be given for tags returned to the North Carolina Division of Marine Fisheries (DMF). Internal anchor tags were inserted into a small abdominal incision made above the midventral line, just beyond the posterior extension of the pelvic fin. Cinch-up tags were inserted dorsally and just posterior to the termination of the second dorsal fin.

Fishery and mortality rates.—Data for red drum catches in North Carolina were obtained from several sources: fishery-specific length frequencies from the DMF biological database (1979 to present); commercial landings from the North Carolina General Canvas Data compiled through the DMF and National Marine Fisheries Service (NMFS) cooperative data collection program (1970 to present); and length-frequency and catch-per-unit-effort (CPUE, catch/trip) data for recreational catches from the North Carolina Marine Recreational Fisheries Statistics Survey (MRFSS; 1987–present).

The Seber (1970) and Robson and Youngs (1971) tag recovery model was selected to estimate a series of survival rates from a sample of fish captured, tagged, and released into the population at roughly the same time each year for five consecutive years (Ricker 1975). To fit the model, only fish of the previous year's cohort that were tagged from July through December were included; this was also the period for first-year recoveries; succeeding recovery periods were the entire year. The number of recaptured fish per year was adjusted for nonreporting, tagging mortality, and tag loss. Cohort-specific survival (S) and exploitation rates (u) were estimated with the computer program ES-TIMATE, which uses the maximum-likelihood method for estimating parameters (Brownie et al. 1985).

Total mortality (Z) was also estimated by catch curve analysis (Ricker 1975). Annual catch in weight was converted to annual catch in numbers at age by the use of length-frequency data by year and gear and annual age-length keys for 1986– 1990. Catch in weight was converted to catch in numbers based on mean weight of red drums estimated from length-frequency data. Catch estimates (both commercial and recreational) and recreational length-frequency data represented North Carolina and Virginia (>95% from North Carolina). Ages 0–5 were included; age 6+ was created by pooling ages 6 and older. Cohort-specific total



FIGURE 2.—Monthly percent occurrence of opaque zones on the margins of red drum otoliths from North Carolina waters, 1987–1990. Total monthly sample sizes ranged from 0 to 251 (sample sizes were less than 10 in January and February).

mortality rates were calculated for the 1985–1988 year-classes. Thus, Z for the 1985 year-class was based on catches of age-1-5 fish from 1986 through 1990, whereas Z for the 1988 year-class was based only on catches of age-1-2 fish during 1989–1990. Red drums were considered fully recruited to both fisheries at age 1. The methods of Boudreau and Dickie (1989) and Pauly (1979) were used to estimate natural mortality (M).

#### Results

#### Age, Growth, and Size and Age Composition

We collected sagittae from 843 red drums (250– 1,346 mm) from 1987 through 1990. Sections had well-defined and easily interpreted translucent and opaque bands. Readers agreement was 97% after the first counting and 100% after the second counting; four sagittae (0.5%) could not be read.

The first opaque zone appeared during the second spring, when fish were 19–21 months old, based on the September 1 birthdate. Marginal-increment analysis confirmed the recurring formation of opaque zones during March-May. During this time 90–100% of the otoliths for all age-classes had opaque margins (Figure 2).

Monthly length-frequency distributions of red drums shorter than 900 mm exhibited 2-3 modes that represented ages 0, 1, or 2. The modes generally corresponded to the lengths of fish with the

same otolith-determined ages (Figure 3). Convergence of modes after age 2 prevented discrimination of older age-groups.

periodicity of opaque zone The annual formation was confirmed by the recapture of red drums injected with OTC. Otoliths from 4 of 118 chemically marked fish were recovered. The OTC mark was on the margin of the sectioned sagittae from two fish at large less than 1 month. A third fish (1,090 mm) was released November 1989 and recaptured August 1990; a fourth fish (1,295 mm) was released November 1989 and recaptured October 1990. The OTC marks on both appeared on the outer margin of a translucent zone beyond which were one opaque and one translucent zone. This zonation confirmed that one opaque zone formed annually during the spring on red drum otoliths. These fish were 40 and 38 years old, respectively, when recaptured.

Red drums grew rapidly during their first 5 years, after which annual growth was much slower; fish attained a maximum age of 56 years (Table 1; Figure 4). Variation within ages was considerable; 1,000--1,100-mm fish were ages 8-52; 1,100-1,200-mm fish were ages 14-56, and 1,200-1,300-mm fish were ages 40-52. The world record red drum (1,499-mm FL; 42.7 kg) was 53 years old, whereas the 55- and 56-year-old fish in this study were 1,165 and 1,145 mm, and each weighed less



FIGURE 3.—Monthly length-frequency distributions of red drums sampled from North Carolina coastal waters, 1979–1990. Horizontal lines represent the observed ranges of lengths for red drums of ages 0-3 each month for which fish were aged by otoliths. Ages were advanced 1 year on September 1.

than 30 kg. Males ranged from 395 to 1,250 mm and from ages 0 to 56. Females ranged from 397 to 1,346 mm and from ages 0 to 52.

Growth was best described by a continuous double von Bertalanffy curve (Vaughan and Helser

1990) for both sexes pooled. The regular von Bertalanffy curve produced a distinct pattern of residuals—underpredicting for ages 2–6 and the oldest ages, and overpredicting for ages 9–23 (Figure 4). Separate double von Bertalanffy growth curves

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TABLE 1.—Predicted and mean observed fork lengths (FL, mm) for red drums sampled in North Carolina, 1987–1990. Sample sizes (N) are in parentheses. Predicted lengths are from the continuous double von Bertalanffy curve.

	Development	Observed FL				
Age	Predicted _ FL	Mean (N)	Range			
0	279	312 (35)	250-400			
ł.	457	421 (123)	271-718			
2	639	647 (197)	518-763			
3	774	752 (74)	641-855			
4	875	835 (31)	733-940			
5	885	889 (10)	859-933			
6	903	904 (9)	791-940			
7	920	911 (13)	870-978			
8	936	965 (13)	890-1,090			
9	951	937 (15)	895-991			
10	965	972 (24)	915-1,050			
11	978	986 (14)	917-1,050			
12	990	967 (35)	880-1,050			
13	1,002	987 (4)	965-1,003			
14	1,012	1,023 (17)	965-1,194			
15	1,022	1,022 (42)	959-1,120			
16	1,032	1,014 (40)	928-1,168			
17	1,030	1,020 (56)	740-1.118			
18	1.049	1,004 (19)	752-1,085			
19	1,056	1,017 (10)	955-1,085			
20	1,063	1,087 (2)	1,075-1,100			
21	1,070	1,070(1)				
22	1,076	1,030(1)				
23	1,082	1,086 (2)	1,0821,090			
24	1,087	1,104 (4)	1,065-1,150			
25	1,092	1,170(1)				
26	1,097					
27	1,101	1,080(1)				
28	1,105	1,122 (2)	1,110-1,135			
29	1,109	1,090 (2)	1,030-1,050			
30	1,113	1,121 (1)				
31	1,116	1,160(1)				
32	1,119					
33	1,122	1,111 (1)				
34	1,125	1.100 (2)	1.070-1.130			
35	1,127	1,150 (4)	1,107-1,194			
36	1,130	1,137 (5)	1,065-1,193			
37	1,132	1,100 (2)	1,060-1,140			
38	1,134	1 120 (3)				
39	1,136	1,139 (3)	1,115-1,183			
40	1,138	1.218 (2)	1,090-1,346			
41	1.140	1,086(1)				
42	1,141	1.104.41				
43 44	1,143	1,194 (1)				
44 45	1,144 1,145	1 125 (2)	1,130-1,140			
4.2	1,145	1,135 (2)	1,150-1,140			
	1,148	1,140 (4)	1,110-1,181			
47 48	1,148	1,140(4)	1,110-1,181			
40	1,149	1,162 (3)	1,090-1,250			
49 50		1,162 (3)	1,020-1,200			
	1,151	1,146 (2)	1 127 1 166			
51 52	1,151 1,152	1,146 (2)	1,137-1,155 1,090-1,220			
52 53	1,152	1.10.7 (.2)	1,070-1,220			
54	1,155					
54 55	1,154	1,165(1)				
55 56	1,154	1,165 (1)				
	1,120	1,145(1)				

were generated for males (N = 329) and females (N = 340). The five parameters from each growth curve were tested, based on their multivariate normal distribution, by initially computing the Hotelling's  $T^2$ -statistic (2.20) and its corresponding F-statistic (0.44) (Morrison 1967; Bernard 1981). Because the computed F-statistic does not exceed the tabled value at P = 0.05 (F  $\sim 2.21$ ; df = 5 and 663), there are no significant differences among the set of underlying parameters describing growth for the two sexes. The double von Bertalanffy growth curve generated for sexes pooled (Figure 4; Table 1) melds two separate regular von Bertalanffy growth curves at  $t_x$  (transition age) = 4.4 years, with  $K_1 = 0.30$ /year,  $K_2 = 0.07$ /year,  $t_1$ = -0.33 year,  $t_2 = -15.4$  years, and  $L_x = 1.163$ mm.

The age composition of red drums sampled from 1988 through 1990 included fish from age 0 to age 56, with 29–34 age-groups represented annually (Figure 5). Age-0–3 red drums accounted for 51% of the combined samples, ages 4–10 for 14%, ages 11-20 for 28%, and ages 20–56 for 6%. In addition to the expected peaks for age-0–3 fish, two other modes were recurrent each season: ages 10 and 13–17 in 1988; ages 11 and 14–18 in 1989; and ages 12 and 15–19 in 1990. Also recurrent were modes representing ages 34–35 in 1988, ages 35–36 in 1989, and ages 36–37 in 1990. This annual progression of age-groups probably reflects strong year-classes and provides further validation of the annual formation of a single opaque zone.

The persistence of strong year-classes in the adult population was also apparent when age composition data for 1968-1972 (W. Foster, North Carolina State University, unpublished) and 1987-1990 were compared (Figure 6). Old red drums in recent samples matched the prevalent 1936–1937, 1940–1942, and 1951–1954 year-classes in the 1968–1972 distribution. The strong year-classes of 1932–1933 were represented by 55- and 56-year-old fish in recent samples.

The weight-length and fork length-total length regressions for red drums in North Carolina are presented in Table 2. Because there was no significant difference between males and females for weight and fork length (F = 0.19; P > 0.66), the sexes were combined.

### Maturity, Spawning Season, and Spawning Grounds

Unsexed, immature specimens were 250-627 mm long and 0-1 years old. The overall sex ratio



FIGURE 4.—Means (boxes) and ranges (vertical lines) of observed fork lengths (FL) of red drums from North Carolina coastal waters, 1987–1990, including comparison of predicted lengths from a regular (single) von Bertalanffy growth curve ( $L_c = 1.114$  mm FL, K = 0.19/year,  $t_0 = -1.48$ ) and a double von Bertalanffy growth curve ( $L_c = 1.163$  mm FL,  $K_1 = 0.30$ /year,  $K_2 = 0.07$ /year,  $t_1 = -0.33$  year,  $t_2 = -15.4$  years,  $t_x = 4.4$  years). The single growth curve is derived from the formula  $L_t = L$ ,  $[1 - e^{-K(t-t_0)}]$ , where  $L_c$  = asymptotic length, K = growth curves for fish younger and older than a transitional age ( $t_x$ ), described by the formula:  $t_x = (K_2t_2 - K_1t_1)/(K_2 - K_1)$ , where  $K_1$  and  $t_1$  are for fish younger than the transitional age and  $K_2$  and  $t_2$  are for fish older than the transitional age.

(349 males:373 females) was not significantly different from 1:1 ( $\chi^2 = 0.80$ ; P > 0.99).

Female red drums in North Carolina waters mature by age 4 (Table 3). No age-0-2 females exhibited vitellogenesis, but 57% of the age-3 and 100% of the age-4 females were mature. Only 14% of the age-3 females had mature (well-developed) ovaries, but 43% were considered mature because their ovaries contained postovulatory follicles or exhibited atretic activity during early fall. The smallest female with ovaries undergoing late-stage vitellogenesis was 773 mm, although a 733-mm female was classified spent. Maximum-likelihood estimates (PROBIT analysis, Murphy and Taylor 1989) of 20-mm increments indicated that 50% were mature at 801-820 mm. All females larger than 860 mm were mature. Two old females (ages 49 and 51) were senescent, with ovaries severely atrophied and oogenic tissue absent; however five other old females (ages 40-52) caught between October and June were spent or resting.

Males matured at an earlier age and smaller size than females (Table 3). Earliest spermiogenesis was observed in an age-1 (23-month-old) male. The youngest ripe male was age 2. More than 50% of the males were mature by age 2, and all were mature by age 3. Spermiogenesis was observed in a 520-mm male, and the smallest ripe male was 700 mm. Fifty percent maturity for males was reached at 621-640 mm (PROBIT), and all males larger than 740 mm were mature.

Peak spawning occurred in August and September, based on maturity stages and gonadosomatic indices (GSI). Gonadogenesis began as early as May in one male and one female, and was exhibited by 52% of the males and 77% of the females by July (Figure 7). Well-developed gonads were observed in females and males July through September. Ripe males were found during August through early October, and two ripe females were collected in August and September. Partially spent fish were collected during September and early



FIGURE 5.—Annual age composition of red drums sampled from North Carolina coastal waters, 1988-1990.

October. In all 3 years, GSI maxima for both sexes occurred in August and September, with the exception of August 1989, when only two small females were collected (Figure 8).

Ripe and partially spent males, with well-developed, ripe, and partially spent females were found in estuarine and nearshore ocean waters. During August and September, ripe males and well-developed females (N = 34) were caught at the mouth of the Pamlico River, in bays between the Pamlico and the Neuse rivers, and in Pamlico Sound, 5-8 km inside of Hatteras and Ocracoke inlets over deep grass flats or channels. Catches of adults from these waters declined during October, but those remaining (N = 5) were all partially spent or spent. During that period, schools of large red drums found 5-10 km offshore of Hatteras Inlet and Ocracoke Island, and red drums



FIGURE 6.—Frequency of cohorts represented in samples of adult red drums (5-56 years old) captured at Cape Hatteras, North Carolina, during 1968-1972 (Foster, unpublished) and in North Carolina coastal waters north of Cape Lookout during 1987-1990.

caught around the outer bars of Hatteras, Ocracoke, and Drum inlets consisted of well-developed, ripe, and partially spent males and females. By September, most (67%) of the adults caught around the inlets were spent. As the number of adults found in estuarine waters declined in October, they became more prevalent around the outer bars of each inlet, and virtually all were spent.

# Fisheries and Size and Age Composition of the Catches

Commercial landings of red drums in North Carolina increased from a mean of 37,681 kg/year during the 1970s to a mean of 91,598 kg/year during the 1980s (Figure 9). Landings were dominated by long-haul seine catches during the 1970s and by gill-net catches during the 1980s. Red drums are a marketable bycatch of most inshore gears but are targeted during the fall with gill nets. Peak landings occurred August through November when the previous year's cohort attained legal size (357 mm FL) and recruited to most gears.

Annual recreational landings of red drums in North Carolina ranged from 40,735 to 146,514 kg (26,258 to 109,469 fish) during 1987 through 1990

Least squares equation	N	Range of lengths	r <sup>2</sup>
$Log_{10}W = -8.008 + 3.035log_{10}FL$	182	250-1.346 mm	0.99
$Log_{10}W = -7.792 + 2.935log_{10}FL$	97	280-1.270 mm	0.99
FL = 25.933 + 0.914TL	586		0.99
TL = -23.00 + 1.087FL	586		0.99

TABLE 2.—Log weight-log length and fork length-total length regressions for red drum in North Carolina; W = weight (kg); FL = fork length (mm); TL = total length (mm).

(DMF, 1987 MRFSS survey, unpublished). Landings were low in 1990 following a severe freeze in December 1989.

Red drums captured by both commercial and recreational fisheries were typically small fish. From 1979 to 1990, 80% of the red drums sampled from commercial catches were 341-460 mm and were caught during late summer or early fall when 10-16 months old; only 4% were greater than 812 mm. From 1987 through 1990, 55-76% of the fish sampled from recreational catches were less than 460 mm; fish greater than 812 mm made up only 2-6% of the samples during 1987-1989, but 16% during 1990.

TABLE 3.—Percent maturity of male and female red drums in specified size-classes and age-classes. Fish captured from September through December were included in the previous age-class to maintain year-class integrity through a spawning season. Number of fish sampled (N) is in parentheses.

	Percent maturity (N)						
Class	Unknown sex	Males	Females				
Fork length (m	im)						
≤400	0 (65)						
401-500	0(18)	0(2)	0(3)				
501-550	0(2)	20 (10)	0(12)				
551-600	0(1)	21 (24)	0(12)				
601-650	0(4)	54 (28)	0 (29)				
651~700		52 (31)	0 (46)				
701-750		86 (22)	8 (25)				
751-800		100 (15)	10 (20)				
801-850		100 (17)	54 (13)				
851-900		100 (15)	93 (14)				
901-950		100 (58)	100 (54)				
951-1,000		100 (89)	100 (117)				
>1,000		100 (89)	100 (117)				
Age (years)							
0	0 (80)	0(1)	0(3)				
1	0(7)	31 (49)	0 (40)				
2	0(1)	67 (70)	0 (93)				
2 3		100 (23)	57 (21)				
4		100 (6)	100 (10)				
5		100 (3)	100 (4)				
6		100 (7)	100 (5)				
7		100 (5)	100 (8)				
8		100 (4)	100 (5)				
9		100 (15)	100 (12)				
10		100 (3)	100 (9)				
>10		100 (135)	100 (125)				

The year-class composition of adult (age-4+) red drums sampled off Cape Hatteras from 1987 through 1990 differed dramatically from samples taken during 1968–1972 (Foster, unpublished; Figure 6). Age-20 and older fish accounted for 67% of the adults in 1968–1972, but only 6.4% of the adults in 1987–1990. There were 46 year-classes represented in 1968–1972 (N = 191) and 40 year-classes in 1987–1990 (N = 381).

#### Tag-Recapture Data and Mortality Rates

The short distance-of-movement patterns of red drums justified treating North Carolina as a closed system for estimating survival rates from tag-recapture data. Of the 1,113 subadult and adult red drums tagged in North Carolina waters and recaptured between 1984 and 1990, 99.7% were caught in coastal or estuarine waters of North Carolina; one age-1 fish and two adults were caught in Virginia waters (Ross and Stevens 1992).

Recapture rates for late age-0 and early age-1 red drums in commercial and recreational fisheries were very high. Tag return rates for the 1985–1989 year-classes of red drums that were tagged when 10–15 months old (July–December) ranged from 18 to 25% by the end of the calendar year they were tagged and from 21 to 28% through 1990 (Table 4). After adjusting the data 50% to allow for nonreporting (Pafford et al. 1990) and 20% for initial tag loss and tagging mortality (Gutherz et al. 1990), the recapture rates by cohort, as the cohorts initially recruited to the fisheries (August– December), ranged from 46 to 62% during the calendar year they were tagged (Table 4).

Total instantaneous mortality rates (Z) for subadult red drums were estimated from both tagrecapture data and catch curve analysis. Estimates of S for the 1985–1989 year-classes, based on the Seber (1970) and Robson and Youngs (1971) tag recovery model, ranged from 6 to 24%; first-year exploitation rates were 46–62% (Table 5). Thus, estimates of Z (=log<sub>e</sub>S) ranged from 1.44 to 2.74 (Table 6). Year-class-specific estimates of Z from catch curves for North Carolina (Table 6) waters ranged from 1.56 (1985) to 2.88 (1988).



FIGURE 7.—Monthly frequency of occurrence of gonad developmental stages of mature red drums sampled in North Carolina waters during 1987–1990.

Because of the longevity of the red drum, natural mortality can be expected to vary with age, in part because fish have fewer predators as they grow, and because adults and juveniles have different habitats (ASMFC 1990; Vetter 1988). We tried two methods to generate more than one estimate of M to reflect a nonconstant M. Natural mortality from Pauly's (1979) equation, with which we used the

double von Bertalanffy growth parameters  $L_{\infty}$ ,  $K_1$ , and  $K_2$  and an average annual water temperature of 19°C (Williams et al. 1973) was 0.47 for ages 0-5 and 0.18 for ages 6-56. These estimates, particularly for ages 0-5, seemed biologically unreasonable for red drum, which has a 56-year life span and few predators after age 1.

An alternative method, based on life history,



FIGURE 8.—Monthly mean gonadosomatic indices (GSI) for red drums, exclusive of immature (stage-1) fish, sampled in North Carolina from May 1988 through December 1990. Monthly sample sizes were 1-51 females and 1-70 males. (Female sample sizes were less than 5 in July, August, October, and December 1988; June and August 1989; and March, May, and October 1990. Male sample sizes were less than 5 in June and July 1988; June 1989; and March, April and July, and November 1990.)



FIGURE 9.—Annual commercial landings of red drum in North Carolina from 1970 through 1990 (source: North Carolina General Canvas Data from cooperative NMFS and DMF collection program) and recreational red drum landings from 1979 to 1990 (source: Marine Recreational Finfish Statistics Survey).

TABLE 4.—Recapture rates of tagged 10–15-month-old red drums from 1985–1989 year-classes by commercial and recreational fishing in North Carolina under two scenarios. Scenario 1: no adjustment for tag loss, tagging mortality, and nonreporting. Scenario 2: a 20% adjustment for initial tagging mortality and tag loss (Gutherz et al. 1990) and a 50% adjustment for nonreporting (Pafford et al. 1990). Year-classes were tagged and released during the following calendar year.

,			Recapture	es by end of ye	ar released	Overall recaptures through 1990			
Year-class (year released) and scenario	Number tagged		Number returned	Adjusted number recaptured	Percent recaptured	Number returned	Adjusted number recaptured	Percent recaptured	
1985 (1986)	1,459		329			410			
Scenario 1		1,459		329	22.6		410	28.1	
Scenario 2		1,167		658	56.4		820	70.3	
1986 (1987)	427		79			100			
Scenario 1		427		79	18.5		100	23.4	
Scenario 2		342		158	46.2		200	58.5	
1987 (1988)	733		142			171			
Scenario 1		733		142	19.4		171	23.3	
Scenario 2		586		284	48.5		342	58.4	
1988 (1989)	270		55			58			
Scenario I		270		55	20.4		58	21.5	
Scenario 2		216		110	50.9		116	53.7	
1989 (1990)	.36		9			9			
Scenario 1		36		9	25.0		9	25.0	
Scenario 2		29		18	62.1		18	62.1	
All	2,925		614			748			
Scenario 1		2,925		614	21.0		748	25.6	
Scenario 2		2,340		1,228	52.5		1,486	56.8	

that provides age-specific estimates of natural mortality from mean weight at age, was suggested by Boudreau and Dickie (1989). This method, applied to weakfish *Cynoscion regalis* (Seagraves 1992) and red drums (Vaughan 1992), sets M =2.88 ×  $W^{-0.33}$ . W being weight converted to kilocalories. With mean weight at age for red drum estimated from age-length data, the following agespecific estimates of M were obtained: 0.41 at age 0, 0.29 at age 1, 0.18 at age 2, 0.15 at age 3, 0.13 at age 4, 0.13 at age 5, and a mean of 0.11 for ages 6–56 (range, 0.13–0.09). The mean of 0.22 for ages 0–5 is a more reasonable estimate of Mthan 0.47 from Pauly's (1979) equation and was thus used to estimate fishing mortality.

The instantaneous fishing mortality rates (F) for subadult red drums were estimated by three methods. The difference between Z (from both catch curves and tag-recapture data) and M produced similar estimates of F for three of four year-classes (Table 6). Estimates of F from year-class-specific exploitation rates (u; Ricker 1975, equation 1.11) generated by the tag-recapture model of Brownie et al. (1985) ranged from 1.06 to 1.49. These values were lower than those estimated by the difference between Z and M. Underestimating tag loss, tagging mortality, and tag nonreporting could all result in underestimating F.

#### Discussion

#### Age and Growth

Sagittae are valid structures for determining the age of red drums in North Carolina. The formation of the first annulus during the second year and yearly annulus formation thereafter during the late winter or early spring occurs in red drums sampled along the U.S. southeast Atlantic coast (Pafford et al. 1990; Wenner et al. 1990) and in the Gulf of Mexico (Beckman et al. 1989; Murphy and Taylor 1990). Direct validation of annuli in adults, based on recaptured OTC-injected fish, was extended by this research from 27-year-olds (Murphy and Taylor 1991) to at least 40-year-olds. The annual progression of strong year-classes in 1987-1990 North Carolina age composition data and the correspondence of old red drums captured during 1987-1990 with strong year-classes hatched in the 1930s and 1940s (Foster, unpublished) would occur only if aging were valid and mortality rates were equal across adult cohorts over time.

Red drums grow rapidly during their first 4-5 years, after which growth slows as both sexes attain full maturity. This pattern of growth was reported in Florida (Murphy and Taylor 1990) and South Carolina (Wenner et al. 1990). The growth equations were not significantly different between

TABLE 5.—Bias-adjusted maximum-likelihood estimates of annual survival rates (S) and exploitation rates (u) based
on recapture matrix of red drums tagged when 10-15 months old, partitioned by year-class (1985-1989) and year of
release (1986-1990) in North Carolina waters. Number of fish tagged is adjusted for 20% tag loss and release mortality:
number of recaptures is adjusted for 50% nonreporting of recaptured tags.
Adjusted

Year Year class released	Adjusted number of fish	number Adjusted numbers of recentured fish in:				in:	Survival rate		Exploitation rate		
	tagged	1986	1987	1988	1989	1990	S	SE	u	SE	
1985	1986	1,167	658	154	4	2	2	23.69	2.05	56.38	1.45
1986	1987	342		158	36	4	2	13.82	1.98	46.20	2.70
1987	1988	586			284	54	4	18.78	2.47	48.46	2.06
1988	1989	216				110	6	6.45	1.95	50.93	3.40
1989	1990	29					18			62.07	9.01

the sexes, which confirms the findings of Vaughan and Helser (1990) for pooled south Atlantic red drum data. No differences in growth rates were found between sexes for 1–3-year-old red drums in Florida (Murphy and Taylor 1990), although Beckman et al. (1989) generated growth models that predicted larger females than males.

Growth was best described by a continuous double von Bertalanffy growth curve, which fits rapid early growth with slower growth in later years and joins them in a continuous curve at some transition age (Vaughan and Helser 1990). This model was biologically reasonable because the transition age separated two distinct growth stanzas and corresponded with full maturity for both sexes as well as the adoption of an adult migratory pattern (Ross and Stevens 1992).

Red drums attain their largest size and maximum life span in waters between Cape Lookout and the Virginia barrier islands. The predicted  $L_x$  (1,163 mm), the observed maximum lengths for males (1,250 mm) and females (1,346 mm), and the world record (1,499 mm FL) exceed maximum

TABLE 6.—Summary of estimates of red drum mortality rates in North Carolina, based on catch curve analysis and tag-recapture data.

Year- class	total n	taneous nortality e (Z)	Instan-	Incta	ntancous fis	hing
	Tag-re-		natural	moi		
	Catch curve (Z <sub>1</sub> )	capture data (Z <sub>2</sub> )	mortality rate (M <sup>a</sup> )		$Z_2 - M$	$\frac{Z_2 u^k}{A}$
1985	1.56	1.44	0.22	1.34	1.22	1.06
1986	1.92	1.98	0.22	1.70	1.66	1.06
1987	2.49	1.67	0.22	3.27	1.45	1.00
1988	2.88	2.74	0.22	2.66	2.52	1.49

<sup>a</sup> Mean *M* for ages 0-5 are from age-specific estimates of *M* from mean weight at age (Boudreau and Dickie 1989; Vaughan 1992).

<sup>b</sup> A tag-recapture model (Ricker 1975, equation 5.3b) was used to calculate *u*; *A* is the actual total mortality.

sizes reported from South Carolina to Texas (Table 7). The oldest fish we sampled were 55 and 56 years old, essentially the same as the maximum ages (56 and 57 years) reported off North Carolina during 1968–1972 (Foster, unpublished). Black drums *Pogonias cromis* have been reported to live at least 58 years (Murphy and Taylor 1989).

The existence of the oldest and largest red drums in the higher latitudes of their range (North Carolina and Virginia) is not unique. Conover (1990) noted that the maximum growth potential for fish may vary inversely with the duration of the growing season. The evolutionary basis for this phenomenon in subadults may be an adaptive response to size-selective winter mortality in more temperate climates (Conover 1990). The attainment of larger maximum sizes and greater longevity may result from increased metabolic costs for reproduction in warmer southern waters (Edwards 1984). Countergradient variation in growth rate was noted for striped bass Morone saxatilus and American shad Alosa sapidissima (Conover 1990), weakfish (Shepherd and Grimes 1983), and Atlantic croaker Micropogonias undulatus (White and Chittenden 1977). The possibility that red drums move to more northern portions of their range during their lifetimes is unlikely. No fish tagged between Florida and South Carolina have been recaptured as adults in North Carolina or Virginia, nor have red drums tagged south of Cape Lookout been recaptured north of Cape Hatteras (Pafford et al. 1990; Wenner et al. 1990; Ross and Stevens 1992).

# Maturity, Spawning Seasonality, and Spawning Grounds

Male red drums mature at earlier ages and smaller sizes than females. In North Carolina, more than 50% of the males were mature at age 2 and 100% were mature by age 3. This corresponds with red

		Oldest	fish	Largest fish				
State (source)	Age	Length	Sex	Date	Weight (kg)	Length	Date	
Virginia (Claude Bain, Virginia Marine Re- sources Commission)		None reported			38.6	1,397 mm TL	1981	
North Carolina (North Carolina Division of Marine Fisheries)	56	1,145 mm FL	м	Oct 1992	42.6	1,499 mm FL (53 years old)	Nov 1984	
South Carolina (Charles Wenner, South Carolina Wildlife and Marine Re- sources Department)	38	1,095 mm TL	F	Oct 1986	34.0		1965	
Georgia (John Pafford, Georgia Department of Natural Resources)	40	1,057 mm FL	м	Nov 1989	21.5	1,066 mm FL	1986	
Florida (Michael Murphy, Florida Department of Natural Resources)	35	1,050 mm FL	м	Dec 1982	26.7		Aug 1983	
Louisiana (Charles Wilson, Louisiana State Univer- sity)	38	1.030 mm FL	F	1990	34.9		Apr 1975	
Texas (Robert Colura, Texas Parks and Wild- life Department)	35	1.055 mm TL	м	1988	23.5	1,284 mm TL	Nov 1967	

TABLE 7.—Maximum reported ages and sizes of red drums (TL is total length; FL is fork length; M is male; F is female).

drums in South Carolina, where most males matured by the beginning of their third year (36 months; Wenner et al. 1990), and Florida, where all males were mature by age 3 (Murphy and Taylor 1990). In North Carolina, 50% of the females were mature at age 3 and 100% were mature by age 4 (>860 mm FL). Similarly, off South Carolina (Wenner et al. 1990) and in the northern Gulf of Mexico (Wilson et al. 1989), initial maturity was reported at age 3, and most females were mature during their fourth year. On the east and west coasts of Florida, females mature at a smaller initial size, but the length at 50% maturity (825–900 mm FL) was similar to those from North Carolina (Murphy and Taylor 1990).

The peak spawning season for red drums in North Carolina waters is August and September. This was corroborated by recruitment of juveniles (10-30 mm) during September-October in statewide estuarine trawl and seine surveys (Ross and Stevens 1992). This confirms speculations of mid-August to October spawning off Chesapeake Bay and in the South Atlantic by Pearson (1929) and Mansueti (1960) and is similar to the spawning season off South Carolina (Wenner et al. 1990). Spawning occurs off both coasts of Florida during September and October (Murphy and Taylor 1990) but may begin in July (Peters and McMichael 1987) and cease in early November (Johnson and Funicelli 1991). In the Gulf of Mexico, red drums spawn from mid-August through mid-October off Louisiana (Wilson et al. 1991), but possibly as late as February off Texas (Matlock 1984).

The presence of gravid and spent adults along the outer bars of inlets and in nearshore ocean waters conforms with observations that red drums from Chesapeake Bay to the east coast of Florida spawn in coastal waters of the Atlantic (Mansueti 1960; Tagatz and Dudley 1961; Yokel 1966). Red drums in South Carolina and Georgia waters leave the estuaries upon reaching maturity to spawn in the sea (Music and Pafford 1984; Wenner et al. 1990). In the Gulf of Mexico, spawning occurs along the beaches, often in the vicinity of passes, and in open waters along the Gulf side of the barrier islands from Florida to Texas (Yokel 1966; Matlock 1984; Murphy and Taylor 1990).

Red drums also spawn in the estuarine waters of North Carolina. Schools of adults occur from August through early October over specific shoal and channel sites in Pamlico Sound near Hatteras and Ocracoke inlets, and around the mouths of bays and rivers in western Pamlico Sound. Virtually all fish caught from these schools were in spawning condition. Spawning in estuarine waters is atypical for the species but not unique. A recently spawned female was caught 7 km inside the mouth of Tampa Bay, Florida (Murphy and Taylor 1990). Plankton tows, coupled with the presence of spawning females far from inlets (Murphy and Taylor 1990; Johnson and Funicelli 1991), indicated spawning in Mosquito Lagoon, Florida, where sonic tracking detected little directed movement of adults during the spawning season (Carr and Smith 1977). This conforms with our observations that the schools of red drums in estuarine waters of North Carolina remained in the same locations for several weeks during August and September.

#### Fishery and Mortality Rates

Recapture rates of tagged subadults by the commercial and recreational fisheries were extremely high, indicating intense fishing pressure. Unadjusted annual (18–25%) and overall (21–28%) return rates for juvenile red drums in North Carolina waters were as high as rates from South Carolina to Texas, or higher. Over a 5-year period, 6–16% in South Carolina (Wenner et al. 1990) and 17– 40% in Georgia (Pafford et al. 1990) were recaptured by the end of the tagging year. In the Gulf of Mexico, annual tag return rates were 11-25%in Florida (Murphy and Taylor 1990) and 8-13%for subadult red drums in Texas lagoons (Green et al. 1985).

Unadjusted recapture rates for red drum were higher than for all other species tagged in North Carolina's coastal waters. Return rates for summer flounder Paralichthys dentatus and southern flounder P. lethostigma were 6% overall and 3-13% annually during a 5-year study (R. Monaghan, DMF, personal communication). Both species were subjected to intensive recreational or commercial fishing pressure, or both, and summer flounder were assessed to be overfished (MAFMC 1990). Tagged Atlantic croakers, which were commercially harvested throughout the year and exhibited signs of growth overfishing, were returned at an overall rate of 3% (1-9% annually; D. DeVries, NMFS, personal communication). Only tag return rates for striped bass were as high as those for red drum. Stocked and tagged juvenile striped bass were returned at an annual rate of 7-29% from 1981 through 1987 and reflected a severely overfished population during the early and mid-1980s (S. Winslow, DMF, personal communication).

Very high estimates of total mortality indicated low survival of female red drums to maturity. Total mortality from both catch curve and tag-recapture data for the 1985–1988 year-classes translates to only 6-24% annual survival. The strong yearclasses of 1982 and 1985 were followed by high commercial landings in 1983–1984 and 1986– 1987. Thus, the contribution of recent year-classes to the adult population, compared with the 1971– 1973 and 1978 year-classes, was low.

Annual survival rates of subadults in North Carolina were as low or lower than reported in the U.S. south Atlantic or Gulf of Mexico. Survival rates from cohort-based catch curves in South Carolina and Georgia were 6-29% and 15-43%, respectively (Vaughan and Helser 1990). In Florida waters, survival rates were 2-13% for 2-4-yearolds in the Gulf of Mexico and 24-50% for 2-6year-olds in Mosquito Lagoon (Murphy and Taylor 1990). Subadult annual survival rates were 12-20% in Texas lagoons, based on tag-recapture data (Green et al. 1983). The populations were considered overexploited in all cases, and strict management measures were recommended. Survival rates in North Carolina waters were similar to the overall rates estimated for the south Atlantic (16-19%; Vaughan and Helser 1990).

Continued excessive fishing pressure on subadult red drums in North Carolina could ultimately reduce the spawning stock below levels sufficient to maintain the population. Vaughan and Helser (1990) estimated that the spawning stock ratio for 1986–1988 ranged from 2 to 3%, well below the South Atlantic Fishery Management Council's goal of 30% (SAFMC 1990).

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