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# Assessing food limitation for marine juvenile fishes in coastal nurseries using a bioenergetic approach

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**Abstract :**

Understanding mechanisms affecting the renewal of populations is critical for species' conservation and living resources management. For fish species, density-dependant mechanisms occurring in young stages are particularly well studied. The food limitation hypothesis assumes that the food availability is the main limiting factor for juveniles' growth and survival in coastal and estuarine nurseries. Although some promising modelling methods appeared to test this hypothesis, it remains debated because of a lack of a clear signal of food limitation. We use a mechanistic approach based on DEB (Dynamic Energy Budget) theory to test the trophic limitation hypothesis from a metabolic point of view. The energy intake of individuals is quantified given the experienced temperatures, and measures of individuals' length-at-age. We reconstruct the food ingested in an "inverse"-DEB modelling. Then, we further explore the potential of inverse-DEB modelling to describe in fine details the energy partitioning between the main metabolic processes (i.e., maintenance, maturation and growth) of an individual, and highlight periods of energy shortage indicating a trophic limitation. As a case study, we implemented this approach for the juveniles of common sole (Solea solea) settled between 2000 and 2014 in the Seine estuarine nursery. Our approach allowed to (i) quantify food assimilation, and identify (ii) a decrease in the growth efficiency, and (iii) the occurrence of nutritional stress. Both the decrease in growth and the periods of nutritional stress coincide with a decrease in individual-specific food availability. Therefore, the inverse-DEB approach is an interesting tool to test the food limitation hypothesis at the individual scale. DEB theory deepens and structures our knowledge on energy intake and energy use, hence suggesting concrete indices of trophic limitation such as periods of non-growing, and nutritional stress due to starvation (i.e. no food intake). Work on the parametrization of the DEB model is progressing rapidly and our method can already be generalized to other fish species. Finally, mechanistic description of food limitation using bioenergetic modelling helps better understanding the ecology of the species in a dynamic environment. This may ultimately help going towards better species' conservation and fisheries management.

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**Highlights**

► Trophic limitation hypothesis is tested for juvenile soles in a coastal nursery. ► Inverse-DEB modelling estimates food ingested from temperatures and fish's lengths. ► Food assimilation and energy partitioning over time are investigated. ► Periods of non-growing and nutritional stress indicate a trophic limitation. ► Food limitation at the individual scale occurs in late summer.

**Keywords** : DEB model, Energy partitioning, Estuaries, Flatfishes, Nutritional stress

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# 1. INTRODUCTION

## 1.1 The food limitation hypothesis in coastal and estuarine nurseries

Understanding mechanisms affecting the renewal of populations is critical for species' conservation and living resources management. For fish species, we know that regulation factors occurring at larval and juvenile stages directly affect their recruitment (*i.e.* when the young fishes reach the adult stock), mainly through size-selective maturation and size selective survival (Daewel et al., 2011; Van Der Veer et al., 1994). The trophic limitation hypothesis assumes that the environment can supply only finite food resources, restraining the number of individuals able to correctly develop, grow and survive (Amara et al., 2000; Nash et al., 2007; Nunn et al., 2012). Trophic limitation might cause nutritional stress (Neill et al., 1994), resulting in reduced growth and body condition (Meyer et al., 2012), and ultimately in death.

Many young fish, including juvenile flatfishes concentrate in coastal and estuarine (C&E) shallow waters to grow and mature before their recruitment. Indeed, C&E areas offer particular conditions (*e.g.*, high food supply, protection against predation) that allow them to act as nursery grounds for marine juvenile flatfishes, often of fisheries interest (Le Pape et al., 2003; Seitz et al., 2014). However, global changes affecting C&E areas (*e.g.* coastline modification or pollution) may have led, in numerous cases, to a decline in their nursery function (Rochette et al., 2010; van der Veer et al., 2022). During the last decade, particular attention was drawn towards the hypothesis of trophic limitation for juvenile flatfishes in C&E nurseries (Le Pape & Bonhommeau, 2015), with growth reduction observed for juveniles in several areas across the North-West Atlantic (Cardoso et al., 2016; Freitas et al., 2012; Poiesz et al., 2020; van der Veer et al., 2010).

## 1.2 Existing methods to identify a trophic limitation

Several approaches were proposed to test the trophic limitation hypothesis for juvenile fishes in C&E nurseries, leading to contrasting conclusions according to the review of Le Pape and

Bonhommeau (2015). When exploring this hypothesis at the individual scale, most rejected it (*e.g.* Gilliers et al., 2006; Selleslagh & Amara, 2013). However, variations in juvenile's condition were observed (*e.g.* for the plaice, Ciotti et al., 2014), and are likely related to starvation. Le Pape and Bonhommeau (2015) explain that, in fact, size-selective mortality and size-selective sampling might hide the effect of food limitation: (1) small individuals in poor condition are more likely to be dead at the time of sampling and (2) they are likely less captured by the classic fishing gears. On the other hand, when focusing at the population scale, studies mainly support the trophic limitation hypothesis. Indirect population scaled approaches revealed indicators of food limitation such as (i) food partitioning (*e.g.* Amara et al., 2001), (ii) link between fishes' distribution and energy availability at the individual scale (*e.g.* Nicolas et al., 2007), or (iii) growth and condition reduction in comparison to optimal environments (Freitas et al., 2012; van der Veer et al., 2010).

Therefore, trophic limitation hypothesis is still discussed because of the lack of an obvious signal of food limitation occurring on surviving juveniles (Le Pape & Bonhommeau, 2015). During the last years, several authors used a direct population scaled approach to test the trophic limitation in C&E nurseries at the juvenile fish community level, based on the calculation of the exploitation efficiency (EE) (Day et al., 2021; Saulnier et al., 2020; Tableau et al., 2019). This method consists in the assessment of a predation pressure, through the calculation of a ratio between the food consumed by predators and the food supplied by prey (Collie, 1987; Vinagre & Cabral, 2008). Food, and thus energy consumed can be approached by a simple model as proposed by Tableau et al. (2019). The recent studies using this method support the trophic limitation hypothesis for juvenile flatfishes in the Seine estuarine nursery, mainly at the end of the growth period (*i.e.,* late summer and autumn) (Day et al., 2021; Saulnier et al., 2020).

These latter approaches seem relevant and promising toward community level as they combine data at population and individual levels. However, they also come with multiple constraints. First, population scale growth rates, distribution or energy consumption datasets are rarely available because of the time-consuming field and laboratory works they require (Saulnier et al., 2020). Regarding the EE model of Tableau et al. (2019), it also requires a lot of work because

of the need to consider the whole community of prey and predators (Tableau et al., 2016). Additionally, energy consumption in this model is assumed proportional to growth, ignoring energy requirements when growth is null. Finally, the growth efficiency coefficient used to convert observed growth into energy consumption is constant in this model, irrespective of environment variations such as temperature. Yet, energy consumption might be very variable, depending on the environment, the season, the size of the individual and the energy required for its maintenance (Kooijman, 2010).

Therefore, although modelling approaches largely improve our knowledge on prey availability for juvenile flatfishes in nursery grounds (Tableau et al., 2019), testing the trophic limitation hypothesis requires new tools to assess individuals food intake and physiological condition in a dynamic environment (Ciotti et al., 2014).

## 1.3 The DEB modelling to test the trophic limitation hypothesis

Dynamic Energy Budget (DEB) theory is an integrative theory of energy allocation that describes and quantifies the metabolism of an individual over its whole lifecycle, in varying environmental conditions, *i.e.* temperature and food availability (Kooijman, 2000; Marques et al., 2018; Nisbet et al., 2000; Van der Meer, 2006). A powerful aspect of models based on DEB theory (DEB models) is also the possibility to back-calculate energy ingestion, based on experienced temperatures and observed growth patterns (Cardoso et al., 2006; Freitas et al., 2009, 2011; Kooijman, 2010; Pecquerie et al., 2012). This inverse-DEB modelling has been used to reconstruct time series of food availability and energy consumption for several bivalves species (e.g. Cardoso et al., 2006; Freitas et al., 2009; Lavaud et al., 2019). Also, Pecquerie et al. (2012) used this method in order to study the capacity of otoliths data to provide more detailed information on the growth history of the individual, and on the energy it assimilated in the field. These studies showed that reconstructing energy ingestion using inverse-DEB modelling constitutes an original and relevant framework to learn more about fluctuations of resources available for the studied species, as well as of their energy intake and use.

DEB modelling might address the difficulties previously referred in the assessment of the trophic limitation in C&E nurseries. DEB model considers that individuals consume energy even when they don't grow, for their maintenance and maturation (Kooijman, 2010). Thus it allows a more accurate information on fishes' energy intake through time than the EE model of Tableau et al. (2019) that considers a constant linear link between observed growth and energy consumption. Therefore, inverse-DEB modelling might constitute a relevant tool to test the trophic limitation hypothesis for juvenile fishes in C&E nurseries. Freitas et al. (2011) used this approach to test trophic limitation hypothesis for the sand goby over the period of nursery residence. Their approach consisted in reconstructing the mean scaled food conditions over the lifetime of individuals, by comparing the observed asymptotic length with the theoretical maximum one (under unlimited food conditions).

We propose here to (i) apply the inverse-DEB modelling approach to a large dataset of growth trajectories of *Solea solea*, and (ii) go further in exploring the potential of DEB models to detect nutritional stress periods in fish based on fine description of their energy partitioning. We focus on the juveniles of the common sole (*Solea solea*) in the Seine estuarine nursery. We first use inverse-DEB modelling to reconstruct the dynamic of individual-specific food conditions in the nursery. Then, we study the energy partitioning, that is the distribution of mobilized energy between the different metabolic processes considered by the DEB model (*i.e.*, maintenance, growth and maturation), under the experienced environmental conditions. This method allows us to identify indices of trophic limitation such as growth reduction and periods of nutritional stress.

# 2. MATERIAL AND METHODS

## 2.1 DEB theory

### 2.1.1 State variables and fluxes

DEB theory describes and quantifies the metabolism of an individual through four state variables that are linked to mass and metabolic processes (see Figure 1) (Kooijman, 2010; Marques *et al.*, 2018;

Van der Meer, 2006). The reserve $E$ ($J$) translates the available energy for metabolic processes such as growth, maintenance, development and reproduction in adults. The structure $V$ ($cm^3$) corresponds to the organism's somatic parts. The maturity compartment $E_H$ quantifies the cumulated energy invested into development (maturation). Finally, the reproduction compartment $E_R$ ($J$), filled once the puberty starts, allows the production of offspring (here $E_R$ is fixed to zero as the study only concerns juveniles). The state variables are supplied in energy at rates ($J.d^{-1}$) that depend on environmental conditions (*i.e.*, temperature and food) and on the state of the organism (Kooijman, 2010; Sousa *et al.*, 2010; Van der Meer, 2006). Before its birth, the individual uses energy stocked into its reserve but does not assimilate energy. From the moment it is born (*i.e.* for fish the beginning of the exotrophic phase of the larvae), the organism feeds and starts assimilating energy from its environment at a rate $\dot{p}_A$. This assimilated energy fills the reserve compartment $E$, from which it will be mobilized at a rate $\dot{p}_C$. From the flow of mobilized energy, a fraction $\kappa\dot{p}_C$ will be allocated to the growth of structure and the somatic maintenance. A primary flow $\dot{p}_M$ goes to the somatic maintenance while the remaining energy will go into growth ($p_G$). The rest of the mobilized energy, (1-κ) $\dot{p}_C$, will be allocated in priority to the maintenance of maturity ($p_J$), and then to the maturity ($\dot{p}_R$). State variables and fluxes considered in the DEB model are described in Table 1 and Figure 1.

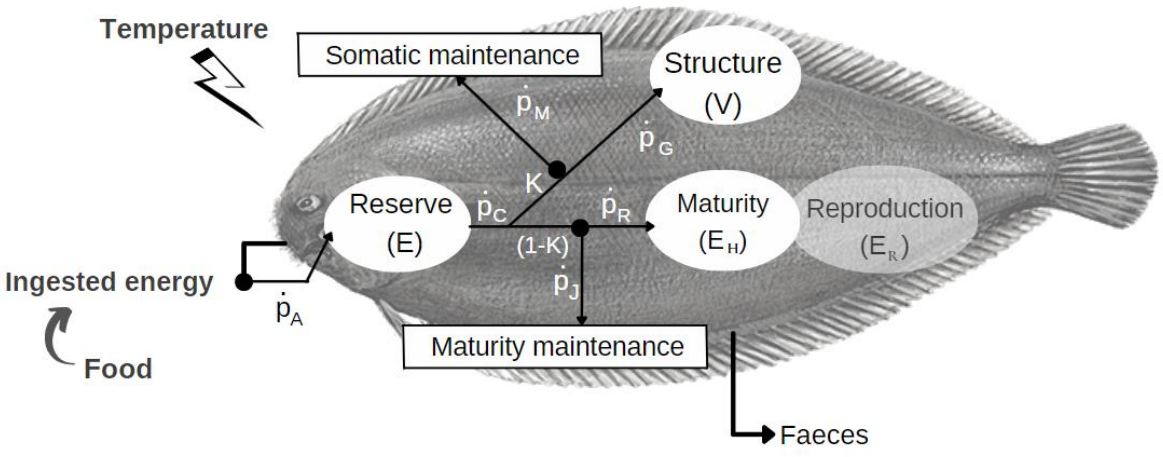



Figure 1: Conceptual representation of the Dynamic Energy Budget (DEB) model. The circles are the state variables: Reserve $E$ (J), structure $V$ ($cm^{-3}$), maturity $E_H$ (J) and reproduction buffer $E_R$ (J). The arrows represent the energy fluxes ($J.d^{-1}$). The rectangles are the maintenance compartments. The temperature and food are the two environmental variables considered in the DEB model.

126 Table 1: Names, equations and units of state variables and metabolic processes in DEB theory for an
127 individual at the juvenile stage (Kooijman, 2010).

| **State variable** | **Differential equation** | **Unit** |
|---|---|---|
| Reserve | $\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$ | J |
| Structure | $if\ \kappa\,\dot{p}_C \geq \dot{p}_M$ : $\frac{dV}{dt} = \frac{\dot{p}_G}{[E_G]}$ \| $if\ \kappa\,\dot{p}_C \leq \dot{p}_M$ : $\frac{dV}{dt} = \frac{\dot{p}_G}{\kappa_G\,[E_G]}$ | $cm^3$ |
| Maturity | $\frac{dE_H}{dt} = \dot{p}_R$ | J |
| Reproduction buffer | $\frac{dE_R}{dt} = 0$ | J |
| **Metabolic processes** | **Equation** | **Unit** |
| Assimilation | $\dot{p}_A = \{\dot{p}_{Am}\} f\ L^2$ | J/d |
| Mobilization | $\dot{p}_C = \frac{[E_G]\,\dot{v}\ V^{-1/3} + [\dot{p}_M]}{\frac{[E_G]}{E} + \frac{\kappa}{V}}$ | J/d |
| Somatic maintenance | $\dot{p}_M = [\dot{p}_M]\ V$ | J/d |
| Growth | $\dot{p}_G = \kappa\ \dot{p}_C - \dot{p}_M$ | J/d |
| Maturity maintenance | $\dot{p}_J = \dot{k}_j\ E_H$ | J/d |
| Maturation | $\dot{p}_R = (1-\kappa)\ \dot{p}_C - \dot{p}_J$ | J/d |

128

129 ### 2.1.2 Consideration of the environment

130 In order to account for the effect of temperature on metabolic rates, the parameters $\{\dot{p}_{Am}\}$, $\dot{v}$,
131 $[\dot{p}_M]$ and $\dot{k}_j$ are corrected by a temperature correction factor *TC* (Kooijman, 2010) (see Appendix A

for further information). In the calculation of $\dot{p}_A$ (see Table 1), the variable *f* is the scaled functional response (Kooijman, 2010), and links the food density in the environment with the actual amount of energy ingested by the animal . *f* allows the energy assimilation rate of the individual to be scaled in relation to the maximum one $\{\dot{p}_{Am}\}$. Therefore, it is usually considered between 0 and 1, with *f*=0 corresponding to a state of starvation (*i.e.* no food intake) and *f*=1 implying an assimilation rate that is equal to the theoretical maximum specific assimilation rate, $\{\dot{p}_{Am}\}$. According to Freitas et al., 2011, f can be used as a proxy of the available food in the environment. However, the term "individual-specific" here highlights that it translates apparent scaled food conditions for an individual and not to the whole amount of food available in the environment. This is important, as f is the integration of multiple factor including energy available in the environment, but also intra and inter-specific competition. In other words, it is related to the energy that can actually be ingested and then assimilated by an individual.

### 2.1.3 Calculating length over time

Given daily temperatures, food availability and the species-specific parameters of the model (see Appendix A), DEB theory can predict the individual structural length *L*, which corresponds to $V^{1/3}$.

When nutritional stress occurs, energy mobilised is no longer sufficient to cover the somatic maintenance requirements, (*i.e.* $\kappa \dot{p}_C < p_M$). In this case, we consider that shrinking of structure is allowed to fulfil these somatic maintenance requirements (implying that $\dot{p}_G$ can be negative). The mobilized energy is assumed to be equal to $\frac{1}{\kappa_G}\frac{dV}{dt}$ (see Table 1), with $\kappa_G$ the growth efficiency, calculated as : $\kappa_G = d_v\, q_v\, /[E_G]$ (Mounier, 2019), where $d_v$, $q_v$ and $[E_G]$ are the density, energy density, and cost per unit of structure (see Appendix A).

The physical length $L_w$ (*cm*) is calculated from the structural length and a shape coefficient δ, assuming isomorphy and no contribution of reserve to physical length: $L_w$ = L/δ. Shape coefficient δ is unitless, and constant post-metamorphosis according to Mounier et al.(2020). It is important to note that a different structure to physical length relationship should be considered when shrinking happens, however we decided to keep δ constant whether the individual is under nutritional stress of not, as in

158 Augustine et al. (2011). This allows simplifying our method, and we consider that the results will not
159 change significantly.

## 160 2.2 Implementing an inverse-DEB modelling to reconstruct food ingestion

161 All the modelling steps of this study (*i.e.* paragraphs 2.2 and 2.3) were implemented in R (R Core
162 Team 2021) and the integrated development environment (IDE) R-studio (Rstudio Team 2020).

163 As a first step, we back-calculated the scaled functional response (*f*) to assess the food ingested by
164 individuals, given the experienced temperatures and observed individuals length-at-age. Age of the fish
165 is estimated in days post fertilization (dpf), assuming a unique fertilization date. To better represent the
166 temporal variability of food ingestion, one *f* value was calculated for each period between two length
167 observations, and independently for individuals of each age class (*i.e.*, each cohort - a cohort represents
168 the individuals born in the same year). Thus, for each period, we estimated *f* by minimising the Mean
169 Relative Error (MRE) between the observed lengths ($L$) and the lengths estimated using the DEB model
170 ($\hat{L}$) for each time point (i) with an observation of the period ( 1 ).

171 $$MRE = \frac{1}{n}\sum_{i=m}^{m+n}\left(\frac{\left|L_i - \hat{L}_i\right|}{L_i}\right) \times 100$$

172 ( 1 )

173 The “optim” function (R Core Team 2021) with the method “L-BFGS-B " (Byrd et al., 1995)
174 was used.

175 To simplify this optimization step, the observed lengths were averaged within each cohort and
176 time point, so that an average individual from each cohort is represented through the three years within
177 the nursery. Figure 2 resumes our methodology for the back-calculation of individual-specific food
178 conditions.

179 During the step of parametrization of the DEB model, the maximum assimilation rate $\{\dot{p}_{Am}\}$ is
180 determined by experiments or found in the literature. In the present study, during the optimization
181 process, we allowed *f* to take values greater than 1. While it is not classical in DEB studies, *f* values can

be greater than 1 as long as *f* is not considered as an explicit functional response for a given food concentration but only as a proxy for the food. In that context, this implies that *f* embeds the uncertainty in both $\dot{p}_X$ and $\{\dot{p}_{Am}\}$ considering that (i) the food quality in the nursery could be better than those used for calibrating the DEB model, and (ii) there is a possible genetic variability in $\{\dot{p}_{Am}\}$ between populations. A *f* greater than 1 implies an assimilation rate superior to $\{\dot{p}_{Am}\}$. This idea is supported by some observations *in natura* of growth rates higher than those simulated by the DEB model for a *f*=1 (*e.g.* for the bivalve *Macoma balthica*, in Cardoso *et al.* (2006)). We therefore allow *f* to take values above 1 and limited it to a maximum of 2. This choice is supported by preliminary calculations of values of *f* that (i) are theoretically allowable and (ii) are already used for predictions, showing satisfying fit of the model to the data for *S. solea* (AmP Solea solea, version 2021/11/30).The final distribution of *f* values is visible in Appendix D. In order to facilitate the interpolation of *f* between two observations (to get a daily value of *f*), we assumed *f* constant during the period between two samplings (see Figure 2).

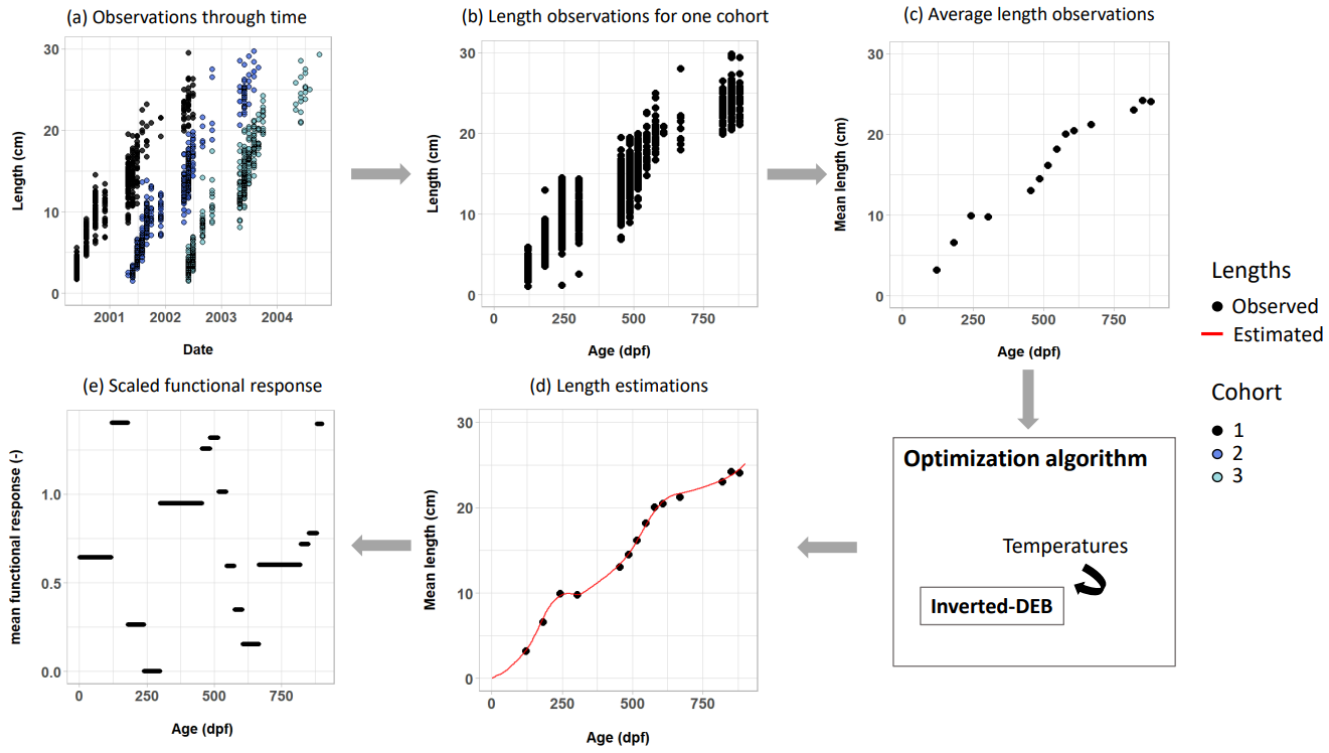



Figure 2: Conceptual representation of the methodology for the reconstruction of individual-specific food conditions (*i.e.* scaled functional response). Length data are available over time (a). From the

lengths of the individuals of one cohort over age in dpf (b), the average lengths were calculated and used in the inverse-DEB modelling (c). By minimizing the MRE between these lengths and the ones estimated by the DEB model (d), we back-calculated the scaled functional response (e). See section 2.2 for further explanations on the values of the scaled functional response in the figure.

## 2.3 Simulate metabolism under experienced conditions

### 2.3.1 Energy intake over time

We simulated the metabolism of an average individual every day for the three years spent in the nursery, under experienced temperatures.

For *Solea solea*, $\{\dot{p}_{Am}\}$ is different between males and females (see Appendix A), and therefore daily assimilated energy in a same environment varies between sexes. However, hereafter we adjusted a value of *f* from the same observed lengths independently for a male and a female. Then we averaged all the simulations to present the results for an average individual, on the assumption that the observations are half from females and half from males.

The daily-assimilated energy $\dot{p}_A$ (see Table 1) actually corresponds to the daily-consumed energy $\dot{P}_X$ divided by a digestibility coefficient $\kappa_X$ (fixed to generalized animal value (Mounier et al., 2020) – see Appendix A). Therefore, the daily-consumed energy was calculated for an average individual as $\dot{p}_X = \dot{p}_A/\kappa_X$.

### 2.3.2 Energy partitioning

Once the energy intake was calculated, we studied the energy partitioning, particularly in order to assess individuals' growth capacity, and to identify potential periods of nutritional stress. To do so, the absolute fluxes towards growth, maturation, maturity maintenance and somatic maintenance were calculated (in *kJ/day*), as well as the percentage of mobilized energy allocated to each metabolic process, respectively.

### 2.3.3 Growth efficiency

The variable that links growth with energy consumption is the growth efficiency coefficient (*k*), *i.e.*, the quantity of energy required by the organism to allocate one energy unit into the structure. The growth efficiency within DEB theory is generally calculated as the ratio between the amount of energy fixed into structure and the amount of ingested energy ($\dot{p}_A/\kappa_X$, or $\dot{p}_X$). However, $\dot{p}_C$ is used here instead of $\dot{p}_A$ in order to avoid calculation issues due to possible null values of $\dot{p}_A$. Therefore, the growth efficiency coefficient *k* is calculated as: $k = (\dot{p}_G\kappa_G)/(\dot{p}_C/\kappa_X)$. $\dot{p}_G$ is the quantity of energy daily allocated to growth, corrected by $\kappa_G$ (*i.e.* growth efficiency), in order to consider the energy that is actually fixed into structure. $\dot{p}_C$ is the daily quantity of mobilized energy, and is divided by $\kappa_X$ (digestibility coefficient, see Appendix A), in order to approximate the daily quantity of consumed energy.

## 2.4 Case study: the common sole in the Seine estuarine nursery

### 2.4.1 Study site

To illustrate our proposal, we used the case study of the juveniles of common sole *Solea solea* in the Seine estuarine nursery. The Seine Estuary is located on the North-West French coast, and opens up in the English Channel (Figure 3). The Seine nursery covers a subtidal shallow area of 360 km², characterized by a mean depth of 8.2m, and muddy-fine sand sediments (Billen et al., 2001).

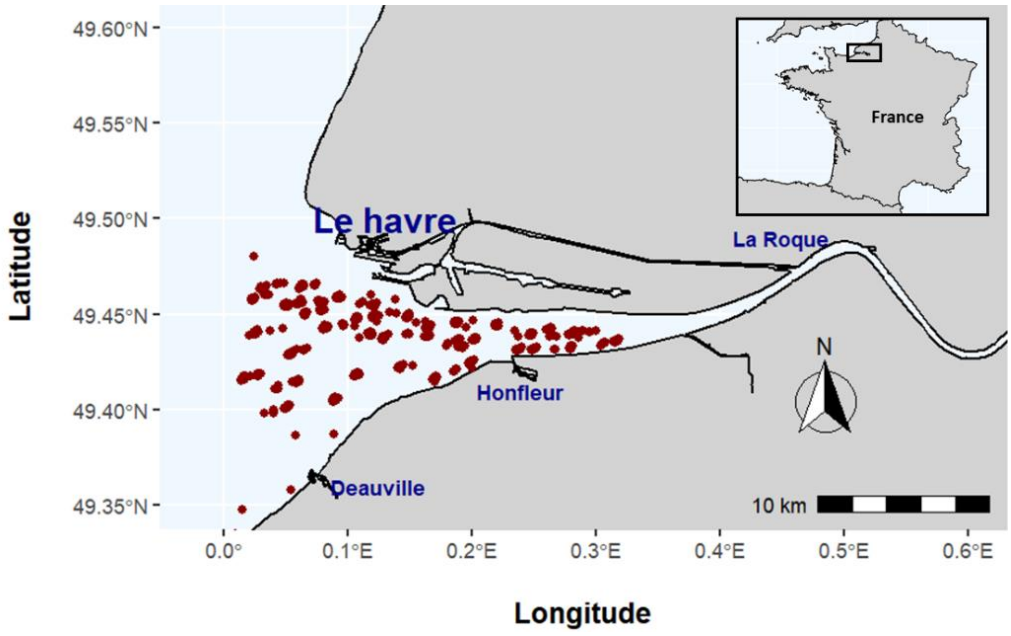



Figure 3: Map of the estuary of the Seine. The red dots represent the position of the stations were juveniles common soles were sampled.

### 2.4.2 Data

The common sole is a bentho-demersal flatfish of fishery interest, found in the muddy and shallow habitats of the Atlantic Ocean, as well as in the Black and Mediterranean seas. Within the nursery, juveniles mainly live in intertidal and subtidal mudflats, where they feed on benthic meiofauna and macrofauna (mainly copepods, shellfish and polychaetes) (Gibson et al., 2014; Morat, 2011).

Fish data were provided by the Cellule de Suivi du Littoral Normand (CLSN, research projects CAPES and Modhanour) from an historic beam-trawling survey conducted between 2000 and 2014 in the Seine estuary. Every month or two months, juvenile fish were sampled and measured in several stations in the estuary (Figure 3). The age-class to which the individuals belonged (*i.e.* G0 for the individuals born in the year, G1 for the ones born one year before the sampling or G2 for the ones born two years before the sampling) was also identified via Gaussian fitting on the size spectra, and provided by the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER). The birthdate was fixed on February 1$^{st}$ for all juveniles.

Satellite-based SST (sea surface temperature) observations were extracted from Pathfinder (1998-2009), Ostia (2010), and Odyssea (2011-2014) products to construct 1998-2014 time series. The observations were re-interpolated over a regular grid with 2.5*2.5 km cells and averaged over the outer Seine estuary on a daily scale (See

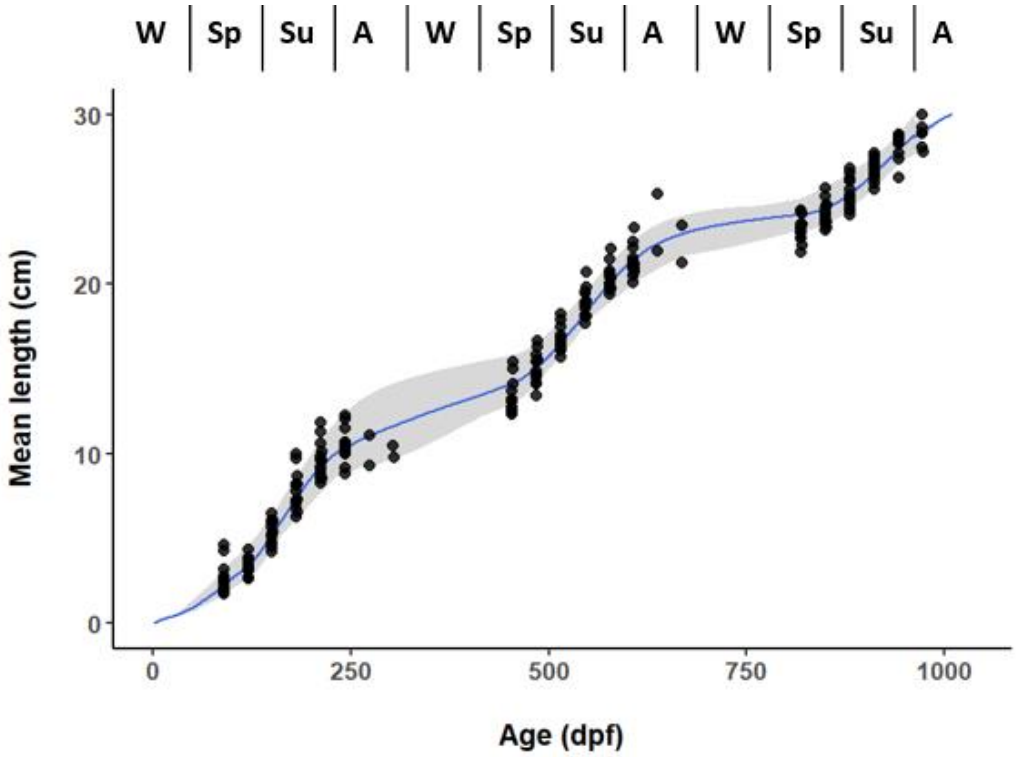
Appendix B for further information on the temperature data).

Concerning the implementation of the DEB model for the sole, we used the sets of DEB parameters calibrated by Mounier et al. (2020) for males and females (see Appendix A).

# 3. RESULTS

## 3.1 Energy intake over time

From the experienced temperatures, individual-specific food conditions were reconstructed to adjust to observed growth data (Figure 4). The fit of the reconstructed growth trajectories with the observed growth data for each cohort separately is shown in Appendix D. We simulated the daily energy consumption of juveniles within the nursery (Figure 5). The daily energy consumption increases with the age of the average individual. In addition, a seasonal pattern can be observed, with a high decrease of energy consumption at the end of the growth season of the common soles (*i.e.*, late summer/autumn). The breaks observed in the values of energy consumption are the consequence of keeping a relative food condition constant between each observation (*i.e.* the average relative food condition for an entire time period between two observations).

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275 Figure 4: Observed mean lengths per dpf per cohort (black dots) over time (in days post fertilization),
276 and estimations of lengths by the DEB model under experienced temperatures and individual-specific
277 food conditions. The blue line represents the average estimated lengths, the grey area represents the
278 range between the upper and lower values of estimated length. Capital letters correspond to the
279 seasons (W = Winter, Sp = Spring, Su = Summer, A = Autumn).

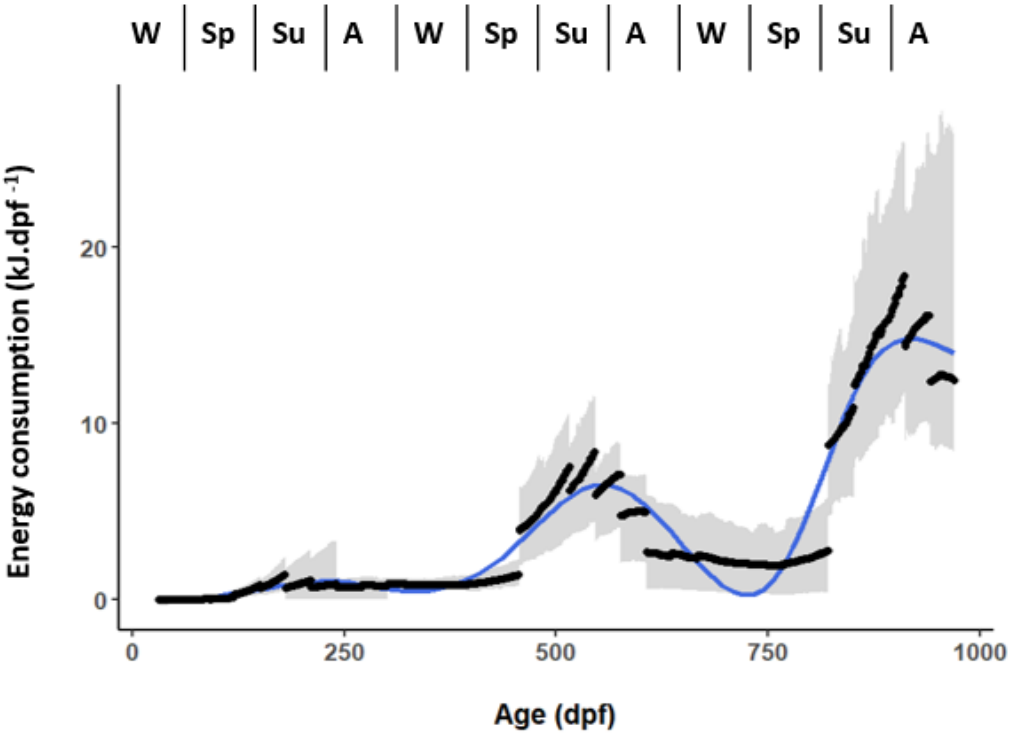
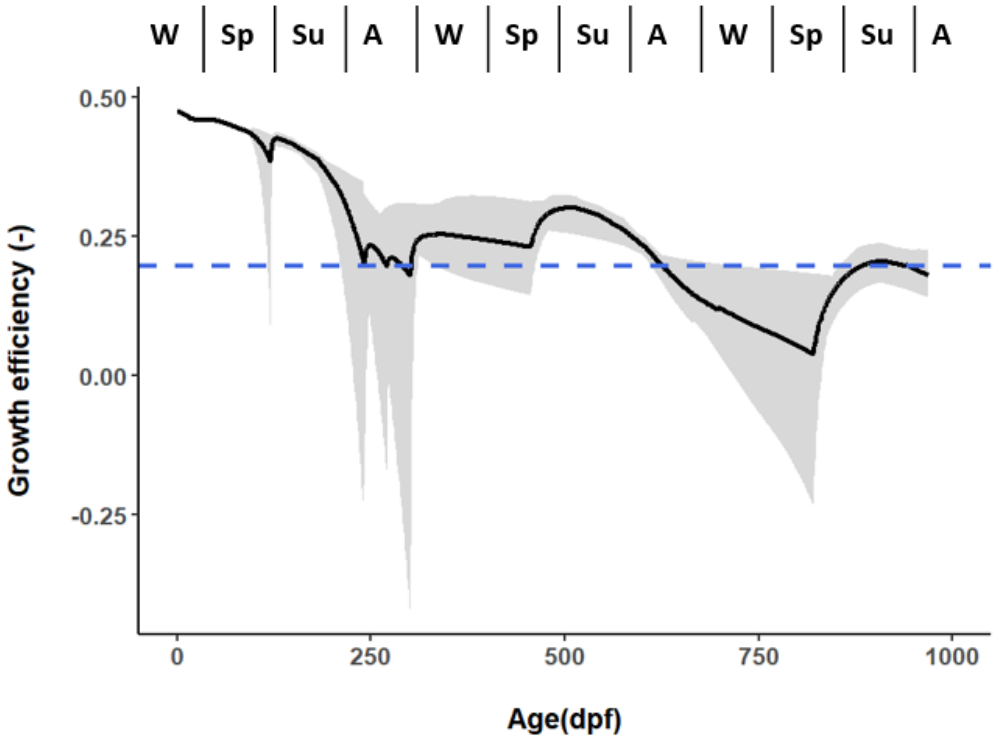



Figure 5: Energy consumption simulated by the DEB model over time (in days post fertilization) under experienced temperatures and individual-specific food conditions. The black dots represent the mean energy consumption for individuals of all cohorts. The blue line is a smoothed function of this energy consumption. The grey area represents the range between the upper and lower values of daily energy consumption. Capital letters correspond to the seasons (W = Winter, Sp = Spring, Su = Summer, A = Autumn).

## 3.2 Dynamic of growth efficiency

The growth efficiency coefficient estimated by the DEB shows a dynamic pattern dependent of the age and the seasons (Figure 6). The growth efficiency coefficient is overall decreasing over time with older individuals investing relatively less assimilated energy in growth compared to young individuals. In late spring, the coefficient increases while in autumn and winter it tends to decrease for all age-classes, with even negative growth coefficients observed for some cohorts. In opposition, the growth efficiency coefficient proposed by Day et al. (2021) for soles based on the model of EE (Tableau et al., 2019) is constant over season and age (blue line in Figure 6). During the first two years in the nursery (approximately between 90 and 730 dpf), the DEB model predicts a growth efficiency

296 coefficient that is generally higher than the one considered in the model of EE, while the opposite is
297 observed during the last year (between 730 and 970).

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299 Figure 6: Evolution of the growth efficiency coefficient for an average individual over time (in days post
300 fertilization). Blue dashed line is the constant growth efficiency coefficient considered by the EE model
301 of Tableau et al. (2019) for the *soleidae* (Day et al., 2021). Black solid line is the mean growth
302 efficiency coefficient estimated by the DEB model. The grey area is the range between the lower and
303 the upper values of the growth efficiency coefficient, for the cohorts between 2000 to 2014. Capital
304 letters correspond to the seasons (W = Winter, Sp = Spring, Su = Summer, A = Autumn).

305 ## 3.3 Link between growth efficiency and relative food availability

306 The mean scaled functional response (*i.e.* individual-specific food availability) shows also a
307 seasonal trend, with highest values in summer and lowest in winter (even null values) (Figure 7).
308 Regarding the link between growth efficiency and the scaled functional response, it appears that periods
309 of shrinking (*i.e.* when the growth efficiency is negative) correspond to periods when the scaled
310 functional response is null or very low, or days following this period (Figure 7).

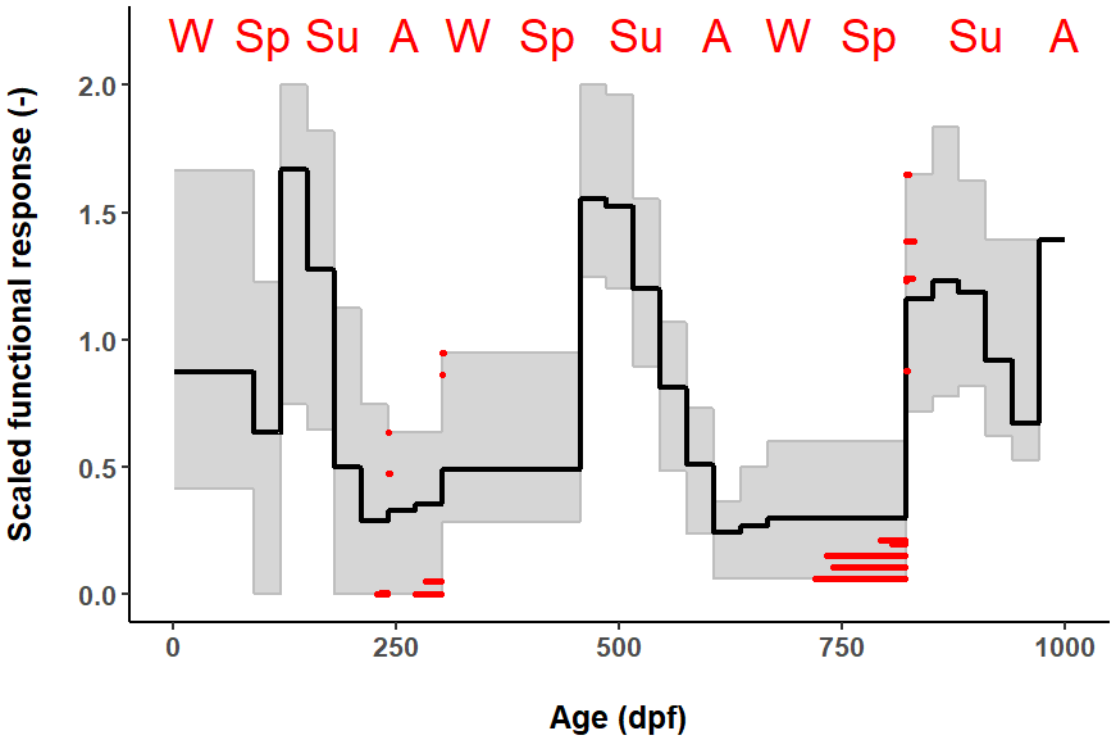


Figure 7: Evolution of the scaled functional response (*i.e.*, individual-scaled food availability) over time (in days post fertilization). The black line corresponds to the average scaled functional response. The grey area corresponds to the range between the lower and upper values of the scaled functional response, for the cohorts between 2000 and 2014. The red dots correspond to values of scaled functional response for days when the growth efficiency (K) is negative. Capital letters correspond to the seasons (W = Winter, Sp = Spring, Su = Summer, A = Autumn).

## 3.4 Energy partitioning

Our method allows studying energy partitioning between the main metabolic processes considered by the DEB model (*i.e.* growth, maturation and maintenance processes) through time, independently for each cohort. The study of the absolute fluxes (*kJ/day*) towards each metabolic process (Figure 8) clearly shows the temporal variability of the energetic fluxes, with very low total energy budget from late autumn to early spring. A decrease in the percentage of energy allocated to the growth during late summer/autumn (around 250 dpf and around 800 dpf) is also observed Figure 9, even with some moments with no energy allocated to growth (Figure 8, Figure 9). The decrease in energy allocation to growth is actually due to the increase in the proportion of maintenance processes to the

total energy budget, mainly the somatic maintenance (Figure 9). Also, during the end of summer/autumn, the cumulative percentage of the energy allocated to the main metabolic processes considered in the DEB model exceeds 100% suggesting a period of high nutritional stress for juveniles during some years.

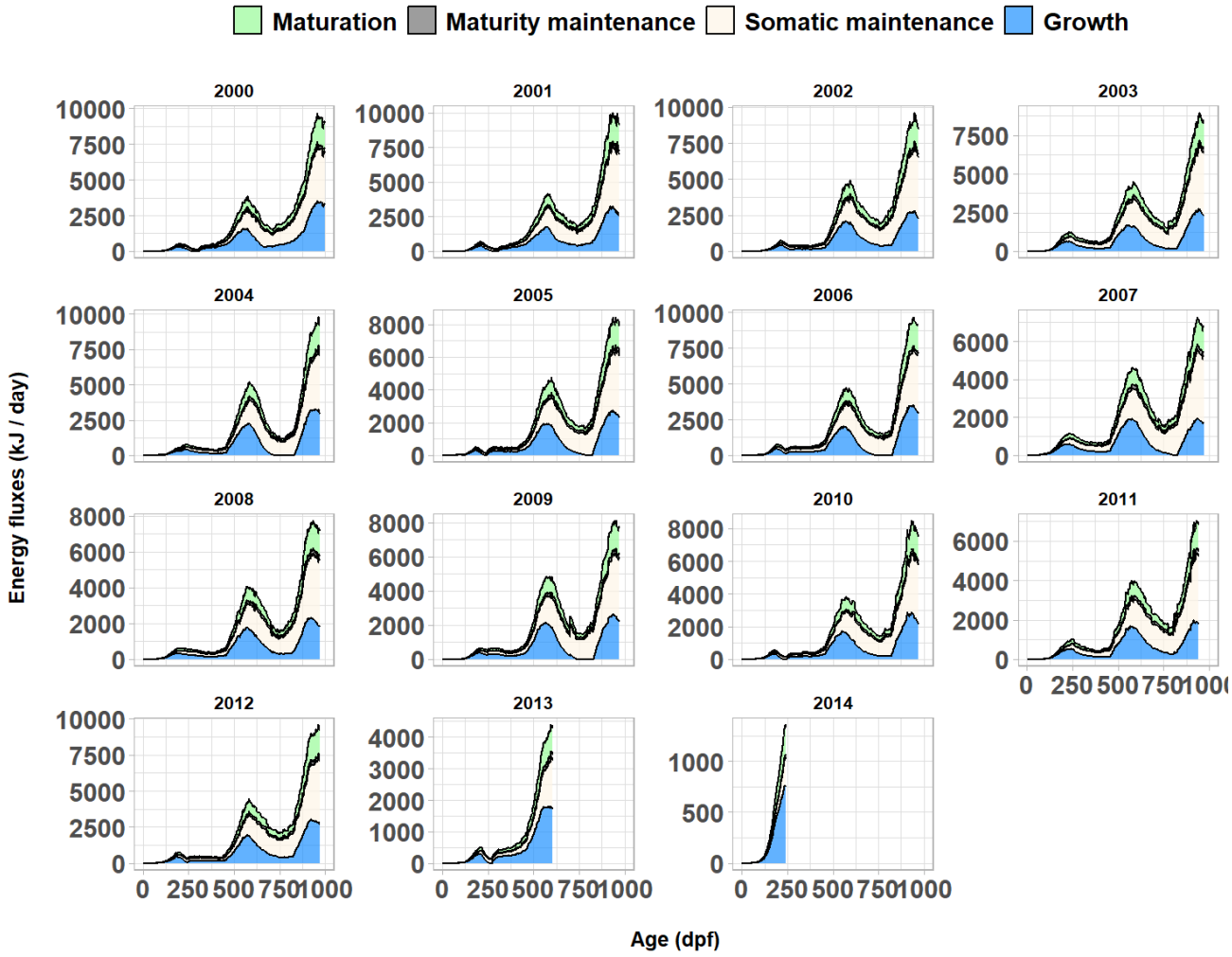


Figure 8: Energy fluxes towards maturation, maintenance of maturity, somatic maintenance and growth for an average individual of cohorts 2000 to 2014. Information for the G2 born in 2013, as well as for the G1 and G2 born in 2014, is not given, as growth data were not provided after 2014.

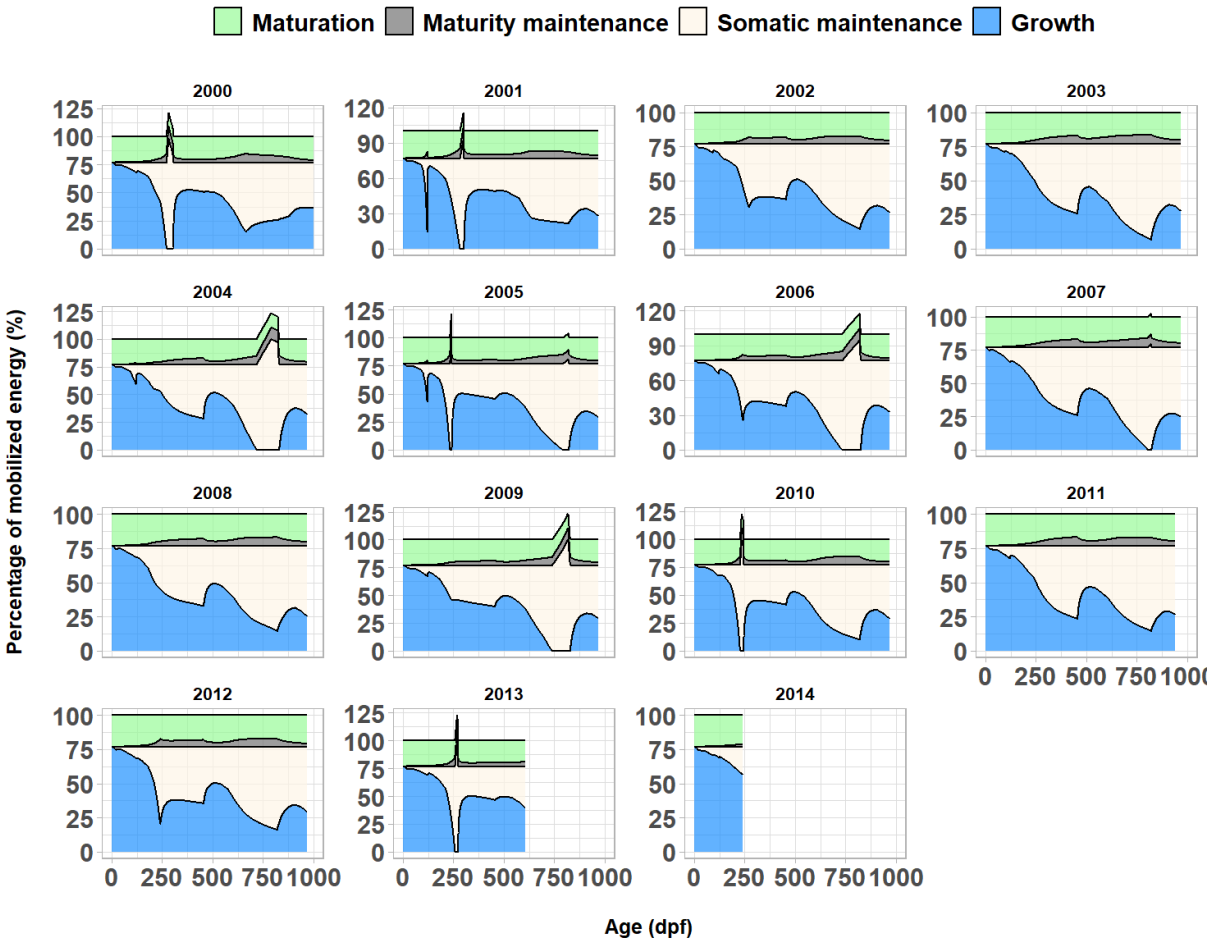


Figure 9: Percentages of mobilized energy allocated to maturation, maintenance of maturity, somatic maintenance and growth for an average individual of cohorts 2000 to 2014. Information for the G2 born in 2013, as well as for the G1 and G2 born in 2014, is not given, as growth data were not provided after 2014.

# 4. DISCUSSION

## 4.1 Highlights

This study applies a bioenergetic approach based on DEB theory to (i) investigate the potential of DEB model to highlight nutritional stresses for individuals and (ii) test the trophic limitation hypothesis for juvenile soles from a metabolic point of view. We reconstructed the scaled functional response, *i.e.*, the individual-specific food availability, from observed growth patterns and the daily temperature experienced by the individuals using inverse-DEB modelling. Although $f$ corresponds to

the food actually ingested by the individual (it takes into account food density, but also competition), it can be used as a proxy of food conditions available in the environment (Freitas et al., 2011). Classic estimations of food availability require extensive samplings of the benthic ecosystem, identification of potential prey and hypotheses on their energetic density. Provided that the model parameters are available and reliable, our method is time- and cost-efficient while accounting for temperature changes over time. This approach allows also describing in an accurate and dynamic way the energy assimilation and energy partitioning for an individual over time, under the experienced environmental conditions, but also in new environments such as those expected in the context of global warming. Finally, our approach allows identifying periods of nutritional stress, consequence of trophic limitation. Altogether, our method supports the hypothesis of trophic limitation during autumn in the Seine estuary, and can help predict energetic needs in marine nurseries and associated ecological consequences.

## 4.2 Food ingestion dynamics from observed growth trajectories

The energy consumption of organisms is particularly difficult to assess, because it depends on several physiological and environmental factors, as well as on the life stage of the individual (Kooijman, 2010; Yamashita *et al.*, 2001). The quantitative study of the individual-specific food availability allowed at a daily scale by the inverse-DEB modelling may interestingly complement other feeding approaches (stable isotopes and gut contents analyses) that can give insights of quantitative contributions of source and prey but not at a fine temporal resolution. The back-calculation of food ingestion and assimilation from growth patterns has already been used for the bay of Biscay Anchovies *Engraulis encrasicolus* (Pecquerie et al., 2012), as well as to test trophic limitation hypothesis for the sand goby over the period of nursery residence (Freitas et al., 2011). However, Pecquerie et al. (2012) did not use the temperatures really experienced by the fish, reducing the precision of the calculation of the food ingestion. In addition, the method used in Freitas et al. (2011) allowed to reconstruct the average individual-specific food conditions over the entire lifespan based on maximum sizes of fish.

We have the capacity with our method to describe fluctuations in the individuals' energy consumption. The decrease in energy consumption in late summer/autumn might be related to the

375 combined effects of (i) the still high temperatures and (ii) the decrease in individual-specific food
376 availability (see Figure 7). This first result showing the reconstructed food ingestion is important
377 because energy consumption of individuals is one of the main factors that allow understanding the
378 trophic limitation, and DEB model directly links energy consumption with individual-specific food
379 availability. Furthermore, the quantitative knowledge on feeding history is essential for the study of the
380 energy partitioning made in this study.

## 381 4.3 Studying energy partitioning to understand the trophic limitation from a
## 382 metabolic point of view

### 383 4.3.1 Energy allocated to growth

384 DEB theory deeply structures our knowledge on energy partitioning, particularly between
385 maintenance and growth during fish's entire life cycle including first life stages (Kooijman, 2010; van
386 der Meer, 2006). A DEB model considers that the individual consumes energy, even when it does not
387 grow, to maintain its organism and to mature. The increase with the age of energy requirement for
388 maintenance processes is the consequence of a maintenance proportional to the volume V and maturity
389 of the organism while assimilated energy is proportional to $V^{2/3}$ (see Table 1). This leads to a decrease
390 over time of the growth efficiency coefficient. This coefficient is also affected by seasonal cycle, with
391 a decrease of relative energy allocated towards growth in late summer/autumn. This decrease coincides
392 with an increase in the proportion of somatic maintenance processes to the total energy budget (Figure
393 9). However, more work is needed in order to investigate whether this increase of proportion of energy
394 allocated to the somatic maintenance is due to (i) an increase in the absolute maintenance requirements,
395 possibly linked to environmental conditions, or (ii) to the observed decrease in the energy assimilation
396 (figure 5). In the latter case, the observed seasonal decrease in energy allocated towards growth could
397 be an index of trophic limitation. Indeed, if the individual cannot assimilate enough energy, it allocates
398 in priority energy to maintenances, rather than growth, and this phenomenon is taken into account in
399 DEB theory (Kooijman, 2010).

### 4.3.2 Nutritional stress

The study of energy partitioning over time shows that for multiple years, the amount of energy theoretically allocated to the metabolic compartment exceeds periodically the energy the fish can mobilize from its environment (Figure 9). This result indicates a potential nutritional stress: the average individual is not able to mobilize sufficient energy from its food to balance energetic needs for maintenance. In this case, DEB theory allows to mobilize energy from the individual's structure (Kooijman, 2001). This is possible via processes of shrinking, observed when k (*i.e.* growth efficiency coefficient) is negative. Our results show that these periods of shrinking correspond to periods when the *f* value (*i.e*. individual-specific food availability) is very low (Figure 7). During a few days just after a period of low individual-specific food availability, k can remain negative, even if the mean value of *f* has risen. We interpret this by a little delay time after a nutritional stress, before the individual can re-allocate energy into growth.

These periods of nutritional stress can reflect critical trophic limitation periods, in late summer/autumn. This is coherent with the results of previous studies on the Seine estuarine nursery that identify this phenomenon at the same period of the year (Day et al., 2021; Saulnier et al., 2020).

## 4.4 Limits and perspectives

Some authors discuss the use of growth data for estimation of trophic limitation of nursery (Le Pape & Bonhommeau, 2015). Indeed, this implies the risk to overestimate the growth, hence energy consumption of individuals because of (i) apparent growth rates of only survival fish, and in this case study (ii) selectivity of the beam trawl or (ii) omitted immigration and emigration processes (bigger fish might migrate to deeper areas). However, if indices of trophic limitation are visible regarding larger individuals, we can assume that this will be even more the case for small individuals. Another limit of our method could be the fitting of the lengths estimated by the DEB model with length-at-age data obtained with a fixed birthdate. It would be interesting to investigate the effect of the birthdate on the results. Indeed, the spawning period, and thus the timing of colonization of estuaries by young stages are variable among sub-populations, depending on environmental conditions (Amara et al., 2000).

Moreover, our approach considers two major environmental factors (*i.e.*, temperature and food availability) on the individual's metabolism. However, other environmental factors affected by global change may influence species' energetic needs. For example, oxygen availability (Gibson, 1994), or pollution (Mounier et al., 2020) constitute stressors that might modify fish's metabolism, including energy assimilation (Sadoul & Vijayan, 2016). This is particularly true in coastal nurseries, where organisms are subjected to important environmental gradients, and rapid human-induced changes (McLusky & Elliott, 2004).

We assumed here that the f reconstructed using the method presented in this paper can be used to explore the potential trophic limitation of nursery grounds as it is, to some extent, representative of the average overall food conditions in the nursery. This is all the more relevant that preliminary results in this direction show for instance that there is a significant and positive link between the mean annual values of the scaled functional response (all individuals considered) and the mean annual values of the scaled functional response for each age class G0, G1 and G2 (see Appendix E). However, although we didn't highlight differences between age-classes (that could be interpreted in terms of competition for instance), a more in-depth year-to-year comparison of results of individual-specific energy availability and energy partitioning by age class, combined with data of environmental conditions (i.e. temperature, juveniles' abundance leading to competition, and prey production) will substantially improve our understanding of trophic limitation.

We carried out this study on an average individual of each cohort, as the aim was to investigate the potential of DEB models to reconstruct energy ingestion and highlight nutritional stresses for individuals. However, the use of this method to simulate several individuals will be particularly interesting, allowing to (i) consider inter-individual variations e.g. in $\{\dot{p}_{Am}\}$, and (ii) to extrapolate our results at the population scale, e.g. by including a probability to die when a nutritional stress occurs, which was not done here.

It would also be interesting to generalize the method to other study sites and to explore how other species belonging to the juvenile fish community can be considered together.

To conclude, our method based on the study of energy intake and energy partitioning at an individual scale responds to some difficulties raised in the concrete identification of signs of a trophic limitation for organisms (Ciotti et al., 2014; Le Pape & Bonhommeau, 2015). We showed that it is possible with our method to assess individual's food intake from their observed lengths, and results of energy partitioning put forward indices of trophic limitation such as growth reduction and periods of nutritional stress. Being able to identify periods of non-growing and nutritional stress is also interesting in the context of species' conservation, and fisheries management, as it extends our knowledge on underlying processes that affect fish populations' renewal, hence dynamic. All this will give a better insight of the nurseries' functioning and its evolution.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORS' CONTRIBUTIONS

***Marion Lefebvre du Prey**: Methodology, Software, Formal analysis, writing – Original draft, Visualization.* ***Jérémy Lobry**: Conceptualization, Methodology, Validation, Writing – Original draft.* ***Anik Brind'Amour**: Investigation, Data Curation, Writing- Review and Editing.* ***Hervé Le Bris**: Investigation, Data curation, Writing – Review and Editing, Supervision.* ***Bastien Sadoul**: Conceptualization, Methodology, Validation, Writing – Original draft, Supervision.*

## DATA AVAILABILITY STATEMENT

The data used for this work will be available upon acceptance of the manuscript on the database data.inrae.fr.

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# APPENDICES

Appendix A: Dynamic Energy Budget model

Parameters of the DEB model for *Solea solea*:

Table A.1: table of parameters of the DEB model for a juvenile of the common sole, *Solea solea*, with their description, unit, and values. All the parameters used in this study were found in Mounier et al. (Mounier et al., 2020). All rate parameters are expressed at the reference temperature $T_{ref}$ = 20°C = 293K).

| **Parameter** | **Description** | **Unit** | **Value** | |
|---|---|---|---|---|
| | | | Females | Males |
| $\{\dot{p}_{Am}\}$ | Maximum assimilation rate | $J.cm^{-2}.d^{-1}$ | 710 | 671 |
| $\dot{v}$ | Energy conductance | $cm.d^{-1}$ | 0.0724 | |
| $\kappa$ | Fraction of energy allocated to growth and somatic maintenance | - | 0.7682 | |
| $[\dot{p}_M]$ | Somatic maintenance rate | $J.cm^{-3}.d^{-1}$ | 39.18 | |
| $[E_G]$ | Cost of structure | $J.cm^{-3}$ | 5430 | |
| $\dot{k}_j$ | Maturity maintenance rate coefficient | $d^{-1}$ | 0.002 | |
| $E_H^b$ | Maturation threshold at birth | $J$ | 0.285 | |
| $E_H^j$ | Maturation threshold at metamorphosis | $J$ | 6.039 | |
| $\delta$ | Shape coefficient | - | 0.171 | |

| | | | |
|---|---|---|---|
| $\kappa_X$ | Digestibility coefficient | - | 0.8 |
| $\kappa_G$ | Growth efficiency | - | 0.7705 |
| $T_L$ | Lower boundary of tolerance range | $K$ | 276 |
| $T_H$ | Upper boundary of tolerance range | $K$ | 303 |
| $T_A$ | Arrhenius temperature | $K$ | 5119 |
| $T_{AL}$ | Rate of decrease at lower boundary | $K$ | 50000 |
| $T_{AH}$ | Rate of decrease at upper boundary | $K$ | 100000 |
| $d_v$ | Density of structure | $g_d.cm^{-3}$ | 0.2 |
| $q_v$ | Energy density of structure | J.$g_d^{-1}$ | 20920 |

Temperature correction factor:

In DEB theory, all metabolic rates are scaled to body temperature evolution thanks to the correction of primary parameters with a temperature correction factor TC. The parameters$\{\dot{P}_{Am}\}$, $\dot{v}$ , $[\dot{P}_M]$ and $\dot{k}_j$ are therefore multiplied by TC. TC is calculated as:

$$TC = \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \times \frac{1 + \exp\left(\frac{T_{AL}}{T_{ref}} - \frac{T_{AL}}{T_L}\right) + exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{ref}}\right)}{1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right) + exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)}$$

Appendix B: Data of temperature

The temperatures used for this study are sea surface temperatures (SST) from satellite observations, because bottom temperature data were not available in the Seine Estuary throughout each sampled year (see figure B.1.a). To ensure the reliability of the use of SST, we compared SST and bottom temperatures for the dates when both data were available. SST and bottom temperatures are significantly correlated, with a Pearson's coefficient of 0.96 (see Figure B.1.b).

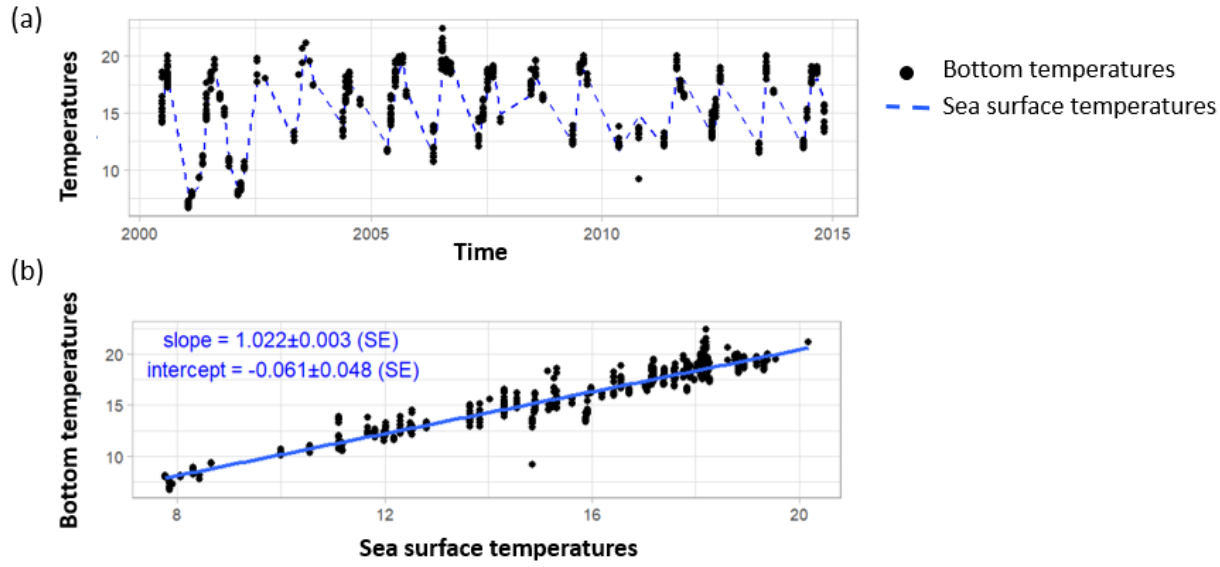


Figure B.1: (a) Temperatures available for the Seine estuary from 1998 to 2014. The black dots represent the bottom temperatures; the blue dashed line represents the sea surface temperatures. (b) Correlation of the sea surface temperatures and the bottom temperatures for the dates between 1998 and 2014 when they are both available in the Seine estuary.

Appendix C: Distribution of the scaled functional response

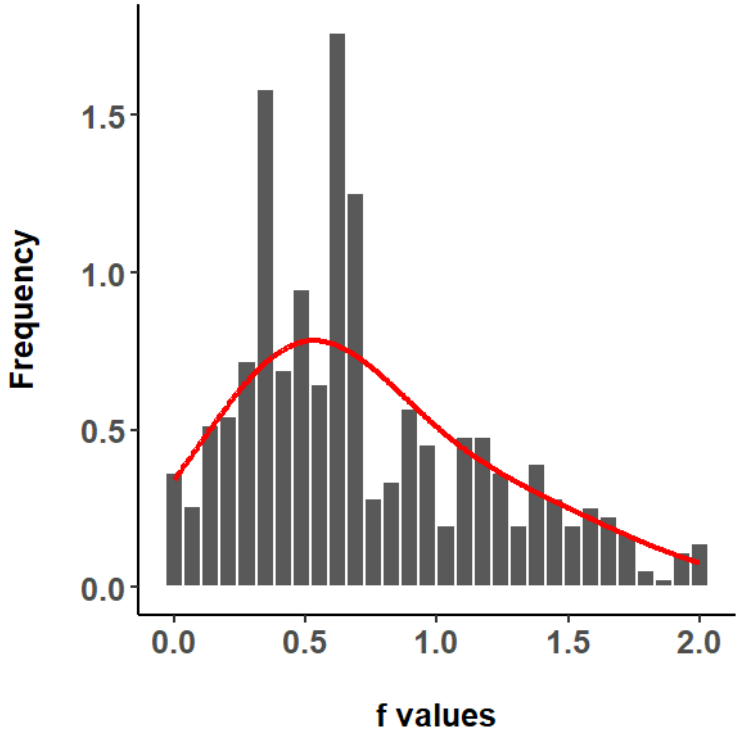


Figure C.1: Histogram and distribution (red line) of values of *f* that are back-calculated in the inverse-DEB modelling from the observed lengths of juvenile fish.

Appendix D: Fit of the growth trajectories reconstructed by the DEB model under experienced environmental conditions with the observed mean lengths data, for each cohort

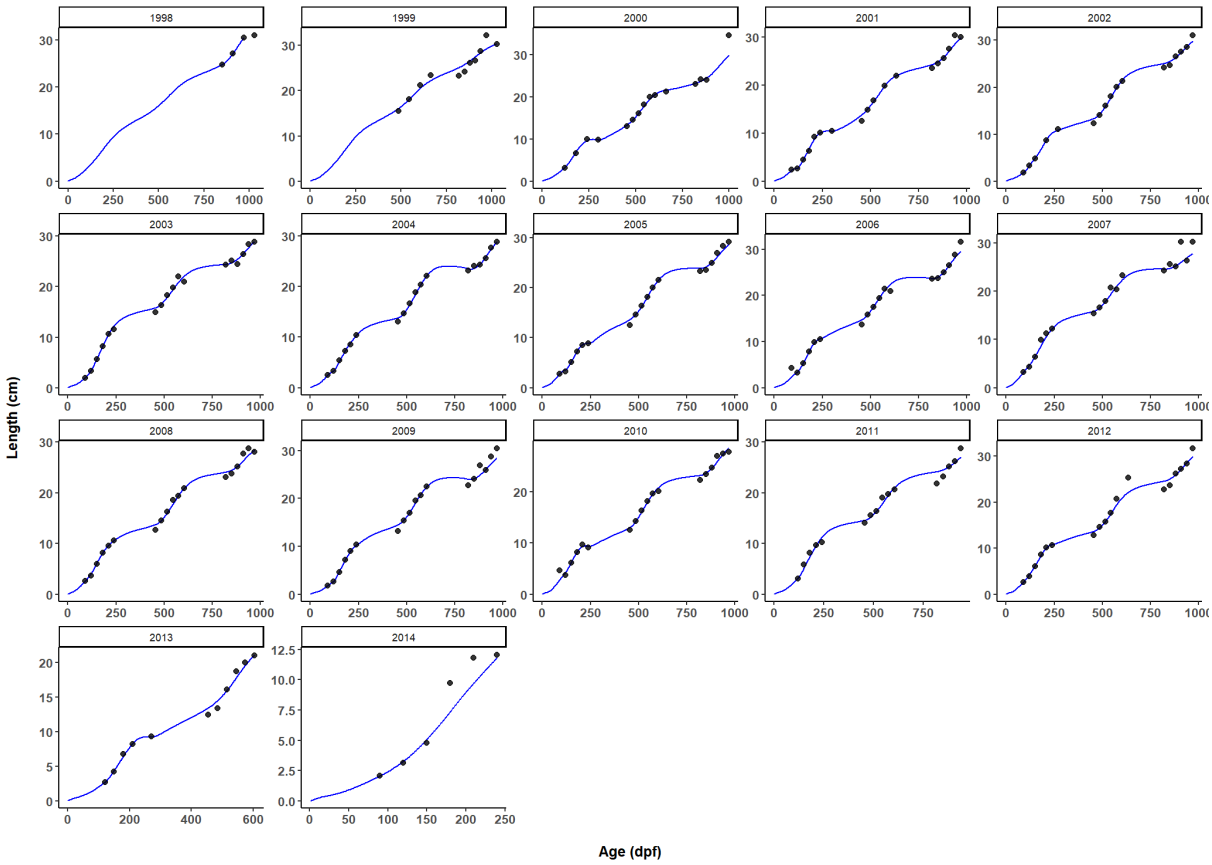


Figure D.1: Observed mean lengths (black dots) over time (in days post fertilization), and estimations of lengths by the DEB model under experienced temperatures and relative food conditions, for each cohort. The blue line represents the average estimated lengths over time for each cohort.

Appendix E: Comparison of mean annual values of the scaled functional response for all individuals and for each age-class.

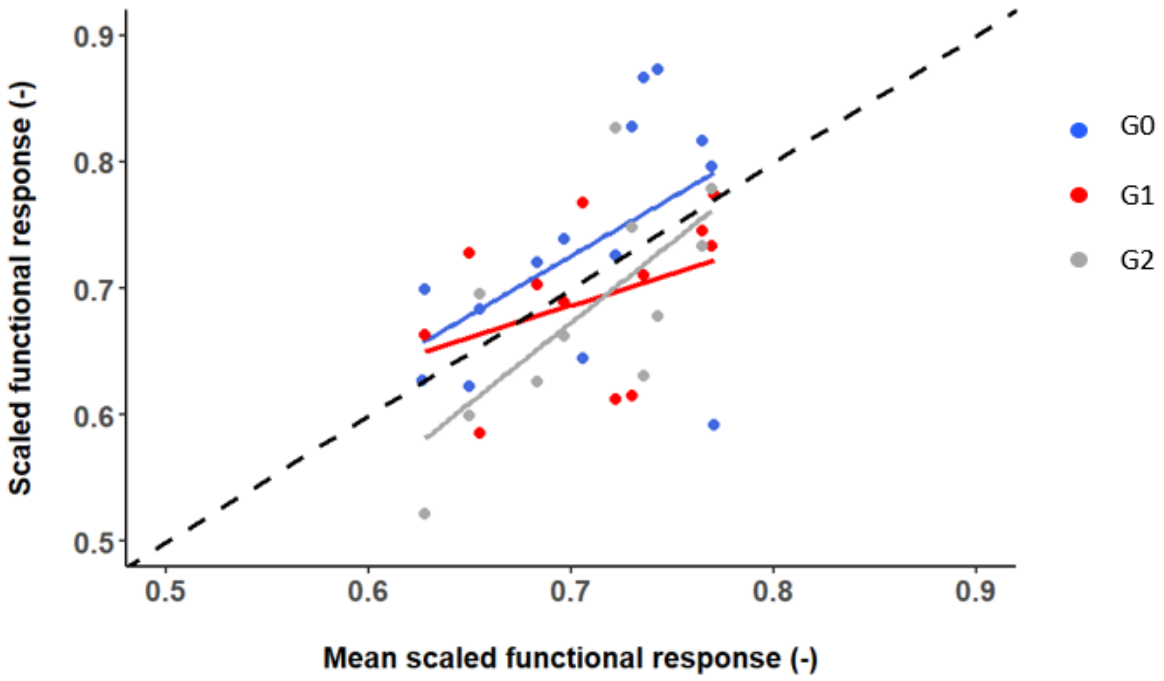


Figure E.1: Mean annual values of the scaled functional response (*f*) for each age-class (G0, G1 and G2) as a function of the mean annual values of the scaled functional response when considering all the individuals present in the nursery. Each point represents a year. The dashed line is the x=y bisector.