A bioenergetics model of the entire life cycle of the three-spined stickleback, gasterosteus aculeatus

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A BIOENERGETICS MODEL OF THE ENTIRE LIFE-CYCLE OF THE THREE-SPINED STICKLEBACK, *GASTEROSTEUS ACULEATUS*

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A whole life-cycle bioenergetic model based on the Dynamic Energy Budget (DEB) theory was proposed for the three-spined stickleback (*Gasterosteus aculeatus*). To develop this model, experiments on growth and reproduction were performed: adult and juvenile growth, size at first reproduction, and amount of eggs spawned by females were monitored under different feeding levels and temperatures. The DEB parameters were estimated, using Bayesian statistics, based on the data produced during these experiments and on other data found in the literature. The model fitted accurately the different data used for the calibration process and, in addition, predicted accurately the datasets used to assess its predictability. Our bioenergetic model of the whole life cycle of the three-spined stickleback accounting for environmental variations could contribute in many ways to improved ecological assessment: supporting change of scale from individual to populations; developing new biomarkers of exposure and effect; analysing ecotoxicity tests with biology-based models.

Key-words: Dynamic energy budget, Bayesian statistics, growth, reproduction, environmental variations

INTRODUCTION

The three-spined stickleback *Gasterosteus aculeatus* is a small-bodied teleost fish which constitutes a major component of shallow water food webs in the Northern hemisphere. Actually, stickleback can play an important role in ecology by dominating fish communities or affecting ecosystem functioning (Harmon *et al.* 2009). For example, it can compete with economically valuable species, such as salmonids or cottids, in resource-limited environments (Hovel *et al.* 2015). The three-spined stickleback is a model species for experimental studies in aquatic evolutionary biology, ecology, and behaviour. For instance, numerous field and laboratory studies on the reproductive behaviour of *G. aculeatus* and on the consequences of global warming for aquatic species were carried out on this species (Wootton 1984). *G. aculeatus* is also considered as a good sentinel fish species in aquatic ecotoxicology (Pottinger *et al.* 2002). Experiments have been carried out in field or semi-field conditions to assess the impacts of pollutants at the population level (Maunder *et al.* 2007; Roussel *et al.* 2007a; De Kermoysan *et al.* 2013).

Mathematical models are increasingly used in ecological risk assessment, due to the rise in demand for ecological realism in regulatory risk assessment (Forbes *et al.* 2011). Models are conveniently used to upscale from individual level to population level (Beaudouin *et al.* 2012; Goussen *et al.* 2013; Martin *et al.* 2013; Beaudouin *et al.* 2015). However, their development requires a large amount of data on the life cycle of the organisms (Péry *et al.* 2003; Goussen *et al.* 2013; Beaudouin *et al.* 2015). Mechanistic models of the bioenergetics of organisms, accounting for environmental variations (for example energy resources, temperature), offer a realistic description of the life cycle of individuals (growth, reproduction, survival…). They can also contribute to reduce the data necessary to develop a model of population dynamics when they explicitly link feeding, growth, and reproduction (Beaudouin *et al.* 2012).

Accounting for energy in population models also allows to assess how energy is shared between different species competing for the same resource, for instance stickleback and economically valuable species (Hovel et al. 2015). Finally, bioenergetics models have already proved to be useful to assess the effects of toxic compounds (Kooijman & Bedaux 1996; Péry *et al.* 2003; Jager *et al.* 2004; Billoir *et al.* 2008; Goussen *et al.* 2013; Goussen *et al.* 2015).

Bioenergetics models were already developed for *G. aculeatus* adults and were used to compare the bioenergetics pathways for a variety of populations in relation to both individual variations and environmental conditions (Wootton and Evans 1976; Wootton *et al.* 1978; Wootton *et al.* 1980; Wootton 1994). However, these models did not integrate the effect of temperature on the physiological parameters (Wootton 1994). Recently, a bioenergetics model has been developed for the three-spined stickleback to determine mass- and temperature-dependent functions for maximum consumption and routine respirations costs (Hovel et al. 2015). However, an integrated model describing the dynamics of energy from larvae to adults, linking feeding, growth and reproduction has still not been developed.

The bioenergetics models commonly found in the literature are based on strong empirical foundations and are very helpful to synthesize data. Theory-driven models such as those based on the Dynamic Energy Budget (DEB) theory (Kooijman 2000), go a step further, by providing a description of the whole life cycle, with parameters able to account for intra-species and inter-species variations as explained by Nisbet *et al.* (2012). As shown by these authors, the traditional bioenergetics models are in fact special cases of a DEB model. When the focus is on the entire life-cycle, and provided the assumptions of standard DEB theory apply, a DEB model would have fewer parameters than common bioenergetics models. DEB theory has been used to answer different questions in ecology of fishes: management in fisheries (Jusup *et al.* 2011), prediction of the growth and reproduction during spawning

74 migration (Pecquerie *et al.* 2009; Einarsson *et al.*, 2011) or under different environmental
75 conditions (Rinaldi *et al.* 2014), and comparison of life strategies between species (van der
76 Veer *et al.* 2001; Freitas *et al.* 2010; Pecquerie *et al.* 2011). Moreover, nesting a DEB model
77 within a population dynamics model provides realistic descriptions and predictions of
78 population dynamics, especially when populations are facing food limitations (Beaudouin *et*
79 *al.* 2015).

80 The aim of this study was to develop an entire life-cycle model, based on the DEB theory,
81 for *G. aculeatus* to predict the main physiological processes (growth, reproduction, puberty)
82 in different environmental conditions, *i.e.*, temperature, feeding. To achieve this aim, we
83 produced and collected data on growth, on larvae development, maturity, and reproduction.
84 The model was calibrated on these data using Bayesian statistics. Before the calibration, a
85 sensitivity analysis of the DEB model was carried out. Finally, the predictive capacity of the
86 model was evaluated.

87 # MATERIALS AND METHODS

88 ## EXPERIMENTAL DESIGN

89 *G. aculeatus* used in laboratory experiments came from field population located in the
90 vicinity on the experimental facilities and were reared in laboratory condition during six
91 months before the experiments (INERIS, Verneuil-en-Halatte, France). The ethics committee
92 of the National Institute of Industrial Environment and Risks (INERIS) approved all the
93 experiments performed and described in this manuscript.

94 In order to develop the DEB model, experiments were performed outdoor in semi-
95 controlled conditions and indoor in controlled conditions. The outdoor experiments were
96 conducted in experimental rivers under natural scenario of temperature (fluctuating) and
97 under natural photoperiod. These experiments aimed to focus on the response of the growth of

juveniles and the fecundity of females to different scenarios of temperature and feeding level. Our experimental rivers are described in detail in de Kermoysan *et al.* (2013). The indoor experiment under controlled conditions (*i.e.* with a constant fixed temperature and photoperiod) aimed to measure the growth of *G. aculeatus* (juveniles and adults) as a function of temperature and feeding level. Fish were placed under a constant photoperiod of 14:10-h light:dark.

Water quality

For all experiments, water temperature was recorded every ten minutes with a water temperature sensor (HOBO0257, Prosensor, Amanvillers, France). Water parameters (pH, conductivity and dissolved oxygen) in the outdoor experiments were monitored and kept suitable for the development of *G. aculeatus*. In the indoor experiments, the tank was filled with denitrified and dechlorinated tap water continuously renewed (1L h^{-1}).

Length measurement of fish

The standard length was measured (from mouth to the base of the caudal fin) by photography. Individuals were placed on a graph paper in a crystallizer containing a few millimetre of water. Then the individuals were measured using the ImageJ software (Rasband 1997).

Feeding

In the experiments, feeding level was adjusted (*i.e.*, mass a food provided) at the time of measurement to be maintained as a constant ratio of the fish mass. The fish weight was deduced from the measured standard length using allometric relationship calibrated on data obtained during previous experiments (Fig 1A and 2A, Supporting Information). Adult food

120 was composed of frozen chironomid larvae and juveniles were fed with Artemia newly
121 hatched.

122 *Experiment 1: Egg development and dynamic of yolk sac absorption*

123 To determine the duration of the embryonic development from fertilization to hatching, a
124 pool of 250 unfertilized eggs obtained from 10 females were in vitro fertilized and incubated
125 at constant temperature (methods presented in Santos, 2013a). The actual temperature was
126 monitored every in continue. The number of hatched eggs was counted four times a day since
127 the first hatching was observed. Hatching was considered achieved when at least 50 % of the
128 eggs are hatched.

129 As above, to determine the dynamic of yolk absorption, a pool of fertilized eggs obtained
130 from 10 females was used to randomly select four groups of 20 individuals which were
131 monitored from hatching to full yolk absorption. The evolution of the size of the yolk sac was
132 monitored three times per day for eight days. To this purpose, the juveniles were observed
133 under a binocular microscope and scored on five (5 for a full yolk sac and 0 for the absorption
134 of the yolk sac). Yolk absorption was considered achieved when at least 50 % of individuals
135 scored 0.

136 The eggs and juveniles were introduced into beakers (diameter: 11.5 cm, height: 4 cm, 400
137 mL of water) placed in a water bath having a nominal temperature of 14.5 °C. Two thirds of
138 the water was renewed every day.

139 *Experiment 2: growth of juveniles under controlled conditions/under natural conditions*

140 The aim of these experiments was to monitor the growth of juveniles under different
141 temperature and feeding scenarios. Each group was composed of 20 juveniles and
142 experiments were initiated with newly hatched juveniles with completely absorbed yolk. A
143 pool of fertilized eggs obtained from 10 females was used to randomly select the individuals

144 of the groups. The daily rations were provided in two feeding events per day. The number of
145 dead fishes was monitored twice a day at the feeding (Table 1A; Supporting Information).
146 The actual food rations (mg of food per individual per day) were computed for each group at
147 the end of experiment. The lengths were measured on photographs taken at the initial time
148 and at the end of the experiment.

149 We placed 43 groups, each in a 15 L aquarium, under controlled conditions. The nominal
150 exposure temperatures were 5, 10, 15, 20, and 22 °C and were maintained constant in time.
151 This range of temperature was chosen according to the study by Lefébure *et al.* (2011). The
152 feeding level varied from 5 to 80% (5, 10, 20, 40, 60, and 80%) of the fish mass. For a given
153 temperature, at least five different feeding levels were tested. Measured average temperatures
154 and feeding level are summarized in Supporting Information A.2. These experiments lasted
155 four days.

156 We placed 9 groups under outdoor conditions in enclosures (20cm x 20cm x 15cm) in
157 experimental rivers. Fish were fed from 10 to 60% of their mass, for six days and the
158 temperature varied from 15.9 °C to 20.4°C. These experiments were performed at different
159 times from May to August.

160 *Experiment 3: growth of adults*

161 To minimize the food competition and facilitate feeding, three mixed-sex fish groups of
162 similar length were defined at the beginning of the experiment: small (length approximately
163 30 mm; 30 unsexed fish), medium (length approximately 40 mm; seventeen females and
164 fourteen males) and large (approximately 60 mm long; nineteen females and eleven males)
165 fish groups. The small and medium groups were placed in tanks of 300 litres. The large group
166 was sub-divided into two groups and placed in 300 litres tanks to lower the density in each
167 tank. The length was monitored in males and females during 55 days and each fish was

168 measured every ten days. Fish were individually marked with alphanumeric tags (method
169 detailed in de Kermoysan *et al.* (2013)) and the sex of the fish was identified at the end of the
170 experiment by examining the gonads under binocular microscope. For this experiment, the
171 tanks were placed indoor with natural light and non-controlled temperature. Dechlorinated
172 and denitrified tap water continuously renewed (1L h^{-1}) was used to fill the tank (very small
173 daily variation) and they were exposed to natural photoperiod (from April to June). The
174 temperature was monitored continuously (daily mean temperature was from 13.9 ± 0.3 to 18.8
175 ± 0.5 °C; mean ± S.D.). Adults were fed *ad-libitum*.

176 *Experiment 4: fecundity of females*

177 The aim of this experiment was to determine the number of eggs by clutch. This
178 experiment was performed under outdoor conditions: fluctuant temperature (from 11.0 to
179 19.3°C) and natural photoperiod (May to August). Three pool of females (15 individuals) kept
180 in tanks of 300 litres and fed *ad-libitum,* were observed daily. Among these females, when
181 one female was ready to spawn, it was selected, anesthetized (MS-222), measured and then
182 stripped, *i.e.* mature eggs were retrieved by gently pressing the abdomen of the female
183 pectoral fin to the tail (the method is detailed in Santos *et al.* (2013b)).

184 During the entire experiment, 34 clutch sizes were collected from 34 females ready to
185 spawn, and were stripped. The females were not marked and we do not know the number of
186 clutches produced by each female. According to our experiments, a margin of error of about
187 5% was observed in the egg recovery (dissection of some females after euthanasia to check
188 the method). After a recovery period, the fish was released in its tank and the eggs released
189 were counted.

190 *Experiment 5: length at maturity of males*

191 The maturity states of 115 males measuring from 23 to 47 mm were determined. Males were
192 caught in the field population (natural temperature and photoperiod) and growth under natural
193 temperature and photoperiod. To this purpose, the fish were killed using a high dose of MS-
194 222. Thereafter, fish standard length was measured, and sex was determined by visual
195 observation of the gonads. Maturity states of the males were determined by observation under
196 a stereo microscope and two groups were distinguished: immature and mature (Craig-Bennett
197 1931; Sokolowska and Kulczykowska 2006). A log-normal distribution was adjusted on the
198 frequency by length classes of male with mature gonads to determine the median length at
199 maturity (Supporting Information A.4).

200 MODEL STRUCTURE

201 In this study, we used a DEB model. The model of the DEB theory describes the rate at
202 which the organism assimilates and uses energy for maintenance, growth, and reproduction as
203 a function of its state (energy density and size) and its environment (*i.e.* food density and
204 temperature; Fig .1). Allocation to growth and somatic maintenance occurs in parallel to
205 allocation to maturation and reproduction (Fig. 1). A description of the DEB model in fish is
206 well detailed in Augustine *et al.* (2011) and Pecquerie *et al.* (2009). All the equations of the
207 DEB model are presented in Supporting Information B. Parameters are listed in Table 1 using
208 standard DEB notation.

209 The growth simulation in the DEB model of *G. aculeatus* starts in a primordial cell (L_0, in
210 mm). Just after hatching, larvae have a yolk sac (energy storage necessary for growth until
211 juvenile stage). Once the yolk sac is absorbed, juveniles start feeding. There is no assimilation
212 during the embryonic period. The metamorphosis between the larvae and the juvenile stage
213 and between the juvenile and the adult stages occurs when energy invested in maturity
214 reaches specific thresholds.

215 Male *G. aculeatus* have a smaller maximal size than females (Wootton 1984) and a smaller
216 growth rate after puberty, as observed in our experiments. To model this difference, we
217 assumed a type R metabolic acceleration (Kooijman, 2014). Contrary to females for which the
218 parameter κ (the fraction of energy allocated to growth and somatic maintenance) is invariant
219 in time, the value of K in males decreases when the individuals reach their maturity (E_H=E_H^p),
220 which gives: $\kappa_{males} = \kappa - \alpha$, with alpha the fraction subtracted for κ in males *G. aculeatus*.

221 Parameter *f*, the feeding ratio, was computed from the following equations:

222 If $W_F < W_{F,\,ad\text{-}lib}$ then $f = \frac{W_F}{W_{F,ad-lib}} = \frac{W_F}{\varphi.L^2}$ (1)

223 If $W_F >= W_{F,\,ad\text{-}lib}$ then $f = 1$ (2)

224 where W_F is the energy available for a fish per day (in J). W_F is computed from the actual
225 daily mass of food (mg) per fish and the energy density for the different preys, 2326, 3730
226 and 3427 J/g wet weight for the nauplii of *Artemia sp*, the larvae of *Chironomus sp* and the
227 *Mysis sp*, respectively (Supporting Information A.6). $W_{F,\,\text{ad-lib}}$ is the amount of food *ad libitum*
228 (in J per day). $W_{F,\,\text{ad-lib}}$ is supposed, as assimilation process in general, to be proportional to
229 the squared length. φ is a proportionality factor.

230 Nauplii of artemia was provided as a volume of solution, and converted in mass using the
231 volume-weight relationships provide in Supporting information A.5. To take into account the
232 uncertainty of this relationship and on the energy density of the nauplii, an uncertainty factor
233 (noted Fc), *a priori* equals to one, was used to modulate the value of W_F (Eq. 3) when fish
234 were fed with brine shrimp nauplii.

235 In ectotherms, physiological processes depend on the environmental temperature. The
236 primary parameters used in the DEB model were corrected depending on the temperature
237 using a temperature correction function approximated with the Arrhenius temperature

(Kooijman 2000). As shown by Lefébure *et al.* (2011) and Hovel *et al.* (2015), the Arrhenius relationship can be assumed for the *G. aculeatus* only within a particular temperature range from the minimal temperature (3-5°C) to the optimal temperature for growth (21-23°C) (Supporting Information B.3). Consequently, in our DEB stickleback model, we proposed to use a temperature correction function defined for warmwater fishes (Kitchell et al. 1977) and adjusted for the stickleback by Hovel *et al.* (2015). This function, named T_{effect}, provided results similar to the function proposed by Lefébure *et al.* (2011) (Supporting Information B.3):

$$T_{effect} = \left(\frac{T_{max}-T_{exp}}{T_{max}-T_{opt}}\right)^{X} . e^{X - X.\left(\frac{T_{max}-T_{exp}}{T_{max}-T_{opt}}\right)} \quad (3)$$

$$X = \frac{Z^2 \times \left(1+\sqrt{1+\frac{40}{Y}}\right)^2}{400} \quad (4)$$

$$Z = log\,(Cq) \times \left(T_{max} - T_{opt}\right) \quad (5)$$

$$Y = log\,(Cq) \times \left(T_{max} - T_{opt} + 2\right) \quad (6)$$

where, T_{max}, is the water temperature above which consumption ceases, T_{opt} is laboratory-derived temperature preferendum, Cq approximates the rate at which the function increases over low temperatures and $Texp$ is the experiment temperature. Parameters$\dot{v}$, the energy conductance (mm d^{-1}), $\{\dot{p}_{Am}\}$, the maximum surface area specific assimilation rate (J mm^{-2} d^{-1}), $[\dot{p}_M]$, the volume specific somatic maintenance costs (J mm^{-3} d^{-1}), $\dot{k}_J$, maturity maintenance rate (d^{-1}) and φ were corrected with this equation. This last parameter is corrected to take into account the acceleration or deceleration of assimilation impacting on the amount of food available.

STATISTICAL METHODS

Statistical analysis of data

First, the effect of the temperature and/or the feeding level on the daily growth in juveniles (experience 2; n = 53) was analyzed using a linear model. Secondly, the effect of the sex (male or female) on the standard size of adults (experience 2, three mixed groups, n = 75) was analyzed using an ANCOVA. The time was used as covariate and the sex as factor. Finally, for the experience 4, we tested whether the clutch size (n = 34) depends of the female standard lengths and the water temperature by using an ANCOVA. The standard length of female was incorporate as covariate and the temperature as factor.

Sub-models for non-measured data

As successive spawns by the same female were difficult to observe, we had to estimate the inter-spawning interval (*i.e.*, the time between two spawns) and the standard length of the female at the beginning of the inter-spawning interval for each spawn observed in our experiments. To this purpose, an equation which predicted the inter-spawning interval (ISI) according to the water temperature (equation 7) was fitted to the data published by (Wootton *et al.* 1980; Bolduc & FitzGerald 1989; Boulé & Fitzgerald 1989).

$$ISI = 0.748 \times \bar{T} + 26.416 \quad (7)$$

where $\bar{T}$ is the daily mean temperature (in °C). This equation gives the number of days between two consecutive spawns. Based on the interval estimated for each female, the length at the beginning of the ISI was estimated assuming growth occurring in optimal conditions. We checked, *a posteriori* that this choice did not affect the calculation of the length by more than 1% compared to the calibrated model (Table 4C and Fig 6C, Supporting information).

Sensitivity analysis

We performed sensitivity analysis of the DEB model to identify the main contributing parameters to changes in model outputs. This was performed using the Sobol' method

283 (Saltelli 2002). This analysis is based on a functional decomposition of the variance, and is
284 recommended in the case where the model is non-linear and non-monotonic. In order to
285 estimate Sobol' indices, a Monte Carlo approach was used. Two input sample matrices ($n \times$
286 p) where n is the sample size (n = 10,000) and p the number of parameters (p = 16 for the SA
287 of females and p = 17 for males) were used. Parameter distributions were uniform and the
288 lower and upper limits were defined ± 10 % around *a priori* values. Then, we calculated the
289 first order (FOI; variance contribution on one parameter) and the total order (TI; main effect
290 of one parameter and all its interactions with the other parameters) Sobol' index. To assess
291 confidence intervals on the estimation of Sobol's indices, bootstrapping was used (1,000
292 times sampled with replacement). The sensitivity analysis was carried out with sensitivity R-
293 package using the function *soboljansen* (Pujol *et al.* 2012) with the statistical computing
294 software R (R Core Team, 2014). Sobol' sensitivity indices were estimated for the growth at
295 20, 100 and 650 days post fecundation (dpf), for the energy invested in maturity at 20, 50 and
296 150 dpf, and for the energy invested in reproduction at 150, 400 and 650 dpf.

297 *Model calibration*

298 The calibration of *G. aculeatus* DEB model was performed using the software R with the
299 *coda* package (Plummer *et al.* 2015) and MCSim, which is designed for Bayesian inference
300 through Markov Chain Monte-Carlo (MCMC) (Bois 2009). We performed three independent
301 MCMC and the quality of convergence was checked by calculating the Gelman-Rubin index
302 (Gelman *et al.* 1996).

303 The likelihood functions were defined assuming that the observations: length, number of
304 eggs per clutch, size at sexual maturity, and length and age at larvae-juvenile metamorphosis
305 (absorption of the yolk sac, first external feeding), were associated with normally distributed
306 residual errors. The standard deviation of the residual errors of the growth and reproduction

was adjusted with a half normal distribution, and fixed at the estimated values on the data for the two other endpoints (Table 2B in Supporting Information B).

The *a priori* distribution of the parameters were defined based our experimental data or using the addmypet database (www.bio.vu.nl/thb/deb/deblab/add_my_pet). When enough data were available for a given parameter, *a priori* distributions of the parameters values were defined by a normal distribution, and otherwise, we used a uniform distribution (Table 1).

EXPERIMENTS USED TO EVALUATE PREDICTIVE CAPACITY

Data were produced to assess the predictability of our DEB model. To evaluate the growth predictions, two different experiments were performed. Each experiment lasted three weeks in semi-controlled conditions (natural scenario of temperature and under natural photoperiod). For each experiment, three groups were introduced in enclosure (25 x 25 x 30 cm with mesh to 500 microns) in experimental river. Experiments were performed at two different periods of the same year (May and July). Juveniles of the first experiment (May, 30 fishes per group) were fed with similar level of food (percentage of the fish mass) for the first and third weeks, and with a smaller during the second week (Table 2A in Supporting Information A). The juveniles of the second experiment (July, 40 fishes per group) were fed to a higher constant level of food (percentage of the fish mass), readjusted at each length measurement (Table 2A in Supporting Information A).

For the reproduction part, the calibration dataset (training set) was constituted using a dataset where eleven out of the 34 clutch sizes were randomly removed (1/3 female) from the data produced in Experiment 4. The eleven clutch sizes randomly removed were used to evaluate the predictive capacity of the model, and then constituted the test set. Finally, once the predictive capacity had been checked, a global calibration was performed with the whole dataset.

RESULTS

EXPERIMENTAL DATA

The embryonic development from fecundation to hatching of 50% of the viable eggs (229 eggs) lasted 12.9 days at 13.1 ± 0.8 °C (mean ± S.D.). The yolk sac absorption in larvae in experiment 1 lasted 48 hours for four groups at 15.7 ± 0.02 °C (mean ± S.D.).

In the experiment 2, the growth of juveniles was significantly altered by the feeding ratio (linear model, $t = 5.81$, $df = 2$, $P < 0.001$, $R^2 = 0.77$) and the temperature (linear model, $t = 11.57$, $df = 2$, $P < 0.001$, $R^2 = 0.77$). There is no interaction between the feeding ration and the temperature (linear model, $t = -0.23$, $df = 3$, $P = 0.82$, $R^2 = 0.77$). The minimal growth was 0.091 mm d^{-1} measured at temperature of 7°C and fish daily fed at 5% of their mass; and, the maximal growth was 0.38 mm d^{-1} at 15.66°C and a daily feeding ratio of 80% of fish mass.

In the experiment 3 (growth of adults under controlled conditions), no significant sex effect was shown (ANCOVA, $F_{1,71} = 3.38$, $P = 0.07$) in the group with small size. However, females were significantly bigger than males for the two other groups (ANCOVA, medium group, $F_{1,153} = 21.64$, $P < 0.001$ and large group, $F_{1,162} = 345.87$, $P < 0.001$). The small and medium groups continued to grow during the 55 days in the experiment (ANCOVA, small group, $F_{1,71} = 319.01$, $P < 0.001$; medium group, $F_{1,153} = 151.00$, $P < 0.001$) whereas the large group ceased to grow (ANCOVA, $F_{1,162} = 3.81$, $P = 0.053$) because the ultimate length was reached. There is no interaction between sex and time for the small group (ANCOVA, $F_{1,71} = 0.77$, $P = 0.38$). In contrast, the growths were not the same between males and females for the medium group (ANCOVA, $F_{1,153} = 9.91$, $P = 0.002$) and the large group (ANCOVA, $F_{1,162} = 4.40$, $P = 0.04$). The average maximal standard length of *G. aculeatus* in our experiments was 61.88 ± 1.86 mm (mean ± S.D.) for females (range: 59.96 – 65.02 mm) and 55.51 ± 2.06 mm (mean ± S.D.) for males (range: 53.94 – 58.42 mm).

In experiment 4, the average clutch size in our data was 101.41 ± 28.38 eggs (mean ± S.D., n = 34) and the average standard length of females was 48.78 ± 3.59 mm (mean ± S.D., n = 34). The clutch size increased with the females' standard length (ANCOVA, $F_{1,27} = 37.32$, $P < 0.001$). However, in our experiment, the clutch size was not impacted by the water temperature (ANCOVA, $F_{2,27} = 2.22$, $P = 0.13$) and by the interaction (ANCOVA, $F_{2,27} = 0.66$, $P = 0.53$).

Linear model fitted on the clutch size data predicts the length for a female with one egg at 30.3 ± 5.01 mm (CI at 95% is from 25.3 to 35.2 mm; clutch size = α.L+β, with α equal to 5.37 ± 0.56 and β equal to -160.29 ± 28.72). The length at maturity for the males was similar: 50 % of the males were mature at 33.1 mm and the smaller mature male in our sample measured 30.5 mm (data presented in Supporting Information).

SENSIVITY ANALYSIS

The sensitivity analysis showed that the main influencing parameters on growth were the same for females and for males (Fig. 2; from Fig. 1C and Fig. 2C in Supporting Information C.1). The parameters δ_M, T_{opt}, $\{\dot{p}_{Am}\}$, κ, $[\dot{p}_M]$ and $\dot{v}$ were the six most influential parameters. The other parameters only slightly influenced growth (Fig. 2A). Regarding reproduction, the parameter $\{\dot{p}_{Am}\}$ had the largest impact on the number of eggs produced by the females (Fig. 2C). This parameter was followed by parameters T_{opt}, $[\dot{p}_M]$, k_R and E_0 for females.

CALIBRATION

The three Markov chains stabilized around the same distribution for each parameter (Supporting Information C.2 and C.3). Indeed, the Gelman-Rubin was lower than 1.2 for all parameters. The mode of *a posteriori* parameters distribution is presented in Table 2. *A*

377 *posteriori* values of parameters differed from *a priori* ones (Tables 1 and 2) except for the
378 parameter L_{egg}.

379 Growth patterns (juveniles, females and males adults) were accurately described by our
380 DEB model regardless the length (Fig. 3A, B and C), the temperature and the feeding level
381 (Fig. 3). The regression line overlapped the diagonal of the Cartesian plan line (slope = 1,
382 intercept = 0; Fig. 3D).

383 We estimated a maximal length for females of 63.28 mm and 56.26 mm for males and a
384 standard length at maturity of 32.84 mm for females and males in *ad-libitum* conditions, at
385 23°C (optimal temperature). Our model could account for the spawn size and the growth of
386 females (in mm) during the reproduction at different temperatures (Fig. 4).

387 PREDICTIVE CAPACITY

388 Our model predictions and the observations are presented for the growth of juveniles in
389 Fig. 5 and for the reproduction in Fig. 6. A majority of the points of the two growth datasets
390 were in the 95% confidence interval for model predictions (Fig. 5A and Fig. 5D). The energy
391 density predicted by our DEB model is presented in Fig. 5B for the experiment 1 (May) and
392 in Fig. 5E for the experiment 2 (July); the feeding ratio is presented in Fig. 5C and Fig. 5F.
393 According to our DEB model, the juveniles were actually not fed *ad-libitum* in the second
394 experiment because the energy density was below E_m (maximal energy density)(Fig. 5E).
395 Furthermore, f (the feeding ratio) did also not reach its maximal threshold which is 1 for the
396 second experiment (Fig. 5F).

397 The reproduction (the cumulated number of eggs spawned according to the standard length
398 of females at the time of the spawns) was well-predicted: only three points were not in the
399 95% confidence interval of the model predictions (Fig. 6).

400 DISCUSSION

401 In this study, comparing to the bioenergetic model developed by Hover et al. (2015), we
402 proposed a model of the entire life-cycle of *G. aculeatus* using a bioenergetics approach.
403 Moreover, our model predicts reproduction. This model adequately fitted the growth and
404 reproduction data used for its calibration, and predicted well the three other datasets (not used
405 for calibration).
406 The Bayesian calibration of our DEB model for *G. aculeatus* appeared to be successful
407 despite the relatively high number of parameters in our model. Convergence was reached, as
408 shown by the Gelman-Rubin convergence statistics (Gelman *et al.* 1996). A Bayesian
409 approach was already used to estimate the parameters of DEB model and showed satisfactory
410 results (Klok *et al.* 2007; Johnson *et al.* 2013; Beaudouin *et al.* 2015). It was also used to
411 estimate parameters in DEBtox model (Billoir *et al.* 2008; Goussen *et al.* 2015). Another
412 method using covariance method is usually also performed (Lika *et al.* 2011a; Lika *et al.*
413 2011b). This approach is based on the frequentist statistical inference (minimization of a
414 weighted sum of squared, maximum likelihood). The main advantage of the Bayesian
415 approach is that *a priori* information on the distribution of the parameters can be used, and *a*
416 *posteriori* distributions informed on the parameter uncertainties.
417 The *a posteriori* distributions were different from *a priori* distribution except for the
418 parameter L_{egg}. This denotes that in our dataset and experiments, no information was available
419 to reduce the uncertainty on this parameter, and complementary experiments should be
420 conducted to refine these posterior distributions. For the parameters for which the
421 distributions were updated, part of this update could be explained by biological differences
422 (relative to growth, size at maturity and reproduction) between *G. aculeatus* used in our
423 experiments and the fish for which data were available to determinate the *a priori* values of

424 parameters. *G. aculeatus* is indeed well-known for its phenotypical plasticity (Baker 1994;
425 McKinnon & Rundle 2002; Wootton 1984)(Table 1D in Supporting Information D).
426 The temperature range of our experiment was from 11 to 20 °C for both the growth and the
427 reproduction experiments. Consequently, the range of the temperature in our experiment was
428 too small to update the three parameters of the temperature correction function and avoid
429 over-fitting. We thus decided to exclude the temperature correction from the calibration. We
430 used the temperature correction function defined for warmwater fishes (Kitchell et al. 1977)
431 and adjusted for the stickleback by Hovel *et al.* (2015). In the case of *G. aculeatus*, the effect
432 of temperature on growth follows a sharp peak: the growth is maximal at an optimum
433 temperature and decreases at lower and upper temperatures (Hovel *et al.* 2015). The model we
434 used accounted for this phenomenon and provided accurate predictions of the effects of
435 temperature.
436 Our experimental results are in agreement with the literature. Thus, the growth of fish is
437 well-known to depend on the water temperature and on the amount of food in the
438 environment (Allen & Wootton 1982; Wootton 1984). Moreover, our predictions of maximal
439 standard length are in conformity with observations in France for female and male *G.*
440 *aculeatus* (Table 1D, Supporting Information D). However, some observations for the
441 maximal length and the standard length at maturity available in the literature are different
442 from the values we estimated (Table 1D, Supporting Information D). Indeed, most of them
443 were bigger than our estimates for our population studied in experimental river. These
444 differences may be due to the large phenotypic plasticity of *G. aculeatus* (McKinnon &
445 Rundle 2002) but also to the differences between confounding environmental factors
446 depending on latitude, such as temperature (Baker 1994). Furthermore, the fact that males and

447 females are sexually mature at the same length is in conformity with the results by Mori &
448 Nagoshi (1987).

449 For the reproduction part of our model, overall, the model gives accurate predictions which
450 are in accordance with literature data: for instance, as predicted by our model, a female about
451 50 mm long is likely to spawn a hundred eggs (Table 1D, Supporting Information D).
452 However, higher residual errors were observed for some reproduction observations (Fig. 5).
453 The literature shows that the number of eggs depends on several factors in sticklebacks
454 (Wootton 1973b; 1984; 1985; Wootton & Fletcher 2009), as among others, the actual length
455 of the female (Wootton 1973; Wootton 1976; Kynard 1978; Baker 1994) and food ratio
456 (Wootton 1973a). The food ratio and standard length may be influenced by intraspecific food
457 competition between females in the tank (Gill & Hart 1996; Milinski 1982; Ward *et al.* 2006).
458 In *G. aculeatus*, bigger fish monopolize the prey (Gill & Hart 1996; Milinski 1982) and
459 subordinate fish have to increase their effort to obtain the same food intake than dominant.
460 Consequently, the net energetic gains may decrease, with consequences for reproductive
461 success (Purser & Radford 2011). In our case, the subordinate females may have fed less than
462 *ad-libitum* and may have spawned a number of eggs lower than expected. In addition, clutch
463 size could be reduced because the dominance hierarchies between female may induce an
464 inhibition of the reproductive processes caused by olfactory cues (Paull *et al.* 2010;
465 Sokolowska & Kulczykowska 2009). For instance, in *Danio rerio*, some steroid glucuronides
466 released into the water by males or by females stimulate the reproductive processes of the fish
467 of the opposite sex but also inhibit the reproductive processes of the fish of same sex (Gerlach
468 2006; Lawrence 2007). In *G. aculeatus*, one study highlighted an increase of genes expression
469 in fish housed in social groups (Greenwood & Peichel 2015). These genes were responsible
470 for social competition (between individuals for the food resources) and reproductive behavior.

Finally, the stress caused by everyday anthropogenic activities (feeding, observation, capture) can increase experimental variability and have a negative impact on foraging efficiency in *G. aculeatus* (Purser & Radford 2011). Another source of residual error could be the uncertainty on the estimation of the inter-spawning interval or growth. Indeed, the data used to estimate the ISI came from different *G. aculeatus* populations living in different habitats with different life strategies (Bolduc & FitzGerald 1989; Boulé & Fitzgerald 1989; Wootton *et al.* 1978) and *G. aculeatus* is a species of fish widely known for phenotypic plasticity, in particular, relative to reproduction parameters (Wootton 1973; Wootton 1976; Wootton & Evans 1976; Boulé & Fitzgerald 1989; Snyder & Dingle, 1989) (Table 1D, Supporting Information).

Our DEB model could be integrated into an individual-based model of *G. aculeatu*s adding other individual and population processes not predicted by the DEB model (behaviour, interactions with the environment …). This population model would allow us to predict impact of compounds at the population level in future works aiming at assessing the ecological impact of chemicals on the fish. For this, the DEB model of *G. aculeatus* will be combined with an individual-based model. DEB-IBM models have already used to others species, and have demonstrated their abilities to extrapolate from ecotoxicological data measured on organisms in laboratory conditions to biological endpoints convenient (Beaudouin *et al.* 2012; Beaudouin *et al.* 2015; Martin *et al.* 2013). Moreover, data on population obtained in our mesocosm (De Kermoysan *et al.* 2013) could be used to improve the DEB model by giving information on the energy budget in male after maturity and during the reproduction season.

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654

CAPTIONS

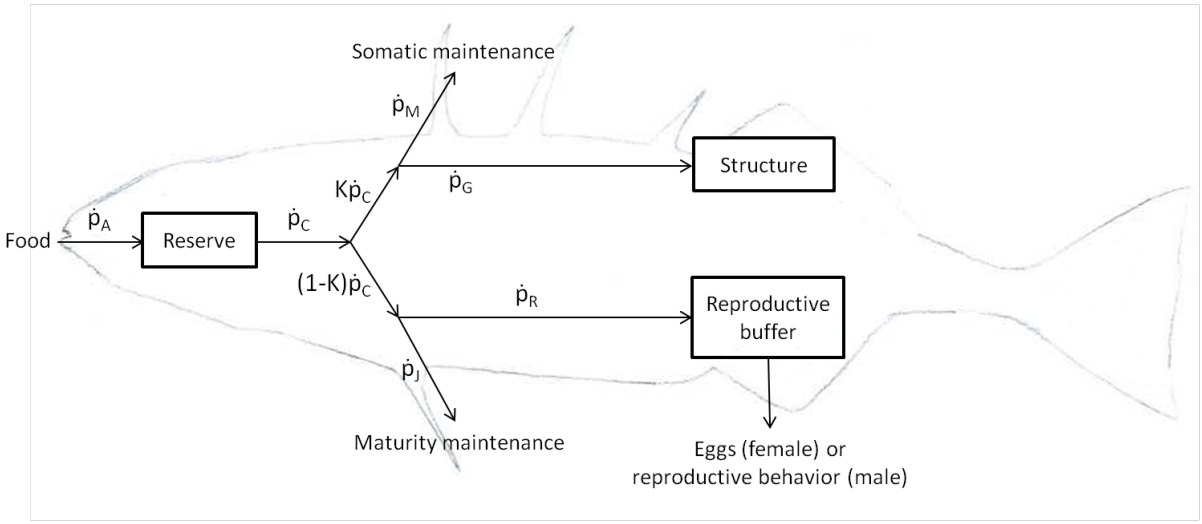


Fig. 1. Schematic representation of the dynamic energy budget model of three-spined stickleback. $\dot{p}_A$ represents energy assimilated from food and $\dot{p}_C$ represents the energy used from reserve. K is the fraction of energy allocated to growth and somatic maintenance. $\dot{p}_M$, $\dot{p}_G$, $\dot{p}_J$ and $\dot{p}_R$ represent the energy flux allocated to somatic maintenance, growth, maturity maintenance and reproduction, respectively.

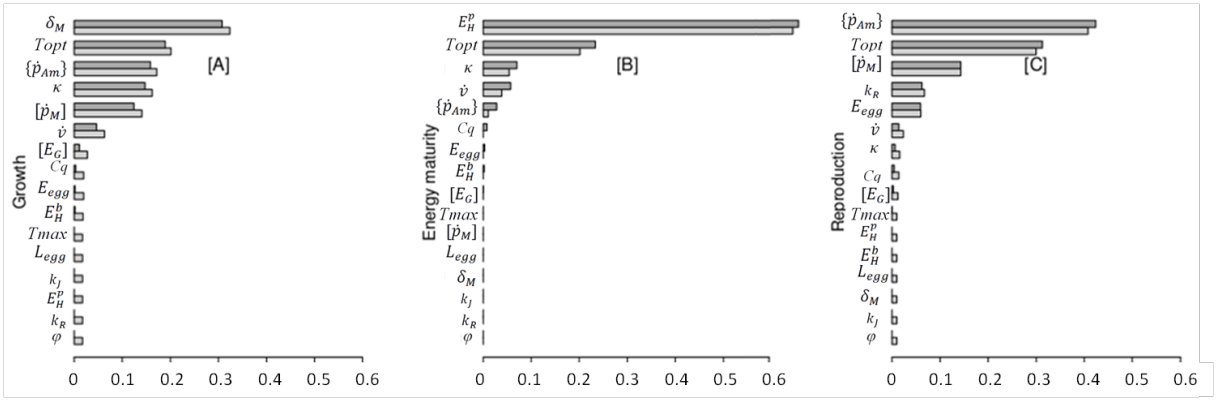
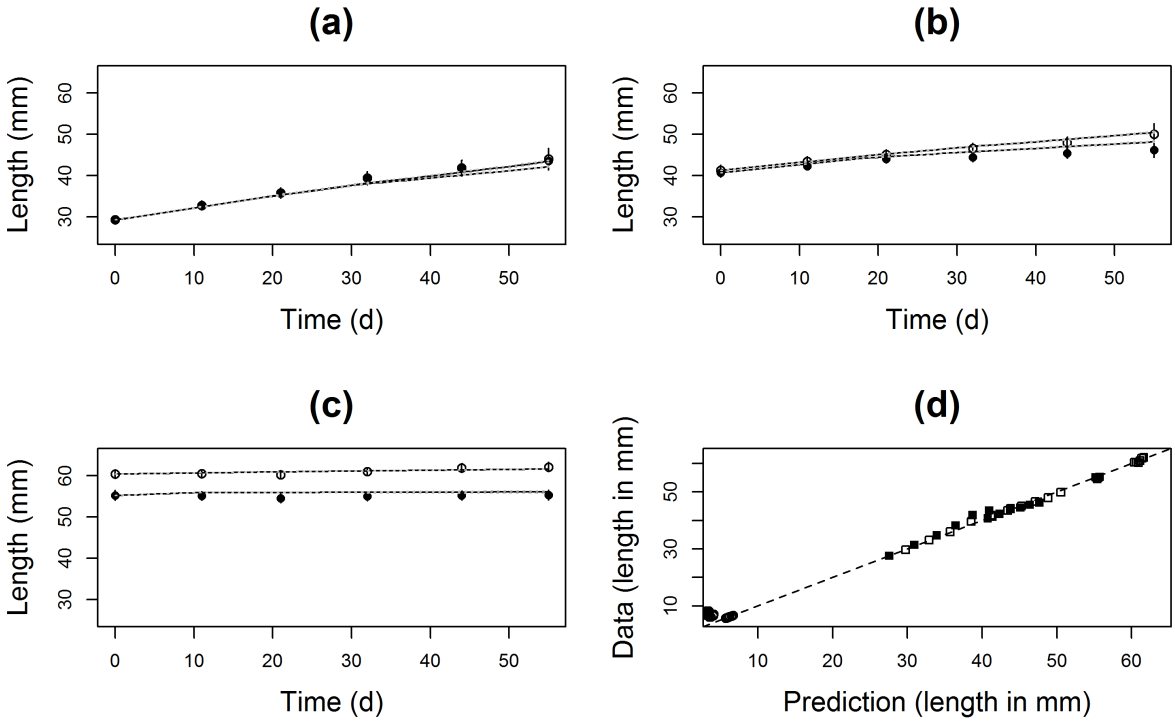


Fig. 2. Sensitivity analysis of the DEB model. The Sobol' sensitivity indices are presented for the males for the growth (A), the energy invested in maturity (B), and the energy invested in reproduction (C).

667 Sobol indices were computed for the growth at 20, 100 and 650 dpf, for the energy
668 invested in maturity at 20, 50 and 150 dpf, and for the energy invested in reproduction at 150,
669 400 and 650 dpf. The water temperature was fixed at 20°C and the food was *ad-libitum* (f=1).

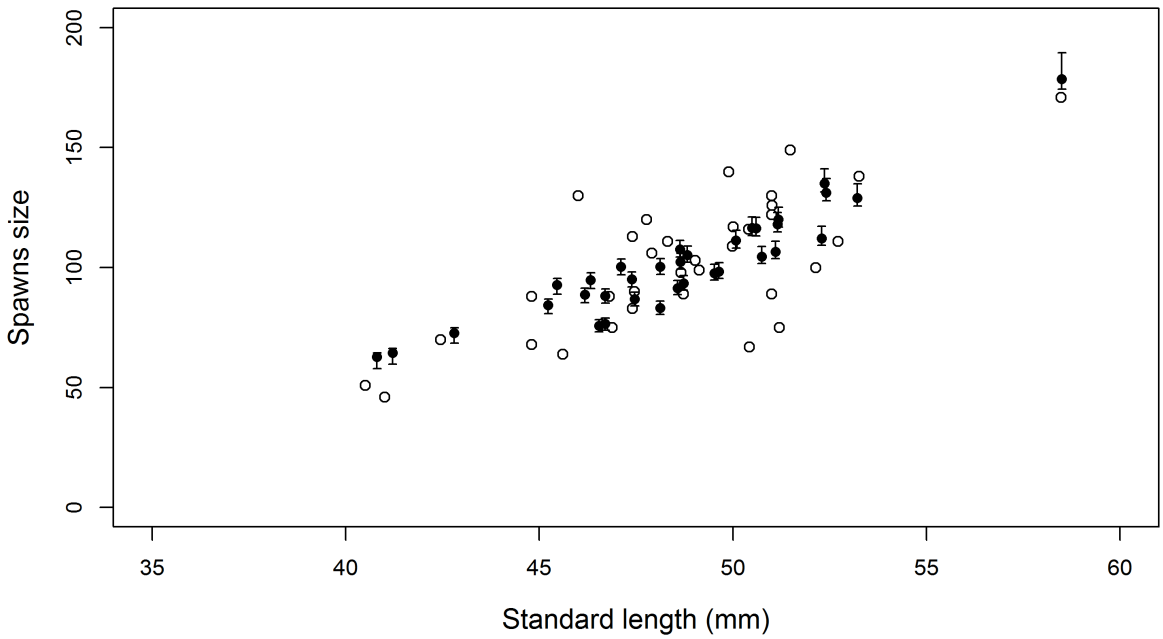
670 Mean of the indices were presented. The total order indices (TI) are presented in dark grey
671 and first order indices (FOI) in light grey. Parameters were ordered according to the total
672 order sensitivity indices.



673

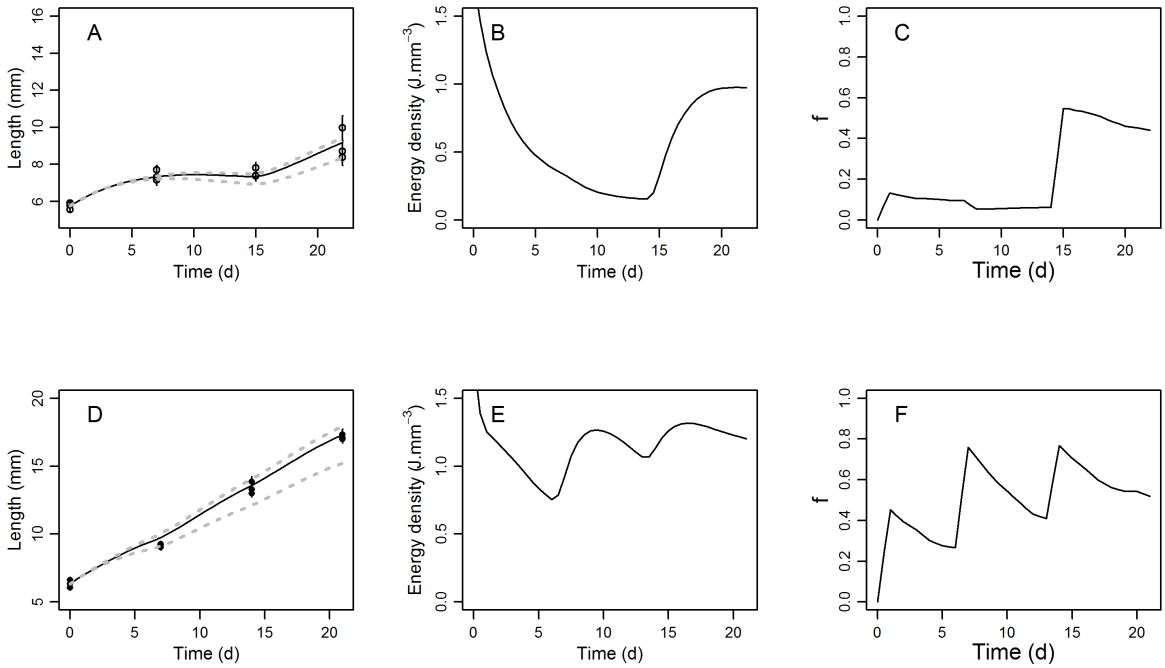
674 *Fig. 3.* Model predictions using the posterior distributions compared to observed standard
675 lengths of fish (snout till end of caudal fin): (A) small fish group, (B) medium fish group and
676 (C) large fish group; monitored for 55 days. ○ and ● represent the mean length of females and
677 males, respectively. The error bar represents the 95% C.I. of the mean (S.E.). Full lines
678 represent the median and dotted grey lines represent the 95% C.I. of the model predictions for
679 females and males, respectively. 95% C.I. of predictions were computed from the posterior
680 distributions. Fig. (D) represents the observations and model predictions (median) for all the

681 growth data. The dotted line is the bisector and ○, □ and ■ are the means of observations for
682 juveniles, females and males respectively for all experiments.



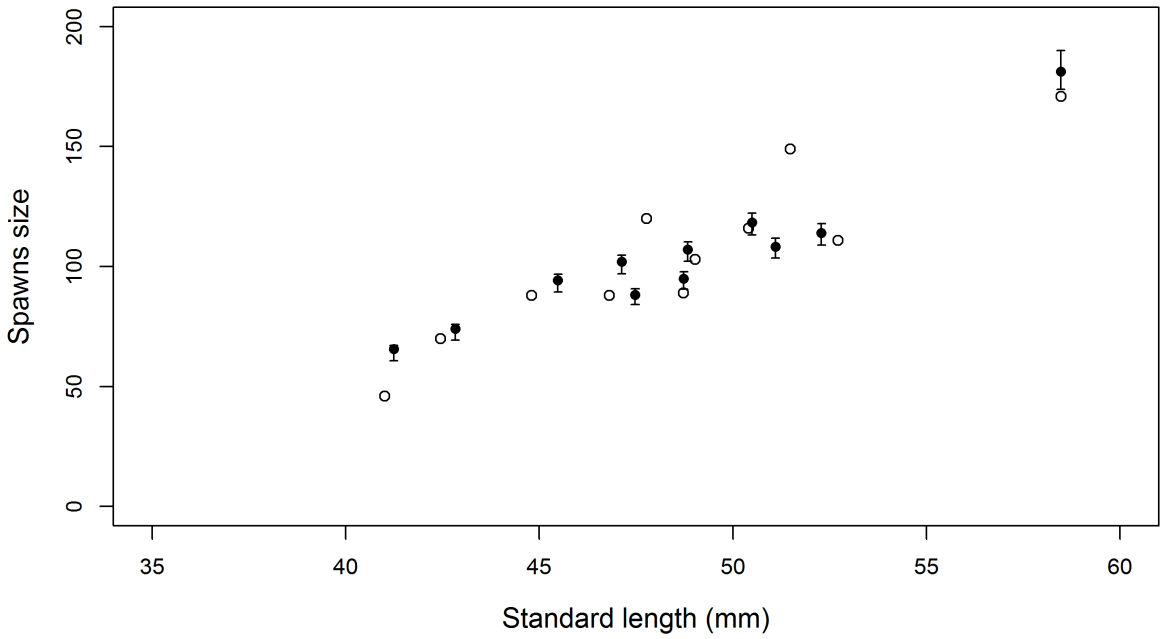
683

684 *Fig. 4*. Model predictions versus observations for the number of eggs spawned according
685 to the standard length of females at the time of the spawns. ○ represent the observations (one
686 female per points under different water temperature) and ● represent the predictions using the
687 mode of posterior distributions. The error bars represent the 95% C.I. of the predictions
688 computed from the posterior distributions. Data were recorded under *ad-libitum* food regime
689 and different water temperature scenarios.



690

691 *Fig. 5.* Assessment of the predictive capacity of the model for the growth: model
692 predictions compared to the observed mean length of fish for the experiment 1 (A) and 2 (D).
693 ○ and ● represent the observations for the experiment 1 and 2 respectively. The error bars
694 represent the 95% C.I. of the observations. Full lines represent the median and dotted grey
695 lines represent the 95% C.I. of the model predictions. 95% C.I. of predictions were computed
696 from the posterior distributions. Fig. (B) and (E) represent the model predictions for the
697 energy density ($J.mm^{-3}$). Full lines represent the median for the energy density and dotted red
698 lines are the maximal energy density in a fish. Fig. (C) and (F) represent the feeding ratio (F)
699 during the experiments. Values are comprised between 0 and 1.



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701 *Fig. 6.* Assessment of the predictive capacity of the model for the female reproduction:
702 model predictions compared to the cumulated number of eggs observed (data not used for
703 calibration process) as a function of standard length at the time of the spawns. ● represent the
704 observations (one female per point with different water temperatures) and ○ represent the
705 predictions using the mode of posterior distributions. The error bars represent the 95% C.I. of
706 the predictions computed from the posterior distributions. Data were recorded under *ad-*
707 *libitum* food regime and different water temperature scenarios.

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Table 1. *A priori* distributions of the parameters of the stickleback DEB model

Symbols	Distribution	Bounds	Definition	Unit	References
δ_M	N(0.25, 0.025)	0.2 - 0.3	Shape coefficient for adults	-	Fitted on our data
E_0	N(8, 1)	5 - 11	Initial reserve	J	Wootton, 1984 ; Wootton, 1994, fitted
E_H^b	N(0.675, 0.3)	0.00001 - 3	Cumulated energy invested in maturity at birth	J	*Addmypet*
E_H^p	N(1000, 250)	100 - 1900	Cumulated energy invested in maturity at puberty	J	*Addmypet*
$\{\dot{p}_{Am}\}$	N(1.5, 0.5)	0.01 - 6	Maximum surface area specific assimilation rate	J mm^{-2} d^{-1}	*Addmypet*
$\dot{v}$	N(1.25, 0.5)	0.01 - 3.5	Energy conductance	mm d^{-1}	*Addmypet*
α	U(0, 1)	0 - 1	Fraction subtracted to κ for obtain κ in males	-	-
κ	N(0.7, 0.1)	0.5 - 0.9999	Specific fraction of energy mobilized from reserve allocated to growth and somatic maintenance	-	*Addmypet*
L_{egg}	N(0.55, 0.05)	0.2 - 0.9	Size of primordial cell	mm	Wallace and Selman, 1979; Baker, 199
$[\dot{p}_M]$	N(0.07, 0.1)	0.001 - 0.3	Volume specific somatic maintenance costs	J mm^{-3} d^{-1}	*Addmypet*
$[E_G]$	N(5.2, 2.5)	0.001 - 10	Cost of synthesis of a unit of structure	J mm^{-3}	*Addmypet*
$\dot{k}_J$	N(0.002 , 0.1)	0 - 0.5	Maturity maintenance rate	d^{-1}	*Addmypet*
k_R	N(0.95, 0.1)	0 - 1	Reproduction efficiency	-	*Addmypet*
φ	N(17, 1.7)	0 - 30	Feeding frequencies during a day to be fed *ad-libitum*	-	Hovel *et al.* (2015)
Tmax	25	-	Water temperature above which consumption ceases	°C	Hovel *et al.* (2015) - Non fitted
Cq	3	-	Rate at which the function increases over low temperatures	-	Hovel *et al.* (2015) - Non fitted
Topt	23	-	Water temperature preferendum	°C	Hovel *et al.* (2015) - Non fitted
Fc	N(1, 0.2)	-	Uncertainty on the artemia nauplii energy (energy density and allometric relationship)	-	

N(μ, σ) denotes a normal distribution with μ the mean and σ the standard deviation
U(α, β) denotes an uniform distribution between α and β
Addmypet : http://www.bio.vu.nl/thb/deb/deblab/add_my_pet_old/Species

Table 2. Mode and standard deviation of the a posteriori parameters of the DEB model

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Parameter	*Mode*	*SD*	*Unit*
δ_M	0.247	0.016	-
E_0	5.72	0.56	*J*
E_H^b	1.39	0.22	*J*
E_H^p	459	165	*J*
$\{\dot{p}_{Am}\}$	2.46	0.17	*J mm^{-2} d^{-1}*
$\dot{v}$	1.26	0.08	*mm d^{-1}*
κ	0.752	0.028	-
α	0.079	0.004	-
L_{egg}	0.551	0.05	*mm*
$[\dot{p}_M]$	0.119	0.01	*J mm^{-3} d^{-1}*
$[E_G]$	0.972	0.12	*J mm^{-3}*
$\dot{k}_J$	0.00056	0.005	*d^{-1}*
k_R	0.962	0.05	-
Tmax	*25*	-	*°C*
Cq	*3*	-	-
Topt	*23*	-	*°C*
φ	16.76	1.69	-
Fc	1.20	0.18	-
Sigma C	0.293	0.015	-

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