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1 EvEel (Evolutionary ecology based model for Eel): a model to explore the role of phenotypic
2 plasticity as an adaptive response of three temperate eels (*Anguilla anguilla*, *A. japonica* and *A.*
3 *rostrata*) to spatially structured environments

4

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24 Keywords: *Anguilla* sp., phenotypic plasticity, adaptive response, EvEel, length-at-silvering, sex-
25 determination, habitat use

26

27 **Abstract**

28 *Anguilla anguilla*, *A. japonica* and *A. rostrata* are three largely distributed catadromous and
29 semelparous species characterized by a long and passive oceanic larval drift between their marine
30 spawning grounds and their nursery areas in continental waters. Their large and spatially
31 heterogeneous environments combined with population panmixia and long and passive larval drift
32 impair the possibility of local adaptation and favour the development of phenotypic plasticity. In
33 this context, we develop EvEel, a model that aims at exploring the role of phenotypic plasticity as
34 an adaptive response of eels. Results suggest that the spatial patterns in terms of sex-ratio, length-at-
35 silvering and habitat use observed at both the distribution area and the river catchment scales may
36 actually be the result of three adaptive mechanisms to maximize individual fitness in spatially
37 structured environments. We think that considering phenotypic plasticity as a paradigm is required
38 to develop appropriate models for this species.

39

40 **Introduction**

41 Phenotypic plasticity has been proposed as an adaptive response to environment variability for
42 many species (Levins 1963; Gotthard and Nylin 1995; Pigliucci 2005). It has been demonstrated
43 that in some cases, fitness gains arise from plastic phenotypes compared to non-plastic ones and that
44 consequently, phenotypic plasticity may be selected by natural selection (Schlichting 1986; Sultan
45 1987; Travis 1994). Moreover, Ernande and Dieckmann (2004) demonstrated that density-
46 dependence favours the selection of plastic phenotypes. The phenotypic plasticity issue is all the
47 more interesting for temperate eels (European eel *Anguilla anguilla*, American eel *A. rostrata* and
48 Japanese eel *A. japonica*) that meet all the conditions favouring the emergence of phenotypic
49 plasticity while impairing the possibility of local adaptation: panmictic populations with large
50 distribution areas and density-dependent population dynamics, concomitantly with a large
51 variability in life history traits, life tactics and demographic attributes.

52 Temperate eels are three semelparous catadromous species displaying remarkable similarities in
53 their life history traits (Daverat et al. 2006; Edeline 2007). All three species have a large distribution
54 area, from Morocco to Norway (Tesch 2003) for the European eel, from ~7°N to ~55°N for *A.*
55 *rostrata* (Helfman et al. 1987; Edeline 2007) and from Northern Philippines to Korea for *A.*
56 *japonica*. The populations are considered as panmictic since no clear genetic difference at neutral
57 loci was observed along the distribution area (Han et al. 2010; Als et al. 2011; Pujolar 2013). All
58 three species are characterised by a long and passive larval drift (larvae are called leptocephali)
59 between spawning grounds (Sargasso Sea for *A. anguilla* and *A. rostrata* (Schmidt 1923; McCleave
60 1993), and west of the Mariana Islands for *A. japonica* (Tsukamoto 1992)) and continental nursery.
61 Leptocephali metamorphose into glass eels when arriving on the continental shelf (Tesch 2003).
62 Then, glass-eels colonise continental waters where they become pigmented yellow eels and remain
63 during their growth phase that lasts several years. After a variable period generally lasting from 3 to
64 15 years, yellow eels metamorphose again into silver eels. They achieve their sexual maturation

65 while migrating back to spawning grounds.

66 As leptocephali drift passively to the continental shelf (McCleave 1993; Kettle and Haines 2006;
67 Bonhommeau et al. 2009), larvae are not able to select the river catchment in which they will grow.
68 Consequently, eels are distributed in contrasted environments (from Mauritania to Norway for
69 example for European eel, or from Northern South-America to Greenland for the American eel),
70 and more specifically with contrasting temperature which is a primary driver of physiological
71 processes, affecting both growth and survival (Brown et al. 2004).

72 Concomitantly with this environmental heterogeneity, a large phenotypic diversity is observed at the
73 distribution area and at the river catchment scales. For example, sex-ratio is spatially highly
74 heterogeneous at the distribution area and at the river catchment scale (Vladykov 1966; Helfman et
75 al. 1987; Oliveira et al. 2001). Vladykov (1966) and Helfman et al. (1987) mentioned a female
76 biased sex-ratio in the northern part of the distribution area. Krueger & Oliveria (1999) and Oliveira
77 et al. (2001) argued that sex-ratio variability can also vary a lot within a limited range of latitudes
78 under the influence of local conditions. A large data collection of existing observations carried out
79 by Kettle et al. (2011) for both *A. rostrata* and *anguilla* confirms this latitudinal pattern. Sex-
80 determination for eel is still poorly known but is controlled by environmental factors (Geffroy
81 2012). Environmentally controlled sex-determination is generally selected by evolution when the
82 environmental factor differentially affects the fitness of males and females (Mayhew 2006).

83 Environmental sex-determination is not rare for fishes, temperature being the main driving factor,
84 though the influence of density or social interactions have also been observed for some species
85 (Devlin and Nagahama 2002). Several factors have been proposed as driving factors for eel sex-
86 determination. Regarding eel density, a male biased sex-ratio is generally observed when eel density
87 is high (Roncarati et al. 1997; Tesch 2003; Han and Tzeng 2006). This has been observed at the
88 catchment scale where males are concentrated in the downstream part of the catchment (Oliveira
89 and McCleave 2000; Tesch 2003), though this observation may result from a more limited
90 colonisation ability of males. More convincing observations come from catchments where

91 modifications of densities have resulted in modifications of the sex-ratio (Poole et al. 1990;
92 Roncarati et al. 1997; Tesch 2003), and by observations in controlled environment experiments
93 (Colombo and Grandi 1996; Beullens et al. 1997; Holmgren et al. 1997). Growth rate in youngest
94 stages is also suspected to play a role in sex-determination, however results are less obvious.
95 Holmgren (1996) and Holmgren and Mosegaard (1996) observed in controlled experiments that fast
96 growing (especially in weight) young eels preferentially turn into males. However results were
97 unclear because of concomitant variation in density. More generally, Geffroy (2012) assumed that
98 the global quality of the environment may be the main factor affecting sex-determination.
99 This issue of sex-determination is of major importance because males and females are supposed to
100 display distinct life tactics (Helfman et al. 1987). The reproduction success of a male does not vary
101 with its body size, consequently males are assumed to follow a time-minimising strategy, leaving
102 continental waters as soon as they have enough energy to migrate to the spawning grounds
103 (Vollestad 1992). This assumption would explain why male silver eels display rather similar
104 weights and sizes (Oliveira 1999) all over the distribution area (Vollestad 1992; Oliveira 1999). Such
105 a size threshold may correspond to the size at which energy stores are sufficient to undergo the
106 transoceanic reproduction migration (Van Den Thillart et al. 2007). By contrast, fecundity and
107 consequently reproduction success of females is mainly influenced by body size. Consequently,
108 females are assumed to follow a size-maximising strategy, adapting their length-at-silvering to local
109 growth and mortality conditions in order to find a trade-off between survival and fecundity.
110 Latitudinal pattern of female silver eel length is often mentioned with larger females in the northern
111 part of the distribution area (slow growth but lower mortality) than in the southern part (Helfman et
112 al. 1987; Davey and Jellyman 2005; Jessop 2010).

113 In addition to sex-ratio and length-at-silvering variability, eels also display a large range of tactics in
114 terms of growth and habitat use, some settling in estuarine waters while others move far upstream in
115 river catchments (Tsukamoto et al. 1998; Daverat et al. 2006; Arai and Chino 2012). Growth rate in
116 salted and brackish downstream parts of catchments is significantly higher than in upper parts of the

117 catchments (Helfman et al. 1984; Melià et al. 2006b; Daverat et al. 2012). A lower mortality in
118 upper parts of river catchments is sometimes assumed to balance the associated lower growth.
119 Consequently, upstream habitats with more limited intraspecific competition may still be favourable
120 especially for females which can adapt their length-at-silvering to balance lower growth rates.
121 Edeline (2007), for example, assumed that catchment colonisation and tactics in habitat use by eels
122 correspond to a conditional evolutionary stable strategy (Gardner et al. 1987). A conditional
123 evolution stable strategy is a generalisation of evolutionary stable strategy in which an individual
124 can express different phenotypes (the tactics of the conditional strategy) depending on its
125 environmental, social and physiological status (cueing trait). According to Edeline (2007),
126 individuals with high energetic status would migrate upstream to avoid competition and then settle
127 (*i.e.* change tactics) when their energetic status becomes too low or when the benefits do not
128 outweigh the costs of migration. This assumption is challenged by Cairns et al. (2009) who did not
129 observe mortality differences large enough to balance variations in growth between different
130 habitats. Cairns et al. (2009) concludes that the decrease of natural mortality (competition) would
131 not outweigh the cost of migration and the decrease in growth rate.

132 As a summary, eels display a large phenotypic and tactical variability at both the distribution area
133 and the catchment scales including sex-determination, females length-at-silvering and use of growth
134 habitats within a catchment with higher density downstream. Since eels meet all conditions
135 favouring phenotypic plasticity, the objective of this paper is to explore if those spatial patterns may
136 result from adaptive responses to spatially structured environments and density-dependence, or if
137 they are a "passive" response to environmental variability (Van Kleunen and Fischer 2005). This
138 analysis is carried out using EvEel (Evolutionary ecology model for Eel): a model exploring the
139 role of phenotypic plasticity as an adaptive response of eels to spatially structured environments.

140 **Material and methods**

141 ***Model rationales and definition of the spatial patterns***

142 The model is based on the assumption that the growth phase of eels in continental waters starts by
143 two successive events, sex-determination and growth habitat selection, which are two adaptive
144 responses to environmental variability. Consequently sex-determination and growth habitat
145 selection are assumed to be two "decisions that maximise expected fitness". Assuming that
146 decisions are made to maximise expected fitness is the main assumption when modelling adaptive
147 life history decisions (Mangel and Clark 1988). For example, in the optimal foraging theory,
148 animals are assumed to move to maximise their food intake which is considered as a proxy of their
149 fitness (Mangel and Clark 1986; Giske et al. 1998; Railsback and Harvey 2013). Similarly, models
150 based on the life history theory posits that the schedule and duration of life traits are the results of
151 natural selection to optimize individual fitness (Giske et al. 1998). For example, McLaren (1963)
152 developed a model of spatial distribution of zooplankton based on habitat profitability, by modelling
153 the effect of water temperature on reproduction rate.(2013) Life-history theory models generally
154 focus on finding an optimal trade-off between age at maturity, fecundity and survival (McNamara
155 and Houston 1992; Clarke 1993; Giske et al. 1998). Alternative migratory tactics of salmonids
156 (anadromous, jacks and freshwater resident) may be interpreted as an adaptation to local
157 environment in the context of life-history theory (Dodson et al. 2013).

158 Assumed that males adopt a time-minimising strategy, their fitness may be approximated by the
159 probability to survive until length-at-silvering. On the other hand, females are assuming to adopt a
160 size-maximising strategy, seeking an optimal trade-off between length-at-silvering (fecundity) and
161 survival, consequently females fitness can be approximated by the product of expected fecundity at
162 the length-at-silvering multiplied by the probability to survive until this length.

163 Following Grimm and Railsback (2012), we applied a pattern-oriented modelling approach by
164 comparing model outputs to the following observed and documented spatial patterns:

- 165 • at the distribution area scale:
- 166 1. male-biased sex ratio in the southern part of the distribution area and female-biased
- 167 sex-ratio in the northern part
- 168 2. male-biased sex-ratio in environment with high density
- 169 3. male-biased sex-ratio in fast growth environment
- 170 • at the river catchment scale:
- 171 4. higher density downstream than upstream
- 172 5. higher length-at-silvering upstream than downstream
- 173 6. male-biased sex-ratio downstream and female-biased sex-ratio upstream

174

175 ***Distribution area scale: sex-determination and length-at-silvering as adaptive***

176 ***mechanisms to a wide variety of spatially structured environmental conditions***

177 We denote r a river catchment where glass-eels arrive. It is characterised at its mouth by:

- 178 • an instantaneous natural mortality rate $M(r)$
- 179 • a Brody growth coefficient $K(r)$ of a Von-Bertalanffy growth curve
- 180 • a mean water temperature $T(r)$

181

182 We assume that female fitness may be approximated by the product of the expected number of eggs

183 at length-at-silvering and the probability to survive until this length-at-silvering $L_{Sf}(r)$, *i.e.* the mean

184 expected number of eggs produced by each female. Following De Leo and Gatto (1995), we assume

185 that growth is well represented by a Von Bertalanffy growth model: $L(t, r) = L_{\infty} \cdot \left(1 - e^{-K(r)(t-t_0)} \right)$

186 with $L(t, r)$ the length at time t of a fish, L_{∞} the asymptotic length and $K(r)$ the Brody growth

187 coefficient.

188 Consequently, age-at-silvering $As_f(r)$ is:

189 1) $As_f(r) = -\frac{1}{K(r)} \cdot \log\left(\frac{L_\infty - L_{S_f}(r)}{L_\infty}\right) + t_0$

190 If we denote L_g the length at recruitment which is supposed to happen at $t=0$, we get:

191 2) $t_0 = \frac{1}{K(r)} \cdot \log\left(\frac{L_\infty - L_g}{L_\infty}\right)$

192 and consequently:

193 3) $As_f(r) = \frac{1}{K(r)} \cdot \log\left(\frac{L_\infty - L_g}{L_\infty - L_{S_f}(r)}\right)$

194 Von Bertalanffy parameters $K(r)$ and L_∞ are generally largely correlated (Pilling et al. 2002;

195 Siegfried and Sansó 2006; Eveson et al. 2007). Regarding eels, Melià et al. (2006a) found a strong

196 linear correlation between the two parameters estimates. Consequently following de Pontual et al.

197 (2006) and Drouineau et al. (2010, 2012) we assume that L_∞ is fixed and that only $K(r)$ varies.

198 This assumption is also consistent with the Dynamic Energy Budget theory in which L_∞ is not

199 affected by temperature variations (Kooijman 2000).

200

201 From equation 3, we can calculate the proportion of individuals that survive till length-at-silvering

202 $p_f(r)$:

203 4) $p_f(r) = e^{-M(r) \cdot As_f(r)} = \left(\frac{L_\infty - L_g}{L_\infty - L_{S_f}(r)}\right)^{\frac{-M(r)}{K(r)}}$

204 and the reproductive output of females which we consider as a proxy of the female fitness $\pi_f(r)$ is

205 5) $\pi_f(r) = (a_1 + a \cdot L_{S_f}(r)^b) \cdot \left(\frac{L_\infty - L_g}{L_\infty - L_{S_f}(r)}\right)^{\frac{-M(r)}{K(r)}}$

206 with a_1 , a and b parameters from a fecundity-at-length relationship proposed by Andrello et al.
207 (2011), in which fecundity is assumed to be a linear function of weight, the latter scaling
208 allometrically to length (Melià et al. 2006a).

209 As previously mentioned, females length-at-silvering is assumed to be a trade-off between
210 fecundity and survival probability, consequently we numerically estimated $Ls_f(r)$ as the value that
211 maximises $\pi_f(r)$ in the growth and survival conditions of r . This trade-off between fecundity is
212 illustrated by Fig. 1.

213

214 Conversely, male reproduction success is assumed to adopt a time minimising strategy, leaving
215 continental waters as soon as they have reached the minimal length to undergo the reproduction
216 migration (Helfman et al. 1987; Vollestad 1992). Consequently, we assume that male length-at-
217 silvering is constant (as observed by Oliveira (1999)) and corresponds to the minimal length to
218 carry out the migration to the spawning grounds. Males fitness $\pi_m(r)$ may thus be approximated by
219 the probability to survive until length-at-silvering:

220 6)
$$\pi_m(r) = \left(\frac{L_\infty - L_g}{L_\infty - Ls_m(r)} \right)^{\frac{-M(r)}{K(r)}}$$

221

222 The ratio $\pi_f(r) / \pi_m(r)$ is then calculated for different values of $K(r)$ and $M(r)$ varying from 0 to 0.3
223 year⁻¹. For each case, the optimal female length-at-silvering $Ls_f(r)$ is also estimated. This produces
224 a diagram of ratio of fitness. A large ratio indicates a marginal fitness gain for females while a
225 smaller ratio indicates a marginal fitness gain for males. This also produces a diagram of females
226 length-at-silvering, as a function of $K(r)$ and $M(r)$. We do not consider any feedback in sex-
227 determination: the expected fitness of choosing male or female does not depend on how many other
228 eels choose which sex.

229

230 Natural mortality and growth rates of living organisms are largely influenced by temperature
231 because of physiological processes (Brown et al. 2004). Correlation between eel natural mortality
232 (Bevacqua et al. 2011b), growth (Daverat et al. 2012) and temperature has been observed.
233 Consequently, all combinations of values of $M(r)$ and $K(r)$ are not physiologically possible. Pauly
234 (1980) has carried out a large meta-analysis linking growth parameters to survival for numerous
235 marine fish species:

$$236 \quad 7) \log(M(r)) = -0.0066 - 0.279 \cdot \log(L_{\infty}) + 0.6543 \cdot \log(K(r)) + 0.4634 \cdot \log(T(r))$$

237

238 We use this relationship with temperatures ranging from 5°C to 25°C, and plot this relation on the
239 diagrams of ratio of fitness and females length-at-silvering as functions of $K(r)$ and $M(r)$, to detect
240 plausible combinations of growth and mortality rates. We also plot hypothetical points of growth
241 and mortality to illustrate how sex-ratio and length-at-silvering may vary between Scandinavia, Bay
242 of Biscay and Mediterranean area: Scandinavia is characterised by a low temperature (we chose 5°C
243 as an illustration) and a slow growth (see (Helfman et al. 1987; Jessop 2010) for description of
244 latitudinal pattern in growth). Mortality rate was then estimated using equation 7, Conversely,
245 Mediterranean area is characterised by a warmer temperature (we chose 25°C as an illustration) and
246 a faster growth.

247

248 Parameters values are presented in the control experiment scenario in table 1.

249

250 ***River catchment scale: habitat selection, sex-ratio and length-at-***
251 ***silvering as adaptive mechanisms within a catchment***

252 A slightly more complex version of the model is developed to be applied to a theoretical river

253 catchment r . In this second step, we consider that sex-determination has already occurred, and we
254 focus on the selection of growth habitat by $N_m(r)$ males and $N_f(r)$ females in the river catchment.

255

256 The river catchment is represented by n contiguous cells, the first cell representing the river mouth
257 while the n -th cell represents the source of the river. As previously mentioned, within river growth
258 rates are significantly faster downstream than upstream. To represent this gradient, we assume that
259 the instantaneous growth rate in cell i , $K(r,i)$ is:

260 8)
$$K(r,i) = K(r,n) + (K(r,1) - K(r,n)) \cdot \text{cauchit}\left(\frac{i}{n}, \gamma_K\right)$$

261 9)
$$\text{cauchit}(x, \gamma) = 1 - \frac{2}{\pi} \cdot \text{atan}\left(\frac{x^2}{\gamma}\right)$$

262 with cauchit a mathematical function similar to the sigmoid function but that allows asymmetrical
263 patterns (by modifying the parameter γ - Fig. 2 illustrates the form of this relationship).

264 Since natural mortality is also sometimes assumed to be smaller upstream than downstream
265 (Moriarty 2003; Daverat and Tomás 2006), we assume that the instantaneous natural mortality in
266 cell i , $M(r,i)$ is:

267 10)
$$M(r,i) = M(r,n) + (M(r,1) - M(r,n)) \cdot \text{cauchit}\left(\frac{i}{n}, \gamma_M\right)$$

268

269 We can notice that assuming that $M(r,1) = M(r,n)$ is equivalent to assuming a constant
270 instantaneous natural mortality all over the river catchment.

271 We denote $M_m(r,i)$ and $M_f(r,i)$ the instantaneous natural mortality rates for males and females.

272 For simplicity, following Lockwood (1980), we assume that natural mortality increases linearly
273 with density (Hixon and Jones 2005) though logarithmic relationship may also be assumed (Myers
274 and Cadigan 1993; Fromentin et al. 2001) and provide similar results:

275 11) $M_m(r, i) = M(r, i) + (N_m(r, i) + N_f(r, i)) \cdot \alpha_m$

276 12) $M_f(r, i) = M(r, i) + (N_m(r, i) + N_f(r, i)) \cdot \alpha_f$

277 with $N_m(r, i)$ and $N_f(r, i)$ the number of males and females in cell i while α_m and α_f are two
 278 parameters that control the intensity of density-dependence.

279

280 In each cell i , males and females fitnesses (denoted $\pi_m(r, i)$ and $\pi_f(r, i)$) are calculated using
 281 equations 5 and 6 and assuming a density-dependent natural mortality (Vollestad and Jonsson 1988;
 282 De Leo and Gatto 1996; Lobón-Cerviá and Iglesias 2008; Bevacqua et al. 2011b) as described in
 283 equations 11 and 12:

284 13) $\pi_f(r, i) = (a_1 + a \cdot L_{S_f}(r, i)^b) \cdot \left(\frac{L_\infty - L_g}{L_\infty - L_{S_f}(r)} \right)^{\frac{-M_f(r, i)}{K(r, i)}}$

285 14) $\pi_m(r, i) = \left(\frac{L_\infty - L_g}{L_\infty - L_{S_m}} \right)^{\frac{-M_m(r, i)}{K(r, i)}}$

286 $L_{S_f}(r, i)$ is estimated as the length maximising $\pi_f(r, i)$ (see Fig .1).

287 For each cell i , we estimate the mean length-at-silvering as:

288 15) $\overline{L_s}(r, i) = \frac{N_m(r, i) \cdot L_{S_m} \cdot \pi_m(r, i) + N_f(r, i) \cdot L_{S_f}(r, i) \cdot \frac{\pi_f(r, i)}{a_1 + a \cdot L_{S_f}(r, i)^b}}{N_f(r, i) \cdot \frac{\pi_f(r, i)}{a_1 + a \cdot L_{S_f}(r, i)^b} + N_m(r, i) \cdot \pi_m(r, i)}$

289 and standardised fitnesses along the riverside as:

290 16) $\pi_{m, std}(r, i) = \frac{\pi_m(r, i)}{\max_j \{\pi_m(r, j)\}}$

291 17) $\pi_{f, std}(r, i) = \frac{\pi_f(r, i)}{\max_j \{\pi_f(r, j)\}}$

292

293 We assume that the N_m males and the N_f females settle in the cell of maximum fitness. Based on this
294 assumption, males and females are distributed in the river catchment by applying the following
295 algorithm:

- 296 • For k from 1 to $\max(N_m, N_f)$
 - 297 ◦ if $k \leq N_m$
 - 298 ▪ k -th male goes in cell i having $\pi_{m, std}(i) = 1$ (maximum fitness)
 - 299 ◦ if $k \leq N_f$
 - 300 ▪ k -th female goes in cell i having $\pi_{f, std}(i) = 1$ (maximum fitness)

301 *i.e.* males and females are put one after the other in the cell of maximum fitness.

302 The procedure is repeated with four different sets of model parameters. Figure 2 summarizes the
303 assumed values of natural mortality and growth rates along the catchment for each set of
304 parameters. It mimics a catchment with a small downstream part with fast growth rate
305 corresponding to brackish waters. Concerning mortality rates, we assume constant rates in three sets
306 and a small gradient in the fourth one.

307

308 For each set, we analyse different outputs: $N_f(r, i)$, $N_m(r, i)$, $\pi_f(r, i)$, $\pi_m(r, i)$, $Ls_f(r, i)$, $M_f(r, i)$
309 and $M_m(r, i)$.

310

311 **Results**

312 ***Distribution area scale: sex-determination and length-at-silvering as adaptive***

313 ***mechanisms to a wide variety of spatially structured environmental conditions***

314 The ratio of fitness for various conditions of $K(x)$ and $M(x)$ (Fig. 3) demonstrates that high mortality

315 tends to favour males as compared to females fitness. If we assume that high density increases
316 mortality because of intra-specific competition, this may explain why males-biased sex-ratios are
317 observed in high density environments.

318 Fast growth rate seems to favour females with respect to males. This is not consistent with the
319 observed pattern of sex-ratio at the distribution area, with female biased sex-ratio in the northern
320 part (slow growth) and male biased sex-ratio in the south (fast growth). However, the physiological
321 relationship (Pauly 1980) between $M(r)$ and $K(r)$ implies that in the southern part (white circle -
322 Fig. 3) fast growth is generally associated with higher natural mortality, and consequently males
323 become favoured with respect to females compared to Northern area (black circle - Fig. 3), which is
324 consistent with observations.

325 Consequently, at the distribution area, the model mimics the geographical pattern of sex-ratio and is
326 consistent with male-biased sex-ratios in high density environment.

327 Looking at length-at-silvering as a function of $M(r)$ and $K(r)$ (Fig. 4), we observe that the model
328 predicts largest females in cold conditions (black circle) than in warm conditions (white circle).
329 This is consistent with the observation of largest silver eels females in the northern part of the
330 distribution than in the southern part (Fig. 4).

331 As a summary, the model mimics all three spatial patterns observed at the distribution area scale
332 (Table 2).

333

334 ***River catchment scale: habitat selection, sex-ratio and length-at-silvering as***
335 ***adaptive mechanisms within a catchment***

336 Without density-dependence (set S0 – Fig. 5), all males and females concentrate downstream the
337 river. In this situation, dispersion in the catchment would not correspond to a conditional
338 evolutionary stable strategy, as suggested by Cairns et al. (2009).

339 If we consider that natural mortality is partly density-dependent (set S1 - Fig. 5), males and females
340 are distributed all along the river, with highest densities downstream the catchment. However, males
341 and females have exactly the same distribution while only females are observed upstream in the
342 field. Relative fitness and length-at-silvering is constant all along the river in this situation.

343 If we assume lower mortality rate upstream than downstream (set S3 - Fig. 5), results are not
344 changed drastically and males and females spatial distributions are still similar.

345 Consequently, dispersion may be a conditional evolutionary stable strategy if we assume that part of
346 the natural mortality is density-dependent. However, it does not explain why the spatial
347 distributions of males and females are different.

348 With set S2 (Fig. 5), we assume that males are less sensitive than females to density-dependence.
349 Set S2 produces results rather similar to field observations. First, males are concentrated in the
350 downstream part of the catchment, where growth is faster, while females are distributed more
351 upstream in zone with lower fish density. When looking at length-at-silvering, silver eels are
352 smaller downstream (where there are more males) than upstream. Moreover, natural mortality is
353 rather constant downstream (where males are concentrated), which may explain why Cairns et al.
354 (2009) do not observe high variations in natural mortality.

355 To conclude, density-dependence is required to mimic catchment colonisation (Table 2) and all the
356 patterns are mimicked if we assume that males are less sensitive than females to density-
357 dependence.

358

359 **Discussion**

360 The aim of this paper was to explore if few assumptions based on evolutionary concepts may
361 explain the spatial patterns observed in the 3 temperate eels in term of sex-ratio, length-at-silvering
362 and habitat distribution, both at the distribution area scale and at the river catchment scale. Six
363 spatial patterns were listed and the model mimics all of them at both distribution area and river

364 catchment scales (Table 2). This does not demonstrate that our assumptions are correct, however, it
365 suggests that sex-determination, length-at-silvering and growth habitat selection may be interpreted
366 as adaptive plasticity selected by evolution to respond to the highly variable and spatially structured
367 environmental conditions encountered by temperate eels. An extension to tropical eels would be
368 interesting in the future.

369 Interestingly, Côté et al. (2009, 2014) and Gagnaire et al. (2012) have recently explored an
370 alternative hypothesis. Côté et al. (2009) observed permanent growth rate differences between eels
371 originating from two different regions that were reared in similar conditions. Gagnaire et al. (2012)
372 observed genetic differences between eels originating from different sites. They assumed that
373 despite population panmixia, local conditions may select adaptive alleles that are then reshuffled
374 again during the next reproduction. The two hypotheses are not totally contradictory: the two
375 mechanisms, *i.e.* phenotypic plasticity and genetic adaptation, may complement each other as
376 adaptive responses. In the future, it would be interested to turn EvEel into a demo-genetic model
377 (Piou and Prévost 2012) or to a quantitative genetic model that incorporates phenotype plasticity
378 similar to the model developed by Baskett et al. (2005). In this model, each individual is
379 characterised by its genotype which corresponds to the genetic predisposition to mature at a given
380 size (that would be length-at silvering for eel). However, the phenotype is assumed to be a balance
381 between the genotype and a response to environment through phenotypic plasticity.

382

383 Within a river catchment, Edeline (2007) proposed that colonisation may correspond to a
384 conditional evolutionary stable strategy, assuming that lower growth rates upstream were
385 compensated by lower mortality rates. This point of view was challenged by Cairns et al. (2009)
386 who did not observe large variations of natural mortality rates in the field. However, our model
387 suggests that, despite these limited variations of natural mortality, the colonisation and the choice of
388 a growth habitat may still correspond to fitness maximisation strategy. If we assume that females
389 are more sensitive to density-dependent mortality than males, males are concentrated downstream

390 where Cairns et al. (2009) made their observations, a zone where the model predicts that their
391 natural mortality rate is rather constant (Fig. 5, scenario S2). It is well known that density-
392 dependence plays a major role in eel dynamics (De Leo and Gatto 1996), especially in migratory
393 behaviour (Geffroy and Bardonnnet 2012). Our assumption of distinct density-dependent sensitivity
394 between males and females, i.e. females suffering a higher density-dependant natural mortality rate
395 than males, is plausible for two main reasons: First, Holmgren et al. (1997) observed that males in
396 young stages have a faster growth in weight, with higher condition indices, and so they may become
397 dominant with respect to females. Secondly, we may assume that males may have evolved to be
398 more adapted to high-density since males biased sex-ratios are observed in high density
399 environments. Gender difference in sensitivity to intraspecific competition has already been
400 observed for insects (Gibbs et al. 2004; Tsurim et al. 2013) and birds (Clobert et al. 1988). For
401 example, Gibbs et al. (2004) demonstrated in controlled experiments that females of a butterfly
402 were more adversely affected by high density than males. In the model, we assumed that density-
403 dependence affects natural mortality because of negative effects of intra-cohort and inter-cohort
404 densities on mortality have been observed in many studies (Vollestad and Jonsson 1988; De Leo
405 and Gatto 1996; Lobón-Cerviá and Iglesias 2008; Bevacqua et al. 2011a, 2011b).

406 In our model, we assume that only natural mortality was impacted by density-dependent processes
407 though intra-specific competition may also result in lower growth rates in reality. However, since
408 fitness is approximated by a function of the ratio of instantaneous natural mortality over Brody
409 growth coefficient in our model (see equations 5 and 6), the results would not change if modelling a
410 density-dependant growth rate.

411 EvEel is based on few evolutionary assumptions: (i) sex-determination is an adaptive response to
412 favour sex with highest fitness in a given environment (assumption consistent with what is observed
413 on many species having an environmental sex-determination (Mayhew 2006)), (ii) since females
414 adopt an size-maximising strategy, fitness may be approximated by the product of fecundity and
415 survival rate, (iii) since males adopt a time-minimising strategy, their fitness may be approximated

416 by their survival rate, (iv) females are more sensitive to intra-specific competition than males and
417 (v) colonisation and growth habitat selection in a catchment is based on the maximisation of the
418 fitness. Only five assumptions are enough to mimic the main spatial pattern of sex-ratios, length-at-
419 silvering and distribution at the distribution area scale and at the river catchment scale. However,
420 mimicking patterns does not validate (or invalidate) those assumptions and controlled experiments
421 would be required to investigate their reliability.

422 Sex-determination, length-at-silvering and habitat selection are not conscious choices of eels.
423 Optimality models assumes that decisions are made to maximize expected future fitness though
424 organisms do not understand the world they live in and are not able to predict the future. However,
425 evolution has selected animals that undertake those types of decisions in given environmental
426 conditions (Giske et al. 1998). Eel plasticity may be influenced by a few environmental factors so
427 that eels may adapt to the wide range of environmental conditions they may encounter. Among
428 these factors, temperature probably plays a major role by affecting growth and mortality rates. Food
429 availability also plays a role through natural mortality and density-dependence. More generally,
430 global environment quality would affect those three mechanisms, as proposed by Geffroy (2012) for
431 sex-determination.

432 Temperature is known to affect most physiological processes (Brown et al. 2004; Clarke 2006).
433 Pauly (1980) proposed a relation between somatic growth, natural mortality and temperature. This
434 relation was fitted mainly at the inter-specific level, however we considered that this relationship
435 was still relevant at the intra-specific level for two reasons. First in the database analysed by Pauly
436 (1980), many species were included more than once (*Gadhus morhu* was considered 8 times for
437 example) with growth and mortality estimates from distinct regions. This tends to demonstrate that
438 the relationship remains correct at the intra-level scale. Secondly, the arguments suggested by Pauly,
439 *i.e.* increased physiological mortality and increased predation, to explain a direct relationship are
440 still valid at the specific level. Indeed, high temperature increases all metabolic rates (Clarke and
441 Johnston 1999; Clarke 2003) leading to higher growth rates (Brown et al. 2004). However, resting

442 metabolic rates (and consequently the energy required for maintenance) (Clarke 2003) and inter-
443 specific interactions (competition, predation...) (Brown et al. 2004) also increase with temperature,
444 potentially leading to higher natural mortality rates.

445 Pauly's equation (1980) describes a general trend in growth and mortality with temperature which is
446 considered correlated to latitude in our study. However, this general trend may be altered by local
447 conditions. Upwellings for example may disrupt (i) the temperature/latitude gradient and (ii) the
448 growth rate/temperature relationship because of high productivity. Specific habitats, such as lakes,
449 may also disrupt the trend and may explain the phenotypic variability observed by Krueger and
450 Oliveira (1999) and Oliveira et al. (2001) at similar latitudes.

451 Provided our assumptions are valid, it is interesting to analyse the effect of various sources of
452 anthropogenic mortalities. Glass-eels fisheries downstream river catchments tend to decrease eel
453 densities which may lead to a change in sex-ratio towards females and to a decrease of the
454 colonisation of upstream habitats. Remaining individuals are consequently located in downstream
455 habitats where growth is faster mitigating the impact of the fishery. An obstacle to upstream
456 colonisation implies higher densities of individuals downstream. An obstacle close to the mouth
457 would result in a change of sex-ratio towards males (impacting undetermined young eels) or block
458 females which are very sensitive to density-dependence.

459 This first version of EvEel is simple. It does not model population dynamics and assume that fishes
460 are omniscient (perfect knowledge of the entire river catchment) and omnipotent (they are able to
461 migrate to any part of the catchment without any delay). Moreover, it assumes that sex-
462 determination and choice of growth habitat are two successive events that occur very early in the
463 growth phase in continental waters. The reality is more complex: sex-determination occurs between
464 20 cm and 30 cm and consequently, colonisation has already started. Moreover, it has been
465 demonstrated that some eels that settle upstream can then move downstream to more favourable
466 habitats when density decreases (Daverat et al. 2006). The model simplicity explains the rough
467 contrasts in the spatial distribution of individuals within a catchment and in the distribution of

468 length-at-silvering. It would be interesting in the future to incorporate population dynamics and to
469 apply the model to a real river catchment. Basin model proposed by MacCall (1990) and diffusion-
470 advection models (Mullen 1989; Bertignac et al. 1998) would be relevant solution to model eel
471 spatial distribution. Diffusion-advection model would allow to incorporate dynamics in EvEel.
472 These types of models are all based on theoretical ecological concepts (fitness) which are often
473 interesting to explore assumptions that may be validated in the future (Willis 2011). These models
474 would probably result in smoother transitions between males and females and in length-at-silvering
475 because of diffusion. It would be very interesting to compare the results of those models to the
476 outputs of mechanistic or statistical models that have been used to model eels spatial distribution
477 (Ibbotson et al. 2002; Lambert et al. 2011; Jouanin et al. 2012).

478 In the current version of the model, we only consider the growth phase in continental waters and we
479 do not consider the larval drift and the spawning migration. Depending on the river catchment,
480 distance to spawning grounds and consequently migration duration may vary. Larval drift being
481 passive, there is probably no systematic inter-individual difference in fitness. Glass-eels may recruit
482 with variable lengths and energetic resources at different latitudes, however our results were not
483 affected when varying Lg . Regarding spawning migration, Clevestam et al. (2011) suggested that
484 silver eels from the Baltic Sea, one of the most distant region from *A. anguilla* spawning grounds,
485 may be too small to undergo the migration. Consequently, it would be interesting to take into
486 account this migration in a future version of the model.

487 Regarding length-at-silvering, the model produces smaller silver eels downstream where males are
488 dominant than upstream where females are dominant. This pattern is consistent with observations.
489 Regarding females length-at-silvering, it is constant over the whole catchment. Possible gradient of
490 female length-at-silvering is sometimes suspected in the literature though evidence is small. By
491 taking into account population dynamics, and especially migration dynamics, in the model, fast
492 migrating females would benefit from upstream habitat with lower density since all females would
493 not be able to reach upstream habitat, resulting in females with slightly larger length-at-silvering.

494 To conclude, the study of phenotypic plasticity has progressed significantly over the past few
495 decades (Pigliucci 2005) and empirical evidences have been accumulated for many taxa (Ernande
496 and Dieckmann 2004). Regarding diadromous fishes, the role of phenotypic plasticity in explaining
497 some geographic gradients in migratory behaviour of salmonids have for example been underlined
498 by Dodson et al (2013). We think that temperate eels are relevant species to work on phenotypic
499 plasticity. Their large distribution area with spatially structured environments, panmixia and passive
500 larval drift limit the possibility of local adaptation and favours phenotypic plasticity as an adaptive
501 response. Phenotypic plasticity in terms of sexual-determination and subsequent sex-ratio (Davey
502 and Jellyman 2005), length-at-silvering (Vollestad 1992), growth rate (Geffroy and Bardonnet
503 2012), natural mortality rate and migration behaviour (Edeline 2007; Cairns et al. 2009) have
504 actually been documented and analysed for a long time. However, they have generally been
505 considered separately, or two by two, without considering the entire continental life cycle of eels.
506 To our knowledge, it is the first time that all those mechanisms are analysed simultaneously in a
507 single model that considers the implications of life history traits and tactical choices as adaptive
508 responses to highly variable environmental conditions. More generally, we think that evolutionary
509 ecology may provide valuable insights to better understand the continental phase of this species.
510 Phenotypic plasticity has been considered as a nuisance parameter in evolutionary study before
511 becoming a paradigm (Pigliucci 2005). Phenotypic variability is also considered as a nuisance
512 (noise) in population dynamic models for eels. We are alike convinced that phenotypic plasticity
513 should become a paradigm to develop appropriate models for this species.

514

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519

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777 **Tables**

778 **Table 1.** Parameters values used in the four sets

	S0 : Control experiment	S1 : Density- dependence	S2 : Differential density-dependence	S3 : Gradient on mortality
n			30	
$N_m(r)$			10000	
$N_f(r)$			10000	
α_1		8846 (Andrello et al. 2011)		
a		1.387119 (Melià et al. 2006a; Andrello et al. 2011)		
b		3.22 (Melià et al. 2006a)		
L_∞		76.2 cm (De Leo and Gatto 1995)		
LS_m		40.5 cm (Vollestad 1992)		
L_g	7.5 cm (Desaunay and Guerault 1997; Dekker 1998; Desaunay et al. 2012)			
$K(r,1)$		0.23 year ⁻¹ (De Leo and Gatto 1995)		
$K(r,n)$		0.115 year ⁻¹		
$M(r,1)$		0.138 year ⁻¹ (Dekker 2000)		
$M(r,n)$		0.138 year ⁻¹		0.103 year ⁻¹
γ_M			0.05	
γ_K			0.05	
α_m	0	0.0001	0.00005	0.0001
α_f	0	0.0001	0.0001	0.0001

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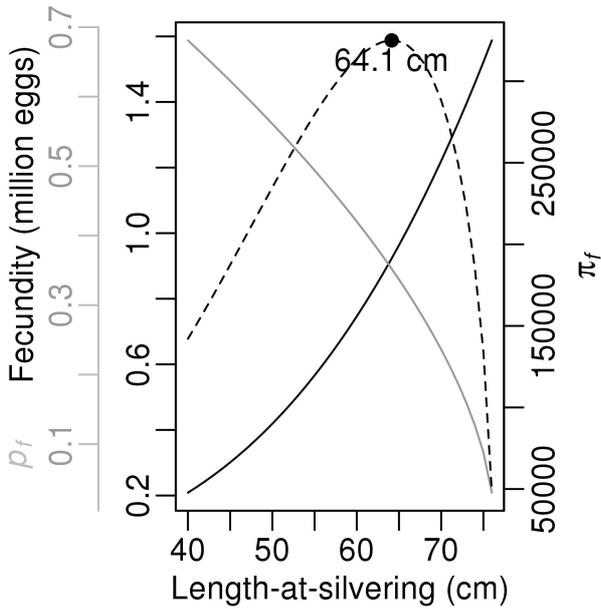
781

782 **Table 2.** Consistency of the model with observed spatial patterns at the river catchment scale and at
 783 the distribution area scale

Patterns				
<i>Distribution area scale</i>				
male-biased sex ratio in the southern part of the distribution area and female-biased sex-ratio in the northern part				yes
male-biased sex-ratio in environment with high density				yes
male-biased sex-ratio in fast growth environment				yes
<i>River catchment scale</i>				
	S0	S1	S2	S3
higher density downstream than upstream	yes	yes	yes	yes
higher length-at-silvering upstream than downstream	no	no	yes	no
male-biased sex-ratio downstream and female-biased sex-ratio upstream	no	no	yes	no

784

785 **Figures**



786

Fig. 1. Illustration of the trade-off between p_f (grey line) and fecundity (black solid line): p_f decreases with length-at-silvering while fecundity increases resulting in a dome-shaped mean expected reproductive output which is considered as a proxy of the fitness π_f (dashed line). The optimal length-at-silvering is 64.1 cm for considered conditions ($M=0.138 \text{ year}^{-1}$ (Dekker 2000) and 0.23 year^{-1} (De Leo and Gatto 1995)).

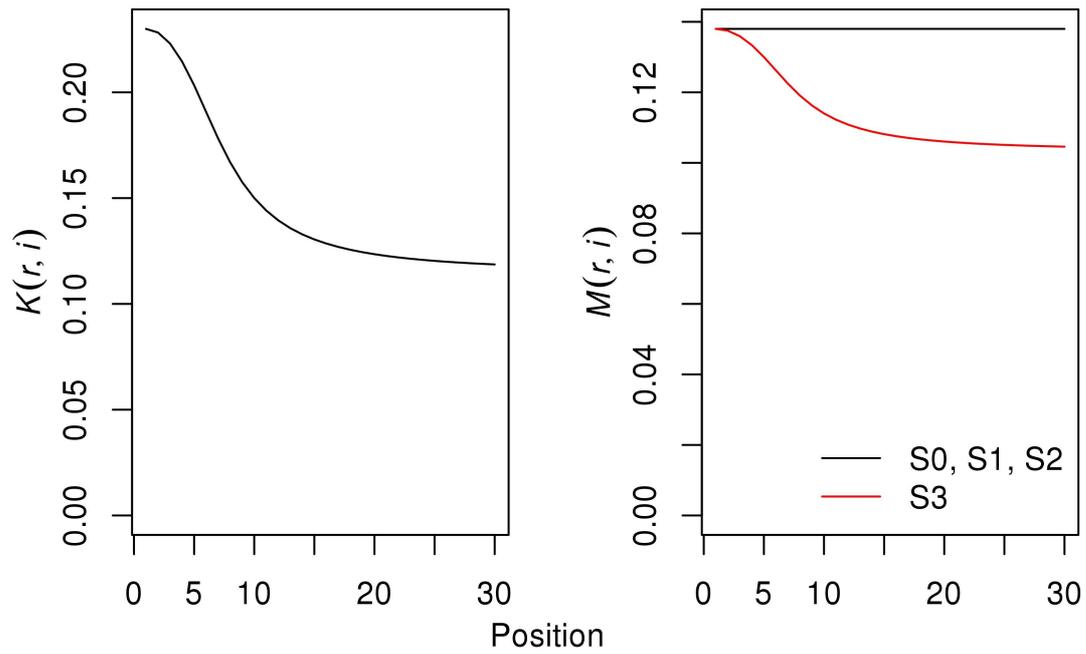


Fig. 2. Instantaneous growth rate (left panel) and instantaneous non density-dependent natural mortality (right panel) corresponding to each set of parameters.

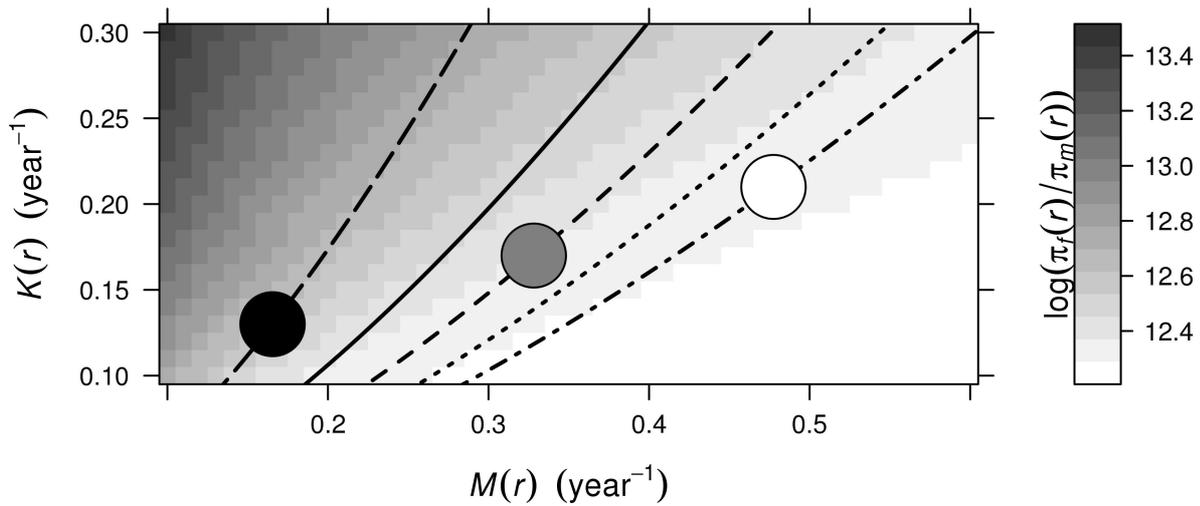


Fig. 3. Fitness ratio $\pi_f(r)/\pi_m(r)$ depending on instantaneous natural mortality rate $M(r)$ and instantaneous growth rate $K(r)$ at the catchment mouth. Dark colours indicate fitness marginal gains for females whereas light colours indicate fitness marginal gains for males. Lines represent the physiologically plausible values of $K(r)$ and $M(r)$ combinations at different temperatures based on Pauly (1980) (5°C longdash, 10°C solid, 15°C dashed, 20°C dotted and 25°C dotdash). Circles indicates putative positions for eels in Scandinavia (black circle), Bay of Biscay (grey circle) and Mediterranean lagoons (white circle)

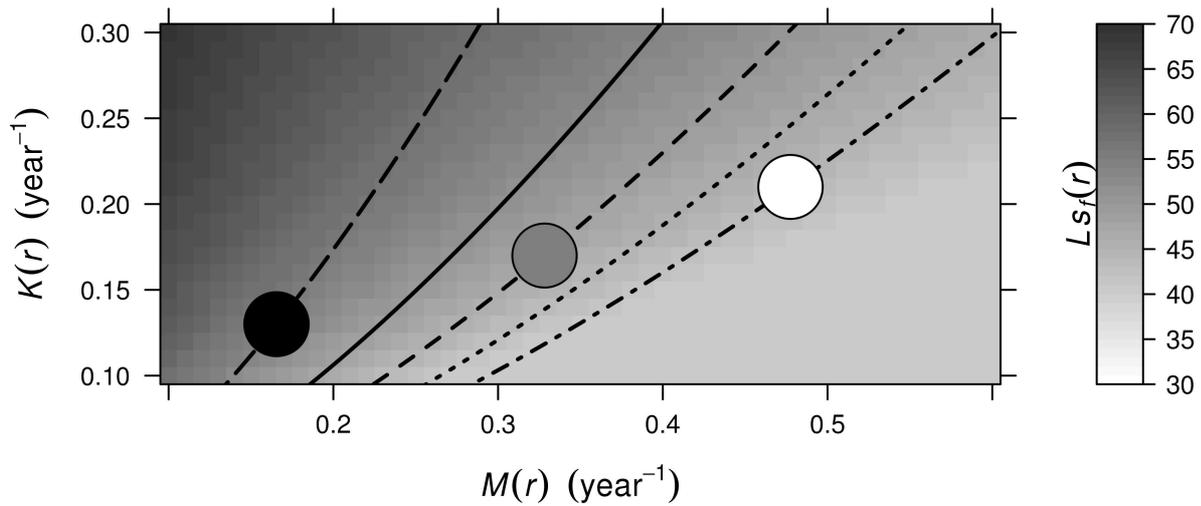


Fig. 4. $L_{sf}(r)$ maximising female fitness as a function of $K(r)$ and $M(r)$. Coloured lines represent the physiologically plausible values of $K(r)$ and $M(r)$ combinations at different temperatures based on Pauly (1980) (5°C longdash, 10°C solid, 15°C dashed, 20°C dotted and 25°C dotdash). Circles indicates putative positions for eels in Scandinavia (black circle), Bay of Biscay (grey circle) and Mediterranean lagoons (white circle).

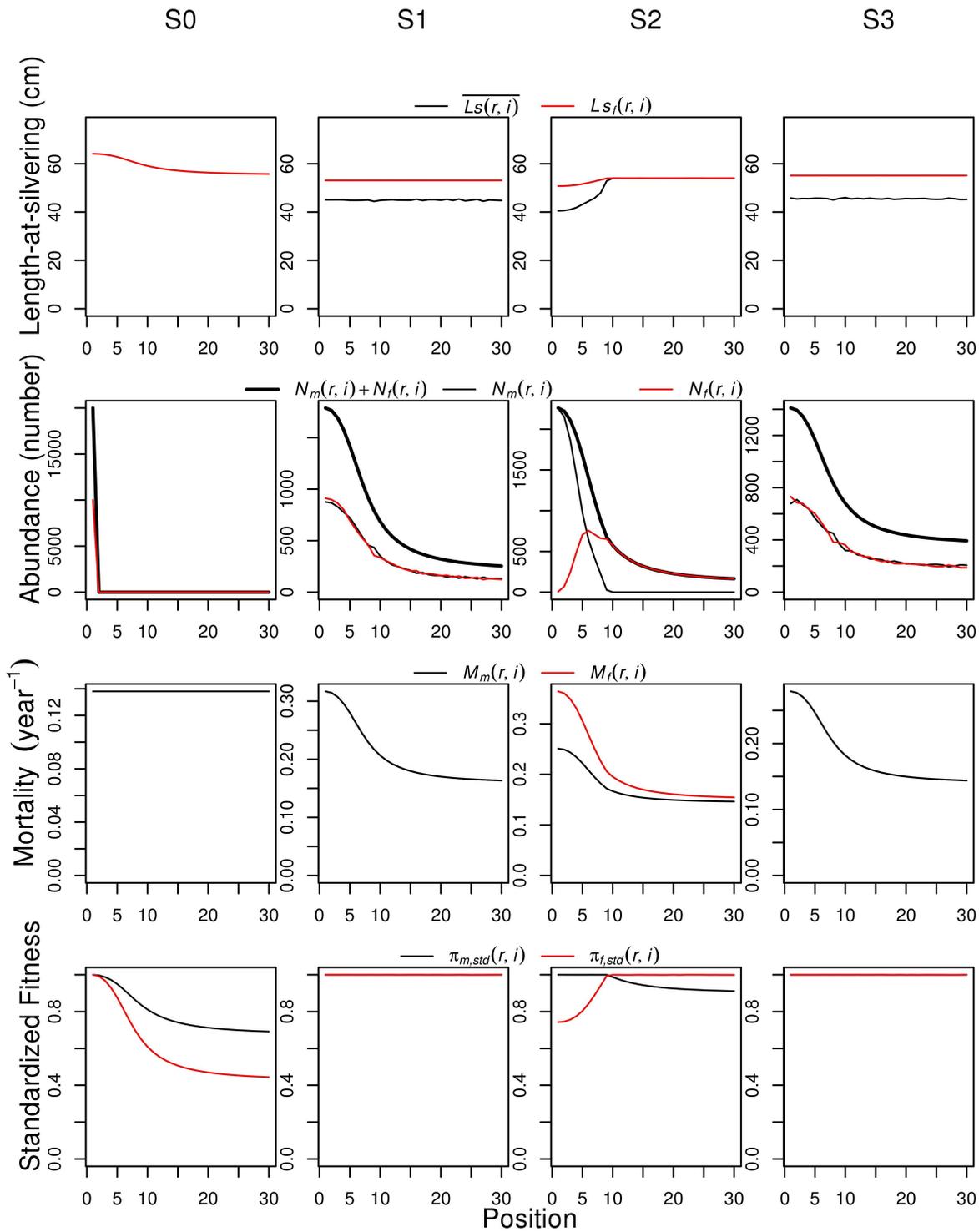


Fig. 5. Length-at-silvering, abundance, natural mortality (including density-dependence), and relative fitness by sex for each set of parameters.