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Simulation of the Impact of Fishing on Reproduction of a Protogynous Grouper, the Graysby

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Abstract.—To determine if protogynous species are, as a result of fishing, more likely to suffer reproductive failure than are gonochoristic species, we modeled the production of fertilized eggs in simulated populations of graysby *Epinephelus cruentatus*. Additionally, we examined the effect of various compensatory mechanisms on maintaining fertilized-egg production despite increasing fishing mortality. These mechanisms included accelerated maturation, accelerated transition to malehood, accelerated growth, and combinations thereof. Protogynous stocks may be far more vulnerable to fishing than are comparable gonochoristic stocks. Stocks exhibiting uncompensated protogyny lost reproductive capacity as fishing mortality increased and failed reproductively (egg production less than 1% of that under natural mortality alone) at a lower fishing mortality rate than did gonochoristic stocks. Compensation through conservation of the numerical sex ratio somewhat reduced the impact of protogyny, and compensation through conservation of the cohort male biomass : fecundity ratio erased all effects of protogyny. All the modeled stocks incurred a drastic reduction in reproductive capacity even at moderate levels of fishing mortality. Delaying harvest of a cohort not only provides increased yield per recruit but also reduces the loss of reproductive capacity caused by fishing.

In this paper we use simulation models to investigate the effects of fishing on the reproductive capacity of populations of a protogynous fish, the graysby *Epinephelus cruentatus*. In addition, we examine a yield-per-recruit model for the graysby and compare the yield-per-recruit model's fishery management implications with those derived from our protogyny–fishing simulation models.

Protogyny is a form of hermaphroditism in which most, if not all, individuals begin life as females and subsequently become males. In some grouper populations substantial numbers of males do not appear until the cohort is 10 years old, and the cohort sex ratio is not equal until age 15 (e.g., *E. morio*; Moe 1969). Many species of grouper attain ages of greater than 20 years (Manooch 1987).

Reef fishery managers have a general concern that fishing might affect the reproductive capacity of protogynous fish stocks more severely than it affects stocks with normal bisexual reproduction (gonochorism; Smith 1982). Protogynous as well as gonochoristic populations tend to lose reproductive capacity as fishing increases because of decrease in stock biomass and, consequently, in egg production. A major concern for protogynous stocks, however, is that increased fishing mortality, by reducing the abundance of older age-classes, might reduce the relative abundance of males and diminish the probability that eggs will be successfully fertilized (Reinboth 1980; Garratt 1985; Buxton and Clarke 1986). In the extreme, fishing might remove all the age-classes that contain males and totally preclude reproduction.

The exploration by Bannerot et al. (1987) of the relationship between protogyny and susceptibility to overfishing revealed that a limited sperm supply rendered protogynous populations more vulnerable to overexploitation than it did gonochoristic populations. Our study begins with the assumption that quantity of sperm can limit reproduction. We proceed further to determine if any of various biological mechanisms that might compensate for removal of males can protect reproductive success of populations.

Evidence exists (e.g., Ross 1981; Shapiro 1981; Nemtzov 1985) that some protogynous reef fish compensate for the removal of males from their populations. For instance, a large female may rapidly become male when the dominant male is removed from the local assemblage. It is largely accepted today that such contingency-based transitions in gender enhance the evolutionary fitness (reproductive potential) of the individual that transforms, not necessarily of the group of which that individual is a member. It is not the purpose of this paper to argue whether sex change is an

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aspect of individual or of group fitness. We wish to explore only whether contingency-based transitions, which are clearly demonstrated to occur in nature, could have any ameliorating effect on the loss of reproductive capability of protogynous stocks enduring fishing. Consequently, we constructed several models to evaluate the effect of compensatory transition in contravening the effects of fishing. We do not know which, if any, compensatory mechanisms exist in grouper populations, nor do we know in detail the timing and rate of sexual transition for most species. The research necessary to obtain specific information on protogyny is slow, expensive, and unlikely to be completed soon. Yet fishery managers have immediate need for information about the interaction of protogyny and fishing. Simulations of protogynous populations provide preliminary guidance. Using models incorporating a range of compensatory mechanisms, we can at least inform managers of the minimum impact fishing might have on protogynous populations.

Groupers are important food and game fishes throughout the tropical and warm-temperate seas of the world. Of the grouper life history studies available, that for the graysby (Nagelkerken 1979) is one of the most complete, and we chose it as a basis for our model. The graysby, one of the smaller groupers, attains a maximum length of about 300 mm total length, is distributed in the western Atlantic from Cape Hatteras, North Carolina, through the Gulf of Mexico to the northern shelf of South America, and inhabits coral and rock reefs to depths of at least 100 m (Breder 1948). Like other groupers it attains its maximum size relatively slowly (growth coefficient, K = 0.13/year; von Bertalanffy 1938). The graysby lives at least 9 years.

Methods

Description of Life History Parameters

Parameters required for our simulations were taken directly from the work of Nagelkerken (1979) or calculated from data presented therein (Figure 1). Growth parameters were taken directly: K = 0.13/year; asymptotic length L_∞ = 41.5 cm; time at 0 size $t_0 = -0.94$ year; and for the length–weight relationship, W (grams) = $0.0121 \cdot L^{3.0821}$, where L = total length in centimeters.

Following Beverton and Holt (1959) we assumed that M (the instantaneous natural mortality rate) = K = 0.13. Pauly (1980–1981) proposed that M is estimated by a logarithmic multiple regression on K, L_∞, and temperature (°C). The Pauly estimate of M for the graysby was 0.41 (based on mean annual seawater temperature of 25°C in the southern Caribbean; U.S. National Oceanic and Atmospheric Administration 1973). Hoenig (1983) suggested M can be estimated using maximum age ($M = e^{1.46} t_{\max}{}^{-1.01}$; for the graysby, M = 0.42). We later discuss implications of a greater M than we used.

Experimental Strategy

Using a proxy (defined below) for the quantity of fertilized eggs produced by a population as an indicator, we measured the reproductive capacity, at different levels of fishing, of populations exhibiting compensated and uncompensated protogyny. Not knowing which, if any, scheme of compensation occurs in graysby populations, we simulated the responses of several schemes (described below) that, based on literature accounts (Ross 1981, 1990; Shapiro 1983; Bentivegna and Cirino 1984; Nemtzov 1985; Breitburg 1987; Lejeune 1987; Cole and Robertson 1988; Lutnesky 1989) and logic, seemed most reasonable to us. We compared responses of protogynous populations to that of a control, a simulated population of an animal like the graysby in all ways except that it was gonochoristic (at each age the sex ratio was 45:55, ♂:♀, which we computed is the graysby's population sex ratio under natural mortality alone).

We considered a population's production of fertilized eggs to be a more useful measure of reproductive potential for this simulation than was the production of reproductive offspring. The latter value represents the true reproductive success of a population but probably is heavily influenced by oceanographic conditions and predation. Fertile-egg production is dependent primarily on stock fecundity and mating success, two factors strongly tied to mortality rate and sex ratio, the variables of interest in this study.

Logic and Computation of the Proxy for Fertilized Egg Production

We computed our proxy (E') for population fertilized egg production (E) by multiplying the total population fecundity (O) by a factor representing the probability of successful fertilization of the egg (Q).

Total population fecundity (O) was determined by

(1) calculating the mean length of females at each age in the population from the von Bertalanffy equation (Nagelkerken 1979);

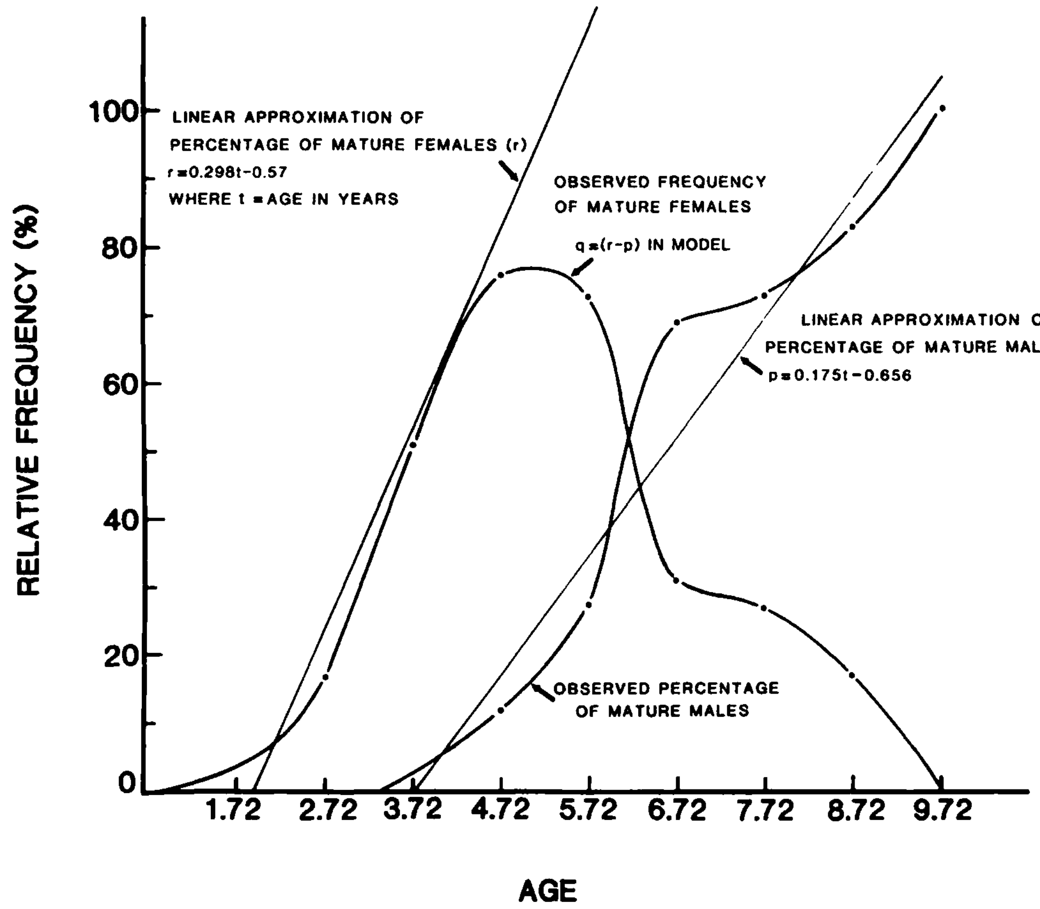

FIGURE 1.—Rates of transition to maturity and to malehood by females of the graysby. (Derived from data of Nagelkerken 1979.)

(2) converting the mean lengths to mean weights by use of the length–weight relationship;

(3) computing the total weight of mature females in each age-class by multiplying the mean weight by the number of females alive in the population under the mortality and transition conditions imposed in any particular simulation;

(4) computing fecundity from the relationship $Y = 1.2512X - 24.5805$, where Y = fecundity in thousands of ripe eggs and X = total population body weight in grams (Nagelkerken 1979); and finally,

(5) computing the total population fecundity of mature females by summing over all ages. Total fecundity probably does not indicate the exact number of eggs spawned, but it is probably a useful index of the egg production of a cohort. We only assume that the proportion of total eggs released, through batch spawning or other mechanisms, remains the same at all levels of fecundity.

Calculating the probability of successful fertilization of eggs (Q) is more complex and hypothetical. The combined effect of fixed maturation, sexual transition, and mortality rates is the establishment of a fixed population age structure and sex ratio. We suggest that evolution ought to result in the combination of M, maturation schedule, and transition rate that results in the optimal sex ratio and age distribution for producing fertilized eggs. The most likely and appropriate expression of the optimum condition for egg fertilization is the ratio of population male biomass to population fecundity under M alone.

Proposing that population male biomass was linearly related to sperm production, we reasoned that the male biomass to population fecundity ratio might be more closely correlated with the probability that eggs were fertilized than was the numerical sex ratio. Large males might produce more milt per spawning or spawn more times per season than would an equal number of small males. Therefore, for our simulations we assumed that the male biomass to fecundity ratio pertaining under M alone furnished a standard by which to judge the fitness of ratios occurring as a result of greater mortality. We assumed a linear decrease in the probability of egg fertilization as fishing mortality changed the ratio from that existing under M. Consequently we computed a factor representing probability of successful egg fertilization (Q) as follows:

$$Q = \frac{\dfrac{\text{population male biomass at } Z}{\text{population fecundity at } Z}}{\dfrac{\text{population male biomass at } M}{\text{population fecundity at } M}};$$

$Z = F + M$ = the total instantaneous mortality rate, and F, the instantaneous fishing mortality rate, was varied from 0 to 1.0. We further constrained that Q was 1 or less, reasoning that an excess of male biomass could not increase the fertilization rate beyond that provided by the optimum ratio. Population male biomass was calculated in the same way as female biomass. In the protogynous populations all males were assumed to be mature. In the gonochoristic population males were assumed to mature at the same rate as females.

Ultimately, the proxy for fertilized egg production (E') is

$$E' = QO.$$

Although the effects of male biomass : fecundity ratio changes might be nonlinear, we believed that linearity was likely and that it provided a good basis for this first set of models. Many models could have been constructed using different combinations of responses and slightly varying rates. The models presented offer a reasonable range of potential response by protogynous populations. We did not model the complex but extant circumstance in which some fish are born as males whereas other males (occasionally most of them) result from sex change (e.g., Nemtzov 1985).

Description of Experimental Populations

Five experimental populations exhibiting the following reproductive patterns were simulated and compared to the gonochoristic control population.

Option 1: uncompensated protogyny. — Regardless of changes in the sex ratio resulting from increased fishing pressure, no compensation through increased rate of transition or earlier onset of maturation or transition occurred in this population. The population parameters remained exactly those derived from Nagelkerken's (1979) work. In this case, rates of maturation and transition were assumed to be intrinsic physiological processes that did not change in response to short-term perturbations of population characteristics, especially sex ratio.

Option 2: number-compensated protogyny, maturation fixed. — In this model the onset and rate of transition to malehood were allowed to change as F increased so that the numerical ratio of males to females in the population remained constant at 45:55. The onset and rate of female maturation was fixed and was regarded as intrinsic. This simulation allowed for modification of physiological events as a response to changed social conditions. We posited that individual fish perceived sex ratio in terms of numbers, and the aggregate population response to these individual perceptions was adjustment of transition rate and onset to maintain a certain frequency of males in the population. Several species (e.g., *Anthias squamipinnis*: Shapiro 1981) respond to removal of a (the) male from the local grouping by the rapid transition of a female to a male. The aggregate effect of that response occurring in many groupings was simulated at the population level in the present model. The mathematical technique of computing adjusted onset ages and rates of transition is presented in the Appendix.

Option 3: number-compensated protogyny, maturation varies. — In this model the onset and rate of attainment of female maturity, as well as onset and rate of transition to malehood, were allowed to vary as F increased. The numerical ratio of males to females was preserved at 45:55. The rationale for compensation was the same as in the preceding model, but the maturation of females also changed as mortality increased (see Appendix for technique).

Option 4: biomass-compensated protogyny, maturation fixed. — This simulation mimicked the reproductive capacity of a population that compensated in response to changes (decreases) in the population male biomass : population fecundity ratio. The onset and rate of female maturation remained constant at all values of F, but the onset and rate of transition to malehood changed so that the ratio of population male biomass to population fecundity stayed the same. (See the Appendix for the necessary computations.)

Option 5: growth-compensated protogyny.—In this simulated population the rate of attainment of maximum size (K from the von Bertalanffy equation) increased in response to increased fishing mortality. We allowed K to increase 50% (from 0.13 to 0.20) linearly as F increased from 0.0 to 0.8, at which point reproduction effectively ceased. No other compensation occurred. Onset and rate of female maturation and transition were constant at all values of F. Comparison of this population was to a gonochoristic model that exhibited the same growth compensation. Many fish species have been observed to grow faster as a result of increased mortality caused by fishing (Gulland 1974; Miller et al. 1990). Such growth compensation is part of the basis of the widely used logistic, or Schaefer (1957), population model. We used what might be an unrealistically large change in K to explore the limit of the ability of changes in growth to improve the population's resistance to fishing.

Scheme for Comparisons

The fertilized egg production proxy (E') was computed for each simulated population at Z values of 0.13 (M alone), and from 0.2 to 1.0 at 0.1 intervals. Then for each population, production at all levels of Z was expressed as a fraction of that population's production at Z = 0.13 to remove the inherent difference in production at M (F = 0) between the gonochoristic and protogynous stocks. This difference resulted from the necessarily different allocation of biomass among ages to the sexes in the two types of populations.

Finally, we estimated relative reproductive success of protogynous versus gonochoristic populations at each level of mortality. The internally relative fertilized egg production of each protogynous population at each Z was expressed as a fraction of the internally relative production of the gonochoristic population (see Figure 2):

$$\text{Relative reproductive success} = \frac{\dfrac{E' \text{ protogynous at } Z}{E' \text{ protogynous at } M}}{\dfrac{E' \text{ gonochoristic at } Z}{E' \text{ gonochoristic at } M}}$$

Yield-per-Recruit Calculations

We compared results from protogyny-fishing models with information from a yield-per-recruit (Y/R) model to see if a different management strategy was required for maintaining adequate reproduction than was necessary for protecting yield from a cohort.

The Y/R model, an abbreviated version of the dynamic pool model (Beverton and Holt 1957) has minimal requirements for 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 still derive general information on which to base management regulations.

The Y/R model predicts the weight or numbers of fish caught during the life span of a cohort divided by 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 and t_r (age at recruitment to the fishery). The growth rate, natural mortality rate, and longevity of the species are the principal parameters influencing the shape of the surface. The algorithm is that of Beverton and Holt as described in Ricker (1975).

Results

There was an extraordinary decline in reproductive capacity as F increased regardless of the mode of reproduction. Under the conditions we imposed even the gonochoristic stock lost over 90% of its intrinsic fertilized egg production (at M) if F was 0.4 and 70% if F was as small as 0.17.

Increased fishing mortality caused decidedly greater losses of reproductive capacity in the stock exhibiting uncompensated protogyny than in that with gonochorism, but some forms of compensation prevented or reduced the extra losses. Without compensation the slope of the relative loss of reproductive potential of the protogynous stock was −0.82 (where Z = 0.13 to 1.0), whereas the slope of decline of the gonochoristic stock was, by definition, 0.0. Compensation through conservation of the male biomass : cohort fecundity ratio (with only onset and rate of transition to malehood allowed to vary) resulted in a reproductive decline identical to that of the gonochoristic stock. Because relatively few females must convert to males to maintain the biomass to fecundity ratio, the decline in reproductive capacity is principally a result of loss of females to fishing. This loss is

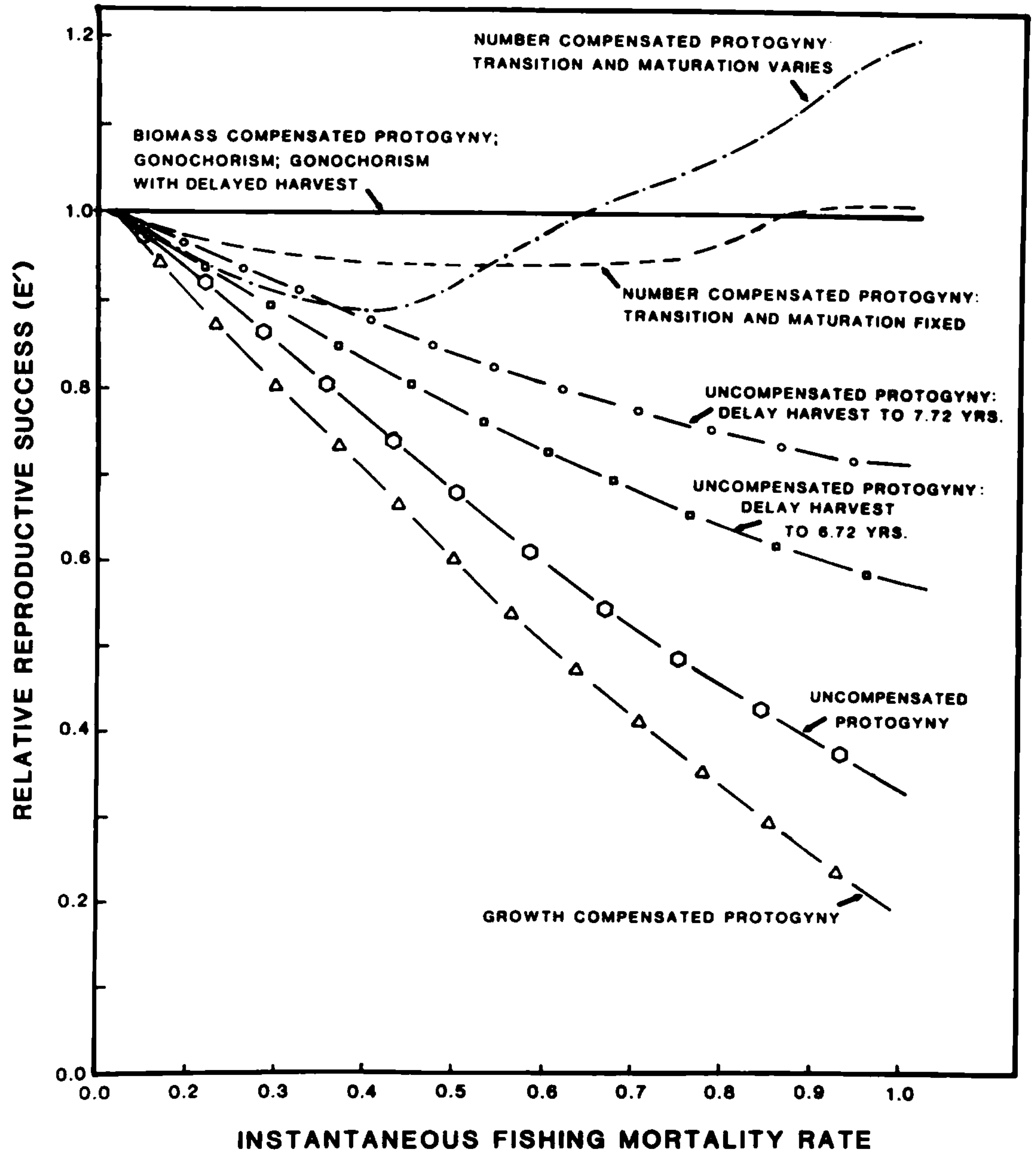

FIGURE 2.—Responses of the proxy for fertilized egg production to fishing in simulated gonochoristic and protogynous populations.

nearly an exact parallel to the removal of females from the gonochoristic stock.

Compensation through conservation of the numerical sex ratio allowed much greater reproductive capacity with increasing F than was displayed by the uncompensated protogynous stock but otherwise produced anomalous and unexpected results. Regardless of whether or not the onset and rate of female maturation were allowed to vary, numerically compensating populations showed greater declines than the gonochoristic stock at lower fishing mortality rates ($F = 0.0$–0.64, when maturation varied, and $F = 0.0$–0.82, when maturation was fixed) and better capacity at higher rates. The impact of the relative increase at higher F may be small, however, because so much ($>85\%$)

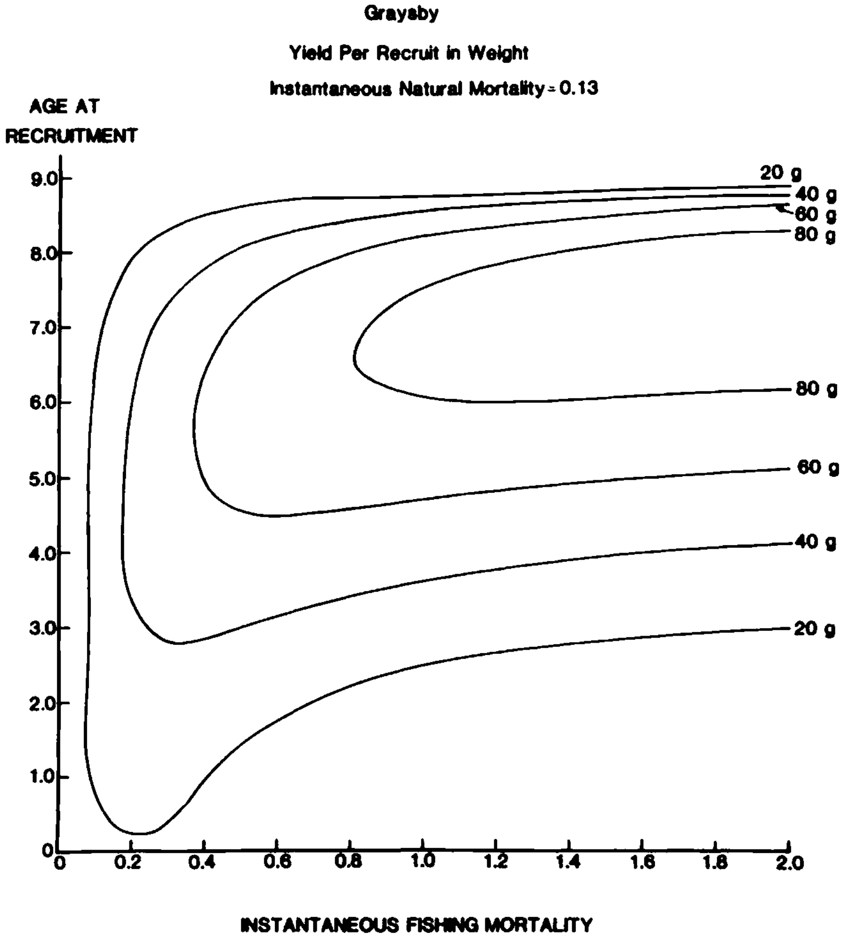

FIGURE 3.—A Beverton and Holt yield-per-recruit model for the graysby at a natural mortality of $M = 0.13$.

of the original actual reproductive capacity had been lost already. The improvement at high *F* results from an increase in the male biomass : cohort fecundity ratio as *F* exceeds the inflection levels (approximately 0.4 and 0.7). At high levels of *F*, maintenance of the numerical sex ratio results in a greater proportion of the population biomass being female than in the gonochoristic population, and the male biomass : cohort fecundity ratio remains adequate for good fertilization. Allowing the onset and rate of female maturation to vary lowers the inflection *F* and increases the rate of improvement in reproductive capacity. Our model allowed females as young as 2 years to mature, although the actual earliest possible age of maturity is unknown.

Decline of reproductive capacity in the growth-compensated model is greater than in the uncompensated model. As expected, the growth-compensated gonochoristic model, to which the growth-compensated protogynous model is compared, performed better with increasing *F* than did the unaltered gonochoristic model.

The yield-per-recruit (*Y*/*R*) model (Figure 3) is similar to those of many reef fish (Huntsman et al. 1983) in that maximal *Y*/*R* is attained by first taking fish at relatively great age (recruitment at 6–7 years for the graysby) if *F* is large (≥ 0.8). Even if *F* is as small as 0.35, only 25% of the maximal yield is lost at those recruitment ages.

Because the *Y*/*R* model suggested that a high recruitment age would ensure the maximal *Y*/*R*, we investigated the effects of imposing size limits in our simulated fisheries. We wanted to determine if maximizing *Y*/*R* by eliminating fishing mortality prior to ages 6.7 or 7.7 (ages chosen for computational simplicity) would have concurrent beneficial effect on reproductive capacity. We established four simulated populations: two controls and two experimental. The controls were, as before, gonochoristic populations, but in this case the initial age of harvest was delayed to either 6.7 or 7.7 years. The experimental populations exhibited uncompensated protogyny, had the initial age of harvest delayed to either 6.7 or 7.7 years, and were compared to the gonochoristic model with the same delay in age of initial harvest (Figure 2).

Delaying recruitment reduced the loss of reproductive capacity, and the benefit of delayed harvest increased as F increased. At $F = 0.3$, delaying harvest for 6.7 years reduced the protogyny-caused relative loss of reproductive capacity by 8% and delay to 7.7 years reduced the loss by 14%. At $F = 0.7$ a delay of 6.7 years decreased the loss by 19%, and a 7.7-year delay reduced the loss by 31%.

Discussion

Within limits imposed by our assumptions and data, we have shown that some protogynous stocks may be far more vulnerable to fishing than are comparable gonochoristic stocks. Stocks exhibiting uncompensated protogyny lose reproductive capacity as fishing mortality increases and fail reproductively (egg production $<1\%$ of that at M) at a lower fishing mortality rate. Compensation through conservation of the numerical sex ratio somewhat reduces the impact of protogyny, and compensation through conservation of the cohort male biomass : fecundity ratio erased all effects of protogyny. Finally, we demonstrated that all the modeled populations, including the gonochoristic, incurred a drastic reduction in reproductive capacity even at moderate levels of fishing mortality. Like Bannerot et al. (1987), we determined that, given a limited sperm supply, uncompensated protogyny renders a fished population more susceptible to reproductive failure. However, even with sperm limitation, some compensatory schemes protect reproductive capacity. We believe that some exploited fish populations are likely to have a limited sperm supply. Sperm limitation may not be normal to populations existing under natural mortality alone (Charnov 1982), but fished populations endure human-induced changes—drastic truncation of their age structure and reduction in population size—that are substantially greater than those characteristic of successful, unmolested populations. For instance, for four of seven studied grouper populations living off the southeastern U.S. Atlantic coast, estimates of the spawning stock biomass per recruit ratio (SSBR, an assumed proxy for reproduction capacity) were below 0.3, and the estimate was 0.002 for warsaw grouper *Epinephelus nigritus* (1.0 is the SSBR condition of an unfished stock; Huntsman et al., in press). The population, in numbers, of all ages (not just spawning adults) of speckled hind *E. drummondhayi* from Cape Hatteras, North Carolina, to the Dry Tortugas, Florida, in 1990 was estimated to be only 7% of that existing in 1973 (Beaufort Laboratory, Southeast Fisheries Science Center, unpublished data). Thus suppositions about sperm limitation based on evolutionary theory may provide little guidance towards events in populations experiencing the extremely rapid and traumatic changes attendant to fishing.

The value of population simulations depends on the accuracy of relationships and assumptions used. A strength of simulations is that one can posit the range in which a relationship might fall and evaluate the effects of the extremes. For some relationships we attempted to provide a single estimate and for others we evaluated the range. We believe most of our single estimates are reasonable because they are based directly on investigations of the graysby life history. Even so the parameter estimates may have two flaws. First, the estimate of M is unconfirmed and will remain so. Because a fishery for graysby was ongoing, it was impossible to separate fishing (F) and natural mortality (M). Nagelkerken (1979) was reluctant even to estimate Z because the graysby age frequency had an unusual form. The Pauly (1980–1981) estimate of M for the graysby is 0.41, a value considerably greater than we used. Greater M would reduce the cohort male biomass : cohort fecundity ratio at M and decrease the sensitivity of Q to increasing F. Thus differences in response between protogynous and gonochoristic stocks would have diminished.

Further, the ongoing fishing may have caused compensatory changes in population parameters before Nagelkerken's study. If compensation occurred, its results would likely have been reduction in the computed differences in response between protogynous and gonochoristic stocks. Only the consummation of research just now beginning, and expected to take many years, will enable the determination of parameters of mortality, maturation, and transition for most groupers.

Another conceivable criticism of our work is that our measure of reproductive success (i.e., the proxy for the amount of fertilized eggs) might be incorrect or irrelevant. First, was our proxy (E') a true one? Second, even if the proxy were correct, is a measure of fertilized egg production of any significance to grouper management? We do not know and do not believe anyone will know in the foreseeable future. Research required to determine the nature and success of egg fertilization is complex, expensive, and time consuming, and is only just beginning (C. Koenig, Florida State University, personal communication). In the meantime the managers' need for information is urgent. Consequently we propose that our proxy, based upon a linear relationship to male abundance, is, at the least, one of several logical measures and serves adequately for initial simulations.

Whether or not fertilized egg production is significant to fishery managers is, in part, a philosophical question. We believe that oceanographic phenomena are immensely important in transporting grouper eggs and larvae, and, probably, in determining their survival. Various groupers are transported by the Gulf Stream as far as the Woods Hole (Massachusetts) region, in spite of a complete absence of spawning adults there. Also, the reef fishery on Jamaica's south shelf is believed to result from transported larvae because spawning adults are rare or extirpated (Munro 1983). Thus, it appears possible, in some cases, to sustain a grouper fishery without local spawning. On the other hand, oceanographic phenomena can only transport eggs and reduce their abundance. There must be an initial source. Until we understand the relationship of grouper stocks to their recruitment source it would be improvident to manage without regard to reproductive potential.

Our results present a strong message to fishery managers: fishes like the graysby, perhaps most groupers, should be subjected to low fishing mortality only. Reproductive capacity diminishes quickly and drastically with increasing F regardless of whether or not protogyny exists. With uncompensated protogyny, the stocks are decidedly more fragile than are gonochoristic ones. Size limits, which increase the age at first harvest, somewhat reduce the impact of uncompensated protogyny, but their benefits cannot override the inherent reproductive weakness of grouper stocks. Various compensation schemes might eliminate the relative differences between protogyny and gonochorism, but they cannot improve the fragile reproductive scheme.

A large fraction of the maximum available yield (yield per recruit) of the graysby, and most other groupers (Huntsman et al. 1983), is available at relatively low F if appropriate minimum age at first harvest is maintained. For instance, 75% of the maximum Y/R is available if $F = 0.4$ (if recruitment ages are greater than 4.5 and less than 7.0), but at this F only 5% of the original reproductive capacity remains in the stock with uncompensated protogyny. But fishing at $F = 0.2$ will result in taking 50% of the maximum available Y/R (if recruitment age is between 3.0 and 7.5) and allow retention of about 25% of the reproductive capacity.

Implementation of effort limitations (to control F) and size limits (to regulate minimum age at first harvest) is often difficult. Effort limitations are politically unpopular and often complex. Implementation of size limits in reef fisheries occasions two major problems. First, groupers taken from relatively deep water (>30 m) receive injuries from internal gas expansion during capture that may preclude the survival of released undersize fish. Second, many reef fisheries are effected with traps, and several species, often of greatly different size, are the simultaneous targets. Consequently, it is difficult to choose a trap mesh size that maximizes Y/R for one species without incurring losses of Y/R for other species (Stevenson 1978). Compounding the theoretical problem of mesh selection is the practical problem that the wire mesh used for traps is available in very few sizes. Consequently imposition of size limits is often impractical and, when the yield of several species is considered, may be counterproductive.

Management of reef fish stocks off the southeastern United States is now largely based on attempts to model reproductive potential as expressed by the spawning stock biomass per recruit ratio (SSBR; Gabriel et al. 1989). However, lack of basic information about the reproductive biology of the managed species and about the interaction of fishing with those patterns precludes substantial confidence in the ability of SSBR modeling, to date, to predict the impact of fishing on protogynous stocks. Our modeling provides clues to essential differences in response to fishing of protogynous and gonochoristic stocks.

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Appendix: Computing Parameters for Compensated Protogyny Models

From Nagelkerken (1979: Figure 33) we have data to estimate the age-specific proportions of fish in three principal sexual categories—immature, male, and female. Nagelkerken's category of "transitionals" was equally apportioned to males and females. These data were best modeled by fitting straight lines to the proportion of immatures and to the proportion of males at each age, and then calculating females by subtraction. Cohort numbers, biomass, and fecundity can then all be calculated in terms of these linear functions. The various compensation options discussed in the text are accomplished by adjusting the slopes (negative for immatures and positive for males).

Let

$R(i)$ = proportion immature at age $i = a + bi$;
$P(i)$ = proportion male at age $i = c + di$;
$N(i)$ = number of fish in ith age-class;
$w(i)$ = mean weight of fish in ith age-class;
$f(i)$ = mean fecundity of females in ith age-class;
S = a sum of $N(i)$ over ages specified by subscript;
SS = a sum of $i \times N(i)$ over ages specified by subscript.

Subscripts are

o = all ages;
r = ages for which $0 \leq R(i) \leq 1$,
$r^{\cdot}$ = ages for which $1 < R(i)$,
p = ages for which $0 \leq P(i) \leq 1$,
$p^{\cdot}$ = ages for which $1 < P(i)$,
rp = ages for which $0 \leq R(i), P(i) \leq 1$;

and superscripts are

$'$ = sums of $N(i) \times w(i)$,
$''$ = sums of $N(i) \times f(i)$.

Then

$$\begin{aligned} N_m &= \text{number of males} \\ &= cS_p + dSS_p + S_{p^{\cdot}}; \end{aligned} \tag{1}$$

$$\begin{aligned} N_I &= \text{number of immatures} \\ &= aS_r + bSS_r + S_{r^{\cdot}}; \end{aligned} \tag{2}$$

$$\begin{aligned} N_F &= \text{number of females} \\ &= S_o - N_M - N_I; \end{aligned} \tag{3}$$

$$
\begin{aligned}
F &= \text{cohort fecundity} \\
&= S_{rp}'' - (aS_r'' + bSS_r'') - (c_pS'' + d_pSS''); \qquad (4)
\end{aligned}
$$

$$
\begin{aligned}
B &= \text{biomass of males} \\
&= cS_p' + dSS_p' + S_{p\cdot}'. \qquad (5)
\end{aligned}
$$

Option 2: Number-Compensated Protogyny, Maturity Fixed (Changes Only d*)*

N_m^* = required number of males to maintain sex ratio at $Q1$ (=sex ratio at M).

$$Q1 = \frac{S_o - N_I - N_m^*}{N_m^*}.$$

$$N_m^* = \frac{S_o - N_I}{Q1 + 1}.$$

From equation (1),

$$d = (N_m^* - cS_p - S_{p\cdot})/SS_p.$$

Option 3: Number-Compensated Protogyny, Maturation Varies (Change d *and* b *to Maintain Sex Ratio at* Q1*)*

$$N_m^* = N_F/Q1.$$

$$d = (N_m^* - cS_p - S_{p\cdot})/SS_p.$$

From equations (2) and (3),

$$N_I = S_o - N_F - N_m^*;$$

$$b = (S_o - N_m^* - N_F - aS_r - S_{r\cdot})/SS_r.$$

Option 4: Biomass-Compensated Protogeny, Maturation Fixed (Change d *to Maintain* B/F *Constant at the Ratio Prevailing Under* M *Alone [*Q2*]).*

From equations (4) and (5),

$$Q2 = \frac{cS_p' + d^*SS_p' + S_{p\cdot}}{S_{rp}'' - (aS_r'' + bSS_r'') - (cS_p'' + d^*SS_p'')};$$

$$d^* = \frac{Q2[S_{rp}'' - (aS_r'' + bSS_r'') - cS_p''] - (cS_p' + S_{p\cdot})}{SS_p' + Q2SS_p''}.$$