Add-my-pet procedure for fathead minnow *Pimephales promelas* and walleye *Sander vitreus*

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1 Introduction

The present document presents a full life cycle model at the individual scale for the growth, reproduction and maintenance in *Pimephales promelas* and *Sander vitreus* based on the Dynamic Energy Budget (DEB) theory [Kooijman, 2010]. Both models are DEB model with type M acceleration, which means that during part of the life cycle metabolism accelerates. This model is a one-parameter extension of standard DEB model. This document is organized as followed. Firstly, we briefly describe the standard DEB model and the DEB model with type M acceleration. Then, we briefly introduce the parameter estimation method that was used in this work. Finally, we present the data used in this parameter estimation and provide a comparison of the models outputs and data used.

2 Methods

2.1 DEB model

The standard DEB model describes the entire life cycle of an organism through three life stages. We here introduce state variables and fluxes (table 2.1) from a life cycle point of view. In DEB theory, life cycle is described in 3 stages and the transition between one stage to the other depends on a state variable, called maturity E_H.
During the first life stage, named the embryonic stage, the organism does not feed, so the flux for assimilation $\dot{p}_A$ is null. The organism uses the available energy in reserve compartment (E), with a fixed allocation rate (κ), to grow in structure (V). So a proportion κ of the mobilization flux $\dot{p}_C$ goes to the structure (V) for its maintenance $\dot{p}_S$ and its growth which thus equals $\kappa\dot{p}_C - \dot{p}_S$. What remains of the mobilization flux (*i.e.* $(1-\kappa)\dot{p}_C$) is allocated to maturity E_H for maintenance ($\dot{p}_J$) and maturity increase. So the increase in maturity is $(1-\kappa)\dot{p}_C - \dot{p}_J$. The maintenance of the structure ($\dot{p}_S$) depends on temperature trough the Arrhenius relationship ($c(T)$), and also on its surface and/or volume. The maintenance of maturity depends on temperature, with the same Arrhenius relationship ($c(T)$), and on the amount of maturity.
The second stage is the juvenile stage. It starts when the organism is able to feed on the environment, *i.e.* when maturity has reached a fixed threshold (E_H^b). Therefore,

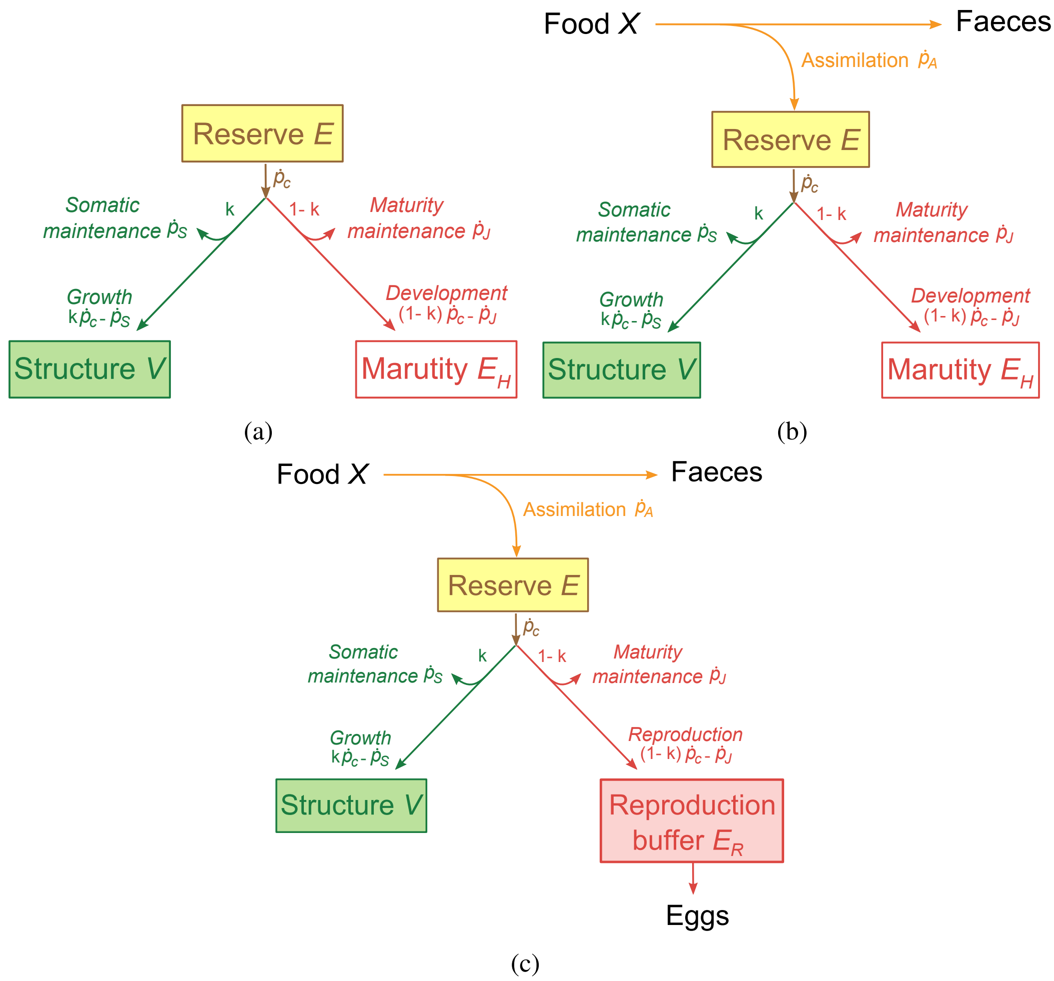


Figure 1: **Schematic representation of the three life stages of the standard DEB model.** (a) An embryo uses reserve to grow and develop. (b) At birth, a juvenile starts feeding, and (c) at puberty, an adult starts allocating energy to reproduction.

the assimilation flux $\dot{p}_A$ is no longer null. The assimilation depends on temperature, environmental food condition ($f(X)$) and the structural surface of the organism. The assimilated energy supplies the reserve compartment from which energy is allocated to growth or maturation, still with the same κ allocation rule.
When maturity has reached a fixed amount of energy (E_H^p), the organism enters the adult stage. From this moment, named puberty, energy that was previously allocated to maturity is now allocated to reproduction. Nevertheless, the maturity maintenance does not cease, and the allocation rate to growth or maturity/reproduction is still the same.

The metabolic acceleration occurs between birth and a moment defined as the metamorphosis (when maturity reaches a threshold value (E_H^j), before puberty) which might or might not correspond with changes in morphology.
For more details on DEB theory, see Kooijman [2010].

Table 1: Equations of the standard DEB model for ectotherm.

Differential equations
$\frac{d}{dt}E = \dot{p}_A - \dot{p}_C$ $\frac{d}{dt}V = \frac{1}{[E_G]}\dot{p}_G = \frac{1}{[E_G]}(\kappa\dot{p}_C - \dot{p}_S)$ $\frac{d}{dt}E_H = (1-\kappa)\dot{p}_C - \dot{p}_J \quad \text{if } E_H < E_H^p, \quad \text{else } \frac{d}{dt}E_H = 0$ $\frac{d}{dt}E_R = 0 \quad \text{if } E_H < E_H^p, \quad \text{else } \frac{d}{dt}E_R = (1-\kappa)\dot{p}_C - \dot{p}_J$
Fluxes equations
$\dot{p}_A = c(T)f(X)\{\dot{p}_{Am}\}L^2 \quad \text{if } E_H \geq E_H^b, \quad \text{else } \dot{p}_A = 0$ $\dot{p}_C = c(T)\{\dot{p}_{Am}\}L^2\frac{ge}{g+e}\left(1 + \frac{L}{gL_m}\right); \quad \text{with } e = \frac{E}{E_m} = \frac{E}{V}\frac{\dot{v}}{\{\dot{p}_{Am}\}} \quad \text{and } L = V^{\frac{1}{3}}$ $\dot{p}_S = c(T)[\dot{p}_M]L^3$ $\dot{p}_J = c(T)\dot{k}_J E_H$
Scaled food and temperature functions
$f(X) = \frac{X}{X+K}$ $c(T) = exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right)$

2.2 Parameter estimation

The parameters of the standard DEB model were estimated using the co-variation method [Lika et al., 2011]. This method uses the simplex method to simultaneously minimize the weighted sum of squared deviations between model predictions and observations for a considerable number of data sets. Two types of data are used: the uni-variate data and the zero-variate data. Uni-variate data consist of sets of time-series observations of an organism, like growth versus time. The zero-variate data are composed of pseudo-data and real-data. Pseudo data are composed of parameter values which are supposed to be highly conserved among all the taxa, so they serve as a kind of prior knowledge on the organism. Real data are observations such as maximum length and weight at birth and/or puberty and/or death, lifetime and number of egg produced. A weight coefficient can be assigned to each uni-variate data set, and both kinds of zero-variate data set. In the present study we chose to assign the same weight to every data set.

Table 2: Parameters, state variables and forcing variables of the standard DEB model.

Symbol	Value	Units	Definition
			State and forcing variables
E		J	Reserve density
V		cm^3	Structural volume
E_H		J	Cumulated energy invested into development
E_R		J	Reproduction buffer energy
X		$J \cdot l^{-1}$	Food density
T		K	Temperature
$f(X)$			Scaled functional response
$c(T)$			Temperature correction factor
			Primary parameters for *Pimephales promelas*
$[\dot{p}_M]$	85.598	$J \cdot cm^{-3} \cdot d^{-1}$	Volume-specific somatic maintenance rate
$\{\dot{p}_T\}$	0	$J \cdot cm^{-2} \cdot d^{-1}$	Surface-area-specific somatic maintenance rate
$[E_G]$	5220.5	$J \cdot cm^{-3}$	Volume-specific cost for structure
$\dot{v}$	0.0201	$cm \cdot d^{-1}$	Energy conductance
κ	0.9105		Fraction reserve used for growth + maintenance
$\dot{k}_J$	0.0020	d^{-1}	Maturity maintenance rate coefficient
E_H^h	0.0768	J	Maturity threshold at hatching
E_H^b	0.1391	J	Maturity threshold at birth
E_H^j	9.3675	J	Maturity threshold at metamorphosis
E_H^p	546.82	J	Maturity threshold at puberty
κ_R	0.95		Fraction of the reproduction buffer fixed into eggs
			Auxiliary and compound parameters for *Pimephales promelas*
T_A	12000	K	Arrhenius temperature
T_{ref}	293.15	K	Temperature
δ_M	0.1609		shape coefficient
			Primary parameters for *Sander vitreus*
$[\dot{p}_M]$	108.990	$J \cdot cm^{-3} \cdot d^{-1}$	Volume-specific somatic maintenance rate
$\{\dot{p}_T\}$	0	$J \cdot cm^{-2} \cdot d^{-1}$	Surface-area-specific somatic maintenance rate
$[E_G]$	5224.5	$J \cdot cm^{-3}$	Volume-specific cost for structure
$\dot{v}$	0.0485	$cm \cdot d^{-1}$	Energy conductance
κ	0.9743		Fraction reserve used for growth + maintenance
$\dot{k}_J$	0.002	d^{-1}	Maturity maintenance rate coefficient
E_H^h	0.1948	J	Maturity threshold at hatching
E_H^b	2.4333	J	Maturity threshold at birth
E_H^j	503.22	J	Maturity threshold at metamorphosis for female
E_H^j	335.73	J	Maturity threshold at metamorphosis for male
E_H^p	1313.2	J	Maturity threshold at puberty for female
E_H^p	81032	J	Maturity threshold at puberty for male
κ_R	0.95		Fraction of the reproduction buffer fixed into eggs
			Auxiliary and compound parameters for *Sander vitreus*
T_A	8000	K	Arrhenius temperature
T_{ref}	293.15	K	Temperature
δ_M	0.1677		shape coefficient

3 Results

3.1 Data versus model outputs for *Pimephales promelas*

Table 3: Real versus estimated data values used for parameter estimation of DEB model for *Pimephales promelas*.

Data (dimension)	Value	Source	Modeled
Age at hatching (d)	4.5	Braunbeck et al. [1998], Jeffries et al. [2015]	4.5
Age at birth for female (d)	6	Sommer [2011]	6.087
Age at birth for male (d)	6	Sommer [2011]	6.678
Age at puberty for female (d)	135	Sommer [2011]	133.8
Age at puberty for male (d)	135	Sommer [2011]	112.7
Age at death (d)	1460	Sommer [2011]	1460
Weight at birth (10^{-4} g)	3.393	Braunbeck et al. [1998]	3.548
Weight at puberty (g)	0.7857	Braunbeck et al. [1998]	0.835
Weight at death for female (g)	3	Sommer [2011]	3.358
Weight at death for male (g)	5	Sommer [2011]	5.185
Length at birth (cm)	0.5	Wang [1986]	0.3552
Length at puberty (cm)	4	Braunbeck et al. [1998]	4.515
Length at death for female (cm)	8.09	Collected from Lab data from SCSU	7.424
Length at death for male (cm)	10.1	Etnier and Starnes [1993]	9.61
Number of egg per day ($\#/d$)	30	Watanabe et al. [2007]	33.35

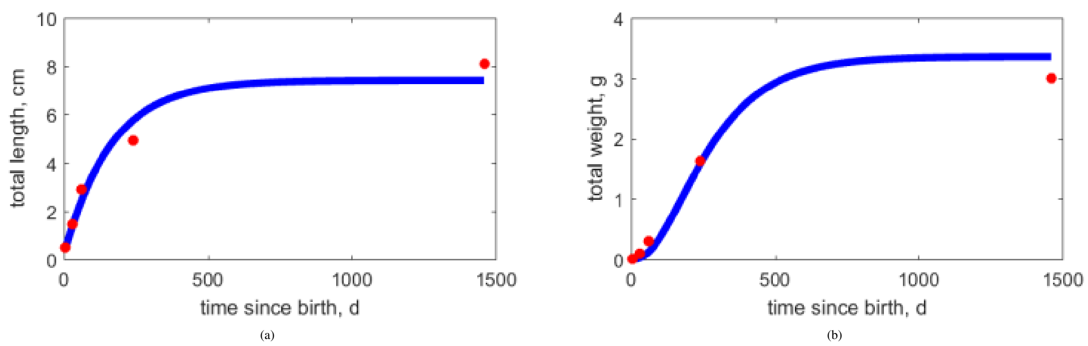


Figure 2: Model outputs versus length data (a) and weight data (b) for female *Pimephales promelas*. Model outputs are the blue lines and data are the red dots.

We used a previously developed version of DEB model for *Pimephales promelas*[1]. We modified some zero-variate data and added some new ones in order to model both female and male fathead minnows (table 3).
We also added uni-variate data on length and weight both for female (figure 2) and male (figure 3). These data were extracted from Saint-Cloud State University (SCSU) laboratory experiments.

[1]`https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Pimephales_promelas/Pimephales_promelas_res.html` - version of 2011/03/17

Zero-variate data (table 3) are accurately reproduced by the model. Life-cycle events (*i.e.* ages at hatching, birth, puberty and death) at different temperatures are particularly well estimated, which guarantees that the DEB model estimations are in accordance with reality. Lengths and weights observed at each of these life-cycle events are also well reproduced by the model as well as the reproduction rate.
Pimephales promelas exhibits a sexual dimorphism that is taken into account by the DEB model. The female (figure 2) and male (figure 3) growth patterns are accurately simulated by the model both for length and weight growth.

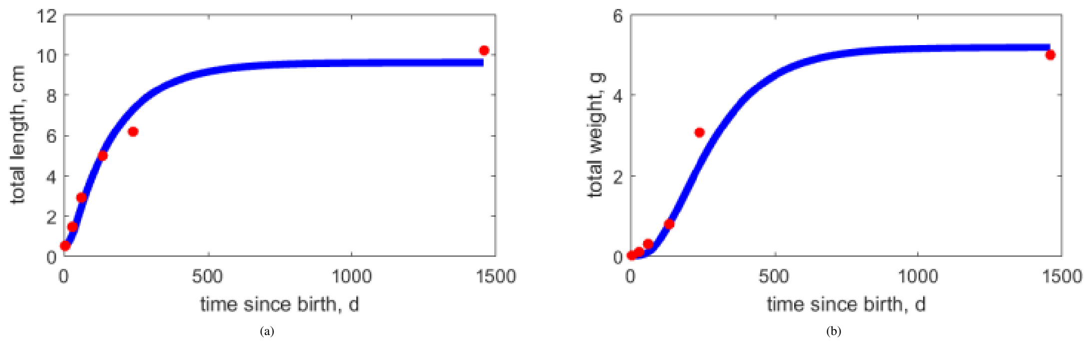


Figure 3: Model outputs versus length data (a) and weight data (b) for male *Pimephales promelas*. Model outputs are the blue lines and data are the red dots.

3.2 Data versus model outputs for *Sander vitreus*

Data used for the parameter estimation were all extracted from literature. Zero-variate data are shown in table 4. Uni-variate data include data on length, growth (figures 4 and 5), weight versus length data (figure 6), egg versus length data (figure 7) and incubation time data versus temperature data (figure 8).

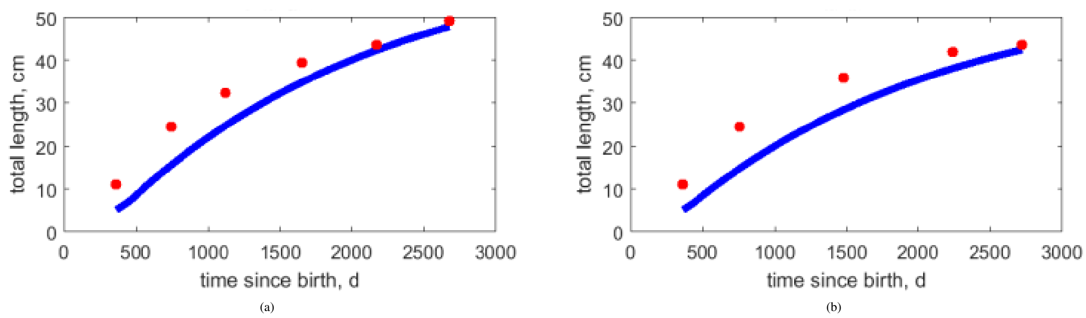
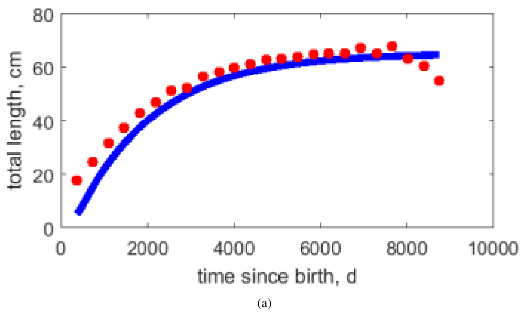


Figure 4: Model outputs versus length data for female (a) and male (b) *Sander vitreus*. Model outputs are the blue lines and data are the red dots. Data are extracted from Colby et al. [1979]

Table 4: Real versus estimated data values used for parameter estimation of DEB model for *Sander vitreus*.

Data (dimension)	Value	Source	Modeled
Age at hatching (d)	14	Nelson [1968]	13.83
Age at puberty for female (d)	1095	Bozek et al. [2011]	827.2
Age at puberty for male (d)	730	Bozek et al. [2011]	792.2
Age at death (d)	6023	Bozek et al. [2011]	6023
Weight at birth (g)	0.031	Bozek et al. [2011]	0.0308
Weight at puberty for female (g)	587.9	Honsey et al. [2017]	660.4
Weight at puberty for male (g)	436.9	Honsey et al. [2017]	417.9
Weight at death for female (g)	2763	Honsey et al. [2017]	2585
Weight at death for male (g)	1605	Honsey et al. [2017]	1727
Length at hatching (cm)	0.65	Nelson [1968]	0.6622
Length at birth (cm)	1.5	Nelson [1968]	1.492
Length at puberty for female (cm)	40	Bozek et al. [2011]	41.45
Length at puberty for female (cm)	35	Bozek et al. [2011]	35.59
Length at death for female (cm)	67	Bozek et al. [2011]	65.33
Length at death for male (cm)	54	Bozek et al. [2011]	57.11
Number of egg per day ($\#/d$)	2055	Bozek et al. [2011]	1034



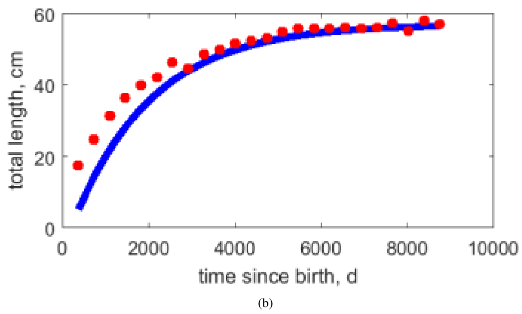


Figure 5: Model outputs versus length data for female (a) and male (b) *Sander vitreus*. Model outputs are the blue lines and data are the red dots. Data are extracted from Honsey et al. [2017]

The DEB model well reproduce all the zero-variate data (tabel 4). Ages at hatching, birth, puberty and death at different temperatures are all well estimated both for the male and the female. Age at puberty for female is slightly underestimated by the model. Nevertheless, both length and weight at puberty for the female walleye are accurately reproduced. Lengths and weights observed at each of the other life-cycle events are also well reproduced by the model. Walleye exhibits a sexual dimorphism. The female grows larger in length and weight compared to the male walleye. This is also accounted in the model and accurately reproduced both for length (figures 4 and 5) and weight (figure 6) for male and female.

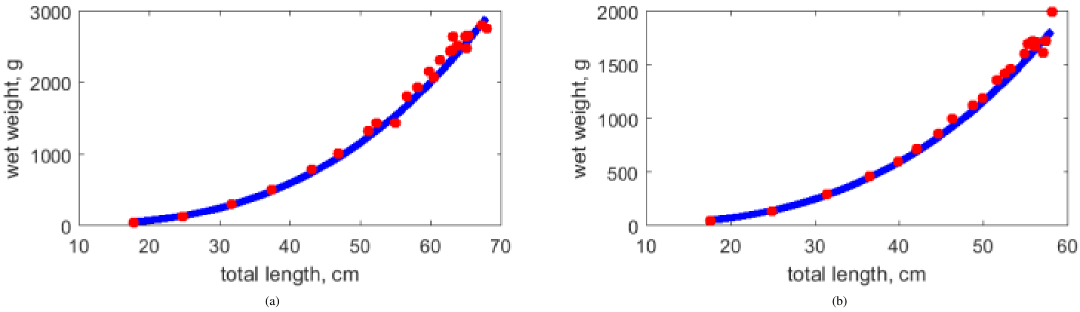


Figure 6: Comparison of model outputs and length versus weight data for female (a) and male (b) *Sander vitreus*. Model outputs are the blue lines and data are the red dots. Data are extracted from Honsey et al. [2017]

Female reproduction (eggs number) as function of length is also well reproduced by the model. Figure 7 shows data on reproduction at two different food and temperature conditions in lake Erie that are well reproduced as well. Incubation time (time to hatch) as function of temperature (figure 8) is accurately reproduced. The accurate reproduction of these data at different food and temperature conditions validate the realistic behavior of the model in different modeling contexts.

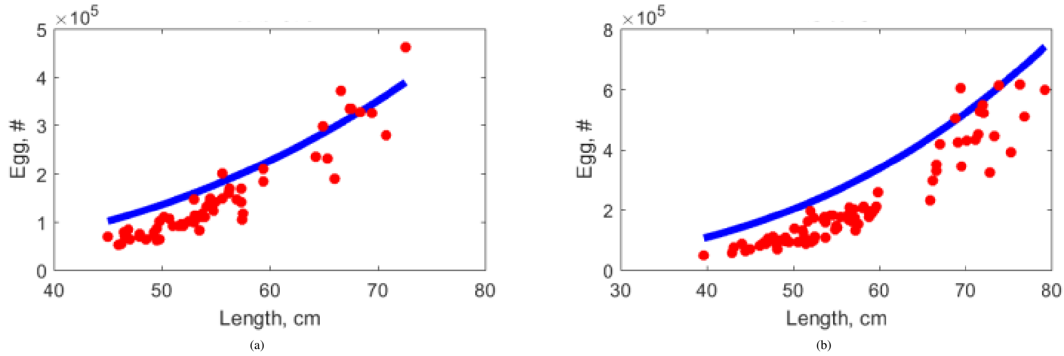


Figure 7: Comparison of model outputs and egg versus length data for East Erie Lake (a) and West Erie Lake (b) for *Sander vitreus*. Model outputs are the blue lines and data are the red dots. Data are extracted from Wolfert [1969]

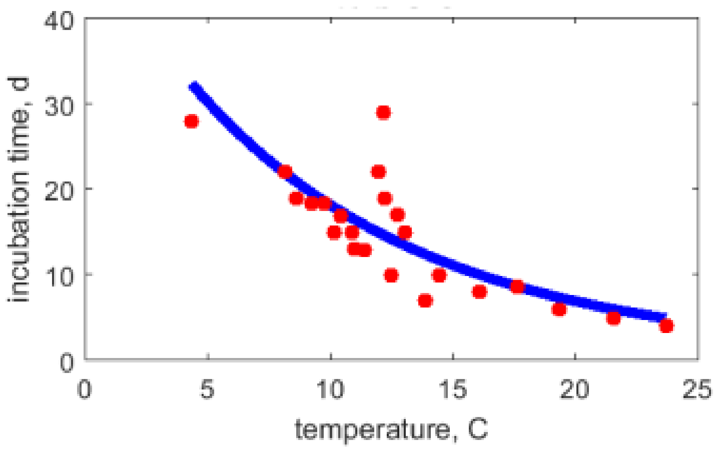


Figure 8: Comparison of model outputs and incubation time versus temperature data for*Sander vitreus*. Model outputs are the blue lines and data are the red dots. Data are extracted from Wolfert [1969]

4 General conclusion

The DEB models calibrated for *Pimephales promelas* and *Sander vitreus* provide an accurate representation of the full life-cycle in different simulation contexts both for male and female individuals.

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