**Modelling historical mesocosm data: Application of a fish bioenergetics model in semi-natural conditions**

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Abstract Developing ecological models for accurately predicting the dynamics of a population and individual physiological processes in field conditions is a challenging task for ecosystem management and ecological risk assessment. Here we propose to assess the relevance of a Dynamic Energy Budget (DEB) model calibrated using data previously generated from laboratory experiments for adult three-spined sticklebacks (*Gasterosteus aculeatus*) living in semi-natural conditions. We compared different ways of integrating different data sets such as temperature and prey abundance obtained in mesocosm experiments in order to assess the predictive capacity of the model. By this study, we provide recommendations for developing an appropriate environmental scenario (*e.g.* natural variations of food and temperature) for using a DEB model in a field context. We conclude that a DEB model calibrated with laboratory data can be used to predict the physiological processes of an organism living in semi-natural conditions, but that the reproductive behavior of the organism can affect the predictions. Finally, we suggest that further studies on the feeding behavior may be necessary for immature organisms.

**Key words** Dynamic energy budget, three-spined stickleback, environmental scenario, mesocosm

# Introduction

Ecosystems have been threatened by human activities for several centuries. The pressure made on habitats, the release of pollutants as well as changes in global climate are among the causes driving biodiversity loss and disturbing ecosystem functioning. Evaluating biological responses to specific anthropogenic stressors such as warming or toxicant releases are of great interest but are often restrained to tests on specific organisms in laboratory conditions. However, laboratory experiments do not include many biological interactions like predation, competition, or variations of environment factors although these ecological factors may significantly modulate the effect of the studied stress ([Forbes et al. 2011](#_ENREF_18), [Beaudouin et al. 2015](#_ENREF_6), [Goussen et al. 2016](#_ENREF_25)). To overcome these limitations, developing ecological models that integrate relevant information on the ecosystem has been proposed as a powerful solution to help ecosystem management and risk assessment ([Forbes et al. 2017](#_ENREF_19)).

Among the existing ecological models, the Dynamic Energy Budget (DEB) Theory has been suggested as a starting point to improve ecosystem management and risk assessment ([Galic and Forbes 2017](#_ENREF_20)). This theory describes the energy fluxes during the whole life cycle of an individual taking into account the effects of both temperature and food level ([Kooijman 2010](#_ENREF_37)). DEB models have been tested on many organisms and used in different applications (*e.g.* global change, ecotoxicology, extrapolation to population-level dynamics) ([Jusup et al. 2017](#_ENREF_36)). However, as environmental data are often difficult to obtain, DEB models are mainly calibrated with laboratory experiments usually performed under standard conditions ([Augustine et al. 2011](#_ENREF_3), [Goussen et al. 2015](#_ENREF_24)). Nevertheless, some studies have already shown that integrating effects of environmental factors (*e.g.* food level or temperature) in DEB models is critical for highlighting the effects of chemical stressors ([Jager and Zimmer 2012](#_ENREF_35), [Cedergreen et al. 2016](#_ENREF_16)). Indeed, the complexity of natural ecosystems explains why the results from laboratory often fail to accurately predict natural processes. Thus, in order to improve ecosystem management, a focus on DEB model predictions using environmental scenarios (*e.g.* natural variations of food and temperature) should be made.

Developing environmental scenarios requires a large amount of data on the seasonal and temporal variations of temperature and food web dynamics. To fill this gap, mesocosm experiments provide a sound basis to reconstruct environmental scenarios and study the biological responses of organisms in semi-natural conditions. Indeed, they have played an important role in improving our understanding of ecology and ecosystem functioning ([Caquet et al. 2000](#_ENREF_15)). For example, these experiments have been used in ecotoxicology to assess direct and indirect effects of toxicants on populations and also investigate responses at different levels of biological organization under natural variations of ecological factors ([Boyle and Fairchild 1997](#_ENREF_13), [Caquet et al. 2000](#_ENREF_15)). Thus, these experiments provide a hazard analysis with an improved ecological realism compared to laboratory experiments ([Beaudouin et al. 2008](#_ENREF_7), [Beaudouin et al. 2012](#_ENREF_5)).

The three-spined stickleback (*Gasterosteus aculeatus*) is a small teleost fish native to the Northern Hemisphere and is a relevant fish species for mesocosm studies ([OECD 2006](#_ENREF_48)) as it has a relatively small size and its habitat is easy to mimic. Furthermore, the ecology and biology of this species is relatively well-known ([Wootton 1984](#_ENREF_65), [Bell and Foster 1994](#_ENREF_8)), and experiments have already been performed in mesocosms to assess the effects of chemicals on stickleback populations ([Roussel et al. 2007](#_ENREF_51), [de Kermoysan et al. 2013](#_ENREF_17)). The effects of environmental factors on the sticklebacks biology has also been extensively studied in laboratory with both temperature and food availability affecting the biology of sticklebacks ([Wootton 1984](#_ENREF_65), [Bell and Foster 1994](#_ENREF_8), [Hopkins et al. 2010](#_ENREF_31), [Hovel et al. 2015](#_ENREF_33)). In addition, a bioenergetic model of the three-spined stickleback, based on the DEB theory ([Kooijman 2010](#_ENREF_37)) and describing its whole life cycle, has already been developed and calibrated using laboratory data ([Leloutre et al. 2018](#_ENREF_42)).

Accordingly, this study aims to assess the relevance of the *Gasterosteus aculeatus* DEB model calibrated with previously generated laboratory data to describe the physiological processes of the organism under semi-natural conditions (variations of temperature and food) using pre-existing data from mesocosm experiments. For this purpose, we tested different ways of integrating temperature and food data into the DEB model to properly formulate the food and temperature scenarios. To build the food scenario, we made different hypotheses on the distribution of food in the mesocosms and on the feeding behavior of sticklebacks. These hypotheses were tested by comparing predicted and observed data on stickleback processes recorded during two different mesocosm experiments.

# Material and methods

*Experiment description*

The present study uses previously generated data from two experiments (1 and 2) performed in lotic mesocosms (INERIS, Verneuil-en-Halatte, France) during two different years with two contrasted sets of environmental conditions (*i.e.* temperature, food dynamics). Each experiment was conducted with 11 mesocosms, thus a total of 22 stickleback populations were monitored. A complete description of the experimental setup can be found in De Kermoysan et al. ([2013](#_ENREF_17)). Briefly, each mesocosm was 20 m long and 1 m wide with a water depth of 30 cm upstream (0–9 m) and 70 cm downstream (11–20 m). A one-meter slope separated the two sections. The water flow for each mesocosm was 0.8 m3.h-1. Each mesocosm was set up between October and December with sediments (80% sand and 20% clay), macrophytes, zooplankton and macroinvertebrates (details provided in Supplementary Information (SI) Section 1). The experiments started at the beginning of March when 15 mature female and 10 mature male sticklebacks (thereafter called the founders) were introduced in each mesocosm. Before their release, founders were measured, weighed and marked with a 1.2 mm × 2.7 mm alphanumeric tag (VI Alpha Tags, NorthwestMarine Technology, Shaw Island, WA, USA). Individuals were selected to have a similar length. The experiments lasted 210 days and 213 days, respectively for experiment 1 and 2. At the end of each experiment, each mesocosm was emptied to collect all sticklebacks which were then sacrificed using a high dose of MS-222, measured, and weighed. Fish sex was determined by visual observation of the gonads. In our study, only the data for which a founder with a visible tag was recovered were used for the DEB model simulations (SI Table S1). Daily background mortality probability of sticklebacks during the experiments was estimated using the method described by Soubeyrand et al. ([2007](#_ENREF_54)).

Macroinvertebrates and zooplankton were sampled every four weeks and identified to the lowest practical taxonomic level. A detailed description of the sampling methodology is provided in SI Section 1 and Table S3. The water temperature was measured every 10 minutes throughout the course of the experiments using two sensors (± 0.1°C, HOBO0257, Prosensor, Amanvillers, France) which were positioned at 5 m and 15 m from the inlet of water, respectively on the surface and at 70 cm-depth (thereafter called Temp5 and Temp15). These sensors were placed in four randomly chosen mesocosms (thus a total of four Temp5 and Temp15 for each experiment).

*DEB model description*

DEB theory describes the rate at which the organism assimilates and uses energy for its energetic processes: maintenance, growth and reproduction. This theory resulted in the κ-rule DEB model which proposes that a fixed fraction κ is allocated to maintenance and growth and that the remaining fraction (1 – κ) is available for maturity and reproduction ([Kooijman 2010](#_ENREF_37)). In the present study, we used the DEB model developed for the whole life cycle of the three-spined stickleback by Leloutre et al. ([2018](#_ENREF_42)). The equations are provided in SI Section 2. Parameters depending on temperature were corrected by the temperature function adapted for sticklebacks by Hovel et al. ([2015](#_ENREF_33)). Male sticklebacks have a smaller maximal length than females, this dimorphism was modeled by a type R metabolic acceleration ([Kooijman 2014](#_ENREF_38)): the value of the parameter κ for males decreases after maturity and the parameter α is the fraction subtracted from κ. This assumes that a higher amount of energy is used for the reproduction which is coherent with the fact that male sticklebacks provide all the parental care during the breeding season.

We adapted the implementation of the feeding level in the DEB model of Leloutre et al. ([2018](#_ENREF_42)) by using a hyperbolic functional response, as suggested by Kooijman ([2010](#_ENREF_37)):

with (1)

Where is the scaled food density and the food density in J which is daily updated, is the necessary amount of food to be fed ad libitum (J/mm2) which depends on the squared structural length L (mm) of the fish. Our definition of the functional response is slightly different from the one in Kooijman ([2010](#_ENREF_37)) as it takes into account the length of the fish. Indeed, for a given amount of food in the environment, two fish predators with different length would not have the same level of satiety. According to Leloutre et al. ([2018](#_ENREF_42)), is a parameter which gives a theoretical value of the demand in energy of the fish to cover all its bioenergetics processes, including all its energy costs.

*Integration of the freshwater temperature in the DEB model*

First, the inter-mesocosm variability was assessed by comparing the temperature data recorded by the same type of sensor in the four mesocosms (four Temp5 and Temp15 per experiments) to their overall mean temperature for each type of sensor.

Then, in order to account efficiently for the effects of the spatial heterogeneity of the water temperature into the mesocosm (intra-mesocosm variability) on the bioenergetic processes of sticklebacks, we performed three simulations of the growth and reproduction of a hypothetical individual using (i) the temperature recorded every 10 minutes on the surface (from Temp5), (ii) in the bottom (from Temp15), or (iii) using the mean of both temperatures recorded every 10 minutes by the sensors. The hypothetical individual was fed ad-libitum and considered immature for the length simulations (Initial length at 10 mm) and mature for the reproduction (Initial length at 35 mm).

Finally, to take into account the effect of the temporal variation of water temperature during the experiments on the bioenergetic processes of sticklebacks, we examined how a temperature scenario could be integrated into a model using discrete time. Three time-steps were tested to understand which precision level is needed in the observations to accurately predict growth and reproduction (SI Figure S3). Simulations of growth and reproduction using the temperature data were either implemented as (i) the daily mean temperature, (ii) the weekly mean temperature, (iii) the mean of the temperature over the experiment or (iv) using all the temperatures recorded every 10 minutes (this simulation was considered as the reference). The results of the three first simulation types were compared to the last simulation considered as the reference. Predictions were performed using the same hypothetical individual and the mean of both temperatures recorded by the sensors.

*Integration of food samples in the model*

Prior to integrating food samples in the DEB model, the uncertainty of zooplankton and macroinvertebrate samples was estimated. For this purpose, specific samples were performed using 13 water samples for the zooplankton and 12 samples of macroinvertebrates using each type of sampling devices (tubes, tiles, or scrubbed walls, see SI Section 1 Tables S5 and S7). The uncertainty was assessed by a bootstrap method with replacement (n=10,000). The uncertainty analysis is detailed in SI Section 4.

Furthermore, of all the zooplankton and macroinvertebrate species encountered in the mesocosm, sticklebacks only predate a subset. This subset was determined by analyzing literature data focusing on the diet of the three-spined sticklebacks ([Hynes 1950](#_ENREF_34), [Walkey 1967](#_ENREF_59), [Allen and Wootton 1984](#_ENREF_2)) and data on the gut contents of 40 sticklebacks obtained in a former mesocosm experiment (SI Tables S9 and S10). Then, the total mesocosm abundance of this subset was estimated by assuming that the quantity of prey was homogeneous throughout the mesocosms and that the density in the sampling devices was representative. Hence, a ratio between the volume/area of the sampling devices and mesocosms was used to convert the abundance of a given species in the sampling devices to the mesocosm abundance (SI Tables S11 and S12). Then, abundance per species was converted into energy by using organism mass/energy content ratio found in literature (SI Tables S13 and S14). Finally, the energy density in the mesocosms was linearly interpolated between the sampling dates.

Finally, three different hypotheses were considered to compute the individual feeding level for founder fish. In all cases, we assumed that founders were dominants compared to other sticklebacks born during the experiments, and thus monopolize the feeding resources in case of limitation. (i) The first hypothesis was to simply consider that sticklebacks were fed ad libitum in the mesocosms and thus, food samples are not required to estimate the feeding level of sticklebacks (hypothesis “ad libitum”).

(ii) Using the food energy in the mesocosms, another hypothesis was to consider that the food level is equally divided between founders. To do that, we calculated a proportion factor relative to the number of founders in mesocosms to equally divide the amount of food between them (hypothesis “equal food partition”)

(iii) Our last hypothesis is based on the stickleback foraging behavior (hypothesis “foraging behavior”). It has been shown that sticklebacks eat in the water column ([Thomas 1974](#_ENREF_57), [Hart and Gill 1994](#_ENREF_29)). We then considered that the food density corresponds to the amount of available food in the water column around the foraging fish. To do that and because the food energy was assumed to be homogenous throughout the mesocosm, we calculated a proportion factor from the total surface of the mesocosm and a surface taking into account the needed distance for foraging. Indeed, sticklebacks have a reaction distance between 102 mm for a pale-yellow daphnids and 260 mm for a 10 mm-long *Gammarus* in turbid water ([Wootton 1984](#_ENREF_65)). Furthermore, the mean distance travelled by sticklebacks after rejection of a food object was calculated ([Thomas 1974](#_ENREF_57)) and was at most 146 mm. This distance is reduced to 60 mm in case of acceptance of the food. Considering these results, we calculated that a distance of 130.8 mm (i.e. median values reported by Thomas ([1974](#_ENREF_57)) in case of rejection of an item) should be sufficient for the stickleback to find its preys. Thus, a proportion factor of 1/1500 was calculated and seemed to be a relevant assumption as it resulted in dividing the mesocosm into 130.8 mm diameter cylinders.

*Model calibration*

A new calibration of the DEB model parameters using the functional response for the feeding level was performed. Model parameters values were inferred by Bayesian numerical calibration ([Bois 2009](#_ENREF_10)) using the same laboratory experiments, likelihood functions and prior distributions as detailed in Leloutre et al. ([2018](#_ENREF_42)) (SI Section 2).

Energy budgets for males were also re-adjusted to assess the level of sexual dimorphism in the mesocosms.For this purpose,parameter α (called α’) was re-calibrated using the male length data from experiment 1 and the calibration was assessed on the data from experiment 2.

Finally, we calibrated the inter-individual variability considering that the DEB parameters related to the feeding processes (surface-area-specific maximum assimilation rate and the proportional factor to be fed ad libitum (φ)) were individual-specific. To fit the parameters, we used a hierarchical population model ([Gelman et al. 1996](#_ENREF_21)) in order to disentangle the inter-individual variability from the uncertainty in parameter estimation ([Gelman et al. 1996](#_ENREF_21), [Bois et al. 2010](#_ENREF_11)) (SI Section 2). The calibration was made on the 83 individual female length data from experiment 1. The calibration of the DEB model was performed using the software R 3.3.1 with the coda package ([Plummer et al. 2016](#_ENREF_50)) and MCSim, which is designed for Bayesian inference through Markov Chain Monte Carlo (MCMC) ([Bois 2009](#_ENREF_10)). Three independant Markov Chains were run for each calibration.

Predictive capacity of the DEB model for mesocosm experiments.

All simulations for growth and reproduction were run with the R 3.3.1 software.The predictive capacity for growth was assessed by comparing the predicted and observed mean length of the founders in the mesocosms at the end of the experiments. The uncertainties over the food availability (1000 different scenarios) and over the DEB parameters (computed from 1000 randomized sets of parameters selected from the last 5000 posterior distributions) were taken into account. To analyze the predictions of the inter-individual variability, we compared the simulated length of each individual trajectory in experiment 2 considering 100 scenarios of food with or without 100 random draws of and φ per individuals to the observed length of the individuals.

As female founder sticklebacks were supposed to be mature, the DEB model predicts the cumulated number of eggs produced by the females. To assess if the order of magnitude of the cumulated number of eggs predicted by the DEB model for female sticklebacks during the breeding period were accurate, we compared the predictions to data provided from literature ([Wootton 1973](#_ENREF_63), [Mori 1993](#_ENREF_46)). The simulations were made considering 100 random draws of and φ and 100 scenarios of food per individual and considering the same breeding period (March to early July) than in Mori ([1993](#_ENREF_46)).

# Results

*Mesocosm description*

Table S1 gives the number of founder males and females used for the analysis and their observed length at the beginning and end of the experiments and Table S2 gives the population characteristics for both experiments. At the end of the experiments, founders were smaller in experiment 2 than in experiment 1 and males were smaller than females in both experiments. Furthermore, the estimated daily mortality probability was 0.21 % for female founders in both experiments and 0.31 % and 0.20 % for male founders in experiment 1 and 2 respectively.

*Integration of the freshwater temperature in the DEB model*

The differences in temperature measured by Temp5 and Temp15 were small between the four different mesocosms (SI Figure S1, 95% of inter-mesocosm differences were smaller than 2.4 %), thus the mean temperature recorded every 10 minutes respectively by all Temp5 and Temp15 for each experiment was kept for the following analyses.

Concerning the intra-mesocosm variability of the temperature, the difference of temperature between Temp5 and Temp15 could reach up to 4°C during the summer period. The results of the simulations using the temperatures recorded every 10 minutes throughout time by Temp5, Temp15 or the mean temperatures of both sensor showed that the use of the mean temperatures would lead to an error of 5 % maximum on growth and reproduction. However, the error can reach 15 % if we only use the temperatures measured either in the surface water (Temp5) or in deeper water (Temp15) (Figure 1a, SI Figure S2).

Regarding the choice of time-steps for temperature to integrate in the model, Figure 1b shows that using the mean temperature per day led to 0.2% of mean error over the entire experiment on growth and reproduction with a maximum of 3% error occurring with the highest temperatures. The error was no larger using a step of 1 week to implement the temperatures (SI Figure S4). Furthermore, the simulation with the mean temperature over the entire experiment led to a good approximation of the mean growth and reproduction at the end of the experiment (error < 1%, data not shown).

*Integration of the food samples in the model*

Zooplankton, higher crustacea (*Gammarus* and *Asellus*), and a diptera family (*Chironomidae*) were among the most frequently found species in the gut contents of sticklebacks (SI Tables S9 and S10). Considering the abundance of these species, we calculated the total amount of available energy obtained from these preys in the mesocosms. Moreover, our uncertainty analysis on food data showed that for zooplankton, at each sampling date, the sampling methodology captures 80 % of abundances estimated with an error less than 25%, 18%, 15% and 11% for *Rotifera, Cladocera, Nauplii* and *Copepoda* respectively (SI Table S6, Figures S5 and S6). For macroinvertebrates, we considered that the uncertainty for *Gammarus pulex, Asellus* *aquaticus* and *Chiromidae* were the same as for *Stylaria lacustris* and were less than 40% in 80 % of the cases (SI Table S8 and Figure S7).

*Model calibration*

For each calibration (DEB model, inter-individual-variability), the Gelman-Rubin index was smaller than 1.1 and the three Markov chains converged around the same value. Parameter values were close to the ones estimated during the last calibration ([Leloutre et al. 2018](#_ENREF_42)). For male sticklebacks, the value of α’ (0.111 ± 0.001 (-)) using mesocosm data was more important than the one obtained with laboratory data (0.082 ± 0.004). For the inter-individual variability, the coefficient of variation of and φ were similar (0.054 ± 0.010 and 0.055 ± 0.010 respectively). All the estimated values for the parameters can be found in the Appendix.

*Predictive capacity of the DEB model for growth in* ***semi-natural conditions***

Figure 2 shows the total amount of available energy and the resulting functional response *f* over the course of the experiments using the different hypotheses for food access. The energy provided by food in the mesocosms was lower in experiment 2 than in experiment 1 (Figure 1a). Using the hypothesis called “foraging behavior”, *f* fluctuated between 0.61 and 0.98 for experiment 2 whereas for experiment 1, *f* was close to 1. Using the hypothesis “equal food partition”, *f* was close to 1 for both experiments (Figure 2b).

Simulations considering that sticklebacks were fed ad libitum led to an overestimation of the length of the founders at the end of both experiments. The difference between the observations and predictions is particularly marked for experiment 2. Indeed the mean female observed length is 56.14 mm against 62.93 mm for the mean predicted length (observed mean length outside the 95% prediction interval), resulting in an error of 12% (Figure 3a).

For females, the simulations including prey abundance and hypothesis “equal food partition” were not relevant as they gave the same results as when female sticklebacks were considered ad libitum (Figure 3b). Simulations considering the hypothesis “foraging behavior” were better for both experiments and the prediction error is reduced to 0.8 % for experiment 2 (Figure 3c): the observed mean female length was inside the 95% prediction interval.

Similarly, predictions for males were more accurate using the hypothesis “foraging behavior” for the food scenario. However, the predictions overestimated the mean length of the male founders by 4% at the end of both experiments (Figure 3c). The use of α’, accounting for the level of sexual dimorphism in mesocosms and calibrated with data from experiment 1, considerably improved the predictions (0.6% of error on the mean predicted length) for experiment 2 (Figure 3c).

Finally, simulations of individual length of sticklebacks which only include the food uncertainty failed to predict the highest observed lengths of male and female founders (Figure 4a,b). However, the introduction of an inter-individual variability (here introduced on parameters and φ) gave a relevant range of length at the end of experiments (Figure 4c,d) as the majority of the observed points were within the 95% prediction interval. The extreme points were also successfully captured.

Predictive capacity of the DEB model for reproduction in semi-natural conditions

Figure 5 gives the cumulated number of eggs observed in field and laboratory and predicted by the DEB model for founder female sticklebacks. Simulations of our DEB model taking into account the hypothesis “foraging behavior” yielded an estimated number of eggs of 1093 ± 138 and 907 ± 92 for the period March to early July for experiments 1 and 2 respectively (Figure 5). Mori ([1993](#_ENREF_46)) estimated that the cumulative number of eggs for females was of 940 eggs at the most for the same period. In the laboratory, the number of eggs can reach 2610 eggs in 13 weeks with a high feeding ration and decrease at 727 eggs with a low feeding ration ([Wootton 1973](#_ENREF_64)).

# Discussion

*Mesocosm description*

Mesocosm experiments provide great insight and understanding of ecosystems. During the mesocosm experiments, the daily mortality probability was more important for male sticklebacks than females in experiment 1. This higher mortality rate for males was expected because of their important parental care during the breeding season. Indeed, during the reproductive period, males have a lower prey encounter rate compared to females which are more mobile: Wootton ([1972](#_ENREF_62)) explained that the amount of time spent at the nest for a male stickleback can reach up to 90% until hatchling emergence. Males are also more exposed to some risks ([Moodie 1972](#_ENREF_45), [Whoriskey and Fitzgerald 1985](#_ENREF_61)) like predation. We did not find the same result for experiment 2 as male and female founders had about the same daily mortality probability. One may hypothesize that males in experiment 2 may have been less active than in experiment 1. Indeed, by definition, the environmental conditions (food density, photoperiod, freshwater temperature) of mesocosms vary between experiments and could have induced a difference in investment in the reproduction processes of male sticklebacks ([Borg 1982](#_ENREF_12), [Stanley and Wootton 1986](#_ENREF_55)).

*Development of the temperature scenario*

To consider temperature effects on the bioenergetic processes of sticklebacks, a focus on the temperature used for the simulations should be made. The habitat of sticklebacks is characterized by relatively shallow water ([Kynard 1978](#_ENREF_41), [Mori 1994](#_ENREF_47), [Kraak et al. 1999](#_ENREF_40)). Inside each mesocosm, sticklebacks were observed in both upstream (-30 cm) and downstream (-70 cm) during the experiments. Given this intra-mesocosm variability, the temperatures recorded by both sensors (Temp5 and Temp15) could be relevant. Our study showed that the variations of temperature in the water column (surface vs depth) may strongly impact the DEB predictions. Thus, the location of the temperature sensor in the experiment should be set according to the ecology of the species of interest. For example, a bottom temperature may be more relevant to use for benthic species whereas the surface temperature would be more relevant for pelagic species. In our temperature scenario (Table S4), we decided to use the mean of both sensors as sticklebacks could be found in both locations.

Furthermore, the temperature regime in the mesocosm experiments corresponds to a small stream (1 m wide and 30 to 70 cm depth) with a relatively low water flow (0.8 m3.h-1). The daily freshwater temperature fluctuations were mostly dependent on the atmospheric temperature. In a natural stream, the water temperature would also be depending on the distance from the source and the water flow, but usually the atmospheric conditions are the main drivers of the seasonal and diurnal temperature fluctuations ([Caissie 2006](#_ENREF_14)). Therefore, integrating these temperature variations in the DEB model was also worthy of interest. However, our study showed that implementing the temperature fluctuations over time did not strongly improve the predictions. Hence, the choice of the temperature step to integrate in the model is not decisive, and should be set in regard to the objective of the model and the computational costs. In our case, to reduce computational costs of the model while keeping temperature variations to assess the effects of both variations of environmental factors (*e.g.* temperature, food) on the predictions, we used the daily mean temperatures from both sensors for the temperature scenario (Table S4).

*Development of the food scenario*

The stickleback’s diet has been extensively studied. We analyzed studies of freshwater populations of sticklebacks from Northern Europe to determine which prey were relevant for our food scenario. The importance of zooplankton, especially copepods, was described in Hynes ([1950](#_ENREF_34)), Walkey ([1967](#_ENREF_59)) and Allen and Wootton ([1984](#_ENREF_2)) as well as for the sticklebacks raised in mesocosms (Tables S9 and S10). Higher crustacea as well as chironomids were also major elements of the diet in both the literature ([Hynes 1950](#_ENREF_34), [Walkey 1967](#_ENREF_59), [Allen and Wootton 1984](#_ENREF_2)) and the mesocosm observations. Furthermore, seasonal variations of the gut content of sticklebacks have been identified but can be interpreted as changes in the food availability rather than seasonal shifts in food preferences of sticklebacks ([Wootton 1984](#_ENREF_65)). As zooplankton and macroinvertebrate populations were sampled every four weeks, the presence of the preys in mesocosms was followed seasonally and was accounted for in the food scenario.

Among the range of possible prey, a selection of a preferred prey type by sticklebacks could be assumed. However, it has been shown that prey selection in sticklebacks is related to prey density. Indeed, when exposed to low food density environments, sticklebacks tend to be less selective and to eat less palatable prey types ([Beukema 1968](#_ENREF_9), [Wootton 1984](#_ENREF_65), [Gill and Hart 1994](#_ENREF_22)). Consequently, we did not include any selection of prey type in the DEB model to leave the possibility to eat all available preys in case of limited food resources.

*Relevance of the DEB model predictions for mesocosms*

First, the fact that simulations considering that sticklebacks were fed ad libitum in the mesocosms led to an overestimation of the length of the founders at the end of both experiments was not surprising since organisms in their natural environment often have to face limiting resources. The importance of food limitation in DEB model predictions has already been described in literature ([Peeters et al. 2010](#_ENREF_49), [Augustine et al. 2011](#_ENREF_4), [Jager and Zimmer 2012](#_ENREF_35)) and food level is also known to affect the growth of sticklebacks ([Allen and Wootton 1982](#_ENREF_1), [Wootton 1984](#_ENREF_65)). Furthermore, the available energy provided by food in experiment 2 was low compared to experiment 1 (Figure 2a) and the observed length of the founders at the end of experiment was also lower than in experiment 1 (SI Table S1). This indicates that the sticklebacks were unlikely to have been feeding ad libitum during experiment 2. This example emphasizes the importance of considering the prey density in mesocosms even if such information is not straightforward to obtain and to handle.

Among the two hypotheses on the limitation of food, only the “foraging behavior” hypothesis led to good predictions of the mean length of founders for both experiments. However, the uncertainty of the predictions for experiment 2 was important but can be explained by the uncertainty of the *f* functional response which was also larger compared to experiment 1 (Figure 2b).

Finally, as the predictions for male sticklebacks were improved using the parameter α’, our study pointed out the effect of the environment on the sexual dimorphism between males and females. Indeed, during the spawning period, male sticklebacks establish and defend their territory, build a nest and take care of their eggs until hatchling emergence ([Van Iersel 1953](#_ENREF_58)): the energy expenditure in parental care is considerable ([Wootton 1994](#_ENREF_66), [Smith and Wootton 1999](#_ENREF_53)). This reproductive behavior was not reproduced during the laboratory experiments used for the calibration, which can explain the overestimation of male predicted lengths at the end of the experiment. We corrected this overestimation by recalibrating the parameter α on the mesocosm data resulting in an increased value. Therefore, assuming an increase in the energy allocation to the reproduction processes. The energy expenditure of male sticklebacks was the main reason for using a type R metabolic acceleration in the DEB model rather than a type A metabolic acceleration that would account for a difference in assimilation rates ([Kooijman 2014](#_ENREF_38)). Indeed, a decrease of the assimilation rates of the food for mature males could explain the smaller length of males compared to females, however this would not have explained the highest energy expenditure of male sticklebacks that was observed thanks to respirometry measurements during parental behavior ([Smith and Wootton 1999](#_ENREF_53)). One could also assume a mix of both approaches for males in reproduction (i.e. a difference in the allocation of energy coupled to a decrease of the assimilation rate), but additional laboratory or field observations on males during the breeding period would be required to explore this hypothesis.

The accuracy of the DEB model in predicting the reproduction of sticklebacks was also assessed as it can be affected by both temperature and food availability. Indeed, it has been shown that food levels can influence the number of spawned eggs ([Wootton 1973](#_ENREF_64), [Wootton and Evans 1976](#_ENREF_67)). Temperature also has an effect, as an increased ambient temperature may disrupt the reproductive behavior of sticklebacks ([Hopkins et al. 2010](#_ENREF_31)). Thermal conditions can affect sperm performance and fertilization success ([Mehlis and Bakker 2014](#_ENREF_44)) Furthermore, increased temperature can affect the egg sizes in a clutch ([Shama 2017](#_ENREF_52)) and disrupt the spawn frequency as shown in the field study of Hovel et al. ([2016](#_ENREF_32)). As the design of mesocosm experiments does not allow accurate recording of the number of spawned eggs in the nests, we compared the model predictions for reproduction with literature data of studies assessing the breeding system of the three-spined stickleback. Mori ([1993](#_ENREF_46)) observed the reproduction of sticklebacks in field conditions during four months (March to early July). This author estimated that females spawned around 3.4 times and that the cumulative egg production during this period was of 940 eggs at the most. In laboratory, females had a higher spawning frequency (until 7.8 spawns per female) depending on the feeding ration ([Wootton 1973](#_ENREF_64)) which strongly positively impacted the number of produced eggs. In mesocosms, the reproductive conditions were closer to the ones in natural field, therefore female sticklebacks were unlikely to spawn a high number of times. Thus, an order of magnitude of a thousand eggs during March to early July in mesocosms using the hypothesis “foraging behavior” was deemed to be reasonably consistent with the literature data.

Additional assumptions on the access to food resources may be required to predict physiological processes of juveniles or younger mature sticklebacks. Indeed, this study only focused on founder sticklebacks. Yet, founders are larger than the other fish in the mesocosms, thus they dominate them and are relatively unaffected by phenomena like competition during foraging ([Gill and Hart 1996](#_ENREF_23)). However, the cohorts which were born during the experiments may be more sensitive to competition. Indeed, intraspecific competition is known to exert powerful selective forces on fishes ([Ward et al. 2007](#_ENREF_60)). For example, the effects of density-dependence on growth resulting from intraspecific competition or predation were demonstrated for wild populations and *Danio rerio* ([Lorenzen and Enberg 2002](#_ENREF_43), [Hazlerigg et al. 2012](#_ENREF_30)). Another point to note is that juvenile and adult stickleback have the same diet ([Wootton 1984](#_ENREF_65)) but the mouth length of the early juvenile sticklebacks can limit the size of the prey they have access to ([Hart and Gill 1992](#_ENREF_28), [Gill and Hart 1994](#_ENREF_22)). Thus, food availability should be reduced to small preys only. Finally, as not all sticklebacks may be mature at the same moment, it would be relevant to integrate an inter-individual variability on the DEB parameters related to the maturity as suggested by Kooijman ([1989](#_ENREF_39)). Finally, we focus on stages when the organisms can assimilate food, and consequently, the relevance of the model predictions should be assessed for the specific stage of the embryo-larvae ([Leloutre et al. 2018](#_ENREF_42)).

Further considerations for wild organisms

The lack of knowledge on parameter values for wild organisms is often one of the limits of DEB models for species of interest ([Galic and Forbes 2017](#_ENREF_20)) but in this study we showed that changing the value of one parameter (α accounting for sexual dimorphism) was sufficient to improve the predictions for semi-natural populations of sticklebacks. Thus, as a first approximation, a DEB model calibrated with laboratory experiments can be used to predict the physiological processes of an organism in field conditions, but users should keep in mind that some parameters, depending on the studied species, may need to be recalibrated with environmental data in order to improve the accuracy of the predictions. Concerning the inter-individual variability, the calibrated values of the coefficients of variation of and φ were consistent with the value of 0.05 suggested by Kooijman ([1989](#_ENREF_39)) and gave good predictions of the range of stickleback lengths. Thus, this value may be used as a first approximation for predicting the inter-individual variability of wild populations.

Furthermore, our study suggests that the energy obtained from food can be calculated by using abundance data of the prey community. It implies that the diet of the species of interest should be well known which is the case for the three-spined stickleback ([Hynes 1950](#_ENREF_34), [Walkey 1967](#_ENREF_59), [Allen and Wootton 1984](#_ENREF_2)) but can be delicate for other species. Particularly, the foraging behavior of the studied species should be well known in order to make assumptions on the access to food. Calculating the amount of available energy per water column can be a relatively simple solution applicable for species for which considering the food availability per volume of environment makes sense ([Kooijman 2010](#_ENREF_37)). For other species for which food availability is most appropriately expressed in terms of biomass per surface area, alternative hypotheses on how to use data form prey samples should be tested.

Additional considerations should be made on the food distribution in natural ecosystems as prey distribution may vary spatially and temporally. Hence, the hypothesis of homogeneous repartition of food may not be relevant. Furthermore, patchily distributed resources may influence the behavior of the studied species. For example, Hansen et al. ([2016](#_ENREF_27)) showed that when resources were patchy in space and time, sticklebacks tend to adopt joining foraging tactics to reduce both search times and the variance in finding food. Another point is that patchily distributed resources could induce a specific behavior of defense of food patches which has been widely observed in a range of both aquatic and terrestrial species ([Taylor et al. 2016](#_ENREF_56)). Juvenile salmonids are a good example of this specific territorial behavior as it is only related to feeding purposes. Indeed, their territory size was shown to decrease with increasing food abundance suggesting that juvenile salmonids can adapt their foraging behavior in function of their environment ([Grant et al. 2017](#_ENREF_26)). These aspects of ecology, food distribution as well as foraging strategies, may be of interest for the use of DEB models in a natural context as they could influence the amount of food organisms have access to.

Finally, the standard DEB model considers one type of food and assumes constant assimilation efficiency ([Kooijman 2010](#_ENREF_37)). In our study, we consider different prey types and used the energy content per prey type found in literature to calculate the food density. However, there were no data to estimate differences on the assimilation efficiency depending on the prey types chosen for the food scenario. Moreover, the morphology and behavior of sticklebacks ([Wootton 1994](#_ENREF_66)) was suggested to strongly affect the level of differences between the assimilation efficiency of two different types of prey. In our case, we had no argument to justify that there were any differences in assimilation efficiency of prey. Nevertheless, further studies should be made on this point as assimilation efficiency may be dependent on the type of prey in natural ecosystems and is likely to have significant implications for the use of standard DEB models for wild organisms. Furthermore, we used multiple food types to develop the food scenario. Especially, *Asellus aquaticus* were the most dominant species in the food scenarios for both experiments due to its high abundance in mesocosms and its relative high energy content. On the contrary, zooplankton species had the lower relative weight in the food scenarios. In the context of assessing fish population resilience to an environment change (*e.i*. climate change or toxic effect), considering different preys in the food scenario is important. Indeed, preys could be differently impacted by a stress which could lead to a shift in the food preferences of the fish. Thus, the effects on the fish population are not straightforward to predict.

In conclusion, this study showed that DEB models calibrated with laboratory experiments may be suitable to extrapolate laboratory data on standard organisms to wild populations, which is one of the challenges of current ecological modelling in the context of developing more relevant risk assessment and ecological management. Minimal assumptions on natural behavior of organisms were necessary to improve the predictions of the DEB model, and were mostly related to the foraging behavior. The study also showed that integrating reproductive behavior can strongly improve the predictions. Thus, this study addresses the concern of developing more relevant environmental scenarios and integrating important aspects of species biology and ecology for the use of DEB models in field conditions.

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# Figure legends

**Figure 1.** Growth predictions of DEB model using different observed data and time-steps to summarize the temperature scenario. (a) Growth predicted from the temperature recorded every 10 minutes by Temp5 (black circles) or by Temp15 (blue crosses) is compared to the growth predicted using the mean temperatures of both sensor. (b) Growth predictions from the temperature scenario defined by the mean of both sensors (Temp5 and Temp15) summarized using a time step of one day (mean per day) or all the data recorded (every 10 min). The growth (mm/d) per day is presented on these two graphics.

**Figure 2.** Total available energy from zooplankton and macroinvertebrates found in mesocosms (a) and the resulting scaled functional response f (b) of founder sticklebacks for experiment 1 (blue lines) and 2 (red lines). On graph b, the full lines are for the hypothesis “foraging behavior” and the dashed lines are for the hypothesis “equal food partition”. Light color zones correspond to the 95 % uncertainty interval.

**Figure 3.** Predicted mean length at the end of the experiments considering that the founders were “ad libitum” (a) or assuming the hypotheses “equal food partition” (b) or “foraging behavior” (c). Blue symbols represent the predictions done for the experiment 1 and red symbols for the experiment 2. Circles represent the predictions for the females and triangles for males. Full symbols represent the simulations for males using the parameter α’, calibrated with mesocosm experiments. The error bars represent the 95% prediction interval computed from the posterior distributions of the DEB parameters and from the food uncertainty.

**Figure 4.** Predictions of the DEB model for the individual length of the founder females (a, c) and males (b, d) in experiment 2 with 100 scenarios of food (.unc) and the hypothesis “foraging behavior” for the access to the food. Simulations were made without inter-individual variability (a, b), or considering the inter-individual variability (var.i) with 100 random draws of and φ (c, d). Simulations for males were made using the parameter α’, calibrated with mesocosm experiments. The black line represents the predicted mean length, dotted black lines represent the 95% prediction interval and grey zones represent the range of the predicted lengths. The points represent the observed lengths at the beginning and end of the experiment.

**Figure 5.** Number of spawned eggs predicted and reported in different studies. Field: estimations from Mori ([1993](#_ENREF_46)) of the minimum and maximum of spawned eggs from field observations during four months. Laboratory: number of spawned eggs from 13-week experiments made by Wootton ([1973](#_ENREF_64)) in laboratory with different amount of food. Experiments 1 and 2: Simulated number of spawned eggs considering the same period than in Mori (Beginning of March to early July).

# Appendix

Table. Mode and standard deviation of the *a posteriori* parameters of the DEB model calibrated with laboratory or mesocosm experiments

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Parameter | Prior | Posterior  Mode | Posterior  SD | Unit | Definition | Calibration data |
|  | N(0.25, 0.025) | 0.250 | 0.014 | - | Shape coefficient | Laboratory |
|  | N(8, 1) | 5.61 | 0.388 | J | Initial reserve | Laboratory |
|  | N(0.675, 0.3) | 1.33 | 0.134 | J | Cumulated energy invested in maturity at birth | Laboratory |
|  | N(1000, 250) | 442 | 154 | J | Cumulated energy invested in maturity at puberty | Laboratory |
|  | N(1.5, 0.5) | 2.42 | 0.262 | J/mm²/d | Maximum surface area specific assimilation rate | Laboratory |
|  | N(1.25, 0.5) | 1.33 | 0.084 | mm/d | Energy conductance | Laboratory |
| κ | N(0.7, 0.1) | 0.757 | 0.016 | - | Specific fraction of energy mobilized from energy from reserved allocated to growth and somatic maintenance | Laboratory |
| α | U(0, 1) | 0.082 | 0.004 | - | Fraction subtracted from κ to obtain κ in males after maturity | Laboratory |
|  | N(0.55, 0.05) | 0.563 | 0.050 | mm | Size of primordial cell in physical length | Laboratory |
|  | N(0.07, 0.1) | 0.111 | 0.017 | J/mm3/d | Volume specific somatic maintenance costs | Laboratory |
|  | N(5.2, 2.5) | 1.10 | 0.183 | J/mm3 | Cost of synthesis of a unit of structure | Laboratory |
|  | N(0.002 , 0.1) | 0.003 | 0.004 | /d | Maturity maintenance rate | Laboratory |
|  | N(0.95, 0.1) | 0.978 | 0.052 | - | Reproduction efficiency | Laboratory |
| φ | N(17, 1.7) | 15.31 | 1.65 | J/mm² | Proportional factor to be fed ad libitum for a given day | Laboratory |
|  | - | 25 | - | °C | Water temperature above which consumption ceases | Hovel et al. (2015) |
|  | - | 3 | - | - | Rate at which the function increases over low temperatures | Hovel et al. (2015) |
|  | - | 23 | - | °C | Optimal water temperature | Hovel et al. (2015) |
| α’ | U(0,1) | 0.111 | 0.001 | - | Fraction subtracted from κ to obtain κ in males after maturity | Mesocosm |
| CV\_Phi | TruncN(0.05, 0.01, 0.01, 1.4) | 0.054 | 0.010 | - | Coefficient of variation of φ | Mesocosm |
| CV\_Pam | TruncN(0.05, 0.01, 0.01, 1.4) | 0.055 | 0.010 | - | Coefficient of variation of | Mesocosm |