FISHERIES-INDUCED EVOLUTION OF ENERGY AND SEX ALLOCATION

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ABSTRACT

Fishing has been identified as a potential cause of the evolution of earlier age and size at maturation in many fish stocks. Several studies have focused on the ecological effects of fisheries on slow-growing, late-maturing hermaphroditic species such as groupers, but few have looked at the potential evolutionary effects of long-term size-selective fishing on hermaphrodites. We present an individual-based energy-allocation life-history model parameterized for *Epinephelus fuscoguttatus* Forsskål, 1775. Individual life-history trajectories are specified by three "genes": length at 50% probability of maturation and the proportions of available energy allocated to reproduction in the female and male phases. A genetic algorithm finds evolutionarily stable life-history strategies (ESS). Age and size at maturation and sex change are thus emergent traits. The model predicts that the grouper hermaphroditic life-history strategy should be very sensitive to even low fishing mortalities. Under increasing fishing mortalities, the ESS showed decreased age and size at maturation and sex change and increased female-to-male sex ratios. The model predicted an alteration in the sex system, under which the population became dioecious (having separate sexes) at intermediate fishing mortalities. The evolutionarily stable yield peaks at fishing mortalities as low as 0.06 yr^{-1}. Fisheries management in the simplest form would, for such species, include implementing a low fishing mortality and choosing proper size limits for the fishery.

Although many plants are simultaneous hermaphrodites, hermaphroditic animals more commonly begin as one sex and change to the other during their lifetime. The direction of sex change is most often to the sex that gains the greater advantage from large size (Ghiselin, 1969). The size advantage may for example arise from female fecundity, as in shrimps like *Pandalus borealis* Knoyer, 1833 (Jensen, 1965; Charnov, 1982) or anemone fish like *Amphiprion clarkii* (Bennett, 1830) (Moyer, 1986); these species first reproduce as males and then change sex to become females. Where territoriality or female choice is part of the mating system, males often need to be large to compete successfully for mates, and sex change goes in the other direction.

Several authors have suggested that the size or age at which sex change occurs can be expressed as a constant proportion of maximum size (or relative to age at maturation) that is invariant across species (Shapiro et al., 1993; Charnov and Skuladottir, 2000; Allsop and West, 2003). This approach has been criticized because spurious relationships may arise when two measures of size are correlated (for example size at sex change and maximum size) and because it leaves much variation unexplained (Buston et al., 2004; Munday et al., 2006).

Time of sex change is also very plastic. For example, in the red lyretail, *Anthias squamipinnis* Peters, 1855 a protogynous serranid living in sedentary social groups with territorial males, removal of a male from the group induced a female to change sex (Shapiro, 1980). Recent studies suggest that sex change is often driven by social interactions in the mating group and takes place when changing sex increases the individual's expected reproductive value (Muñoz and Warner, 2004; Munday et al., 2006). The individual that changes sex is not necessarily the largest: when the male

is removed from a haremic mating group of the bucktooth parrotfish, *Sparisoma radians* Cuvier and Valenciennes, 1840, the largest female does not change sex if her fecundity is greater than the fecundity of the rest of the females in the group combined (Muñoz and Warner, 2003).

Population dynamics is often different in hermaphroditic than in dioecious species, because maturation and sex ratio follow a different pattern in relation to size. The difference may also have implications for how harvest affects hermaphroditic and dioecious species, and one might expect different and more diverse consequences. For example, harvest normally truncates age and size distributions (Jennings et al., 2001) and in the case of sequential hermaphrodites can virtually remove one of the sexes (Alonzo and Mangel, 2004). In protogynous species, sperm limitation can then lead to population collapse (Alonzo and Mangel, 2004). The severity of this effect depends on the flexibility of the sex-changing rule (Alonzo and Mangel, 2005). In shrimp, the proportion of early-maturing females (individuals that skip the male phase and reproduce as females in their first reproductive season) responds to the composition of the population and is higher in years when many females have been removed by fishing (Jensen, 1965; Charnov, 1982). This response suggests a flexible mechanism that incorporates social cues about the size and abundance of conspecifics as well as state-dependent information about the individual to achieve adaptive timing of sex change. At the other extreme, many dioecious species have genetically coded and irreversible sex determination.

Attention has recently been devoted to the rapid evolutionary changes that may result from harvest. Fisheries often concentrate on specific parts of the population, for example large or mature fish, and this practice has been shown to lead to life-history evolution on time scales as short as years or decades (Law and Grey, 1989; Conover and Munch, 2002; Olsen et al., 2004). The aim of our study was to investigate the effects of fisheries on life-history evolution of a protogynous population of groupers. We have developed a model that is based on a mechanistic description of energy allocation to growth and reproduction. The model is individual-based and therefore allows for flexible sex-changing rules that assess expected reproductive value in a population of conspecifics. Because we model individual life-history strategies by means of the energy-allocation mechanism, a suite of individual and population characteristics emerge: individual growth rates, age and size at maturation and sex change, and population dynamics, as well as age and size composition of the population and the catch.

Our motivation for this study was a rapidly expanding export-oriented grouper fishery in the Maldives that began in the mid-1990s (Shakeel and Ahmed, 1996). Because of the abrupt intense fishing activity on many species of groupers, the fishery reached its peak in 1997, and in the absence of management, catch rates have since declined. The numbers of both spawning fish and spawning aggregations have also decreased for the Nassau grouper, *Epinephelus striatus* Bloch, 1792 since fisheries began in the Caribbean (Sadovy and Domeier, 2005). Groupers are slow-growing, long-lived, and late-maturing species (see Heemstra and Randall, 1993, for a review of the biology of groupers). They inhabit coral-rich areas of lagoon and seaward reefs in almost all tropical and temperate areas at depths ranging from 4 to 100 m and feed mostly on crustaceans and small fishes (Heemstra and Randall, 1993).

Our model is parameterized for *Epinephelus fuscoguttatus* Forsskål, 1775 (common names brown marbled grouper, flowery cod), which in 2006 contributed ap-

proximately 43% toward the live grouper exports from the Maldives (S. A. Sattar, unpubl. data). This species matures around 9 yrs of age and may reach ages of up to 40 yrs and lengths up to 100 cm (Pears et al., 2006). Like the similarly slow-growing and late-maturing sharks and rays (Stevens et al., 2000), groupers are highly susceptible to overfishing, and overfishing is encouraged by the high market demand and export prices reaching \$100 kg^{-1}.

Against this background, our aim is to assess the evolutionary consequences of harvest for energy and sex allocation in groupers. To what extent are hermaphroditic life-history strategies amenable to evolutionary change resulting from harvest-induced mortality; what types of changes are expected; and how would such changes affect population dynamics and the fisheries itself?

Model Description

Structure

The model presented here is based on the model by Alonzo and Mangel (2004, 2005) for a protogynous hermaphrodite and is extended by inclusion of energy allocation as a mechanism for exploring life-history variation and of genetic algorithms that allow for life-history evolution. Individuals in the model go through the processes of growth, maturation, sex change, and reproduction with mutation. Each individual is described by an attribute vector and a strategy vector. The attribute vector describes the state of the individual and contains information about age, length, maturity status, and sex. The strategy vector specifies the individual's life-history strategy and contains three phenotypic traits that evolve in the model: (1) allocation of energy to reproduction in the female phase, α_F; (2) allocation of energy to reproduction in the male phase, α_M; and (3) length at 50% probability of maturation L_m. Although the evolving traits are phenotypic, we assume that they have a genetic underpinning and will describe the evolution of the traits analogously to that of genes on a chromosome. This assumption is not critical, because we do not focus on the evolutionary trajectories (see Fig. A2 of the online appendix for an example) but only analyze the evolutionary endpoints, i.e., the evolutionarily stable strategies.

The model is based on a mechanistic description of energy allocation. The energy obtained through feeding can be allocated to growth, which increases body length, or to reproduction, which results in egg or sperm production. The model uses a genetic algorithm to simulate an evolving population (Holland, 1992): offspring inherit their traits, with mutations, from successful parents. The model thus leads to the emergence of evolutionarily stable life-history strategies under various levels of fishing.

Simulations are run for a time limit of 20,000 yrs and a maximum population size of 10,000 individuals (but because of mortality, the breeding population is 250–500 individuals, depending on their life-history strategies and the mortality level). The time resolution of the model is in yrs. Mutation, mortality, maturation, size at hatch, and food variability are processes that include stochasticity and result in differences between individuals with otherwise identical strategy vectors. Because the model simulates population dynamics, emergent properties include age and size at maturation and sex change; breeding population size; and age, size, and sex distribution of the population and of the catch.

Model Processes

The most central processes are briefly described below. Most of them are as in Alonzo and Mangel (2004, 2005), but growth, fecundity, and sperm production are modeled from energy allocation, and the fitness of individuals is in terms of number of offspring. In addition, our model does not have a function for fertilization probability, as we consider only one large spawning aggregation. Please refer to the online appendix for a more detailed description and a sensitivity analysis for some key parameters.

Energy Intake and Growth.—The weight W [g] of an individual is a function of its length L [cm] as $W = 0.01 \cdot L^3$. Energy intake I [J] is length dependent and is subject to stochastic variability χ:

$$I = \chi \cdot 11.0 \cdot L^{2.1}$$

A proportion of the available energy $(1 - \alpha)$ is then used for growth in length as:

$$L_{t+1} = \left(L_t^3 + (1 - \alpha_{(sex)})I \right)^{\frac{1}{3}}$$

where L_{t+1} is length in the next year, L_t is length in current year, and $\alpha_{(sex)}$ is specified by the strategy vector for females and males, whereas $\alpha = 0$ for immatures. The remainder of the energy is used for reproductive purposes (see below).

Maturation and Sex Change.—The probability that an individual will mature, $P_m(L)$, is given by a logistic function of length L

$$P_m(L) = \frac{1}{1 + \exp(-q(L - L_m))}$$

In the model, sex change occurs when an individual's size-dependent expected reproductive success is greater as a male than as a female (identical to rule 4 "reproductive success" of Alonzo and Mangel, 2005). Briefly, we assumed that sex change occurs once a year in rank order downward in size from the largest female. The model predicts the expected number of fertilizations for an individual of the same size for both sexes, given average feeding conditions and the current population composition, and the individual changes sex to become male if doing so increases reproductive success. We furthermore assumed that individuals change sex only once in their lifetime (from female to male), and that they must be mature females for at least 1 yr before they can change sex. Muñoz and Warner (2003) suggested that the largest female would not change sex if her fecundity was greater than the combined fecundity of all the remaining females in the mating group. Although such effects are probably important in species reproducing in small mating groups, the effect is much less probable in the one large spawning aggregation we model here.

Reproduction.—We assume that female fecundity ε is proportional to the energy allocated to reproduction:

$$\varepsilon = \alpha_F \cdot I$$

For males, sperm production, σ, also depends on length in accordance with the size-advantage hypothesis:

$$\sigma = \alpha_M \cdot I \cdot L^{0.1}$$

The term $L^{0.1}$ could represent any mechanism that would increase probability of fertilizing eggs as body size increases. Although it is here formulated as an increase in sperm production, size-dependent competition among males for access to females or female preference for larger body size would work in analogous ways. In addition, mortality declines with body size (see below), another type of size advantage applying to the two sexes equally.

Individuals produce numbers of offspring proportionally to gamete production, and each sex contributes half the offspring in the next generation. *Epinephelus fuscoguttatus* aggregate to spawn in groups that can exceed a thousand individuals (Johannes et al., 1999); we therefore assumed that spawning takes place once a year in one large spawning aggregation. We further assumed that all gametes are completely mixed. When total egg and sperm production in the population are denoted E and S, respectively, then the number of offspring $n_{0,i}$ produced by parent i is

$$n_{0,i} = \left(\frac{\varepsilon}{E}\right)\left(\frac{N_0(t)}{2}\right) \text{ if the parent is female, and}$$

$$n_{0,i} = \left(\frac{\sigma}{S}\right)\left(\frac{N_0(t)}{2}\right) \text{ if the parent is male.}$$

Here $N_0(t)$ is the total number of offspring produced in the population that year, determined by a Beverton-Holt density-dependent process (see the online appendix for details).

Natural Mortality and Fishing Selectivity.—Like Alonzo and Mangel (2004), we assume that natural mortality, M, is size dependent and is modeled as a power function of length (Peterson and Wroblewski, 1984; McGurk, 1986). The function for M gives mortality rates in the range of those observed for groupers (0.1–0.68 yr^{-1}; Pauly, 1980), and the lowest rate is restricted to $M_0 = 0.15$ yr^{-1}, which is the estimated natural mortality rate for adult *E. fuscoguttatus* (Grandcourt, 2005). Natural mortality is therefore size dependent as

$$M = (25L^{-0.5}) + 0.15$$

The fishery is size selective, and fishing selectivity, C, is a logistic function of length; 50% probability of being selected occurs at length L_f. The results shown are for $L_f = 30$ cm and $r = 1$.

$$C(L) = \frac{1}{1 + \exp(-r(L - L_f))}$$

For a fishing mortality F, survival probability P_S is therefore

$$P_S = e^{-M(L) - C(L) \cdot F}$$

Observations.—The evolving populations were simulated for 20,000 yrs to reach evolutionary equilibrium, and results were observed for the last 1000 yrs. These results thus show the evolutionary endpoint or the evolutionarily stable strategies

(ESS). The 20,000 yrs do not imply that evolution would be slow but is an assumption intended to standardize conditions for finding the ESS. The reasons to focus on ESSs rather than evolutionary trajectories on ecological time-scales were (i) that little evidence addresses the question of which elements of the hermaphroditic life histories are regulated genetically and which are expressed as a result of social control; (ii) additive genetic variation or heritabilities for these traits are poorly known; and (iii) evolutionary rates would probably depend on mating structure, for which we only investigate one large well-mixed spawning aggregation.

Results

Evolution of Life History Traits

Life histories are sensitive to even low fishing mortalities. The ESSs are characterized by decreased age and length at maturation and at sex change with increasing fishing mortalities (Fig. 1). These are the types of response that one could observe in survey or catch data. With increasing fishing mortality, mean age at maturation in the population decreased from 9–11 yrs to 4 yrs (Fig. 1A), and mean length at maturation from approximately 54–60 cm to 25 cm (Fig. 1C). Mean age at sex change decreased from approximately 14 yrs to 6 yrs (Fig. 1B), and mean length at sex change from approximately 65 cm to 30 cm (Fig. 1D). Each point in Figure 1 represents the mean phenotypic trait value for an ESS given a constant level of fishing mortality, and multiple points for each fishing mortality indicate replicates.

The responses in age and size at maturation are due to evolution of the underlying life-history strategies (Fig. 2). Allocation to reproduction in the male phase is quite
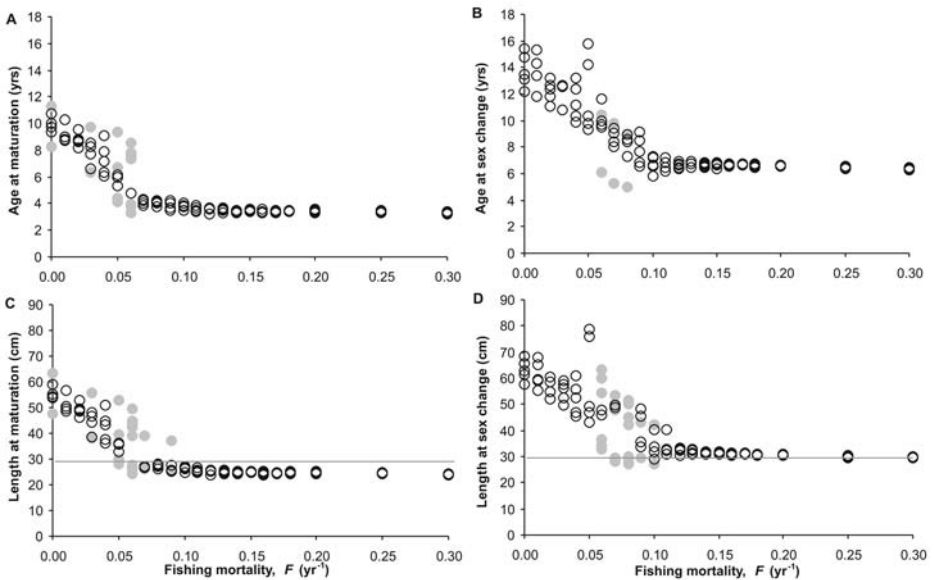

Figure 1. Evolved phenotypes (life history strategies) for a modeled grouper (*Epinephelus fuscoguttatus*) population subjected to varying levels of harvest intensity. (A) Age at maturation. (B) Age at sex change. (C) Length at maturation. (D) Length at sex change. The minimum size limit is L_f 30 cm (indicated by gray line in panels C and D), and the values are mean trait values in the population (open circles) or the two peaks if the distribution was bimodal (gray circles).
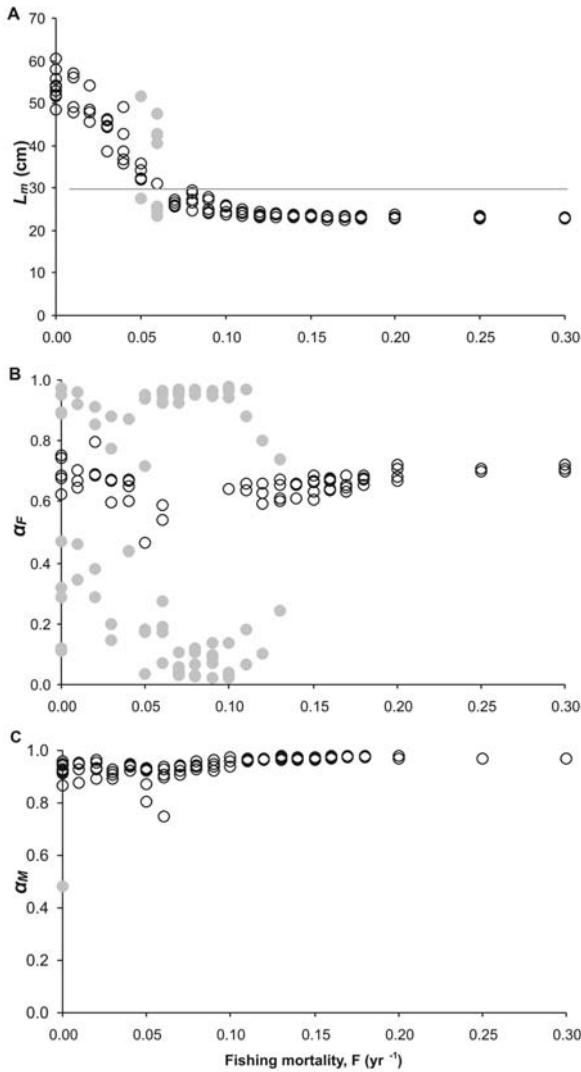
Figure 2. Evolutionarily stable life-history strategies in a modeled grouper population (parameterized for *Epinephelus fuscoguttatus*) under various levels of harvest. The three panels correspond to three "genes" that specify a life-history trajectory: (A) Length at 50% probability of maturation L_m. (B) Energy allocation to reproduction in the female phase, α_f. (C) Energy allocation to reproduction in the male phase, α_M. The minimum size limit is $L_f = 30$ cm (indicated by gray line in panel A). Symbols as in Figure 1.

stable and high regardless of fishing mortality (Fig. 2C). The response to fishing is seen primarily in the two other traits. Under intense fishing (F > 0.06 yr^{-1}), the gene for length at maturity, L_m, evolved to values lower than the length at which individuals are recruited to the fishery, $L_f = 30$ cm (Fig. 2A). That size provides a refuge from fishing mortality, and life histories did not change when fishing mortality was increased beyond this level. Bimodality in L_m at a fishing mortality around 0.06 yr^{-1} indicates that the population was composed of some individuals who were maturing at smaller sizes and some individuals who were maturing at larger sizes later in life (Fig. 2A). This bimodality must be viewed together with the allocation to reproduc-

tion in the female phase (Fig. 2B). These two traits interact and must be interpreted in light of the mating system.

Hermaphroditism vs Dioecism

At low fishing mortalities (0–0.05 yr⁻¹) individuals followed a hermaphroditic strategy. In the female phase, either all allocated about 70% of energy to reproduction and 30% to growth or allocation was bimodally distributed in the population, such that one group allocated more to reproduction and the other less (Fig. 2B). This bimodality in female allocation means that the two groups are biased toward the female and male sex, respectively. The individuals that allocated almost all their energy to reproduction in the female phase virtually stopped growing, and few of them changed sex to become males later in life. The other group allocated almost nothing to reproduction but continued growing, sooner or later becoming large enough to change sex. This bimodal distribution of female allocation values was observed as the ESS for fishing mortalities between 0.05 and 0.12 yr⁻¹ (Fig. 2B) and resembles dioecism (separate sexes). The model therefore predicts a continuum of life-history strategies ranging from normal hermaphroditism, in which individuals reproduce as both females and males during their lives, to almost purely dioecious strategies.

Bimodality was also apparent in the gene for length at maturation but for a narrower range of fisheries mortalities (0.05–0.06 yr⁻¹) (Fig. 2A). In these cases, the individuals following the male-biased strategy matured at larger size than did those following the female-biased strategy. Because of the low allocation to reproduction the male-biased individual also continued to grow through the female phase. The population therefore contained a few very large males, visible as a long tail in the male size distribution for $F = 0.05$ (Fig. 3D).

At fishing mortalities > 0.1 yr⁻¹, the ESSs again reflected pure hermaphroditism (Fig. 2B). At such high fishing mortalities the fish matured and spent most of their life history at sizes below those vulnerable to fisheries (Fig. 1).

Age and Size Composition of the Population

With increasing fishing mortalities, the age and size at which females and males appear in the ESS population tended toward earlier ages and smaller sizes (Fig. 3). The modal length of females decreased from 58 cm (no fishing) to 30 cm ($F = 0.1$ yr⁻¹), and that of males from approximately 70 cm (no fishing) to 30 cm ($F = 0.1$ yr⁻¹) (Figs. 3B and 3F, respectively). The appearance of males and females at smaller sizes is due to the evolution of earlier maturation at high fishing mortalities. Size at maturation and sex change evolved to fall below L_f when L_f was 50 cm (Fig. A10 in the online appendix).

Yield and Fisheries Management

The long-term sustainable yield, after life histories have adapted to the prevailing fisheries mortality, followed a dome-shaped curve peaking around a fishing mortality $F = 0.06$ yr⁻¹ and stabilizing above $F = 0.12$ yr⁻¹ (Fig. 4A). Immature individuals contributed most to the yield at low fishing mortalities, whereas males contributed most at higher fishing mortalities.

The evolutionarily stable yield was highest when L_f was low ($L_f = 30$) and fisheries mortality moderate ($F = 0.06$ yr⁻¹). Yield never fell to zero within the range of given fishing mortalities and L_f. The fishing mortality that produced the maximum yield depended on the L_f (Fig. 4B).
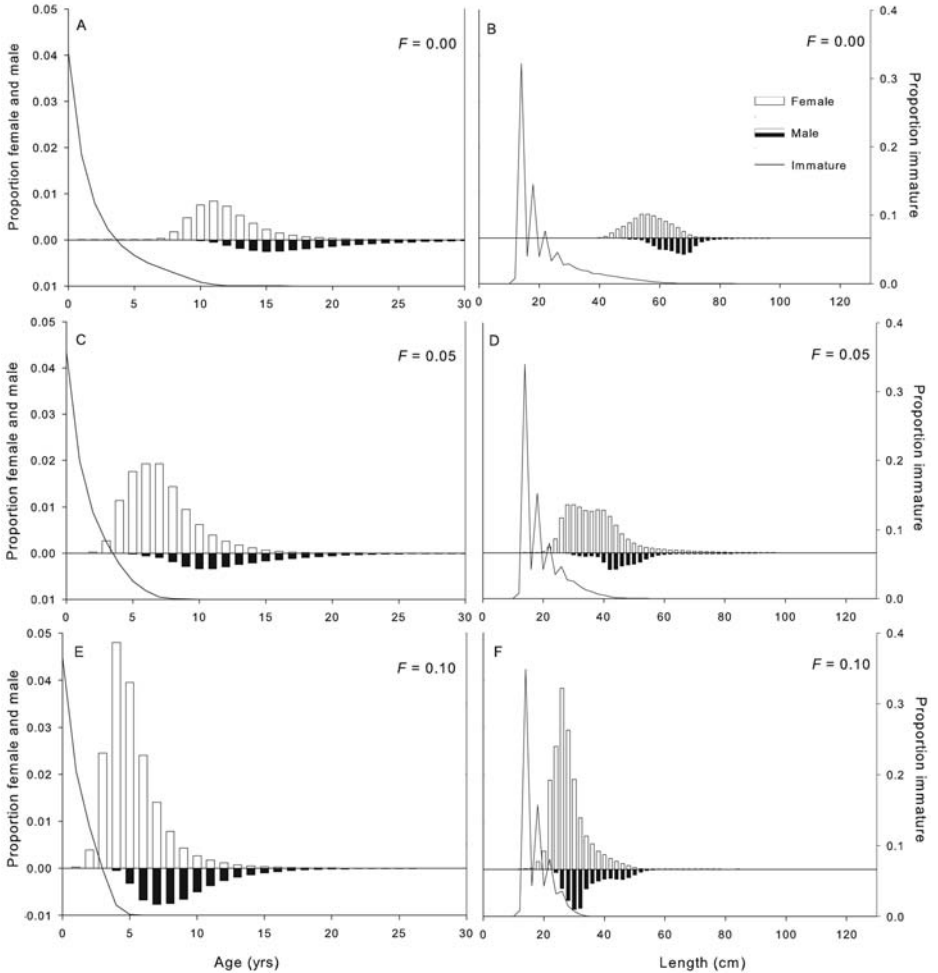
Figure 3. Age (left column) and size (right column) distribution of a modeled population of grou-
pers (*Epinephelus fuscoguttatus*) following the evolved evolutionarily stable life-history strate-
gies under various levels of harvest intensity (the annual harvest rate, F [yr^{-1}], is indicated on each
panel). The size selectivity of the fishery was $L_f = 30$ cm. The proportion of the population that
consists of immatures is shown on the right hand axis, and proportions of females and males on
the left axis.

DISCUSSION

Charnov's (1982) comprehensive treatment of sex allocation theory was popu-
lation-based and frequency-dependent, and has proven to be an excellent tool for
training intuition and elucidating variation in sex systems. Empirical studies have
since confirmed many of the theory's predictions but also highlighted that matura-
tion and sex change are indeed individual life-history events, often resulting from
complex evaluations of individual fitness consequences within the mating group
(Muñoz and Warner, 2003), as in the case of the bucktooth parrotfish, in which the
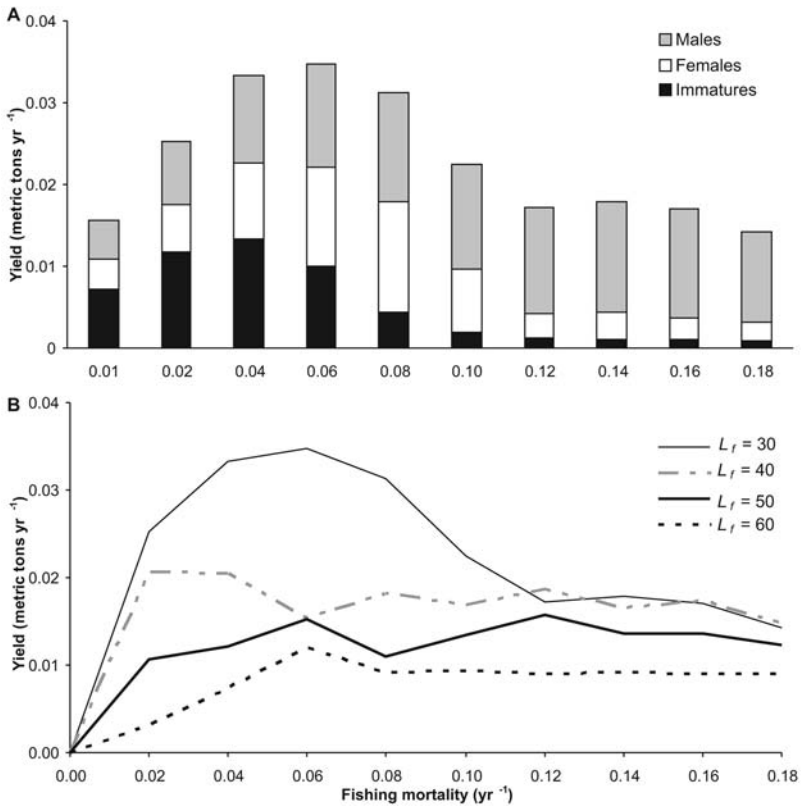largest female deferred sex change to smaller females if her fecundity was higher

Figure 4. Yield in a modeled grouper fishery where the population followed evolutionarily stable life-history strategies adapted to increasing levels of harvest intensity. The model was parameterized for *Epinephelus fuscoguttatus*. (A) The contribution of immatures, females, and males to the total yield. The minimum size limit in the fishery was L_f = 30 cm. (B) Total yield under different management regimes. The minimum size limit, L_f, was varied between 30 cm and 60 cm.

than the total fecundity of all other females in the reproductive group (Muñoz and Warner, 2004). In larger mating groups, as for example in our model, this situation would rarely arise, and the largest female would be expected to change sex first. Such studies emphasize that sex-allocation strategies are both flexible with respect to the individual's state and influenced by the local environment, including the other individuals in the mating group.

Flexibility in the timing of a life history event depends on how strictly it is genetically determined. Individual traits that respond to social cues or the state of the environment can quickly result in population changes. The composition of the breeding population can then respond rapidly to altered selection pressures, in principle on a time-scale shorter than a generation. Traits that are more strictly genetically controlled, on the other hand, would require evolutionary change of gene frequencies before the population would adapt. In our model, maturation size is genetically coded and responds slowly, whereas sex change can be flexible from year to year because it is based on a rule that evaluates the composition of the breeding population. Similar flexible strategies have been suggested to govern sex change in several species (e.g., by Charnov, 1981; Muñoz and Warner, 2004).

The flexibility with which a life-history trait responds to external forcing may in turn have consequences for population dynamics. Interestingly, a strategy for sex change that relies on social cues may potentially increase vulnerability to fishing because compensatory mechanisms in individual life histories may mask typical signs of overexploitation, for example altered sex ratios or reduced recruitment (Alonzo and Mangel, 2005). In our study, we analyzed only the ESSs, the evolutionary endpoint, given a fishing intensity and selectivity. We therefore do not make predictions about the evolutionary trajectories—the transient periods before the population has reached a new evolutionary equilibrium—or the ecological vulnerability of the population during a period of evolutionary change.

Correspondence Between Modelled and Observed Life-History Strategies

Only a few studies of life-history traits in *E. fuscoguttatus* have been published and none from the Maldives; Pears et al. (2006) presented the most comprehensive set of data collected from Australia's Great Barrier Reef, and we will use those for comparison. No time series for life-history traits in harvested populations of *E. fuscoguttatus* are available, nor are any comparisons between areas that have experienced different harvest rates. The comparison between the model and field data is therefore limited to the situation with no fishing mortality. In general, the model agrees with field observations: a hermaphroditic strategy in which females allocate energy to both growth and reproduction until they later become males, an asymptotic growth pattern, and occurrence of most of the growth in the immature and female phases (Pears et al., 2006). That individuals in the male phase showed no growth implies that they allocated nearly all their energy to reproduction. The model also agrees with the observation that > 90% of the available energy was diverted to reproduction in the male phase across all fishing mortalities, with only a few minor exceptions.

For maturation, the model predicts larger size (55 cm) and later age (10 yrs) than suggested by gonad observations (30 cm and 2 yrs and onwards; Pears et al., 2006), but Pears et al. (2006) observed a strong pattern linking size and sexual activity among female *E. fuscoguttatus;* smaller females were less active in reproduction than were larger females. In fact, most females < 10 yrs old (corresponding to a length of approximately 60 cm) had gonads too small for reproduction (Pears et al., 2006). Energy must therefore be primarily invested in growth at smaller sizes, and the model and the field data agree on the size and age at which females become reproductively functional.

At zero and very low fishing mortality (< 0.05 yr^{-1}), some of the replicate simulations predicted bimodal distributions of female allocation to reproduction, in which the lowest female allocation value was still well above zero. These two life-history pathways, one biased toward the female and the other toward the male sex, both follow a hermaphroditic strategy. This type of bimodality in allocation values is different from the more pure dioecism that is predicted at fishing mortalities between 0.05 and 0.10 yr^{-1}, where the sexes are more or less functionally separate.

Effects of Harvest on Life-History Strategies

The selection regime in the wild has shaped populations so that the growth period before maturation maximizes the trade-off between survival on the one hand and the benefits that come with size on the other—i.e., increased fecundity among fe-

males and all ecological mechanisms that contribute to size advantage among males. Under harvest, however, this size advantage is offset by fishing mortality: survival until reproduction matters more than large body size. The ESS will therefore be a strategy that reduces exposure to fishing, i.e., in which maturation takes place earlier in life. Numerous studies have demonstrated harvest-induced evolution toward lower maturation age on decadal time scales (Law and Grey, 1989; Conover and Munch, 2002; Olsen et al., 2004).

In a similar model, but without evolution, Alonzo and Mangel (2005) predicted their hermaphroditic population to crash under high fishing mortalities when the rule for sex change was based on reproductive success and when fishing included younger year classes. In contrast, individuals in the model presented here evolved earlier maturation, and earlier sex change following from altered population dynamics. Earlier maturation evolved also when fisheries selected larger fish (Figs. A9, A10). That fish life histories can evolve as a result of size-selective harvest has recently been highlighted by Swain et al. (2007). From back-calculated size at age in a Canadian cod (*Gadus morhua* Linnaeus, 1758) stock, they suggested that fishing has selected first for increased size at age 4 yrs and thereafter for reduced size at age (but see also Heino et al., 2008). Such evolution of traits under selection pressure that prevents extinction has been termed "evolutionary rescue" (Ferrière et al., 2004). Evolutionary rescue enables the population to persist in times of environmental degradation or other external selection forces such as intense fishing mortality. Such an evolutionary process would rely on rearrangements of available genetic variance or new mutations, both processes that were included in our model. Evolution does not need to be beneficial to the population, however. Adaptation can also modify traits in ways that cause the population to go extinct, a process called "evolutionary suicide" (Ferrière et al., 2004). An evaluation of the consequences of adaptation, an evolutionary risk assessment so to speak, cannot therefore be based on generalizations about the nature of evolution but requires detailed understanding of each specific case.

Harvest of Sequential Hermaphrodites

In species where one sex is larger than the other, the selection for earlier maturation will normally be stronger on the larger sex because of its longer growth phase. The evolutionary consequence will be that the sexes evolve to more similar size as survival probability swamps the effects of size advantage. The reduced importance of size advantage, which maintained and stabilized sequential hermaphroditism in the first place, is the mechanism behind our model's prediction that fishing for a sequentially hermaphroditic species can lead to the evolution of strongly female- and male-biased strategies that approach dioecism. Also, the ESS strategies under higher harvest rates are for individuals to mature and reproduce before they become vulnerable to the fisheries. Because survival probability is only little affected by fishing, size advantage is reestablished, and hermaphroditism is again the predicted evolutionary outcome.

Individuals showing strategies of dioecism within hermaphroditic life histories, that is, a part of the population that develops directly to the terminal sex, have also been termed "early maturers," (Charnov, 1982; early maturing males in our model). In reality these are pure males, and our model concomitantly predicted that the remaining individuals in the population would increase their allocation in the female phase, thus becoming pure females. Technically, in the model all individuals are

forced to go through a female phase. This formulation might at first seem confusing but it is a flexible one that allows for both dioecious and hermaphroditic strategies. Individual allocation values in the population typically followed one of two patterns. In the first, individuals did not differ markedly, and all allocated energy to reproduction during both female and male phases. The result was a typically hermaphroditic life-history strategy in which the largest among the females changed sex to become males. In the second pattern, two strategies cooccurred in the population. One allocated nothing to reproduction in the female phase but continued to grow; these individuals reproduced only as males. The other strategy allocated almost 100% to reproduction during the female phase, and because these individuals stopped growing, only rarely did they later become males. These two coexisting strategies thus conform to dioecism. Individuals with the male-biased strategy also matured at a smaller size, but because they had one year of growth while technically in the female phase (they did not allocate energy to reproduction), males and females typically became reproductively functional at approximately the same age and size.

Management of Hermaphroditic Species

Several studies have stressed the importance of considering life-history characteristics before introducing management strategies (King and McFarlane, 2003). Not only do life-history traits determine individual trajectories for growth and reproduction, but these individual characteristics also scale up to population-level properties such as productivity, biomass fluctuations, resilience, and yield. Heppell et al. (2006) compared the effects of reduced fishing mortality on different life-history stages of the gag grouper [*Mycteroperca microlepis* (Goode and Bean, 1879)]. Their results showed that sustainable management of a gag grouper population requires a management plan that encompasses the optimal solutions for population recovery, biomass, sex ratio, and fertility (Heppell et al., 2006). On the basis of our results, we can add the potential consequences of fisheries-induced evolution to that list. Our model suggests that species like slow-growing groupers are especially sensitive to fishing mortality. Not only did evolution toward maturation and sex change at earlier ages and smaller sizes take place at very low fishing mortalities, but the selective pressures maintaining hermaphroditism itself may erode under fishing. It would be instructive to study models that explore a wider parameter range to identify which parameters or ecological conditions make hermaphrodites especially vulnerable to fisheries-induced changes. Although the species may evolve to accommodate to the new selection pressure, it simultaneously evolves away from the life-history strategy that was favored by natural selection. At present, we know too little about the ecological interactions to predict what consequences such an evolutionary shift of life-history strategies may imply for the species and the ecological community. Potentially, ecological consequences range from behavior and mating success through reproduction and recruitment to population dynamics. In turn, these can lead to altered interactions with other species in the reef ecosystems.

Results from our model as well as those from Alonzo and Mangel (2005) reveal the importance, in implementation of a management strategy for hermaphrodites, of considering the size selectivity of the fishing pattern in conjunction with the mechanism for sex change. This finding is supported by our model, which predicts that hermaphroditic life histories are sensitive to fishing and might evolve even at low fishing mortalities. Also, models, including the one presented here, tend to assume

that individuals time their sex change on the basis of perfect knowledge. The effects of incomplete knowledge may be different when a population is subject to fishing. Along the same lines, incorporating the particular cues individuals use in their assessment of when to change sex would be instructive.

The rate of natural mortality being experienced by grouper populations is uncertain. Most life-history models are sensitive to mortality rates, and with higher natural mortality rates, our model predicts an even stronger evolutionary response (a sensitivity analysis is presented in the online appendix). We tested two values for the size selectivity of the fishery (L_f = 30 cm, Figs. 1 and 2; L_f = 50 cm, Figs. A9 and A10). In both cases, the life histories evolved toward individuals' maturing and changing sex before they became vulnerable to fishing. Within this range, these results suggest that, the more intense fisheries selection is, the larger the magnitude of the evolutionary response will be.

Does the high sensitivity of the grouper life history to fisheries-induced selection mean that one must either accept the occurrence of these evolutionary changes, which will have at present unknown ecological consequences, or stop harvesting, thereby dramatically affecting people's livelihoods? First, our model does not address evolutionary rates, so although the ESS changes substantially when the grouper life history is subject to long-term fisheries mortality, we cannot conclude from our model whether these changes will be fast or slow. Second, one potential remedy that remains to be properly investigated would be to create marine reserves where only natural selection acts on life histories, thereby maintaining the selection pressures that favored hermaphroditism in the first place. Marine reserves represent a promising avenue for restricting the effects of mortality on population dynamics and potentially also on life-history evolution (Baskett et al., 2005). How evolution within the reserve and that in fished areas outside the reserve would interact, or whether one would dominate the other, depends on whether dispersive life-history stages exist and, if so, the connectivity between the areas (Baskett et al., 2005). On the basis of the unanticipated effects of fishing on the mating system itself, models that test the efficacy of marine reserves must address hermaphroditic life-history strategies specifically. Such models must also take into account that many groupers are mostly solitary and do not occur in groups except during spawning periods.

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