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Modeling fish growth and reproduction in the context of the Dynamic Energy Budget theory to predict environmental impact on anchovy spawning duration

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Abstract:

Spawning location and timing are critical for understanding fish larval survival. The impact of a changing environment on spawning patterns is, however, poorly understood. A novel approach is to consider the impact of the environment on individual life histories and subsequent spawnings. In the present work, we extend the Dynamic Energy Budget (DEB) theory to investigate how environment variability impacts the spawning timing and duration of a multiple-batch spawning species. The model is successfully applied to reproduce the growth and reproduction of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. The model captures realistically the start and ending of the spawning season, including the timing of the spawning events, and the change in egg number per batch. Using a realistic seasonal forcing of temperature and food availability derived from a bio-physical model, our simulation results show that two thirds of the total spawned mass already accumulates before the start of the spawning season and that the condition factor increases with body length. These simulation results are in accordance with previous estimations and observations on growth and reproduction of anchovy. Furthermore, we show how individuals of equal length can differ in reproductive performance according to the environmental conditions they encounter prior to the spawning season. Hatch date turns out to be key for fecundity at age-1 as it partly controls the ability to build up reserves allocated to reproduction. We suggest the model can be used to realistically predict spawning in spatially and temporally varying environments and provide initial conditions for bio-physical models used to predict larval survival.

Keywords: DEB Theory; Reproductive Biology; Multiple-Batch Spawning;

Condition factor, Environmental conditions, Starvation, *Engraulis encrasicolus*, Bay of Biscay

1 Introduction

The variability of the spawning success and the relationship between spawning and recruitment are among the least understood aspects of the dynamics of fish populations. Bio-physical studies have largely contributed to improve our understanding of the factors that potentially control recruitment success (Werner *et al.*, 2001; Gallego *et al.*, 2007) by showing in particular how spawning location and timing influence larval transport (Huret *et al.*, 2007a) and how the inter-annual variability of the environmental conditions encountered by the larvae determines recruitment variability (Allain *et al.*, 2007b). However, spawning location and timing depend on the environmental conditions encountered by the adults (Slotte, 2001) and therefore are difficult to predict and to take into account in bio-physical studies.

James *et al.* (2003) showed statistically that the longer the spawning season for a population, the higher the probability to find suitable conditions for larval survival, and hence the higher the recruitment level. In the case of multiple-batch spawners, larger individuals spawn earlier and longer than small individuals (Parrish *et al.*, 1986; Millán, 1999). Therefore, the study of the length structure of the population is of importance to understand the variability of the individual spawning patterns.

The size of an individual remains however only a proxy for its spawning duration; for multiple-batch spawners, it is the amount of reserves available for reproduction that determines the number of egg batches an individual will spawn. To evaluate this amount is particularly challenging for multiple-batch spawners with indeterminate fecundity such as small pelagic species (e.g. Le Clus, 1979; Hunter and Leong, 1981; Motos, 1996). These species develop new batches of eggs during the spawning season ; fecundity and number of egg batches per season cannot be assessed prior to the spawning season unlike for species with determinate fecundity such as cod (Kjesbu *et al.*, 1998) and herring (Kurita *et al.*, 2003). Northern anchovy, *Engraulis mordax* (Hunter and Leong, 1981) and Peruvian anchovy, *E. ringens* (Cubillos *et al.*, 2001) acquire part of the energy reserves for reproduction few months before the spawning season, during the productive period. However, to predict the impact of the environment on the amount available at the time of spawning remains a

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challenge. The impact of environmental conditions on the reserve available for reproduction of an individual fish has been recently studied in a mechanistic way for cod (Jørgensen and Fiksen, 2006) and perch (van de Wolfshaar *et al.*, 2008), which are determinate fecundity species. To our knowledge, such model for small pelagic species has however never been developed.

In the present work, we aimed to predict the spawning duration and the number of spawning events of an individual fish with indeterminate fecundity as a function of the environmental conditions it encounters. To this end, we applied the Dynamic Energy Budget (DEB) theory (Kooijman, 2000; Nisbet *et al.*, 2000) to model individual growth and reproduction, with a focus on the reserves available for reproduction and the batch fecundity at the time of spawning. We extended the standard DEB model with a module for batch preparation based on the recent evaluation of the cost of an egg by Kooijman (2009). DEB theory has been successfully applied to a large range of marine taxa (e.g. van der Veer *et al.*, 2001; Pouvreau *et al.*, 2006; van der Veer *et al.*, 2006; Maury *et al.*, 2007; Bodiguel *et al.*, 2009). It makes explicit use of mass and energy balances and covers the full life cycle of an individual (Kooijman, 2000). This theory provides a conceptual and quantitative framework to quantify jointly growth and reproduction of an individual given seasonally varying food and temperature conditions.

We applied the model to the Bay of Biscay anchovy (*E. encrasicolus*) that can spawn twenty times per season on average (Motos, 1996). Allain *et al.* (2003, 2007a,b) studied larval transport in the Bay of Biscay with a particle-tracking model and showed that larval growth and survival could be driven by the environmental conditions encountered by larvae along their trajectories. Although the average spawning pattern of the Bay of Biscay anchovy is well described (Motos *et al.*, 1996; Motos, 1996), inter-annual variations in spawning location and timing, i.e. the initial conditions of the larval drift model, remain unknown. Hence, the development of a mechanistic approach to study the factors that potentially generate inter-annual variations in spawning pattern is critical but remains challenging. We based our approach on the development of a model that reproduces known patterns of growth and reproduction in fish in general and for our case study in a realistic seasonal environment. Then we assessed the ability of the model to reproduce the observed variability of length and condition among individuals to be able to analyze further the factors that generated different spawning patterns in our simulations.

The standard DEB model as well as the features of the reproduction module that was implemented are first summarized. We then present the results for three different simulations. The first simulation was designed to validate the ability of the model to reproduce the average growth and reproduction patterns of an individual anchovy. The second simulation was designed to validate the predictions of the model under prolonged starvation conditions. The third simulation aimed to quantify the impact of variable temperature and food conditions on the spawning pattern of a given population. We both studied an inter-annual and an inter-individual variability in the temperature and food conditions. We finally discuss the consistency of our simulation results with observations on fish species with both determinate and indeterminate fecundity and observations on our case study.

2 Model structure

2.1 Standard DEB model

The standard model of the DEB theory (Kooijman, 2000, 2001; Nisbet *et al.*, 2000; van der Meer, 2006) describes the rate at which the organism assimilates and utilizes energy for maintenance, growth and reproduction as a function of its state and its environment (i.e. food density and temperature) (Fig. 1). The standard DEB model deals with one type of food, one type of reserve and one type of structure for an isomorph, i.e. an individual that does not change in shape during growth.

[Fig. 1 about here.]

An individual is described by three state variables: the structural volume V (cm^3), the reserve energy E (J), and the reproduction energy buffer E_R (J). Equations of the model are given in Appendix A. Reserve is continuously used and replenished, while structural material is continuously degraded and reconstructed as a result of somatic maintenance (Kooijman, 2000). Assimilation is taken to be proportional to the surface area of the structural volume and maintenance is taken to be proportional to structural volume. We further assume that reserve hardly contributes to physical length (i.e. the length we measured). So physical length L (cm) relates to volumetric length as follows: $L_V = \delta L$, with δ the shape coefficient and $L_V = V^{1/3}$ (cm). The rate parameters depend on temperature (see Eq. 4 in Appendix A), but are constant otherwise. The transitions between the embryo and the juvenile stages, and between the juvenile and the adult stages occur at fixed lengths L_{Vb} and L_{Vp}, where the subscripts b and p refer to birth and puberty respectively. At birth, the individual starts feeding; at puberty, allocation to maturation is redirected to reproduction.

2.2 *Specific handling rules of the reproduction buffer for multiple-batch spawners*

The model was original in two ways compared to the standard DEB model (Kooijman, 2000): (1) the reproduction buffer could be used as a source of energy during starvation to pay maintenance costs and (2) the handling rules for the reproduction buffer were specified to reproduce a multiple-batch spawning pattern with indeterminate fecundity.

The assumptions for the use of the reproduction buffer are detailed in Table 1 and the equation is given in Appendix A (Eq. 3). Covering maintenance requirements from the reproduction buffer in limiting conditions has been previously applied by Pouvreau *et al.* (2006) to oyster (*Crassostrea gigas*). In the present study, it was a determinant component as it regulated the number of batches an individual could release during the spawning season. Use of the reserves allocated to reproduction to cover maintenance costs could typically occur during the bleak season prior to the start of the spawning season, but it could also occur during the spawning season. In this case, it was related to atresia, i.e. the resorption of vitellogenic oocytes in the gonads (Hunter and Macewicz, 1985).

[Table 1 about here.]

We developed simple rules to convert the energy stored in the reproduction buffer into eggs spawned in different batches during the spawning season (see equations in Appendix B). We used temperature as an external trigger to start batch preparation. We did not consider mechanisms for egg maturation but we aimed at reproducing a realistic batch spawning frequency during the spawning season. At spawning, the amount of energy spawned by the female depended on its structural volume. The energy content per egg, and hence the number of eggs per batch, depended on the state of the female. A female with a large reserve density $[E] = E/V$ (J cm^3) would produce eggs with a large amount of reserves. Therefore, two females of the same length but different reserve density will spawn the same amount of energy but the female with a larger reserve density will produce larger but fewer eggs. To end the spawning season, an internal trigger was defined: when reserves available for reproduction were depleted, the last batch was spawned and spawning ceased until the next season.

3 Application to the Bay of Biscay anchovy

The European anchovy *E. encrasicolus* is a small pelagic species with a short life span (4 years). In the Bay of Biscay area, adults spawn between March and

August with a peak in May-June (Motos *et al.*, 1996) and rebuilt their reserves in late summer - autumn. Individuals grow fast during their first year and are mature after their first winter (Motos, 1996). The bulk of the population used to be composed of these age-1 individuals before the sharp recruitment decline the recent years (ICES, 2006). The small age-1 individuals spawn during the peak of the season, in May-June, while large individuals start spawning earlier in spring. Motos (1996) estimated that on average, an individual can spawn 20 times per season.

3.1 Data

Data on spawning adults were collected during Ifremer's spring pelagic acoustic surveys PELGAS (Petitgas *et al.*, 2003), which are yearly undertaken in May during the peak of the anchovy spawning season. The main objective of these surveys is to assess the biomass of small pelagic species in the Bay of Biscay. Individual data on length, weight and age are available for the period 2000-2005. Here, we considered the growth of the 2000 cohort (Pecquerie, 2007). The juvenile data were collected during Ifremer's autumn pelagic acoustic surveys for juveniles, which were undertaken in 1999 and 2003 (JUVESU and JUVAGA, Allain *et al.*, 2003; Petitgas *et al.*, 2004). These data were used to calculate the average length- and weight-at age of an adult and the average weight-length relationship for a juvenile. This information, in turn, was used to estimate parameter values (see Parameter estimation section).

3.2 Links between observations and state variables

To calibrate and validate the model, we defined variables that can be compared with available data such as the weight and the condition factor of individual fish. These quantities contain information relative to both growth and reproduction that we aimed to disentangle and interpret. In particular, we aimed to study the link between the condition factor and the energy available for reproduction in our simulations. No data are presently available on the number of egg batches an individual anchovy spawns in a given environment; we studied the possibility to use the condition factor as a proxy for this number.

Weight W (g) has contributions from the structure (W_V), the reserve (W_E) and the reproduction buffer (W_{E_R}). Thus, weight is not an explanatory variable in the standard DEB model, but is useful to calibrate and/or validate the model (Kooijman *et al.*, 2008). It is defined as follows:

$$W = W_V + W_E + W_{E_R} \tag{1}$$

$$= d_V V + \frac{E + E_R}{\rho_E} \tag{2}$$

where V (cm^3) is the structural volume, E (J) the reserve energy, E_R (J) the reproduction energy buffer, d_V the density of the structural volume (g cm^{-3}) and ρ_E the energy content of one gram of reserve (J g^{-1}). In the model, the reserve and the reproduction buffer have the same composition and therefore the same energy content.

We also defined the condition factor K as the ratio of the total weight W and the weight of the structure W_V:

$$K = \frac{W}{d_V V} = 1 + \frac{E + E_R}{d_V \rho_E V} \tag{3}$$

In the DEB context, the condition factor K indicates the state of the individual in terms of reserve and reserve allocated to reproduction per gram of structure. We studied the weight-length relationship and the relationship between length and the condition factor K for the Bay of Biscay anchovy in the data and compared them with our simulation results in variable environmental conditions (see the Simulation design section).

3.3 Forcing variables: temperature and food density

The annual temperature cycle is obtained from the outputs of the 3D hydrodynamical model MARS3D applied to the French continental shelf (0-200m isobaths, and from the Spanish coast to 48°N) over the period 1999-2003. Details on MARS3D can be found in Planque *et al.* (2004) and Lazure and Dumas (2008). We assumed that juveniles live in the 0-20 m layer and experience the average temperature of this layer until they recruit to the adult population (Petitgas *et al.*, 2004). Adults are then supposed to experience the average temperature of the water column; anchovy forms schools close to the bottom during day time and disperses at surface during night time (Massé, 1996).

The average annual cycle of primary production was given by a biogeochemical model coupled to MARS3D (Loyer, 2001; Huret *et al.*, 2007b). Zooplankton is the main diet of the Bay of Biscay anchovy (Plounevez and Champalbert, 1999). We used the primary production as a proxy for zooplankton biomass (e.g. Ware and Thomson, 2005).

We fitted a Fourier series to the outputs of the biogeochemical model to have simple analytical functions of the forcing variables (temperature, surface temperature and food density). This allowed a substantial reduction of the computation time during the parameter estimation procedure.

3.4 Parameter estimation

In a context of little information on the Bay of Biscay anchovy physiology, we scaled the reserve and the reproduction buffer to remove the 'energy' dimension (see Eqs 1 to 3, Appendix A). This scaling procedure reduced the number of degrees of freedom for the parameter estimation (Kooijman *et al.*, 2008).

Anchovy was assumed to be isomorphic. We obtained an approximate value of the shape coefficient by fitting a weight-length relationship of the type $W = (\delta L)^3$ to the juvenile data. We neglected the contribution of the reserve to the total weight and considered that juveniles have no reserve available for reproduction ($E_R = 0$). We found the shape coefficient equal to 0.172 ($n = 148$, $p < 0.001$). The (physical) length at puberty was 9 cm, which corresponded to the smallest fish caught with active gonads during the spring surveys. Hence, L_{Vp} the (volumetric) length at puberty was $9 \times 0.172 = 1.548\,\text{cm}$.

We used the Arrhenius temperature, T_A (K), to express the effects of temperature on biological rates, and we assumed all rates were affected in the same way (Kooijman, 2000). Regner (1996) obtained the following relationship between egg development time D (d) and temperature T (K) for *E. encrasicolus*: $D = 1788.42(T - 273)^{-2.29}$. When plotting $\ln(1/D)$ against $1/T$, we obtained the value of $T_A = 9800$ K, the slope of the linear regression ($n = 14$, $r^2 = 0.99$) (see Eq. 4 and Kooijman, 2000, pp.53–54).

Motos *et al.* (1996) reported that Bay of Biscay anchovy mainly spawned when sea surface temperature ranged between 14 and 18°C, but spawning could occur at 13°C (Irigoien *et al.*, 2007). The temperature threshold T_R to start batch preparation was set at 13°C (= 286 K) which corresponded to mid-April for the upper 20 m using MARS3D outputs.

To estimate the other model parameters such as the saturation constant X_K, the energy conductance v, the somatic maintenance rate coefficient k_M, the investment ratio g, the fraction of mobilized reserve allocated to growth and maintenance κ, the scaled energy density of one batch $[U_B]$ and the scaled energy content of the reserve $\{p_{Am}\}/\rho_E$, we used a minimization algorithm with a defined simulation setting. We used a Nelder-Mead method implemented in the Matlab routine '`nmregr`' of the DEBtool software (Kooijman, 2008). This routine minimized the weighted sum of squares deviation between model predictions and observations.

We compared model predictions to the following observations: (1) length-at-age and (2) weight-at-length in spring for adults, (3) an average number of batches per individual N_B equal to 20 batches per season (Motos, 1996), (4) a relative batch fecundity F_V of 600 eggs/cm^3 (after Motos, 1996) and (5) a maximum length of 26 cm (Pecquerie, 2007). Parameter estimates are given in Table 2.

[Table 2 about here.]

Model predictions were obtained by running the model for an individual hatched on June 1st which lived until the end of the spawning season at age 3. This individual experienced average annual environmental conditions (Figs. 2a and b). Initial conditions at time t_0 were set at metamorphosis at the age of 65 days (Ré, 1996). The (physical) length at metamorphosis $L(t_0) = L_j$, where subscript j refers to metamorphosis, was 4 cm ($L_V(t_0) = 0.688$ cm). The scaled reserve density $e(t_0) = e_j = [E_j]/[E_m]$ with $[E_j]$ the reserve density at metamorphosis (J cm^{-3}) and $[E_m]$ the maximum reserve density (J cm^{-3}) (see Eq. 1, Appendix A) was equal to the scaled functional response $f(t_0)$. The model was however not sensitive to the initial condition for e_j (not shown). The reproduction buffer $U_R(t_0)$ was empty as the individual was a juvenile.

3.5 Simulation design

We designed three simulations to study the properties of the model under different environmental scenarios. Model properties were validated using an average annual environmental cycle (Simulation 1) and under starving conditions (Simulation 2). We then evaluated the impact of different environmental conditions before the spawning season on individuals that have the same length at the beginning of the spawning season (Simulation 3).

3.5.1 Simulation 1: Effect of hatching dates on growth and reproduction patterns in a seasonal environment

The objectives were twofold: (i) evaluate the impact of hatching dates on the spawning pattern of the individuals the following year and (ii) validate the model by comparing the variability in the model outputs with the variability of the observed values. We compared results for the individual hatched during the peak of the spawning season (June 1st) - that we used to calibrate the model parameters - with the results for two individuals that lived in the same environment but that hatched early (April 1st) and late (August 1st) in the spawning season.

The temperature and food conditions for the simulation are given in Figs. 2a and b. Food and temperature varied seasonally but there was no inter-annual variation. The three individuals were juveniles at the beginning of the simulation with the same initial conditions: $L(t_0) = 4\,\mathrm{cm}$, $e(t_0) = f(t_0)$ at the beginning of the simulation and $U_R(t_0) = 0\,\mathrm{cm}^2\,\mathrm{d}$. We evaluated growth in length and weight for the three individuals that we compared to the length- and weight-at-age observed spring (see Data section). We also examined the changes of the condition factor during each of the spawning season (three spawning seasons per individual).

[Fig. 2 about here.]

3.5.2 Simulation 2: Effect of temperature and individual length on the use of reserve allocated to reproduction to cover maintenance requirements under starvation conditions

The objectives were the followings: (i) evaluate the dynamics of the reserve under starvation conditions for individuals of different sizes at different temperature levels and (ii) validate the model predictions with the experiment of Hunter and Macewicz (1985). During this experiment, female anchovies (*E. mordax*) were kept without food at 16°C and atresia was observed after three days of starvation.

In this simulation, each individual experienced a constant temperature for 20 days during which the food index was set to $X = 0$ (Figs. 2c and d). We considered eight temperature levels from 10 to 24°C and for each temperature level four different initial lengths were considered: 9, 13, 18 and 21 cm. The individuals were adults at the beginning of the simulation with a scaled energy density $e(t_0) = 1$, as if they were fed *ad libitum* before the beginning of the experiment ; the level of reserves in the reproduction buffer was function of the structural volume of the individual ($U_R(t_0) = 170 \times V$), which corresponded to an average value for the individuals in Simulation 1 prior to the beginning of the spawning season. We evaluated the time at which individuals started to use the reserve allocated to reproduction to cover maintenance requirements under starvation conditions.

3.5.3 Simulation 3: Effect of the environmental conditions preceding spawning on the duration of the spawning season

The objectives of this simulation were to evaluate (i) the inter-annual variability and (ii) the inter-individual variability of the spawning season for groups of individuals of different lengths that experienced different environmental conditions prior to the spawning season.

The average temperatures and food indices we used for this simulation are shown in Figures 2e and f. We were interested in the spawning seasons of four different years from 2000 to 2003. We simulated the growth and reproduction of the individuals starting August 15th of the year that preceded the spawning season of interest. Environmental conditions were the same for each individual after May 1st: we used the climatology of the environmental conditions for the period 2000-2003 given by the hydrodynamical and the biogeochemical models. Before May 1st, we assumed individuals were moving within the area we considered (South Bay of Biscay) and hence were experiencing different environmental conditions. To generate different environmental conditions for each individual, we added some white noise to the temperature and food functions. This white noise was a random number chosen from a normal distribution with mean 0 and a standard deviation equal to the standard deviation of the outputs of the environmental model for the area of interest. When negative values were generated, they were set to 0. We then smoothed these functions (temperature and food) with a 5-day moving average to add autocorrelation, assuming the environment of a particular day is correlated to the environment some days before and after this date.

For each period (1999-2000 to 2002-2003), we considered a group of individuals with 12 different length classes, from 8 to 19 cm, at the beginning of the experiment. Each length class had the same number of individuals (30 individuals) to evaluate inter-individual variability. At the beginning of the simulation, individuals were adults but they had an empty reproduction buffer ($U_R(t_0) = 0$ cm^2 d) as the simulation started at the end of the (previous) spawning season (Motos, 1996). Their scaled reserve density was in equilibrium with the environment ($e(t_0) = f(t_0)$).

From our simulations, we evaluated the egg production per day during the four different spawning seasons. We examined the simulated length distribution in mid-May of the different 'populations' as well as the condition factor of the individuals just prior to the first spawning. Simulated condition factor values were compared to the range of observed values. We finally determined from our simulation the inter-individual variability in terms of number of egg batches released during the spawning season for two particular length classes (14 and 18 cm individuals in May) to evaluate how different could be the spawning pattern of individuals of the same size in May but that experienced different environmental conditions prior to the spawning season.

4 Results

4.1 Simulation 1: Hatching dates generated variability among individuals in growth and reproduction traits at age 1

4.1.1 Average growth and reproduction patterns in a seasonal environment for an individual hatched during the peak of the spawning season

We were successful in finding a set of parameters (Table 2) for which the model reproduced both the growth pattern in spring and the reproduction pattern described in the Parameter estimation section for an individual hatched during the peak of the spawning season (June 1^{st}). The simulated average length- and weight-at-age of an individual in May were consistent with the length- and weight-at-age observed at the same period during surveys (Fig. 3). The three spawning seasons we simulated spanned over April-July (Table 3) with a number of egg batches per season ranging between 20 and 31 batches per season spawned every three or four days and an average relative batch fecundity F_V of 720 eggs per batch per unit of structure (Table 3), which was consistent with observations from Motos *et al.* (1996) and Motos (1996).

[Fig. 3 about here.]

[Table 3 about here.]

Using the forcing variables (food and temperature) given in Figs. 2a and b, the model simulated a seasonal growth in length with no growth during winter (Fig. 3a). The larger the individual, the longer the non-growing period. This period lasted 76 days the first winter when the individual was 11.2 cm and doubled the second winter (135 days) when the individual was 16 cm, although the winter conditions were the same. The simulated growth in weight was also seasonal with no significant variation in winter (Fig. 3b). During the spawning season, the individual significantly lost weight at ages 2 and 3 (22% on average) but not at age 1 as the individual was still substantially growing (Fig. 4b).

We found that two third of the energy used for reproduction was stored before the spawning season (Table 3), which is in agreement with the estimations of Hunter and Leong (1981) for Northern anchovy *E. mordax*. The individual spawned on average 25 batches of eggs per spawning season but fewer batches of eggs at age 1 compared to age 2 and 3. Age-1 spawning season was at least one month shorter (until mid-June) compared to age-2 and -3 spawning seasons (until the end of July and mid-July respectively) (Table 3), which is in agreement with observations from Motos (1996). We also simulated an average batch fecundity F of 8 000, 17 000 and 20 000 eggs at age 1, 2 and 3 respectively, which reproduced the observations that large females spawn more batches of eggs with a larger batch fecundity F than small individuals (Table 3; Motos, 1996). It is noteworthy that at age 3, the individual had a slightly shorter spawning season than at age 2: mobilization of reserve is inversely proportional to the length of the individual (see Eq. 1) and individuals close to their asymptotic size allocate less energy to the reproduction buffer.

4.1.2 Condition factor depended on individual length

We found a significant relationship between the condition factor and the length of the individual in the data, $K = 0.03L + 0.82$ ($n = 847$, $p < 0.001$, Fig. 4a). Only 20% of the variability of the condition factor was explained by the length of the individuals ($r^2 = 0.2$). We also found in our simulation that the average condition factor K over the spawning season was an increasing function of the length of the individual (Fig. 4b). It is noteworthy that the simulated condition factor showed a decrease as the season progressed at all ages (Fig. 4b) and the range of simulated values was comparable to the range of observed values.

[Fig. 4 about here.]

4.1.3 Effect of hatching dates still visible at age 1

In a seasonal environment, an individual hatched late in the season did not compensate its growth delay the following spring (Fig. 3a). The individuals hatched early in the season, during the peak and at the end of the spawning season were 13.7 cm, 13 cm and 11.5 cm respectively on May 15th of the following year (Fig. 3a). The individual hatched late in the season compensated most of its growth delay during its second year. The three individuals were all 17.8 cm in May at age 3 (Fig. 3a).

Hatching dates also generated inter-individual variability in the condition factor values (Fig. 4b) and the spawning pattern at age 1: the individual hatched early in the season spawned 22 times during its first spawning season while the two individuals hatched during the peak and late in the season spawned 20 and 14 times respectively. Hatching dates hardly influenced age-2 and -3 spawning seasons.

4.2 Simulation 2: Validation of the dynamics of the reserve by simulating starvation conditions

We estimated that reserves available for reproduction were used to cover maintenance costs after 3-4 days of starvation at 16 °C (Fig. 5), which is fully consistent with the observations of Hunter and Macewicz (1985) who observed atresia after three days of starvation at the same temperature in females *E. mordax*. Hence, we were able to validate both the rate at which reserve was depleted under starvation conditions and the ability of the model to regulate the reserves available for reproduction under limiting food conditions.

[Fig. 5 about here.]

Under starving conditions, the higher the temperature, the more rapidly the reserve was depleted and the earlier the individuals required energy from the reproduction buffer to pay maintenance costs. At 10°C, the reserve was not sufficient to cover maintenance requirements after an average period of 7.5 days under starving conditions (Fig. 5) but this time period depended on the length of the individual: nine days for an 9 cm individual and six days for a 21 cm individual. At 24°C, all the individuals started to use their reserves allocated to reproduction to pay maintenance costs after two days of starvation.

4.3 Simulation 3: Duration of the spawning season depended on individual length but also on environmental conditions encountered prior to the spawning season

4.3.1 Winter conditions in 2001 in particular and in 2003 led to shorter spawning seasons

Using different environmental conditions prior to the spawning season in our simulation, we found that conditions in 2000 and 2002 led to similar spawning durations (May to August) and similar egg production which corresponded to a total average of 610 000 eggs per individual during the season (Fig. 6). Spawning seasons in 2001 and 2003 were shorter with a spawning season ending one month and half earlier in 2001 compared to both 2000 and 2002. Egg production at the peak of the season was also 25% less in 2001 compared to both 2000 and 2002.

[Fig. 6 about here.]

4.3.2 Average individual length is smaller in 2001 at the beginning of the season

A shorter spawning season in our simulation is linked to a smaller average individual length at the beginning of the spawning season (Figs. 6 and 7). An ANOVA study of the length distributions of the four different simulated periods showed that the average simulated length in May 2001 was significantly different from the average length in 2002 and 2003 respectively ($p < 0.001$ in both cases) (Figs. 7c, d and e).

[Fig. 7 about here.]

4.3.3 Condition factor as a proxy for the number of egg batches per individual

We found a linear positive relationship between the condition factor K of an individual prior to the spawning season and the number of egg batches N_B that it released during the spawning season (Fig. 8). The condition factors prior to the first spawning were on average the same in 2000 and 2002 (K = 1.6) but higher than in 2001 and 2003, with individuals in 2001 having the lowest average condition factor (K = 1.3; Fig. 8). This was in agreement with the shorter spawning season in 2001 (Fig. 6).

[Fig. 8 about here.]

4.3.4 Individuals of the same length can have different spawning patterns

We obtained a large variability in condition factors at the beginning of the spawning season (Fig. 4c). The range of the simulated values compared well with the data (Fig. 4a). Although the average K value was on average higher than the average observed value, we calculated these values just prior the first simulated spawning whereas observations were carried out during the spawning season when the condition factor had already decreased due to previous spawnings.

We found particularly interesting that the number of egg batches spawned per individual was highly variable for a given length class both within and among years (Fig. 9). We focused on the 14 and 18 cm length classes but this pattern was also observed for the range of simulated length as shown by the variability of condition factors for a given length class in Fig. 4c. Furthermore, the variability of the number of egg batches per individual was larger for the large individuals (Figs. 4c and 9). Individuals of 14 cm and 18 cm spawned between 12 and 25 egg batches and between 8 and 34 egg batches respectively, all years confounded. It is noteworthy that in 2001, individuals relatively different in lengths (14 and 18 cm) spawned on average the same number of egg batches (Fig. 9).

[Fig. 9 about here.]

5 Discussion

In the present study, we aimed at studying in a mechanistic way how the spawning pattern of a small pelagic fish with indeterminate fecundity was impacted by variable environmental conditions. We developed our model in the framework of the DEB theory and to our knowledge, this is the first spawning model for fish with indeterminate fecundity. We simulated the growth and reproduction of an individual fish depending on the environmental conditions it encountered, and in particular the date of each spawning event, the batch fecundity and the egg energy content per batch. Calibrated for the Bay of Biscay anchovy for the period 2000-2005, the model successfully reproduced the main features of individual growth and reproduction in this area. Furthermore, we found that individuals of the same length can spawn substantially different numbers of egg batches both within and among years if the environmental conditions they encountered prior to the spawning season differed. This variability increased with the length of the individual. Although individual length can be used as a qualitative proxy for the spawning duration of an individual (i.e. a large individual would have a longer spawning duration than a small individual), our study demonstrated that the study of the environmental conditions encountered by the individuals prior to the spawning season is critical if we aim at predicting quantitatively the duration of the anchovy spawning season each year.

5.1 Model properties are consistent with known growth and reproduction patterns in fish

5.1.1 Properties of the model in a constant environment

In a constant environment, the model first reproduces a von Bertalanffy growth and provides a physiological interpretation of von Bertalanffy parameters (Kooijman, 2000). Second, the model reproduces two other common observations in fish studies: a positive relationship between the (Fulton) condition factor and the length of the individuals (Froese, 2006) and large individuals spawn more eggs than small individuals. In the context of the DEB theory, the latter actually provides a mechanism for the former observation.

As a matter of fact, we defined a condition factor K (Eq. 3) that is comparable to the Fulton's condition factor $K_F = \beta W/L^3$ with $\beta = 100$ cm^3 g^{-1} (Froese, 2006). Our condition factor K relates to K_F as follows: $K = (\beta d_V \delta^3)^{-1} K_F$. Being an increasing function of length is a well-known property of the Fulton's condition (Froese, 2006). If the weight of an individual is described by an allometric function $W = aL^b$, then $K_F = \beta a L^{b-3}$ which is indeed an increasing function of length if $b > 3$.

The relationship between individual length and the condition factor appears in constant environmental conditions as Eq. 3 simplifies greatly. DEB theory assumes that the reserve density of an individual is constant: $[E] = E/V =$

$f[E_m]$, with f the scaled functional response and $[E_m]$ the maximum reserve density (J cm^{-3}). Eq. 3 becomes

$$K = 1 + \frac{1}{d_V \rho_E} \left(f[Em] + [E_R] \right) \tag{4}$$

with $[E_R] = E_R/V$, the density of the reserve allocated to reproduction. At constant food, $[E_R]$ is a polynomial of the third degree in length with positive coefficients (see Eq. 3, Appendix A), i.e. large individuals accumulate more reserves for reproduction relative to their length than do small individuals. Although Hensen (1899, in Froese 2006) dismissed the measure of K_F as having no obvious advantage because it depends on the length of the individual, we suggest K and K_F (prior to spawning) can be interpreted as a proxy for the amount of energy invested into reproduction in a constant environment.

5.1.2 Properties of the model in a dynamic environment

The amount of reserves available for spawning is regulated, i.e. is reduced, according to the limiting conditions an individual encountered during the spawning period (Simulation 2) or during winter conditions (Simulation 3). Atresia phenomenon, which is widely observed in fish and which reduces individual fecundity both in determinate and indeterminate fecundity species, can thus be modeled mechanistically according to the state of the individual and the conditions it encounters. In this model, the state variable E_R can be compared with the notion of reversible mass developped by Claessen *et al.* (2000) and applied recently in van de Wolfshaar *et al.* (2008). However, our approach differs significantly from e.g. Jørgensen and Fiksen (2006). Our rule for energy allocation to reproduction is fixed, i.e. depends on the environment and the state of the individual but does not make use of a rule that maximizes fitness in a given environment, and hence does not require the definition of a fitness index.

Egg size and egg energy content are also known to vary among female fish in natural populations (e.g. Kjesbu *et al.*, 1996; Heins *et al.*, 2004). It has been interpreted as an adaptation of the female to the temperature conditions experienced by larvae (Kjesbu *et al.*, 1996; Heins *et al.*, 2004): a large egg results in a larger length at hatching which increases the survival of the larvae in unfavorable conditions at the beginning of the spawning season. The reproduction module we developed simulates variations in egg energy content according to the state of the female, i.e. the model reproduced a maternal effect, with well-fed females producing eggs with higher energy content. This mechanism offers a new interpretation to this decrease in egg size during the season that is not based on an optimization argument if the food conditions of the females decrease as the spawning season progresses. To validate our assumption requires further data acquisition on egg energy content together with individual lengths and conditions.

Fish species with indeterminate fecundity are able to develop new batches of eggs as the season progresses and eventually produce more batches if the conditions during the spawning season are favorable. Thus, we needed to define an internal trigger to end spawning to allow the production of more batches if conditions permit: if reserves available for reproduction are exhausted, spawning stops. And this availability of reserves for reproduction depended on two continuous fluxes during the spawning season: the allocation of reserves to reproduction and the use of these reserves to produce eggs. This component of the model was key to generate variability of spawning patterns and could be applied to other multiple-batch species with indeterminate fecundity.

5.2 Impact of the environment on the growth of the Bay of Biscay anchovy

5.2.1 Average growth in a seasonal environment

Our model not only captured common pattern in fish but also the average growth and reproduction patterns of the Bay of Biscay anchovy quantitatively. A calibration of the parameters made on different datasets still produced a goodness of fit with the length- and weight-at-age observed in spring for the different age classes of the Bay of Biscay anchovy. In particular, the fast juvenile growth was captured by assuming that the juveniles are present in the upper layer of the water column in summer-early autumn, which was observed during the JUVAGA surveys (Petitgas *et al.*, 2004). During the juvenile period, the temperature of the upper layer was on average three degrees higher than the temperature averaged over the first 150m (Fig. 2a), which greatly enhanced growth assuming food quantity was sufficient.

5.2.2 Variability in length among individuals

We showed that individual length determines the potential for the reserves available for reproduction an individual can store in a non limiting environment. Therefore, elucidating the factors that generate variability in growth is critical to understand the potential variability of the spawning pattern of the Bay of Biscay anchovy.

By simulating differences in hatching dates in a seasonal environment, we obtained a substantial variability of length the following year (Fig. 3a). This suggests that the large observed variability in length at age 1 in the data might be explained by the duration of the previous spawning season. However, the variability in length-at-age decreased at age 2 and age 3 in Simulation 1 as the individuals experienced the same seasonal environment.

By contrast, we generated significant differences among years in average lengths by assuming an implicit random spatial distribution of the individuals (Simulation 3; Fig. 7). Environmental scenarios that would take explicitly into account the spatial variability of the environmental conditions could hence generate the observed variability in lengths at age 2 and 3. Further simulations may also take genetic differences among individuals into account. Body size scaling relationships that apply among species (Kooijman, 2000) could be applied at the population level, i.e. maximum length L_{Vm} could differ among individuals. In the same environment, individuals would therefore have different growth patterns, even at age 2 and 3.

5.3 Impact of the environment on the condition and the reproduction pattern of the Bay of Biscay anchovy

5.3.1 Condition factor as a proxy for the number of egg batches per individual

In natural conditions, the condition factor in spring is still positively correlated with length, although the relationship only explained 20% of the observed variability. In the data collected by Ifremer in spring for the Bay of Biscay anchovy, we found $W = 0.0042L^{3.2}$ ($n = 4404, p < 0.001$). As mentioned in the previous section, having a coefficient $b = 3.2$ is in agreement with the positive relationship that we found between K and the length of the individuals in the data (Fig. 4a). It should also be noted for comparison purposes that our condition factor is almost twice as high as the Fulton's condition factor ($K = 1.97K_F$) using parameter values in Table 2.

Results of the present study showed that even when the environmental condition are not constant, the condition factor K can be used as a quantitative indicator of the number of spawning events per individual (Figs. 4 and 8). The results of Simulations 1 and 3 suggest that the variability in the condition factor observed in the data for a given length could be explained by two factors: *(i)* individuals are observed at different moments of their spawning season (beginning or end of the season, see Simulation 1, Fig. 4b) and *(ii)* individuals may have been limited in food during winter and have used their reserves allocated to reproduction for survival before the start of the spawning season (Figs. 4c and 9).

It should be noted that reserve had a limited contribution to the total weight compared to the reproduction buffer and the structure (not shown), which validated our procedure to estimate the shape coefficient δ and allowed us to use the condition factor at the beginning of the spawning season as a proxy for the number of spawning events per individual. Experiments in controlled conditions with varying food levels would confirm the relative contributions of reserve, structure and reserves available for reproduction to the weight of an individual (Kooijman *et al.*, 2008).

5.3.2 Impact of the environment on the variability of the anchovy spawning pattern

Our objective was to evaluate to which extent the spawning pattern of the Bay of Biscay anchovy could vary among years and which factors could generate this variability. We found that differences between years might be explained by different length distributions at the beginning of the spawning season, but also by the different individual life histories that determined the actual energy available for reproduction at the beginning of the spawning season. Although the variability of number of batches per season cannot be observed at the individual level in natural conditions, we made the assumption that the simulated variability we obtained for the Bay of Biscay anchovy was realistic for the three following reasons: the model compared well quantitatively with the average reproductive traits described by Motos (1996) (Simulation 1, Table 2), we reproduced a large part of the observed variability in the condition factor (Fig. 4) and atresia phenomenon was well reproduced (Simulation 2, Fig. 5).

If an adult population is mainly composed of Age 1 individuals during the spawning season, as it used to be the case for the Bay of Biscay anchovy before the sharp recruitment decline the recent years (ICES, 2006), we showed that the variability in the number of spawning events per individual might be high. Hatching dates had a substantial impact on the condition of the individuals at the beginning of the spawning season (Fig. 4b) and hence on the subsequent spawning season. Only few more months of favorable growth in spring-summer made the difference as anchovy is a fast-growing species. It allowed the older individuals to reach the length at puberty early in autumn and to accumulate substantial reserves for their first reproduction.

Our results also showed that the length of the individual was a qualitative but not a quantitative indicator of the number of spawning events per individual (Fig. 9). An individual could reach a certain size but then experience limiting conditions that impact on its subsequent spawning season. Part of the variability in the number of spawning events per individual would have been missed if we did not track growth together with the amount of reserves available for reproduction at the individual level. We evaluated that two third of the reserves available for reproduction were stored during the period preceding the spawning season. Hence, we focused our scenarios analysis to this period. We showed that, as it is the case for determinate fecundity species, limiting food conditions distant in time from the spawning season can regulate the number of spawning events per individual for multiple-batch spawners.

Furthermore, we showed that the variability of the number of batches per season increased with the length of the individual in a variable environment. We explained this observation by the fact that a large individual has a greater ability to store reserves for reproduction but its maintenance requirements are also higher. Hence, in a limiting food conditions, a large individual would use more reserves previously stored for reproduction to cover its maintenance requirements.

5.4 Future work

To better understand how the environment can generate different spawning patterns among years, we suggest two areas where the model and its application to the Bay of Biscay anchovy could be further improved: *(i)* a more mechanistic approach to simulate the start of the reproduction period and *(ii)* a better description of the magnitude of the variations of the food conditions for the Bay of Biscay anchovy.

We had simple rules to trigger the spawning season by starting the allocation of energy to the eggs at a temperature threshold. Hence, we did not reproduce the pattern where large individuals start spawning earlier than small individuals (Motos, 1996). To reproduce this pattern, we could describe egg maturation in a more mechanistic way - at the cost of additional parameters - by letting the energy allocation to eggs be a function of the structural volume.

The validation of the storage and the use of reserves at a higher temporal resolution requires more information on the food availability and the state of the individuals. In particular, the identification of the food-limited periods is critical and may change some parameter values, and the primary parameters that determine $[E_m] = \{p_{Am}\}/v$, the maximum reserve density in particular. For instance, Dubreuil and Petitgas (2009) recently studied the energy content and the dry weight of individual anchovy in the Bay of Biscay area collected during three different months - March, May and September of two recent years. This type of data could be included in future work on anchovy and other species but a careful attention should be paid first to the water composition of the different state variables of a DEB model as there is a linear relationship between the energy density and the water content of the whole organism in fish in general (Hartman and Brandt, 1995) and for the Bay of Biscay in particular (Dubreuil and Petitgas, 2009).

Further environmental scenarios could consider more food limiting conditions during winter, but specific rules to survive starvation conditions when the reserves available for reproduction are exhausted might be necessary. Compared to Simulation 1 (Fig. 3b), a significant weight loss in winter might then be simulated. Data describing to which extent individuals might lose weight during this period would be very useful to validate the simulations and specify these starvation rules.

Indication of a food-limited period in the Bay of Biscay area at the end of the spawning season is given by the analyses of the otolith opacity pattern of age-2 individuals. For the 2000-2005 period, between 8 and 50% of these otoliths presented a translucent check between the annual rings of the first and the second winters (see Petitgas and Grellier, 2003, for the 2000-2002 period). As all Age 1 individuals had an opaque otolith border during Ifremer surveys in May, we can reasonably assume this check was formed in summer. Using a food function that decreases during the spawning season and becomes limiting in summer would result in a decrease in egg size in the simulations, a pattern that could be (in)validated if egg size data could be collected throughout the spawning season.

Small pelagic species are key components of ecosystem dynamics and world fisheries. The timing of the spawning events and the egg energy content might play a significant role in the larval survival of these species. In a context of rapid climate change, we made a significant step towards a mechanistic approach of the impact of the environmental conditions on these reproductive traits. Applications of this general framework to other multiple-batch species, with determinate or indeterminate fecundity, might help revealing the common mechanisms that control the different reproductive traits observed in natural fish populations.

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A Equations of the standard DEB model

A.1 Scaled state variables

In our application for the Bay of Biscay anchovy, we used scaled state variables to remove the 'energy' dimension. Equations for non scaled variables are given e.g. in Pouvreau *et al.* (2006). The reserve density $[E] = E/V$ was scaled by the maximum reserve density $[E_m]$ ($\mathrm{J\,cm^{-3}}$) and the reproduction buffer by $\{p_{Am}\}$ the maximum surface-area specific assimilation rate ($\mathrm{J\,cm^{-2}\,d^{-1}}$) at a reference temperature. The change in scaled reserve density $e = [E]/[E_m]$, volumetric length $L_V = V^{1/3}$ (cm), and scaled reproduction buffer $U_R = E_R/\{p_{Am}\}$ ($\mathrm{cm^2\,d}$) were defined as follows:

$$
\begin{aligned}
\frac{d}{dt}e &= \frac{v}{L_V}(f - e) && (1)\\
\frac{d}{dt}L_V &= \frac{v}{3(e+g)}\left(e - \frac{L_V}{L_{Vm}}\right) \quad \text{if} \quad e \geq \frac{L_V}{L_{Vm}} && (2)\\
&= 0 \quad \text{otherwise} &&\\
\frac{d}{dt}U_R &= 0 \quad \text{if } L_V < L_{Vp} && (3)\\
&= (1-\kappa)\left[\frac{eL_V^2}{e+g}\left(g + \frac{L_V}{L_{Vm}}\right) - \frac{L_{Vp}^3}{L_{Vm}}\right] \quad \text{if} \quad L_V \geq L_{Vp} \quad \text{and} \quad e \geq \frac{L_V}{L_{Vm}} &&\\
&= (1-\kappa)\left[\frac{eL_V^2}{e+g}\left(g + \frac{L_V}{L_{Vm}}\right) - \frac{L_{Vp}^3}{L_{Vm}}\right] - \frac{\kappa L_V^3}{L_{Vm}} \quad \text{otherwise} &&
\end{aligned}
$$

with $f = X/(X + X_K)$ the scaled functional response, X the food density, X_K the saturation constant, v the energy conductance ($\mathrm{cm\,d^{-1}}$), g the investment ratio, k_M the maintenance coefficient ($\mathrm{d^{-1}}$), κ the fraction of the utilization rate spent on maintenance plus growth, $L_{Vm} = v/(k_M g)$ the maximum volumetric length (cm) and L_{Vp} the volumetric length at puberty (cm).

A.2 Temperature

All physiological rates depend on body temperature. For a species-specific range of temperatures, the model considers a temperature effect given by

$$p(T) = \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right) p(T_1) \tag{4}$$

where T is the absolute temperature(K), T_1 a chosen reference temperature (K), T_A the Arrhenius temperature (K), p a physiological rate (e.g. ingestion rate or respiration rate) (J d^{-1}). Parameters v, k_M and $\{p_{Am}\}$ depend on temperature. Thus, the variables and fluxes that were scaled by the parameter $\{p_{Am}\}$ were corrected for temperature effect as well.

B Equations of the reproduction module

We specified the equations with non-scaled state variables for generality purposes. Allocation to the reproduction buffer was initiated at $L_V = L_{Vp}$ and then occurred at rate $p_R = (1-\kappa)p_C - p_J$, with p_C the flux of mobilized reserve and p_J the maturity maintenance flux (see Fig. 1 and Kooijman, 2000). The reproduction module specified the handling rules for the reproduction buffer.

Batch preparation was initiated if surface temperature exceeded T_R. A batch was completed if the batch size was equal to $E_B^* = \min(E_R, [E_B]L_V^3)$ (J). The rate of batch preparation was given by:

$$p_B = \frac{\kappa_R}{\lambda}\left[(1-\kappa)p_{Cm} - p_J\right] \tag{1}$$

$$\text{with } p_{Cm} = [E_m]\frac{vL_V^2 + k_M L_V^3}{1 + 1/g} \tag{2}$$

with p_B the batch preparation rate (J d^{-1}), p_{Cm} a flux that was equal to the maximum flux of mobilized reserve (J d^{-1}), i.e. as if the individual was fed *ad libitum* ($e = 1$), $(1 - \kappa_R)$ the overhead costs of reproduction$and\lambda$ a constant ($\lambda < 1$) that relates to the maximum fraction of the year during which the fish would spawn if it was fed at libitum. The rate p_B still depended on the length of the individual but could not be smaller than p_R. This allowed us to avoid an unbounded accumulation in the reproduction buffer at abundant food. Notice that only in the last batch of the spawning season the batch size was smaller than the target size $E_B = [E_B]L_V^3$.

At spawning the reproduction buffer made a step down of E_B^* if enough was available, else it was fully emptied. With t_B denoting the time point at a spawning event, we had:

$$E_R(t_B + dt) = E_R(t_B) - E_B^* \tag{3}$$

$$\text{and} \quad E_B(t_B + dt) = 0 \tag{4}$$

The fecundity per batch (number of eggs) was given by $F = E_B^*/E_0$, with E_0

(J) the egg energy content. The energy content of an egg depended on the state of the female at the time of spawning. As stated by Kooijman (2000, 2009), we assumed that an offspring at birth would have the same scaled reserve density as the female at spawning ; a well fed female would produce offsprings in good condition. Hence, the reserve at birth is given by $E_b = e_b V_b[E_m] = e_\varphi V_b[E_m]$ with the subscript b referring to birth, e_b the scaled reserve density at birth, V_b the structural volume at birth (cm^3) and e_φ the scaled reserve density of the mother at spawning. Based on the assumption that the reserve and structure dynamics (Eqs. 1 and 2) also apply to embryos in the absence of food intake, the routine '`initial_scaled_reserve`' of the freely downloadable software DEBtool (Kooijman, 2008) was designed for calculating E_0 for different female conditions e_φ and parameters values. Further details of this calculation are provided in Kooijman (2000, pp.96–108) and Kooijman (2009).

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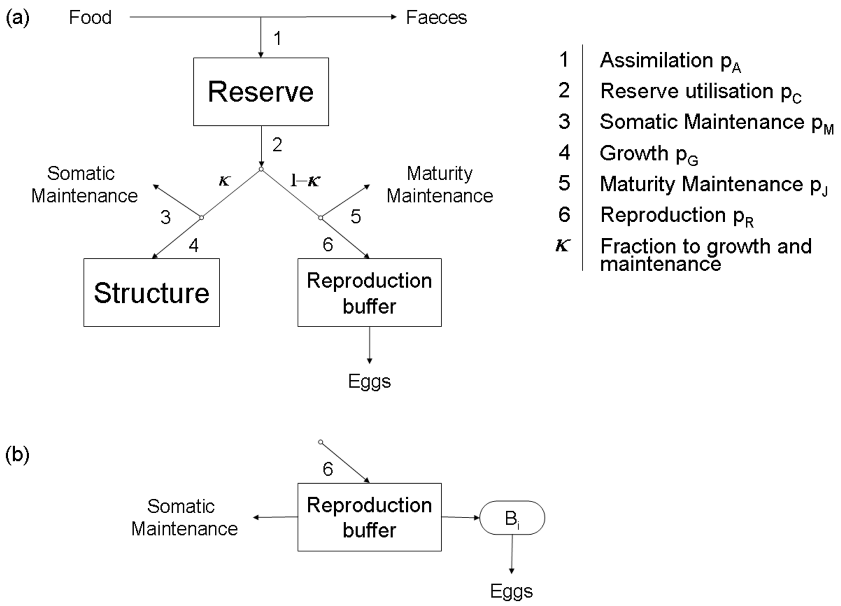

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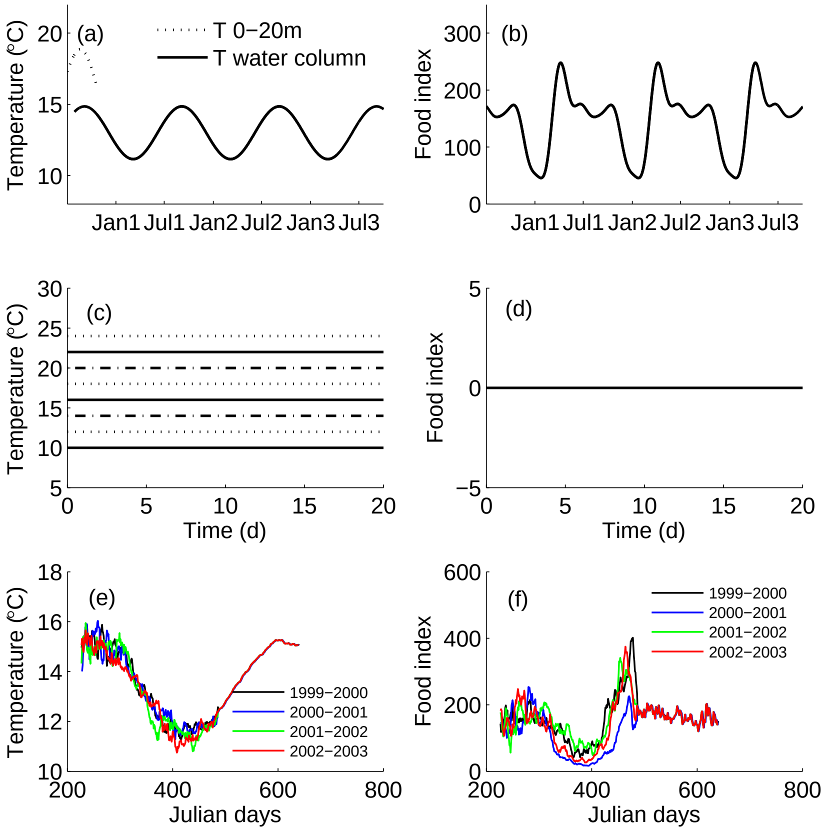

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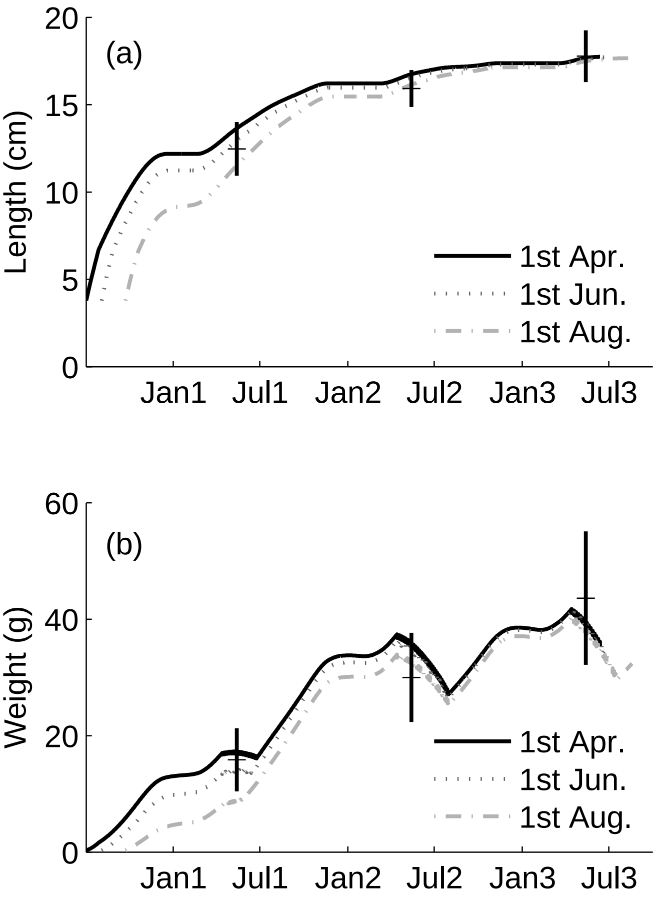

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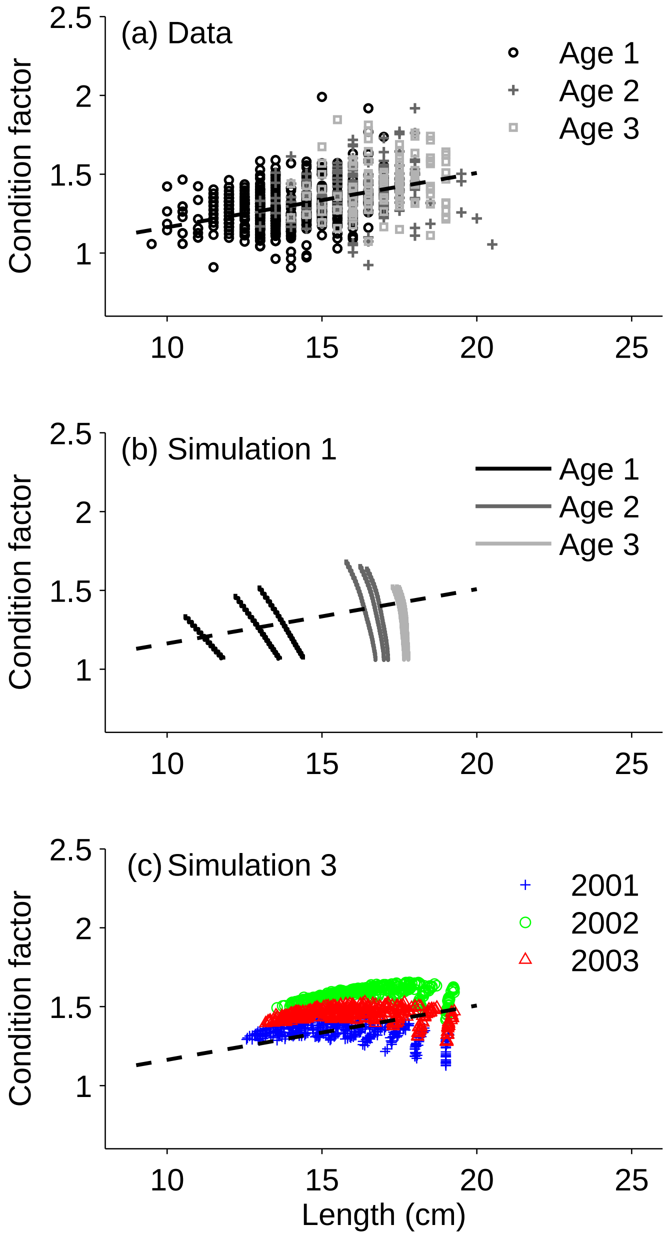

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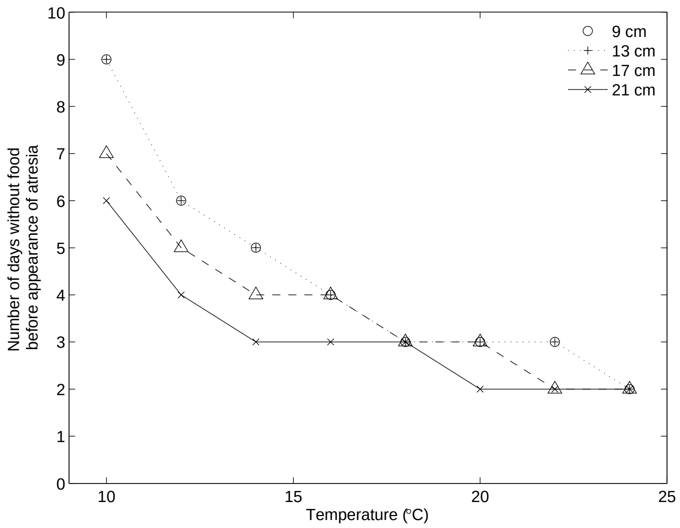

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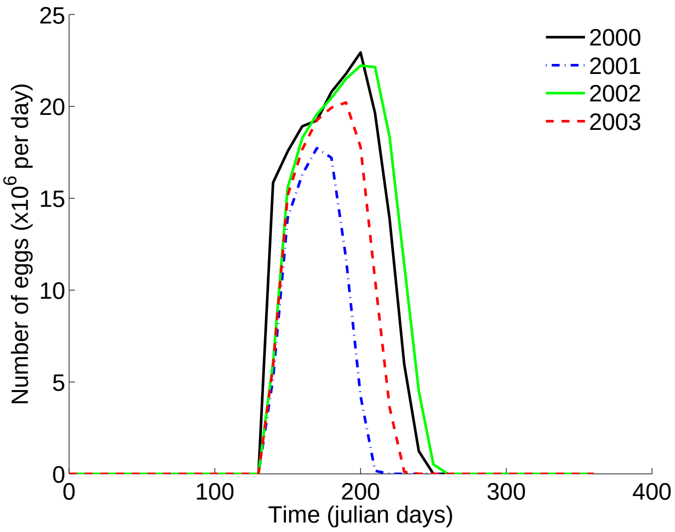

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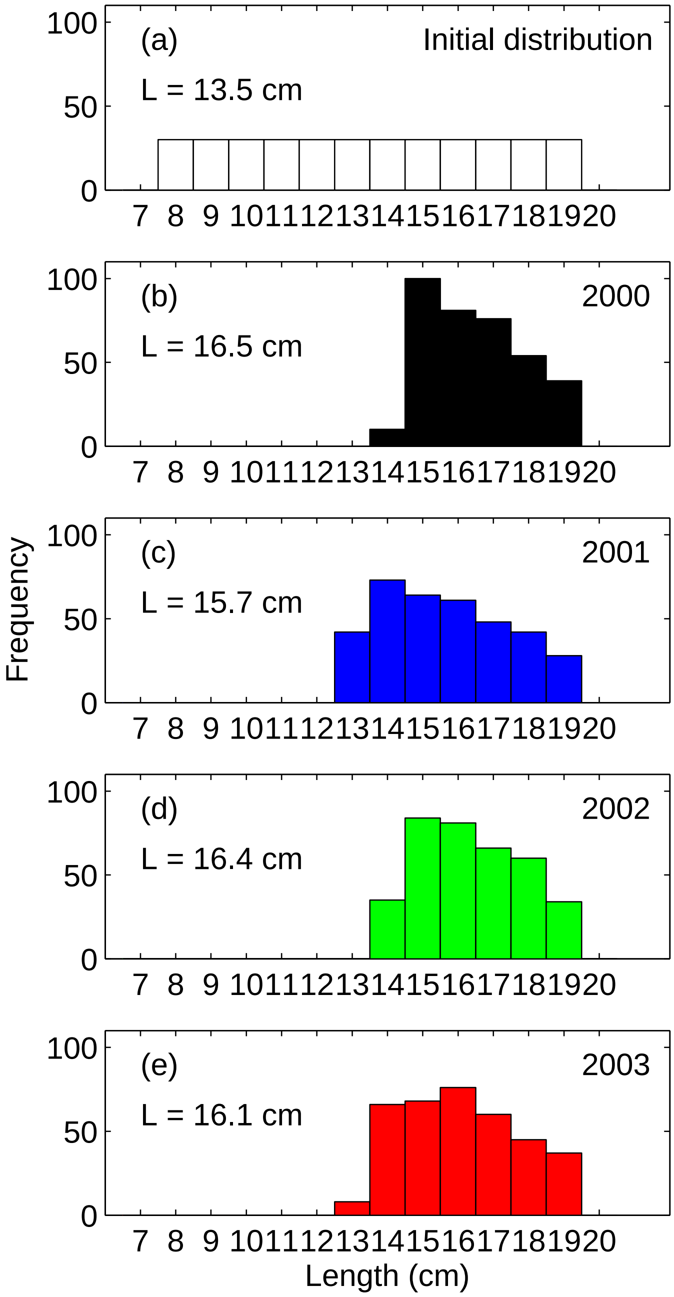

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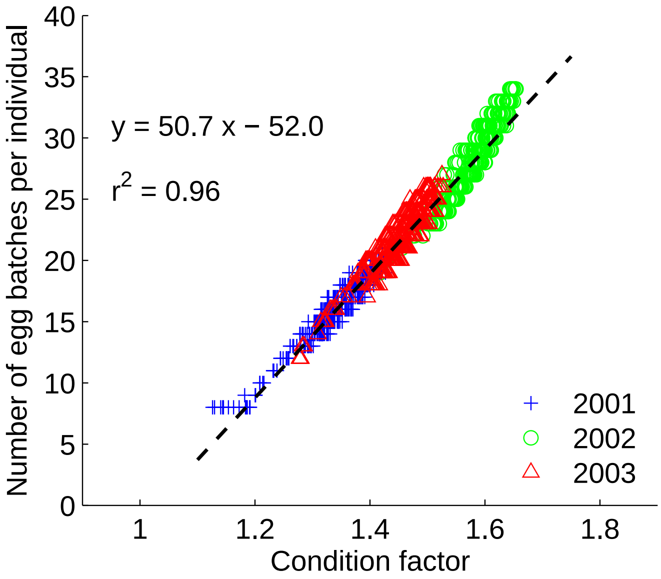

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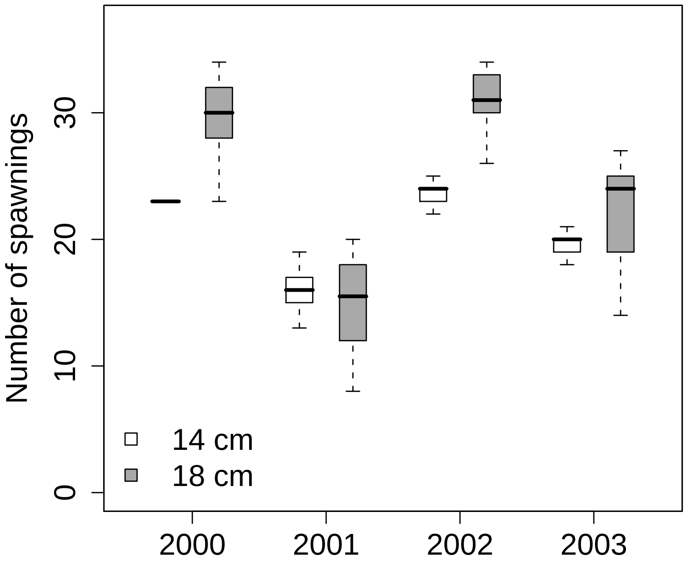

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Table 1

Assumptions on the use of the reproduction buffer for a multiple-batch spawning species

(1) If somatic maintenance costs cannot be paid from reserve, they are paid from the reproduction buffer.

(2) If the reproduction buffer is empty and if the somatic maintenance costs cannot be paid from reserve, the individual dies.

(3) When the surface temperature reaches a certain threshold T_R, batch preparation starts (external trigger).

(4) The energy density $[E_B]$ of a spawned batch is constant, except for the last batch which empties the reproduction buffer and ends the spawning season (internal trigger).

(5) Timing of spawning is determined by the time required to fill a batch up to the threshold $[E_B]V$ from the reproduction buffer

(6) The rate of energy allocation from the reproduction buffer to a batch equals the maximum rate of energy allocation from reserve to the reproduction buffer of a fish of the current size (to avoid accumulation in the reproduction buffer in *ad libitum* conditions).

(7) All eggs in a batch have the same energy content, which depends on the reserve density of the female at the timing of spawning. Hence, egg energy content can vary among batches.

Table 2

Parameter values and initial conditions (at time t_0) used to calibrate the parameters. Rates are given at the reference temperature $T_1 = 286$ K (= 13°C). Parameters calibrated during the estimation procedure (see Parameter estimation section) are noted 'calib.'

Symbol	Value	Units	Definition	Reference
T_R	286	K	Temperature threshold for spawning	Motos *et al.* (1996)
T_A	9800	K	Arrhenius temperature	after Regner (1996)
X_K	75		Saturation coefficient	calib.
k_M	0.015	d^{-1}	Somatic maintenance rate coefficient	calib.
g	6		Investment ratio	calib.
v	0.4	cm d^{-1}	Energy conductance	calib.
κ	0.65		Fraction allocated to somatic maintenance + growth	calib.
κ_R	0.95		Fraction allocated to eggs	Kooijman (2000)
$[U_B]$	0.1	d cm^{-1}	Scaled batch reserve density	calib.
λ	0.5		Maximum fraction of the year for spawning	calib.
δ	0.172		Shape coefficient	Ifremer surveys [a]
L_{Vb}	0.086	cm	Volumetric length at birth	after Ré (1996)
L_{Vp}	1.548	cm	Volumetric length at puberty	Ifremer surveys[a]
d_V	1	g cm^{-3}	Structure density	van der Veer *et al.* (2001)
$\{p_{Am}\}/\rho_E$	0.00275	g cm^{-2} d^{-1}	Scaled reserve to mass converter	calib.
$a(t_0)$	65	d	Age at metamorphosis	Ré (1996)
$e(t_0)$	$f(t_0)$		Scaled reserve density	
$L_V(t_0)$	0.688	cm	Volumetric length	after Ré (1996)
$U_R(t_0)$	0	cm^2 d	Scaled reserve allocated to reproduction	

[a] Unpublished data

Table 3
Description of the average spawning pattern of an individual hatched June 1$^{\mathrm{st}}$ as a function of its age (Simulation 1): season, average length L (cm) and weight W (g), number of batches N_B (#), average batch fecundity F (#), and relative batch fecundity F_V (# cm^{-3}), average spawning period Δt (d) and proportion of energy used for reproduction accumulated before the season γ

	Season	L	W	N_B	F	F_V	Δt	γ
Age 1	14 Apr. - 20 Jun.	12.9	13.7	20	7950	724	3	0.64
Age 2	15 Apr. - 31 Jul.	16.6	31.4	31	17035	718	3	0.65
Age 3	15 Apr. - 19 Jul.	17.6	35.8	26	20070	717	4	0.64