

1 Fisheries-induced evolution of energy- and sex-allocation

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9 **Abstract:**

10 Fishing has been identified as a potential cause for the evolution of earlier age and size at
11 maturation in many fish stocks. For slow-growing, late-maturing hermaphroditic species such as
12 groupers, several studies have focused on the ecological effects of fisheries. Few studies have,
13 however, looked at the potential evolutionary response of long-term size-selective fishing on
14 hermaphrodites. We present an individual-based energy-allocation life-history model
15 parameterized for *Epinephelus fuscoguttatus*. Individual life history trajectories are specified by
16 three ‘genes’: length at 50% probability of maturation, and two values for the proportions of
17 available energy allocated to reproduction in the female and male phases, respectively. A genetic
18 algorithm finds evolutionarily stable life history strategies (ESS). Age and size at maturation and
19 sex change are thus emergent traits. The model predicts that the grouper hermaphroditic life
20 history strategy is very sensitive to even low fishing mortalities. Under increasing fishing
21 mortalities, the ESS showed decreased age and size at maturation and sex change, and increased
22 female to male sex ratios. The model predicted an alteration in the sex system, where the
23 population becomes dioecious (having separate sexes) at intermediate fishing mortalities. The
24 evolutionarily stable yield peaks at fishing mortalities as low as 0.06 year^{-1} . Fisheries
25 management in the simplest form would for such species include implementing a low fishing
26 mortality and choosing proper size limits for the fishery.

27 **Introduction**

28 While many plants are simultaneous hermaphrodites, hermaphroditic animals are more
29 commonly sequential and change from one sex to the other during their lifetime. The direction of
30 sex change can often be explained by the latter sex has having a higher advantage of being large
31 (Ghiselin, 1969). The size-advantage may for example be linked to female fecundity, as in
32 shrimps *Pandalus borealis* (Jensen, 1965; Charnov, 1982) or anemone fish *Amphiprion clarkii*
33 (Moyer, 1986); these species first reproduce as males and then change sex to become females.
34 Where territoriality or female choice is part of the mating system, males often need to be large to
35 compete successfully for mates, and sex change goes in the other direction.

36 Several authors have suggested that the size or age at which sex change occurs can be
37 expressed as a constant proportion of maximum size (or relative to age at maturation) that is
38 invariant across species (Shapiro et al., 1993; Charnov and Skuladottir, 2000; Allsop and West,
39 2003) This approach has been criticized because spurious relationships may arise when two
40 measures of size are correlated against each other (for example size at sex change versus
41 maximum size) and because it leaves large variation unexplained (Buston et al., 2004; Munday et
42 al., 2006).

43 There is also great plasticity in when sex change occurs. For example, in the red lyretail
44 *Anthias squamipinnis*, a protogynous serranid living in sedentary social groups with territorial
45 males, removal of a male from the group induced a female to change sex (Shapiro, 1980). Recent
46 studies suggest that sex change is often driven by social interactions in the mating group, and
47 takes place when changing sex increases the individual's expected reproductive value (Muñoz
48 and Warner, 2004; Munday et al., 2006). This does not necessarily coincide with size: when the
49 male is removed from a harem mating group, the largest female does not change sex if her
50 fecundity is greater than the fecundity of the rest of the females in the group combined (Muñoz
51 and Warner, 2003).

52 Population dynamics is often different for hermaphroditic compared to dioecious species,
53 because maturation and sex ratio follow a different pattern in relation to size. This may also have
54 implications for how harvest affects hermaphroditic compared to dioecious species, and one may
55 expect different and more diverse consequences. For example, one effect of harvest is that it
56 normally truncates age- and size-distributions (Jennings et al., 2001), which in the case of
57 sequential hermaphrodites can virtually remove one of the sexes (Alonzo and Mangel, 2004). In

58 protogynous species, sperm limitation can then lead to population collapse (Alonzo and Mangel,
59 2004). The severity of this effect depends on how flexible the sex changing rule is (Alonzo and
60 Mangel, 2005). In shrimp, the proportion of early maturing females (individuals that skip the
61 male phase and reproduce as females already in their first reproductive season) responds to the
62 composition of the population, and is higher in years when many females have been removed by
63 fishing (Jensen, 1965; Charnov, 1982). This suggests a flexible mechanism that incorporates
64 social cues about the size and abundance of conspecifics as well as state-dependent information
65 about the individual to achieve adaptive timing of sex change. At the other extreme, many
66 dioecious species have genetically coded and irreversible sex-determination.

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

79 Our motivation for this study is a rapidly expanding export-oriented grouper fishery in the
80 Maldives that began in mid 1990s (Shakeel and Ahmed, 1996). The abrupt intense fishing
81 activity on many species of groupers resulted in the fishery reaching its peak in 1997, and with no
82 management in place catch rates have since declined. Also for the Nassau grouper *Epinephelus*
83 *striatus* in the Caribbean, the numbers of both spawning fish and spawning aggregations have
84 decreased since fisheries began (Sadovy, 2002). Groupers are slow-growing, long-lived and late-
85 maturing species (see Heemstra and Randall, 1993, for a review of the biology of groupers). They
86 inhabit coral-rich areas of lagoon and seaward reefs in almost all tropical and temperate areas at
87 depths ranging from 4 to 100 m and feed mostly on crustaceans and small fishes (Heemstra and
88 Randall, 1993). This model is parameterized for *Epinephelus fuscoguttatus* (common names:

89 brown marbled grouper or flowery cod), which in 2006 contributed approximately 43% towards
90 the live grouper exports from the Maldives (S. A. Sattar, unpublished). This species matures
91 around ~9 years of age and may reach ages of ~40 years and lengths up to 100 cm (Pears et al.,
92 2006). Similar to sharks and rays (Stevens et al., 2000), the slow life histories make groupers
93 highly susceptible to over-fishing, and this effect is amplified by the high market demand and
94 export prices reaching \$100 per kg.

95 Against this background, the aim of this paper is to assess the evolutionary consequences of
96 harvest on energy and sex allocation in groupers; To what extent hermaphroditic life history
97 strategies are amenable to evolutionary change due to harvest-induced mortality; what types of
98 changes are expected; and how would such changes affect population dynamics and the fisheries
99 itself?

100 ***Model description***

101 **Structure**

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

117 The model is based on a mechanistic description of energy allocation. The energy obtained
118 through feeding can be allocated towards *growth*, which increases body length, or towards

119 reproduction, which results in egg/sperm production. The model uses a genetic algorithm to
 120 simulate an evolving population (Holland, 1992): offspring inherit the traits, with mutations,
 121 from successful parents. The model thus leads to the emergence of evolutionarily stable life
 122 history strategies under various levels of fishing.

123 Simulations are run for a time limit of 20 000 years and a maximum population size of 10 000
 124 individuals (but due to mortality the breeding population is 250-500 individuals depending on
 125 their life history strategy and the mortality level). The time resolution of the model is in years.
 126 Mutation, mortality, maturation, size-at-hatch, and food variability are processes that include
 127 stochasticity and result in differences between individuals with otherwise identical strategy
 128 vectors. Since the model simulates population dynamics, emergent properties include age and
 129 size at maturation and sex change, breeding population size, age-, size-, and sex-distribution in
 130 the population and in the catch.

131 **Model processes**

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

138 *Energy intake and growth*

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

$$141 \quad I = \chi \cdot 11.0 \cdot L^{2.1}$$

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

$$143 \quad L_{(t+1)} = \left(L_{(t)}^3 + (I - \alpha_{(sex)})I \right)^{\frac{1}{3}}$$

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

147 *Maturation and sex change*148 The probability that an individual will mature $P_m(L)$ is given by a logistic function of length L

149
$$P_m(L) = \frac{I}{1 + \exp(-q(L - L_m))}$$

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

163 *Reproduction*164 We assume that female fecundity ε is proportional to the energy allocated to reproduction:

165
$$\varepsilon = \alpha_F \cdot I$$

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

168
$$\sigma = \alpha_M \cdot I \cdot L^{0.1}$$

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

174 Individuals produce offspring proportionally to gamete production, and each sex contributes
 175 half the offspring in the next generation. *E. fuscoguttatus* aggregate in groups up to and

176 exceeding a thousand individuals to spawn (Johannes et al., 1999); we therefore assumed that
 177 spawning takes place once a year in one large spawning aggregation. We furthermore assumed
 178 that all gametes are completely mixed. Denoting total egg and sperm production in the population
 179 E and S , respectively, then the number of offspring $n_{0,i}$ produced by parent i is:

$$180 \quad n_{0,i} = \left(\frac{\varepsilon}{E} \right) \left(\frac{N_0(t)}{2} \right) \quad \text{if the parent is female, and}$$

$$181 \quad n_{0,i} = \left(\frac{\sigma}{S} \right) \left(\frac{N_0(t)}{2} \right) \quad \text{if the parent is male.}$$

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

184 *Natural mortality and fishing selectivity*

185 Similar to Alonzo and Mangel (2004), we assume that natural mortality M is size-dependent, and
 186 is modelled as a power function of length (Peterson and Wroblewski, 1984; McGurk, 1986). The
 187 function for M gives mortality rates in the range of what has been observed for groupers (0.1–
 188 0.68 year⁻¹; Pauly, 1980), and the lowest rate is restricted to $M_0 = 0.15$ year⁻¹ which is the
 189 estimated natural mortality rate for adult *E. fuscoguttatus* (Grandcourt, 2005). Thus, natural
 190 mortality is size-dependent as:

$$191 \quad M = (25L^{-0.5}) + 0.15 .$$

192 Fishery is size-selective and fishing selectivity C is a logistic function of length with a 50%
 193 probability of being selected at length L_f . The results shown are for $L_f = 30$ cm and $r = 1$.

$$194 \quad C(L) = \frac{I}{1 + \exp(-r(L - L_f))} .$$

195 Hence for a fishing mortality F , survival probability P_S is thus:

$$196 \quad P_S = e^{-M(L) - C(L) \cdot F}$$

197 *Observations*

198 The evolving populations were simulated for 20 000 years to reach evolutionary equilibrium,
 199 and results were observed for the last 1000 years. These results thus show the evolutionary
 200 endpoint or the evolutionarily stable strategies (ESS). The 20 000 years do not mean that
 201 evolution would be slow but is an assumption to standardize conditions for finding the ESS. The
 202 reasons to focus on ESSs rather than evolutionary trajectories on ecological time-scales were *i)*

203 there is little evidence for which elements of the hermaphroditic life histories are regulated
204 genetically and which are expressed due to social control, *ii*) additive genetic variation or
205 heritabilities for these traits are poorly known, and *iii*) evolutionary rates would probably depend
206 on mating structure, for which we only investigate one large well-mixed spawning aggregation.

207 **Results**

208 **Evolution of life history traits**

209 Life histories are sensitive to even low fishing mortalities. The evolutionarily stable strategies
210 show decreased age- and length-at-maturation and -sex change with increasing fishing mortalities
211 (Fig. 1). These are the type of responses that one could observe in survey or catch data. With
212 increasing fishing mortality, mean age at maturation in the population decreased from 9-11 years
213 to 4 years (Fig. 1a) and mean length at maturation decreased from approximately 54 - 60 cm to
214 25 cm (Fig. 1c). Mean age at sex change decreased from approximately 14 years to 6 years (Fig.
215 1b) and mean length at sex change decreased from approximately 65 cm to 30 cm (Fig. 1d). Each
216 point on the graph represents the mean phenotypic trait value for an evolutionarily stable strategy
217 given a constant level of fishing mortality, and multiple points for each fishing mortality indicate
218 replicates.

219 The responses in age and size at maturation are due to evolution of the underlying life
220 history strategies (Fig. 2). Allocation to reproduction in the male phase is quite stable and high
221 regardless of fishing mortality (Fig. 2c). The response to fishing is mostly seen in the two other
222 traits. Under intense fishing ($F > 0.06 \text{ year}^{-1}$), the gene for length at maturity, L_m , evolved to
223 values lower than the length at which individuals are recruited to the fishery, $L_f = 30 \text{ cm}$ (Fig. 2a).
224 The small size thus provides a refuge from the fishing mortality, and life histories did not change
225 when fishing mortality was increased beyond this level. Bimodality in L_m at a fishing mortality
226 around 0.06 year^{-1} indicates that the population was composed of some individuals who were
227 maturing at smaller sizes and some individuals who were maturing at larger sizes later in life
228 (Fig. 2a). This bimodality has to be viewed together with the allocation to reproduction in the
229 female phase (Fig. 2b). These two traits interact and must be interpreted in light of the mating
230 system.

231 **Hermaphroditism versus dioecism**

232 At low fishing mortalities (0 to 0.05 year⁻¹) the individuals followed a hermaphroditic strategy.
 233 Either, all allocated around 70% of the energy to reproduction and 30% to growth in the female
 234 phase, or allocation in the female phase was bimodally distributed in the population, with one
 235 group allocating more and the other group allocating less (Fig. 2b). This bimodality in female
 236 allocation means that the two groups are biased towards the female and male sex, respectively.
 237 The individuals that allocated almost all their energy to reproduction in the female phase virtually
 238 stopped growing and few of them changed sex to become males later in their life. The other
 239 group allocated next to nothing to reproduction but would continue growing, sooner or later
 240 becoming large enough to change sex. These bimodal distributions of female allocation values
 241 were observed as the ESS for fishing mortalities between 0.05 and 0.12 year⁻¹ (Fig. 2b) and
 242 resemble dioecism (separate sexes). The model thus predicts a continuum of life history strategies
 243 ranging from normal hermaphroditism, where individuals reproduce as both female and male
 244 during their lives, to almost purely dioecious strategies.

245 There was also bimodality in the gene for length at maturation but for a narrower range of
 246 fisheries mortalities (0.05-0.06 year⁻¹) (Fig. 2a). Here, the male-biased strategy matured at larger
 247 size than the female-biased strategy. Due to the low allocation to reproduction it also continued to
 248 grow through the female phase. The population thus contained a few very large males, visible as
 249 a long tail in the male size distribution for $F = 0.05$ (Fig. 3d).

250 At fishing mortalities greater than 0.1 year⁻¹, the ESSs again showed pure
 251 hermaphroditism (Fig. 2b). At such high fishing mortalities the fish matured and spent most of
 252 their life history at sizes below what is vulnerable to fisheries (Fig. 1).

253 **Age and size composition of the population**

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

261 **Yield and fisheries management**

262 The long term sustainable yield, after life histories have adapted to the prevailing fisheries
263 mortality, follows a dome-shaped curve peaking around a fishing mortality $F = 0.06 \text{ year}^{-1}$ and
264 stabilising above $F = 0.12 \text{ year}^{-1}$ (Fig. 4a). Immature individuals contribute most to the yield at
265 low fishing mortalities while males contribute most at higher fishing mortalities.

266 The evolutionarily stable yield is highest when L_f is low ($L_f = 30$) and fisheries mortality
267 moderate ($F = 0.06 \text{ year}^{-1}$). Yield never falls to zero within the range of given fishing mortalities
268 and L_f , due to the adaptive component given to the populations in the model. Fishing mortality
269 which gives the maximum yield depends on the L_f (Fig. 4b).

270 **Discussion**

271 Charnov's (1982) comprehensive treatment of sex allocation theory was population-based and
272 frequency-dependent, and has proven to be an excellent tool for training intuition and
273 understanding variation in sex systems. Empirical studies have since confirmed many of the
274 theory's predictions, but also highlighted that maturation and sex change are indeed individual
275 life history events, often resulting from complex evaluations of individual fitness consequences
276 within the mating group (Muñoz and Warner, 2003). For example, it has been experimentally
277 shown in the bucktooth parrotfish *Sparisoma radians* that it is not always the largest female
278 which changes sex: the largest female deferred sex change to smaller females if her fecundity was
279 higher than the total fecundity of all other females in the reproductive group (Muñoz and Warner,
280 2004). In larger mating groups, as for example in our model, this situation would rarely arise, and
281 the largest female is expected to change sex first. Such studies emphasise that sex allocation
282 strategies are 1) flexible with respect to the individual's state, and 2) influenced by the local
283 environment, including the other individuals in the mating group.

284 Flexibility in the timing of a life history event depends on how strictly it is genetically
285 determined. Individual traits that respond to social cues or the state of the environment can
286 quickly translate into population changes. The composition of the breeding population can then
287 respond rapidly to altered selection pressures, in principle on a time-scale shorter than a
288 generation. Traits that are more genetically hardwired, on the other hand, would require
289 evolutionary change of gene frequencies before the population would adapt. In our model,
290 maturation size is genetically coded and responds slowly, whereas sex change can be flexible

291 from year to year because it is based on a rule that evaluates the composition of the breeding
292 population. Similar flexible strategies have been suggested to govern sex change in several
293 species (e.g., Charnov, 1981; Muñoz and Warner, 2004).

294 The flexibility with which a life history trait responds to external forcing may in turn have
295 consequences for population dynamics. Interestingly, a strategy for sex change that relies on
296 social cues may potentially increase vulnerability to fishing because compensatory mechanisms
297 in individual life histories may mask typical signs of over-exploitation, for example altered sex
298 ratios or reduced recruitment (Alonzo and Mangel, 2005). In this paper we only analyse the
299 evolutionarily stable strategies, or the evolutionary endpoint, given a fishing intensity and
300 selectivity. Thus, we do not make predictions about the evolutionary trajectories – the transient
301 periods before the population has reached a new evolutionary equilibrium – or the ecological
302 vulnerability of the population during a period of evolutionary change.

303 **Correspondence between modelled and observed life history strategies**

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

316 When it comes to maturation, the model predicts larger size (55 cm) and later age (10 years)
317 than suggested by gonad observations (30 cm and 2 years and onwards; Pears et al., 2006).
318 However, Pears et al. (2006) observed a strong pattern linking size and sexual activity among
319 female *E. fuscoguttatus*, where smaller females were less active in reproduction than larger
320 females. In fact, most females younger than 10 years (corresponding to a length of approximately
321 60 cm) had gonads too small for reproduction (Pears et al., 2006). This indicates that energy is

322 primarily invested in growth at smaller sizes, and that the size and age at which females become
323 reproductively functional agree between the model and field data.

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

331 **Effects of harvest on life history strategies**

332 The selection regime in the wild has shaped populations so that the growth period prior to
333 maturation maximizes the trade-off between survival on the one hand and the benefits that come
334 with size on the other, i.e. increased fecundity among females and all ecological mechanisms that
335 contribute to size-advantage among males. Under harvest, however, this size-advantage is offset
336 by fishing mortality: it matters more to survive until reproduction than it does to have a large
337 body size. The ESS will therefore be a strategy that reduces exposure to fishing, i.e. where
338 maturation takes place earlier in life. Numerous studies have demonstrated harvest-induced
339 evolution towards lower maturation age on decadal time-scales (Law and Grey, 1989; Conover
340 and Munch, 2002; Olsen et al., 2004).

341 In a similar model but without evolution, Alonzo and Mangel (2005) predicted their
342 hermaphroditic population to crash under high fishing mortalities when the rule for sex change
343 was based on reproductive success and when fishing included younger year-classes. In contrast,
344 individuals in the model presented here evolve earlier maturation, with earlier sex change
345 following from altered population dynamics. Earlier maturation evolved also when fisheries was
346 selective for larger fish (Figs. A9, A10). That fish life histories can evolve due to size-selective
347 harvest has recently been highlighted by (Swain et al., 2007). From back-calculated size-at-age in
348 a Canadian cod (*Gadus morhua*) stock they suggested that fishing has selected first for increased
349 size at age four years and thereafter for reduced size-at-age. Such evolution of traits under
350 selection pressure so as to escape extinction has been termed 'evolutionary rescue' (Ferrière et
351 al., 2004). Evolutionary rescue enables the population to persist in times of environmental
352 degradation or other external selection forces such as intense fishing mortality. Such an

353 evolutionary process would rely on rearrangements of available genetic variance or new
354 mutations, both processes which are included in our model. Evolution does not need to be
355 beneficial to the population, however. Adaptation can also modify traits so that the population
356 goes extinct, a process called ‘evolutionary suicide’ (Dieckmann and Metz, 2006). An evaluation
357 of the consequences of adaptation, an evolutionary risk assessment so to speak, can therefore not
358 be based on generalizations about the nature of evolution but requires detailed understanding in
359 each specific case.

360 **Harvest on sequential hermaphrodites**

361 In species where one sex is larger than the other, the selection towards earlier maturation will
362 normally be strongest on the largest sex due to their longer growth phase. The evolutionary
363 consequence will be that the sexes evolve to more similar size as survival probability swamps the
364 effects of size-advantage. The reduced importance of size-advantage, which maintained and
365 stabilized sequential hermaphroditism in the first place, is the mechanism behind our model’s
366 prediction that fishing on a sequentially hermaphroditic species can lead to the evolution of
367 strongly female- and male-biased strategies that approach dioecism. Also, the ESS strategies
368 under stronger harvest rates mature and reproduce before they become vulnerable to the fisheries.
369 Since survival probability is only little affected by fishing, size-advantage is re-established, and
370 hermaphroditism again predicted as the evolutionary outcome.

371 Dioecious strategies within hermaphroditic life histories have also been termed ‘early
372 maturers’, where part of the population develops directly to the terminal sex (Charnov, 1982; i.e.
373 ‘early maturing males’ in this model). In reality these are pure males, and the model
374 concomitantly predicted that the remaining fraction of the population would increase their
375 allocation in the female phase, thus becoming pure females. Technically, in the model all
376 individuals are forced to go through a female phase. This might at first seem confusing but is a
377 flexible formulation that allows for both dioecious and hermaphroditic strategies. Individual
378 allocation values in the population typically followed one of two patterns: *i*) Individuals did not
379 differ markedly, and for all there was allocation to reproduction during both female and male
380 phases. This resulted in a typically hermaphroditic life history strategy where the largest among
381 the females changed sex to become males. *ii*) There was two co-occurring strategies in the
382 population. One strategy allocated nothing to reproduction in the female phase but continued to
383 grow; these individuals only reproduced as the male sex. The other strategy allocated almost

384 100% to reproduction during the female phase, and because they stopped growing only rarely did
385 they later become males. These two co-existing strategies thus conform to dioecism. The male
386 strategy also matured at a smaller size, but because it had one year of growth when it was
387 technically in the female phase but did not allocate to reproduction, both males and females
388 typically became reproductively functional at approximately the same age and size.

389 **Management of hermaphroditic species**

390 Several studies have stressed the importance of considering life history characteristics prior to
391 introducing management strategies (King and McFarlane, 2003). Not only do life history traits
392 determine individual trajectories for growth and reproduction, but these individual characteristics
393 also scale up to population-level properties such as productivity, biomass fluctuations, resilience,
394 and yield. Heppell et al. (2006) compared the effects of reduced fishing mortality on different life
395 history stages of the gag grouper (*Mycteroperca microlepis*). Their results showed that to manage
396 a gag grouper population sustainably, one has to formulate a management plan which
397 encompasses the optimal solutions for population recovery, biomass, sex ratio, and fertility
398 (Heppell et al., 2006). Based on the results obtained in this study, we can add the potential
399 consequences of fisheries-induced evolution to that list. Our model suggests that species such as
400 slow growing groupers may be especially sensitive to fishing mortality. Not only did evolution
401 towards maturation and sex change at earlier ages and smaller sizes take place at very low fishing
402 mortalities, but the selective pressures maintaining hermaphroditism itself may erode under
403 fishing. It would be instructive to study models that explore a wider parameter range to identify
404 which parameters or ecological conditions make hermaphrodites especially vulnerable to
405 fisheries-induced changes. Although the species may evolve to accommodate to the new selection
406 pressure, it simultaneously evolves away from the life history strategy that was favoured by
407 natural selection. At present, we know too little about the ecological interactions to predict what
408 consequences such an evolutionary shift of life history strategies may imply for the species and
409 the ecological community. Potentially ecological consequences range from behaviour and mating
410 success via reproduction and recruitment to population dynamics. In turn, this can lead to altered
411 interactions with other species in the reef ecosystems.

412 Results from our model as well as those from Alonzo and Mangel (2005) show how important
413 it is that the implementation of a management strategy for hermaphrodites considers the size-
414 selectivity of the fishing pattern in conjunction with the mechanism for sex change. This finding

415 is supported by our model, which predicts that hermaphroditic life histories are sensitive to
416 fishing and might evolve even at low fishing mortalities. Also, models, including the one
417 presented here, tend to assume that individuals time their sex change based on perfect knowledge.
418 The effects of incomplete knowledge may be different when a population is subject to fishing.
419 Along the same lines, it would be instructive to incorporate the particular cues individuals use in
420 their assessment of when to change sex.

421 There is uncertainty of the rate of natural mortality being experienced by grouper populations.
422 Most life history models are sensitive to mortality rates, and with higher natural mortality rates
423 the model predicts an even stronger evolutionary response (a sensitivity analysis is presented in
424 the online appendix). We tested two values for the size selectivity of the fishery ($L_f = 30$ cm,
425 Figs. 1 and 2; $L_f = 50$ cm, Figs. A9 and A10). In both cases, the life histories evolved to mature
426 and change sex before they became vulnerable to fishing. Within this range, these results suggest
427 that the more intense fisheries selection is, the larger will the magnitude of the evolutionary
428 response be.

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

446 **Acknowledgements**

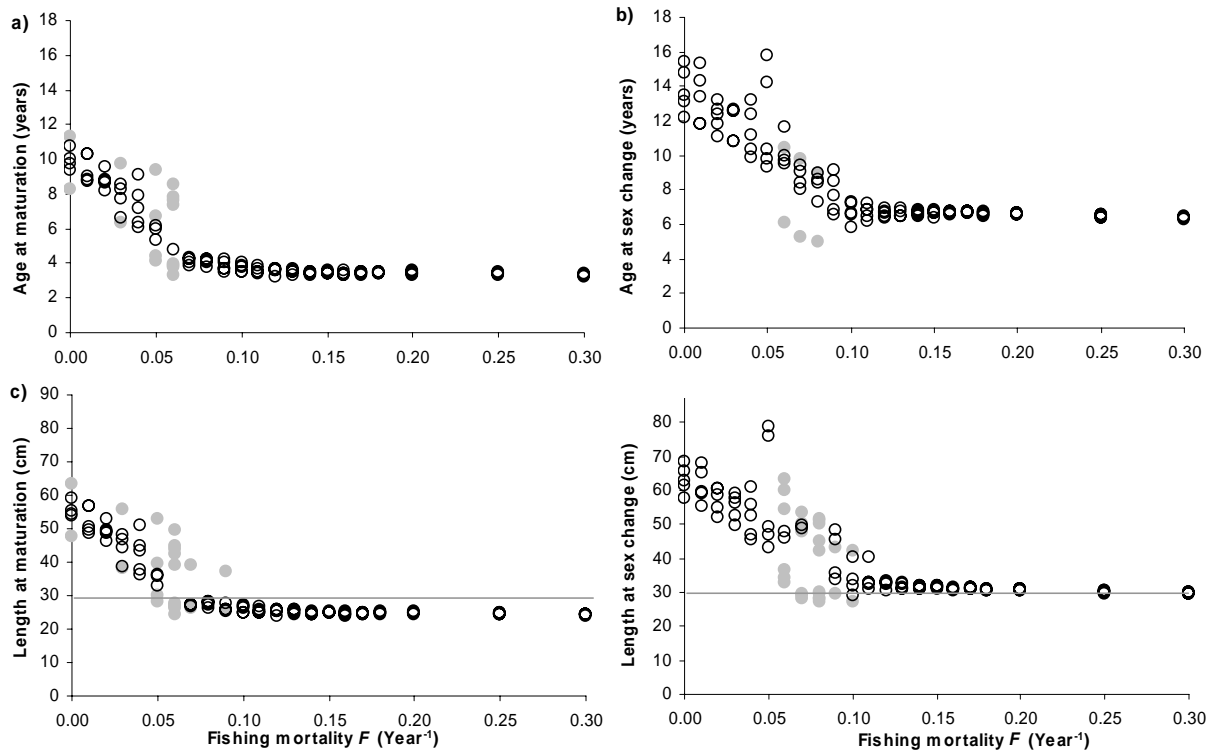
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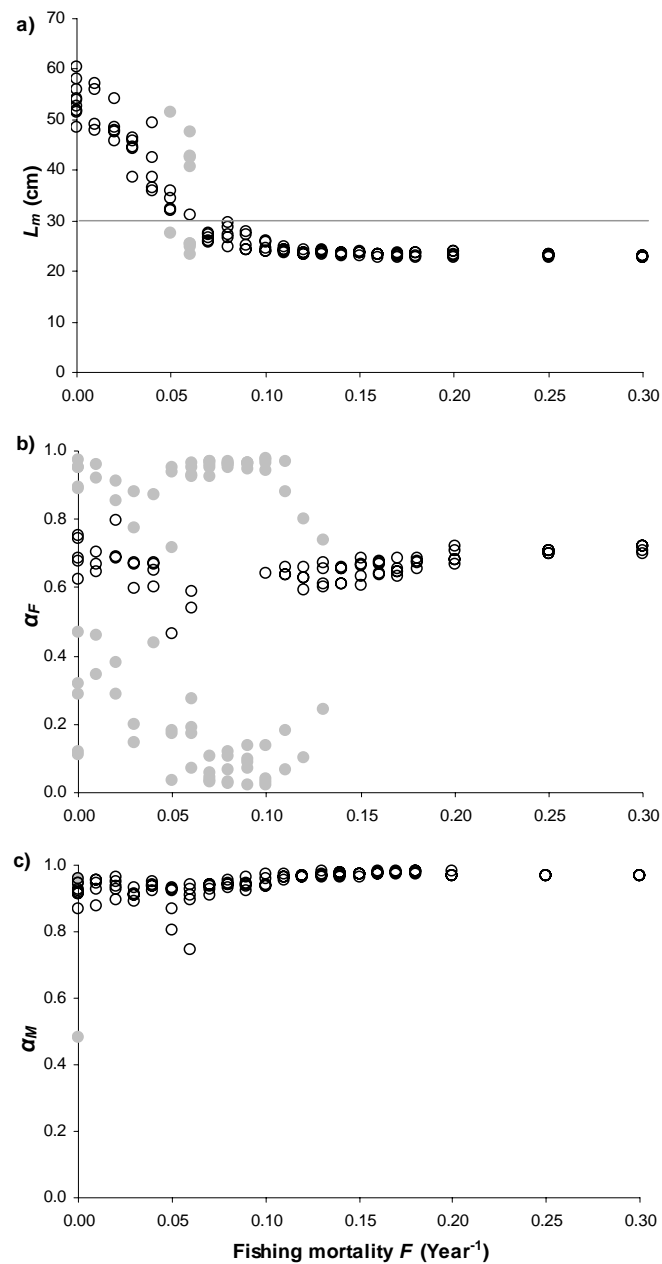
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537



538
539

540 **Figure 1.** Evolved phenotypes (life history strategies) for a grouper population (*E. fuscoguttatus*)
 541 subjected to varying levels of harvest intensity. a) Age at maturation. b) Age at sex change. c)
 542 Length at maturation. d) Length at sex change. The minimum size limit is $L_f = 30$ cm (indicated
 543 by grey line in panels c and d) and the values are mean trait values in the population (open
 544 circles) or representing each of two peaks if the distribution were bimodal (grey circles).

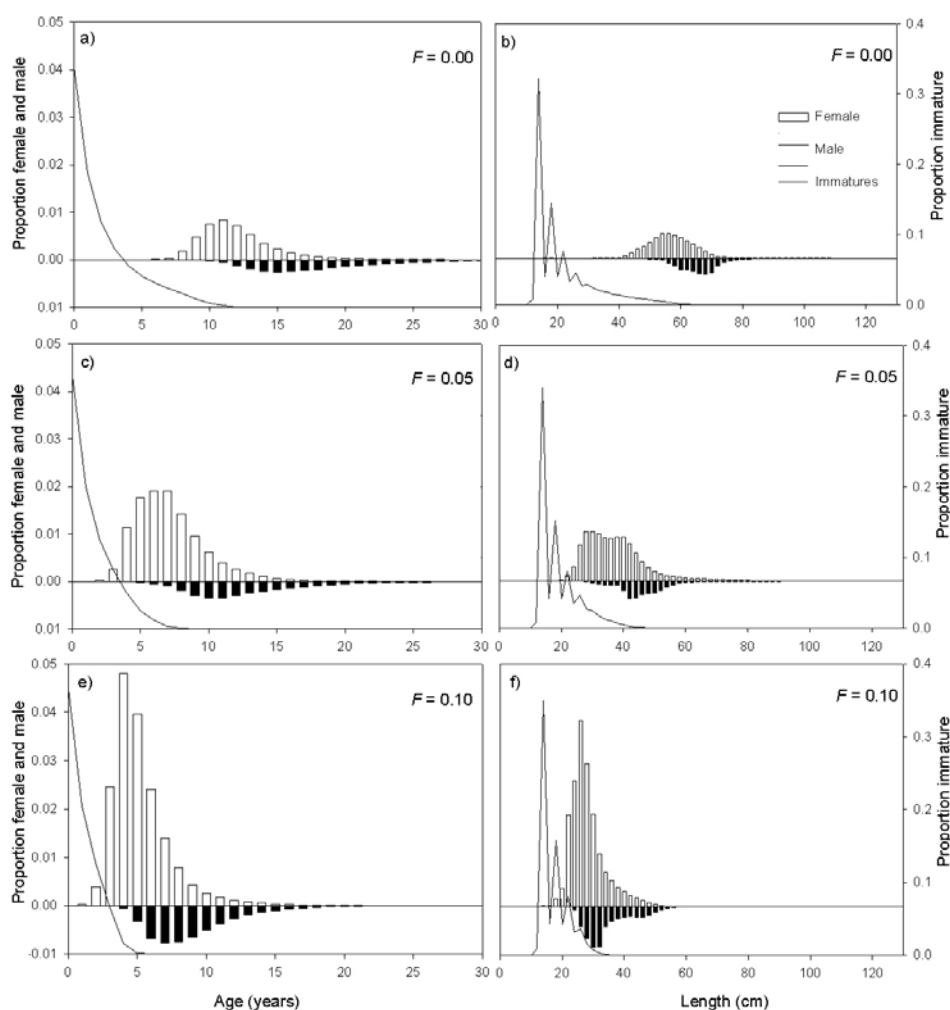


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547 **Figure 2.** Evolutionarily stable life history strategies in a grouper population (parameterized for
 548 *Epinephelus fuscoguttatus*) under various levels of harvest. The three panels correspond to three
 549 ‘genes’ that specifies a life history trajectory: a) length at 50% probability of maturation L_m ; b)
 550 energy allocation to reproduction in the female phase α_F ; and c) energy allocation to reproduction
 551 in the male phase α_M . The minimum size limit is $L_f=30$ cm (indicated by grey line in panel a).
 552 Legend as in Figure 1.

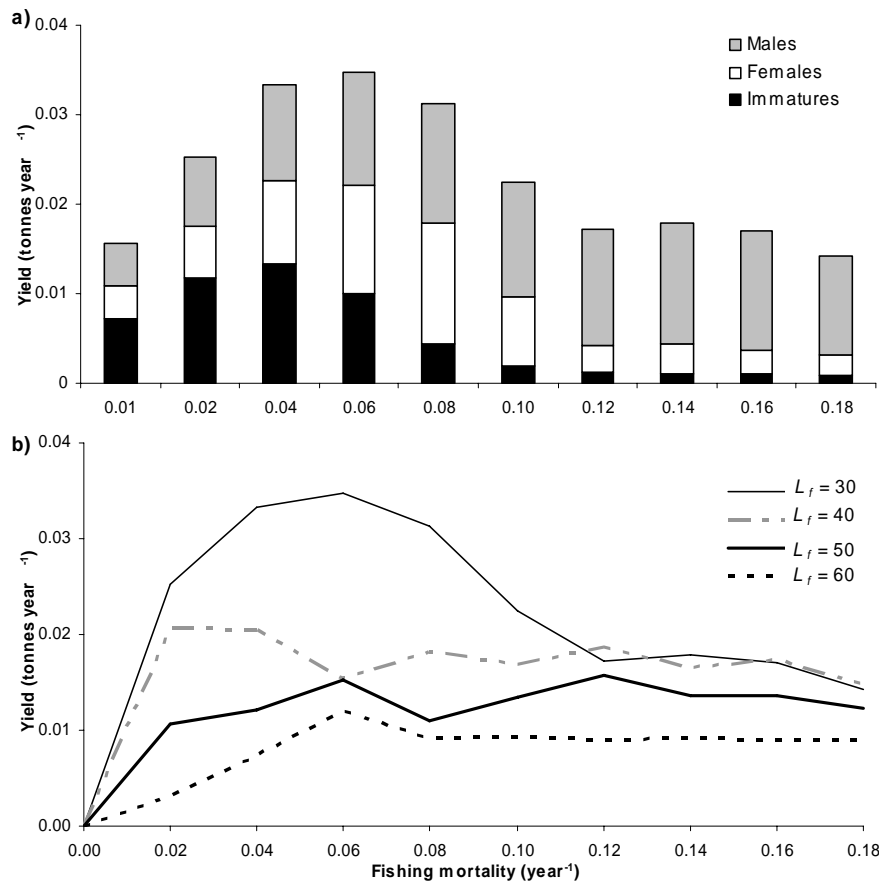
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555

556 **Figure 3.** Age (left column) and size (right column) distribution of a population of groupers (*E.*
 557 *fuscoguttatus*) following the evolved evolutionarily stable life history strategies under various
 558 levels of harvest intensity (the annual harvest rate F [year^{-1}] is indicated on each panel). The size-
 559 selectivity of the fishery was $L_f = 30$ cm. The proportion of the population that consists of
 560 immatures is shown on the right hand axis, and proportions of females and males are shown on
 561 the left axis.



562

563

564 **Figure 4.** Yield in a grouper fishery where the population followed evolutionary stable life
 565 history strategies adapted to increasing levels of harvest intensity. The model was parameterized
 566 for *Epinephelus fuscoguttatus*. a) The contribution of immatures, females, and males to the total
 567 yield. The minimum size limit in the fishery was $L_f = 30$ cm. b) Total yield under different
 568 management regimes. The minimum size limit L_f was varied between 30 cm and 60 cm.

Online Appendix

Part 1 - Model description

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

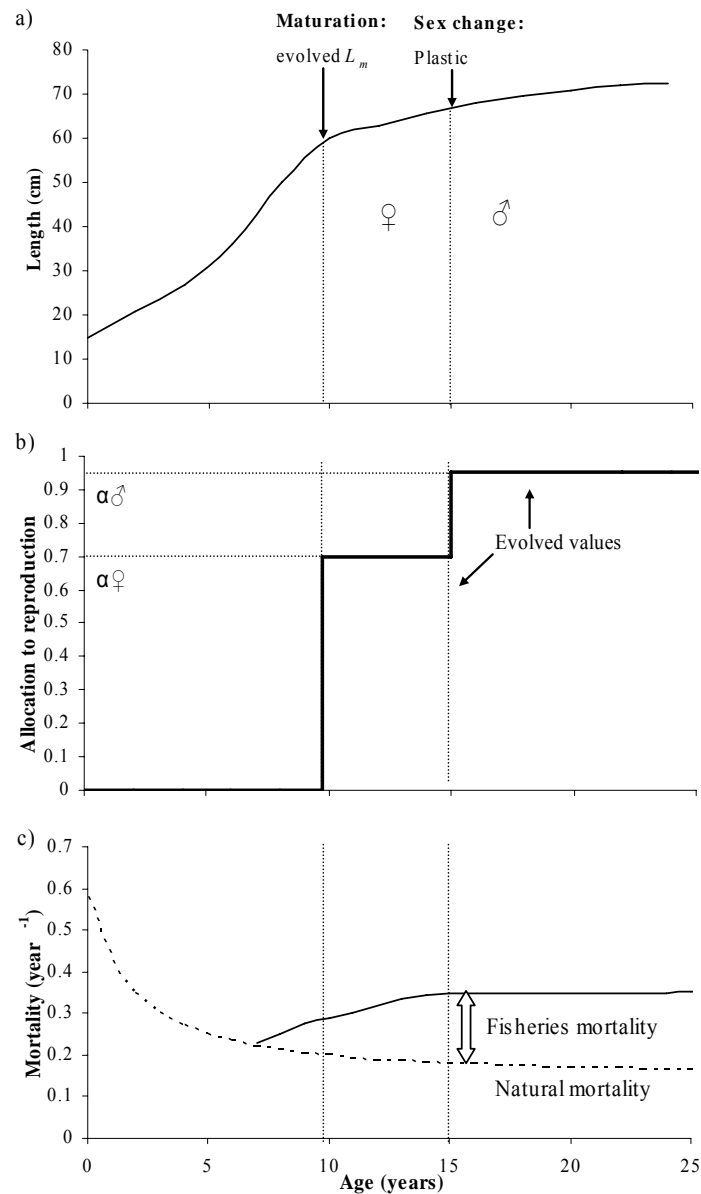
Purpose

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 (α_F and α_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.

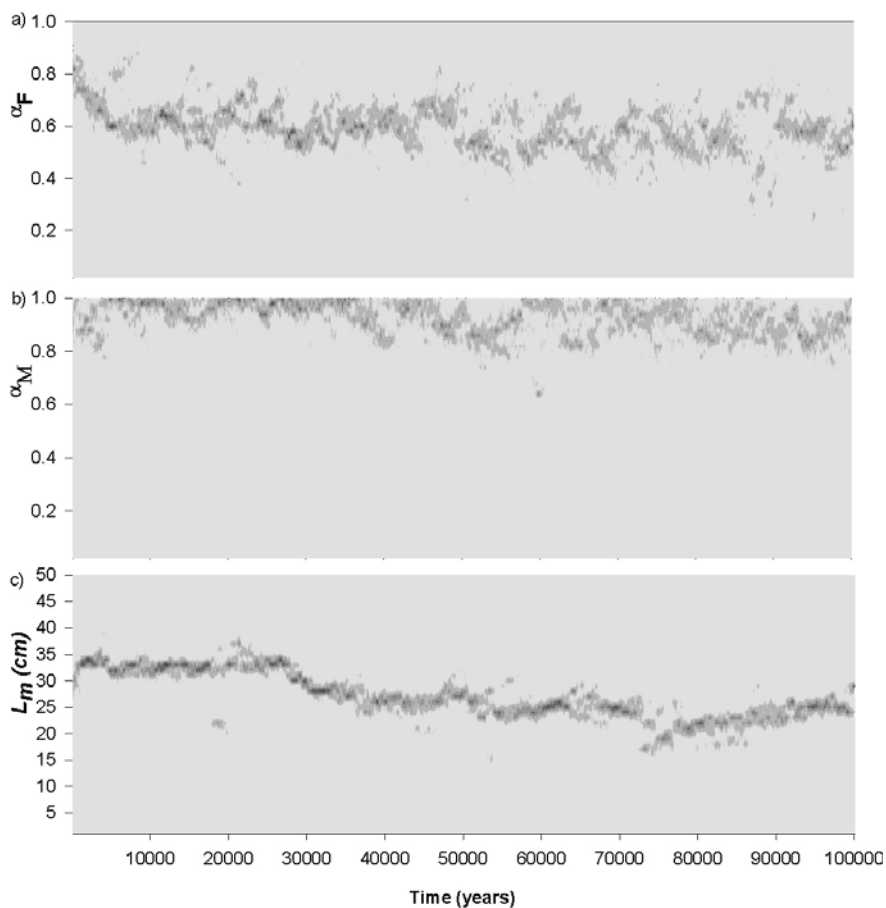


32

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 (α_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, α_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 α_F , 2) energy
 50 allocation to reproduction in the male phase α_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, α_F (a), male
 58 phase, α_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*

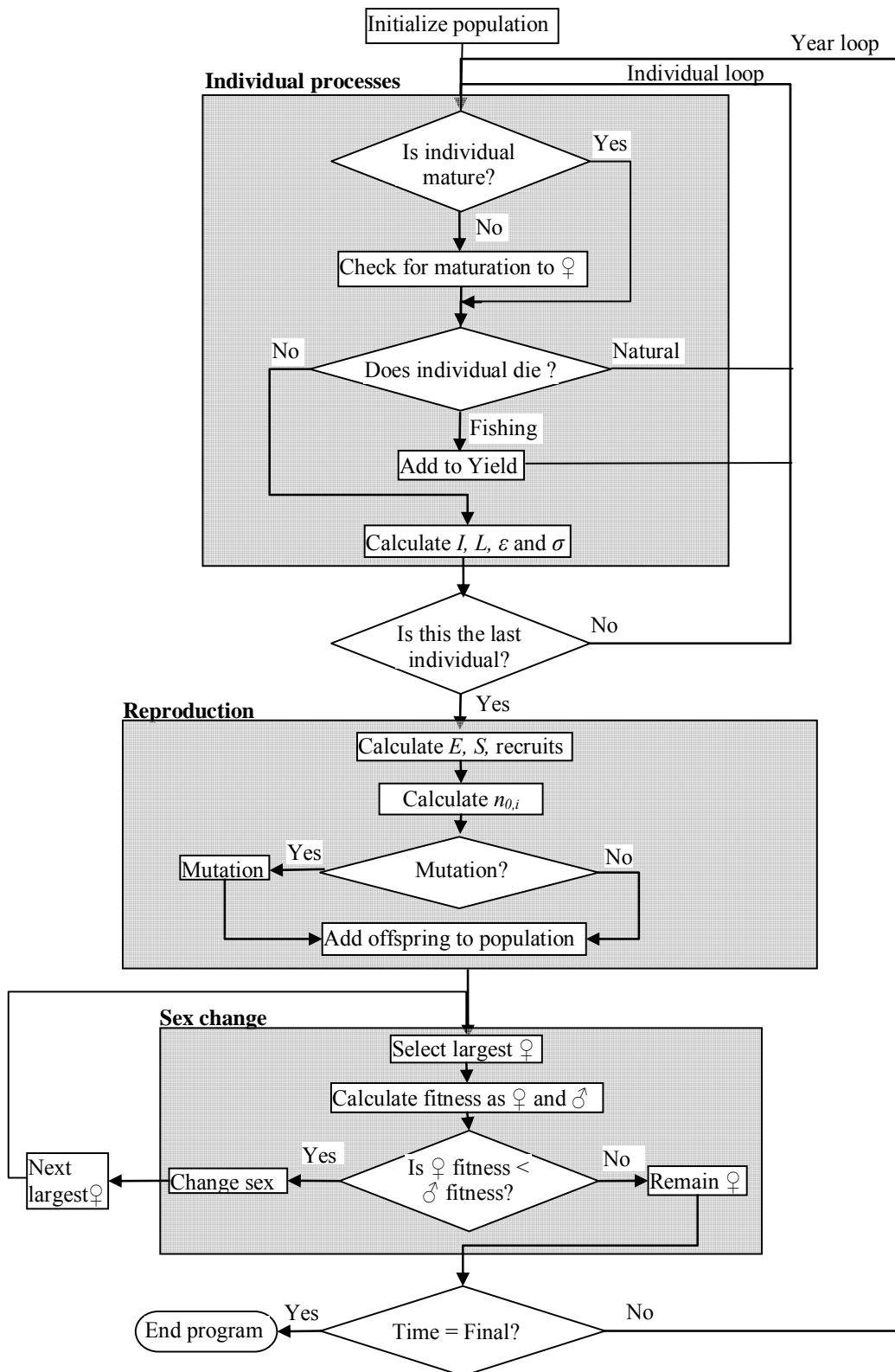
81 At the time of reproduction, each individual is able to assess its fitness as female and male by
82 assessing the population structure and the sex ratio. If the given individual's fitness as a male is
83 greater than as a female it will change sex and hence increase its fitness by being a male. The
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 (α_F) and 0.95 for males (α_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.

122

123 ***Submodels***

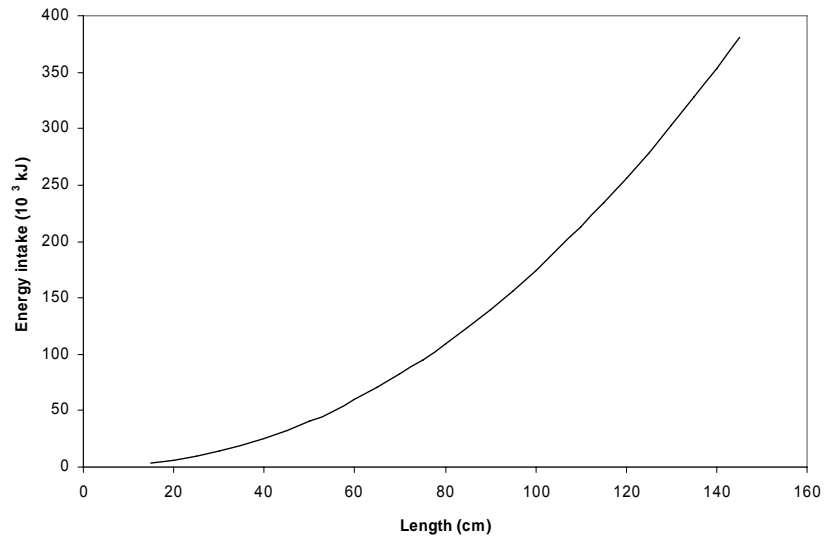
124 A summary of all parameters used in the model is given in Table A1.

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, α 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 ± 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 α_F and α_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 α 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

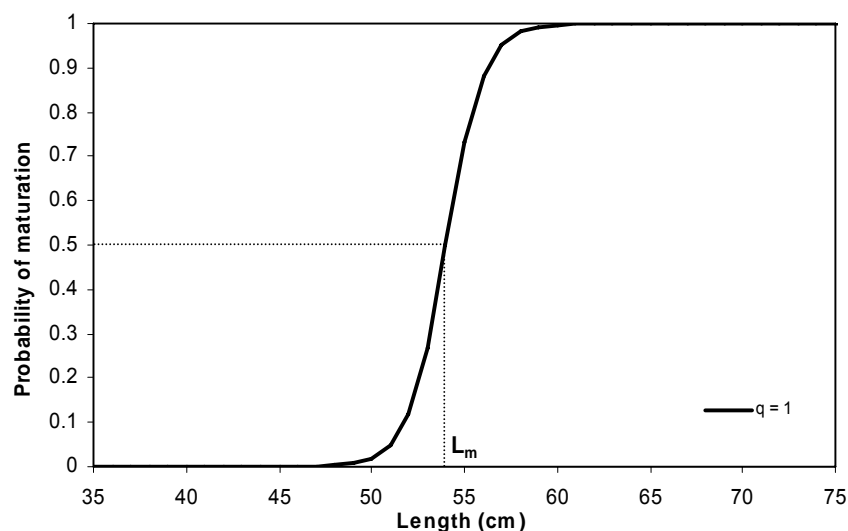
$$153 \quad \sigma(L) = I\alpha_M L^{0.1} \quad (5)$$

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 ε_* if female and the expected sperm production σ_* 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

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

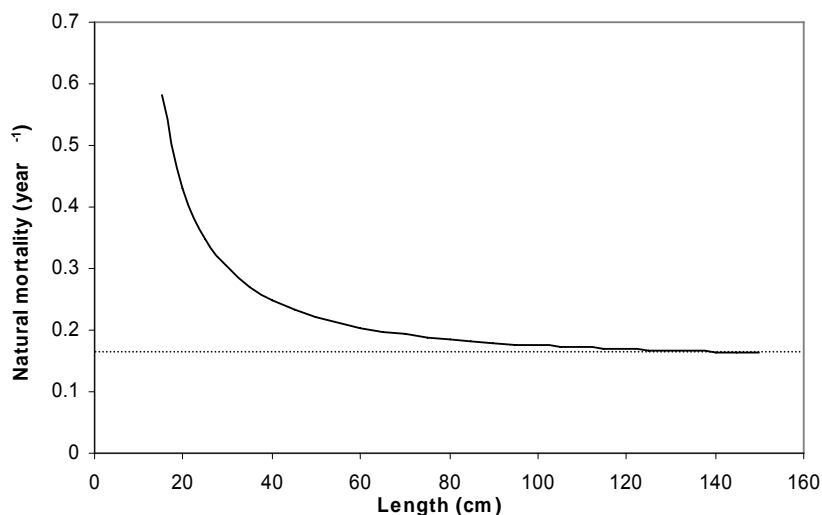
197 If the fitness of the individual as a male (V_M), is greater than that as a female (V_F), the individual
 198 changes sex and functions as a male for the rest of its life. This is in contrast to Alonzo and
 199 Mangel (2005) where they assume that an individual will change sex if its expected fecundity 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 μ 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⁻¹. This value is close to the estimated value of natural mortality for *E. fuscoguttatus* (0.14
 210 year⁻¹) (Grandcourt, 2005) and is an average of estimated natural mortality values for this genus.
 211 The values for μ 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⁻¹) (Pauly, 1980).

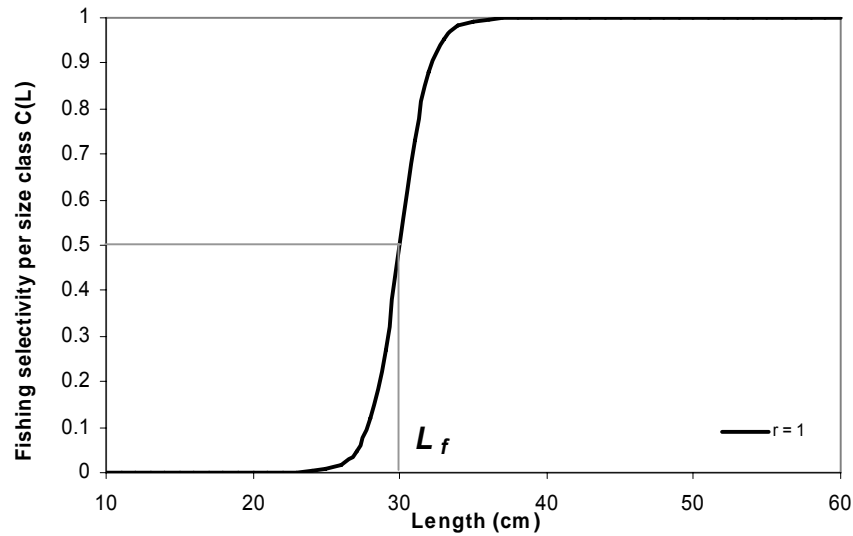


213
 214 **Figure A6.** Varying natural mortality with length. Individuals suffer a higher natural mortality at smaller
 215 sizes. Natural mortality of individuals decreases with increasing size.
 216

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⁻¹), total mortality $Z(L)$ (year⁻¹) 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*

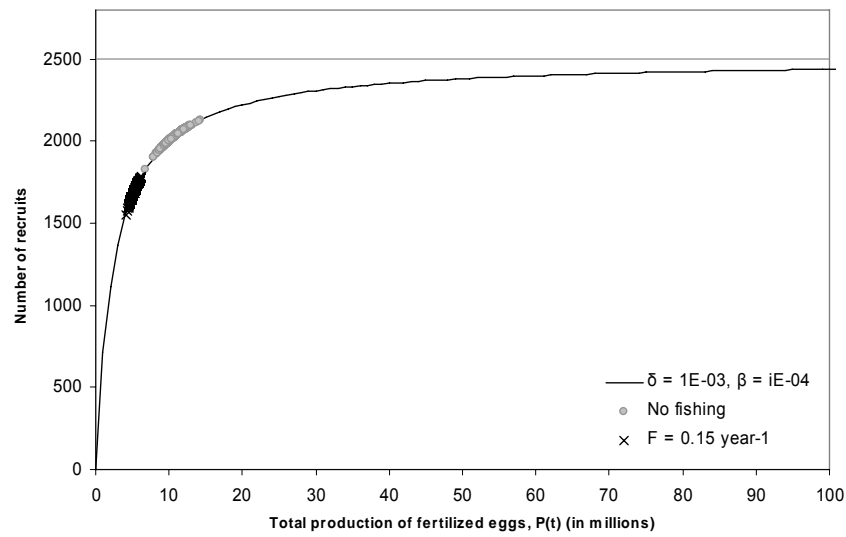
238 In every time step, the age and length of all individuals from the previous time step is updated
 239 given that the individual remains alive. Recruitment into the population is determined by the total
 240 production of fertilized eggs $P(t)$ (which is equivalent to total fecundity of the population 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 δ/β 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. δ and β
 251 respectively. δ/β 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 δ , 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>
Strategy vector			
L_m	54	cm	length at which there is 50% probability of an individual that size maturing
α_F	0.7	-	energy allocation to reproduction by females
α_M	0.95	-	energy allocation to reproduction by males
Attribute vector			
Age		years	age of individual
L		cm	length of individual
Sex		-	0 - immatures, 1 - females, 2 - males
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	year ⁻¹	base-line natural mortality rate
r	1	-	steepness of fishing selectivity curve
F	0 - 0.3	year ⁻¹	fishing mortality
L_f	30 - 60	cm	varying length at which there is 50% probability of an individual that size being caught
Maturity and Reproduction			
q	1	-	shape parameter in the maturity function
β	4E-07	-	larval recruitment function parameter
Mutation			
P_{Mut}	0.05	-	probability of mutation
Variables			
Age_{min}	0	years	age at which individuals are initialised in the population
L_0	15 ± 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_*
ε_*		eggs	expected fecundity of largest female
σ_*		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 ⁻¹	natural mortality
Z		year ⁻¹	total mortality
P_S		-	annual survival probability
m_F		-	probability of death due to fishing
Y		tonnes year ⁻¹	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 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 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*

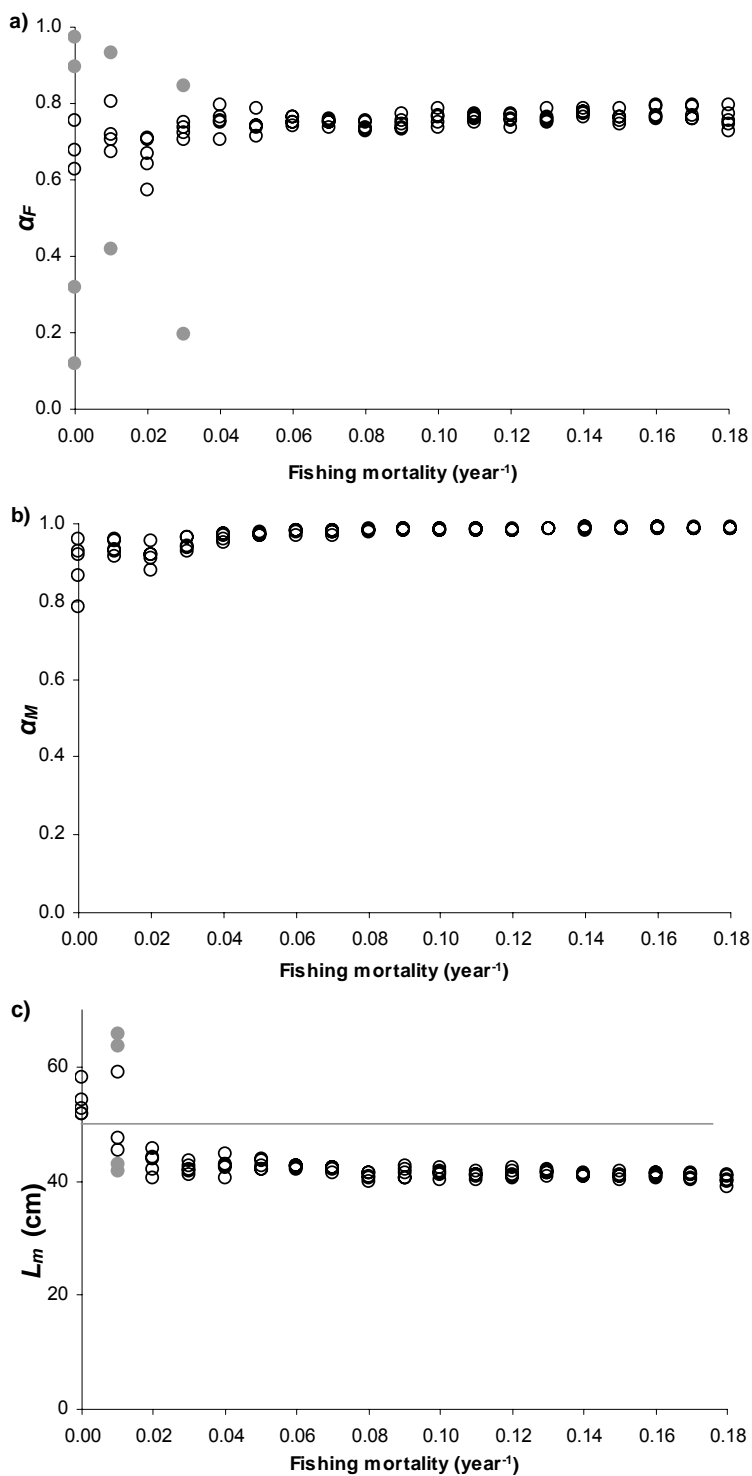
286 When minimum size limit in the fishery is high, evolution of traits occur at lower fishing
287 mortalities than when fishing includes smaller size classes. Energy allocation to reproduction in
288 the female phase α_F shows that individuals favor a hermaphroditic strategy over dioecious
289 strategy for all fishing mortalities (Fig. A9a). Bimodality in α_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 α_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.

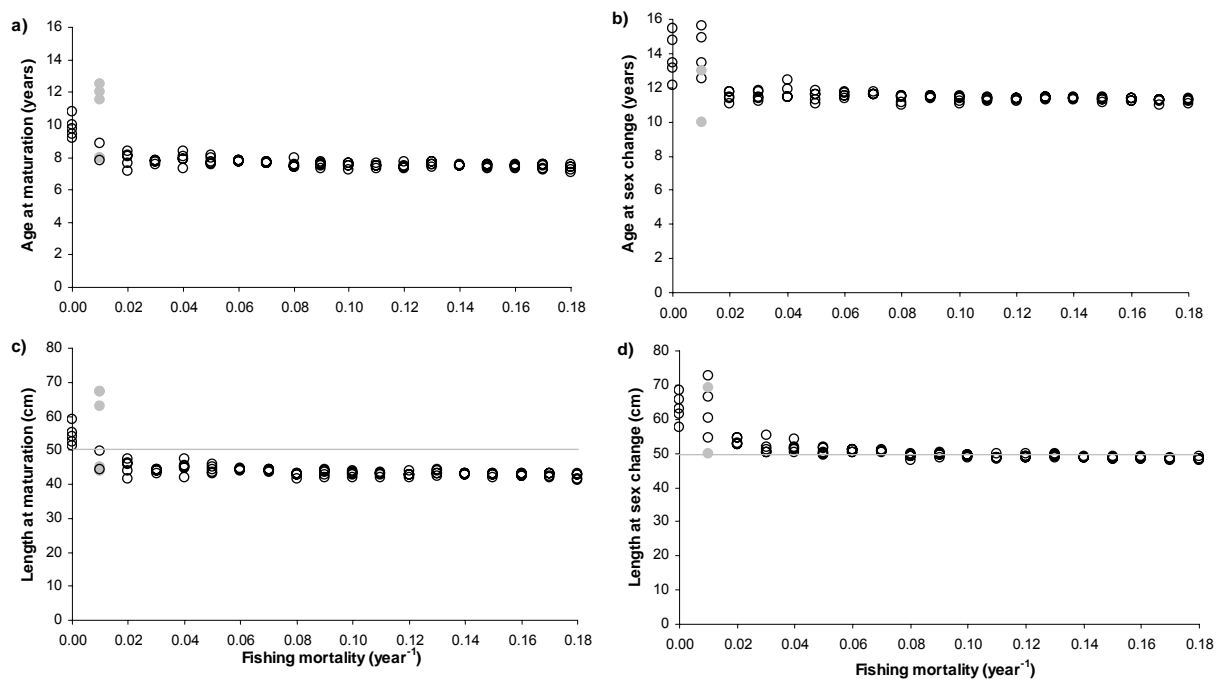
298

299 L_m decreases and evolves to lengths below the L_f of 50 cm at very low fishing mortalities (0.01
300 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 α_F (a), energy allocation to reproduction in the
 306 male phase α_M (b) and length at which there is 50% probability of maturation L_m (c).

307



308

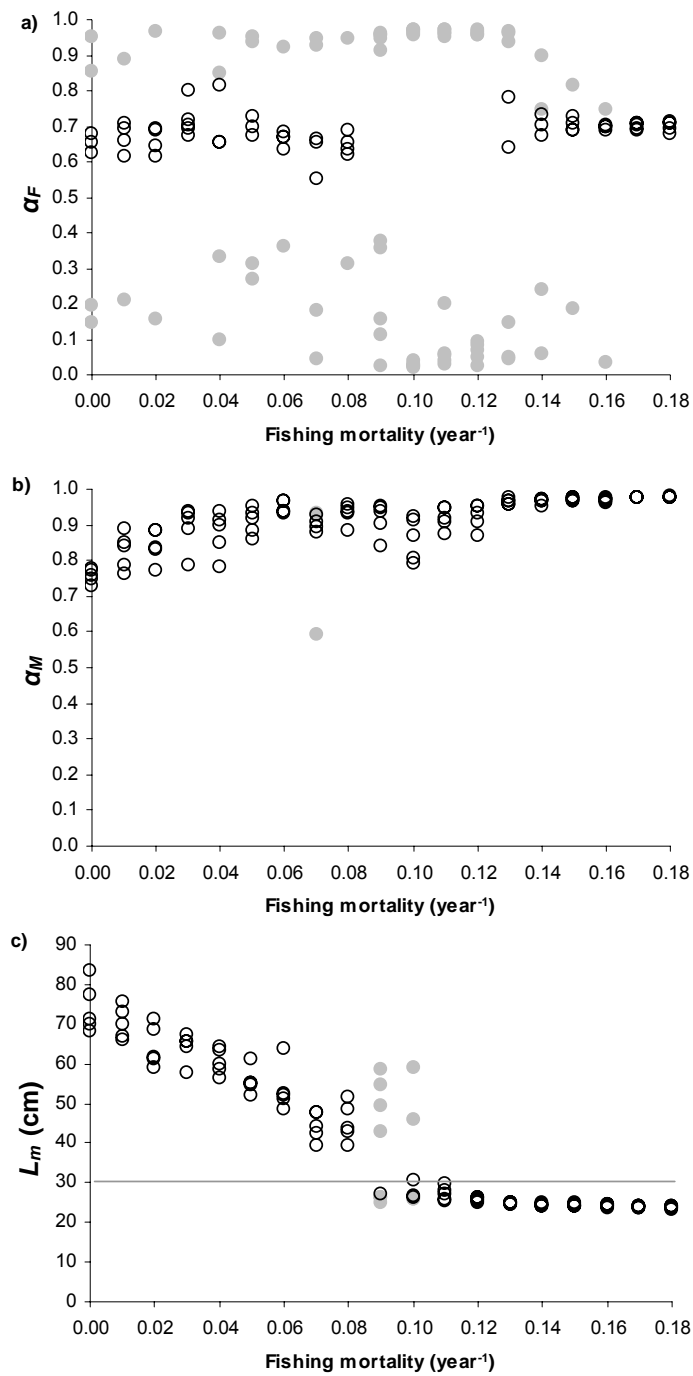
309 **Figure A10.** Evolved life history strategies (phenotypes) for a grouper population subjected to varying
 310 levels of harvest intensity. Mean values for age and length at maturation and sex change at different
 311 fishing mortalities and L_f of 50 cm (indicated by grey line). Age at maturation (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 year^{-1} . Similar to what was observed for the gene (L_m), the length at
 319 maturation at fishing mortality of 0.01 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*

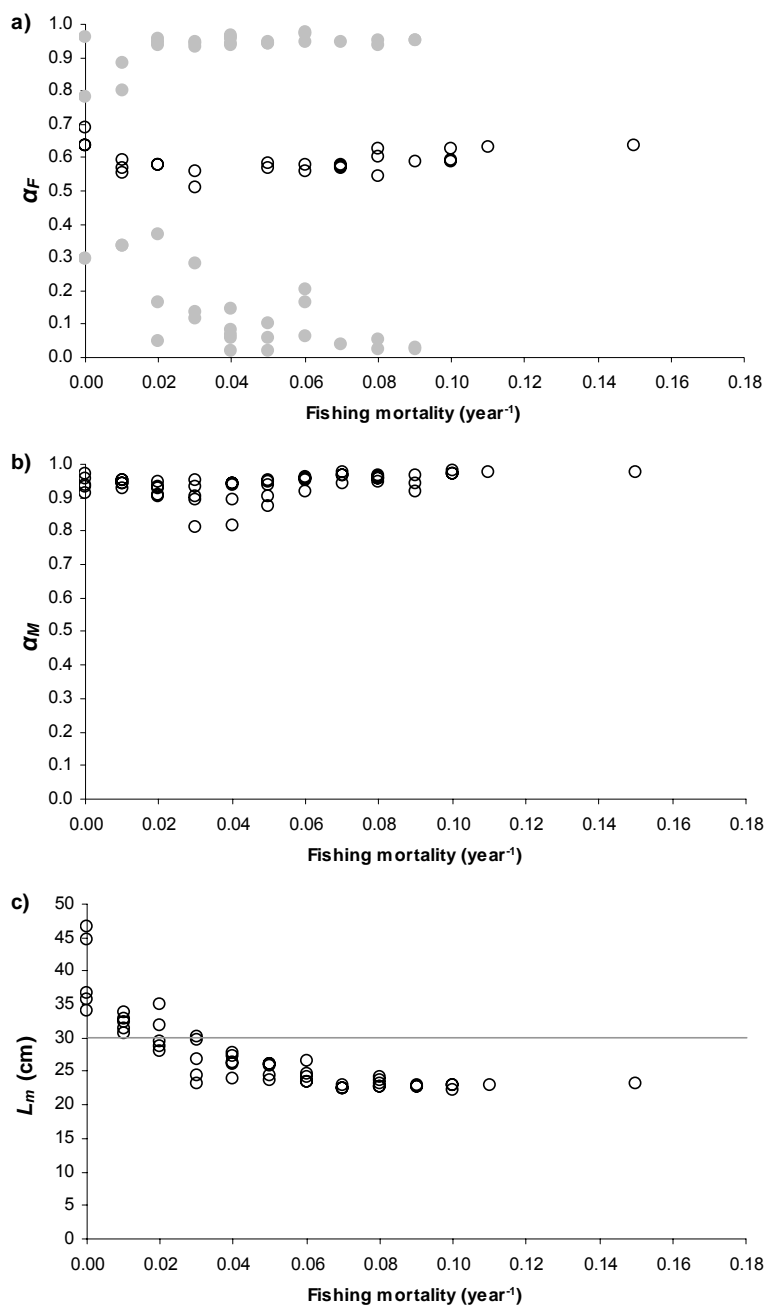
323 *Sensitivity of life history traits in the model to natural mortality*
 324 Sensitivity of life history traits to varying M_0 shows different patterns for different values of M_0
 325 and evolution of the population occurs at lower fishing mortalities when M_0 is equal to 0.2 year^{-1} .
 326 When $M_0 = 0.1 \text{ year}^{-1}$ hermaphroditism is more often favored over a dioecious strategy at low
 327 fishing mortalities (Fig. A11a). However distinct bimodality in α_F at fishing mortalities between
 328 0.09 and 0.12 year^{-1} indicate that populations are following a separate sex strategy.
 329 Hermaphroditism is once again observed at fishing mortalities greater than 0.12 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 α_F (a), energy allocation
 335 to reproduction in the male phase α_M (b) and length at which there is 50% probability of maturation L_m (c).

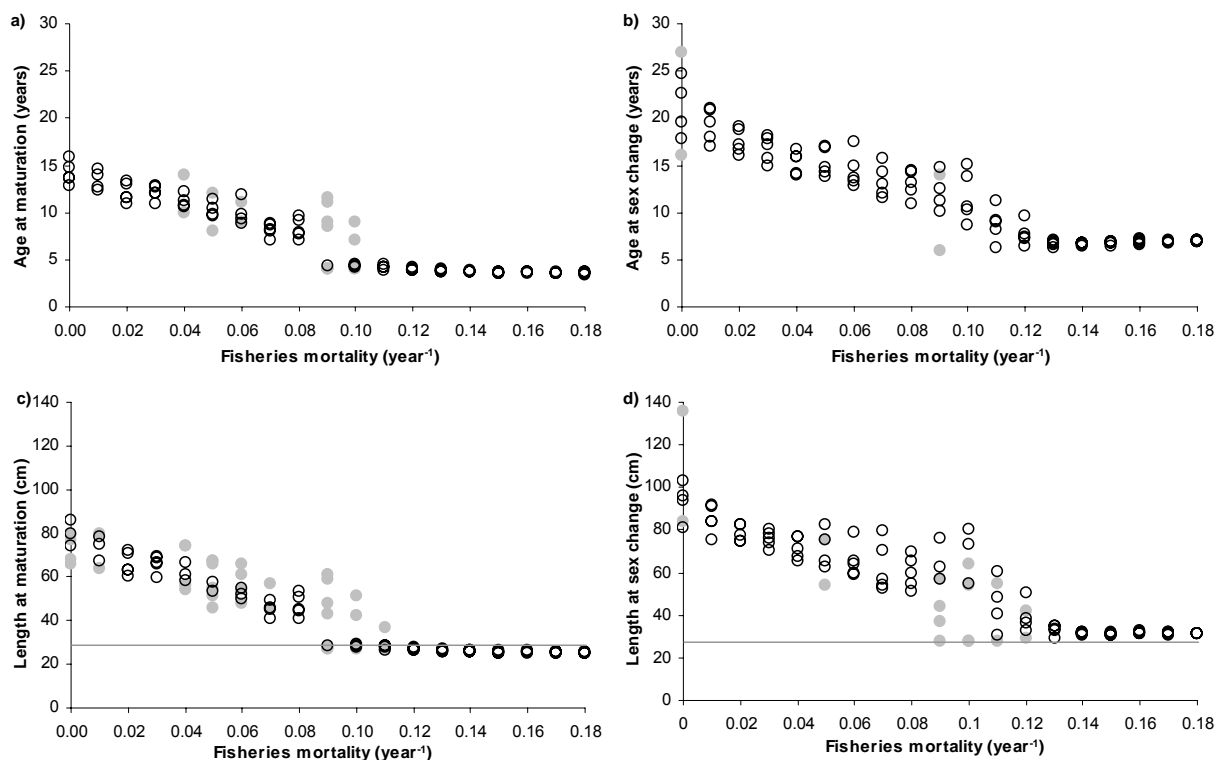


336
 337 **Figure A12.** Evolution of genes coding for life history strategies in a grouper population subjected to
 338 harvest. Mean values for genes evolved with varying fishing mortalities, L_f of 30 cm (indicated by grey
 339 line) and $M_0 = 0.2 \text{ year}^{-1}$. Energy allocation to reproduction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

346 L_m evolves between fishing mortalities of 0 and 0.09 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 year^{-1} .

350
 351 When $M_0 = 0.2 \text{ year}^{-1}$ α_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 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 year^{-1} . Fishing mortalities greater than 0.09 year^{-1} show a purely
 355 hermaphroditic strategy. α_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 year^{-1} (Fig. A12c) evolving to lengths below
 359 the imposed L_f at fishing mortalities of 0.03 and 0.04 year^{-1} . No further evolution of L_m occurs for
 360 fishing mortalities greater than 0.08 year^{-1} .

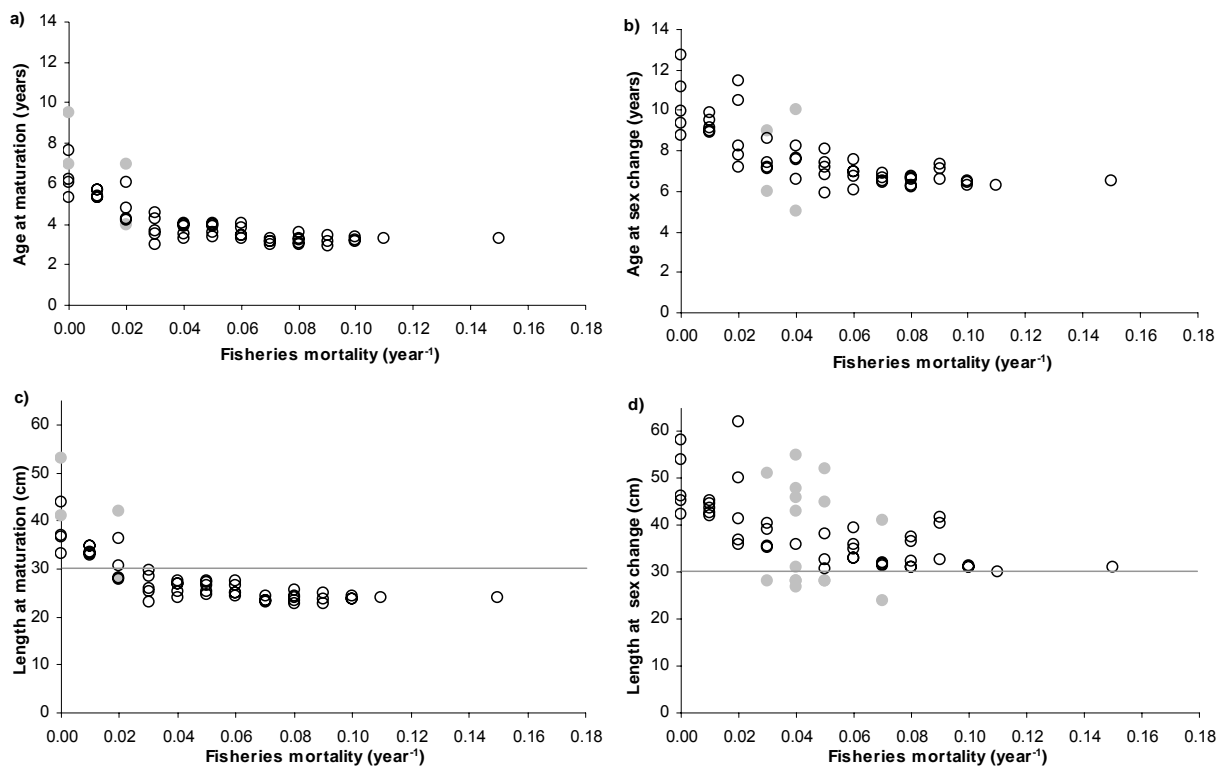


361
 362 **Figure A13.** Evolved life history strategies (phenotypes) for a grouper population subjected to varying
 363 levels of harvest intensity. Mean values for age and length at maturation and sex change at different
 364 fishing mortalities, L_f of 30 cm (indicated by grey line) and $M_0 = 0.1 \text{ year}^{-1}$. 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 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 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 $0.1 - 0.11 \text{ year}^{-1}$.

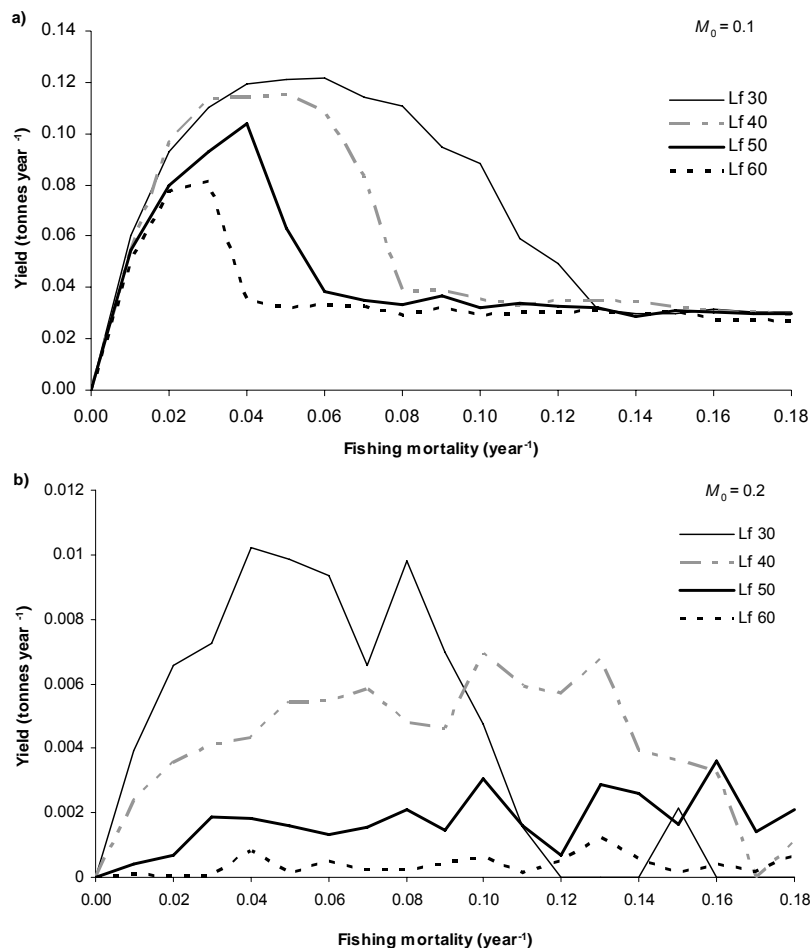


379
 380 **Figure A14.** Evolved life history strategies (phenotypes) for a grouper population subjected to varying
 381 levels of harvest intensity. Mean values for age and length at maturation and sex change at different
 382 fishing mortalities, L_f of 30 cm (indicated by grey line) and $M_0 = 0.2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

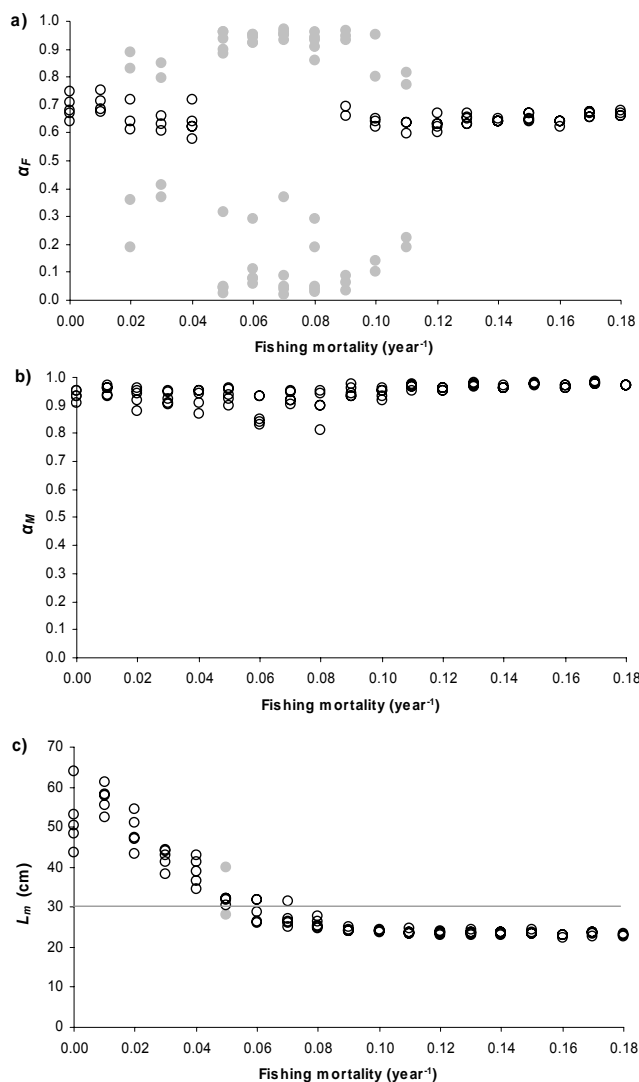
395

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 year^{-1} . Highest evolutionary stable
 399 yield is obtained at a fishing mortality of 0.06 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 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 α_F (a), energy
 410 allocation to reproduction in the male phase α_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*

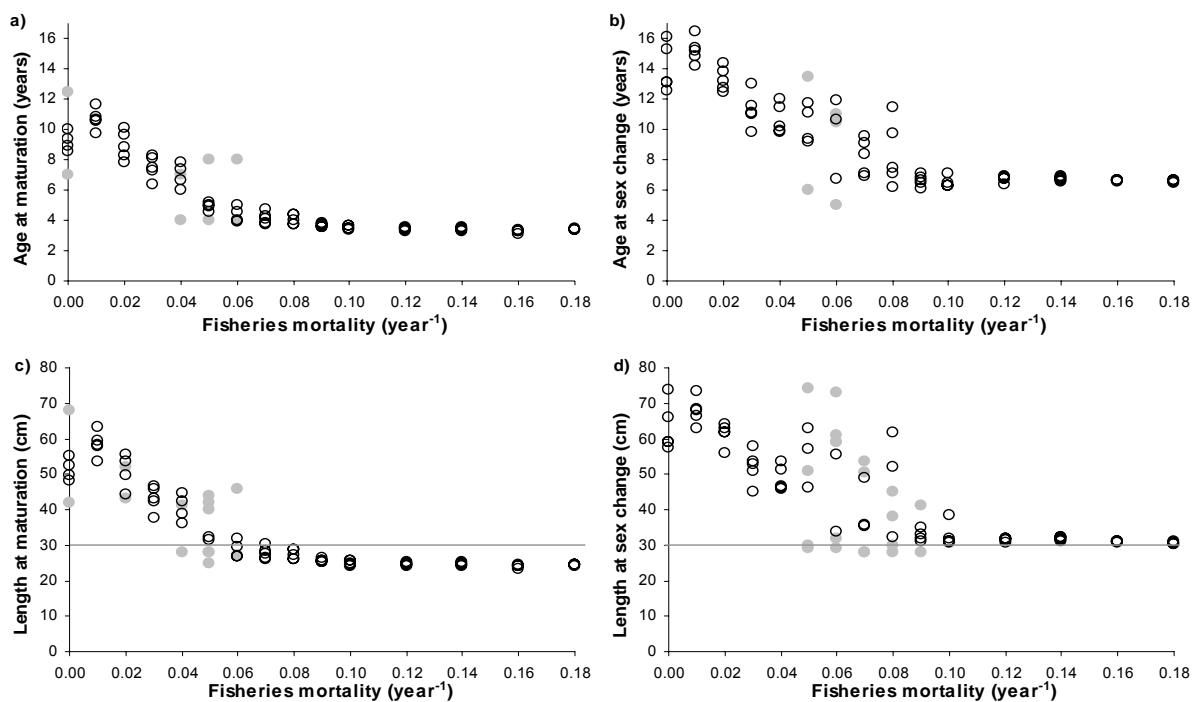
415 In contrast to what would be expected, removal of size advantage in males results in the
 416 population favoring hermaphroditism over dioecy more frequently (Fig. A 16a). There is no

417 bimodality in α_F in the absence of fishing and dioecy is observed for fishing mortalities between
 418 0.03 and 0.08 year⁻¹.

419
 420 α_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⁻¹, explaining
 426 the preference for a hermaphroditic strategy at fishing mortalities greater than 0.08 year⁻¹ (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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