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

Authors:

- Hilaire DROUINEAU (corresponding author)
    - affiliations: Irstea, UR EABX Ecosystèmes aquatiques et changements globaux / Pôle Écohydraulique Onema-INP-Irstea
    - address: 50, avenue de Verdun - 33 612 CESTAS Cedex – FRANCE
    - tel : +33 (0)5 57 89 27 09
    - fax: +33 (0)5 57 89 08 01
    - mail: hilaire.drouineau@irstea.fr
- Christian RIGAUD
    - affiliations: Irstea, UR EABX Ecosystèmes aquatiques et changements globaux / Pôle Écohydraulique Onema-INP-Irstea
    - mail: christian.rigaud@irstea.fr
- Françoise DAVERAT
    - affiliations: Irstea, UR EABX Ecosystèmes aquatiques et changements globaux
    - mail: francoise.daverat@irstea.fr
- Patrick LAMBERT
    - affiliations: Irstea, UR EABX Ecosystèmes aquatiques et changements globaux

- mail: patrick.lambert@irstea.fr

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Abstract

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

Introduction

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

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

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

Concomitantly with this environmental heterogeneity, a large phenotypic diversity is observed at the distribution area and at the river catchment scales. For example, sex-ratio is spatially highly heterogeneous at the distribution area and at the river catchment scale (Vladykov 1966; Helfman et al. 1987; Oliveira et al. 2001). Vladykov (1966) and Helfman et al. (1987) mentioned a female biased sex-ratio in the northern part of the distribution area. Krueger & Oliveria (1999) and Oliveira et al. (2001) argued that sex-ratio variability can also vary a lot within a limited range of latitudes under the influence of local conditions. A large data collection of existing observations carried out by Kettle et al. (2011) for both *A. rostrata* and *anguilla* confirms this latitudinal pattern. Sex-determination for eel is still poorly known but is controlled by environmental factors (Geffroy 2012). Environmentally controlled sex-determination is generally selected by evolution when the environmental factor differentially affects the fitness of males and females (Mayhew 2006). Environmental sex-determination is not rare for fishes, temperature being the main driving factor, though the influence of density or social interactions have also been observed for some species (Devlin and Nagahama 2002). Several factors have been proposed as driving factors for eel sex-determination. Regarding eel density, a male biased sex-ratio is generally observed when eel density is high (Roncarati et al. 1997; Tesch 2003; Han and Tzeng 2006). This has been observed at the catchment scale where males are concentrated in the downstream part of the catchment (Oliveira and Mccleave 2000; Tesch 2003), though this observation may result from a more limited colonisation ability of males. More convincing observations come from catchments where modifications of densities have resulted in modifications of the sex-ratio (Poole et al. 1990; Roncarati et al. 1997; Tesch 2003), and by observations in controlled environment experiments (Colombo and Grandi 1996; Beullens et al. 1997; Holmgren et al. 1997). Growth rate in youngest stages is also suspected to play a role in sex-determination, however results are less obvious. Holmgren (1996) and Holmgren and Mosegaard (1996) observed in controlled experiments that fast growing (especially in weight) young eelspreferentially turn into males. However results were unclear because of concomitant variation in density. More generally, Geffroy (2012) assumed that the global quality of the environment may be the main factor affecting sex-determination.

This issue of sex-determination is of major importance because males and females are supposed to display distinct life tactics (Helfman et al. 1987). The reproduction success of a male does not vary with its body size, consequently males are assumed to follow a time-minimising strategy, leaving continental waters as soon as they have enough energy to migrate to the spawning grounds (Vollestad 1992). This assumption would explain why male silver eels display rather similar weights and sizes (Oliveira 1999)all over the distribution area (Vollestad 1992; Oliveira 1999). Such a size threshold may correspond to the size at which energy stores are sufficient to undergo the transoceanic reproduction migration (Van Den Thillart et al. 2007). By contrast, fecundity and consequently reproduction success of females is mainly influenced by body size. Consequently, females are assumed to follow a size-maximising strategy, adapting their length-at-silvering to local growth and mortality conditions in order to find a trade-off between survival and fecundity.

Latitudinal pattern of female silver eel length is often mentioned with larger females in the northern part of the distribution area (slow growth but lower mortality) than in the southern part (Helfman et al. 1987; Davey and Jellyman 2005; Jessop 2010).

In addition to sex-ratio and length-at-silvering variability, eels also display a large range of tactics in terms of growth and habitat use, some settling in estuarine waters while others move far upstream in river catchments (Tsukamoto et al. 1998; Daverat et al. 2006; Arai and Chino 2012). Growth rate in salted and brackish downstream parts of catchments is significantly higher than in upper parts of the catchments (Helfman et al. 1984; Melià et al. 2006b; Daverat et al. 2012). A lower mortality in upper parts of river catchments is sometimes assumed to balance the associated lower growth. Consequently, upstream habitats with more limited intraspecific competition may still be favourable especially for females which can adapt their length-at-silvering to balance lower growth rates. Edeline (2007), for example, assumed that catchment colonisation and tactics in habitat use by eels correspond to a conditional evolutionary stable strategy (Gardner et al. 1987). A conditional evolution stable strategy is a generalisation of evolutionary stable strategy in which an individual can express different phenotypes (the tactics of the conditional strategy) depending on its environmental, social and physiological status (cueing trait). According to Edeline (2007), individuals with high energetic status would migrate upstream to avoid competition and then settle (*i.e.* change tactics) when their energetic status becomes too low or when the benefits do not outweigh the costs of migration. This assumption is challenged by Cairns et al. (2009) who did not observe mortality differences large enough to balance variations in growth between different habitats. Cairns et al. (2009) concludes that the decrease of natural mortality (competition) would not outweigh the cost of migration and the decrease in growth rate.

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

Material and methods

Model rationales and definition of the spatial patterns

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

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

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

- at the distribution area scale:
    1. male-biased sex ratio in the southern part of the distribution area and female-biased sex-ratio in the northern part
    2. male-biased sex-ratio in environment with high density
    3. male-biased sex-ratio in fast growth environment
- at the river catchment scale:
    4. higher density downstream than upstream
    5. higher length-at-silvering upstream than downstream
    6. male-biased sex-ratio downstream and female-biased sex-ratio upstream

Distribution area scale: sex-determination and length-at-silvering as adaptive mechanisms to a wide variety of spatially structured environmental conditions

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

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

We assume that female fitness may be approximated by the product of the expected number of eggs at length-at-silvering and the probability to survive until this length-at-silvering $Ls_f(r)$, *i.e.* the mean expected number of eggs produced by each female. Following De Leo and Gatto (1995), we assume that growth is well represented by a Von Bertalanffy growth model: $L(t,r) = L_\infty \cdot \left(1 - e^{-K(r)(t-t_0)}\right)$ with $L(t,r)$ the length at time *t* of a fish, L_∞ the asymptotic length and $K(r)$ the Brody growth coefficient.

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

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

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

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

and consequently:

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

Von Bertalanffy parameters $K(r)$ and L_∞ are generally largely correlated (Pilling et al. 2002; Siegfried and Sansó 2006; Eveson et al. 2007). Regarding eels, Melià et al. (2006a) found a strong linear correlation between the two parameters estimates. Consequently following de Pontual et al. (2006) and Drouineau et al. (2010, 2012) we assume that L_∞ is fixed and that only $K(r)$ varies. This assumption is also consistent with the Dynamic Energy Budget theory in which L_∞ is not affected by temperature variations (Kooijman 2000).

From equation 3, we can calculate the proportion of individuals that survive till length-at-silvering $p_f(r)$:

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

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

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

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

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

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

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

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 year^{-1}. For each case, the optimal female length-at-silvering $Ls_f(r)$ is also estimated. This produces a diagram of ratio of fitness. A large ratio indicates a marginal fitness gain for females while a smaller ratio indicates a marginal fitness gain for males. This also produces a diagram of females length-at-silvering, as a function of *K(r)* and *M(r)*. We do not consider any feedback in sex-determination: the expected fitness of choosing male or female does not depend on how many other eels choose which sex.

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

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

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

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

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

A slightly more complex version of the model is developed to be applied to a theoretical river catchment *r*. In this second step, we consider that sex-determination has already occurred, and we focus on the selection of growth habitat by $N_m(r)$ males and $N_f(r)$ females in the river catchment.

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

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

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

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

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

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

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

We denote $M_m(r,i)$ and $M_f(r,i)$ the instantaneous natural mortality rates for males and females. For simplicity, following Lockwood (1980), we assume that natural mortality increases linearly with density (Hixon and Jones 2005)though logarithmic relationship may also been assumed (Myers and Cadigan 1993; Fromentin et al. 2001) and provide similar results:

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

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

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 parameters that control the intensity of density-dependence.

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

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

14) $\pi_m(r,i) = \left(\dfrac{L_\infty - Lg}{L_\infty - Ls_m}\right)^{\frac{-M_m(r,i)}{K(r,i)}}$

$Ls_f(r,i)$ is estimated as the length maximising $\pi_f(r,i)$ (see Fig .1).

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

15) $$\overline{L_s(r,i)} = \frac{N_m(r,i) \cdot Ls_m \cdot \pi_m(r,i) + N_f(r,i) \cdot Ls_f(r,i) \cdot \dfrac{\pi_f(r,i)}{a_1 + a \cdot Ls_f(r,i)^b}}{N_f(r,i) \cdot \dfrac{\pi_f(r,i)}{a_1 + a \cdot Ls_f(r,i)^b} + N_m(r,i) \cdot \pi_m(r,i)}$$

and standardised fitnesses along the riverside as:

16) $\pi_{m,std}(r,i) = \dfrac{\pi_m(r,i)}{\max\limits_j\left(\pi_m(r,j)\right)}$

17) $\pi_{f,std}(r,i) = \dfrac{\pi_f(r,i)}{\max\limits_j\left(\pi_f(r,j)\right)}$

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

```
• For $k$ from 1 to max($N_m$, $N_f$)
    ○ if $k<=N_m$
        ▪ $k$-th male goes in cell $i$ having $\pi_{m,std}(i)=1$ (maximum fitness)
    ○ if $k<=N_f$
        ▪ k-th female goes in cell $i$ having $\pi_{f,std}(i)=1$ (maximum fitness)
```

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

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

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

Results

Distribution area scale: sex-determination and length-at-silvering as adaptive mechanisms to a wide variety of spatially structured environmental conditions

The ratio of fitness for various conditions of *K(x)* and *M(x)* (Fig. 3) demonstrates that high mortality tends to favour males as compared to females fitness. If we assume that high density increases mortality because of intra-specific competition, this may explain why males-biased sex-ratios are observed in high density environments.

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

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

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

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

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

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

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

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

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

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

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

Discussion

The aim of this paper was to explore if few assumptions based on evolutionary concepts may explain the spatial patterns observed in the 3 temperate eels in term of sex-ratio, length-at-silvering and habitat distribution, both at the distribution area scale and at the river catchment scale. Six spatial patterns were listed and the model mimics all of them at both distribution area and river catchment scales (Table 2). This does not demonstrate that our assumptions are correct, however, it suggests that sex-determination, length-at-silvering and growth habitat selection may be interpreted as adaptive plasticity selected by evolution to respond to the highly variable and spatially structured environmental conditions encountered by temperate eels. An extension to tropical eels would be interesting in the future.

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

Within a river catchment, Edeline (2007) proposed that colonisation may correspond to a conditional evolutionary stable strategy, assuming that lower growth rates upstream were compensated by lower mortality rates. This point of view was challenged by Cairns et al. (2009) who did not observe large variations of natural mortality rates in the field. However, our model suggests that, despite these limited variations of natural mortality, the colonisation and the choice of a growth habitat may still correspond to fitness maximisation strategy. If we assume that females are more sensitive to density-dependent mortality than males, males are concentrated downstream where Cairns et al. (2009) made their observations, a zone where the model predicts that their natural mortality rate is rather constant (Fig. 5, scenario S2). It is well known than density-dependence plays a major role in eel dynamics (De Leo and Gatto 1996), especially in migratory behaviour (Geffroy and Bardonnet 2012). Our assumption of distinct density-dependent sensitivity between males and females, i.e. females suffering a higher density-dependant natural mortality rate than males, is plausible for two main reasons: First, Holmgren et al. (1997) observed that males in young stages have a faster growth in weight, with higher condition indices, and so they may become dominant with respect to females. Secondly, we may assume that males may have evolved to be more adapted to high-density since males biased sex-ratios are observed in high density environments. Gender difference in sensitivity to intraspecific competition has already been observed for insects (Gibbs et al. 2004; Tsurim et al. 2013) and birds (Clobert et al. 1988). For example, Gibbs et al. (2004) demonstrated in controlled experiments that females of a butterfly were more adversely affected by high density than males. In the model, we assumed that density-dependence affects natural mortality because of negative effects of intra-cohort and inter- cohort densities on mortality have been observed in many studies (Vollestad and Jonsson 1988; De Leo and Gatto 1996; Lobón-Cerviá and Iglesias 2008; Bevacqua et al. 2011a, 2011b).

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

EvEel is based on few evolutionary assumptions: (i) sex-determination is an adaptive response to favour sex with highest fitness in a given environment (assumption consistent with what is observed on many species having an environmental sex-determination (Mayhew 2006)), (ii) since females adopt an size-maximising strategy, fitness may be approximated by the product of fecundity and survival rate, (iii) since males adopt a time-minimising strategy, their fitness may be approximated by their survival rate, (iv) females are more sensitive to intra-specific competition than males and (v) colonisation and growth habitat selection in a catchment is based on the maximisation of the fitness. Only five assumptions are enough to mimic the main spatial pattern of sex-ratios, length-at-silvering and distribution at the distribution area scale and at the river catchment scale. However, mimicking patterns does not validate (or invalidate) those assumptions and controlled experiments would be required to investigate their reliability.

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

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

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

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

This first version of EvEel is simple. It does not model population dynamics and assume that fishes are omniscient (perfect knowledge of the entire river catchment) and omnipotent (they are able to migrate to any part of the catchment without any delay). Moreover, it assumes that sex-determination and choice of growth habitat are two successive events that occur very early in the growth phase in continental waters. The reality is more complex: sex-determination occurs between 20 cm and 30 cm and consequently, colonisation has already started. Moreover, it has been demonstrated that some eels that settle upstream can then move downstream to more favourable habitats when density decreases (Daverat et al. 2006). The model simplicity explains the rough contrasts in the spatial distribution of individuals within a catchment and in the distribution of length-at-silvering. It would be interesting in the future to incorporate population dynamics and to apply the model to a real river catchment. Basin model proposed by MacCall (1990) and diffusion-advection models (Mullen 1989; Bertignac et al. 1998) would be relevant solution to model eel spatial distribution. Diffusion-advection model would allow to incorporate dynamics in EvEel. These types of models are all based on theoretical ecological concepts (fitness) which are often interesting to explore assumptions that may be validated in the future (Willis 2011). These models would probably result in smoother transitions between males and females and in length-at-silvering because of diffusion. It would be very interesting to compare the results of those models to the outputs of mechanistic or statistical models that have been used to model eels spatial distribution (Ibbotson et al. 2002; Lambert et al. 2011; Jouanin et al. 2012).

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

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

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

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Tables

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			
a_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

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

Patterns				
Distribution area scale				
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			
River catchment scale	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

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doi : 10.1139/cjfas-2014-0090

Figures

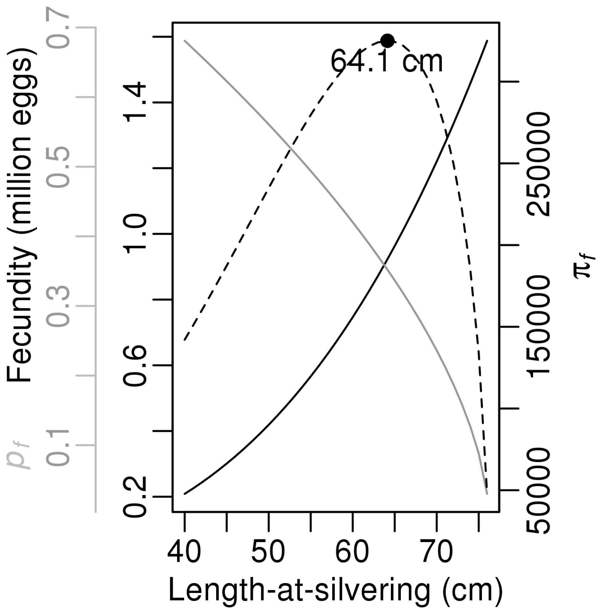

Fig. 1. Illustration of the trade-off between p_f (grey line) and fecundity (black solid line): p_f decreases with length-at-silvering while fecundity increases resulting in a dome-shaped mean expected reproductive output which is considered as a proxy of the fitness π_f (dashed line). The optimal length-at-silvering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

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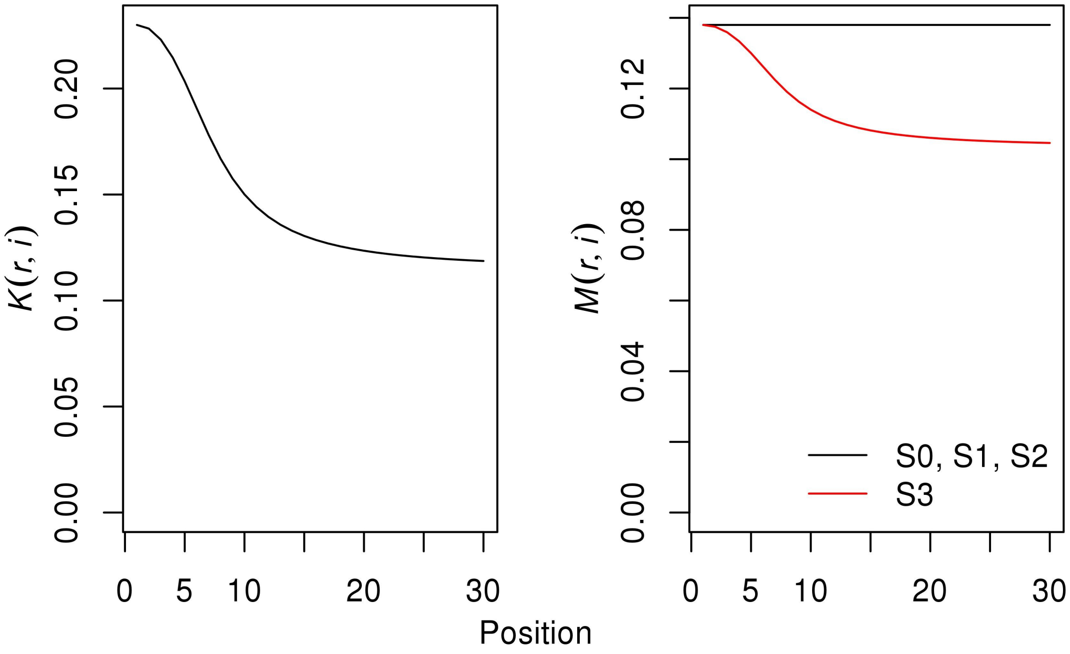

Fig. 2. Instantaneous growth rate (left panel) and instantaneous non density-dependent natural mortality (right panel) corresponding to each set of parameters.

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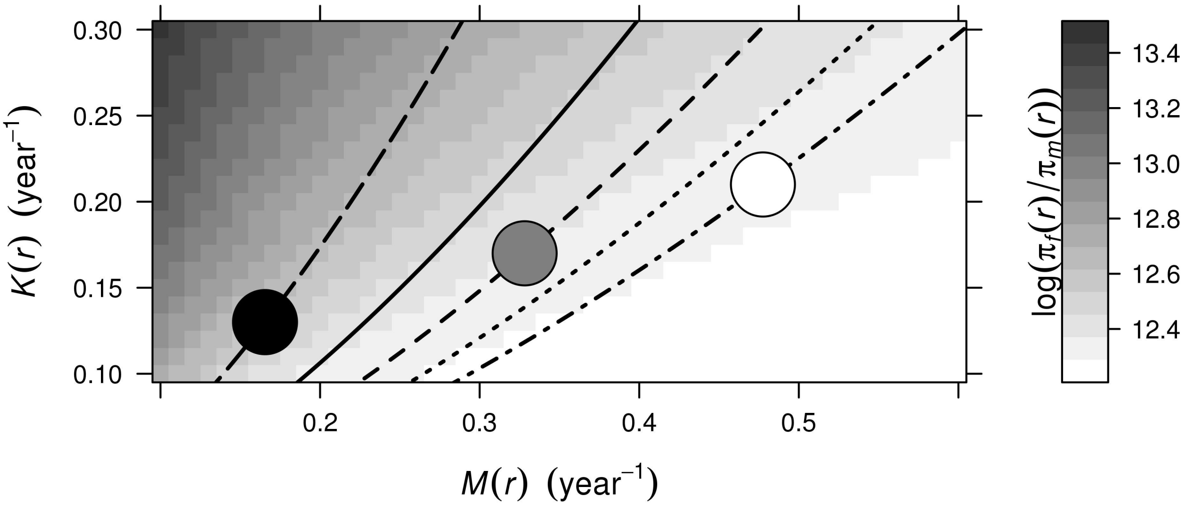

Fig. 3. Fitness ratio $\pi_f(r)/\pi_m(r)$ depending on instantaneous natural mortality rate *M(r)* and instantaneous growth rate *K(r)* at the catchment mouth. Dark colours indicate fitness marginal gains for females whereas light colours indicate fitness marginal gains for males. Lines represent the 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)

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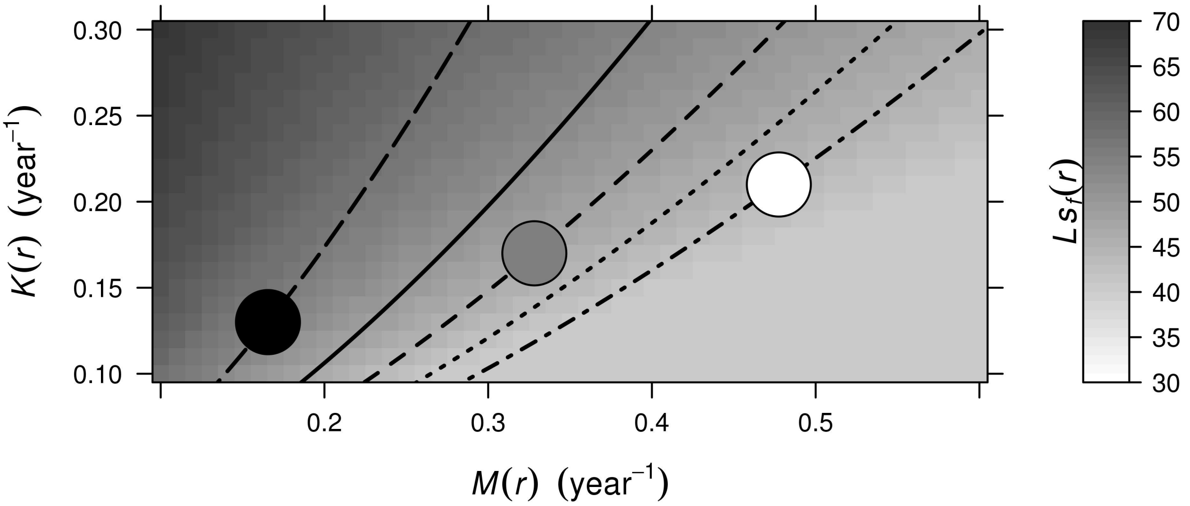

Fig. 4. *$Ls_f(r)$* maximising female fitness as a function of *K(r)* and *M(r)*. Coloured lines represent the physiologically plausible values of *K(r)* and *M(r)* combinations at different temperatures based on Pauly (1980) (5°C longdash, 10°C solid, 15°C dashed, 20°C dotted and 25°C dotdash). Circles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

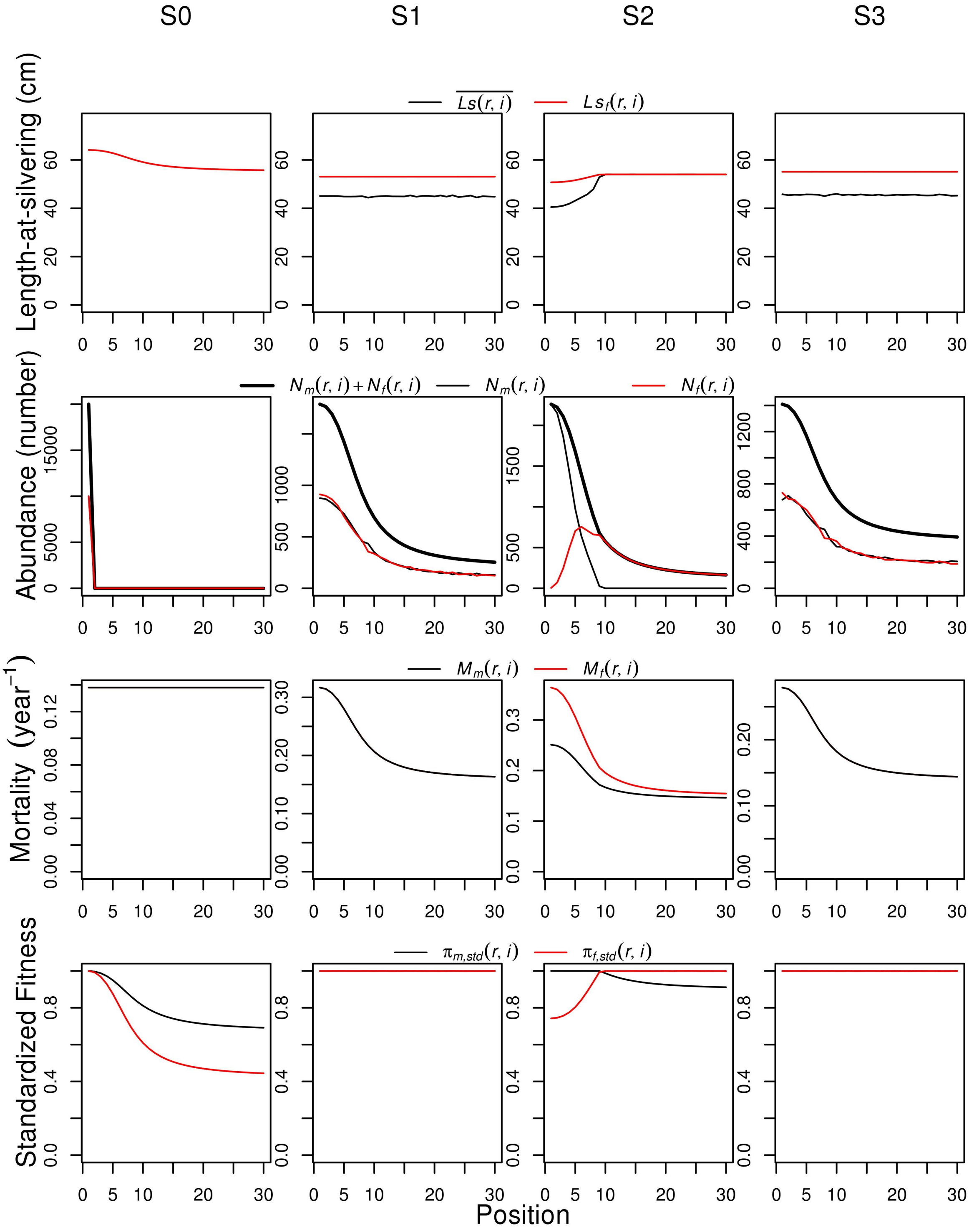

Fig. 5. Length-at-silvering, abundance, natural morality (including density-dependence), and relative fitness by sex for each set of parameters.