

## Online Appendix

### Part 1 - Model description

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

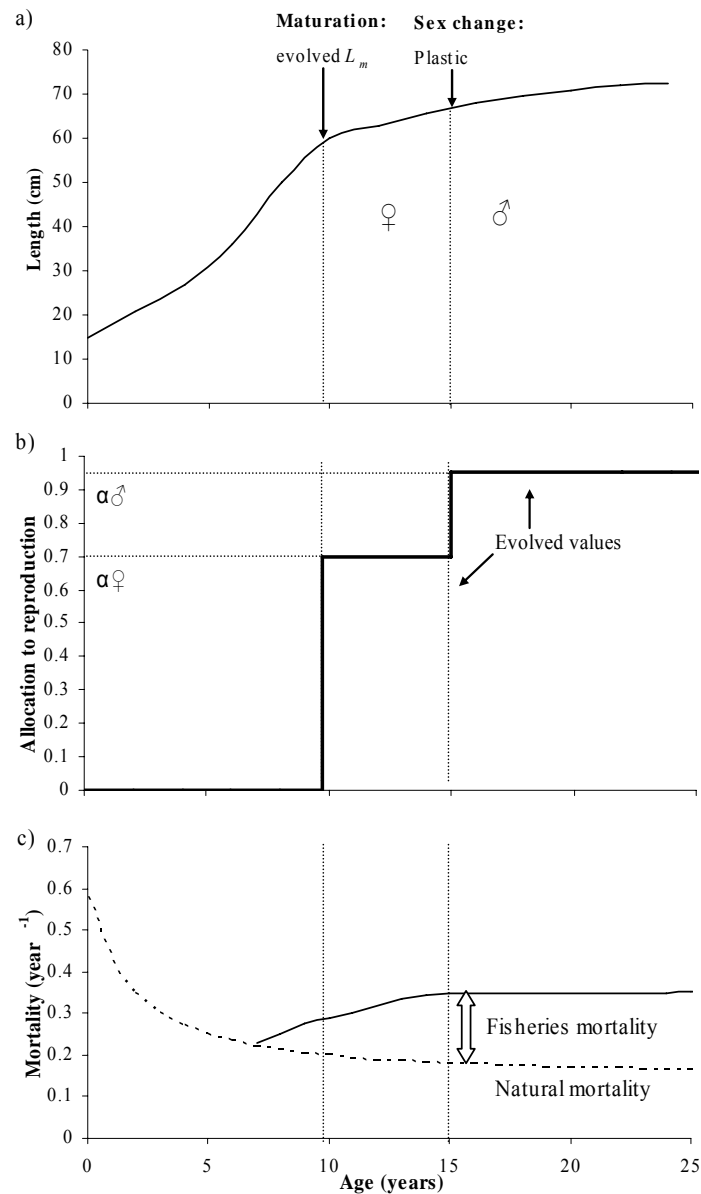
#### *Purpose*

The aim of this study is 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 phase for a population subject to fisheries. Growth rates emerge from energy allocation to growth versus reproduction. 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 by allowing for life history evolution. Figure A1 shows the life history pathway of protogynous hermaphrodites such as groupers. Individuals start as immatures, 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 towards reproduction in the female and male phase ( $\alpha_F$  and  $\alpha_M$  respectively) and length at which there is 50% probability of maturation,  $L_m$ . 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 a function of length (Fig. A1). Population simulations were run for 10,000 individuals and there is stochasticity in the model 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 evolutionary 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.

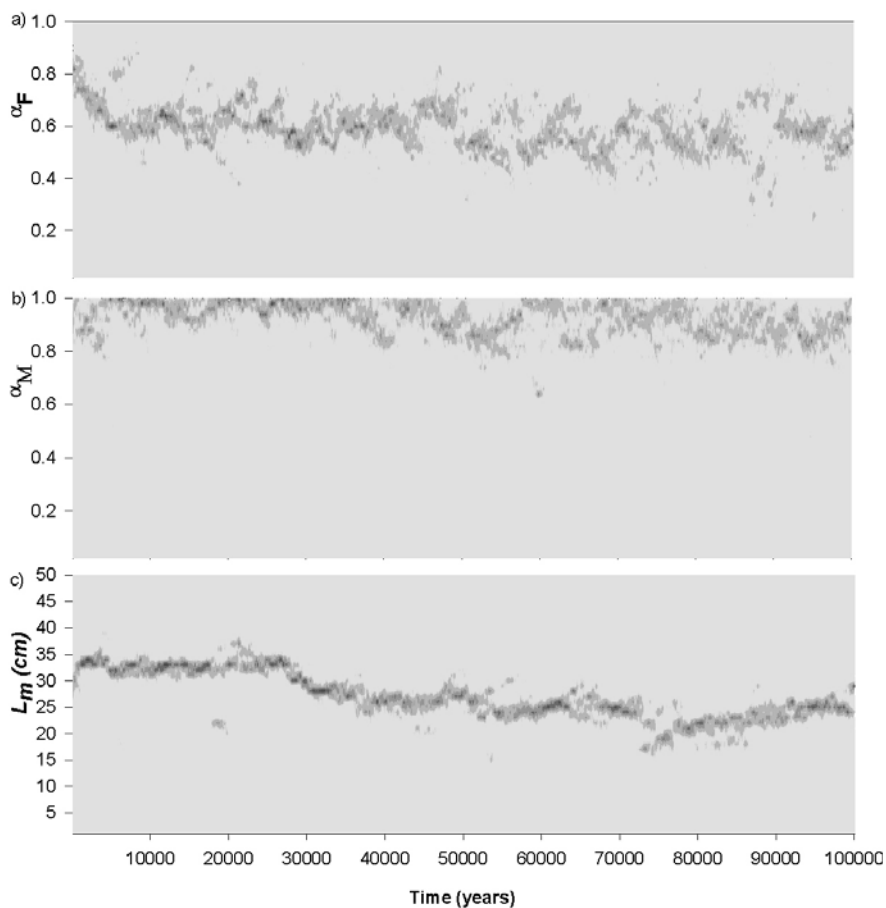


32

33 **Figure A1.** Example of a life history pathway for an individual grouper in a life history model. Each  
 34 individual goes through an immature phase until it matures to become a reproductive female. Later the  
 35 individual then undergoes the process of sex change to function as a male for the rest of its life (a). In the  
 36 immature phase, the individual allocates all its energy to growth. Once it matures (determined by the gene  
 37 for length at which there is 50% probability of maturation,  $L_m$ ) it goes through the mature female phase  
 38 where it allocates certain amount of energy to reproduction ( $\alpha_F$ ) and to growth ( $1-\alpha_F$ ). Having functioned  
 39 as female for at least a year, the individual may change sex (length at sex change is plastic) and function  
 40 as a male for the rest of its life. In the male phase the individual allocates a proportion,  $\alpha_M$  of its energy to  
 41 reproduction. Levels of energy allocation to reproduction in the female and male phase are also  
 42 determined by individual genes and are evolved in the population together with the gene for length at  
 43 maturity (b). Prior to exposure to fisheries individuals only suffer natural mortality which decreases with  
 44 age (dotted line). Once fisheries is introduced its contribution towards the mortality of older age classes  
 45 increases total mortality (solid line) suffered by the population (c).

46 **Processes**

47 The model simulates an evolving population. Individuals in the model go through the processes  
 48 of growth, maturation, sex change and reproduction including recombination and mutation. The  
 49 model uses three genes: 1) energy allocation to reproduction in the female phase  $\alpha_F$ , 2) energy  
 50 allocation to reproduction in the male phase  $\alpha_M$  and 3) length at maturity  $L_m$ . An example of the  
 51 evolutionary trajectory of the genes is shown in Figure A2. Energy allocated towards growth  
 52 increases body length, while the energy allocated towards reproduction is used for egg/sperm  
 53 production. The model simulates an evolving population using a genetic algorithm (Holland,  
 54 1992) leading to the emergence of evolutionary stable life history strategies under varying levels  
 55 of fishing.



56  
 57 **Figure A2.** Evolution of genes for energy allocation to reproduction in the female phase,  $\alpha_F$  (a), male  
 58 phase,  $\alpha_M$  (b) and length at which there is 50% probability of maturation,  $L_m$  (c).

## 59 *Concepts*

### 60 *Fitness*

61 The model has endogenous fitness i.e. the fitness of any strategy comes from within the  
62 population and is determined by the reproductive success of the individual which is a function of  
63 the individual's fecundity (if female), sperm production (if male). The model does not impose a  
64 fitness function which states the number of offspring which should be produced by an individual  
65 of certain length.

### 66 *Emergence and adaptation*

67 Emergence takes place at two levels. First individuals differ in their genetic composition (the life  
68 history strategy) and the environment they experience; this leads to the emergence of population  
69 dynamics including age and size at maturity and sex change as well as age, size and sex  
70 distributions in the population. Second, the genetic algorithm simulates evolution, and over time  
71 life history strategies adapt to the biotic and abiotic environment. This leads to the emergence of  
72 evolutionarily stable life history strategies.

### 73 *Interaction*

74 There is no competition for food resources. Interaction occurs during reproduction as competition  
75 for mates and during sex change when individuals assess their future fitness of being female or  
76 male relative to the others in the population. Fitness depends on the amounts of eggs and sperm  
77 produced by each individual relative to other members of the population. There is also density  
78 dependent juvenile survival, as the recruitment function limits the number of recruits which can  
79 be added to the population per year.

### 80 *Prediction*

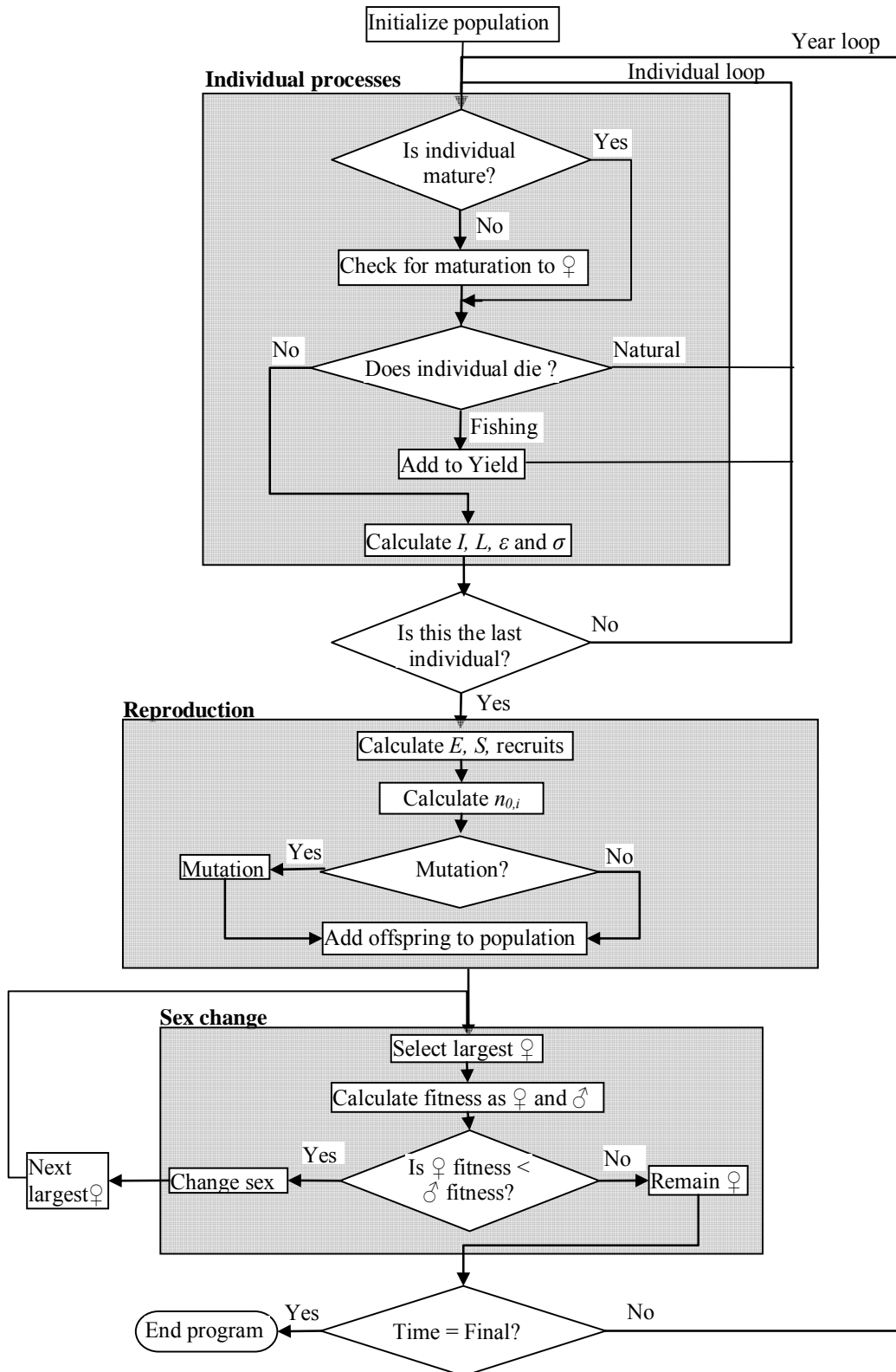
81 At the time of reproduction, each individual is able to assess its fitness as female and male by  
82 assessing the population structure and the sex ratio. If the given individual's fitness as a male is  
83 greater than as a female it will change sex and hence increase its fitness by being a male. The  
84 individual maximizes its reproductive success by changing sex when fitness of being a male is  
85 greater than that of being a female.

86 *Stochasticity*

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

93 *Scheduling*

94 The model runs in time steps of years. All immature individuals feed, grow or die due to natural  
95 mortality. The survivors, once they reach a length greater than or equal to length at which there is  
96 50% probability of them being fished, i.e.  $L_f$  are also susceptible to fisheries mortality (which is a  
97 function of length) in addition to natural mortality. Individual processes take place in the  
98 following order: Maturation, stochastic energy intake, allocation of available energy, growth and  
99 egg/sperm production. Egg and sperm production is summed at the population level, and used to  
100 calculate density-dependent offspring production. Offspring are divided between individuals  
101 proportional to their fitness and the strategy vector undergoes mutations with given probabilities.  
102 At the end of the year, females assess the population structure and change sex if future male  
103 fitness is higher than fitness of continuing as a female. A flowchart of the model is shown in  
104 Figure A3.



105  
 106 **Figure A3.** The structure and flow of the model

107 ***Initialization***

108 All individuals are initialized in the model at age 0 years. Each individual is described by its  
 109 attribute vector and strategy vector. Initial body length is drawn from a normal distribution with a  
 110 mean of 15 cm (immature) and standard deviation of 2 cm. The initial energy allocation to  
 111 reproduction is set to 0.7 for females ( $\alpha_F$ ) and 0.95 for males ( $\alpha_M$ ) and the initial length at which  
 112 there is 50% probability of an individual of that length maturing ( $L_m$ ) is set to 54 cm with  
 113 standard deviations of 0.1 for energy allocation and 3 cm for  $L_m$ . These values were averages  
 114 obtained in the no-fishing scenario. Each evolving population was simulated for 20 000 years for  
 115 to reach the Evolutionarily Stable Strategy (ESS). The 20 000 years do not mean that evolution  
 116 would be slow but is an assumption to standardize conditions for finding the ESS. The reasons to  
 117 focus on ESSs rather than evolutionary trajectories on ecological time-scales were *i*) there is little  
 118 evidence for which elements of the hermaphroditic life histories are regulated genetically and  
 119 which are expressed due to social control, *ii*) additive genetic variation or heritabilities for these  
 120 traits are poorly known, and *iii*) evolutionary rates would probably depend on mating structure,  
 121 for which we only investigate one large well-mixed spawning aggregation.

123 ***Submodels***

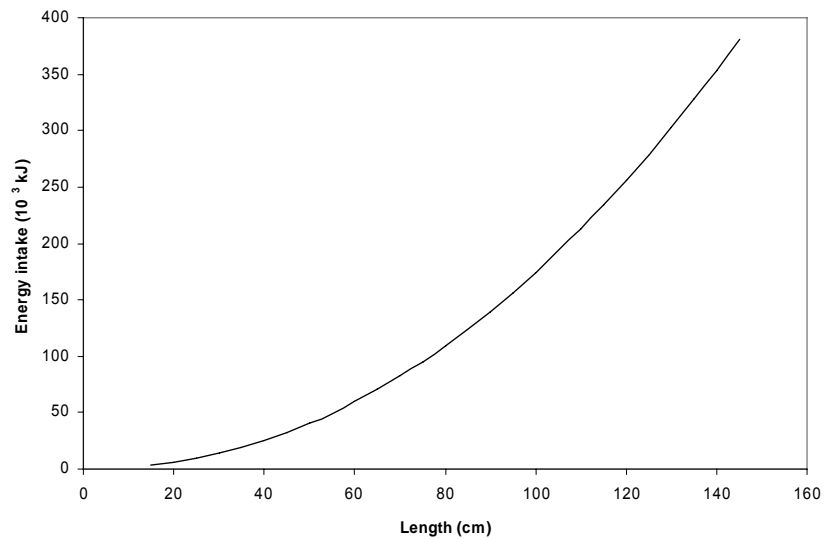
124 A summary of all parameters used in the model is given in Table A1.

125 ***Energy intake and allocation to growth and reproduction***

126 Growth is calculated in discrete time steps of years, while taking energy intake  $I$  [J] and energy  
 127 allocation to reproduction,  $\alpha$  into consideration.

$$128 \quad I = X \cdot kL^a, \quad (1)$$

129 where  $L$  [cm] is length and  $k$  and  $a$  are constants in growth trajectories (Fig. A4) and  $X$  is a  
 130 stochastic random variable drawn from a normal distribution ( $1 \pm 0.2$ ) to introduce variation  
 131 between individuals.



132  
 133 **Figure A4.** Energy intake with increasing length. The energy intake function increases exponentially with  
 134 length, giving larger individuals the benefit of higher intake in terms of quantity.  
 135

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

139  
 140 All energy goes towards growth for immatures ( $\alpha = 0$ ), while it takes the genetically adapted  
 141 values  $\alpha_F$  and  $\alpha_M$  in the female and male phase respectively.  
 142

143 Length  $L$  [cm] in the next year  $t+1$  is then:

$$144 \quad L_{(t+1)} = \left( L_{(t)}^3 + (1 - \alpha)I \right)^{\frac{1}{3}} \quad (2)$$

145 where value of  $\alpha$  depends on the sex of the individual.

146  
 147 In this model, weight  $W$  [g] is a deterministic function proportional to length cubed;

$$148 \quad W = 0.01L^3 \quad (3)$$

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

$$151 \quad \varepsilon(L) = I\alpha_F \quad (4)$$

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

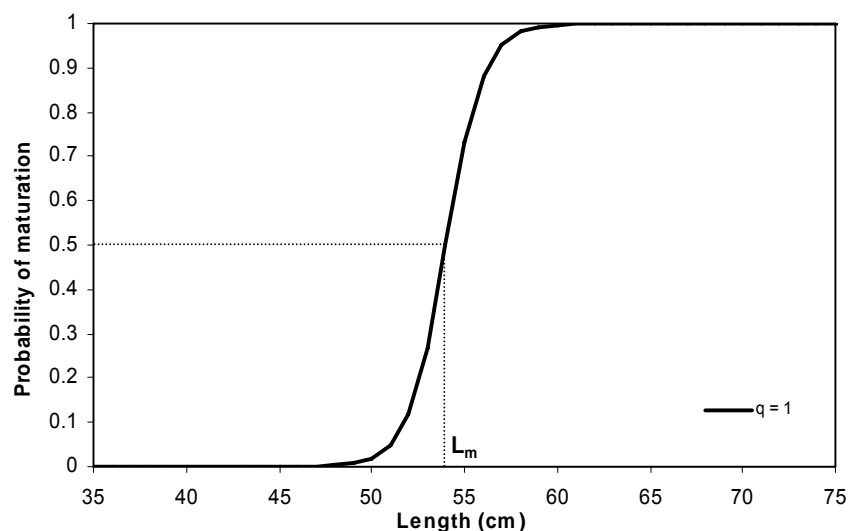
$$153 \quad \sigma(L) = I\alpha_M L^{0.1} \quad (5)$$

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

### 159 *Maturation*

160 The probability that an individual will mature  $P_m(L)$  is a function of length  $L$ . Following Alonzo  
 161 and Mangel (2004), we let  $L_m$  represent the length at which there is 50% probability of an  
 162 individual of that size maturing and  $q$  determine the steepness of the probability function (Fig.  
 163 A5):

$$164 \quad P_m(L) = \frac{1}{1 + \exp(-q(L - L_m))} \quad (6)$$



165  
 166 **Figure A5.** The function for the probability of maturation.  $L_m$  denotes the length at which there is 50%  
 167 probability of an individual that length maturing. A value of  $q = 1$  was used in the model.

### 168 *Sex change*

169 Alonzo and Mangel (2005) investigated for different rules for sex change, using absolute or  
 170 relative size of the individual. Their rules were fixed size, relative size, relative frequency, and  
 171 reproductive success (see Alonzo and Mangel, 2005, for more detailed descriptions). In our  
 172 model we use reproductive success (rule 4 in Alonzo and Mangel, 2005) to determine the  
 173 probability of sex change occurring in an individual of a given length. In this rule, sex change  
 174 occurs when an individual's size-dependent expected reproductive success (fitness) is greater as a  
 175 male than as a female (Alonzo and Mangel, 2005). Several studies suggest that sex change is

176 socially controlled and may respond to own and other individual's size (Muñoz and Warner,  
 177 2003; Muñoz and Warner, 2004; Munday et al., 2006), and we therefore chose the reproductive  
 178 success rule rather than the other less responsive rules explored by Alonzo and Mangel (2005).  
 179 Sex change occurs once a year in a rank order from the largest female to the next largest until it  
 180 no longer pays to change sex. Individuals change sex only once in their lifetime and they have to  
 181 be mature females for at least one year before they can change sex.

182  
 183 At the time of sex change the individual will assess her fitness as a female or male based on her  
 184 performance using average energy intake quantities (function of her length) and total fecundity  
 185 and sperm production for the population for the previous mating season. If  $L_*$  represents the  
 186 length of the largest female then her energy intake  $I_*$  during the breeding season is:

$$187 \quad I_* = kL_*^a \quad (7)$$

188 Then her expected fecundity  $\varepsilon_*$  if female and the expected sperm production  $\sigma_*$  if she became a  
 189 male would be:

$$190 \quad \varepsilon_* = I_* \alpha_F \quad (8)$$

$$191 \quad \sigma_* = I_* \alpha_M \left( \left( L_*^3 + (1 - \alpha_M) I_* \right)^{\frac{1}{3}} \right)^{0.1} \quad (9)$$

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

$$193 \quad V_F = \left( \frac{\varepsilon_*}{\varepsilon_* + E} \right) * 0.5 \quad (10)$$

194 If the large female was to become a male, her expected fitness as a male,  $V_M$  then depends on her  
 195 expected proportion of sperm production and is given by

$$196 \quad V_M = \left( \frac{\sigma_*}{\sigma_* + S} \right) * 0.5 \quad (11)$$

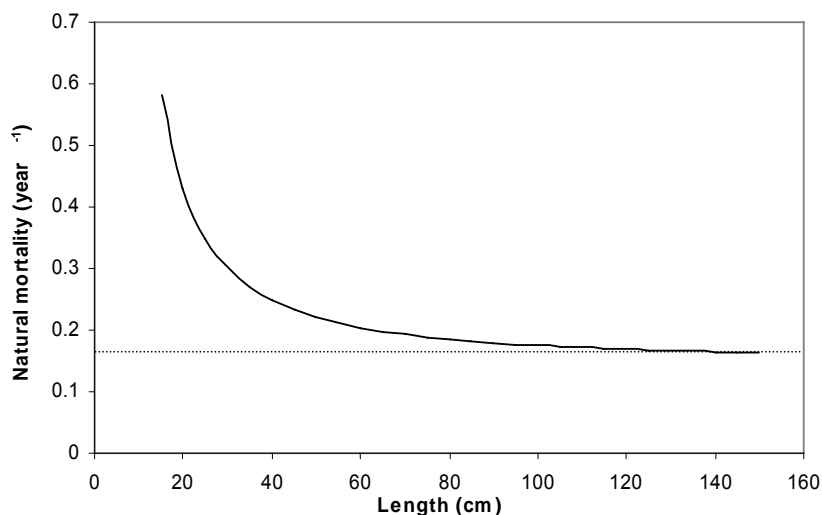
197 If the fitness of the individual as a male ( $V_M$ ), is greater than that as a female ( $V_F$ ), the individual  
 198 changes sex and functions as a male for the rest of its life. This is in contrast to Alonzo and  
 199 Mangel (2005) where they assume that an individual will change sex if its expected fecundity at a  
 200 given length is exceeded by the individuals' paternity at the site (i.e. total egg production  
 201 multiplied by the individuals' sperm production).

202 *Fishing selectivity and survival*

203 Similar to Alonzo and Mangel (2004), we assume that natural mortality  $M$  is size dependent, and  
 204 is modeled as a power function of length (Peterson and Wroblewski, 1984; McGurk, 1986;  
 205 Lorenzen, 1996) (Fig. A6). If  $\mu$  is the natural mortality rate at  $L = 1$  cm, and  $b$  is the allometric  
 206 scaling factor then  $M$  is

$$207 \quad M(L) = (\mu L^b) + M_0 \quad (12)$$

208  $M_0$  is set to 0.15 in the model and thus ensures that the natural mortality never goes below 0.15  
 209 year<sup>-1</sup>. This value is close to the estimated value of natural mortality for *E. fuscoguttatus* (0.14  
 210 year<sup>-1</sup>) (Grandcourt, 2005) and is an average of estimated natural mortality values for this genus.  
 211 The values for  $\mu$  and  $b$  in the mortality function were adjusted to give a range of mortality rates  
 212 which have been obtained for grouper species (0.1–0.68 year<sup>-1</sup>) (Pauly, 1980).

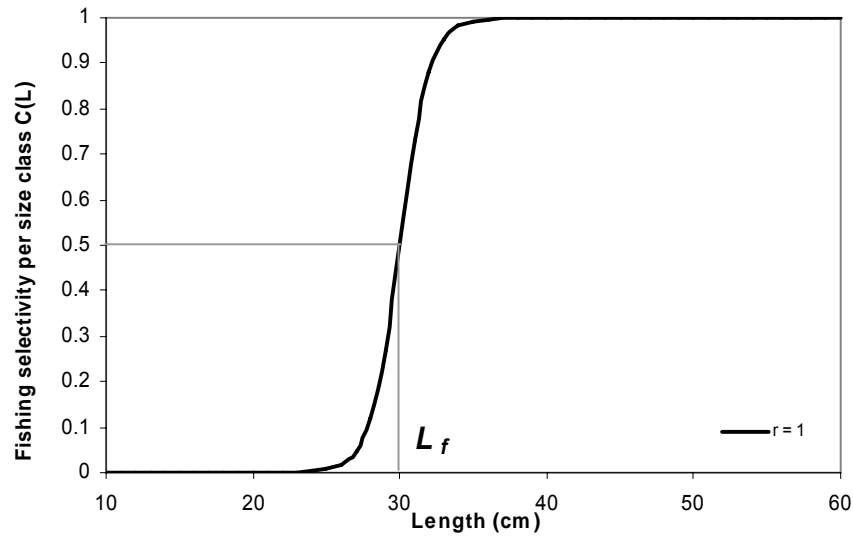


213  
 214 **Figure A6.** Varying natural mortality with length. Individuals suffer a higher natural mortality at smaller  
 215 sizes. Natural mortality of individuals decreases with increasing size.  
 216

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

$$220 \quad C(L) = \frac{I}{1 + \exp(-r(L - L_f))} \quad (13)$$

221 where  $r$  gives the steepness of the curve (Fig. A7).



222  
 223 **Figure A7.** Varying fishing selectivity patterns with different values of  $r$ .  $r$  is influenced by the difference  
 224 between  $L$  and  $L_f$ .  $L_f = 30$  cm.  
 225

226 With fishing mortality  $F$  (year<sup>-1</sup>), total mortality  $Z(L)$  (year<sup>-1</sup>) and survival probability,  $P_S$  is  
 227 calculated as:

$$228 \quad Z(L) = M(L) + FC(L) \quad (14)$$

$$229 \quad P_S = e^{-M(L) - C(L) \cdot F} \quad (15)$$

### 230 *Yield*

231 Given that the individual dies, the law of total probability is used to calculate the probability of  
 232 death due to fishing,  $m_F$ , which is a function of  $L$ :

$$233 \quad m_F(L) = \frac{1 - \exp(-FC(L))}{(1 - \exp(-FC(L))) + (1 - \exp(-M(L)))} \quad (16)$$

234  
 235 If the cause of death is fishing (determined by a stochastic process) then the weight of this fish is  
 236 added to the yield,  $Y$ . Size, age and sex of the catch is also recorded.

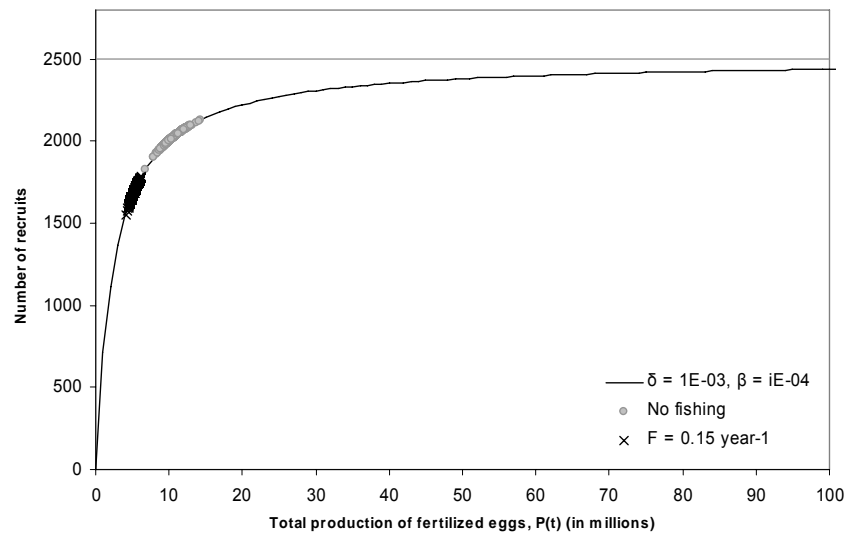
### 237 *Population dynamics*

238 In every time step, the age and length of all individuals from the previous time step is updated  
 239 given that the individual remains alive. Recruitment into the population is determined by the total  
 240 production of fertilized eggs  $P(t)$  (which is equivalent to total fecundity of the population as  
 241 fertilization probabilities remain stable at high values) and the number of recruits which survive  
 242 from this total (Fig. A8). A Beverton-Holt recruitment function (Jennings et al., 2001) is used to  
 243 calculate the number of eggs surviving ( $N_0$ ) to recruit in year  $t$ :

$$244 \quad N_0(t) = \frac{\delta P(t)}{1 + (\beta P(t))} \quad (17)$$

245 where  $\delta/\beta$  gives the maximum number of recruits per year.

246  
 247 The main assumption of the Beverton-Holt recruitment function is that the mortality rate  
 248 established due to competition between juveniles is linearly dependent on the number of fish  
 249 alive in the cohort at any given time (Hilborn and Walters, 1992, p. 259). The recruitment  
 250 function has both density-independent and density-dependent components i.e.  $\delta$  and  $\beta$   
 251 respectively.  $\delta/\beta$  gives the maximum number of recruits produced every year in and ensures that  
 252 this does not exceed the maximum population size.



253  
 254 **Figure A8.** Effect of varying  $\delta$ , on the recruitment function. Recruitment increases towards an asymptote  
 255 with increasing values of  $P(t)$ . Maximum number of recruits per year is indicated by grey line.

256  
 257 *Reproduction*

258 Individuals produce offspring proportionally to their gamete production, and each sex contributes  
 259 half the offspring in the next generation. Reproduction is thus asexual and mutation-limited.  
 260 These assumptions imply that we can only study ESS strategies and not evolutionary trajectories.  
 261 Denoting total egg and sperm production in the population  $E$  and  $S$ , respectively, then the number  
 262 of offspring  $n_{0,i}$  produced by parent  $i$  is:

$$263 \quad n_{0,i} = \left( \frac{\varepsilon}{E} \right) \left( \frac{N_0(t)}{2} \right) \quad \text{if the parent is female, and} \quad (18)$$

$$264 \quad n_{0,i} = \left( \frac{\sigma}{S} \right) \left( \frac{N_0(t)}{2} \right) \quad \text{if the parent is male.} \quad (19)$$

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

267 *Mutation*

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

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

<i>Parameter</i>	<i>Baseline value</i>	<i>Units</i>	<i>Definition</i>
<b>Strategy vector</b>			
$L_m$	54	cm	length at which there is 50% probability of an individual that size maturing
$\alpha_F$	0.7	-	energy allocation to reproduction by females
$\alpha_M$	0.95	-	energy allocation to reproduction by males
<b>Attribute vector</b>			
Age		years	age of individual
$L$		cm	length of individual
Sex		-	0 - immatures, 1 - females, 2 - males
<b>Growth</b>			
$k$	11	-	constant in energy intake function
$a$	2.1	-	exponent in energy intake function
<b>Mortality and fishing</b>			
$\mu$	25	-	natural mortality rate when $L = 1$ cm
$b$	-1.5	-	length exponent in natural mortality function
$M_0$	0.15	year <sup>-1</sup>	base-line natural mortality rate
$r$	1	-	steepness of fishing selectivity curve
$F$	0 - 0.3	year <sup>-1</sup>	fishing mortality
$L_f$	30 - 60	cm	varying length at which there is 50% probability of an individual that size being caught
<b>Maturity and Reproduction</b>			
$q$	1	-	shape parameter in the maturity function
$\beta$	4E-07	-	larval recruitment function parameter
<b>Mutation</b>			
$P_{Mut}$	0.05	-	probability of mutation
<b>Variables</b>			
$Age_{min}$	0	years	age at which individuals are initialised in the population
$L_0$	$15 \pm 2$	cm	length at which individuals are initialised in the population
$I$		joules	energy intake
$W$		grams	weight of individual
$\varepsilon(L)$		eggs	female fecundity
$\sigma(L)$		sperms	sperm production
$E$		eggs	total fecundity
$S$		sperms	total sperm production
$P(t)$		eggs	total egg production
$P_m(L)$		-	probability of maturation
$I_*$		joules	energy intake by largest female based on her length, $L_*$
$\varepsilon_*$		eggs	expected fecundity of largest female
$\sigma_*$		sperms	sperm production by largest female if she was to be a male
$V_F$		fertilized eggs	fitness of the largest female
$V_M$		fertilized eggs	fitness of the largest female if she was to be a male
$n_{0,i}$		inds	number of offspring produced per parent
$C(L)$		-	fishing selectivity
$M(L)$		year <sup>-1</sup>	natural mortality
$Z$		year <sup>-1</sup>	total mortality
$P_S$		-	annual survival probability
$m_F$		-	probability of death due to fishing
$Y$		tonnes year <sup>-1</sup>	yield
$N_0$		inds	number of surviving recruits

## 277 **Part 2 - Sensitivity analysis**

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

283

### 284 ***Sensitivity to fishing selectivity***

#### 285 *Sensitivity of life history traits in the model to fishing selectivity*

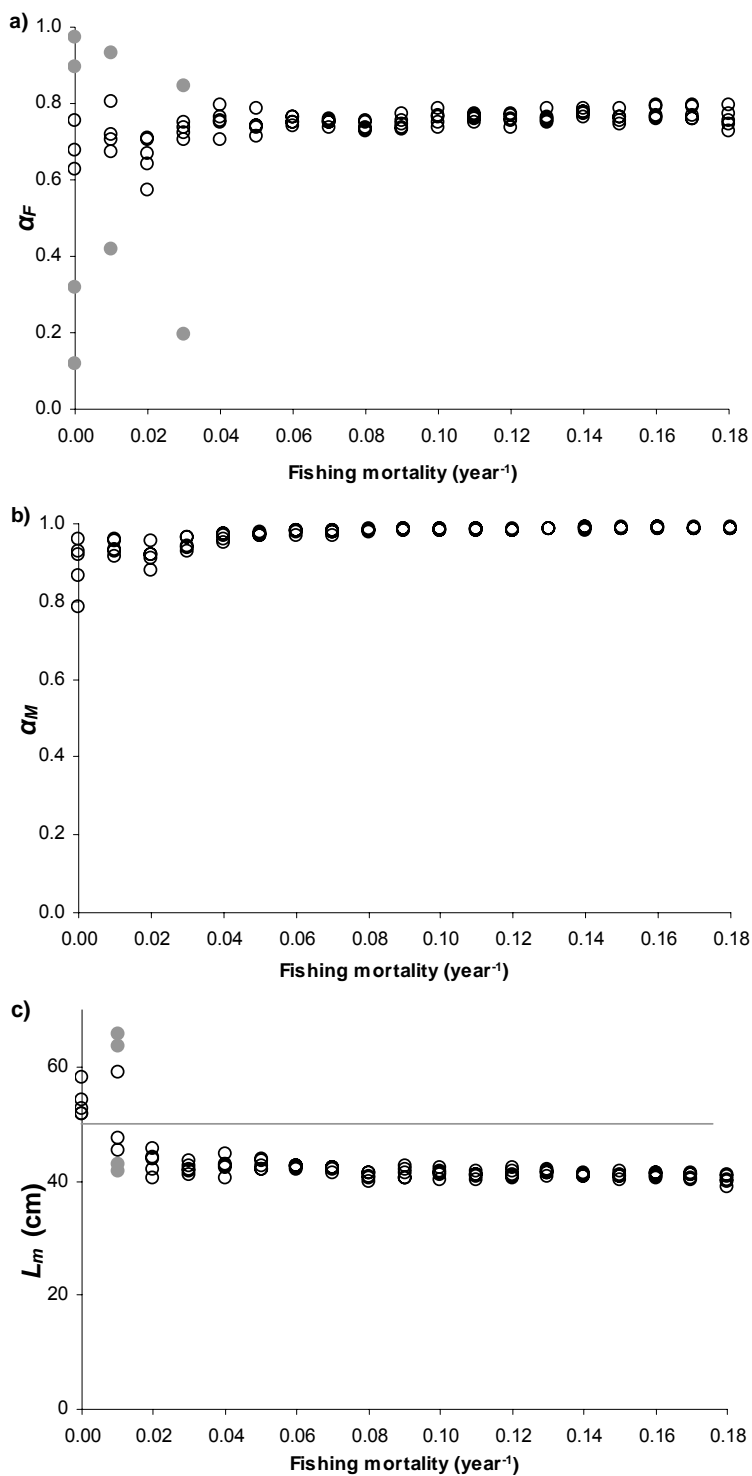
286 When minimum size limit in the fishery is high, evolution of traits occur at lower fishing  
287 mortalities than when fishing includes smaller size classes. Energy allocation to reproduction in  
288 the female phase  $\alpha_F$  shows that individuals favor a hermaphroditic strategy over dioecious  
289 strategy for all fishing mortalities (Fig. A9a). Bimodality in  $\alpha_F$  indicates that some individuals are  
290 allocating very little energy to reproduction in the female phase and some are allocating high  
291 amounts of energy to reproduction in the female phase. In comparison to the results obtained for  
292  $L_f$  30 cm (Figs. 1–3 in main paper), using an  $L_f$  of 50 cm does not drive the population towards  
293 becoming a dioecious population at high fishing mortalities.

294

295 Energy allocation to reproduction in the male phase  $\alpha_M$  remains quite stable at almost maximum  
296 energy allocation levels to reproduction (Fig. A9b). Hence individuals are not growing in the  
297 male phase.

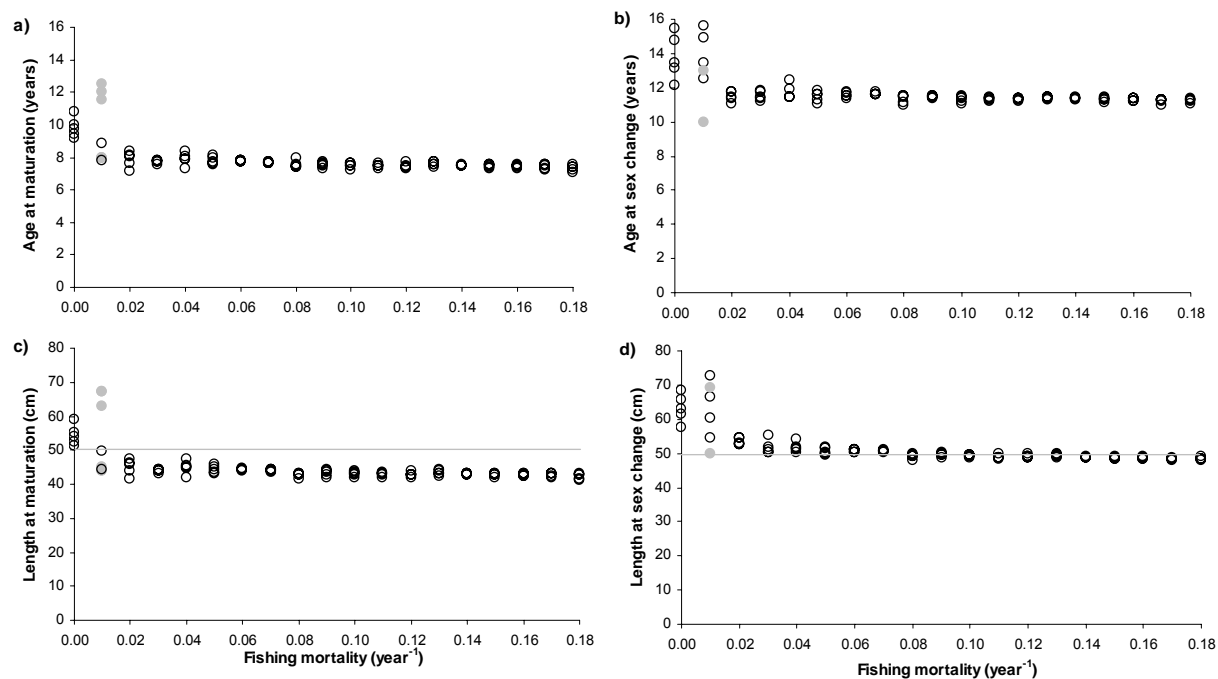
298

299  $L_m$  decreases and evolves to lengths below the  $L_f$  of 50 cm at very low fishing mortalities ( $0.01$   
300  $\text{year}^{-1}$ ) (Fig. A9c). This evolution is the reason for continued hermaphroditism in the population  
301 even at high fishing mortalities.



302  
 303 **Figure A9.** Evolution of genes coding for life history strategies in a grouper population subjected to  
 304 harvest. Mean values for genes evolved with varying fishing mortalities and  $L_f$  of 50 cm (indicated by grey  
 305 line). Energy allocation to reproduction in the female phase  $\alpha_F$  (a), energy allocation to reproduction in the  
 306 male phase  $\alpha_M$  (b) and length at which there is 50% probability of maturation  $L_m$  (c).

307



308

309 **Figure A10.** Evolved life history strategies (phenotypes) for a grouper population subjected to varying  
 310 levels of harvest intensity. Mean values for age and length at maturation and sex change at different  
 311 fishing mortalities and  $L_f$  of 50 cm (indicated by grey line). Age at maturation (a), age at sex change (b),  
 312 length at maturation (c) and length at sex change (d).

313

#### 314 *Sensitivity of life history strategies in the model to fishing selectivity*

315 Mean age- and length-at-maturation and sex change follow the same trend as that observed for  
 316 the genes (Fig. A10). All four phenotypes decrease with increasing fishing mortalities and mean  
 317 length-at-maturation and sex change evolves to lengths at or below the imposed  $L_f$  of 50 cm at a  
 318 low fishing mortality of  $0.01 \text{ year}^{-1}$ . Similar to what was observed for the gene ( $L_m$ ), the length at  
 319 maturation at fishing mortality of  $0.01 \text{ year}^{-1}$  shows that some individuals are maturing at larger  
 320 lengths while some are maturing at smaller lengths.

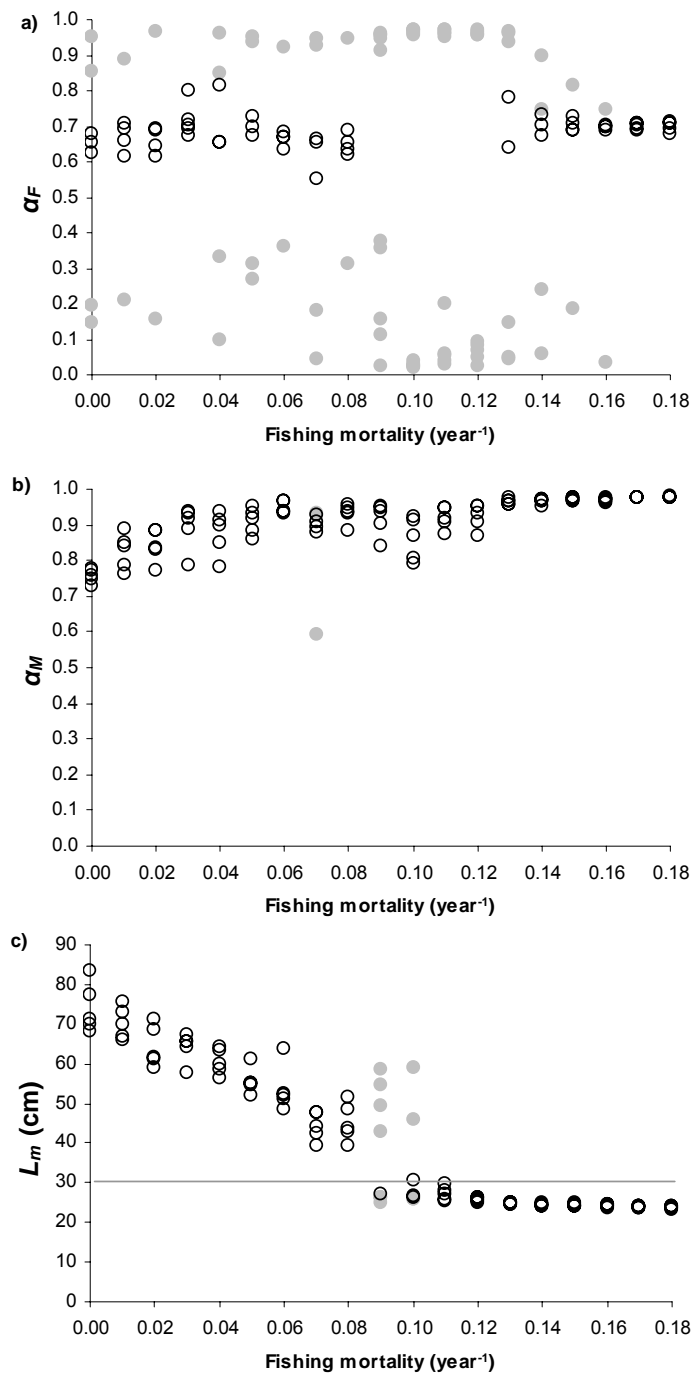
321

#### 322 *Sensitivity to natural mortality*

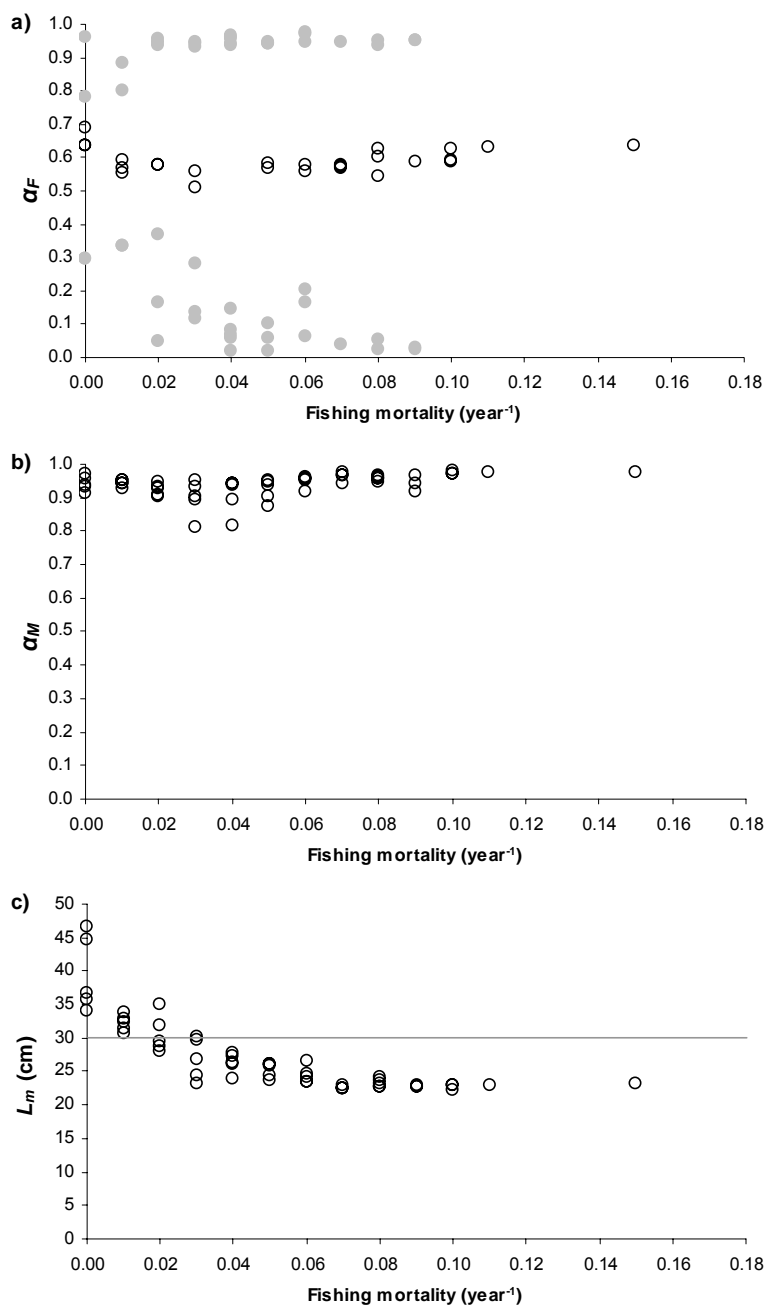
##### 323 *Sensitivity of life history traits in the model to natural mortality*

324 Sensitivity of life history traits to varying  $M_0$  shows different patterns for different values of  $M_0$   
 325 and evolution of the population occurs at lower fishing mortalities when  $M_0$  is equal to  $0.2 \text{ year}^{-1}$ .  
 326 When  $M_0 = 0.1 \text{ year}^{-1}$  hermaphroditism is more often favored over a dioecious strategy at low  
 327 fishing mortalities (Fig. A11a). However distinct bimodality in  $\alpha_F$  at fishing mortalities between  
 328  $0.09$  and  $0.12 \text{ year}^{-1}$  indicate that populations are following a separate sex strategy.  
 329 Hermaphroditism is once again observed at fishing mortalities greater than  $0.12 \text{ year}^{-1}$ .

330



331  
 332 **Figure A11.** Evolution of genes coding for life history strategies in a grouper population subjected to  
 333 harvest. Mean values for genes evolved with varying fishing mortalities,  $L_f$  of 30 cm (indicated by grey  
 334 line) and  $M_0 = 0.1 \text{ year}^{-1}$ . Energy allocation to reproduction in the female phase  $\alpha_F$  (a), energy allocation  
 335 to reproduction in the male phase  $\alpha_M$  (b) and length at which there is 50% probability of maturation  $L_m$ (c).

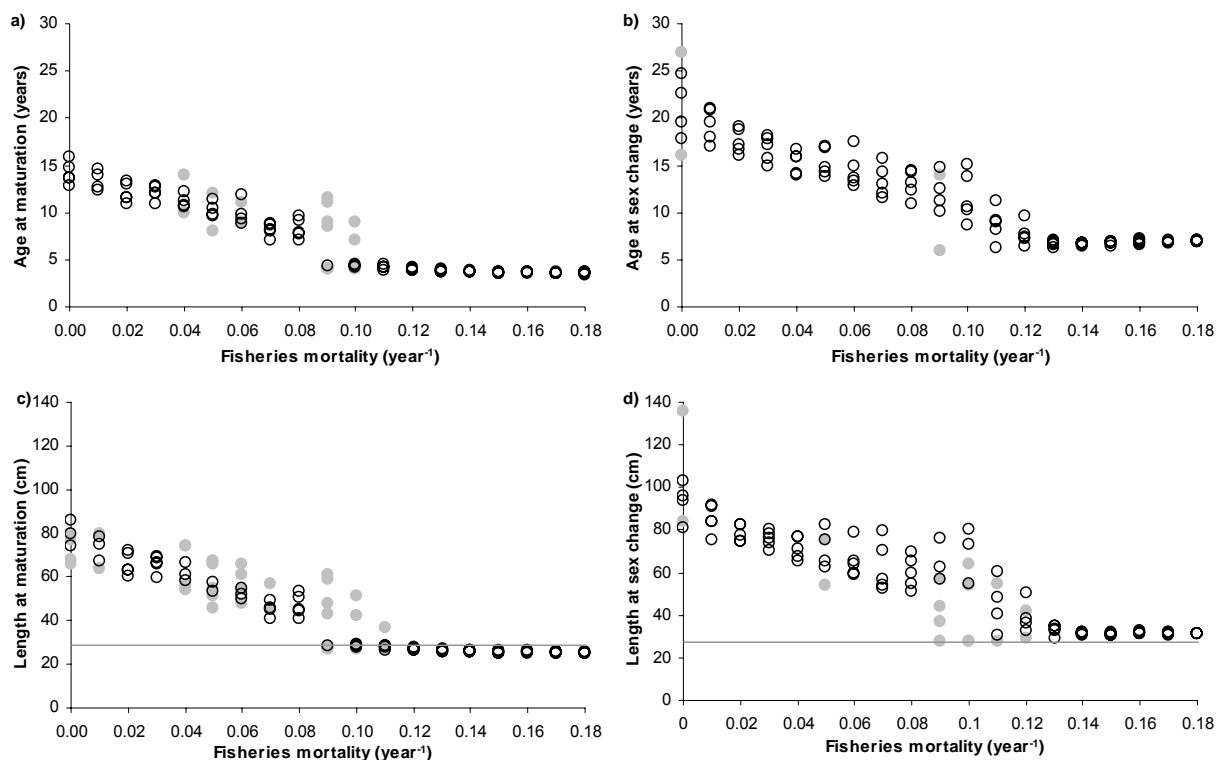


336  
 337 **Figure A12.** Evolution of genes coding for life history strategies in a grouper population subjected to  
 338 harvest. Mean values for genes evolved with varying fishing mortalities,  $L_f$  of 30 cm (indicated by grey  
 339 line) and  $M_0 = 0.2 \text{ year}^{-1}$ . Energy allocation to reproduction in the female phase  $\alpha_F$  (a), energy allocation  
 340 to reproduction in the male phase  $\alpha_M$  (b) and length at which there is 50% probability of maturation  $L_m$ (c).  
 341  
 342 There is some variation in  $\alpha_M$  at lower fishing mortalities indicating the some individuals are still  
 343 allocating energy to growth (Fig. A11b). However from fishing mortalities of  $0.12 \text{ year}^{-1}$   $\alpha_M$   
 344 stabilizes at almost maximal values.  
 345

346  $L_m$  evolves between fishing mortalities of 0 and  $0.09 \text{ year}^{-1}$  (Fig. A11c). There is some bimodality  
 347 in values for  $L_m$  at this fishing mortality indicating that parts of the population are maturing at  
 348 smaller lengths while others are maturing at larger sizes. No further evolution of  $L_m$  occurs for  
 349 fishing mortalities greater than  $0.12 \text{ year}^{-1}$ .

350  
 351 When  $M_0 = 0.2 \text{ year}^{-1}$   $\alpha_F$  indicates that both hermaphroditism and dioecy are observed in the  
 352 populations (Fig. A12a). In contrast to when  $M_0$  was equal to  $0.1 \text{ year}^{-1}$  pure dioecy is not  
 353 observed for any fishing mortality. A mix of hermaphroditism and dioecy is observed upto a  
 354 fishing mortality of  $0.09 \text{ year}^{-1}$ . Fishing mortalities greater than  $0.09 \text{ year}^{-1}$  show a purely  
 355 hermaphroditic strategy.  $\alpha_M$  shows little variation if any and remains quite stable at almost  
 356 maximal values (Fig. A12b).

357  
 358  $L_m$  evolves between fishing mortalities of 0 and  $0.04 \text{ year}^{-1}$  (Fig. A12c) evolving to lengths below  
 359 the imposed  $L_f$  at fishing mortalities of  $0.03$  and  $0.04 \text{ year}^{-1}$ . No further evolution of  $L_m$  occurs for  
 360 fishing mortalities greater than  $0.08 \text{ year}^{-1}$ .

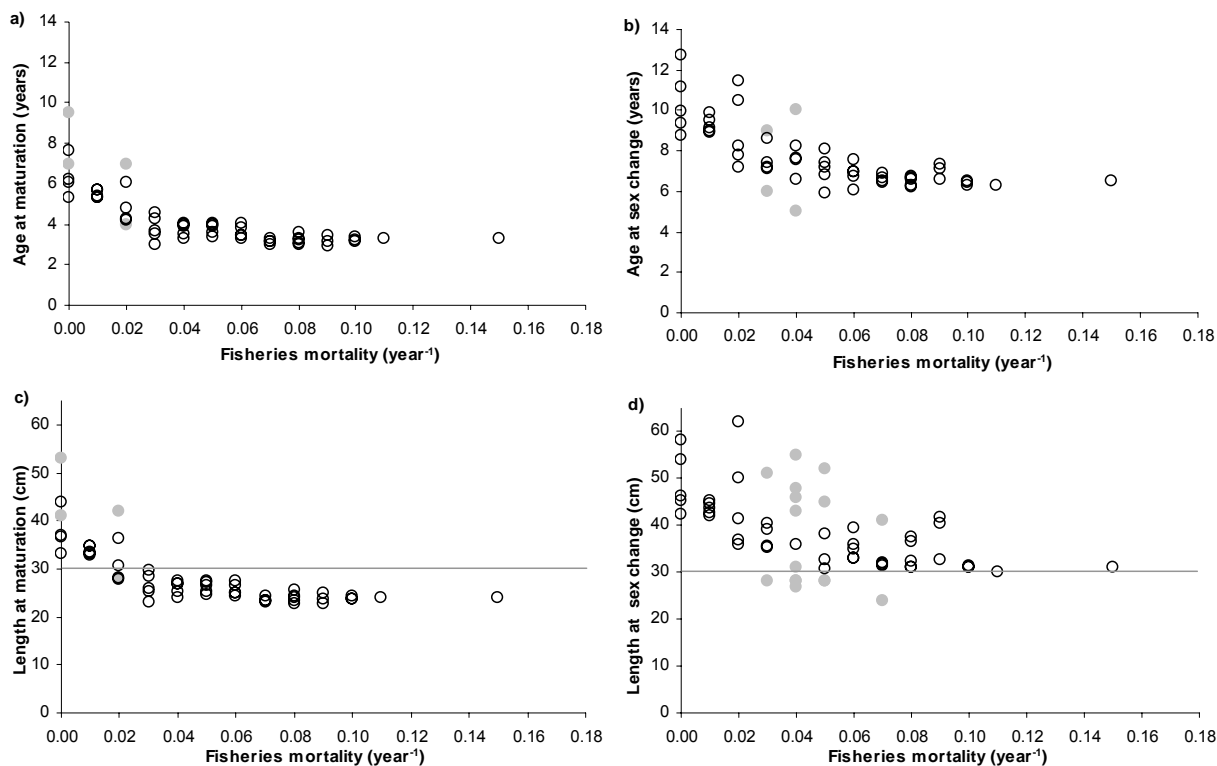


361  
 362 **Figure A13.** Evolved life history strategies (phenotypes) for a grouper population subjected to varying  
 363 levels of harvest intensity. Mean values for age and length at maturation and sex change at different  
 364 fishing mortalities,  $L_f$  of 30 cm (indicated by grey line) and  $M_0 = 0.1 \text{ year}^{-1}$ . Age at maturation (a), age at  
 365 sex change (b), length at maturation (c) and length at sex change (d).  
 366

367 *Sensitivity of life history strategies in the model to natural mortality*

368 Similar to the genotypes, sensitivity of the phenotypes to varying  $M_0$  also shows different patterns  
 369 for different values of  $M_0$  and evolution of the population occurs at lower fishing mortalities  
 370 when  $M_0$  is equal to  $0.2 \text{ year}^{-1}$ . All four phenotypes decrease with increasing fishing mortalities  
 371 and mean length-at-maturation and sex change evolves to lengths at or below the imposed  $L_f$  of  
 372 30 cm

373  
 374 When  $M_0$  is equal to  $0.1 \text{ year}^{-1}$  mean age at maturation and sex change decreases from 15 to 4  
 375 years and 20-25 years to 8 years respectively (Figs. A13 a and b). Mean length at maturation and  
 376 sex change decreases from 70 cm to 28 cm and 80–100 cm to 31 cm respectively (Figs. A13 c  
 377 and d). Evolution of the length at maturation to values lower than the imposed  $L_f$  at fishing  
 378 mortalities around  $0.1 - 0.11 \text{ year}^{-1}$ .

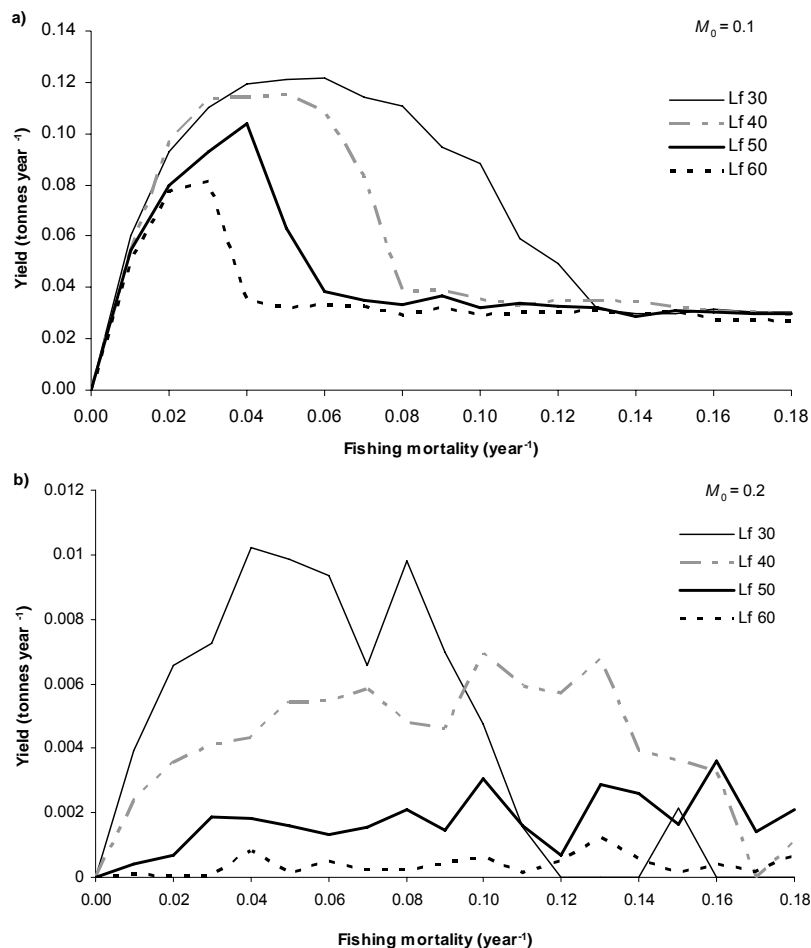


379  
 380 **Figure A14.** Evolved life history strategies (phenotypes) for a grouper population subjected to varying  
 381 levels of harvest intensity. Mean values for age and length at maturation and sex change at different  
 382 fishing mortalities,  $L_f$  of 30 cm (indicated by grey line) and  $M_0 = 0.2 \text{ year}^{-1}$ . Age at maturation (a), age at  
 383 sex change (b), length at maturation (c) and length at sex change (d).  
 384

385 When  $M_0$  is equal to  $0.2 \text{ year}^{-1}$  mean age at maturation and sex change decreases from 6-8 years  
 386 to 3 years and 9 - 11 years to 6 years respectively (Figs. A 14 a and b). Mean length at maturation

387 decreases from 35 – 45 cm to 25 cm (Fig. A 14 c) and mean length at sex change decreases from  
 388 45 - 60 cm to 30 cm (Fig. A 14d). Mean length at sex change shows more variation at each  
 389 fishing mortality than was observed when  $M_0$  was equal to  $0.1 \text{ year}^{-1}$ .

390



391

392 **Figure A15.** Varying yield patterns given by a grouper population subject to varying levels of harvest  
 393 intensity, fishing selectivity  $L_f$  and background mortality  $M_0$ .  $M_0 = 0.1 \text{ year}^{-1}$  (a) and  $M_0 = 0.2 \text{ year}^{-1}$  (b).  
 394 **Note the different scales on yield axis.**

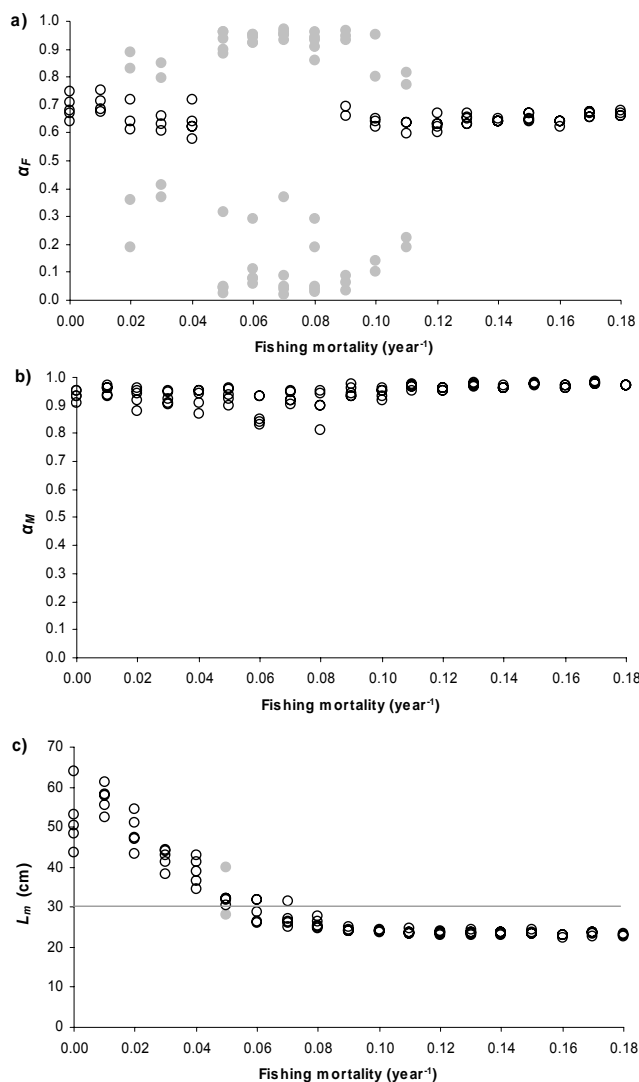
395

396 *Sensitivity of yield to natural mortality and fishing selectivity*

397 When  $M_0 = 0.1 \text{ year}^{-1}$  yield follows a dome-shaped curve for all fishing selectivity patterns  
 398 indicated by  $L_f$ . Yield levels off at a fishing mortality of  $0.13 \text{ year}^{-1}$ . Highest evolutionary stable  
 399 yield is obtained at a fishing mortality of  $0.06 \text{ year}^{-1}$  when  $L_f = 30\text{cm}$ . Yield decreases with  
 400 increasing  $L_f$ .

401

402 With  $M_0 = 0.2 \text{ year}^{-1}$  yield quantities are lower than when  $M_0 = 0.1 \text{ year}^{-1}$ . For the given range of  
 403 fishing mortalities, yield is seen to crash when  $L_f = 30$  and 40 cm. With  $L_f$  of 30 cm yield crashed  
 404 at lower fishing mortalities ( $0.12 \text{ year}^{-1}$ ) than for  $L_f$  of 40 cm ( $F = 0.17 \text{ year}^{-1}$ ).



405  
 406  
 407 **Figure A16.** Evolution of genes coding for life history strategies in a grouper population subjected to  
 408 harvest. Mean values for genes evolved with varying fishing mortalities,  $L_f$  of 30 cm (indicated by grey  
 409 line) and no size advantage in males. Energy allocation to reproduction in the female phase  $\alpha_F$  (a), energy  
 410 allocation to reproduction in the male phase  $\alpha_M$  (b) and length at which there is 50% probability of  
 411 maturation  $L_m$ (c).  
 412

### 413 *Sensitivity to size advantage*

#### 414 *Sensitivity of life history traits in the model to size advantage*

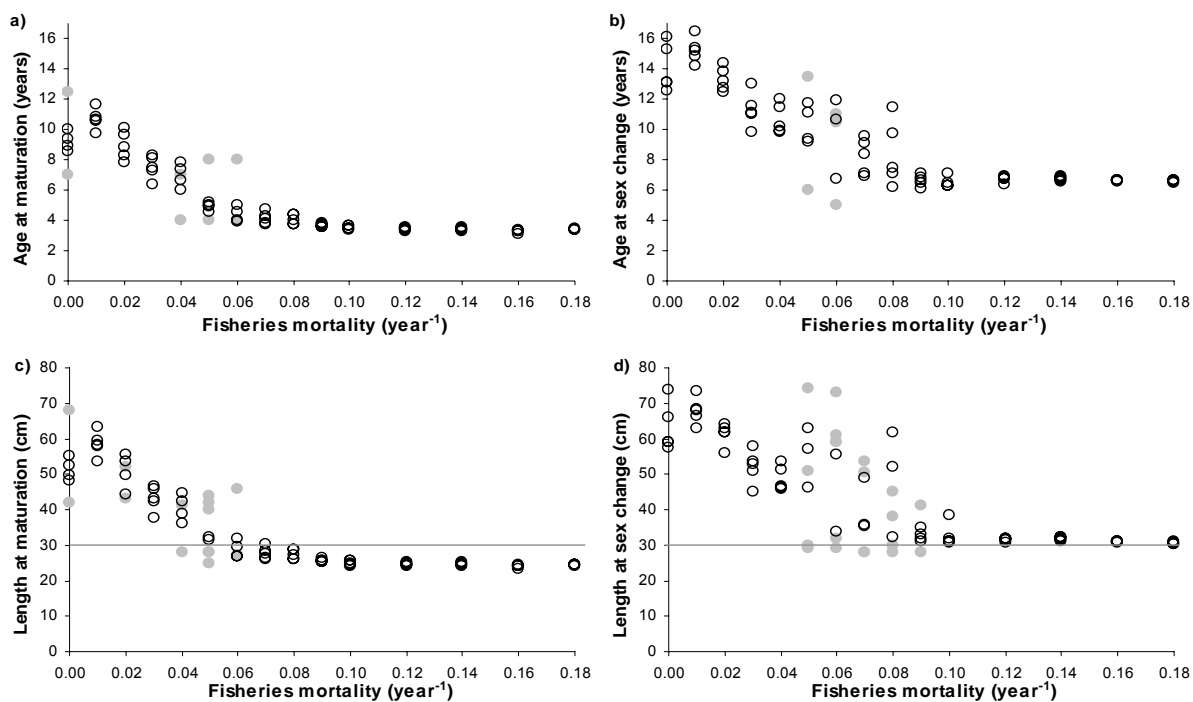
415 In contrast to what would be expected, removal of size advantage in males results in the  
 416 population favoring hermaphroditism over dioecy more frequently (Fig. A 16a). There is no

417 bimodality in  $\alpha_F$  in the absence of fishing and dioecy is observed for fishing mortalities between  
 418 0.03 and 0.08 year<sup>-1</sup>.

419  
 420  $\alpha_M$  is stable at almost maximal values indicating that once in the male phase all individuals are  
 421 allocating all their energy to reproduction and none to growth (Fig. A 16b). This is expected in  
 422 the absence of size advantage in males, as continuing to grow in the male phase will not give any  
 423 additional benefits.

424  
 425  $L_m$  decreases evolving to lengths smaller than  $L_f$  at a fishing mortality of 0.08 year<sup>-1</sup>, explaining  
 426 the preference for a hermaphroditic strategy at fishing mortalities greater than 0.08 year<sup>-1</sup> (Fig. A  
 427 16c).

428



429  
 430 **Figure A17.** Evolved life history strategies (phenotypes) for a grouper population subjected to varying  
 431 levels of harvest intensity. Mean values for age and length at maturation and sex change at different  
 432 fishing mortalities,  $L_f$  of 30 cm (indicated by grey line) and no size advantage in males. Age at maturation  
 433 (a), age at sex change (b), length at maturation (c) and length at sex change (d).

434

435 *Sensitivity of life history strategies in the model to size advantage*

436 Mean age and size at maturation and sex change in the population decreases and mean length at  
 437 maturation evolves to lengths below the imposed  $L_f$ . In general the population follows a similar  
 438 pattern to what is observed when males are given a size advantage.

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