YIELD PER RECRUIT MODELS OF SOME REEF FISHES OF THE U.S. SOUTH ATLANTIC BIGHT

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ABSTRACT

Yield per recruit models for red porgy, Pagrus pagrus; vermilion snapper, Rhomboplites aurorubens; white grunt, Haemulon plumieri; red snapper, Lutjanus campechanus; black sea bass, Centropristis striata; gag, Mycteroperca microlepis; scamp, M. phenax; snowy grouper, Epinephelus niveatus; and speckled hind, E. drummondhayi, the most important species to both recreational and commercial fishing off North Carolina and South Carolina, are strikingly similar, and suggest that there is a single strategy for managing reef fishes in the South Atlantic Bight. For all species, yield per recruit at median recruitment ages increased rapidly in response to increasing F (instantaneous fishing mortality rate) until F = 0.3-0.4. Thereafter, only small increases in yield resulted from large increases in F. Major gains in yield at all but very small values of F ($F \leq 0.15$), resulted if recruitment to the fishery was delayed to age 3 or older. The value of M (instantaneous natural mortality rate) affected the magnitude of yield/recruit but had little effect on the shape of the response surfaces.

The annual total recreational and commercial catches of reef fishes provides a preliminary estimate of maximum sustainable yield if the following assumptions are accepted: 1) $F \ge 0.3$, 2) recruitment ages approximate those required to produce maximum yield per recruit, and 3) recruitment is sufficient to saturate the available habitat. Preliminary estimates of the relative fishing power (per day) of different components of the fishery are headboats, 1.0; commercial handline boats, 1.3-1.5; and reef trawlers, 3.8-5.2.

In this paper we examine the implications of yield per recruit models to management of the reef fishery in the South Atlantic Bight. We examined models for each of the several important species in this fishery to determine if there was a single pattern of yield response that, in turn, would allow development of a coherent management philosophy.

The Fishery

Warm Gulf Stream-influenced water and irregular rocky substrates allow occupancy of the outer continental shelf of the U.S. South Atlantic Bight (Cape Hatteras to Cape Canaveral) by a community of primarily Caribbean, deep reef fishes. Principal species include groupers (*Mycteroperca* and *Epinephelus*), snappers (*Lutjanus* and *Rhomboplites*), porgies (*Calamus* and *Pagrus*), and grunts (*Haemulon*) (Huntsman 1976a). The black sea bass, *Centropristis striata*, is abundant at more temperate reefs nearer shore.

Reef fishes support both recreational and commercial fisheries in the area. About 40 headboats, about

260 charter boats (usually six passengers or fewer), and numerous private boats operate in the recreational fishery. The last two groups exert a greater fraction of the fishery effort in Georgia and Florida than in the Carolinas. The commercial fishery has two main segments-handline vessels and trawlers. Traps are also used occasionally, especially for black sea bass. Handline fishing is with hook and line retrieved by hydraulic or electric reel. Trawling is relatively new in the area and had little acceptance until Sea Grant programs in South Carolina and Georgia introduced the "high-rise" trawl in 1975 (Ulrich et al. 1977). When used by knowledgeable snapper fishermen skilled in fathometer reading, the high-rise trawl can be exceptionally effective in taking reef fish.

The magnitude of the recreational catch is only partly known. Headboats landed about 773 t annually from 1972 through 1974 at North Carolina and South Carolina ports (Huntsman 1976a), and the catch for the entire bight averaged 972 t from 1976 through 1980.³ Catches by charter and private boats are unknown, except for an estimate by Manooch et al. (1981) of the 1978 charter boat catch in North Carolina (about 91 t).

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The offshore commercial catch cannot be accurately calculated from commercial fishery statistics. In the Carolinas in 1973 and 1974 the headboat catch of snappers and groupers appeared to be 3 or 5 times greater (depending on the inclusion of vermilion snapper) than the commercial catch (Huntsman 1976b). Beginning in 1975 the commercial landings in the Carolinas increased greatly and were 836 t of snappers and groupers in 1980. Commercial snapper-grouper landings for the entire bight were 1,308 t for 1980.⁴

Both commercial and recreational fishermen prefer groupers and any of three species known in the trade as red snapper—*Lutjanus campechanus*, *L. vivanus*, and *L. buccanella*. Recreational fishermen and trawlers usually take whatever species is most available, but commercial handline fishermen often leave white grunts or red porgies and seek red snappers and groupers. Since 1976, however, commercial handline fishermen have responded to an improved market for small species by being less selective.

Potential Management Problems

Public Law 94-265 requires that fisheries within the United States extended jurisdiction zone (the area between 3 and 200 mi seaward of the U.S. coast) be managed so that an optimum yield is attained. Optimum yield is an allocation of the yearly harvest to recreational, commercial, and nonexploitive users that is usually equal to, or less than, the maximum sustainable yield (MSY). Minor conflicts and polarized viewpoints have arisen between the various users, primarily because of differing goals and differing methods of fishing. At present there is no objective way of allocating the catch among the various groups, because there is an insufficient understanding of stock productivity. Institutional provisions for the allocation of the catch exist, but the understanding of stock productivity necessary for the allocation is lacking.

Insight into stock productivity may be achieved through mathematical models. But neither the dynamic pool (Beverton and Holt 1957) nor the surplus-yield (Schaefer 1957) population models is presently useful to us because both require data that do not exist. The dynamic pool model requires parameter estimates (such as the relationship of stock size to recruitment) that are unavailable for the stocks involved and the surplus yield model requires a fairly long series of annual catch and effort measurements.

Despite initiation of fishery censuses in 1880, there is a lack of interpretable records of annual commercial catches for the South Atlantic snapper-grouper fishery. Serious problems in the data series include, among others:

- Missing or faulty species distinctions. At least 10 species of grouper are listed only as grouper, and porgies include both inshore estuarinedependent and oceanic reef species. The red snapper listing includes at least three species of *Lutjanus* and, depending on the year, may or may not include vermilion snapper, *Rhomboplites aurorubens*.
- 2) Missing records, often covering decades, in the series of records begun in 1880.
- Catches reported by area of landing instead of by area of fishing (e.g., snappers landed on Florida's east coast may have come from North Carolina or the Bahamas).
- 4) No useful or reliable effort data.

Matching catch and effort data available for the headboat fishery from 1972 to 1980 in North Carolina and South Carolina (Huntsman 1976a, b; footnote 3) and from 1976 to 1980 in Georgia and North Florida, (footnote 3) are nearly useless for yield-model construction without concurrent commercial data.

Enough information is available to develop an abbreviated version of the full dynamic pool model the yield per recruit model (Beverton and Holt 1957). The yield per recruit model, which can be used for partial analysis, is especially useful if one must prepare management schemes from incomplete information. An advantage of the yield per recruit model is that it has minimal requirements of parameter estimates but allows easy evaluation of the response of yield to changes in fishing mortality and recruitment age. Even if the exact relationship between effort and fishing mortality is unknown, one can derive general information on which to base management regulations.

The yield per recruit model predicts the ratio of the weight or numbers of fish caught during the life span of a cohort to the initial number of individuals of the cohort that enter the fishing grounds. It expresses these yields as a surface responding to the independent variables F (instantaneous fishing mortality rate) and t_r (age at recruitment to the gear). The growth rate, natural mortality rate, and longevity of the species are the principal parameters influencing the shape of the surface.

⁴Unpublished data, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, Miami, FL 33149-1099.

Yield per recruit models may be especially appropriate to the snapper-grouper fishery, because carrying capacity and growth, rather than recruitment, are apparently the principal limiting factors (Ehrlich 1975). Since reef habitat occupies a relatively small proportion of the outer continental shelf (Parker and Colby in press), recruitment is probably always sufficient to replace losses from fishing mortality and natural mortality. New reefs, such as wrecks and artificial fishing reefs, are almost immediately colonized (Anonymous 1971; Stone et al. 1979; Stone⁵).

MATERIALS AND METHODS

Species Studied

Species were selected on the basis of their importance to the recreational and commercial catch and, to a lesser extent, on the amount and quality of information available. Huntsman's (1976a, b) and Huntsman and Dixon's (1976) descriptions of the headboat fishery, and Ulrich et al.'s (1977) description of the handline and trawl fisheries suggested the inclusion of:

- 1) red porgy, Pagrus pagrus;
- 2) vermilion snapper, Rhomboplites aurorubens;
- 3) white grunt, Haemulon plumieri;
- 4) red snapper, Lutjanus campechanus;
- 5) black sea bass, Centropristis striata;
- 6) Epinephelus groupers (the important species are the speckled hind, E. drummondhayi, and snowy grouper E. niveatus);
- Mycteroperca groupers (gag, M. microlepis, and scamp, M. phenax, are the most important species).

Estimates of Growth and Mortality Parameters

In general, reliable estimates of growth parameters are available (Table 1) from both published and unpublished sources. Reliable estimates of M(instantaneous natural mortality rate) are not available. Determining M is a difficult but common problem solved by many authors by assuming single (Low 1981) or multiple (Houde 1977a, b; Chittenden 1977; Breiwick et al. 1980; Lenarz et al. 1974) values. M can be reasonably estimated by computed estimates of Z (instantaneous total mortality rate), which provide maximum estimates of M, and by the relationship of growth parameters to M, described generally by Beverton and Holt (1959) and more specifically by Pauly (1980-81).

For most species we provided two or more estimates (Table 1), one of which was, or was very close to, the Pauly estimate. For three groupers (scamp, snowy grouper, and speckled hind), we used only the Pauly estimate because the other analyses indicated that changing M had little effect on the pattern of yield response.

Yield Per Recruit Computations

Computer program BM007,⁶ which requires a relatively small amount of memory, is written in FORTRAN and can be used on most computer systems for calculating yields per recruit. The program output is tabular and must be transposed by hand to graph paper if isometric yield lines are to be drawn.

$$Y/R = FW_{\infty} \left(\frac{1 - e^{-Z\lambda}}{Z} - \frac{3e^{-Kr}(1 - e^{-(Z+k)\lambda})}{Z+K} + \frac{3e^{-2Kr}(1 - e^{-(Z+2K)\lambda})}{Z+2K} - \frac{e^{-3Kr}(1 - e^{-(Z+3K)\lambda})}{Z+3K}\right)$$

,			
and	t _r	=	age at recruitment to the gear
	t _o	=	theoretical age at length "0"
	t_{λ}	==	maximum age in fishery
	F	====	instantaneous rate of fishing mor-
			tality
	М	=	instantaneous rate of natural mor-
			tality
	Z	=	instantaneous rate of total mortal-
			ity, $M + F$
	L_{∞}		asymptotic length of a fish
	W_{∞}	==	asymptotic weight of a fish
	K		growth coefficient from von Berta-
			lanffy growth equation for length
	r	-	$t_r - t_0$, theoretical age of cohort en-
			tering fishery
	λ	_	$t_{\lambda} - t_{\nu}$, amount of time cohort is in
	••		fishery
	Y	_	5
	1	_	yield in weight

- R = number of recruits at t_r
- Y/R = yield per recruit.

³R. B. Stone, Office of Fisheries Management, National Marine Fisheries Service, NOAA, Washington, DC 20235, pers. commun. 1975.

⁶Written by John E. Hollingsworth, Southeast Fisheries Center Beaufort Laboratory, NMFS, NOAA, Beaufort, NC 28516-9722 and Larry L. Massey, Southeast Fisheries Center, NMFS, NOAA, Virginia Key, Miami, FL 33144-1099.

							von Bertalanffy parameters						
Species	ĸ	L∞ (mm)	to (yr)	Source	8	b	Source	м	Source	۲ _۲ (۲۲)	Source	τλ (γη	Source
Red porgy. Pagrus pagrus	0.096	763	-1.88	Manooch and Huntsman 1977	2.524 × 10 ⁸	2.8939	Manooch and Huntsman 1977	0.35	Catch curves (Manooch and Huntsman 1977)	1	Manooch and Huntsman 1977	13	Manooch and Huntsman 1977
Vermilion snapper, Rhomboplites aurorubens	0.198	627	0.13	Grimes 1978	1,722 × 10 ⁻⁸	2.9456	Grimes 1978	0.20 0.25 0.40	Relationship to K Relationship to K For sensitivity analysis	1	Grimes 1978	10	Grimes 1978
								0.50	Catch curve minimum				
White grunt, <i>Haemulon</i> aurolineatum	0.108	640	-1.01	Manooch 1977	1,452 × 10 ⁻⁸	3.0214	Manooch 1977	0.57 0.30	Catch curves Choice of lower values for sensitivity analysis	2	Manooch 1977	13	Manooch 1977
Red snapper, Lutjanus campechanus L vivanus L buccanella	0.160	975	0.00	Nelson and Manoch 1982	315 × 10 ⁻⁷	2.887	Nelson and Manooch 1982	0.16 0.25 0.34 0.40	Relationship to K Higher value sensitivity analysis Pauly 1980-81 Higher value for sensitivity analysis	1	Nelson and Manooch 1982	16	Nelson and Manooch 1982
Black sea bass, Centropristes striatus	0.219	350	0.183	Mercer 1978 (Based on standard length ¹)	2,654 × 10 ^{−8}	3.024	Cupka et al. 1973	0.30 0.50	Relationship to K and \mathcal{T}_{λ} For sensitivity	1	Cupka et al. 1973	10	Cupka et al. 1973
Speckled hind, Epinephelus drummondhayi	1,100.088	1,105	-1.92	Matheson and Huntsman ²	1.1 × 10 ⁻⁸	3.073	Matheson and Huntsman ²	0.20	analysis Pauly (1980-81) estimate Matheson and Huntsman ²	1	Matheson and Huntsman ²	25	Matheson and Huntsman ²
Snowy grouper, Epinephelus niveatus	0.063	1.350	-2.32	Matheson and Huntsman ²	7.0×10 ⁸	2.755	Matheson and Huntsman ²	0.13	Pauly (1980-81) estimate Matheson and Huntsman ²	1	Matheson and Huntsman ²	25	Matheson and Huntsman ²
Gag, Mycteroperca microlepis	0.112	1,290	-1.13	Manooch and Haimovici 1978	12 × 10 ^{−7}	2.996	Manooch and Haimovici 1978	0.20 0.35	Relationship to K Higher value for sensitivity analysis	1	Manooch and Haimovici 1978	13	Manooch and Haimovici 1978
Scamp, Mycteroperca phenax	0.067	1,090	-3.91	Matheson et al. ³	2,400 × 10 ⁸	2.910	Matheson et al. ³	0.17	Pauly (1980-81) estimate Matheson et al. ³	1	Matheson et al. ³	25	Matheson et al. ³

TABLE 1.—Parameter estimates for yield per recruit models.

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¹TL = -11.2 + 1.34 SL (Cupka et al. 1973).

² R. H. Matheson, and G. R. Huntsman. 1983. Growth, mortality, and yield per recruit models for speckled hind, *Epinephelus drummondhayi*, and snowy grouper, E. niveatus, from the U.S. South Atlantic Bight. Unpubl. manuscr., 13 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

³R. H. Matheson III, C. S. Manooch III, and G. R. Huntsman. 1983. Growth, mortality, and yield per recruit models for the scamp, Mycteroperca phenax. Unpubl. manuscr., 14 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOA, Beaufort, NC 28516-9722. Parameters t_0 and K are derived from the von Bertalanffy (1938) growth equation, and W_{∞} is estimated as the weight corresponding to the asymptotic length (L_{∞}) based on a length-weight regression. Growth was assumed to be isometric.

The Beverton and Holt model implies instantaneous or "knife edge" recruitment with respect to age. Knife edge recruitment is not an apparent attribute of the hook-and-line fishery for at least two reasons. First, relatively large variation in size of fish of a single nominal age (resulting in part from long spawning seasons, e.g., vermilion snapper, Grimes and Huntsman 1980) makes it difficult to specify the initial age of capture. Second, the probability of a fish being taken by hook appears to increase somewhat more gradually with size than do probabilities associated with other gears.

Specifying an age at first recruitment is critical to determining the yield being taken from a stock. We believe that the mean age of recruitment provides a practical estimate of recruitment age for species which enter fisheries gradually.

Determination of Mean Age at Recruitment

Computation of mean age at recruitment occurs in three steps:

1) A minimum size at which fish first become vulnerable to the gear is determined from inspection of catch length frequencies. We designated the lower limit of the first class interval containing substantial numbers (usually five or more) of observations as the minimum size of vulnerability. This designation was usually unambiguous, but for species where it was not we evaluated more than one size.

- 2) The probability that a fish of a given age will equal or exceed the minimum size of vulnerability is determined on the assumption of a normal distribution of lengths about the mean length at age.
- 3) The probability for each age is multiplied by the numerical age value (e.g., 0.5×3). The products and probabilities are summed over all ages and the sum of the products is divided by the sum of the probabilities. The success of this treatment depends on exclusion from the calculations of ages beyond the first age at which all ($P \ge 0.99$) fish are vulnerable.

The estimation described here should be successful if the specified minimum size at vulnerability is accurate and if the relationship between size and recruitment is strong.

RESULTS

Regardless of the estimate of M, all models had a strikingly similar response to F (Table 2, Figs. 1-18). For median recruitment ages there was a rapid increase in yield as F increased, then an abrupt change as the rate of increase in yield declined at about F = 0.3, and finally a broad plateau of yield near the maximum. In general the absolute maximum yield per recruit was attained at a very high F relative to that needed to achieve 80 to 90% of the maximum yield. At the lowest estimate of M for all species examined, about 87%, on the average, of the maximum yield could be taken with an F = 0.3, which is

TABLE 2.—Summary of yield per recruit (γ/R) models for South Atlantic reef fish. M = instantaneous rate of natural mortality; F = instantaneous rate of fishing mortality; $t_r =$ age at recruitment to the gear.

Species	For the model with M =	Maximal <i>Y/R</i> (g)	Where F =	and $t_r =$	At <i>F</i> =	and $t_r =$	<i>Y/R</i> is (q)	Percent max. Y/R	At $F =$	and $t_r =$	Y/R is (g)	Percent max. <i>Y/R</i>	Fig. no.
Red porgy	0.35	150	0.80	2.9-4.0	0.50	≤5.5	130	87	0.50-0.30	1.0-5.6	110	73	1
	0.20	300	0.50	5.5-7.3	0.10	3.0-7.5	225	75					2
Vermilion	0.50	100	1.75	3.5-4.0	0.70	2.5-4.0	90	90	0.40	2.5-4.0	80	80	3
snapper	0.40	140	1.50	4.0-4.5	0.65	1.5-3.5	130	93	0.45	1.5-3.5	120	86	4
	0.25	250	0.55	4.5-5.0	0.30	2.5-5.5	200	80					5
White grunt	0.30	180	0.60	4.0-5.0	0.30	2.5-5.0	160	88	0.20	2.0-5.0	140	78	6
	0.57	30	0.55	4.5	0.25	2.7-5.0	25	83					7
Red snapper	0.16	1,600	0.50	6.5-8.0	0.30	5.5-7.5	1,500	94	0.20	4.0-7.5	1,300	81	8
	0.25	900	0.50	≥5.0	0.30	4.0-5.0	800	88	0.20	3.0-6.5	700	78	9
	0.34	550	0.60	4.0-4.5	0.38	3.5-4.5	500	91	0.20	2.0-5.0	400	73	10
	0.40	400	0.45	3.0-4.5	0.20	2.0-5.0	300	75					11
Black sea bass	0.50	50	0.90	2.5-3.5	0.30	2.5	40	80	0.20	1.0-3.5	30	60	12
	0.30	100	0.70	4.0	0.30	2.5-5.0	80	80					13
Speckled hind	0.20	1,200	0.50	5.0-7.0	0.25	4.0-7.0	1,100	92	0.19	3.0-7.0	1,000	83	14
Snowy grouper	0.13	1,300	0.38	9.0-11.0	0.20	7.0-10.0	1,200	92	0.15	5.0-11.0	1,100	85	15
Gag	0.35	900	3.25	4.5	0.70	3.5	850	94	0.30	2.0-4.8	700	78	16
	0.20	1,875	2.20	7.0	0.70	5.5-7.0	1,800	96	0.35	4.0-7.0	1,600	85	17
Scamp	0.17	900	0.72	6.5	0.23	3.0-7.0	800	89	0.15	1.0-8.0	700	78	18



FIGURE 1.—Yield per recruit in weight of red porgy where M = 0.35.

less than half the average F needed to take the maximum. At the lower estimates of M for white grunt, vermilion snapper, red porgy, and black sea bass those species that supply the greatest numbers and most weight to the headboat catch—86, 80, 92, and 80%, respectively, of the maximum yield can be taken with an F = 0.3. This is only 50, 55, 60, and 43% of F



FIGURE 3.—Yield per recruit in weight of vermilion snapper where M = 0.50.

FIGURE 2.—Yield per recruit in weight of red porgy where M = 0.20.



of vermilion snapper where M = 0.25.

needed to take the maximum. At the highest estimates of M, 73, 60, 83, and 90% of maximum yield can be taken with an F of 0.3, which is 55, 17, 38, and 33%, respectively, of the effort needed for maximum yield.

For less numerous, larger species, conservative harvest strategies would be even more successful than for smaller fishes. For instance, for speckled hind, snowy grouper, scamp, and for gag and red snapper at their lowest M estimates, 94, 95, 89, 94, and 78% of the maximal yield per recruit can be taken if F = 0.3 which is 60, 79, 42, 14, and 60% of the F required to take that maximum. Even at the high estimate of M for gag and red snapper, 78 and 88% of the maximal yield per recruit are available if F = 0.3. This F is only 9 and 42% of that needed to take the maximum.

While the absolute relationship of recruitment age to yield varies according to species, it is true for all species that the lower the fishing mortality, the greater the range of recruitment ages at which the highest available yield may be taken. At F = 0.3, recruitment age, regardless of M, could range over 4 or more years for 9 of the 18 models without substantial loss of yield; for the remaining models it could range over 3 yr.





White Grunt M. 0.30 Yield Per Recruit in Weight

FIGURE 6.—Yield per recruit in weight of white grunt where M = 0.30.

It is apparent that on a yield per recruit basis the fishery response to an increase in F is a nonlinear decrease in catch per unit effort (CPUE). The CPUE decreases most rapidly after F exceeds about 0.3 for most species. Further, the range of recruitment ages at which any given yield is available increases rapidly as F decreases.

STATUS OF THE FISHERY

Despite slight differences in the periods when each species was studied, reasonable generalizations can be made about the state of reef fish stocks off North Carolina and South Carolina in the mid to late 1970's.



FIGURE 7.—Yield per recruit in weight of white grunt where M = 0.57.

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GURE 9.— Yield per recruit in weight of red snappe where M = 0.25.

F



Red Snapper

M= 0.34

FISHING MORTALITY (F)

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FIGURE 12.—Yield per recruit in weight of black sea bass where M = 0.5.

Regardless of the M estimates chosen, of the recruitment ages specified, or of whether the recreational or commercial fishery is discussed, it is apparent that most of the important species in the headboat fishery were providing the bulk of their readily available yield per recruit (Table 3). At the lowest M estimates all species studied (except deep water black sea bass) were subjected to sufficient fishing mortality on the headboat grounds to provide at least 70% (mean = 87%) of the maximal yield per recruit. Even at the estimates provided by the highest M values and least favorable recruitment ages, 50% or more (mean = 68%) of the maximal yield per recruit was taken for all species except red snapper (40%).

Stocks available to the commercial fishery (including those on the headboat grounds) were similarly exploited. At the lowest M estimates, at least 70% of the maximal yield per recruit was harvested for all species (black sea bass and white grunt were not taken commercially) except speckled hind for which 50% was taken. The mean for all species was 81%. At the high M estimates, 40% was the minimum taken (for red snapper) and the mean for all commercial species was 67%.

It appears that by the late 1970's most of the practically available yield was being taken from the grounds fished at that time. Several species were incurring sufficient F to provide virtually all the yield per recruit possible while F for most others was at the level beyond which increased yield per recruit comes only with very large increases in effort and concomitant large decreases in CPUE.

DISCUSSION

Any value of our models lies in their utility to management of reef fish stocks. Some information about management can be derived directly from the models without resort to adjunct information; for instance, the models alone reveal that if recruitment age can be kept moderately high, yield per recruit will stay high regardless of how great F becomes. Thus protection of yield per recruit can be obtained without having to know what F is, or without having to



FIGURE 13.—Yield per recruit in weight of black sea bass where M = 0.3.







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FIGURE 15.—Yield per recruit in weight of snowy grouper where M = 0.13 (from Matheson and Huntsman, see Table 1).

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TABLE 3.—Status of fishery. $M =$ instantaneous rate of natural mortality; $F =$ instantaneous rate of fishing mortality; $Z = F + M$ instan-
taneous rate of total mortality; Y/R = yield per recruit.

	М	<u>Z</u>				Recruitment	Age	Y/R available		Percent
Species	estimates	Value	Period	Source	Fishery	size (mm)	(71)	at F =	g	max. Y/A
Red porgy	0.20	0.65	1972-74	Manooch and	Headboat	300	4.1	0.30	120	80
	0.35			Huntsman 1977		07		0.45	280	93
						325	4.3	0.30	120	80
					6		4.1	0.45	290	97
					Commercial	300		0.30	120	80
					handline Commercial	200	2.1	0.45 0.30	280 125	93 83
					trawl	200 or	2.6	0.30	225	75
					11 d VVI	250	2.0	0.45	125	83
						200			250	83
Vermilion	0.25	0.67	1972-73	Grimes,	Headboat	225	3.5	0.32	225	90
snapper	0.40			pers.		or		0.27	100	71
	0.50			commun.1		250		0.17	60	60
						200	3.8	0.32	225	90
								0.27	100	71
								0.17	60	60
					Commercial	300	4.5	0.32	225	90
					Handline			0.27	100	71
								0.17	60	60
					Commercial	200	3.3	0.32	225	90
					trawl			0.27	100	71
								0.17	60	60
White grunt	0.30	0.73	1972-75	Manooch 1977	Headboat	250	4.4	0.43	175	92
	0.57					or		0.16	15	50
						300	5.9	0.43	170	90
					.			0.16	15	50
					Commercial handline and trawl	speci rarely ta				
Red snapper	0.16	0.38	1974-78	Nelson and	Headboat and	500	6.0	0.22	1,300	81
neu anappei	0.10	0.36	13/4-70	Manooch 1982	commercial	500	6.0	0.13	575	64
	0.34 (²)			Manooch 1982	handline			0.04	200	40
	()				Commercial	450	5.0	0.22	1,300	81
					trawl	450	0.0	0.13	500	56
								0.04	200	40
Black sea	0.30	0.83	1978	Low 1981	Headboat	400	4.0	0.53 shallow	98	98
bass		(depth						0.30 deep	80	80
		<40m) 0.60 (depth >40M)			Commercial handline and trawl	species i takei				
	0.50				Headboat	40	4.0	0.33 shallow	35	70
								0.10 deep	10	20
Speckled hind	0.20	0.35	1976-79 headboat	Matheson and Huntsman ³	All fisheries	365	3.3	0.15	950	79
		0.25	1976-79 commercia! handline					0.05	600	50
Snowy grouper	0.13	0.38	1976-79 headboat	Matheson and Huntsman ³		365	3.3	0.25	950	73
		0.24	1976-79 commercial	nunsman				0.11	920	70
Gag	0.20	No	handline	Manooch and	Headboat	_	1.0	⁴ 0.36	1,050	58
		estimate ⁴		Haimovici 1978	Commercial	750	6.6	40.68	1.800	100
					handline	800	8.0	40.68	1,700	94
	0.36		1978-79		Headboat	-	1.0	40.36	650	67
			commercial		Commercial	-	6.6	40.68	650	72
_			handline		handline		8.0	40.68	480	53
Scamp	0.17	0.53	1976-79 headboat	Matheson et al. ⁵	Headboat 1972-75	500	5.4	0.36	850	94
			1976-79		Headboat 1977-79	350	3.1	0.36	800	89
		0.85	commercial handline		Commercial handline	400	4.0	0.68	900	100

¹Churchill B. Grimes, Department of Horticulture and Forestry, Rutgers University, P.O. Box 231, New Brunswick, NJ 08903. ²M of 0.40 omitted because it was greater than estimated F.

³R. H. Matheson, and G. R. Huntsman. 1983. Growth, mortality, and yield per recruit models for speckled hind (Epinephelus drummondheyi) and snowy grouper (E. niveatus) from the U.S. South Atlantic Bight Unpubl. manuscr. 13 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-

from the U.S. South Atlantic Bight Unpubl. manuscr. 13 p. Southeast Fisheries Center Descript Lauviatory, national manuscr. Islands Cartes, national 9722. 9722. ⁴F for gag assumed to be same as for scamp which occupies same habitat and is taken simultaneously with same gear. ⁵R. H. Matheson III, C. S Manooch III, and G. R. Huntsman. 1983. Growth, mortality, and yield per recruit models for the scamp, *Mycteroperca phenax*. Unpubl. manuscr., 14 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.



F

weight of gag where M = 0.20.



FIGURE 18.—Yield per recruit in weight of scamp where M = 0.17 (from Matheson, Manooch and Huntsman, see Table 1).

For instance, we believe that our yield per recruit models allow preliminary estimates of MSY, estimates required in fishery management plans promulgated under the Fishery Conservation and Management Act. Current catches are an estimate of MSY if three fairly safe assumptions, concerning fishing effort, amount of recruitment, and recruitment ages, are fulfilled. The first is that current effort is sufficient to take most of the yield. As early as 1975, F for most important species was great enough that 70 to 85% of the maximum yield was taken. The most cursory observation would reveal that commercial fishing has increased an enormous amount since 1976. Consequently F should now be more than sufficient to take all the yield practically available. The second assumption is that recruitment was sufficient to fully populate the reefs. The major factor limiting reef fish abundance is the scarcity of habitat (Ehrlich 1975), rather than scarcity of recruits. Reef fishes in general have long-lived larval stages allowing replenishment of local populations from distant spawning stocks. Observations of natural and artificial reefs suggest that recruits are almost always abundant (e.g., Anonymous 1971; Stone et al. 1979). The third assumption is that recruitment ages remain within a range that will allow maximum yields. It appears that current recruitment ages for major species either are within, or close to, this range.

Allocation of the catch to various sectors of the fishery may eventually become important. Allocators

will need to understand the relative impact of various types of gear on the stock and the relationship between effort and mortality. To provide a preliminary estimate of relative impact, we calculated a crude measure of the relative fishing power of the three most important vessel types in the Carolina area. Handline vessels operating from South Carolina ports averaged 321 kg/d (Ulrich et al. 1977), "highrise" trawlers took 958 kg, and headboats caught 208 to 250 kg (Huntsman 1976b; Huntsman et al 1978). Thus handline boats were about 1.3 to 1.5 times as effective and trawlers about 3.8 to 5.2 times as effective as headboats. We cannot perfectly equate the three types, however, because each takes different species (Ulrich et al. 1977).

The disparity in species vulnerability might allow partitioning the resource without conflict—red snapper to trawlers; groupers to handliners; porgies, grunts, and vermilion snapper to headboats. But we do not believe such partitioning is desirable. Large trophy fish constitute only a small portion of the headboat catch but are probably extremely important in motivating the fishermen. Further we believe pursuit of large fish catalyzes the taking of smaller and more abundant species in offshore areas. Only about 30,000 groupers and red snapper (totaling about 182 t) were taken annually by headboats in North Carolina and South Carolina from 1972 to 1974, compared with some 400,000 individuals of other species (excluding black sea bass) totaling about 409 t (Huntsman 1976b). If the opportunity for catching large fish were removed, anglers might prefer to patronize smaller and less expensive boats that fish inshore where large catches of smaller fish can also be made.

Relating fishing mortality to fishing effort is difficult because we lack a long series of concurrent effort and mortality estimates. Catch curves for red porgy, vermilion snapper, and white grunt suggest that if M is indeed low, F through 1974 was about 0.3 to 0.4 and was mostly attributable to headboats. Headboat activity for North Carolina and South Carolina was reported as 48,989 angler days in 1972, 59,515 in 1973, and 85,608 in 1974 (Huntsman 1976a). Because we know effort was underestimated, we used the 1975 data to determine the percentage of vessels omitted in earlier years. Our adjusted estimates for 1972, 1973, and 1974 were 71,902, 85,561, and 88,513 angler days, respectively. The 3yr mean was 81,922, corresponding to about 2,350 headboat trips (using the 1974 average of 34.87 anglers/trip). We suggest than an F of about 0.35 was generated by this effort.

Because F on the headboat grounds was quite likely 0.3 to 0.4 in the period 1972-74, the annual catch (450 to 600 t exclusive of black sea bass) for that period should be an estimate of MSY. This catch could be taken with about 2,350 headboat trips (1 d), 1,679 handline vessel days (1.0 handline vessel day = 1.4 headboat day), 522 d of trawling (the range is 452 to 618 d depending on the coversion factor selected), or with some combination of these vessel efforts. Additionally, a headboat fishery at the 1972-74 level should take about 273 t of black sea bass, if the trap fishery remained at the 1972-74 level.

It should not be surprising that near-maximum yields could be taken by a small and apparently inefficient fishery. Historically, reef fish stocks have been vulnerable even to primitive fisheries. Munro et al. (1971) described Jamaica's reef fish stock as overexploited. Brownell and Rainey (1971) reported that inshore reef fishes in the U.S. Virgin Islands were heavily fished, even though handlines and primitive traps fished from unpowered vessels were the only gear. The hook-and-line red snapper fishery in the northern Gulf of Mexico has been sustained by constant expansion of the fishing grounds rather than by continued good catches on existing grounds (Crowley 1983).

Continued laissez-faire management of the snapper-grouper fishery may result in a disproportionate allocation of the catch. If the trawl and handline sectors reduce the abundance of large species to such a level that an acceptable CPUE of trophy fish cannot be experienced by headboat fishermen, the headboat fishery might be weakened. During hundreds of hours spent mingling with the public while sampling headboat catches, we have observed that large (>10 kg) snappers and groupers are very important in promoting headboat ticket sales. Many headboat operators use mounted specimens of large fish to attract customers. Headboat fishing is arduous and expensive (40-50/d in 1982) and large catches of small fish can usually be made easily and cheaply from piers and small boats in the Carolinas.

In this paper we have employed yield per recruit models to suggest guidelines for managing the South Atlantic Bight reef fishery. We believe that we have shown that large and intensive fisheries probably are not needed to fully harvest reef fish in the South Atlantic Bight and that the Carolina headboat fishing grounds are probably fully exploited. A low intensity fishery should take most of the yield available, produce large, high value fish, and allow a sufficient number of fish to live to ages of maturity and sexual transition to allow sustained high yields.

LITERATURE CITED

ANONYMOUS.

- 1971. Small fish sighted on artificial reef near Adelaide. Aust. Fish. 30 (2):12-13.
- BEVERTON, R. J. H., AND S. J. HOLT.
 - 1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.) Ser. II, 19, 533 p.
 - 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In G. E. Wolstenholme and M. O'Connor (editors), The lifespan of animals, p. 142-180. Little and Brown, Boston.
- BREIWICK, J. M., E. D. MITCHELL, AND D. G. CHAPMAN.
 - 1980. Estimated initial population size of the Bering Sea stock of bowhead whale, *Balaena mysticetus*: an iterative method. Fish. Bull., U.S. 78:843-853.

BROWNELL, W. N., AND W. E. RAINEY.

1971. Research and development of deepwater commercial and sport fisheries around the Virgin Islands plateau. Caribb. Res. Inst. V.I. Ecol. Res. Stn., Contrib. 3, 88 p.

CHITTENDEN, M. E., JR.

1977. Simulations of the effects of fishing on the Atlantic croaker, *Micropogon undulatus*. Proc. Gulf Caribb. Fish. Inst. 29:68-86.

CROWLEY, M.

1983. Management plan still in limbo as red snapper landings drop. Natl. Fisherman 63(2):10-11.

CUPKA, D. M., R. K. DIAS, AND J. TUCKER.

- 1973. Biology of the black sea bass, *Centropristis striata* (Pisces: Serranidae) from South Carolina waters. Completion report, Commercial Fisheries Research and Development Act PL 88-309, Project No. 2-138-R, South Carolina, [91] p.
- EHRLICH, P. L.

^{1975.} The population biology of coral reef fishes. Annu. Rev.

Ecol. Syst. 6:211-247.

GRIMES, C. B.

- 1978. Age, growth and length-weight relationship of vermilion snapper, *Rhomboplites aurorubens* from North Carolina and South Carolina waters. Trans. Am. Fish. Soc. 107:454-456.
- GRIMES, C. B., AND G. R. HUNTSMAN.
 - 1980. Reproductive biology of the vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina. Fish. Bull., U.S. 78:137-146.
- HOUDE, E. D.
 - 1977a. Abundance and potential yield of round herring, *Etrumeus teres*, and aspects of its early life history in the eastern Gulf of Mexico. Fish. Bull, U.S. 75:61-89.
 - 1977b. Abundance and potential yield of Atlantic thread herring, *Opisthonema oglinum*, and aspects of its early life history in the eastern Gulf of Mexico. Fish. Bull., U.S. 75:493-512.
- HUNTSMAN, G. R.
 - 1976a. Offshore headboat fishing in North Carolina and South Carolina. Mar. Fish. Rev. 38(3):13-23.
 - 1976b. Offshore bottom fisheries of the United States south Atlantic coast. In H. R. Bullis and A. C. Jones (editors), Proceedings: Colloquium on snapper-grouper fishery resources of the western central Atlantic Ocean, p. 192-221. Fla. Sea Grant Program Rep. 17.

HUNTSMAN, G. R., D. R. COLBY, AND R. L. DIXON.

1978. Measuring catches in the Carolina headboat fishery. Trans. Am. Fish. Soc. 107:241-245.

HUNTSMAN, G. R., AND R. L. DIXON.

- 1976. Recreational catches of four species of groupers in the Carolina headboat fishery. Proc. 29th Annu. Conf. Southeast. Assoc. Game Fish Comm. 29:185-194.
- LENARZ, W. H., W. W. FOX, JR., G. T. SAKAGAWA, AND B. J. ROTHSCHILD.
 - 1974. An examination of the yield per recruit basis for a minimum size regulation for Atlantic yellowfin tuna, *Thunnus albacares*. Fish. Bull., U.S. 72:37-61.

Low, R. A., Jr.

1981. Mortality rates and management strategies for black sea bass off the southeast coast of the United States. North Am. J. Fish. Manage. 1:93-103.

MANOOCH, C. S., III.

1977. Age, growth, and mortality of the white grunt, Haemulon plumieri Lacépède (Pisces: Pomadasyidae), from North Carolina and South Carolina. Proc. 30th Annu. conf. Southeast. Assoc. Fish Wildl. Agencies 30:58-70.

1981. A biological and economic analysis of the North Car-

olina charter boat fishery. Mar. Fish. Rev. 43(8):1-11.

- MANOOCH, C. S., III, AND M. HAIMOVICI.
 - 1978. Age and growth of the gag, Mycteroperca microlepsis, and size-age composition of the recreational catch off the southeastern United States. Trans. Am. Fish. Soc. 107:234-240.
- MANOOCH, C. S., III, AND G. R. HUNTSMAN.

1977. Age, growth, and mortality of the red porgy, *Pagrus pagrus*. Trans. Am. Fish. Soc. 106:26-33.

MERCER, L. P.

1978. The reproductive biology and population dynamics of black sea bass, *Centropristis striata*. Ph.D. Thesis, College of William and Mary, Williamsburg, Va., 195 p.

MUNRO, J. L., P. H. REESON, AND V. C. GAUT.

1971. Dynamic factors affecting the performance of the Antillean fish trap. Gulf Caribb. Fish. Inst., Proc. 23d Annu. Sess., p. 184-194.

NELSON, R. S., AND C. S. MANOOCH III.

1982. Growth and mortality of the red snapper, Lutjanus campechanus, in the west-central Atlantic and northern Gulf of Mexico. Trans. Am. Fish. Soc. 111:465-475.

PARKER, R. O., JR., AND D. R. COLBY.

In press. Estimated amount of reef habitat on U.S. South Atlantic and Gulf of Mexico continental shelf. Bull. Mar. Sci.

PAULY, D.

RICKER, W. E.

- 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191, 382 p.
- SCHAEFER, M. B.
 - 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 2:245-285.
- STONE, R. B., H. L. PRATT, R. O. PARKER, JR., AND G. E. DAVIS. 1979. A comparison of fish populations on an artificial and natural reef in the Florida Keys. Mar. Fish. Rev. 41(9):1-11.
- ULRICH, G. F., R. J. RHODES, AND K. J. ROBERTS.
 - 1977. Status of the commercial snapper-grouper fisheries off South Carolina. Proc. Gulf Caribb. Fish. Inst. 29:102-125.

VON BERTALANFFY, L.

1938. A quantitative theory of organic growth. II. Inquiries on growth laws. Hum. Biol. 110:181-213.

MANOOCH, C. S., III, L. E. ABBAS, AND J. L. ROSS.

^{1980-81.} On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 39:175-192.