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Growth, Mortality, and Yield-per-Recruit Models for Speckled Hind and Snowy Grouper from the United States South Atlantic Bight

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Abstract

Opaque rings on cross-sectioned otoliths from speckled hind *Epinephelus drummondhayi* and snowy grouper *E. niveatus*, taken off North Carolina and South Carolina, were determined to be annuli. Annulus formation occurred primarily between April and June for speckled hind, and from May through July for snowy grouper. The length–weight relationship for speckled hind was $W = 1.1 \times 10^{-8}L^{3.075}$ and for the snowy grouper was $W = 7.0 \times 10^{-8}L^{2.755}$, where W = weight in kilograms and L = total length in millimeters. Back-calculated mean lengths (mm) of speckled hind from ages 1 to 15 were 186, 317, 408, 475, 528, 572, 613, 645, 678, 709, 739, 774, 804, 839, and 861. For snowy grouper ages 1 to 17, they were 210, 328, 403, 462, 514, 562, 605, 647, 686, 721, 762, 798, 832, 874, 900, 924, and 958. The maximum age of both species was at least 25 years. The von Bertalanffy growth equations for speckled hind and snowy grouper (t = age in years) are $L_t = 967\{1 - \exp[-0.13(t + 1.01)]\}$ and $L_t = 1{,}255\{1 - \exp[-0.074(t + 1.92)]\}$. Instantaneous annual mortality rates for speckled hind, determined from catch curves, increased from 0.26 to 0.40 in the headboat fishery between 1975 and 1979, and fluctuated between 0.23 and 0.32 in the commercial hook-and-line fishery. Snowy grouper mortality increased from 0.19 to 0.57 in the headboat fishery between 1972 and 1978, but remained stable at 0.24 to 0.25 in the commercial fishery from 1977 to 1979. Yield-per-recruit models for both species indicated that the headboat and commercial fisheries are harvesting between 60% and 80% of the maximum available yield per recruit.

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In this report, we describe growth, mortality, and yield models for speckled hind *Epinephelus drummondhayi* and snowy grouper *E. niveatus* from waters off North Carolina and South Carolina. There are no published results of any previous research on age and growth research on these species and studies of other groupers in the genus *Epinephelus* are few (Moe 1969; Burnett-Herkes 1975; Nagelkerken 1979; Olsen and LaPlace 1979; Muhlia Melo 1975).

Speckled hind, or Kitty Mitchell grouper[1], are found at Bermuda (Smith 1971), in the Gulf of Mexico, and along the United States' Atlantic coast north to Cape Hatteras, North Carolina (Roe 1976; Huntsman and Dixon 1976). Although occurring to a depth of 165 m on the Campeche Banks (Roe 1976), they are usually caught at depths of 45 to 100 m (Huntsman 1976).

Snowy grouper are more widely distributed, occurring from Brazil north through the Bahamas and Florida to Cape Hatteras, North Carolina (Smith 1971; Huntsman and Dixon 1976), as well as in the eastern Pacific (Miller and Lea 1976; Fitch and Schultz 1978). Reports from Woods Hole, Massachusetts (Smith 1971), undoubtedly were based on juveniles transported by Gulf Stream drift. The snowy grouper is most common in deep water (60 to more than 185 m) (Huntsman and Dixon 1976; Roe 1976), although juveniles and small adults (to about 400 mm long) occasionally occur in water as shallow as 35 m.

[1] Kitty Mitchell was supposedly the red-haired and freckled proprietor of a popular Panama City, Florida, brothel in the early days of the Gulf of Mexico snapper–grouper fishery. Fishermen, seeing a likeness of the well-known madame's complexion and pelage in the white-flecked, maroon coloration of *E. drummondhayi*, named the fish in the famous lady's honor.

Fishing for both species is concentrated at the shelf-break (Struhsaker 1969; Grimes 1976), an area of steep cliffs, rocky ledges, and swift currents. Sport and commercial fishermen are attracted by the large size (7 to 11 kg) that these groupers frequently attain. North Carolina and South Carolina headboats landed an average of 11,908 kg of speckled hind and 6,482 kg of snowy grouper annually between 1972 and 1980. South Carolina hook-and-line commercial vessels landed an average of 7,488 kg of speckled hind and 35,340 kg of snowy grouper annually from 1976 through 1981 (North Carolina grouper landings are not reported by species).[2] Commercial grouper landings prior to 1976 were occasional and generally small.

Methods

Sampling

From 1972 to 1979, lengths and weights from 1,141 speckled hind and 936 snowy grouper were recorded from the headboat fishery (Huntsman 1976) in North Carolina and South Carolina. Most fish were caught between Cape Lookout, North Carolina, and Charleston, South Carolina, and from February through November. The Cape Lookout sampling area included all of Raleigh Bay and the northern half of Onslow Bay, the Cape Fear area included the southern half of Onslow Bay and the northern third of Long Bay, and the Cape Romain area encompassed the remainder of Long Bay and the Atlantic Ocean south to Savannah, Georgia.

Because grouper scales are small, usually regenerated, and useless for age determinations, we instead used dry-stored otoliths which we took from 463 speckled hind and 536 snowy groupers. We exposed otoliths by cutting the skull transversely with a hacksaw or by scraping away the side of the otic capsule (Barans et al. 1979). The latter method is easily mastered and does not deface fish that might be mounted or sold. Left otoliths were used if available and for both species accounted for 78% of the otoliths read. Because an analysis of covariance revealed no significant differences ($P < 0.05$) in total-length–otolith-radius regressions of left and right otoliths for either species, data from left and right otoliths were combined.

Otolith Analysis

We sectioned otoliths with the apparatus and techniques described by Berry et al. (1977) and Matheson (1982), which were derived from Nichy's (1977) methods. The plane of sectioning is of major importance for successful analysis. Characteristics of a suitable plane are constancy of otolith symmetry in the plane throughout the size range of otoliths to be sectioned, clarity of the ring patterns, and absence of protrusions or indentations along the section margin. Otoliths for speckled hind were sectioned along the plane that included the focus and area anterior to the lateral (dorsal) projection (Moe 1969). For snowy grouper the plane included the focus and area posterior to the lateral projection (Matheson 1982).

Rings were counted and measured with an ocular micrometer while viewed in a darkened watch glass through a binocular microscope. Illumination consisted of reflected, high-intensity light projected at a 45° angle. Speckled hind otoliths were viewed at 20× magnification (1 ocular unit = 0.05 mm) and the larger otoliths of snowy grouper at 10× (1 unit = 0.1 mm).

Reflected light revealed white opaque rings and dark translucent (hyaline) rings. Opaque rings, which we hypothesized represented the end of one year's growth, were counted and the distance from the focus to the distal edge of each was measured. We also recorded the radial distance (focus to edge) for all otoliths and the distance from the distal edge of the last opaque ring to the cross-section edge. Ninety-seven percent ($N = 463$) of cross sections from speckled hind and 89% from snowy grouper ($N = 536$) were legible (showed rings).

Using an otolith-radius–fish-length regression of the form $L = a + b(OR)$ where L = total length (mm), OR = otolith radius (mm), and a and b are constants, we back-calculated mean lengths at each age by substituting the means of the distances from the focus to each annulus for OR. The von Bertalanffy (1938) growth equation $L_t = L_\infty\{1 - \exp[-K(t - t_0)]\}$ was fitted to back-calculated lengths; t = age in years, L_∞ = asymptotic maximum length, and K = Brody growth coefficient.

[2] Unpublished data, Southeast Fisheries Center, National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, Florida 33149.

Yield-per-Recruit Computations

Computer program MAREA[3] was used to calculate Ricker (1975) type yield-per-recruit models. Weights at age were determined from the length–weight equation and from lengths at age predicted by the von Bertalanffy growth equation. Some estimates of M, the instantaneous natural mortality rate, were obtained through use of the Pauly (1980) multiple regression of M on K, L_∞, and annual mean water temperature. Based on field observations, our estimates of the annual mean water temperature were 17 C for speckled hind and 12 C for snowy grouper.

Mortality

Catch curves were used to estimate mortality rates (Everhart et al. 1975; Ricker 1975). Regressions were fit to the data for all ages from the modal age plus one through the greatest age in the sample. The age–length-key approach was used to obtain age frequencies for fish from which otoliths had not been taken. Fish of known age and of unknown age were grouped separately by 25-mm length intervals. Length groups of unaged fish were allocated to age groups in the same proportions as those of aged fish. Length frequencies from recreational catches were obtained from the National Marine Fisheries Service headboat survey, 1972 to 1979 (Huntsman 1976). Length frequencies from commercial catches were supplied by the South Carolina Marine Resources Research Institute, Charleston, South Carolina.

Mean Age of Recruitment

Determination of the status of the two grouper fisheries required estimates of F (instantaneous fishing mortality rate) and of t_r, the age at recruitment. To estimate the average age at recruitment, we determined, by inspection of length frequencies, the minimum length at which each species became fully vulnerable to the fishing gear. Based on the normal distribution, the probability that fish of each age would achieve the minimum fully vulnerable length was ascertained, and those probabilities were used to calculate a weighted mean age at recruitment (Huntsman et al., in press)

[3] William H. Lenarz (La Jolla Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, Post Office Box 271, La Jolla, California 92038) and Sheryan P. Epperly and Larry L. Massey (Beaufort Laboratory, Southeast Fisheries Center, National Marine Fisheries Service, Beaufort, North Carolina 28516), A generalized computer program for yield per recruit analysis of a migrating population with area specific growth rates, exploited over multiple areas (MAREA).

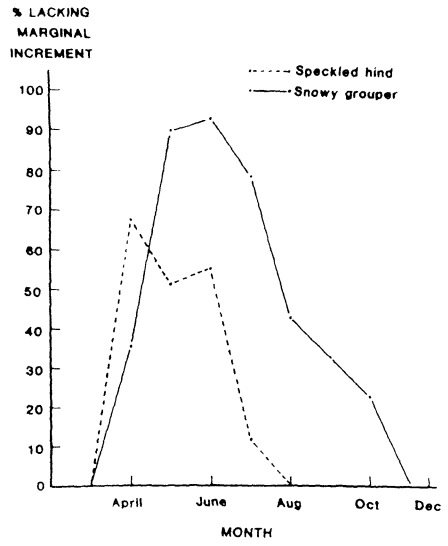

FIGURE 1.—*Time of annulus formation on cross-sectioned otoliths from speckled hind and snowy grouper.*

Results and Discussion

Validation of Ages

Rings on otolith cross-sections from both species were identified as annuli because they satisfied the criteria of Van Oosten (1929). Otolith cross-section radius correlated well with body length; the number of rings increased with size and putative age marks maintained the same position on the otoliths of fish of different ages. Mean back-calculated lengths closely agreed with mean observed lengths at each age.

Radial measurements of otolith cross sections were directly proportional to total lengths for both species. Prediction equations were, for speckled hind: $L = 198.8OR - 106.9$; $r = 0.96$; $N = 463$; and for snowy grouper: $L = 132.8OR - 45.5$; $r = 0.97$; $N = 536$.

Opaque rings formed on otoliths of both species at about the same time of year (Fig. 1). Otoliths from 241 speckled hind (175–500 mm) and 18 snowy grouper (150–500 mm) were examined for marginal increments. The frequen-

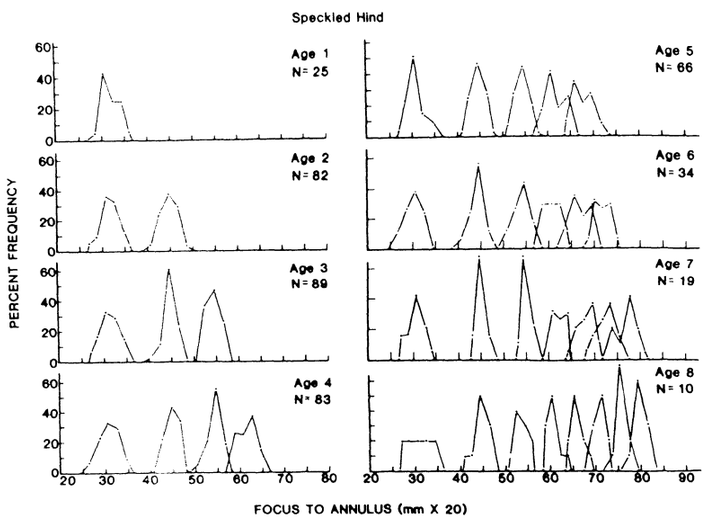

FIGURE 2.—*Frequency of occurrence for focus-to-annulus measurements from otoliths of speckled hind.*

cy of absence of a marginal increment (distance between the last opaque ring and cross-section edge) suggests that annuli form from April to July for speckled hind and from April to October for snowy grouper. Annulus formation occurs most often from April to June for speckled hind and from May to July for snowy grouper.

The frequency plots (Figs. 2 and 3) of the distance from the focus to each opaque ring for both species further support the hypothesis that opaque rings were annuli. The number of rings increased with length, one mode occurred for each ring, and modes were consistently located for each annulus in progressively older fish.

Growth

Back calculated total lengths for speckled hind were 186, 317, 408, 475, 528, 572, 613, 645, 678, 709, 739, 774, 804, 839 and 861 mm for ages 1 to 15, and for snowy grouper were 210, 328, 403, 462, 514, 562, 605, 647, 686, 721,

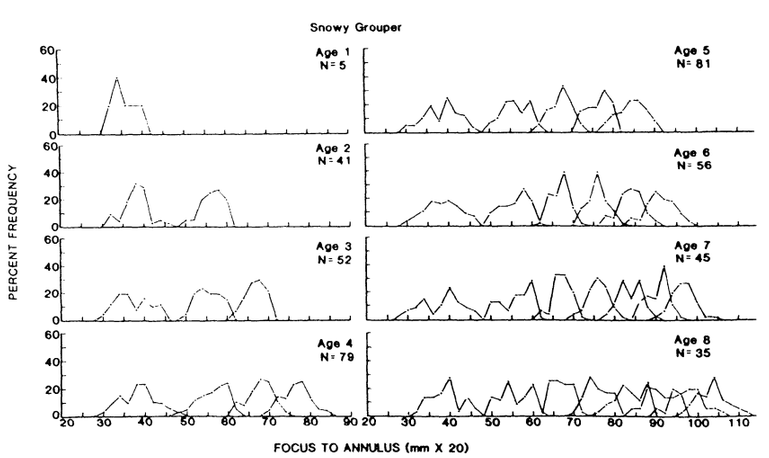

FIGURE 3.—*Frequency of occurrence for focus-to-annulus measurements from otoliths of snowy grouper.*

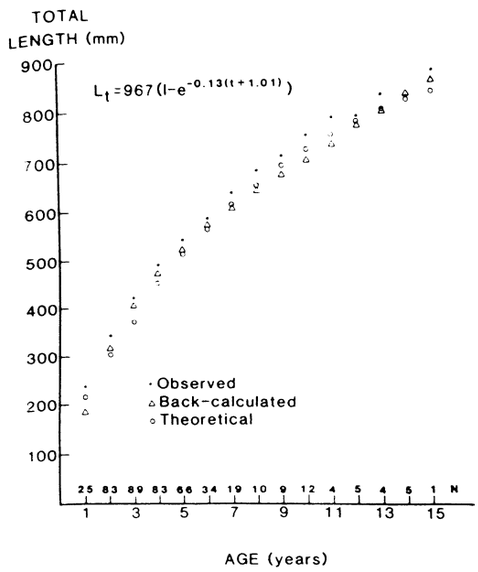

FIGURE 4.—*Observed, back-calculated, and theoretical growth curves for speckled hind.* L *is length;* t *is age.*

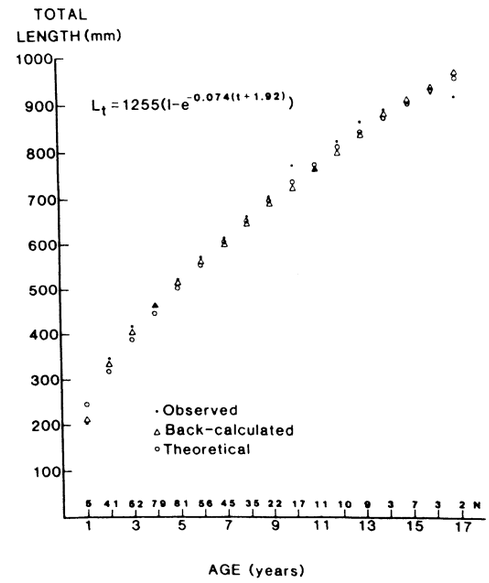

FIGURE 5.—*Observed, back-calculated, and theoretical growth curves for snowy grouper.* L *is length;* t *is age.*

762, 798, 832, 874, 900, 924 and 958 mm for ages 1 to 17. The von Bertalanffy growth equation for speckled hind was $L_t = 967\{1 - \exp[-0.13(t + 1.01)]\}$ and for snowy grouper was $L_t = 1{,}255\{1 - \exp[-0.074(t + 1.92)]\}$ where L_t = total length in millimeters at year t.

Observed, back-calculated, and modeled growth curves agree closely (Figs. 4 and 5). Observed mean lengths were larger than back-calculated lengths because of growth between times of annulus formation and capture.

The values of L_∞ agree closely with observed maximum sizes. We measured a speckled hind 1,096 mm long, believed to be the largest on record, at Morehead City, North Carolina, on September 30, 1977. The largest snowy grouper sampled in North Carolina and South Carolina between 1972 and 1979 was 1,130 mm long, only 11% greater than the L_∞ calculated.

Length–Weight Relationships

For speckled hind the length–weight relationship was $W = 1.1 \times 10^{-8}L^{3.073}$; $N = 462$; $r = 0.99$; W = kilograms; L = total length (mm). Slopes and intercepts of relationships calculated for each sampling area were not significantly different (t-tests; $P < 0.05$) (Table 1). The length–weight relationship for snowy grouper is $W = 7.0 \times 10^{-8}L^{2.755}$; $N = 428$; $r = 0.98$. The regression for Cape Lookout samples was significantly different ($P < 0.01$) from that for Cape Romain samples, and from the equation for all samples combined. We have not identified a cause for this difference. We could not calculate length–weight equations by sex because samples were not so sorted. Groupers are hermaphroditic and sex can be determined accurately only after histological examination.

TABLE 1.—*Total-length–weight relationships of speckled hind and snowy grouper by geographic areas.* W *is kilograms;* L *is millimeters.*

Area	Speckled hind	Snowy grouper
Overall	$W = 1.1 \times 10^{-8}L^{3.073}$	$W = 7.0 \times 10^{-8}L^{2.755}$
Offshore Cape Lookout	$W = 0.7 \times 10^{-8}L^{3.154}$	$W = 3.6 \times 10^{-8}L^{2.868}$
Offshore Cape Fear	$W = 1.4 \times 10^{-8}L^{3.043}$	No observations
Offshore Cape Romain	$W = 1.0 \times 10^{-8}L^{3.087}$	$W = 7.6 \times 10^{-8}L^{2.753}$

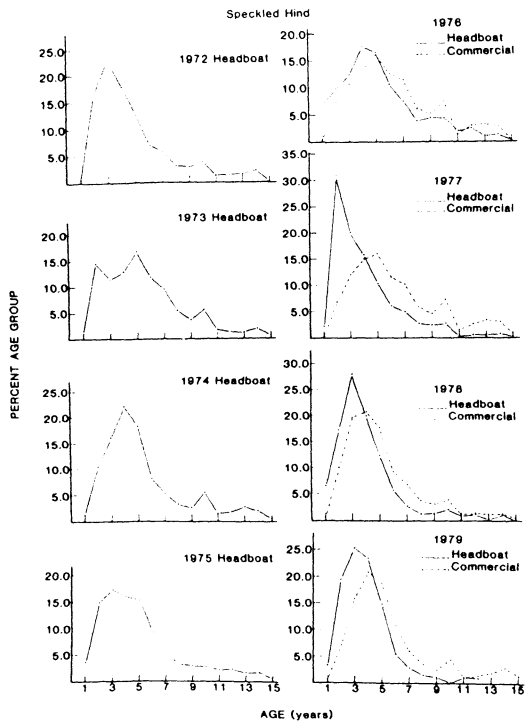

FIGURE 6.—*Annual age composition of speckled hind sampled from headboat and commercial catches, 1972–1979.*

Age Composition and Mortality

From 1972 to 1979 there were changes in several parameters (including modal ages, skewness, kurtosis, and geometric mean age, Table 2) of age distribution (Figs. 6 and 7) that are most dramatically expressed by mortality rates (Table 3). Estimation of mortality rates from catch curves is subject to a number of limitations, the most important of which is the assumption of equal recruitment in each year. However, the catch-curve method is probably the best of those procedures that use samples taken within a single year (Ricker 1975), and recognizing the limitations, we used catch curves.

After 1975, apparent mortality determined from samples from the headboat fishery increased markedly (Table 3) apparently as a result of great increases in commercial fishing (Ulrich et al. 1977). However, mortality rates determined from commercial fishery samples remained low. Of two similar explanations for this anomaly—(1) that the commercial fishery was constantly expanding to new grounds while the headboat fishery, because of vessel cruising ranges, remained on the same area, or (2) that samples from the commercial fishery represent

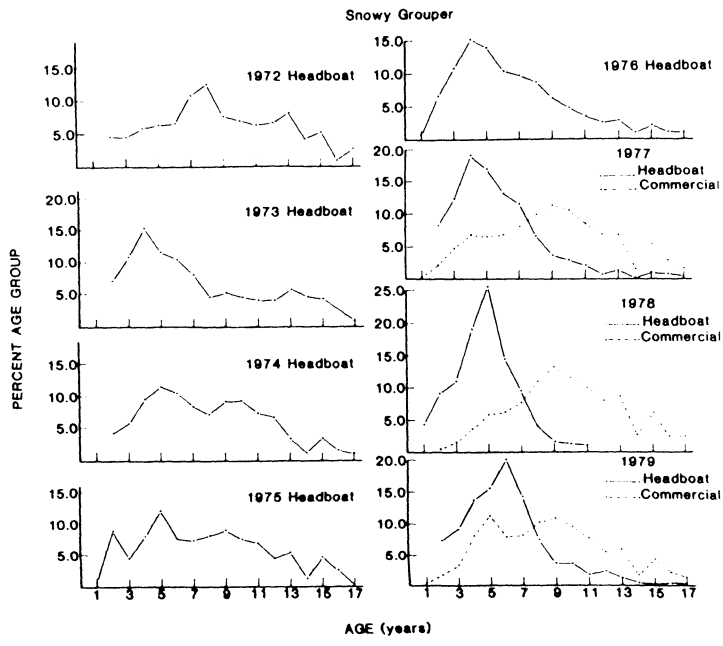

FIGURE 7.—*Annual age composition of snowy grouper sampled from headboat and commercial catches, 1972–1979.*

TABLE 2.—*Geometric mean ages of speckled hind and snowy grouper by year and means of capture.*

	Speckled hind						Snowy grouper					
	Headboat			Commercial			Headboat			Commercial		
Year	Mean age	SE	*N*	Mean age	SE	*N*	Mean age	SE	*N*	Mean age	SE	*N*
1972	4.8	0.046	156				7.8	0.076	60			
1973	4.2	0.036	241				6.1	0.097	43			
1974	4.6	0.041	172				7.0	0.034	241			
1975	4.2	0.044	177				6.7	0.046	168			
1976	4.4	0.067	89	5.6	0.036	203	5.7	0.037	213			
1977	3.5	0.046	145	5.6	0.016	1,042	5.1	0.043	122	8.1	0.015	1,030
1978	3.5	0.048	135	4.5	0.022	512	4.3	0.073	47	9.1	0.011	1,307
1979	3.5	0.095	26	5.0	0.021	576	5.4	0.067	47	7.8	0.014	1,078

populations from a large fishing area of which the headboat grounds are only a portion—the latter seems most likely. Commercial fishermen, with more mobile and dispersed vessels, appeared to be using most of the grounds off North Carolina and South Carolina very soon after 1976.

Yield-per-Recruit Models

We used the yield-per-recruit model to estimate the potential yield of each species. The model estimates the total weight of fish taken from a cohort divided by the number of individuals of that cohort that entered the fishing grounds. In comparison with the full dynamic-pool model (Beverton and Holt 1957), it only requires values for easily estimable parameters. Instantaneous natural mortality (M), growth parameters, instantaneous fishing mortality (F), and age at recruitment to the fishery (t_r) shape the response surface. Estimation of M is a common and often insoluble problem. The Pauly (1980) multiple-regression method appears to provide reliable nonarbitrary estimates, yet even these are suspect for reef fish. For instance, the Pauly estimate of M for mutton snappers *Lutjanus analis* (0.37) is greater than Z (0.32) estimated from a catch curve (C. S. Manooch III, National Marine Fisheries Service, Beaufort, North Carolina, personal communication). For speckled hind, the Pauly estimate of M was 0.27, yet reviewers of this manuscript opined that even 0.20 was probably too great (and we agree). For speckled hind, we constructed yield-per-recruit models for $M = 0.27$, 0.20, and 0.15. The results are similar, and we present and discuss only the model for $M = 0.20$. For snowy grouper, the model is based on the Pauly estimate of M, 0.15. We estimated the maximum attainable age for both species to be 25 years, even though the greatest ages for which we back-calculate lengths are 15 and 17 years, because there occur substantially larger fish than those we could precisely age. Moreover, overestimating maximum age has little impact on yield per recruit because very few fish attain great age.

Both species have similar response surfaces. For speckled hind at $M = 0.20$ (Fig. 8), the maximal yield per recruit (1.2 kg) is available at a minimal $F = 0.65$, given a recruitment age between 6.0 and 7.0 years.

For snowy grouper at $M = 0.15$ (Fig. 9), the estimated maximum yield per recruit (1.4 kg) is available if t_r is between 8.0 and 9.0 years and if F equals a minimum of 0.60. However, for both species, a substantial fraction of the maximal yield per recruit can be taken at very low F. For speckled hind, 1.0 kg, 83% of the maximum, can be taken with an F of 0.20 if t_r is between 4.0 and 7.0 years. For snowy grouper, 1.3 kg, 93% of the maximum, can be taken at $F = 0.30$ if t_r is between 6.0 and 9.0 years.

TABLE 3.—*Annual instantaneous mortality rates (Z) of speckled hind and snowy grouper by year and means of capture.*

	Speckled hind		Snowy grouper	
Year	Head-boat	Commer-cial	Head-boat	Commer-cial
1972	0.30		0.19	
1973	0.30		0.15	
1974	0.28		0.21	
1975	0.26		0.19	
1976	0.29	0.32	0.24	
1977	0.36	0.23	0.33	0.25
1978	0.35	0.31	0.57	0.24
1979	0.40	0.26	0.41	0.25

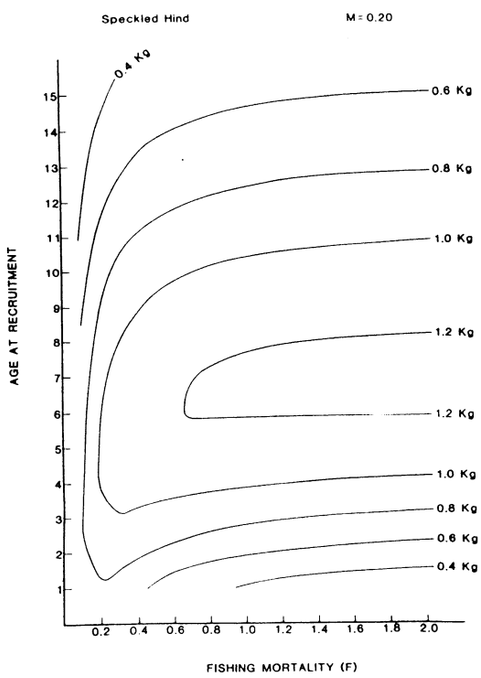

FIGURE 8.—*Yield per recruit in weight of speckled hind at natural mortality* M = *0.20.*

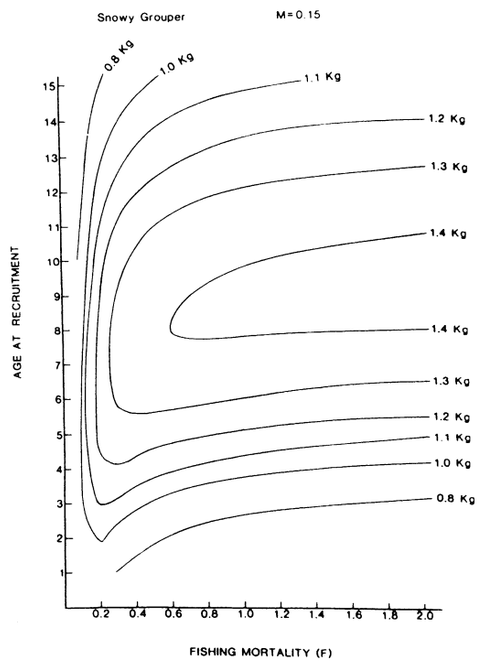

FIGURE 9.—*Yield per recruit in weight of snowy grouper at natural mortality* M = *0.15.*

Status of the Fisheries 1977 to 1979

Because mortality rates determined from samples from the commercial fishery were different from those derived from samples from the headboat fishery, we provide two assessments of the status of the fisheries. The assessment based on samples from the commercial fishery represents the average conditions over an area from Cape Hatteras, North Carolina, south to Savannah, Georgia, from land to about the 200-m isobath. This area includes both the grounds fished only by commercial fishermen and, within the overall area, grounds fished by both commercial and recreational fishermen. The assessment based on mortality rates from the recreational fishery applies only to those grounds fished by both groups, principally areas within an 80-km radius of the major inlets of North Carolina and South Carolina. Underlying the two assessments is the assumption that groupers susceptible to fishing are relatively immobile; that is, they remain in the general vicinity of their home reef after recruitment as juveniles. This assumption, although not conclusively proven by a tagging study, is indicated by limited tagging work, by observations by divers, and by the locality-specific nature of fishing success, and is generally accepted by biologists studying deep-reef fisheries.

We estimated that existing commercial and recreational fisheries in 1977 to 1979 were taking 75% of the maximal yield per recruit of speckled hind on the headboat grounds, and 67% from the area as a whole. For these estimates, we calculated t_r to be 3.3 years and assumed that $F = (Z - M) = 0.17$ on the headboat grounds and 0.07 overall. For both species, our assessments are based on the mean Z for the period 1977 through 1979. Small increases in effort (to $F = 0.3$) might increase the yield per recruit of speckled hind to 83% of the practical maximum (1.2 kg), but effort increases beyond $F = 0.3$ would result in decreased yield per recruit. Only by raising the age of first harvest (up to 6.0 years) could yield per recruit be increased if $F = 0.3$ or more.

For the period 1977 to 1979, we estimated

that 80% of the maximal yield per recruit of snowy grouper was taken on the headboat grounds and 60% was taken over the entire area. We estimated t_r to be 3.3 years, that F was 0.29 on the headboat grounds and 0.10 for the entire area. For both species, the system was assumed to be in equilibrium. While increasing F to 0.25 on the grounds as a whole would produce a 38% increase in yield per recruit, further increases in F there would decrease yield per recruit, and F on the headboat grounds was already greater than optimal. Substantial increases in yield per recruit will result only from increasing age at first recruitment (to about age 6) if F exceeds 0.25.

The growth patterns described here are much like those for other groupers. Maximum size is attained slowly, even more slowly than by any other grouper studied (K = 0.088 and 0.063 for the speckled hind and snowy grouper, respectively). Other reported K values include 0.11 for red grouper *E. morio* (Muhlia Melo 1975), 0.13 for graysby *E. cruentatus* (Nagelkerken 1979), 0.18 for red hind *E. guttatus* (Burnett-Herkes 1975) and Nassau grouper *E. striatus* (Olsen and LaPlace 1979), and 0.12 for gag *Mycteroperca microlepis* (Manooch and Haimovici 1978).

Rapid and marked changes in the age structure of the populations studied, especially of speckled hind, suggest that fishing caused a major impact. Further, yield-per-recruit models of both species showed that fishing mortality rates were close to, or beyond, those which maximized yield per recruit at the recruitment age observed (3.3 years). If even small increases in F occur, yield per recruit only can be augmented if the age at first recruitment is increased. An increased recruitment age might also help to maintain long-term yield by ensuring that enough individuals of these apparently protogynous species live long enough to become males and contribute to reproduction. A high recruitment age (>4.0 years) will be very difficult to ensure, however. Most speckled hind and snowy grouper are so damaged by gas expansion during capture that they cannot be released alive. Even small groupers have large mouths and are caught on large hooks.

If recruitment age cannot be manipulated, control of fishing mortality is the only management tool remaining. Managers might choose to allow pulsed fishing or to effect some control of effort through seasons, limited entry, or control of catch. Pulse-fishing, which is analogous to clear-cut logging, probably would cause loss of yield per recruit because F would be too great and recruitment age too low. However, if F could be kept low (around 0.2), managers could take advantage of the downward dip of yield isopleths at low F and be assured that at whatever recruitment age prevailed, yield per recruit would be maximal for that F.

At present no management measures have been chosen for speckled hind and snowy grouper.

Acknowledgments

We thank Glenn Ulrich of the South Carolina Marine Resources Research Institute who allowed us to use the information on landings of groupers in South Carolina. Robert Dixon and numerous temporary samplers collected biological materials from headboat catches. Alex Chester, William Nicholson, John Merriner, and Russell Nelson gave unselfishly of their time to review the manuscript.

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