Online Appendix to

FISHERIES-INDUCED EVOLUTION OF ENERGY AND SEX ALLOCATION

Shahaama Abdul Sattar, Christian Jørgensen, and Øyvind Fiksen

PART 1—MODEL DESCRIPTION

The model description follows the layout given by Grimm et al. (2006).

Purpose

The purpose of our study was to investigate evolutionary effects of fisheries on the life history of a protogynous population of groupers. The model tests the effect of fisheries on maturation and sex allocation in groupers, which in turn determine the age and size of maturity and sex change. The model finds evolutionarily stable energy allocation to reproduction by individuals in the female and male phases for a population subject to fisheries. Growth rates emerge from proportion of energy allocated to growth. The model simulates an evolving population using a genetic algorithm and thus includes overlapping ecological and evolutionary time scales.

Structure

The model presented here is based on the model of Alonzo and Mangel (2004, 2005) for a protogynous hermaphrodite and is extended to allow for life-history evolution. Figure A1 shows the life-history pathway of protogynous hermaphrodites such as groupers. Individuals start as immatures and mature into females before they change sex to become males.

The model is individual based and predicts reproduction, size distribution, and sex ratio in populations as a function of different fishing mortalities. Each individual in the model is described by a strategy vector and an attribute vector. The strategy vector is defined by energy allocation to reproduction in the female and male phases (α_F and α_M respectively) and length at which probability of maturation is 50%, L_m. The state of each individual in the population is described by the attribute vector, which is defined by age, length, and sex. Energy intake, weight, maturity status, mortality due to natural causes or fishing, and sex change are all functions of length (Fig. A1). Population simulations were run for 10,000 individuals, and the model includes stochasticity, which results in further individual differences. The model finds population dynamics such as age and size at maturation and sex change as well as age, size, and sex distribution in the population. Other emergent properties are evolutionarily stable life-history strategies. The model was parameterized so as to duplicate the life history of the slow-growing, late-maturing grouper *Epinephelus fuscoguttatus*. The time resolution of the model is in years.
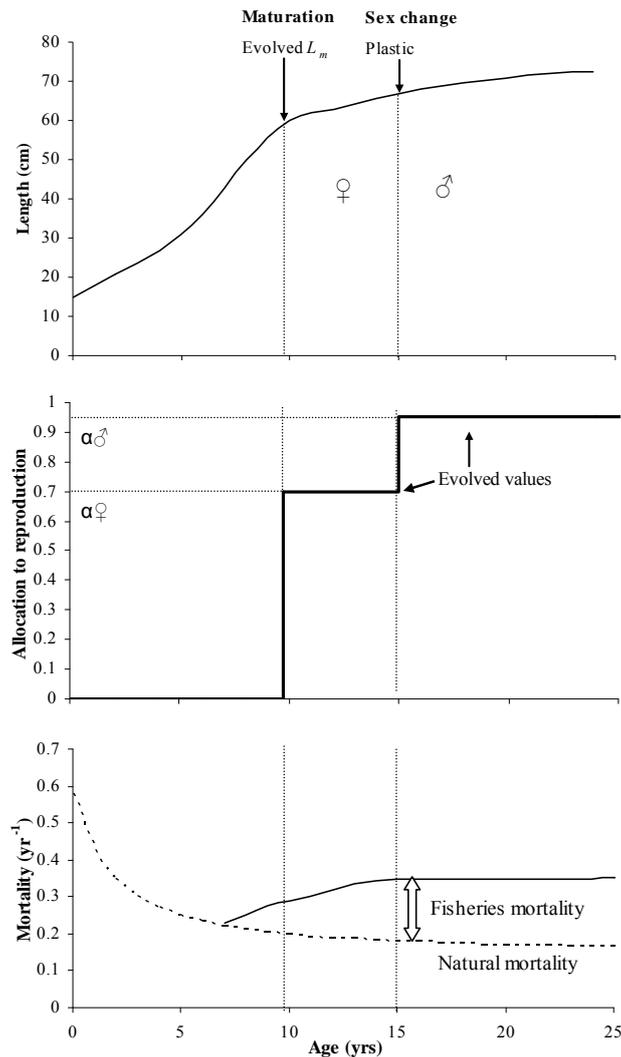
Figure A1. Example of a life-history pathway for an individual grouper in a life-history model. Each individual goes through an immature phase until it matures to become a reproductive female. Later the individual then undergoes the process of sex change to function as a male for the rest of its life (upper panel). In the immature phase, the individual allocates all its energy to growth. Once it matures (at a time determined by the gene for length at which probability of maturation is 50%, L_m) into the mature-female phase, it allocates a certain proportion of energy to reproduction (α_F) and to growth ($1 - \alpha_F$). Having functioned as a female for at least a year, the individual may change sex (length at sex change is plastic) and function as a male for the rest of its life. In the male phase the individual allocates a proportion, α_M, of its energy to reproduction. Levels of energy allocation to reproduction in the female and male phases are also determined by individual genes, which evolve in the population, together with the gene for length at maturity (middle panel). Before exposure to fisheries, individuals suffer only natural mortality, which decreases with age (dotted line). Once fisheries mortality is introduced, its contribution to the mortality of older age classes increases total mortality (solid line) suffered by the population (lower panel).

Processes

The model simulates an evolving population. Individuals in the model go through the processes of growth, maturation, sex change, and reproduction, including recombination and mutation. The model uses three genes: (1) energy allocation to reproduction in the female phase α_F, (2) energy allocation to reproduction in the male phase α_M, and (3) length at maturity L_m. An example of the evolutionary trajectory of the genes is shown in Figure A2. Energy allocated to growth increases body length, whereas the energy allocated to reproduction is used for production of eggs or sperm. The model simulates an evolving population by means of a genetic algorithm (Holland, 1992) that leads to the emergence of evolutionarily stable life-history strategies under varying levels of fishing.
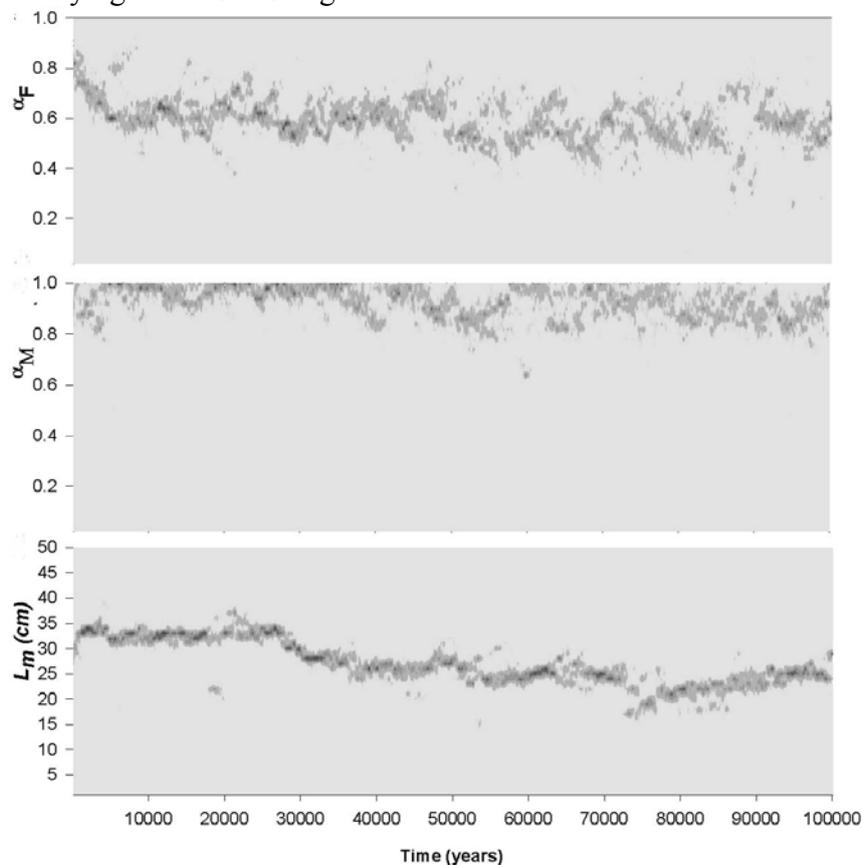

Figure A2. Evolution of genes for energy allocation to reproduction in the female phase, α_F (upper panel), that in the male phase, α_M (middle panel), and length at which probability of maturation is 50%, L_m (lower panel).

Concepts

Fitness.—The model has endogenous fitness; i.e., the fitness of any strategy comes from within the population and is determined by the reproductive success of the individual, which is a function of the individual's fecundity (if female) or sperm production (if male). The model does

not impose a fitness function that states the number of offspring that should be produced by an individual of certain length.

Emergence and Adaptation.—Emergence takes place at two levels. First, individuals differ in their genetic composition (the life-history strategy) and the environment they experience, and the differences lead to the emergence of population dynamics, including age and size at maturity and sex change as well as age, size, and sex distributions in the population. Second, the genetic algorithm simulates evolution, and over time life-history strategies adapt to the biotic and abiotic environment. This adaptation leads to the emergence of evolutionarily stable life-history strategies.

Interaction.—No competition for food resources takes place. Interaction occurs during reproduction as competition for mates and during sex change when individuals assess their future fitness as females or males relative to the others in the population. Fitness depends on the numbers of eggs and sperm produced by each individual relative to other members of the population. Juvenile survival is also density dependent, as the recruitment function limits the number of recruits that can be added to the population per year.

Prediction.—At the time of reproduction, each individual is able to assess its fitness as female or male by assessing the population structure and the sex ratio. If the given individual's fitness as a male is greater than that as a female, it will change sex and thereby increase its fitness and maximizes its reproductive success.

Stochasticity.—The outcome is stochastic for all probabilities used in the model—maturation, natural and fisheries mortality, and total number of offspring produced by each parent. Equations for the functions are given below. A random number between 0 and 1 is drawn, and if the value is less than the probability value, the event takes place. The model also applies a random normal distribution to vary the amount of energy intake by individuals, as well as the frequency of mutations in the offspring.

Scheduling.—The model runs in time steps of years. All immature individuals feed, grow, or die as a result of natural mortality. The survivors, once they reach a length greater than or equal to the length at which probability of capture is 50%, i.e. L_f, are susceptible to fisheries mortality (which is a function of length) in addition to natural mortality. Individual processes take place in the following order: maturation, stochastic energy intake, allocation of available energy, growth, and egg/sperm production. Egg and sperm production is summed at the population level and used to calculate density-dependent offspring production. Offspring are divided among individuals proportional to their fitness, and the strategy vector undergoes mutations with given probabilities. At the end of the year, females assess the population structure and change sex if future male fitness is higher than fitness of continuing as a female. A flowchart of the model is shown in Figure A3.
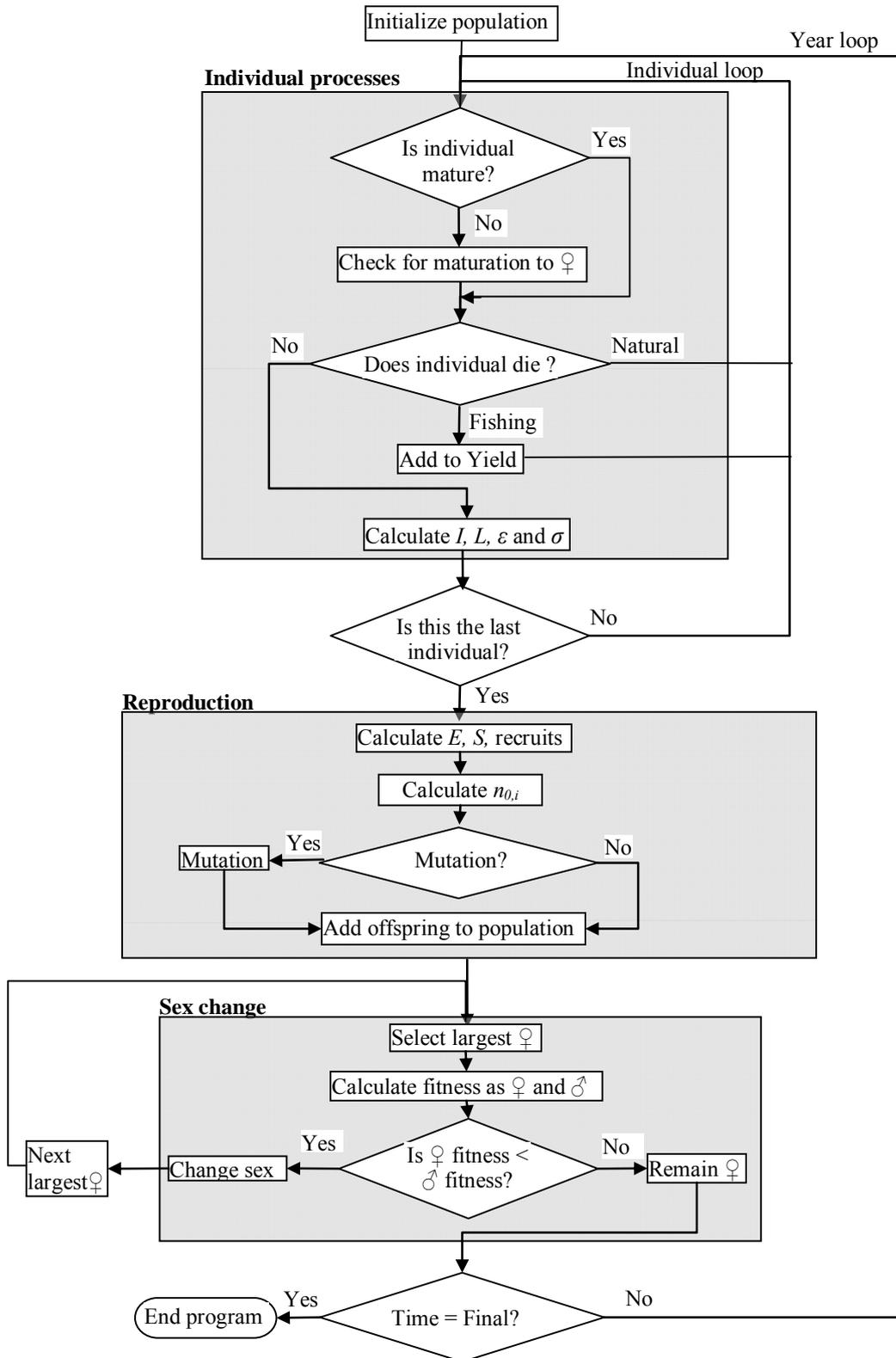
Figure A3. The structure and flow of the model.

Initialization

All individuals are initialized in the model at age 0 yrs. Each individual is described by its attribute vector and strategy vector. Initial body length is drawn from a normal distribution with a mean of 15 cm (immature) and standard deviation of 2 cm. The initial energy allocation to reproduction is set to 0.7 for females (α_F) and 0.95 for males (α_M), and the initial length at which probability of maturing for an individual of that length is 50% (L_m) is set to 54 cm with standard deviations of 0.1 for energy allocation and 3 cm for L_m. These values were averages obtained in the no-fishing scenario. Each evolving population was simulated for 20,000 yrs to reach the evolutionarily stable strategy (ESS). The 20,000 yrs do not indicate that evolution was expected to be slow but was 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 indicates which elements of the hermaphroditic life histories are regulated genetically and which are expressed as a result of social control, (*ii*) that additive genetic variation or heritabilities for these traits are poorly known, and (*iii*) that evolutionary rates would probably depend on mating structure, and we only investigate one large well-mixed spawning aggregation.

Submodels

A summary of all parameters used in the model is given in Table A1.

Energy Intake and Allocation to Growth and Reproduction.—Growth is calculated in discrete time steps of years, while energy intake, I (J), and energy allocation to reproduction, α, are taken into consideration.

$$I = X \cdot kL^a \tag{1}$$

where L (cm) is length, k and a are constants in growth trajectories (Fig. A4), and X is a stochastic random variable drawn from a normal distribution (1 ± 0.2) to introduce variation among individuals.
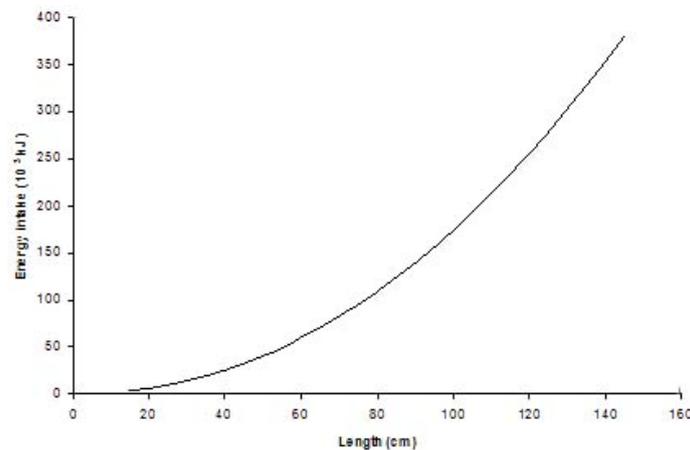

Figure A4. Energy intake with increasing length. The energy intake function increases exponentially with length, giving larger individuals the benefit of higher intake.

Values for *k* and *a* were selected to resemble the length-at-age plot given by Pears et al. (2006) for *E. fuscoguttatus*, given only natural mortality (no fishing). The emerging growth pattern from the ESS was compared to data given by Pears et al. (2006).

All energy goes toward growth for immatures ($\alpha = 0$), but allocation takes the genetically adapted values α_F and α_M in the female and male phases respectively.

Length, *L* (cm), in the next year $t + 1$ is then:

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

(2)

where the value of α depends on the sex of the individual.

In this model, weight, *W* (g), is a deterministic function proportional to length cubed;

$$W = 0.01L^3$$

(3)

We assume that female fecundity, $\varepsilon(L)$, is proportional to the individual's energy allocated to reproduction:

$$\varepsilon(L) = I\alpha_F$$

(4)

For males sperm production, $\sigma(L)$, is given by

$$\sigma(L) = I\alpha_M L^{0.1}$$

(5)

Males have an added advantage in length (the term $L^{0.1}$) to mimic increased mating success with size, so reproductive success increases more rapidly with length in males than in females, in agreement with the size advantage hypothesis (Ghiselin, 1969), which states that sex change occurs when the benefits of being the larger size in the latter sex is greater than the benefits of being larger in the initial sex.

Maturation.—The probability that an individual will mature $P_m(L)$ is a function of length, *L*. Following Alonzo and Mangel (2004), we let L_m represent the length at which probability of maturing for an individual of that size is 50% and *q* determine the steepness of the probability function (Fig. A5):
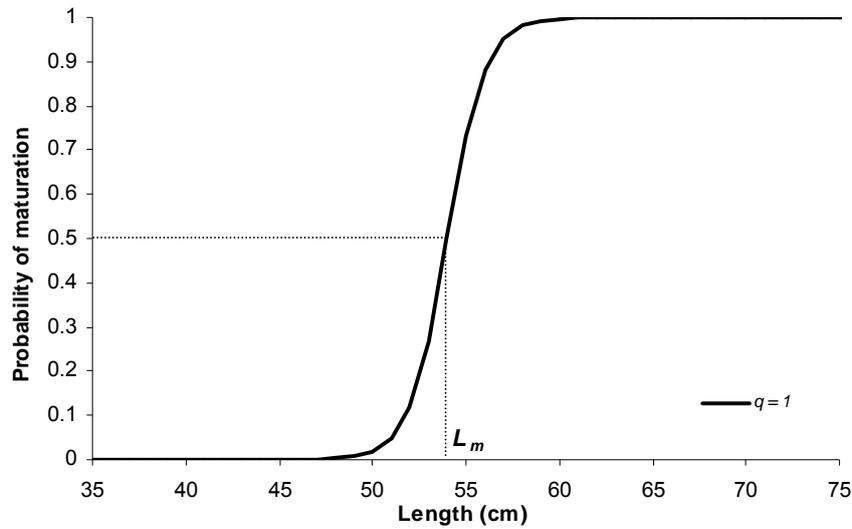
$$P_m(L) = \frac{1}{1 + exp(-q(L - L_m))}$$

(6)

Figure A5. The function for the probability of maturation. L_m denotes the length at which the probability of maturing for an individual of that length is 50%. A value of $q = 1$ was used in the model.

Sex Change.—Alonzo and Mangel (2005) investigated four different rules for sex change, using absolute or relative size of the individual: fixed size, relative size, relative frequency, and reproductive success (see Alonzo and Mangel, 2005, for more detailed descriptions). In our model we use reproductive success (rule 4 of Alonzo and Mangel, 2005) to determine the probability of sex change in an individual of a given length. Under this rule, sex change occurs when an individual's size-dependent expected reproductive success (fitness) is greater as a male than as a female (Alonzo and Mangel, 2005). We chose this rule because several studies suggest that sex change is socially controlled and that individuals respond to their own and other individual's sizes (Muñoz and Warner, 2003, 2004; Munday et al., 2006). Sex change occurs once a year in a rank order from the largest female to the next largest until a female is reached for whom it does not pay to change sex. Individuals change sex only once in their lifetimes, and they must be mature females for at least 1 yr before they can change sex.

At the time of sex change, each individual assesses her fitness as a female and that she would have as a male on the basis of her performance, using average energy intake quantities (a function of her length) and total fecundity and sperm production for the population for the previous mating season. If L_* represents the length of the largest female, then her energy intake, I_*, during the breeding season is

$$I_* = kL_*^a \tag{7}$$

Then her expected fecundity, ε_* if female, and the expected sperm production, σ_* if she became a male, would be

$$\varepsilon_* = I_* \alpha_F \tag{8}$$

$$\sigma_* = I_* \alpha_M \left(\left(L_*^3 + (1 - \alpha_M) I_* \right)^{\frac{1}{3}} \right)^{0.1} \tag{9}$$

Her fitness if she remains female, V_F, then depends on her relative fecundity and is given by

$$V_F = \left(\frac{\varepsilon_*}{\varepsilon_* + E} \right) * 0.5 \tag{10}$$

Here E is the sum of the eggs produced by all the other females, and similarly, S in the next equation is the sperm production of all other males. If the large female were to become a male, her expected fitness as a male, V_M, would then depend on her expected proportion of sperm production and is given by

$$V_M = \left(\frac{\sigma_*}{\sigma_* + S} \right) * 0.5 \tag{11}$$

If her fitness as a male (V_M) is greater than that as a female (V_F), she changes sex and functions as a male for the remainder of life. This pattern differs from that of Alonzo and Mangel (2005), who assume that an individual will change sex if its expected fecundity at a given length is exceeded by its paternity at the site (i.e., total egg production multiplied by the individuals' sperm production).

Fishing Selectivity and Survival.—Like Alonzo and Mangel (2004), we assume that natural mortality, M, is size dependent and model it as a power function of length (Peterson and Wroblewski, 1984; McGurk, 1986; Lorenzen, 1996) (Fig. A6). If μ is the natural mortality rate at $L = 1$ cm, and b is the allometric scaling factor, then M is

$$M(L) = \left(\mu L^b \right) + M_0 \tag{12}$$

M_0 is set to 0.15 in the model and thus ensures that the natural mortality never goes below 0.15 yr^{-1}. This value is close to the estimated value of natural mortality for *E. fuscoguttatus* (0.14 yr^{-1}; Grandcourt, 2005) and is an average of estimated natural mortality values for this genus. The values for μ and b in the mortality function were adjusted to give a range of mortality rates that have been obtained for grouper species (0.1–0.68 yr^{-1}; Pauly, 1980).
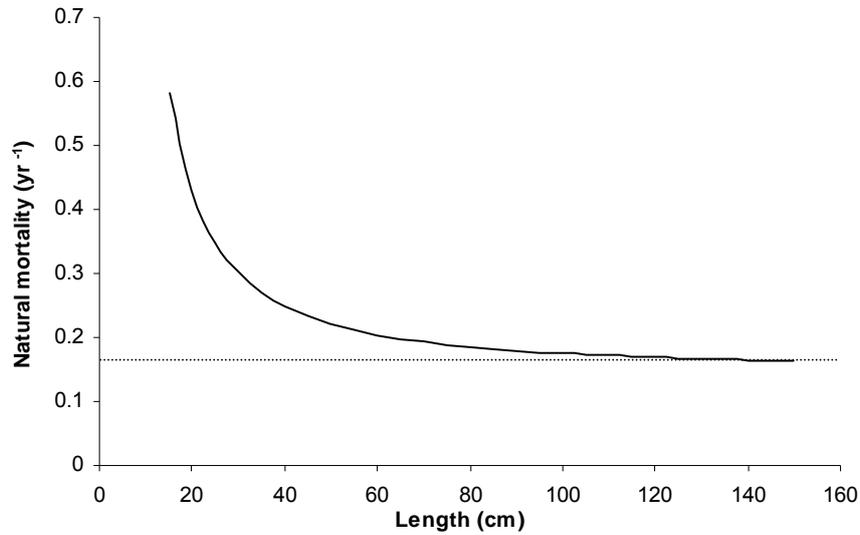
Figure A6. Varying natural mortality with length. Natural mortality of individuals decreases with increasing size.

The fishery is size selective, and given that L_f represents the length at which there is 50% chance that a fish of that size will be caught, fishing selectivity as a function of length $C(L)$ is calculated as:

$$C(L) = \frac{1}{1 + exp(-r(L - L_f))} \tag{13}$$
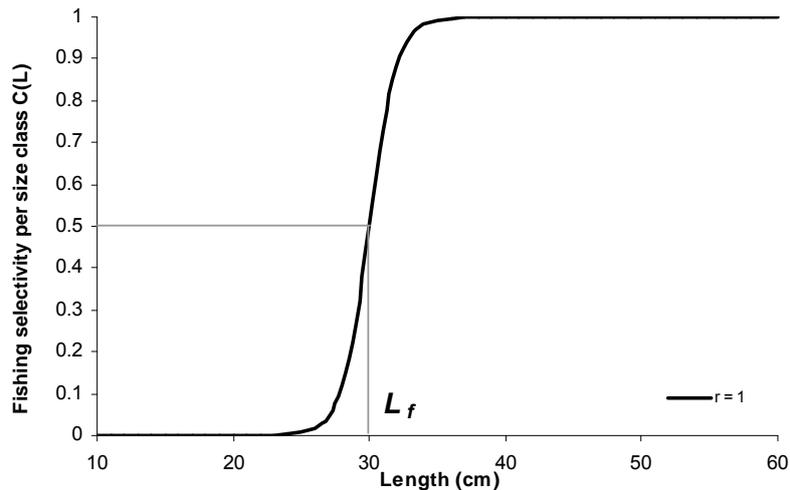
where r gives the steepness of the curve (Fig. A7).

Figure A7. Varying fishing selectivity patterns with different values of r. r is influenced by the difference between L and L_f. $L_f = 30$ cm.

With fishing mortality, F (yr^{-1}), total mortality, $Z(L)$ (yr^{-1}), and survival probability, P_S, are calculated as

$$Z(L) = M(L) + FC(L) \tag{14}$$

$$P_S = e^{-Z(L)} \tag{15}$$

Yield.—Given that the individual dies, the law of total probability is used to calculate the probability of death due to fishing, m_F, which is a function of L:

$$m_F(L) = \frac{1 - \exp(-FC(L))}{(1 - \exp(-FC(L))) + (1 - \exp(-M(L)))} \tag{16}$$

If the cause of death is fishing (as determined by a stochastic process), then the weight of the individual is added to the yield, Y. Size, age, and sex of the catch are also recorded.

Population Dynamics.—In every time step, the ages and lengths of all individuals remaining alive from the previous time step are updated. Recruitment into the population is determined by the total production of fertilized eggs $P(t)$ (which is equivalent to total fecundity of the population, as fertilization probabilities remain stable at high values) and the number of recruits that survive from this total (Fig. A8). A Beverton-Holt recruitment function (Jennings et al., 2001) is used to calculate the number of eggs surviving (N_0) to recruit in year t:

$$N_0(t) = \frac{\delta P(t)}{1 + (\beta P(t))} \tag{17}$$

where δ / β gives the maximum number of recruits per year.

The main assumption of the Beverton-Holt recruitment function is that the mortality rate established by competition between juveniles is linearly dependent on the number of fish alive in the cohort at any given time (Hilborn and Walters, 1992: 259). The recruitment function has both density-independent and density-dependent components, δ and β respectively. δ/β gives the maximum number of recruits produced every year and ensures that this number does not exceed the maximum population size.
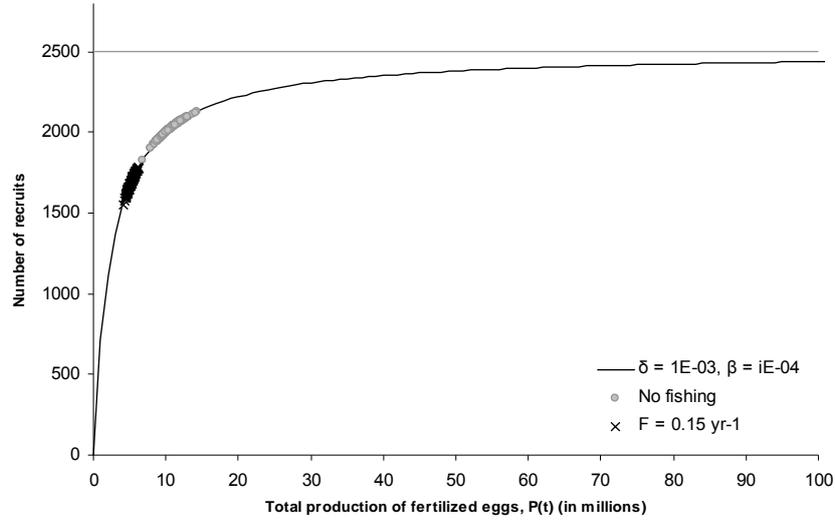
Figure A8. Effect on the recruitment function of varying δ. Recruitment increases toward an asymptote with increasing values of $P(t)$. Maximum number of recruits per year is indicated by the gray line.

Reproduction.—Individuals produce offspring proportionally to their gamete production, and each sex contributes half the offspring in the next generation. Reproduction is thus asexual and mutation limited. These assumptions imply that we can only study ESS strategies and not evolutionary trajectories. If 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

$$n_{0,i} = \left(\frac{\varepsilon}{E}\right)\left(\frac{N_0(t)}{2}\right) \text{ if the parent is female, and} \tag{18}$$

$$n_{0,i} = \left(\frac{\sigma}{S}\right)\left(\frac{N_0(t)}{2}\right) \text{ if the parent is male.} \tag{19}$$

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

Mutation.—Before being added to the population, the offspring undergo mutation of the genes in their strategy vectors. Individuals inherit all genes from one parent. Mutations occur with a probability of 5%, and new gene values are normally distributed around the old value but have a small probability of making large mutational jumps to arbitrary values. This process gives additional variability to the strategy vectors in the model. These unrealistically high mutation rates would have consequences if we were studying evolutionary trajectories, but as we focus only on the ESS, these assumptions do not affect the evolutionary outcomes.

Table A1. List of parameters and variables used in this model.

Parameter	Baseline value	Units	Definition
Strategy vector			
L_m	54	cm	Length at which probability of maturing is 50%
α_F	0.7	cm	
α_M	0.95	cm	
Attribute vector			
Age		yrs	Age of individual
L		cm	Length of individual
Sex			0, immature; 1, female; 2, female
Growth			
k	11		Constant in energy-intake function
a	2.1		Exponent in energy-intake function
Mortality and fishing			
μ	25		Natural mortality rate when $L = 1$ cm
b	–1.5		Length exponent in natural mortality function
M_0	0.15	yr^{-1}	Base-line natural mortality rate
r	1		Steepness of fishing selectivity curve
F	0–0.3	yr^{-1}	Fishing mortality
L_f	30–60	cm	Varying length at which probability of capture is 50%
Maturity and reproduction			
q	1		Shape parameter in the maturity function
β	4×10^{-7}		Larval recruitment function parameter
Mutation			
P_{Mut}	0.05		Probability of mutation
Variables			
Age_{min}	0	yrs	Age at which individuals are initialized in the population
L_0	15 ± 2	cm	Length at which individuals are initialized in the population
I		J	Energy intake
W		g	Weight of individual
$\varepsilon(L)$		eggs	Female fecundity
$\sigma(L)$		sperm	Sperm production
E		eggs	Total fecundity
S		sperm	Total sperm production
$P(t)$		eggs	Total egg production
$P_m(L)$			Probability of maturation
I_*		J	Energy intake by largest female, based on her

		length, L_*
ε_*	eggs	Expected fecundity of largest female
σ_*	sperm	Sperm production by largest female if she were a male
V_F	fertilized eggs	Fitness of the largest female
V_M	fertilized eggs	Fitness of the largest female if she were a male
$n_{0,i}$	inds	Number of offspring produced per parent
$C(L)$		Fishing selectivity
$M(L)$	yr^{-1}	Natural mortality
Z	yr^{-1}	Total mortality
P_S		Annual survival probability
m_F		Probability of death from fishing
Y	metric tons yr^{-1}	Yield
N_0	inds	Number of surviving recruits

PART 2–SENSITIVITY ANALYSIS

The model is quite sensitive to natural mortality and size advantage in males. The effects of increasing fishing mortality on life-history traits and phenotypes is shown for different natural mortalities ($M_0 = 0.1$ yr^{-1} and 0.2 yr^{-1}) and with a fishing selectivity $L_f = 50$ cm. Yield and management implications are also tested for different natural mortalities ($M_0 = 0.1$ and 0.2 yr^{-1}) and L_f (30, 40, 50 and 60 cm).

Sensitivity to fishing selectivity

Sensitivity of Life History Traits in the Model to Fishing Selectivity.—When minimum size limit in the fishery is high, evolution of traits occurs at lower fishing mortalities than when fishing includes smaller size classes. Energy allocation to reproduction in the female phase, α_F, shows that individuals favor a hermaphroditic strategy over a dioecious strategy for all fishing mortalities (Fig. A9A). Bimodality in α_F indicates that some individuals are allocating very little, and some very high amounts of, energy to reproduction in the female phase. In contrast to the results obtained for L_f of 30 cm (Figs. 1–3 in main paper), using an L_f of 50 cm does not drive the population toward becoming a dioecious population at high fishing mortalities.

Energy allocation to reproduction in the male phase, α_M, remains quite stable at almost maximum energy allocation levels to reproduction (Fig. A9B), so individuals do not grow in the male phase.

L_m decreases and evolves to lengths below the L_f of 50 cm at very low fishing mortalities (0.01 yr^{-1}) (Fig. A9C). This evolution is the reason for continued hermaphroditism in the population even at high fishing mortalities.
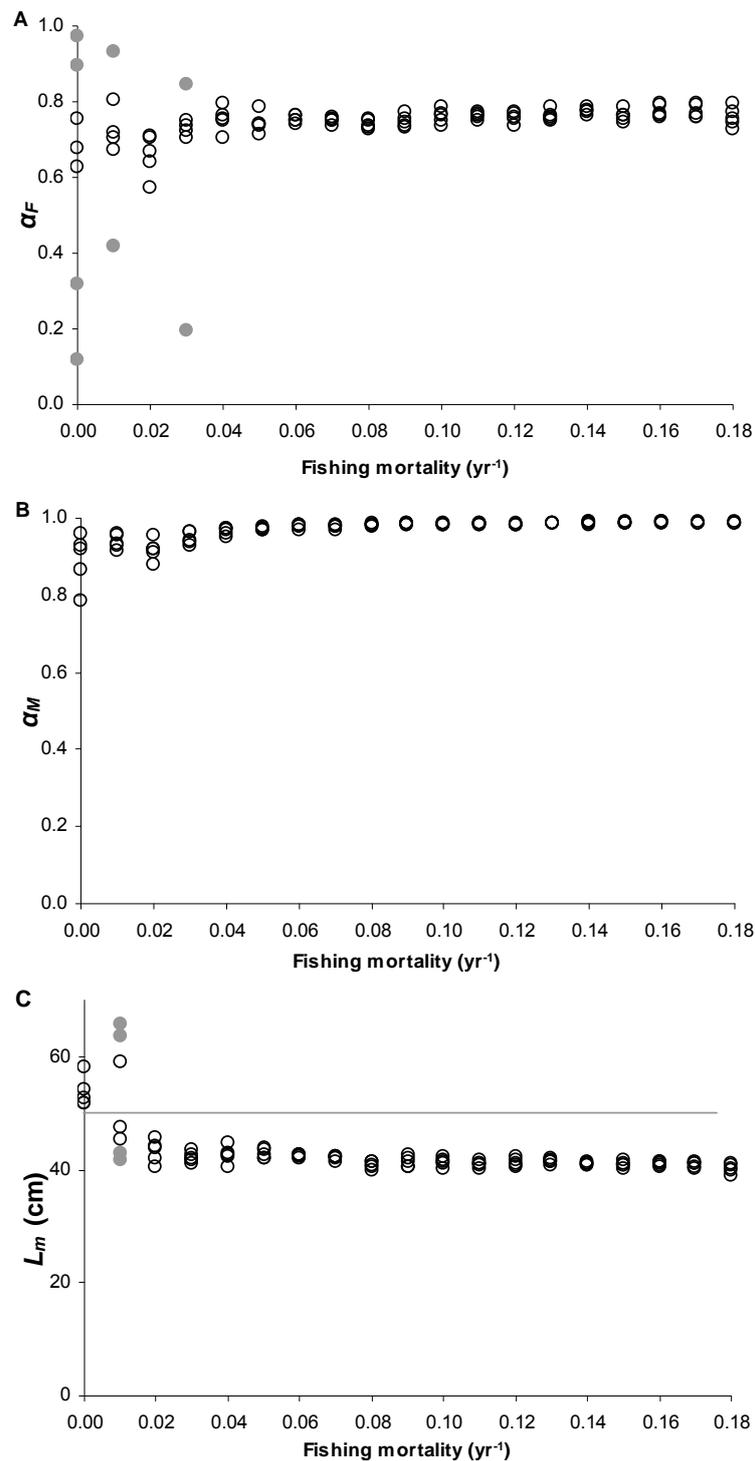
Figure A9. Evolution of genes coding for life-history strategies in a modeled grouper population subjected to harvest. Mean values for genes evolved with varying fishing mortalities and L_f of 50 cm (indicated by gray line). A. Energy allocation to reproduction in the female phase, α_F. B. Energy allocation to reproduction in the male phase, α_M. C. Length at which probability of maturation, L_m(c), is 50%.
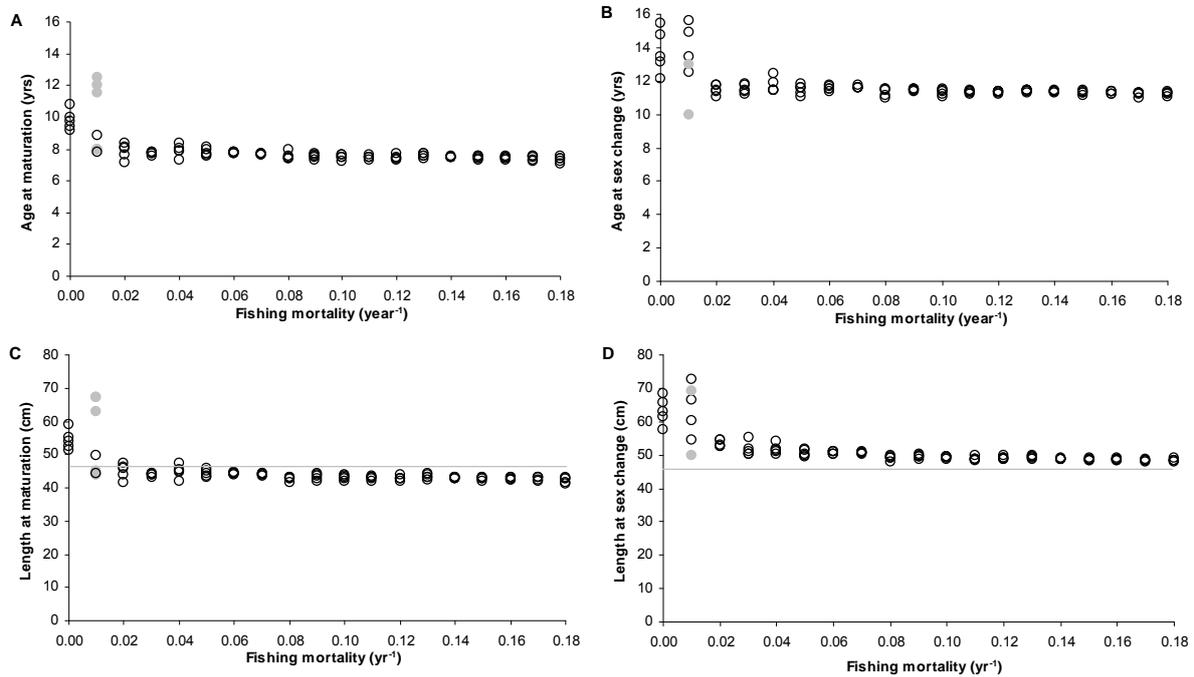
Figure A10. Evolved life history strategies (phenotypes) for a modeled grouper population subjected to varying levels of harvest intensity. Mean values for age and length at maturation and sex change at different fishing mortalities and L_f of 50 cm (indicated by gray line). A. Age at maturation. B. Age at sex change. C. Length at maturation. D. Length at sex change.

Sensitivity of Life-History Strategies in the Model to Fishing Selectivity.—Mean age and length at maturation and sex change follow the same trend as that observed for the genes (Fig. A10). All four decrease with increasing fishing mortalities, and mean length at maturation and sex change evolve to lengths at or below the imposed L_f of 50 cm at a low fishing mortality of 0.01 yr^{-1}. As was observed for the gene (L_m), the length at maturation at fishing mortality of 0.01 yr^{-1} shows that some individuals are maturing at higher, and some at lower, lengths.

Sensitivity to natural mortality

Sensitivity of Life-History Traits in the Model to Natural Mortality.—Sensitivity of life-history traits to varying M_0 shows different patterns for different values of M_0, and evolution of the population occurs at lower fishing mortalities when M_0 is equal to 0.2 yr^{-1}.

When $M_0 = 0.1$ yr^{-1}, hermaphroditism is more often favored over a dioecious strategy at low fishing mortalities (Fig. A11A), but distinct bimodality in α_F at fishing mortalities between 0.09 and 0.12 yr^{-1} indicates that populations are following a separate-sex strategy. Hermaphroditism is once again observed at fishing mortalities greater than 0.12 yr^{-1}.
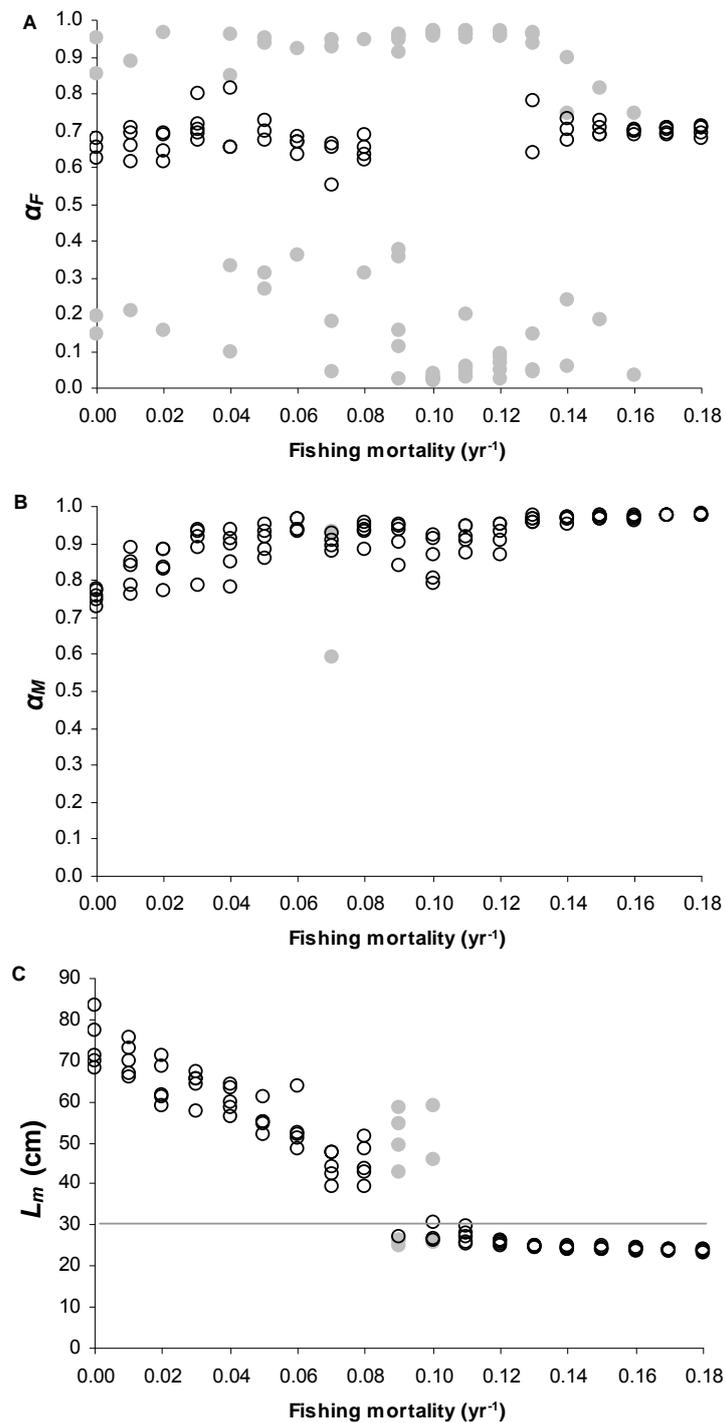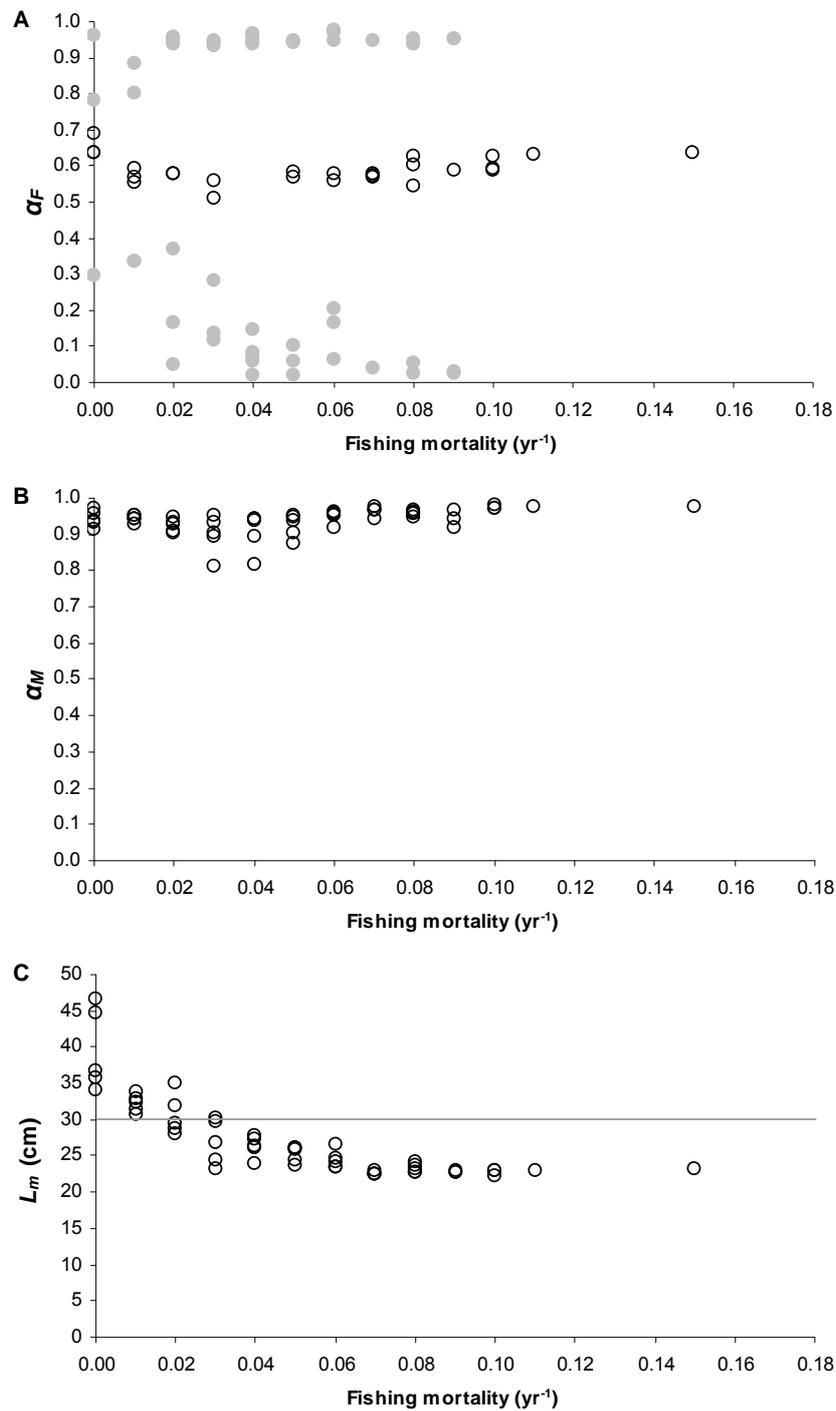
Figure A11. Evolution of genes coding for life-history strategies in a modeled grouper population subjected to harvest. Mean values for genes evolved with varying fishing mortalities, L_f of 30 cm (indicated by gray line), and $M_0 = 0.1$ yr^{-1}. A. Energy allocation to reproduction in the female phase, α_F. B. Energy allocation to reproduction in the male phase, α_M. C. Length at which probability of maturation, L_m(c), is 50%.

Figure A12. Evolution of genes coding for life-history strategies in a modeled grouper population subjected to harvest. Mean values for genes evolved with varying fishing mortalities, L_f of 30 cm (indicated by gray line), and $M_0 = 0.2$ yr^{-1}. A. Energy allocation to reproduction in the female phase α_F. B. Energy allocation to reproduction in the male phase α_M. C. Length at which probability of maturation, $L_m(c)$, is 50%.

α_M shows some variation at lower fishing mortalities, indicating that some individuals are still allocating energy to growth (Fig. A11B), but from fishing mortalities of 0.12 yr^{-1}, α_M stabilizes at almost maximal values.

L_m evolves between fishing mortalities of 0 and 0.09 yr^{-1} (Fig. A11C). Values for L_m show some bimodality at this fishing mortality, indicating that parts of the population are maturing at smaller and others at larger sizes. No further evolution of L_m occurs for fishing mortalities greater than 0.12 yr^{-1}.

When $M_0 = 0.2$ yr^{-1}, α_F indicates that both hermaphroditism and dioecy are observed in the populations (Fig. A12A). In contrast to the case in which M_0 was equal to 0.1 yr^{-1}, pure dioecy is not observed for any fishing mortality. A mix of hermaphroditism and dioecy is observed up to a fishing mortality of 0.09 yr^{-1}. Fishing mortalities greater than 0.09 yr^{-1} show a purely hermaphroditic strategy. α_M shows little variation, if any, and remains quite stable at almost maximal values (Fig. A12B).

L_m evolves between fishing mortalities of 0 and 0.04 yr^{-1} (Fig. A12C), evolving to lengths below the imposed L_f at fishing mortalities of 0.03 and 0.04 yr^{-1}. No further evolution of L_m occurs for fishing mortalities greater than 0.08 yr^{-1}.
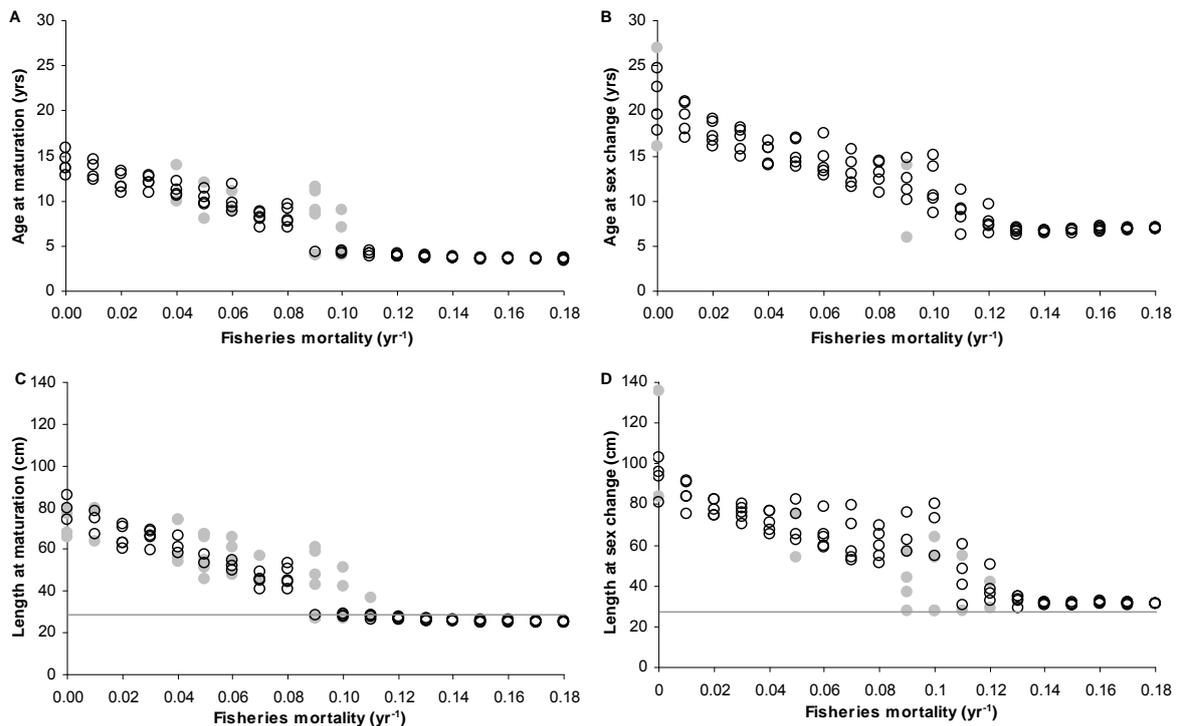
Figure A13. Evolved life-history strategies (phenotypes) for a modeled grouper population subjected to varying levels of harvest intensity. Mean values for age and length at maturation and sex change at different fishing mortalities, L_f of 30 cm (indicated by gray line), and $M_0 = 0.1$ year^{-1}. A. Age at maturation. B. Age at sex change. C. Length at maturation. D. Length at sex change.

Sensitivity of Life-History Strategies in the Model to Natural Mortality

Sensitivity of the phenotypes to varying M_0, like that of the genotypes, shows different patterns for different values of M_0, and evolution of the population occurs at lower fishing mortalities when M_0 is equal to 0.2 yr^{-1}. All four phenotypes decrease with increasing fishing mortalities, and mean length at maturation and sex change evolve to lengths at or below the imposed L_f of 30 cm.

When M_0 is equal to 0.1 yr^{-1}, mean age at maturation and sex change decrease from 15 to 4 years and 20–25 years to 8 years, respectively (Fig. A13A, B). Mean length at maturation and sex change decrease from 70 to 28 cm and 80–100 to 31 cm, respectively (Fig. A13C, D). Length at maturation evolves to values lower than the imposed L_f at fishing mortalities around 0.1–0.11 yr^{-1}.
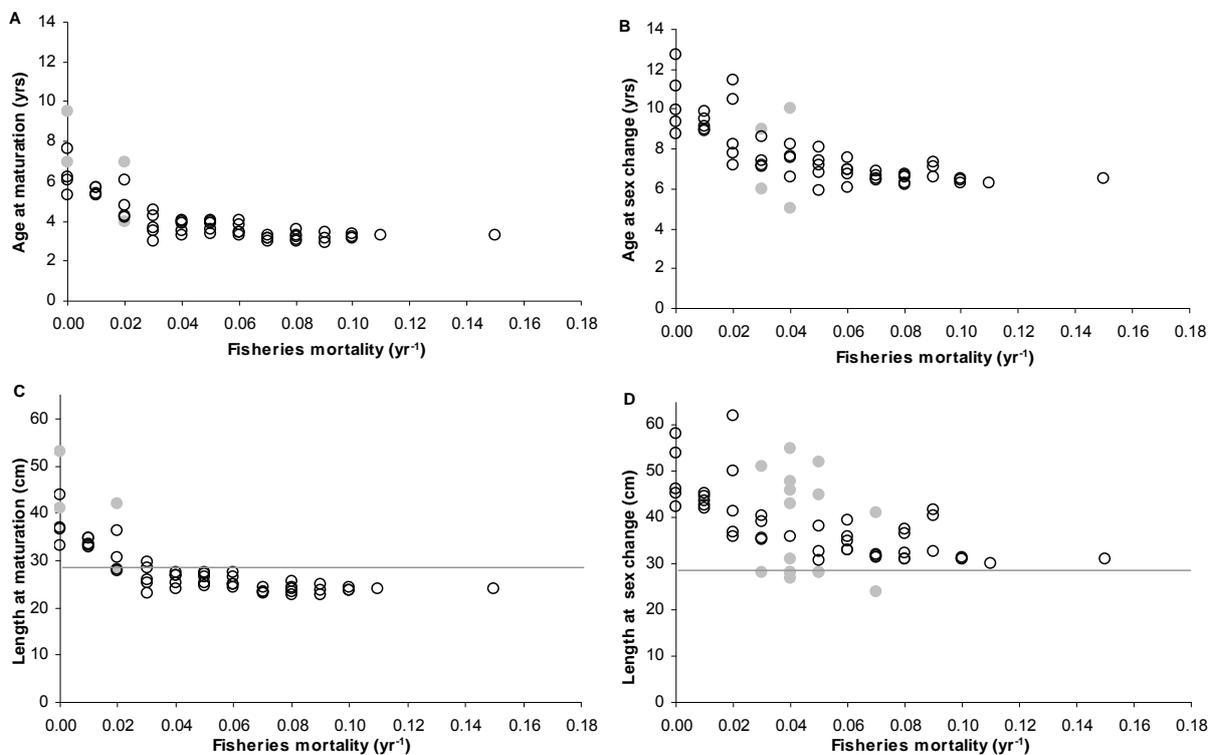

Figure A14. Evolved life history strategies (phenotypes) for a modeled grouper population subjected to varying levels of harvest intensity. Mean values for age and length at maturation and sex change at different fishing mortalities, L_f of 30 cm (indicated by gray line), and $M_0 = 0.2$ yr^{-1}. A. Age at maturation. B. Age at sex change. C. Length at maturation. D. Length at sex change.
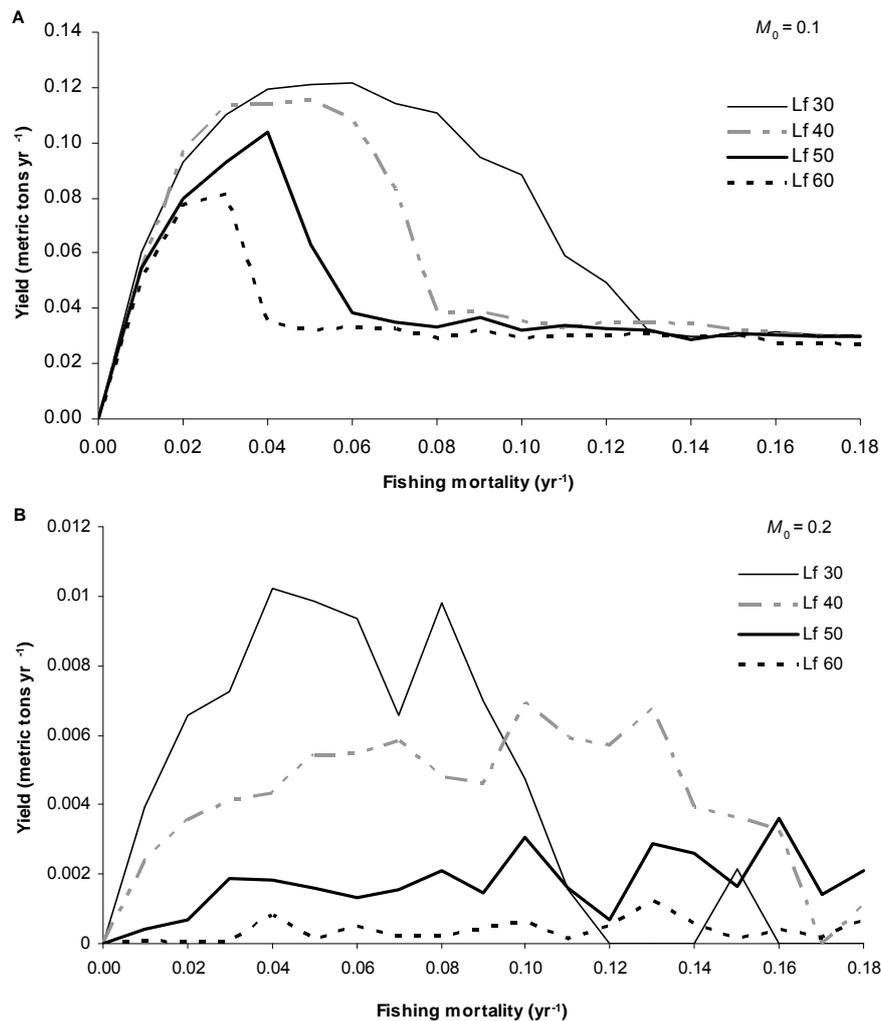
Figure A15. Varying yield patterns in a modeled grouper population subject to varying levels of harvest intensity; fishing selectivity, L_f; and background mortality, M_0. A. $M_0 = 0.1$ yr^{-1}. B. $M_0 = 0.2$ yr^{-1}. Note the different scales on yield axis.

Sensitivity of Yield to Natural Mortality and Fishing Selectivity.—When $M_0 = 0.1$ yr^{-1}, yield follows a dome-shaped curve for all fishing selectivity patterns indicated by L_f. Yield levels off at a fishing mortality of 0.13 yr^{-1}. Highest evolutionarily stable yield is obtained at a fishing mortality of 0.06 yr^{-1} when $L_f = 30$ cm. Yield decreases with increasing L_f.

With $M_0 = 0.2$ yr^{-1}, yield quantities are lower than when $M_0 = 0.1$ yr^{-1}. For the given range of fishing mortalities, yield is seen to crash when $L_f = 30$ and 40 cm. With L_f of 30 cm, yield crashed at lower fishing mortalities (0.12 yr^{-1}) than it did when L_f was 40 cm ($F = 0.17$ yr^{-1}).
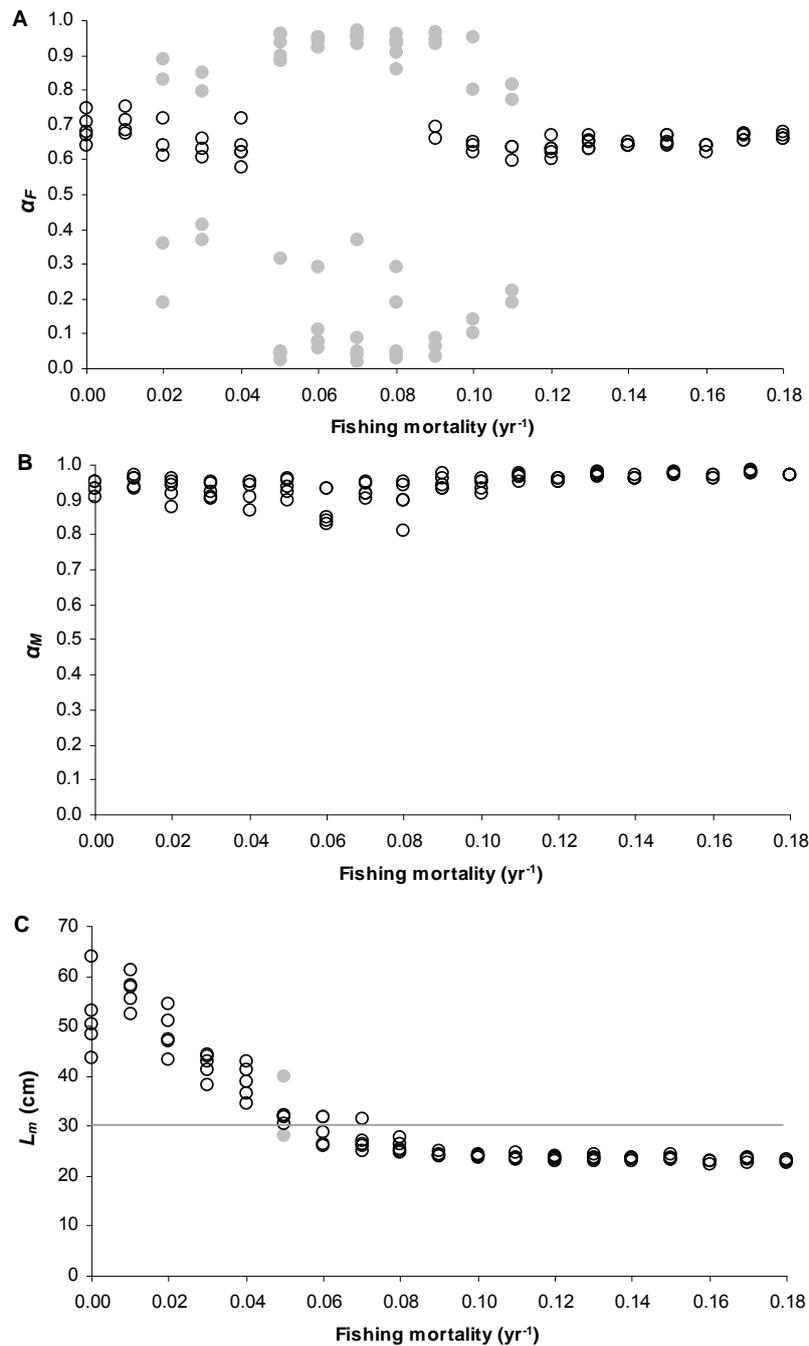
Figure A16. Evolution of genes coding for life-history strategies in a modeled grouper population subjected to harvest. Mean values for genes evolved with varying fishing mortalities, L_f of 30 cm (indicated by gray line), and no size advantage in males. A. Energy allocation to reproduction in the female phase α_F. B. Energy allocation to reproduction in the male phase α_M. C. Length at which is 50% probability of maturation L_m.

Sensitivity to Size Advantage

Sensitivity of Life-History Traits in the Model to Size Advantage.—Contrary to expectation, removal of size advantage in males causes the population to favor hermaphroditism over dioecy more frequently (Fig. A16A). No bimodality is observed in α_F in the absence of fishing, and dioecy is observed for fishing mortalities between 0.03 and 0.08 yr^{-1}.

α_M is stable at almost maximal values, indicating that, once in the male phase, all individuals allocate all their energy to reproduction and none to growth (Fig. A16B). This result is expected in the absence of size advantage in males, as continuing to grow in the male phase will not yield any additional benefits.

L_m decreases, evolving to lengths smaller than L_f, at a fishing mortality of 0.08 yr^{-1}, explaining the preference for a hermaphroditic strategy at fishing mortalities greater than 0.08 yr^{-1} (Fig. A16C).
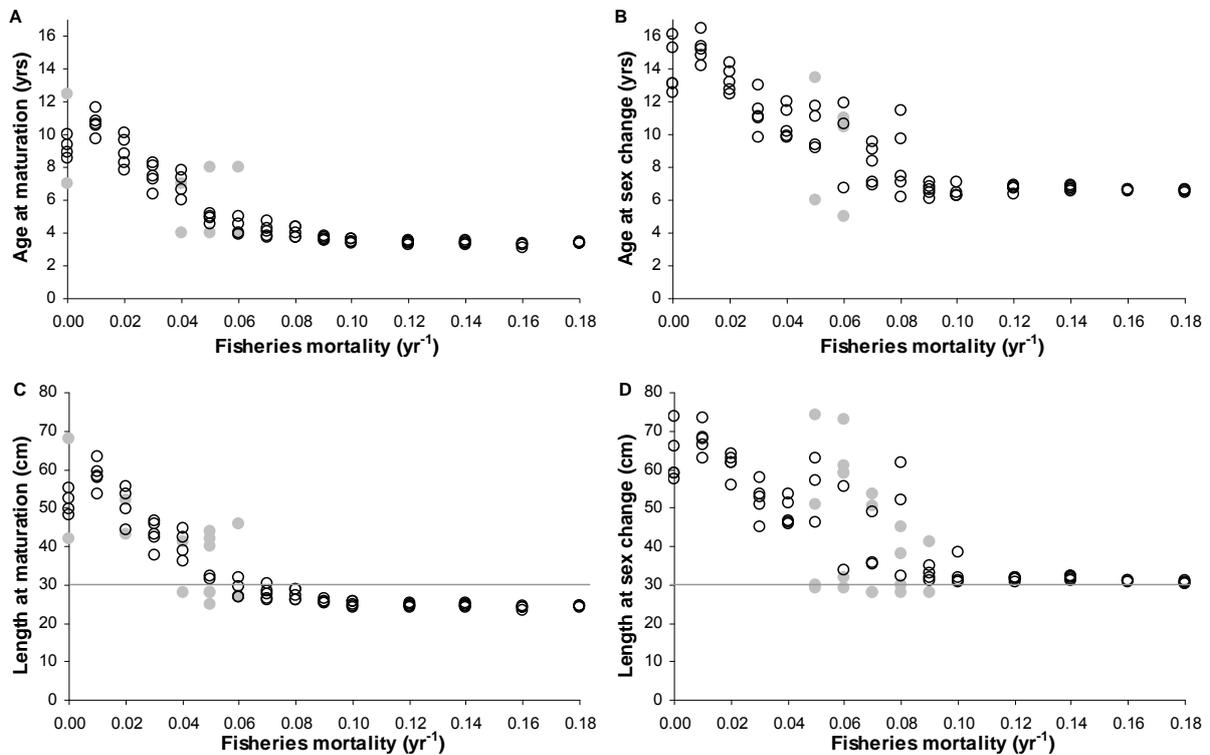

Figure A17. Evolved life history strategies (phenotypes) for a modeled grouper population subjected to varying levels of harvest intensity. Mean values for age and length at maturation and sex change at different fishing mortalities, L_f of 30 cm (indicated by gray line), and no size advantage in males. A. Age at maturation. B. Age at sex change. C. Length at maturation. D. Length at sex change.

Sensitivity of Life-History Strategies in the Model to Size Advantage.—Mean age and size at maturation and sex change in the population decrease, and mean length at maturation evolves to

lengths below the imposed L_f. In general the population follows a pattern similar to that observed when males are given a size advantage.

LITERATURE CITED

Alonzo, S. H. and M. Mangel. 2004. The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. Fish. Bull., U.S., 102: 1–13.

Alonzo, S. H. and M. Mangel. 2005. Sex-change rules, stock dynamics, and the performance of spawning-per-recruit measures in protogynous stocks. Fish. Bull., U.S., 103: 229–245.

Ghiselin, M. T. 1969. Evolution of hermaphroditism among animals. Quart. Rev. Biol. 44: 189–208.

Grandcourt, E. 2005. Demographic characteristics of selected epinepheline groupers (family: Serranidae; subfamily: Epinephelinae) from Aldabra Atoll, Seychelles. Atoll Res. Bull. 593: 200–216.

Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard, T. Grand, S. K. Heinz, G. Huse, A. Huth, J. U. Jepsen, C. Jørgensen, W. M. Mooij, B. Müller, G. Pe'er, C. Piou, S. F. Railsback, A. M. Robbins, M. M. Robbins, E. Rossmanith, N. Rüger, E. Strand, S. Souissi, R. A. Stillman, R. Vabø, U. Visser, and D. L. DeAngelis. 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Model. 198: 115–156.

Hilborn, R. and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Holland, J. H. 1992. Adaptation in natural and artificial systems: an introductory analysis with application to biology, control and artificial intelligence. MIT press, Cambridge, Massachusetts.

Jennings, S., M. J. Kaiser, and J. D. Reynolds. 2001. Marine fisheries ecology. Blackwell Science, Malden, Massachusetts.

Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. J. Fish Biol. 49: 627–642.

McGurk, M. D. 1986. Natural mortality of marine pelagic fish eggs and larvae—role of spatial patchiness. Mar. Ecol. Prog. Ser. 34: 227–242.

Munday, P. L., P. M. Buston, and R. R. Warner. 2006. Diversity and flexibility of sex-change strategies in animals. Trends Ecol. Evol. 21: 89–95.

Muñoz, R. C. and R. R. Warner. 2003. A new version of the size-advantage hypothesis for sex change: incorporating sperm competition and size-fecundity skew. Am. Nat. 161: 749–761.

Muñoz, R. C. and R. R. Warner. 2004. Testing a new version of the size-advantage hypothesis for sex change: sperm competition and size-skew effects in the bucktooth parrotfish, *Sparisoma radians*. Behav. Ecol. 15: 129–136.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. J. Cons. Cons. Inter. Explor. Mer 39: 175–192.

Pears, R., J. H. Choat, B. D. Mapstone, and G. A. Begg. 2006. Demography of a large grouper, *Epinephelus fuscoguttatus*, from Australia's Great Barrier Reef: implications for fishery management. Mar. Ecol. Prog. Ser. 307: 259–272.

Peterson, I. and J. S. Wroblewski. 1984. Mortality rates of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. 41: 1117–1120.

ADDRESSES: *Department of Biology, University of Bergen, P.O. Box 7803, N-5020 Bergen, Norway. (S.A.B.) Present address: Marine Research Centre, Ministry of Fisheries, Agriculture and Marine Resources, Malé, Republic of Maldives. E-mail: <sasattar@mrc.gov.mv>.*