Abstract.—Sagittae (n=2,263) and gonads (n=870) from snowy grouper, *Epinephelus niveatus*, caught primarily with longlines, Kali poles, snapper reels, and chevron traps off North Carolina and South Carolina were examined 1) to compare growth rates, population age structure, and sex ratio between two periods 1979–85 and 1993–94, and 2) to determine reproductive seasonality, size and age at maturity, and size and age at sex change. There were several indications that the population off North Carolina and South Carolina is overfished: 1) size at age of specimens caught with longlines and snapper reels has increased noticeably since the 1980s (possibly a a density-dependent population response to a high level of fishing mortality); 2) 81% of the fish caught with commercial longlines during 1993–94 were ages 1–6, the majority (56%) of which were immature females; 3) the percentage of males in the population appears to have decreased significantly, from 7–23% in the 1970s and 1980s to 1% in the 1990s; and 4) mean length of fish landed in the longline fishery has steadily decreased from 65–80 cm in the early 1980s to 50–60 cm in the mid-1990s. There was a positive trend between water depth and total length in fishery-independent samples. Histological examination of gonads revealed that mature gonads were present in 4% of the females at age 3, 52% at age 5, 95% at age 7, and 100% at ages >7 during 1993–94. The smallest mature female was 469 mm TL, and the largest immature female was 575 mm. Estimates of $Length_{50}$ and Age_{50} were 541 mm (95% CI=529–553 mm) and 4.92 yr (95% CI=4.65–5.21 yr), respectively. Spawning females were caught during April through September on the upper continental slope off South Carolina at depths of 176–232 m. The size (767–1090 mm) and age (8–29 yr) of 97 male specimens and the capture of two specimens undergoing sex change provided conclusive evidence that snowy grouper are protogynous hermaphrodites.

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Growth, population age structure, and aspects of the reproductive biology of snowy grouper, *Epinephelus niveatus*, off North Carolina and South Carolina*

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The snowy grouper, *Epinephelus niveatus*, is a commercially important deepwater species that occurs in the western Atlantic from North Carolina (Cape Hatteras) to Brazil, including the Gulf of Mexico and the Bahamas (Smith, 1971). It also occurs in the eastern Pacific from California to Mexico (Miller and Lea, 1976; Fitch and Schultz, 1978). Along the coast of the southeast United States, adult snowy grouper are predominantly found on the upper continental slope (>75 m; Lee et al., 1985) at depths of 116–259 m (Low and Ulrich, 1983; Moore and Labisky, 1984; Parker and Ross, 1986), whereas juveniles are more common at shallower depths (Moore and Labisky, 1984). Low and Ulrich (1983) noted a positive correlation between total length (TL) and water depth off South Carolina. Most fishing for this species occurs in habitats characterized by rocky ledges, cliffs, and swift currents (Matheson and Huntsman, 1984).

Snowy grouper are captured primarily in commercial fisheries of the southeastern United States (Parker and Mays, 1998). Most are caught with bottom longlines and snapper reels[1] (handlines). Starting in 1991, the longline fishery was restricted to waters deeper than 91 m by the South Atlantic Fishery Management Council (SAFMC, 1991). Fishing for snowy grouper has occurred off North Carolina and South Carolina (the Carolinas) since the mid-1950s (Huntsman, 1976); annual landings from the Carolinas averaged 119,657 kg during 1981–96 (Moran[2]). According to the spawning stock ratio (SSR), the population off the Atlantic coast of the United States is considered to be overfished (SAFMC, 1993).

Population age structure and individual growth rates in the snowy grouper population have not been assessed since the mid-1980s and should be assessed again given the sustained fishing pressure on the population. Studies of other fish populations have shown that size at age is often affected by the level and duration of exploitation (Haug and Tjemsland, 1986; Harris and McGovern, 1997; Helser and

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1 Snapper reels are commonly known as "bandits" or "one-armed bandits" by fishermen owing to the remote similarity between early snapper reels and gambling slot machines, and because luck is involved in what is caught. The early mechanical reels have typically been replaced by 12 volt DC automobile starter motors or hydraulic systems.

2 Moran, J. 1996. S. Carolina Dept. of Natural Resources, P.O. Box 12559, Charleston, SC 29422. Personal commun.

Almeida, 1997; Zhao et al., 1997; Goodyear and Schirripa[3]), thus trends in growth can be indicators of population stability. Additionally, nothing is known about trends in sex ratio. Recent studies along the southeast Atlantic coast and in the Gulf of Mexico have documented sharp decreases in the proportion of males in other grouper, gag (*Mycteroperca microlepis*) and scamp (*M. phenax*), populations (Coleman et al., 1996; McGovern et al., 1998). This and other factors have led to reduced genetic diversity in the gag population along the southeast coast, a cause for serious concern, although the ramifications are not clearly understood (Chapman et al., 1999).

Little is known about the reproductive biology of snowy grouper off the Carolinas because the only previous study (Moore and Labisky, 1984) was conducted in the Florida Keys. Using a histological technique, Moore and Labisky (1984) showed that the snowy grouper is a protogynous hermaphrodite; females reach sexual maturity at ages 3–5 and change to males as early as age 6. The objectives of the present study were 1) to compare individual growth rates, population age structure, and sex ratio between two periods, 1979–85 and 1993–94, and 2) to determine reproductive seasonality, size and age at maturity, and size and age at sex change for snowy grouper off the Carolinas.

Materials and methods

Specimen acquisition

Snowy grouper were obtained from commercial boats, research vessels, and headboats, primarily off North Carolina and South Carolina (Table 1). All specimens were collected between 31°09'N and 34°44'N at depths of 42–302 m. Only seven specimens were caught south of 32°04'N. Fishery-independent samples were collected during cruises of the MARMAP (Marine Resources Monitoring Assessment and Prediction) program with bottom longlines, Kali poles (an off-bottom longline; Russell et al., 1988), snapper reels, rods and reels, and chevron traps (Collins, 1990). Specimens caught with longlines were collected primarily off South Carolina, whereas specimens caught with snapper reels were collected off South Carolina in the 1980s and primarily off North Carolina in the 1990s (Fig. 1). Total length (mm) was measured for all specimens and all length measurements in the text refer to total length (TL).

During 1993–94, samples from the commercial fishery usually included the total catch of snowy grouper from a vessel or a random subsample; on three of 20 occasions, the catches from vessels that landed fish in South Carolina were subsampled to collect otoliths from small and large specimens. No documentation on sampling design was available for fishery-dependent samples that were collected with snapper reels during 1979–85.

Age and growth

The left sagitta, and the right sagitta when time permitted, was removed and stored dry prior to processing. Each otolith was embedded in paraffin (1979–85) or Araldite epoxy resin (1993–94) and sectioned along a dorsoventral plane through the focus with a single high-concentration diamond wheel on a Buehler Isomet low-speed saw. Otolith sections were mounted on glass slides with Crystalbond thermoplastic or Accu-mount 60, covered with cedar wood oil, and examined under a dissecting microscope (10–63×) with reflected and transmitted light.

We examined otoliths from 1937 specimens and used the age determinations (n=326) of Waltz[4] for specimens collected with snapper reels from 1979 to 1985. The width of the translucent zone along the margin of the section was measured to assess the periodicity of increment formation. Increments were counted independently by two readers for 1853 of 1937 specimens. In older fish, all increments could not be counted along one axis in many specimens. Counting commenced on one of three axes (ventral, ventromedial, or adjacent to the sulcus acousticus) and shifted to another axis by following an increment to the new axis. If counts differed, both readers examined the otolith by projecting the image onto a TV monitor. The otolith was rejected if agreement could not be reached.

A small portion (n=129) of the 1937 otoliths that we examined were used for an earlier MARMAP study (Waltz[4]). Age assessments were compared to determine if annual increment structure was being interpreted in a similar manner. The specimens selected for the comparison were collected with longlines or Kali poles on research cruises during 1982–85. Age data from specimens collected with these two gear types were combined because they were fished simultaneously in the same area and were deployed with the same hook type and bait.

The sagittae of three young-of-the-year (YOY) specimens were hand-polished to thin (approx. 5µm)

[3] Goodyear, C. P., and M. J. Schirripa. 1993. The red grouper fishery of the Gulf of Mexico, Report MIA 92/93-75. Miami Laboratory, Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Dr., Miami, FL 33149.

[4] Waltz, W. 1986. The size and age of snowy grouper (*Epinephelus niveatus*) in the South Atlantic Bight. MARMAP Analytical Report, 16 p. S. Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422.

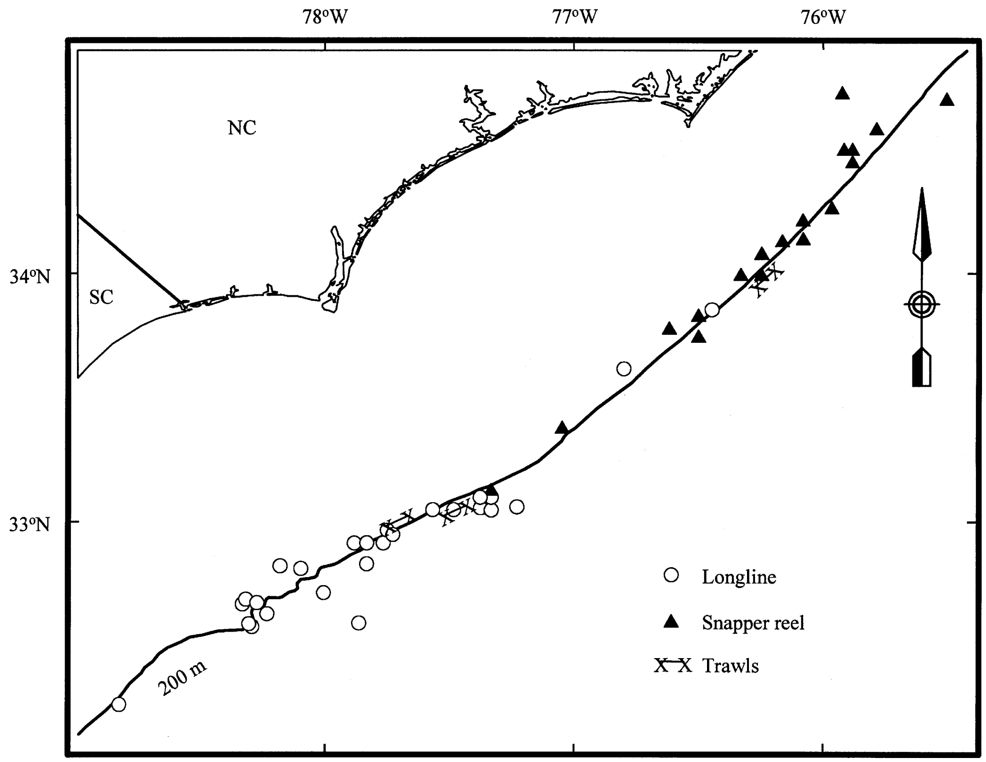

Figure 1

Approximate locations of commercial fishing effort with longlines and snapper reels for snowy grouper off North Carolina and South Carolina between June 1993 and September 1994. Snowy grouper were also caught in trawls in June 1978 during an exploratory squid cruise conducted by the government of Spain and the National Marine Fisheries Service on the RV *Pescapuerta Segundo*. Trawl site off Georgia is not shown.

Table 1

Numbers of specimens of snowy grouper for which otoliths and gonad samples were examined by gear type. C = commercial landings; H = headboats sampled by National Marine Fisheries Service, Beaufort, North Carolina; R = research cruises conducted by Marine Resources Monitoring Assessment and Prediction Program (MARMAP).

Gear	Source	Period	Otoliths	Gonads
Snapper reel	C, R	1979–85	326	309
Longline and Kali pole	most R, C	1982–85	190	180
Rod and reel	most H, R	1973–81	0	90
Other	C, R	1980–84	0	10
Snapper reel	C	1991–95	335	32
Longline	C	1993–94	1332	146
Chevron trap	R	1991–95	78	100
Other	R	1993–95	2	3
Total			2263	870

transverse sections according to the methods of Secor et al. (1992) and examined with a compound microscope. We counted the regular concentric rings, similar to those reported as daily growth increments in other species, to estimate age. Assumed daily rings were visible, with the exception of a large opaque core area, on the smallest otolith but were only distinguishable at discrete locations on the other two otoliths. For these two otoliths, age was estimated by extrapolating the increment count per unit distance to the total radial measurement of the ventral axis, excluding the core. Radial measurement from the core to the first annulus was made for a subsample of 23 specimens that were age 1 and compared with the measurements from the three YOY to establish the position of the first annulus.

Age-length keys were formed by obtaining a matrix of numbers at age by length interval for each gear type (longline and snapper reel) in two periods (1980s and 1990s). Besides the differing selectivities of longlines and snapper reels, another reason for developing keys by gear type was the difference in sampling area in 1993–94 (Fig. 1) and potential differences in sampling depth due to the restriction (SAFMC, 1991) that limits the use of longlines to waters deeper than 91 m. Additional keys were generated to address two questions: 1) Do data from specimens with age estimates of lower precision affect the accuracy of the key for specimens caught with longlines in the 1990s? and 2) Are there differences in the keys for specimens caught with longlines or Kali poles during 1982–85 that were examined in the present study and in an earlier study by Waltz?[4] To address the first question, keys based on all specimens and specimens for which there was a difference of 0–1 increments between readers were compared.

All analysis of age and growth data was conducted with SAS software (SAS Institute, Inc., 1990). Fisher's exact test (Siegel, 1956) was used to compare the age distributions of two age-length keys by 25-mm length intervals. The FREQ procedure was used to run this test. A comparison was made only if each key had >6 specimens in an interval because of the low power associated with small sample sizes (Bennett and Hsu, 1960). The large number of tests required to compare age-length keys necessitated compensating for experimentwise error by computing an adjusted significance level (α^*) using the formula presented by Hayes (1993).

Nonlinear regression analysis with Marquardt's algorithm (NLIN procedure) and the NLIN weight statement were used to fit the von Bertalanffy growth model to observed length at age data (von Bertalanffy, 1938). Lengths were weighted by the inverse of the number of fish at each age to moderate the effect of large and small sample sizes on the estimates of growth parameters. Age-length keys were applied to length data collected through the Trip Interview Program (TIP) in the Carolinas to generate an age-frequency distribution. TIP is a commercial fisheries data collection program funded by the National Marine Fisheries Service (NMFS).

Reproduction

Gonads were obtained during 1979–95 from 870 specimens collected on research cruises and from fish landed whole by fishermen (Table 1). Ninety gonad samples from the headboat fishery during 1973–1981, collected in association with the study of Matheson and Huntsman (1984), were obtained from the Beaufort Laboratory of the NMFS. The posterior portion of the gonad was fixed in 10% seawater-formalin for 1–2 weeks and transferred to 50% isopropanol for 1–2 weeks. Gonad samples were processed, sectioned, and stained with double-strength Gill hematoxylin and eosin-y by using the methods of Schmidt et al. (1993).

Sex and reproductive state were assessed primarily by one reader using histological criteria (Table 2), without reference to body length or date of capture. A second reader examined sections from 75 specimens to ensure accurate interpretations. If the assessments of the two readers differed, the section was viewed simultaneously by the readers and rejected if agreement could not be reached. Specimens with developing, ripe, spent, or resting gonads were considered sexually mature. For females, this definition of sexual maturity included specimens with oocyte development at or beyond the cortical granule stage and specimens with beta, gamma, or delta stages of atresia (see Hunter and Macewicz, 1985). To ensure that females were correctly assigned to either the immature or resting categories, the length-frequency histogram of females with evidence of certain maturity (e.g. those that were developing, ripe, or spent) was compared with the histograms for immature and resting females. Females of uncertain maturity (Table 2) were excluded from data analyses. To estimate length at 50% maturity (L_{50}) and age at 50% maturity (A_{50}), the PROBIT procedure (SAS Institute, Inc., 1990) was used to fit gompit, logit, or probit models to maturity data in 25-mm length intervals or one year increments. The LOGISTIC procedure was used to determine which model to use in the PROBIT procedure.

Females with hydrated oocytes or postovulatory follicles were considered to be in spawning condition. Macroscopic observations of snowy grouper caught in June 1978 during trawls (Fig. 1) of an exploratory squid cruise conducted jointly by the government of Spain and the Northeast Fisheries Center of NMFS in Woods Hole, Massachusetts, on the RV *Pescapuerta Segundo* were also used to define the area and timing of spawning.

Results

Age and growth

An age was assigned to 91.6% of 1937 otoliths that we examined (Table 1). Otoliths were rejected if the

Table 2

Histological criteria used to determine reproductive stage in snowy grouper (see Hunter and Goldberg, 1980; Wallace and Selman, 1981; Hunter and Macewicz, 1985; Wenner et al., 1986; West, 1990).

Reproductive stage	Criteria
Immature	Previtellogenic oocytes only, no evidence of atresia. In comparison with resting female, most previtellogenic oocytes are <70 µm, area of transverse section of ovary is smaller, lamellae lack muscle and connective tissue bundles and are not as elongate, oogonia are abundant along margin of lamellae, and ovarian wall is thinner.
Developing	Oocytes undergoing cortical granule (alveoli) formation through nucleus migration and partial coalescence of yolk globules.
Ripe	Completion of yolk coalescence and hydration in the most advanced oocytes. Zona radiata becomes thinner.
Developing, recent spawning	Developing stage as described above plus presence of postovulatory follicles.
Spent	More than 50% of vitellogenic oocytes in alpha or beta stage of atresia.
Resting	Previtellogenic oocytes only with traces of atresia possible. In comparison with immature female, most previtellogenic oocytes >70 µm, area of transverse section of ovary is larger, lamellae have muscle and connective tissue bundles, lamellae are more elongate and convoluted, oogonia are less abundant along margin of lamellae, and ovarian wall is thicker and exhibits varying degrees of expansion owing to previous spawning.
Uncertain maturity	Immature or resting. Inactive ovaries, previtellogenic oocytes only. Reproductive stage is uncertain.
Transitional	Proliferation of spermatogonia through limited spermatogenesis within lamellae of resting ovary, accompanied by development of peripheral sinuses in musculature of ovarian wall.

readers could not agree on the age or if the section was not adequate. Ages ranged from 1 to 29 yr and lengths from 226 to 1137 mm. From a subsample (n=274) of 3–10 yr old specimens, we found that the mean width of the sagittal marginal translucent zone was smallest in April and May, indicating the period of increment formation (Fig. 2). The unimodal nature of the data indicated that one increment was deposited per year.

Data from longlines and snapper reels showed that size at age was greater during 1993–94 than during the previous decade (Figs. 3 and 4). Snowy grouper captured with longlines in 1993–94 exhibited a nearly constant growth rate until approximately age 10, after which there was a notable decrease. A similar growth pattern was noted for snowy grouper caught with snapper reels, although the trend was less definitive owing to smaller sample sizes. Estimates of theoretical maximum length (L_∞) were reasonable when compared with maximum observed lengths (Table 3). Data from both gear types indicated that L_∞ has increased 169–231 mm in the last decade. The application of the age-length key for samples caught with longlines during 1993–94 to TIP length data for the same period revealed recruitment to the fishery as early as age 1, and a modal age for recruitment of 5 (Table 4).

The increase in size at age since the 1980s was also evident in comparisons of age-length keys between periods for each gear type. For longline gear, the comparisons in 8 of 8 length intervals exceeded the adjusted significance level (P<0.00639; Table 5). The

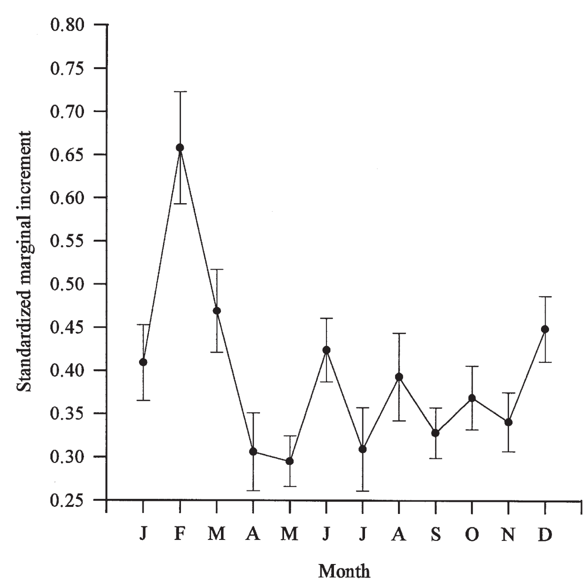

Figure 2

Mean width (±SE) of marginal translucent zone in transverse sections of sagittae from 248 snowy grouper that were 3–10 yr old.

Table 3

Von Bertalanffy parameters (± SE) describing the growth in mm total length of snowy grouper collected with snapper reels and longlines and Kali poles (LL, KP) during two decades. Mean observed length at age data were used to generate parameter estimates. Estimates from two earlier studies, generated using back-calculated lengths, are included for comparison.

Study	Gear and source	Period	n	Maximum observed length	L_∞	k	t_0
Waltz (1986)	Snapper reels commercial, research	1979–85	326	1090	970 (24)	0.109 (0.001)	–2.123 (0.336)
Present	Snapper reels commercial	1993–94	311	1110	1201 (34)	0.103 (0.008)	–1.149 (0.231)
Present	LL, KP, research	1982–85	163	1034	948 (28)	0.122 (0.017)	–0.668 (0.681)
Present	LL, commercial	1993–94	1218	1137	1117 (13)	0.119 (0.004)	–1.409 (0.121)
Matheson and Huntsman (1984)	Hook and line, headboat	1972–79	536	1130	1255	0.074	–1.92
Moore and Labisky (1984)	Hook and line, research	1978–81	118	1180	1320	0.087	–1.013

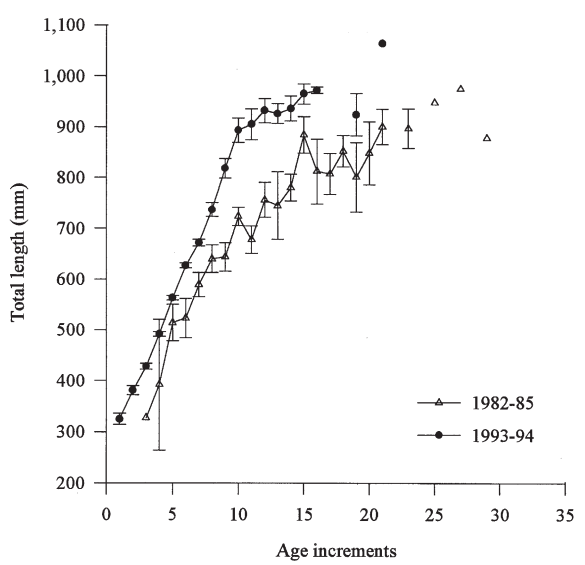

Figure 3

Mean observed size at age (±SE) for snowy grouper collected with longlines and Kali poles during 1982–85 (n=163) and longlines during 1993–94 (n=1,218) off North Carolina and South Carolina.

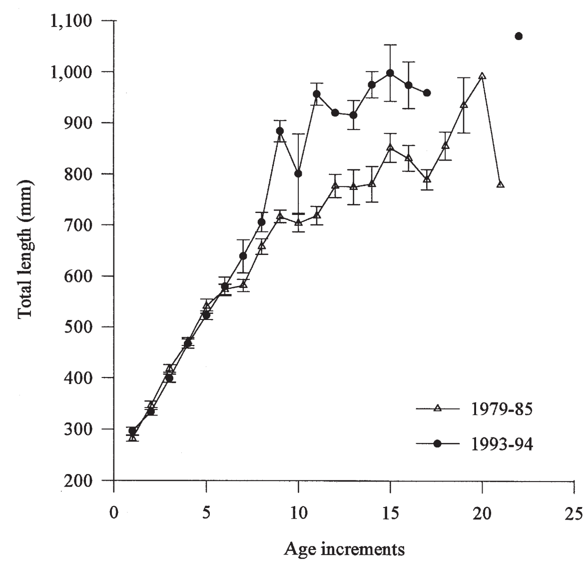

Figure 4

Mean observed size at age (±SE) for snowy grouper collected with snapper reels during 1979–85 (n=326) and 1993–94 (n=311) off North Carolina and South Carolina.

trend was not as strong for snapper reel gear because comparisons in 5 of 13 intervals exceeded the 0.05 level; only one comparison exceeded the adjusted significance level (P<0.00394; Table 5). The age-length keys for the two gear types were very similar in 1993–94 because comparisons in only 3 of 17 intervals exceeded the 0.05 level, none of which exceeded the adjusted significance level (P<0.00284; Table 5).

Initial agreement between independent readers was 24.2% for the 1853 otoliths examined by two readers; however, there was a difference of 0–1 increments between readers for 61.3% of the otoliths. The difference was >1 increment for 30.8% of the otoliths and 7.9% were rejected as uninterpretable. The inclusion in the data sets of age data for otoliths that were difficult to interpret did not affect the assessment of population age distribution for snowy grou-

Table 4

Population age structure of snowy grouper captured with longlines in North Carolina and South Carolina from July 1993 through May 1994. Age-length key was applied to length data from the same period collected during Trip Interview Programs.

Age	Number
1	5
2	32
3	77
4	172
5	209
6	163
7	82
8	23
9	13
10	8
11	6
12	7
13	4
14	2
15	3
16+	3
Total	809

Table 5

Comparison of age distributions by length interval with Fisher's exact test for snowy grouper collected off North Carolina and South Carolina with snapper reels during two periods (1979–85 and 1993–1994), with longlines during two periods (1982–85 and 1993–94), and with longlines and snapper reels during 1993–94. Dashed lines indicate that the sample size was less than seven in one or both groups.

mm TL	Snapper reel, 1979–85 vs. 1993–94	Longline, 1982–85 vs.1993–94	Longline vs. snapper reel, 1993–94
226–250	—	—	—
251–275	—	—	—
276–300	—	—	0.177
301–325	0.570	—	0.841
326–350	—	—	0.074
351–375	0.020	—	0.488
376–400	0.933	—	0.730
401–425	0.057	—	0.407
426–450	1.000	—	0.502
451–475	0.021	—	0.036
476–500	0.630	—	0.595
501–525	0.430	—	0.043
526–550	0.019	—	0.753
551–575	0.001*	—	0.323
576–600	0.209	—	0.972
601–625	0.045	<0.001*	0.200
626–650	—	<0.001*	0.668
651–675	0.064	<0.001*	0.438
676–700	—	<0.001*	—
701–725	—	<0.001*	0.005
726–750	—	0.002*	—
751–775	—	<0.001*	—
776–800	—	—	—
801–825	—	0.003*	—
826–850	—	—	—
851–875	—	—	—
876–900	—	—	—
901–925	—	—	—
926–950	—	—	—
951–975	—	—	—
976–1000	—	—	—
α^1	0.00394	0.00639	0.00284

* $P < \alpha^1$. α^1 = adjusted significance level.

per caught with longlines in 1993–94. Comparisons of age-length keys based on all specimens and specimens for which there was a difference of 0–1 increments between readers revealed a strong similarity in age distribution for 20 intervals (P>0.00256; Table 6).

Slightly less initial agreement was noted when our age estimates were compared with those of Waltz[4] for specimens caught in 1982–85 with longlines and Kali poles. Ages were assigned to 85.3% of 129 specimens that were examined in both studies. The same age was assigned to 18.2% of the specimens and there was a difference of 0–1 increments between studies for 40.0% of the specimens. Although the percent agreement was low, the estimates of mean size at age were similar (Fig. 5). Age distributions in the five length intervals that could be tested were similar (P>0.01021; Table 6). Given the similarity of age distributions, we decided to use the age data of Waltz[4] for snowy grouper caught with snapper reels in 1979–85 without reexamining the otoliths.

The low initial agreement between readers was due to a lack of a readily discernible growth pattern in many otoliths. Typical abnormalities included crystalline areas that obscured increments (Fig. 6A) and rounded opaque deformities that distorted increment spacing (Fig. 6B). In addition, the axis of otolith growth frequently changed direction at least once after 6–7 increments (Fig. 6C). Despite our inability to make linear measurements for back calculations, counts of increments were usually possible, although easily interpreted otoliths (Fig. 6D) were the exception.

We attempted to identify the first annulus 1) by examining daily increment structure in the sagittae of three specimens that were most likely YOY, and

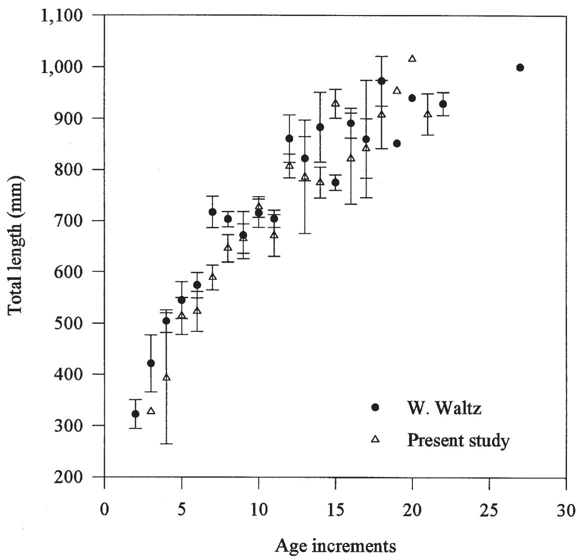

Figure 5

Mean observed size at age (±SE) for snowy grouper caught with longlines and Kali poles in the 1980s. The sagittae were examined by Waltz (n=132; see Footnote 3 in the main text) and investigators in the present study (n=129).

2) by comparing the measurements of otolith radius in these three specimens with the radial measurement to the first annulus in a subsample of 23 specimens that were age 1. Examination of sagittae from YOY revealed that fish lengths of 37, 156, and 172 mm were associated with estimated ages of 35, 159–201 and 191–291 days, respectively. Radial measurement to the edge in these three otoliths was less than the radial measurement to the first annulus in a subsample of 23 age-1 specimens.

Reproduction

Histological examination of 599 sexually mature snowy grouper in four data sets from three periods (1970s, 1980s, and 1990s) suggested that the number of males in the population has substantially decreased. The percentage of males was 7.2%, 19.5%, and 22.9% for samples collected with hook and line during 1973–81, snapper reels during 1980–84, and longlines and Kali poles during 1982–85, respectively, whereas males represented 1.2% of samples collected with longlines during 1993–94 (Table 7). Although sample sizes were <100 for two data sets, especially the 1993–94 data set, the mean total length ($\bar{x}$=63.6 cm, SE=1.0) of specimens in the 1993–94 data set was larger than the mean length of specimens measured through the TIP in North Carolina (1993: $\bar{x}$=58.0 cm, SE=0.6; 1994: $\bar{x}$=56.0, SE=1.4) and South Carolina (1993: $\bar{x}$=59.1, SE=0.7; 1994: $\bar{x}$=53.8, SE=0.6) for the same years, indicating that our data set was not biased toward smaller specimens.

Table 6

Comparison of age distributions by length interval with Fisher's exact test for snowy grouper collected off North Carolina and South Carolina. These comparisons included 1) all specimens that were caught with longlines during 1993–94 and assigned an age versus those for which the difference in age assignment between readers was 0–1 increments (Best), and 2) specimens caught with longlines during 1982–85 that were examined in the present study and by Waltz (Footnote 4 in the main text). Dashed lines indicate that the sample size was less than seven in one or both groups.

mm TL	Best vs. all	Longline, present study vs. Waltz
251–275	—	—
276–300	—	—
301–325	—	—
326–350	1.000	—
351–375	1.000	—
376–400	0.852	—
401–425	0.855	—
426–450	0.980	—
451–475	0.978	—
476–500	0.951	—
501–525	0.853	—
526–550	0.966	—
551–575	0.932	—
576–600	0.997	—
601–625	0.993	0.669
626–650	1.000	0.669
651–675	0.955	—
676–700	0.663	—
701–725	0.832	0.242
726–750	0.943	1.000
751–775	0.902	0.660
776–800	—	—
801–825	1.000	—
826–850	0.795	—
851–875	—	—
876–900	—	—
901–925	—	—
926–950	—	—
951–975	—	—
976–1000		—
α^1	0.00256	0.01021

α^1 = adjusted significance level.

There were ninety-seven males and two transitional specimens in the four sex-ratio data sets.

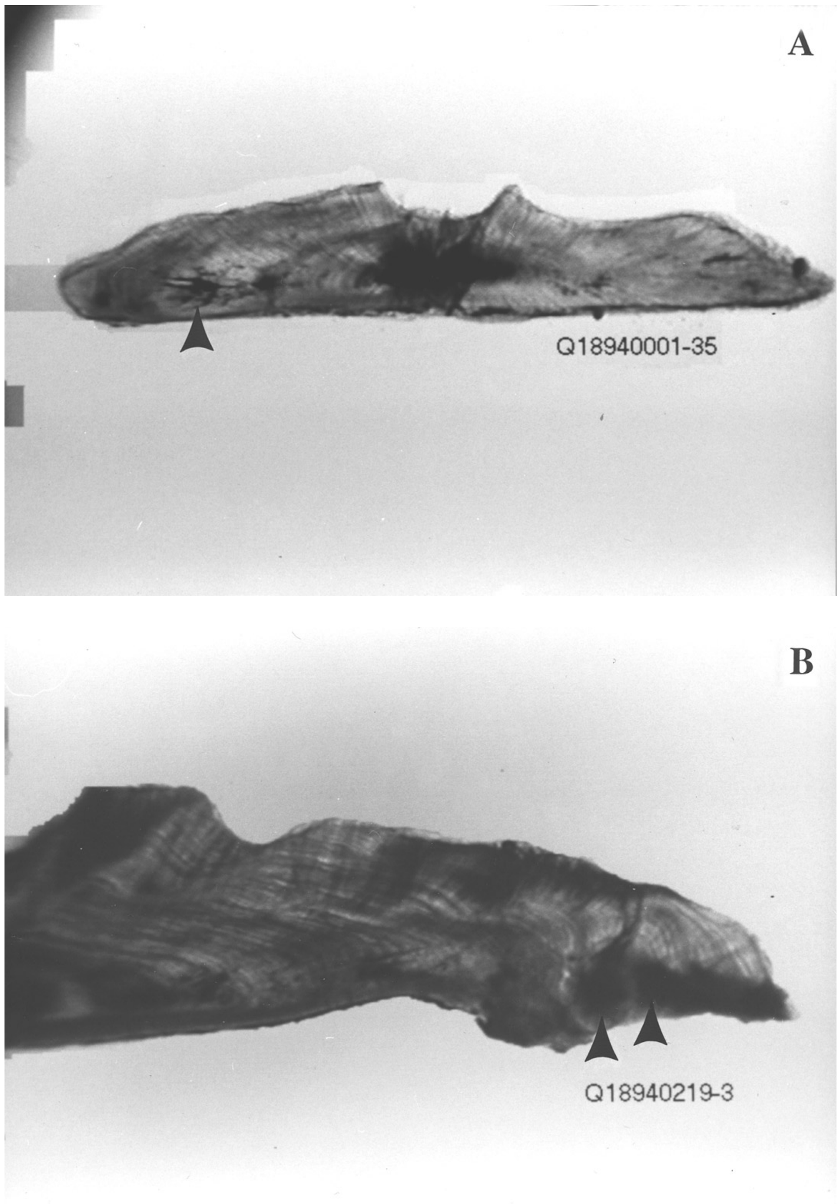

Figure 6

Transverse sections of snowy grouper sagittae displaying (**A**) crystalline area in an age-1 fish that obscures increments, (**B**) opaque deformities (arrows) in an age-5 fish that distort increment spacing, (**C**) change in growth axis in an age-9 fish, and (**D**) easily interpreted increments in an age-6 fish. S = sulcus acousticus axis, VM = ventromedial axis, V = ventral axis.

Males were collected during March through September and their length range was 767–1090 mm (median=918, $\bar{x}$=919 mm, SE=7). Age was assessed for 47 males and ranged from 8 to 29 yr (median=16, $\bar{x}$=16.87, SE=0.63). Transitional specimens (787 mm and unknown age, 1000 mm and age 13) were collected in July and September. The 787 mm specimen was in the latter stage of sexual change (Fig. 7); male tissue was predominant, although previtellogenic oocytes were still numerous.

The near overlap in the length distributions of female snowy grouper that were definitely mature and females that were resting indicated that specimens were correctly assigned to immature and rest-

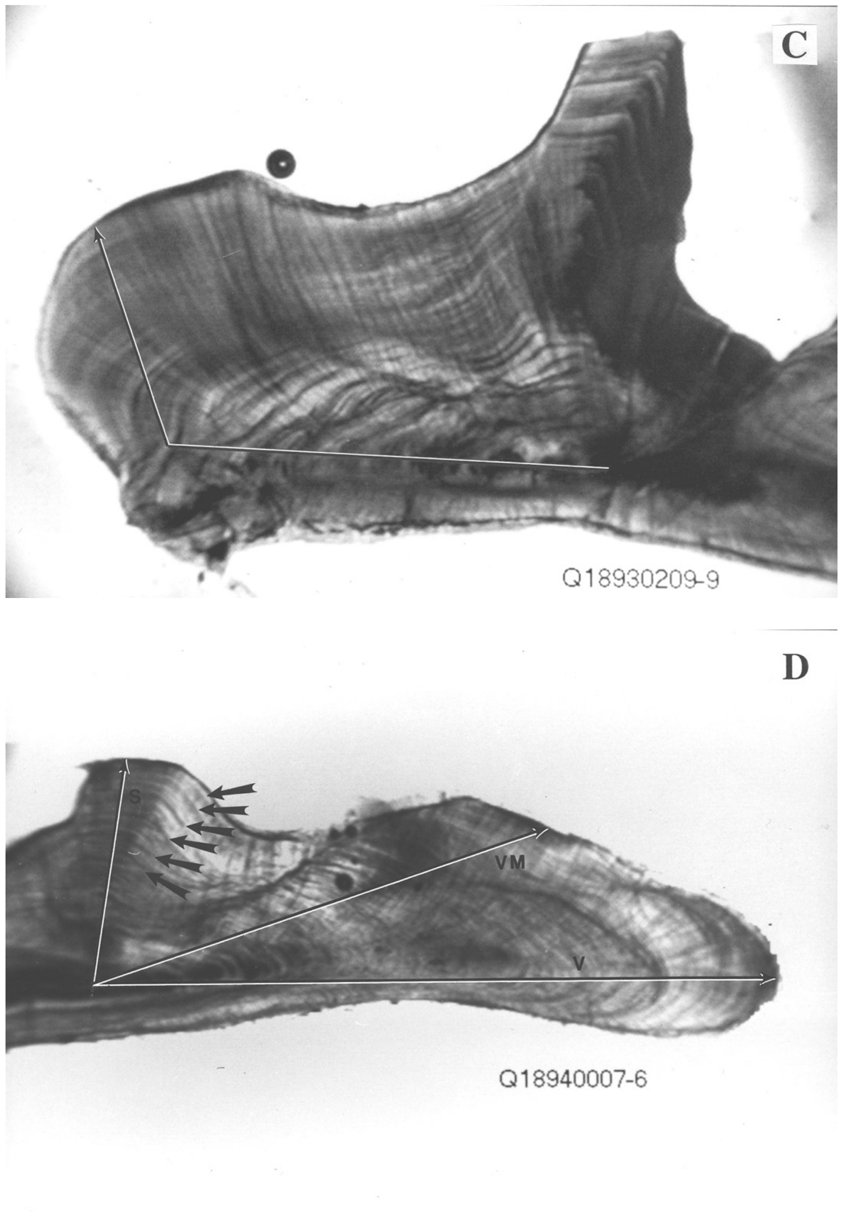

Figure 6 (continued)

ing categories (Fig. 8); only 29 females of uncertain maturity were excluded from analyses. Samples collected primarily with longlines and chevron traps in 1991–95 revealed that snowy grouper become sexually mature at lengths of 451 to 575 mm (ages 3–7; Tables 8 and 9). Mature gonads were present in 4% of females at age 3, 52% at age 5, 95% at age 7, and 100% at ages >7 (Table 9). The smallest mature female was 469 mm, and the largest immature female was 575 mm. Estimates of L_{50} and A_{50} were 541 mm (gompit model; 95% CI=529–553 mm) and 4.92 yr (probit model; 95% CI=4.65–5.21 yr).

Samples collected primarily with bandit reels and longlines in 1980–85 showed that snowy grouper reached sexual maturity at similar lower limits of length and age, 476–500 mm and age 3, although sample sizes were small (<10) in the length and age intervals near the lower limit (Tables 8 and 9). Upper limits of size and age at maturity were higher, 626–650 mm and age 9, during this period and better defined owing to larger sample sizes in comparison to those for 1991–95. Mature gonads were present in 33% of females at age 3, 62% at age 5, 91% at age 7, 95% at age 9, and 100% at ages >9 (Table 9). The smallest

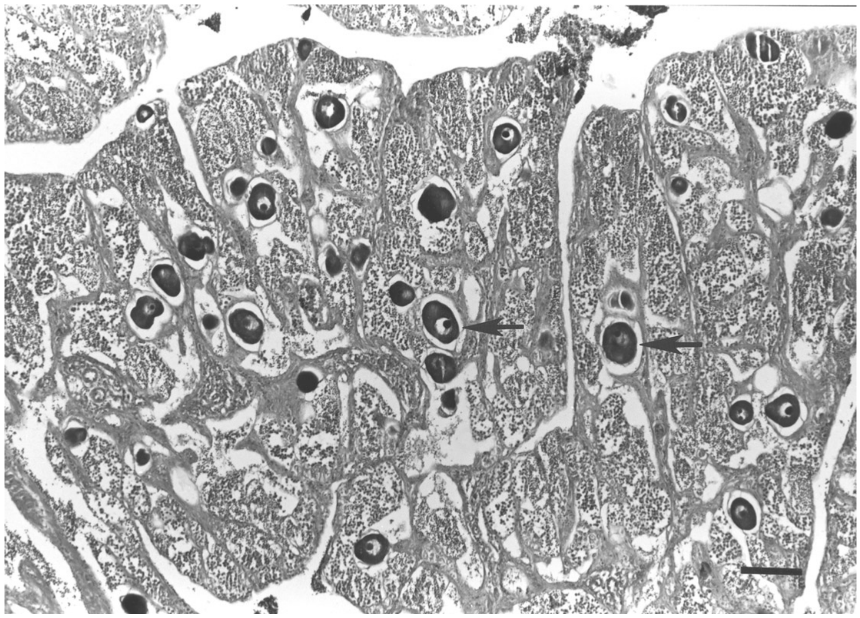

Figure 7

Histological section of gonad tissue from a 787-mm-TL snowy grouper captured in July in which transition to male is nearly completed. Chromatin nucleolar (arrows) and perinucleolar oocytes are still present. Bar = 100µ.

Table 7

Sex ratios of snowy grouper, *Epinephelus niveatus*, (M=male; F=female; T=transitional) collected off North Carolina and South Carolina during 1973–94. Ratios based on sexually mature individuals. LL=longline; KP=Kali pole.

Gear and source	Period	*n*	%*M*	%*F*	%*T*
Rod and reel headboat	1973–81	83	7.2	91.6	1.2
Snapper reels commercial, research	1980–84	281	19.5	80.5	0.0
LL, KP, research	1982–85	153	22.9	76.4	0.7
LL, commercial	1993–94	82	1.2	98.8	0.0

mature female was 483 mm, and the largest immature female was 634 mm. The estimate of L_{50} was 486 mm (logit model; 95% CI=449–509 mm) and A_{50} was not estimated owing to the absence of specimens younger than age 3. A third data set, specimens collected by NMFS during 1973–81 primarily from headboats, exhibited a pattern of size at maturity similar to that found for the 1980–85 samples, though sample sizes were <10 in every length interval and only three specimens were <551–575 mm (Table 8).

Snowy grouper were in spawning condition from April through September based on the presence of hydrated oocytes (Fig. 9A) and postovulatory follicles (Fig. 9B), with no obvious peak period (Fig. 10). Given the small sample sizes for October through March, the spawning season could be longer. Ninety-nine female specimens were captured in spawning condition. Seventy-two percent of the specimens were collected on research vessels off South Carolina (32°28' to 32°50'N) at depths of 176–232 m, primarily during May and July through September. The remaining 27 fish in spawning condition were collected during April through August on headboats off South Carolina, on research vessels off North Carolina between Cape Fear and Cape Lookout, and by commercial fishermen on the upper continental slope off North and South Carolina; exact location data were not recorded. Commercial fishermen reported approximate locations of 32°36' to 33°51'N and depths of 189–302 m for spawning fish.

Trawl collections during exploratory squid cruises in June 1978 also provided evidence that snowy grouper spawn on the upper continental slope (Fig. 1). Four large catches (1160 fish/8776 kg), which were made at depths of 180–316 m off North Carolina, South Carolina, and Georgia (not shown), ranged from 90 to 520 snowy grouper per tow. Tow distance ranged from 7.4 to 18.5 km and estimates of snowy grouper density ranged from 2.2 fish/ha to 10.9 fish/ha (13.5 kg/ha to 79.5 kg/ha). Although the reproduc-

Table 8

Percentage of mature specimens by length interval for female snowy grouper collected off North Carolina and South Carolina with 1) primarily bandit reels and longlines during 1980–85, 2) primarily longlines and chevron traps during 1991–95, and 3) primarily from headboats during 1973–81. Specimens in the developing, ripe, spent, or resting stages were considered mature. All specimens were examined histologically. n = number of specimens.

mm TL	1980–85 n = 372 % (n)	1991–95 n = 235 % (n)	1973–81 n = 74 % (n)
251–275	0 (1)	0 (3)	—
276–300	—	0 (6)	—
301–325	0 (1)	0 (10)	—
326–350	0 (1)	0 (12)	—
351–375	—	0 (10)	0 (1)
376–400	0 (5)	0 (11)	—
401–425	0 (3)	0 (11)	—
426–450	0 (1)	0 (17)	0 (1)
451–475	0 (2)	4 (22)	—
476–500	67 (6)	35 (17)	—
501–525	88 (8)	18 (17)	—
526–550	80 (15)	29 (7)	0 (1)
551–575	100 (20)	70 (20)	100 (7)
576–600	90 (21)	100 (13)	86 (7)
601–625	92 (24)	100 (9)	100 (6)
626–650	97 (31)	100 (12)	100 (8)
651–675	100 (25)	100 (7)	100 (9)
676–700	100 (31)	100 (7)	100 (7)
701–725	100 (39)	100 (7)	100 (3)
726–750	100 (35)	100 (4)	100 (6)
751–775	100 (28)	100 (3)	100 (7)
776–800	100 (15)	100 (1)	100 (3)
801–1025	100 (59)	100 (3)	100 (8)
No length	100 (1)	100 (5)	—

Table 9

Percentage of mature specimens by age class for female snowy grouper collected off North Carolina and South Carolina with 1) primarily bandit reels and longlines during 1980–85, and 2) primarily longlines and chevron traps during 1991–95. Specimens in the developing, ripe, spent, or resting stages were considered mature. All specimens were examined histologically. n = number of specimens.

Age (yr)	1980–85 n = 219 % (n)	1991–95 n = 197 % (n)
1	—	0 (5)
2	—	0 (22)
3	33 (3)	4 (26)
4	80 (5)	23 (43)
5	62 (8)	52 (40)
6	86 (21)	83 (29)
7	91 (32)	95 (21)
8	93 (30)	100 (7)
9	95 (20)	100 (1)
10	10 (26)	100 (1)
11	100 (15)	100 (1)
>11	100 (59)	100 (1)

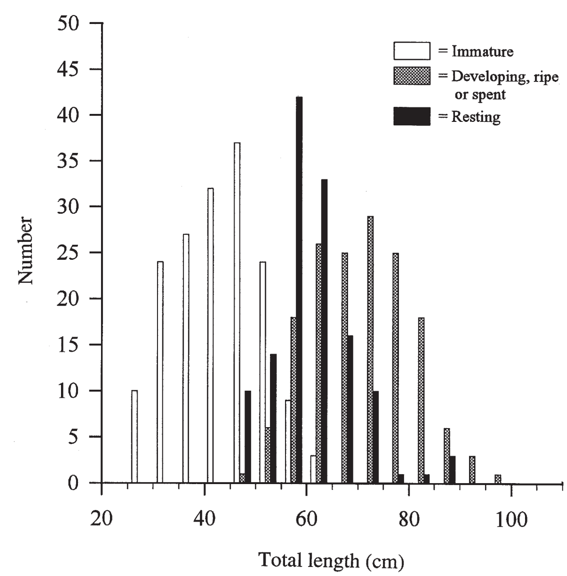

Figure 8

A comparison of length-frequency histograms for snowy grouper specimens collected during 1973–95 that were categorized as immature (n=166), definitely mature (n=158), or resting (n=130). Definitely mature specimens were developing, ripe, or spent.

tive stage of individual fish was not determined, it was noted that milt flowed freely from males in a collection of 420 fish from a depth of 278 m off South Carolina (32°57' to 33°02'N). Nearly all of the specimens were sexually mature as the mean lengths of subsamples collected off North Carolina and off South Carolina and Georgia combined were 67.3 (48–96 cm; n=89) and 79.2 (60–97 cm; n=98), respectively.

Depth distribution

There was a moderately positive trend (r^2=0.53) between water depth and total length in fishery-independent samples. Snowy grouper were caught at depths of 46–258 m. Larger adults were caught more frequently in upper continental slope waters >100 m, whereas small adults and juveniles (<600 mm) were caught more frequently at depths <100 m (Fig. 11).

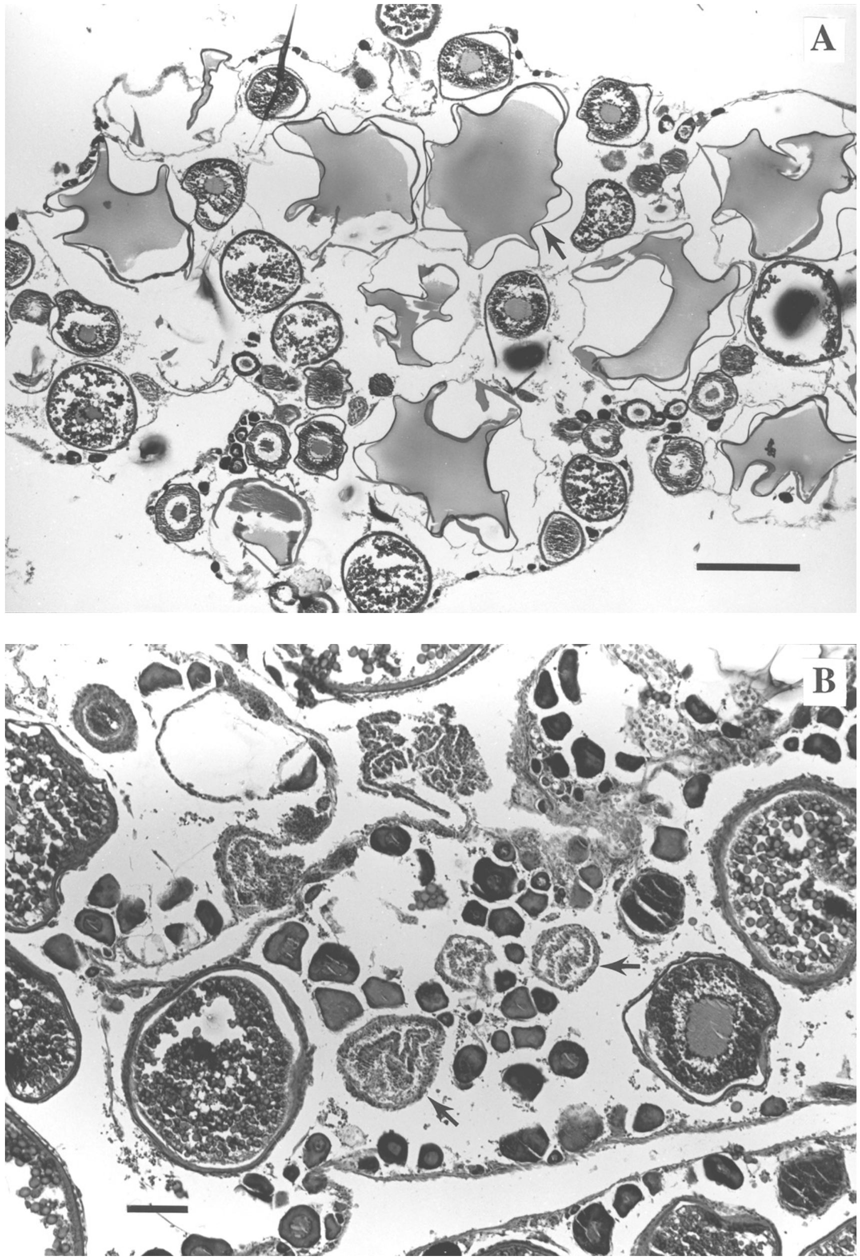

Figure 9

Histological sections of ovarian tissue from female snowy grouper with evidence of imminent or recent spawning: (**A**) hydrated oocytes (arrow) in a 744-mm-TL specimen captured in May (bar=400µ), and (**B**) age 24–48 h postovulatory follicles (arrows) in a 546-mm-TL specimen captured in August (bar=100 µ).

The fishery

Historically, most snowy grouper landings along the Atlantic coast of the United States, as reported through TIP, have occurred in North Carolina and South Carolina (Fig. 12). Although landings statistics are reported by state, fish are often caught throughout the region, especially by vessels fishing with longlines. Landings have varied widely, with peaks noted in 1983 and 1990 for South Carolina and in 1990 and 1992 for North Carolina. These fluctuations have often been the result of changes in effort. For example, the peak in 1983 reflected an approximate doubling in the number of vessels as

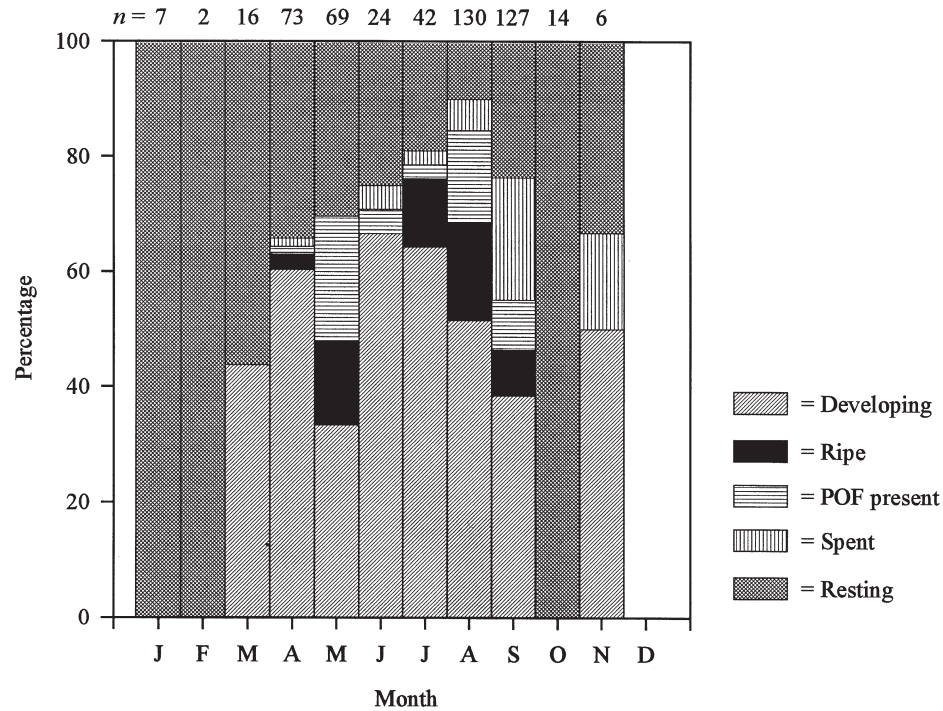

Figure 10

Percentage composition (based on histological criteria) of reproductive stages by month for 510 female snowy grouper. Number of specimens examined is above each bar. POF = postovulatory follicle.

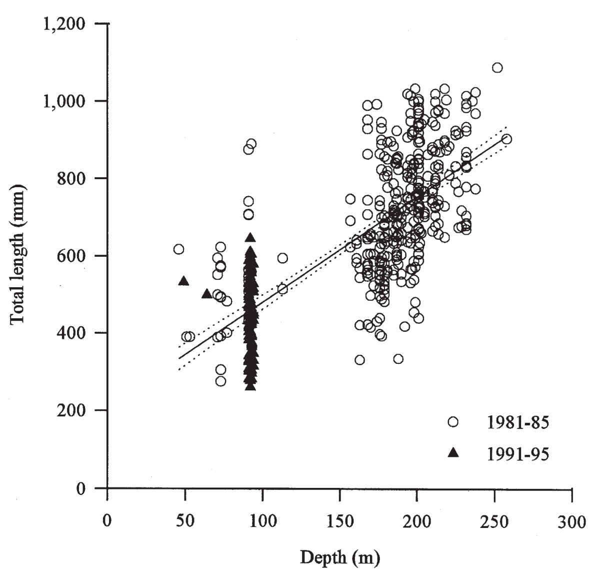

Figure 11

Relationship between length of snowy grouper and depth of capture in fishery-independent sampling off North Carolina and South Carolina primarily with longlines, Kali poles, and snapper reels during 1981–85 (n=359) and primarily with chevron traps during 1991–95 (n=114).

the bottom longline fishery developed. The decreases in 1984 and 1985 reflect a shift in effort to the pelagic longline fishery for swordfish (Low et al., 1987).

In South Carolina, the mean length of snowy grouper caught with longlines decreased steadily from 66 to 72 cm during 1983–84 to a low of 49 cm in 1996 (Fig. 13). No trend was evident in the length data for snowy grouper caught with snapper reels. The snowy grouper caught with snapper reels were consistently smaller than those caught with longlines because snapper reels were deployed in shallower water (Fig. 14).

Length data from North Carolina for snowy grouper caught with longlines showed a similar decreasing trend, though with greater interannual variation (Fig. 15). The mean length of snowy grouper caught with snapper reels has fluctuated, with peaks noted in 1985 and 1993.

Discussion

Status of the fishery

There are several indications that the snowy grouper population off the Carolinas is overfished: 1) size at age of specimens caught with longlines and snapper reels has increased noticeably since the 1980s (Table 3), which could be a density-dependent population response to a decrease in competition for resources, 2) 81% of the specimens caught with longlines were ages 1–6, the majority (56%) of which were immature females (Tables 4 and 9), 3) the percentage of males appears to have decreased significantly, from 7% to 23% in the 1970s and 1980s to 1% in the 1990s (Table 7), 4) spawning stock ratio for the snowy grouper population in the South Atlantic Bight was 0.15 in the most recent assessment (SAFMC, 1993)—below the 0.30 level which means that the SAFMC considers the stock overfished, and 5) mean length of fish landed in the longline fishery has steadily decreased from 65 to 80 cm in the early 1980s to 50–60 cm in the mid-1990s (Figs. 13 and 15; see also Low, 1998).

Snowy grouper are susceptible to rapid depletion in a localized area through fishing efforts. A study on a previously unexploited deep reef off North Carolina found that fishing can remove 3% of the reef population daily (Epperly and Dodrill, 1995). In less than three months, the catch per unit of effort and mean size of snowy grouper at that reef were reduced to levels comparable to other exploited sites. The mean size of snowy grouper landed in North and South Carolina during most of the 1990s (Figs. 13 and 15) is comparable to the size Epperly and Dodrill (1995) reported for exploited sites.

The increase in size at age over a ten-year period for fish from both gear types is noteworthy because this trend has been documented in populations that had experienced moderate to high levels of fishing mortality. Increases in size at age have been noted for silver hake (Helser and Almeida, 1997) and Atlantic halibut (Haug and Tjemsland, 1986) in the north Atlantic and several reef fish species (gag, red grouper, and red porgy) off the southeast coast of the United States and in the Gulf of Mexico (Johnson et al., 1993; Johnson and Collins, 1994; Harris and McGovern, 1997; Goodyear and Schirripa[3]). In our study, the increase in size at age may represent density-dependent growth in response to an increase in fishing mortality (Rothschild, 1986). Decreases in the abundance (Low, 1998) of co-occurring species on a similar trophic level, such as gray tilefish (*Caulolatilus microps*) and tilefish (*Lopholatilus chamaeleonticeps*), also may reduce competition for food and shelter in deepwater habitats. Snowy grouper and gray tilefish feed on macroinvertebrates, particularly crabs (Brachyura), and fishes closely associated with the substrate (Ross, 1982; Dodrill et al., 1993).

Density-dependent increases in growth rate generally indicate that a population or community is heav-

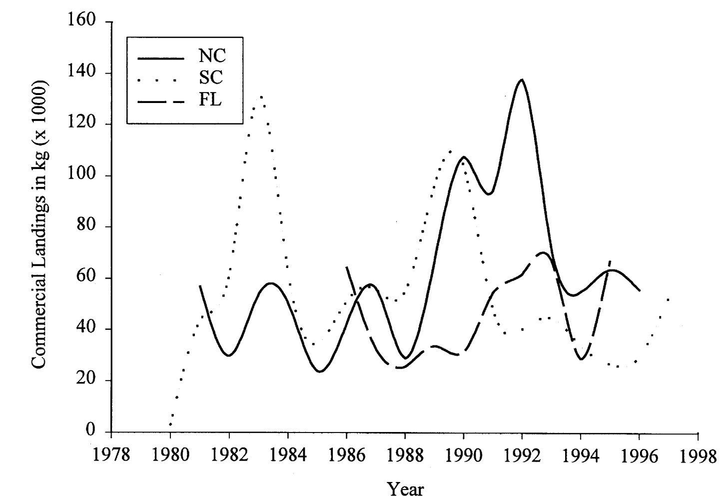

Figure 12

Commercial landings of snowy grouper in North Carolina, South Carolina, and Florida for all gear types, primarily longlines and snapper reels. Data were collected in individual states through their Trip Interview Program (TIP).

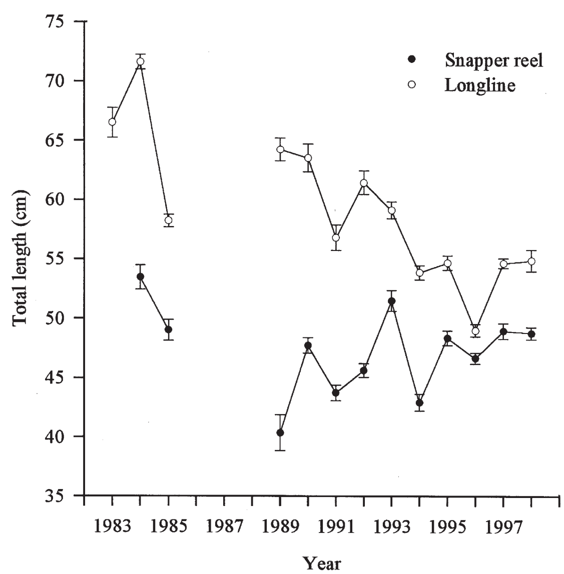

Figure 13

Mean length (±SE) of snowy grouper landed in South Carolina in the longline and snapper reel fisheries. Data were collected through the Trip Interview Program (TIP) at the South Carolina Department of Natural Resources. Sample sizes ranged from 22 to 851.

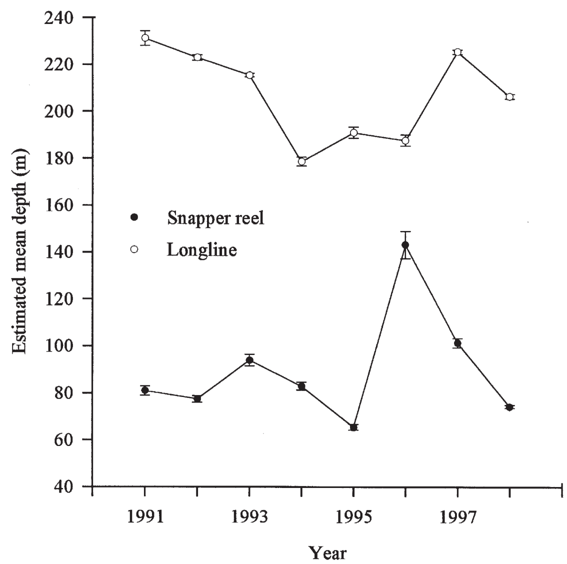

Figure 14

Estimated mean water depth (±SE), based on minimum and maximum depths provided by captains, during fishing efforts in the longline and snapper reel fisheries. Data were collected through the Trip Interview Program (TIP) at the South Carolina Department of Natural Resources from vessels landing their catches in South Carolina. Sample sizes ranged from 141 to 851.

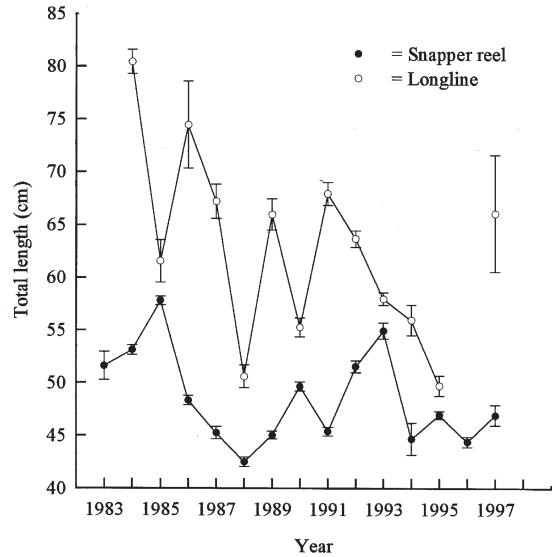

Figure 15

Mean length (±SE) of snowy grouper landed in North Carolina in the longline and snapper reel fisheries. Data were collected through the Trip Interview Program (TIP) at the North Carolina Department of Health, Environment, and Natural Resources. Sample sizes ranged from 5 to 1908 fish.

ily exploited and possibly overexploited. A situation of greater concern would be one where size at age has decreased after a sustained high level of fishing-induced mortality, as has been reported for red porgy, *Pagrus pagrus*, and vermilion snapper, *Rhomboplites aurorubens*, in our study region (Harris and McGovern, 1997; Zhao et al., 1997). There is evidence that faster-growing individuals in the populations of red porgy and vermilion snapper have been effectively eliminated, thus causing a decrease in size at age. Red porgy exhibited a density-dependent response after an initially high level of fishing mortality, but the sustained high level of mortality eventually removed the faster-growing individuals. Size at age should be monitored to ensure that this does not occur in the snowy grouper population.

The age composition of the snowy grouper landings also needs to be monitored because the longline fishery is presently supported by younger age classes (1–6). The present study showed that snowy grouper can attain an age of 29 yr, but only 19% of the fish caught on longlines were >age 6 (Table 4). The low percentage of older age classes in the landings supports the preliminary sex ratio data from the 1990s, showing that the percentage of males had significantly decreased.

Age and growth

A comprehensive comparison of growth data in our study with previously published results was not possible because 1) lack of large and old specimens and small sample sizes, and 2) differences in study area (Florida Keys in Moore and Labisky [1984]). One or more of these factors could explain the differences in size at age, k, and L_∞ between the results of two published studies (Matheson and Huntsman, 1984; Moore and Labisky, 1984) and our results for longline and snapper reel data from the 1980s. A primary reason for higher values of L_∞ in the published studies (Table 3) is that the growth curves do not exhibit asymptotes, which is probably due to low numbers of specimens greater than approximately 900 mm and older than 15–17 yr. In our study, all the data sets (2 bandit reel and 2 longline) had individuals over 1000 mm and at least 21 yr old. Sample sizes in two data sets were very small (<200): our longline or Kali pole data set (n=163) and the data set of back calculations (n=118) in Moore and Labisky (1984). Important factors that could not be evaluated on the basis of previous publications were 1) similarity of fishing gear, 2) method of increment interpretation, and 3) whether or not a weighting factor was used when fitting the von Bertalanffy growth model.

We feel confident that our assessment of the age structure in the snowy grouper population off the Carolinas was accurate, even though interpretation of growth increments was difficult and a minimal number of YOY specimens was available. The difficulty of assigning an age to the sagittae of snowy grouper had not been reported by other investigators, although it has been reported for other deepwater species of continental slopes. The clarity of the hyaline and opaque zones in otoliths (presumably sagittae) from hoki, *Macruronus novaezelandidae*, off New Zealand is highly variable and is divided into six categories based on internal features which are related to the ease of counting increments (Kuo and Tanaka, 1984). When otoliths are difficult to interpret, one option is to base population age structure only on the specimens for which age is easily assessed. Alternatively, ages can be estimated for nearly all specimens despite the difficulties, as we did in our study, with the assumption that the larger sample will represent the population better. We found that limiting the data set to only those specimens for which the difference in counts between readers was 0–1 increments did not improve the accuracy of the age-length key for specimens caught with longlines (Table 6). Thus, we advocate using the entire sample of specimens assigned an age. Crabtree and Bullock (1998) found that rejected otoliths tend to be from slower-growing older specimens, which could introduce bias into analyses. This bias was minimal in their study of growth in black grouper, *M. bonaci*, where each otolith was examined three times by two independent readers. Parameter estimates for the von Bertalanffy model based on all black grouper with ages were within one standard error of those based only on specimens for which the coefficient of variation of the six readings was ≤12%.

An important consideration in age determination is positive identification of the first annulus and any settling mark that may be deposited prior it. We believe that we have identified the first annulus because the largest YOY specimen (172 mm) had an estimated age of 191–291 days and the measurements of otolith radius for all YOY (n=3) were less than radial measurements to the first annulus in a subsample of 23 specimens that were age 1. Evidence to support our conclusion that these three specimens were YOY was found in another sampling effort, where six specimens 4–5 cm in length were caught with a trawl during August and September (Machowski[5]), the last two months of the spawning season. Moore and Labisky (1984) considered 150–175 mm specimens to be YOY, although they did not examine daily increments.

[5] Machowski, D. 1998. S. Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC, 29422. Personal commun.

Validation of a technique for aging snowy grouper with otoliths has been weakly supported by previous studies. We found that marginal increments form annually and there is a peak in April and May that corresponds to the beginning of the spawning season. This finding concurs with the limited results of Matheson and Huntsman (1984) and Moore and Labisky (1984) who found that increment formation appeared to begin in April and peaked in June. Matheson and Huntsman (1984) measured marginal increments in 18 specimens collected during April through October and Moore and Labisky (1984) examined specimens collected during March through July (n not reported). Waltz[4] found a wider period of increment formation, April through September, although he was not able to conclude that increments form annually because samples were lacking for four months.

Reproduction

The reproductive pattern of snowy grouper needs to be investigated more comprehensively and the sex ratio should be assessed again, given the small sample size in 1993–94 (n=82), because there is evidence that reef fish species, particularly grouper, which change sex and aggregate to spawn, are more susceptible to size-selective mortality and overexploitation (Bannerot, 1987; Huntsman and Schaaf, 1994; Coleman et al., 1996). The capture of only one male in the 1993–94 samples, which appeared to be representative of the population based on commercial landings, is reason for concern because the percentage of males has apparently decreased from the 7–23% for samples collected with three gear types in the 1970s and 1980s (Table 7).

Large decreases in the number of males have been documented for two other grouper species in the southeast region. Percentages of males in populations of gag and scamp in the Gulf of Mexico, groupers that are known to form small spawning (10's to 100's of individuals) aggregations, decreased from 17% to 1% and 38% to 18%, respectively, between the 1970s and early 1990s (Coleman et al., 1996). A similar decrease, from 20% to 6%, was noted for gag along the Atlantic coast of the southeastern United States during the same period (McGovern et al., 1998). The resultant decrease in genetic diversity has been documented for gag (Chapman et al., 1999), and its ramifications are currently of great concern to many fishery scientists in the southeast region.

The size (767–1090 mm) and age (8–29 yr) of 97 male specimens in the present study and the capture of two specimens in the process of changing from female to male is conclusive evidence that snowy grouper are protogynous hermaphrodites. Moore and Labisky (1984) reported males as young as age 6 and some males with evidence of recent sex change. It is likely that we collected only two transitional specimens because sex change occurs after a female finishes spawning, during months when sample sizes in our study were small. Sex change in other grouper species, gag for example, occurs primarily during the first two to three months after the spawning season (McGovern et al., 1998), before males and females become spatially separated (Coleman et al., 1996).

Our findings on age at maturity and spawning season are in general agreement with the results of Moore and Labisky (1984) for snowy grouper in the Florida Keys. They found that the smallest mature female and largest immature female were age 3 and age 5, respectively, whereas the smallest mature female from 1980 to 1985 in our study was also age 3, but small percentages (<10%) of the age 7–9 females were immature (Table 9). Females and males in the Florida Keys were in spawning condition from April through July, although no mature fish were sampled in other months (Moore and Labisky, 1984). We found that females off the Carolinas spawn from April through September—possibly longer owing to small sample sizes in October through March.

The capture of 1160 specimens, some of which were assessed macroscopically as spawning, in four trawl collections on the exploratory squid cruise in June 1978 suggests that snowy grouper may form spawning aggregations. Estimates of density would have been much higher than 13.5–79.5 kg/ha calculated from the trawl data if the fish were caught in only a small part of the area sampled during tows of 7.4–18.5 km. Dodrill and Epperly (1995) reported that the initial density of exploitable snowy grouper on a 2700-m^2 virgin reef off North Carolina was 11 kg/m^2.

Depth distribution

Fishery-independent data collected over several years and with various gear types show that fish length is positively correlated with water depth (Fig. 11). Longlines, Kali poles, and snapper reels were the primary gear types deployed in waters >150 m and the waters <100 m were sampled primarily with chevron traps. Chevron traps are not known to be selective for snowy grouper <600 mm. Dodrill et al. (1993) speculated that the low abundance of adults in shallow waters may in part reflect years of intensive fishing pressure in 40–120 m depths and only relative recent fishing activity at depths >183 m off North Carolina. Alternatively, we propose that snowy grouper may migrate to deeper water toward the end of the juvenile stage.

Fish length and water depth data from the commercial fisheries (Figs. 13 and 14) concurred with the positive correlation noted in the Florida Keys (Moore and Labisky, 1984) and off Georgia and South Carolina (Low and Ulrich, 1983), although depth data from fishermen may be less accurate than fishery-independent data. We found small juveniles in shallow water, a finding that agrees with the results of Moore and Labisky (1984) and with observations from submersible dives that documented juvenile snowy grouper (<300 mm) between 46 and 91 m, but not in deeper waters (Parker[6]).

Accurate assessment of population parameters requires knowledge of juvenile and adult distributions of snowy grouper as well as characteristics of the fishery. The snapper reel fishery catches a greater proportion of younger age classes than does the longline fishery because fishing efforts are generally restricted to areas <100 m in depth (Figs. 13 and 14). The longline fishery presently catches a greater proportion of older age classes than does the snapper reel fishery because regulations established by the SAFMC restrict longlines to waters deeper than 91 m.

Conclusions

As other investigators have suggested, rebuilding grouper populations may require a novel approach such as long-term area closures or individual transferable quotas (Epperly and Dodrill, 1995; Coleman et al., 1996). At present, the regulations enacted to rebuild the snowy grouper population include an annual quota of 245,082 kg, with a trip limit of 1134 kg (SAFMC, 1993). Traditional management measures such as minimum size limits will not be effective because snowy grouper experience fatal embolisms while being brought to the surface from deep waters (Matheson and Huntsman, 1984). Future research should focus on improving our understanding of reproductive pattern (e.g. spawning behavior, spatial and temporal aspects of distribution) and include a thorough assessment of sex ratio and an updated assessment of population age structure.

Acknowledgments

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[6] Parker, R., Jr. 1997. National Marine Fisheries Service, 101 Pivers Island Rd., Beaufort, NC, 28516. Personal commun.

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