Individual Based Models for the fathead minnow *Pimephales promelas* and the walleye *Sander vitreus*

M.Vaugeois, P.A. Venturelli, V.E. Forbes

1 Introduction

This document first provides a description of the DEB-IBM models developed for the fathead minnow *Pimephales promelas* and the walleye *Sander vitreus* following the ODD protocol (Overview, Design concepts, Details) for describing individual- and agent-based models [Grimm et al., 2006, 2010]. Then, it presents the simulations results and conclusions about this study.

2 Methods

The two models are developed in Java using the "SimAquaLife" framework [Dumoulin, 2007], which is an individual-based process-oriented framework for aquatic life simulation. Both models are based on same methodologies and share the same objective which is to predict population-level effects of exposure to estrone in different river systems. Therefore, the IBMs are very similar and only differ by the value of their parameters, the initialization and the reproduction sub-models.
The following description is written as the description of one model. We will clearly specify any difference between the two models.

2.1 Purpose

The purpose of this model is to predict effects of exposure to estrone at the population level for different river system types and for different species.

2.2 Entities, state variables, and scales

There are two types of entities in the model, the individuals and spatial units. We used the scaled version of the Dynamic Energy Budget (DEB) model with metabolic acceleration to represent the energy budget of individuals. Individuals are characterized by four state variables (see table 1), namely: the structure (noted L, with the dimension of cm); the scaled reserve (U_E, d.cm); the scaled maturity (U_H, d.cm); and the scaled reproduction (U_R, d.cm). For more details or introduction on Dynamic Energy Budget theory [Kooijman, 2010], see [van der Meer, 2006, Nisbet et al., 2000, Sousa et al., 2010, Jusup et al., 2016]. The ageing of individuals is set the same way as in [Martin et al., 2012]. Briefly, in DEB theory ageing is described by two state variables, namely the damage inducing compounds ($\ddot{q}$), and damage ($\dot{h}$). This is based on the idea that free radicals cause irreversible damage on DNA (damage inducing compounds) that creates damage, and probability to die by ageing is proportional to the amount of damage. Regarding the inter-individual variability, we set it by introducing a normally distributed number ($\mu = 1$ and $\sigma = 0.05$), the scatter multiplier, which impacts four of the eight standard DEB parameters (table 2).

Table 1: State variables.

Name	Notation	Dimension
Volumetric structural length	L	cm
Scaled reserve	U_E	$d.cm^2$
Scaled maturity	U_H	$d.cm^2$
Scaled reproduction	U_R	$d.cm^2$
Ageing acceleration	$\ddot{q}$	$d.cm^2$
Hazard rate	$\dot{h}$	$d.cm^2$
Prey density	X	$J.cm^{-2}$

The model has ten spatial units, each representing one hectare zone of a river. Individuals decide to move upstream or downstream or to stay in their current zone with an equal probability (see 2.3).
Each zone is characterized by 3 quantitative state variables: the prey density (X, $J.cm^{-2}$), the temperature (T, in C) and the surface area (in m^2). The prey density changes daily (*i.e.* at each time step) and independently in each zone according to a logistic growth minus what is eaten by fishes in the zone. The logistic growth function has two parameters, the intrinsic growth rate (here noted a_E, with the dimension of d^{-1}) and the carrying capacity (here noted k_E, with dimension of $J.m^{-2}$). Temperature is the same in all zones and changes daily according to temperature data recorded in Kawishiwi River, MN. Data were downloaded from USGS website (https://waterdata.usgs.gov/nwis).

The model integration is done following the classical Runge-Kutta method thanks to Apache Commons Math library (release 3). One time step represents one day and simulations are run for 20 years. When considered, exposure to estrone starts at 15 years.

2.3 Process overview and scheduling

At each time step, the following action are executed. First, individuals are listed zone by zone. Then, in each zone, individuals first update their DEB state variables. Consequently to this update, organisms can die for 3 reasons: or they can no longer pay their maintenance cost (starvation), or their death is due to ageing, or they die by predation (stage-dependent

Table 2: Parameters.

Name	Notation	Dimension
Standard parameters		
Fraction of mobilized energy to soma	κ	wd
Fraction of reproduction energy fixed in eggs	κ_R	wd
Somatic maintenance rate coefficient	$\dot{k}_M$	d^{-1}
Maturity maintenance rate coefficient	$\dot{k}_J$	d^{-1}
Scaled maturity at hatching	U_H^h	$d.cm^2$
Scaled maturity at metamorphosis	U_H^j	$d.cm^2$
Scaled maturity at birth	U_H^b	$d.cm^2$
Scaled maturity at puberty	U_H^p	$d.cm^2$
Energy conductance	$\dot{v}$	$cm.d^{-1}$
Energy investment ratio	g	wd
Ageing parameters		
Weibull ageing acceleration	$\ddot{h}_a$	d^{-2}
Gompertz stress coefficient	S_G	wd

survival rate to predation). Starvation death is deterministic (depends on state variable) and the other two (*i.e.* ageing and predation) are stochastic (*i.e.* depends on a random selection, see 2.3). The next process is the reproduction. Only adult individuals with a certain amount of energy allocated to reproduction (U_R, d.cm) are able to reproduce. Females can only reproduce if a ready-to-reproduce male is present in the zone. The last process executed is the movement. This process is also a stochastic process. Individuals have 50 percent chance to move or to stay in their current zone. If they choose to move, they have 50 percent chance to move upstream or downstream.

2.4 Design concepts

2.4.1 Basic principles

The model is based on Dynamic Energy Budget theory for describing the energetic of individuals. The DEB model describes how individuals feed, allocate energy for growth and reproduction, and die. Food is limited in our model and its availability depends both on fish density and the logistic growth parameter of food defined in the spatial units. DEB model allow to represent two kinds of mortalities, ageing or starvation. We introduced a third one that represent the mortality due to predation.

The goal of this model is to estimate the population scale effects of exposure to Estrone in different river system types. Consequently we will model different system types, each one characterized by different sets of parameters.

2.4.2 Emergence

All the following measurements emerge from the behavior of individuals, their metabolism, the indirect interaction of individuals through competition for food and the predation: fish density, average individual size (length and weigh), average number of reproducing events per female, average number of eggs per reproducing events, population level mortality rates (starvation and predation), Fulton's condition index [Shin et al., 2005] (*i.e.* ratio of weight of cubic length).

2.4.3 Adaptation

While DEB parameters are different among individuals, they stay constant over the simulation for each individuals. So, there is no adaptive behavior. At any time, individuals can chose to stay or to move from one zone to another.

2.4.4 Objectives

The objective of this work is to compare effects of estrone at the population scale level for different types of river systems. In order to do that, we modeled a river environment with two controlling precesses, the food availability and the stage-dependent predation. Then, several simulations were ran with different sets of parameters for food logistic growth and stage-dependent survival rates to predation. Finally, we analyze the outputs to see in which conditions (*i.e.* set of parameters) a realistic population pattern is observed.
The pattern we want to reproduce is based on literature data and is as follow for the fathead minnow:

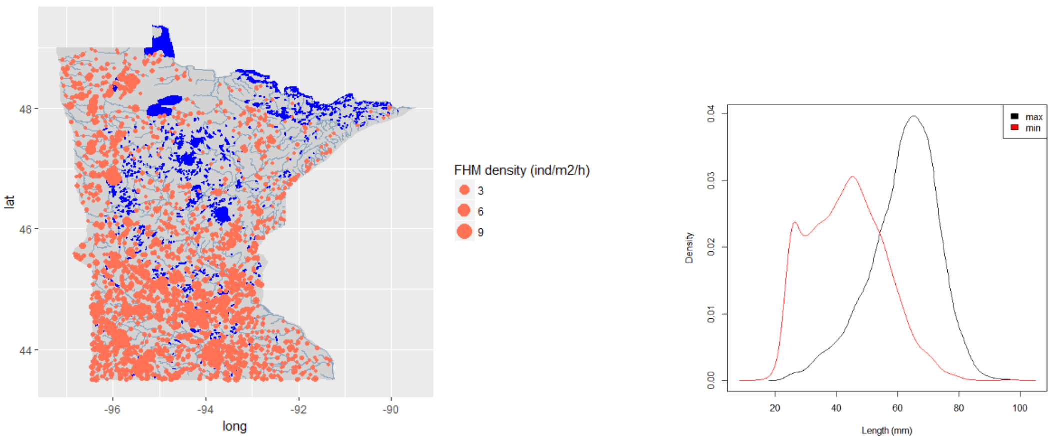
1. The average fish population (individuals between 1.5 and 9.8 cm) density must be between 1 individuals per m^{-2} and 16 individuals per m^{-2} based on the Minnesota Pollution Control Agency (MPCA) (see figure 1);
2. The average number of reproduction events per female per year must be between 14 and 26 [Gale and Buynak, 1982];
3. The average spawning interval (average time between two reproduction events) for female must be between 2.5 and 5.5 days [Watanabe et al., 2007, Jensen et al., 2001];
4. The average number of eggs per clutch must be between 80 and 140 [Watanabe et al., 2007, Ankley et al., 2001].

Regarding the walleye, the pattern we want to reproduce is based on literature data and is as follow:

1. Proportional stock density (PSD) must be comprised between 10 and 60 [Cichosz, 2009, Nate et al., 2011]. PSD is a population structure index that is calculated as follow [Anderson, 1996]: $PSD = 100 * \frac{Numberoffishwithlength>=38cm}{Numberoffishwithlength>=25cm}$
2. Relative stock density (RSD) must be comprised between 1 and 40 [Cichosz, 2009]. RSD is another population structure index that is calculated as follow [Anderson, 1996]: $RSD = 100 * \frac{Numberoffishwithlength>=45cm}{Numberoffishwithlength>=25cm}$

3. Reproduction rate (number of eggs per reproduction) must be comprised between 50000 and 700000 per female individuals Bozek et al. [2011].

4. Number of adults walleye per hectare must be comprised between 1 and 60 [Nate et al., 2011].



(a) (b)

Figure 1: Fathead minnow density in Minnesota (a). Distribution functions of maximum (black) and minimum (red) size measured when fish were collected by electro-fishing (b). Minimum size limit is 1.5 cm and maximum size limit is 9.8cm. Data obtained from the Minnesota Pollution Control Agency.

2.4.5 Learning

There is no learning process in the present model.

2.4.6 Prediction

There is no prediction process in the model.

2.4.7 Sensing

There is no Sensing process in the present model.

2.4.8 Interactions

Individuals interact via reproduction. Individuals interact indirectly via competition for food.

2.4.9 Stochasticity

Some DEB parameters change among individuals. We followed the same methodology than [Martin et al., 2012], based on [Kooijman et al., 1989], to set variability among individuals. Briefly, the surface area specific maximum ingestion rate $\{\dot{J}_{XAm}\}$ is multiplied by a scatter multiplier to introduce differences between individuals. It impacts 4 DEB parameters: the half-saturation coefficient K (see equation **??**) that is multiplied by the value of the scatter multiplier; the energy investment ratio g, that is divided by the value of the scatter multiplier as it equals $\frac{[E_G]\dot{v}}{\kappa\{\dot{P}_{Am}\}}$, with $\{\dot{P}_{Am}\} = \{\dot{J}_{XAm}\}\kappa_X\mu_X$; and the scaled maturity threshold for birth U_H^b and puberty U_H^b, that are divided by the value of the scatter multiplier because we use the scaled DEB model (which is the standard DEB model scaled by $\{\dot{P}_{Am}\}$, see [Kooijman et al., 2008] for more details on scaling standard DEB model).
Another source of stochasticity comes from the order with which organisms are updated. In this work, individuals are randomly selected at each time step, zone by zone.
Another source of stochasticity comes from destination decision (stay or upstream or downstream).
The last sources of stochasticity comes from the probability to die by ageing and the probability to to die by predation.

2.4.10 Collectives

There is no aggregation behavior in the model.

2.4.11 Observations

We collected observations on fish density, number of eggs per reproductive event per female, number of reproducing event per female, average time between two reproductive events (spawning interval) for female, average size of individuals (length and weigh), average population Fulton's condition index (ratio of weight over cubic length).

2.5 Initialization

At the beginning of each simulation food density is set to the value of the carrying capacity in all zones.
For the fathead minnow, all simulations starts at the 151^{th} day of the year in accordance with the reproduction period. For the first 3 years of simulation, 40 individuals are introduced (at the egg stage, with a sex ratio of 0.5) each day with a temperature higher than 15 degree Celsius.
For the walleye, all simulations starts at the 91^{th} day of the year. At this day, 1000 larvae are introduced (with a sex ratio of 0.5). This is repeated for the first 4 years of simulation at this day of the year.

We introduced variability among individuals as described in part 2.4.9. The initial set of DEB parameters (*i.e.* the one on which we apply a scatter multiplier) is the one from the add-my-pet procedure (see the document entitled "Add-my-pet procedure"). The initial value of the DEB state variables are: $L = 0.001$; $U_R = 0$; $U_H = 0$. The initial amount of scaled reserve U_E is calculated for each individuals from the bisection method, as in [Martin et al., 2012].

2.6 Input data

One temperature data set (recorded in Kawishiwi River, MN), provided by the USGS, is inputed in the model. The temperature is the same in every zone of the river and is set identical from one year to the other.

2.7 Sub-models

There are 4 sub-models. 2 sub-models concern individual life cycle: the *Deb sub-model*, which includes DEB state variables update, death due to starvation, ageing and prey dynamics ; and the *mortality sub-model*, which includes the death due to ageing and predation. The other 2 sub-models are for reproduction and movement.

2.7.1 DEB sub model

- Calculate delta reserve considering feeding and mobilized energy
- If maturity is inferior to maturity threshold for puberty, then calculate delta maturity. Otherwise calculate delta reproduction buffer
- Calculate delta length ; If delta length is inferior to 0, then recalculate structure, reserves, maturity, and reproduction buffer based on starvation rules
- If mobilized energy is inferior to energy needed for maintenance, then die
- Calculate delta ageing acceleration
- Calculate delta hazard based on ageing (*i.e.* probability of dying related to ageing)
- Calculate delta prey density based on feeding
- Update prey density
- Update DEB state variables

2.7.2 Mortality sub-model

- If random number is inferior to probability of dying related to ageing, then die
- If random number is inferior to probability of dying related to predation, then die

2.7.3 Reproduction sub-model

For the fathead minnow:

- If the environmental temperature is superior or equal to 15 degree Celcius:
  - If female reproduction buffer is superior to threshold for reproduction and if a ready to reproduce male is in the zone, then reproduce:
    - calculate egg initial energy amount
    - calculate number fertilized eggs spawned
    - update reproduction buffer accordingly
  - If male reproduction buffer is superior to threshold for reproduction and if a ready to reproduce female is in the zone, then reproduce:
    - calculate energy amount needed for reproduction event
    - update reproduction buffer accordingly

For the walleye:

- If the environmental temperature is comprised between 4 and 11 degree Celcius and the time in the year is before the 151^{th} day of the year:
  - If female reproduction buffer is superior to threshold for reproduction and if a ready to reproduce male is in the zone, then reproduce:
    - calculate egg initial energy amount
    - calculate number fertilized eggs spawned
    - update reproduction buffer accordingly
  - If male reproduction buffer is superior to threshold for reproduction and if a ready to reproduce female is in the zone, then reproduce:
    - calculate energy amount needed for reproduction event
    - update reproduction buffer accordingly

2.7.4 Movement

- If not egg, then:
  - If random number is inferior to probability of moving, then move
  - If random number is inferior to probability of moving upstream, then move upstream

2.8 Simulations

2.8.1 Preliminary simulations for the fathead minnow

We ran 20 replicates of each simulation. A simulation has a specific combination of 4 parameters:

- The intrinsic growth rate::
  $a_E \in [0.4, 0.8, 1.5]$;
- The carrying capacity:
  $k_E \in [500.00, 2000.0, 4000.0]$;
- The juvenile annual survival rate:
  $asr_J \in [0.005, 0.01, 0.025, 0.05, 0.1]$;
- The adult annual survival rate:
  $asr_A \in [0.4, 0.8]$.

The total number of simulations is thus 1800. From these simulations, we selected the ones that reproduced the pattern described in the part 2.4.4. The number of selected sets of parameters was 50 out of 90 possible. Each one of this 50 selected sets of parameters represent a different river system.

2.8.2 Preliminary simulations for the walleye

We ran 20 replicates of each simulation. A simulation has a specific combination of 4 parameters:

- The intrinsic growth rate::
  $a_E \in [0.4, 0.8, 1.5]$;
- The carrying capacity:
  $k_E \in [5000.00, 10000.0, 20000.0]$;
- The egg annual survival rate:
  $asr_E \in [0.02, 0.05, 0.1]$;
- The larvae annual survival rate:
  $asr_L \in [4.73e^{-8} 1.44e^{-5}]$;
- The juvenile annual survival rate:
  $asr_J \in [0.09, 0.15]$;
- The adult annual survival rate:
  $asr_A \in [0.6, 0.8]$.

The total number of simulations is 4320. From these simulations, we selected the ones that reproduced the pattern described in the part 2.4.4. The number of selected sets of parameters was 31 out of 216 possible. Each one of this 31 selected sets of parameters represent a different river system.

2.8.3 Simulations with exposure to estrone

Effect on larval survival rate to predation for fathead minnow:

The observed effects of exposure to estrone indicated that temperature does not strongly or consistently modulate the effects of estrone on reproduction, development, and egg survival. However, results suggested that estrone alter larval predator avoidance performance [Ward et al., 2017] which motivated the set up of a predation experiment. Based on the results of this experiment [Korn, 2018], we set up simulations in which the larval survival probability was affected by 10 and 25 percent, the latter corresponding to the observed effect during the experiments.
For each previously selected set of parameters, we ran 20 replicates of simulations in which fish are exposed to estrone starting at the year 15. We then measured effects at the population scale after 5 years exposure.

Effect on egg survival rate to predation for fathead minnow:

Experiments showed that the number of aggressive acts by male fathead minnow decreased when they were exposed to estrone [Ward et al., 2017]. A reduced aggressiveness in male fathead minnow could result in a reduced efficiency to defend the nest from predator. Consequently, the egg survival rate to predation could be affected. In order to investigate how a potential reduction of male nest defense ability could translate at the population scale, we set up simulations in which the egg survival probability was affected by 25 percent.
For each previously selected set of parameters, we ran 20 replicates of simulations with exposure to estrone starting at the year 15. We then measured effects at the population scale after 5 years exposure.

Simulations with combined effects of estrone exposure on larval and egg survival rates to predation for fathead minnow:

For each previously selected set of parameters, we ran 20 replicates of simulations with exposure to estrone starting at the year 15. The considered effects were a 25 percent decrease of both larval and egg survival rate to predation. We then measured effects at the population scale after 5 years exposure.

Simulations for the walleye:

For the walleye, we considered two effects. First, we considered that walleye larvae could be affected in the same way as the fathead minnow when exposed to estrone. We thus ran simulations with a 25 percent decrease of the larval survival rate to predation.
Secondly, taking into account the results of the fathead minnow IBM that showed a population decrease due to exposure to estrone when food was limiting, we also ran simulations with the walleye IBM in which food availability was reduced.
We did not considered effects on egg survival rates to predation because walleye are broadcast spawners.
For each previously selected set of parameters, we ran 20 replicates of simulations with exposure to estrone starting at the year 15. We then measured effects at the population scale after 5 years exposure. We ran 3 sets of simulations:

- The considered effect was a 25 percent decrease of larval survival rate to predation.

- The considered effect was a 25 percent decrease of the environmental food carrying capacity.
- The considered effect was a combination of the two previously considered effects (25 percent decrease for both).

3 Results

3.1 IBMs simulations for fathead minnow:

3.1.1 Effect on larval survival rate to predation:

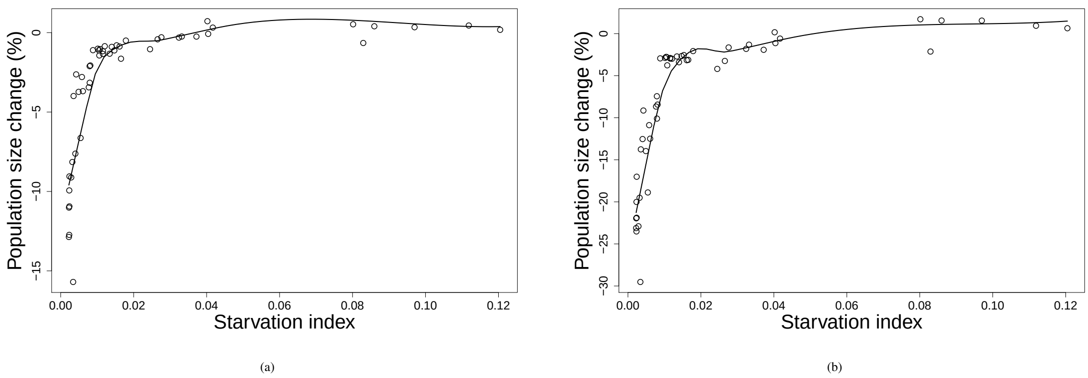
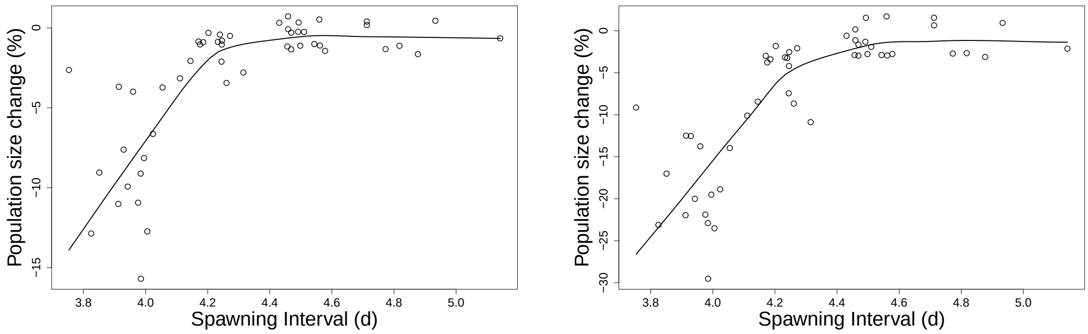


Figure 2: Relative population decline (in percent) after 5 year exposure to estrone as function of the starvation index. Considered effect is a 10 percent (a) and a 25 percent (b) decrease of the larval survival rate to predation. Each point represents the average value of 20 simulations of one particular system. The line is a non-parametric regression of the points (LOESS).

The figure 2 presents how population density changes when fish are exposed to estrone. We can see that all river system types do not show the same answer. For a 10 percent decrease in larval survival rate to predation, the consequence on the fish population density can either be null or decrease by more than 15 percent. Similarly, the population density can either decrease by about 30 percent or do not decrease at all when a 25 percent decrease in larval survival rate is considered. Actually, the population-level effect depends on whether the fish population is more controlled by predation or by food availability. Both control types occur in any system but one of the two has more hold on the population size than the other.
Depending on the relative strength of these two controlling processes, individuals will be more likely to die by starvation or by predation. Therefore, we can characterize the different types of system by comparing the different ratios of individuals who died by starvation over all dead individuals in the systems. This index, that we will named starvation index, will inform us on which is the major process controlling the population size. If it is low,

we can say that the system is more controlled by predation than food availability and vice versa. On the figure 2, we can see that the more a system is controlled by predation, the more it is likely to be importantly impacted by an exposure to estrone.



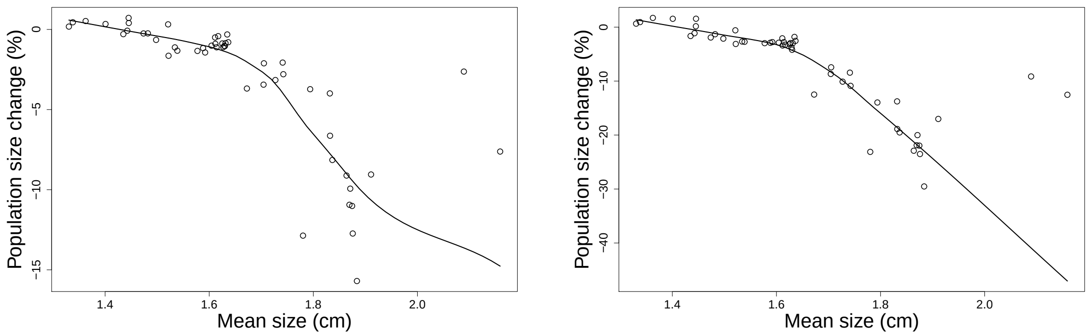
(a) (b)

Figure 3: Relative population decline (in percent) after 5 year exposure to estrone as function of the Fulton's condition index (noted K index) before exposure to estrone. Considered effect is a 10 percent (a) and a 25 percent (b) decrease of the larval survival rate to predation. Each point represents the average value of 20 simulations of one particular system. The line is a non-parametric regression of the points (LOESS).

The figure 3 shows how a relative decrease in population size is related to the value of the Fulton's condition index (ratio of weight over cubic length, noted K index) before the exposure to estrone. We can see that the K index value before exposure to estrone is high (around 0.75 $10^2.cm^{-3}$) in the case of a system which population density will be strongly impacted by the exposure. On the opposite, this value is small (around 0.55) in systems that will not be impacted by exposure to estrone. This means that individual are bigger before exposure in systems that will be strongly impacted by an exposure to estrone.
We can see the same pattern on the figure 4. This figure shows the average size of individuals in different system before being exposed to estrone as function of the relative population decrease after exposure. Here again, we can note that systems with smaller average individual size will be the less impacted by exposure to estrone, whereas the systems with higher average individual size will be more likely be strongly impacted.
Figure 5 presents population changes after exposure as function of the average female spawning interval before any exposure to estrone. It shows that the systems that will be the more impacted are the ones that show a short spawning interval before exposure (*i.e.* higher reproduction rate). On the contrary, systems with longer average spawning intervals before exposure show almost no population decline after exposure.

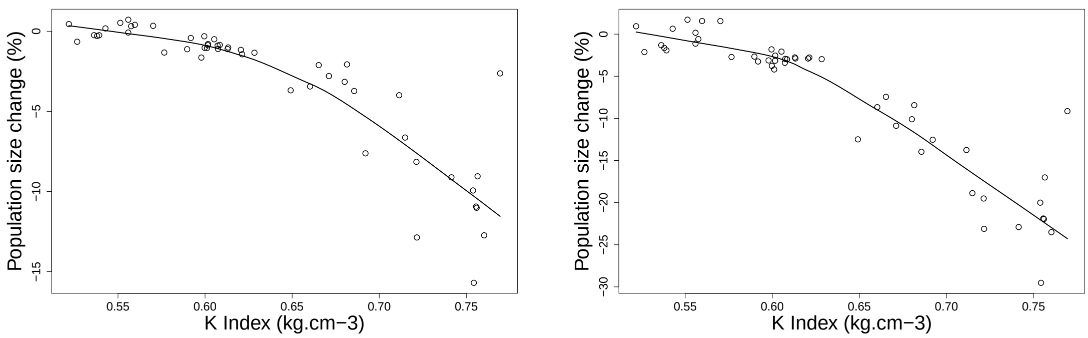
3.1.2 Effect on egg survival rate to predation:

In these simulations with a decreased egg survival rate to predation, we observed the same pattern as we did with the simulations in which we considered a decrease in larval survival rate to predation. The systems that are more controlled by predation (those with a low



(a) (b)

Figure 4: Relative population decline (in percent) after 5 year exposure to estrone as function of the mean individual size before exposure to estrone. Considered effect is a 10 percent (a) and a 25 percent (b) decrease of the larval survival rate to predation. Each point represents the average value of 20 simulations of one particular system. The line is a non-parametric regression of the points (LOESS).



(a) (b)

Figure 5: Relative population decline (in percent) after 5 year exposure to estrone as function of the spawning interval before exposure to estrone. Considered effect is a 10 percent (a) and a 25 percent (b) decrease of the larval survival rate to predation. Each point represents the average value of 20 simulations of one particular system. The line is a non-parametric regression of the points (LOESS).

starvation index) are the ones that show the biggest impacts on fish population density after exposure to estrone (figure 6(a)). Nevertheless, the strength of the population decline is more important than it was with simulations considering effects on larval survival rate. Firstly, a decrease in 25 percent of the egg survival rate to predation can causes a population decline as high as 50 percent. Moreover, systems that were not strongly impacted before (with starvation index between 0.01 and 0.04) are now significantly more impacted.

The relationship between relative population decline after exposure and Fulton's condition index before exposure (figure 6(b)) shows a slightly different pattern compared to the previous case. It is now convex whereas it was concave before.

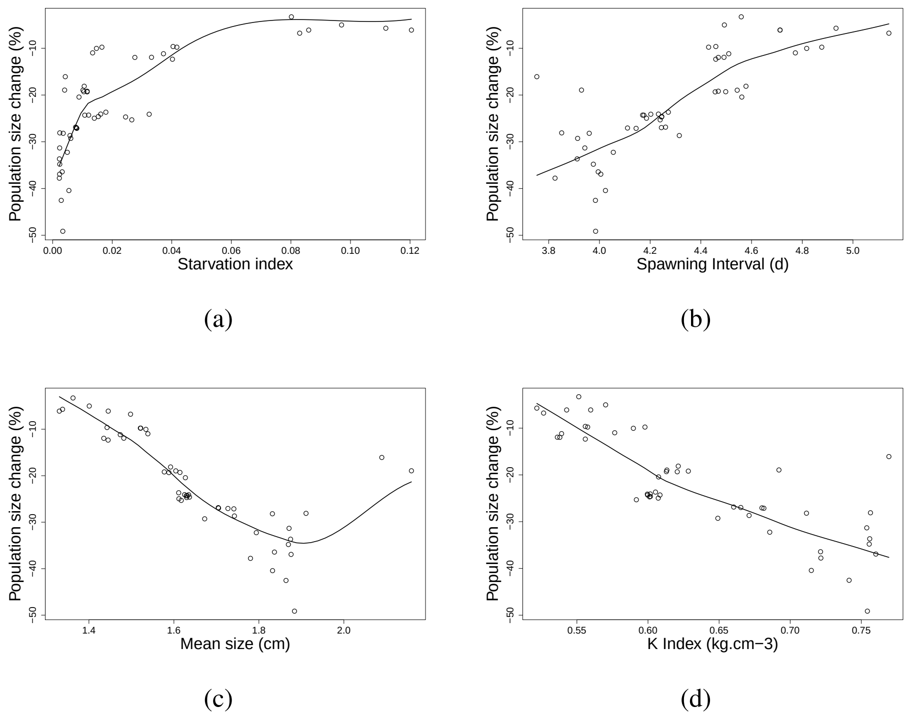


Figure 6: Relative population decline (in percent) after 5 year exposure to estrone as function of the starvation index (a), the Fulton's condition index (noted K index) before exposure to estrone (b), the mean individual size before exposure to estrone (c) and the spawning interval before exposure to estrone (d). Considered effects are a 25 percent decrease of egg survival rate to predation. Each point represents the average population decline for 20 simulations of one particular system. The line is a non-parametric regression of the points (LOESS).

The pattern of fish population decline after exposure as function of the average individual size before exposure (figure 6(c)) has also changed compared to the previous case. It is now more linear at the beginning instead of being concave.
The shape of the relationship between relative population decline after 5 year exposure to estrone as function of spawning interval before exposure (figure 6(d)) is more linear compared to the simulations in which a decrease in the larval survival rate was considered. All these different patterns indicate that the population-level effects of impact on egg survival rate are stronger than those on larval survival rate, both in intensity and in the spectrum wideness of potentially impacted systems.

3.1.3 Combined effects on egg and larval survival rates to predation:

Figure 7 shows how population is affected when a 25 percent decrease of both egg and larval predation rate is considered. We can notice that all types of system are impacted. The minimum impact is a 10 percent population decrease and the maximum impact is a 50 percent decrease. Moreover, a large proportion of systems shows a population decrease of 20 percent or more. This proportion as well as the intensity of the impacted river systems are higher to what was observed when we considered the two effects separately. The patterns of both the Fulton's condition index, the average size and the reproduction rate (spawning interval) are identical to what was observed when we considered the two effects separately.

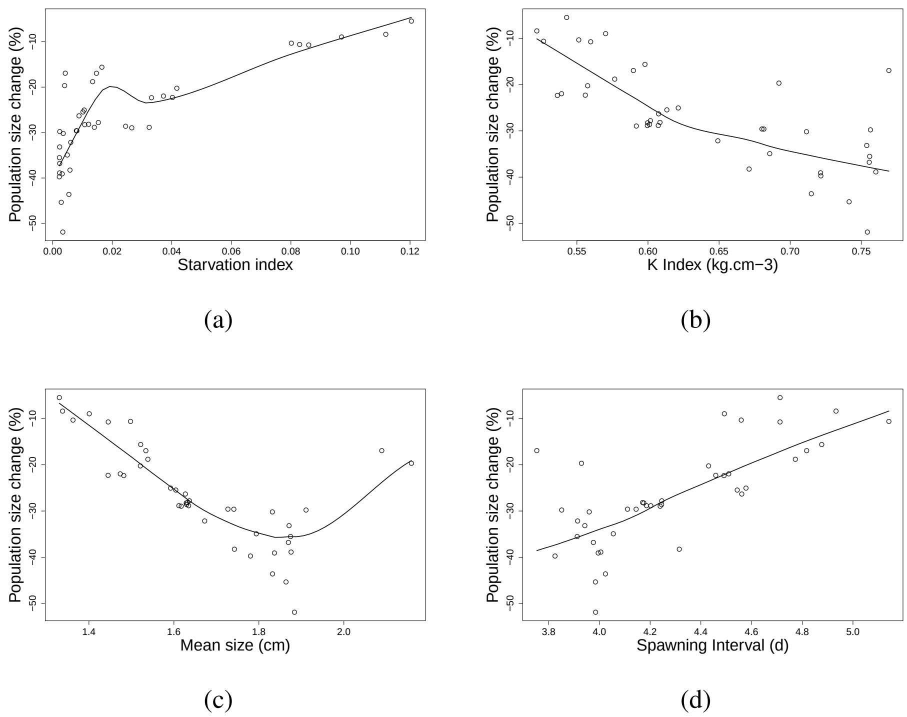
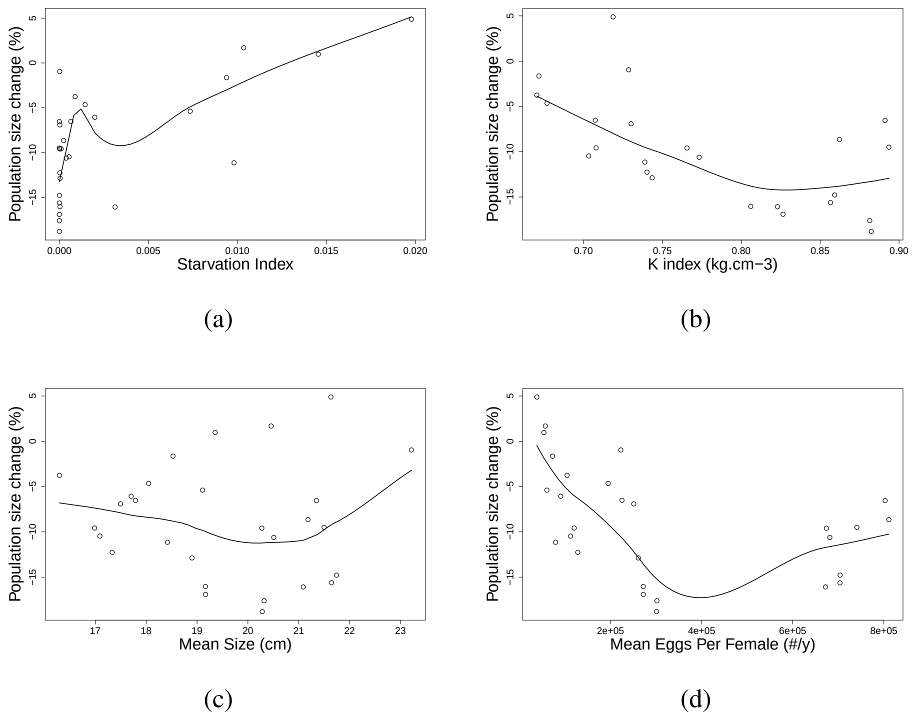


Figure 7: Relative population decline (in percent) after 5 year exposure to estrone as function of the starvation index (a), the Fulton's condition index (noted K index) before exposure to estrone (b), the mean individual size before exposure to estrone (c) and the spawning interval before exposure to estrone (d). Considered effects are a 25 percent decrease of both the egg and the larval survival rates to predation. Each point represents the average population decline for 20 simulations of one particular system. The line is a non-parametric regression of the points (LOESS).

3.2 IBMs simulations for walleye:

3.2.1 Effect on larval survival rate to predation:

the population-level effects of a decrease in larval survival rate to predation for the walleye (figure 7) are very similar to those observed for the fathead minnow. Similarly to what we observed for the fathead minnow, the figure 7(a) shows that the population size change is dependent on the river system type. Nevertheless, the intensity of the observed effect on population size is lower than what was observed for the fathead minnow. The maximum population decrease is between 15 and 20 percent whereas it was between 25 and 30



(a) (b) (c) (d)

Figure 8: Relative population decline (in percent) after 5 year exposure to estrone as function of the starvation index (a), the Fulton's condition index (noted K index) before exposure to estrone (b), the mean individual size before exposure to estrone (c) and the number of eggs per female before exposure to estrone (d). Considered effect is a 25 percent decrease of the larval survival rate to predation. Each point represents the average population decline for 20 simulations of one particular system. The line is a non-parametric regression of the points (LOESS).

percent for the fathead minnow.
The pattern of Fulton's condition index versus population size change is also similar to what was previously observed with the fathead minnow. It is lower in less affected systems (figure 7(b)) and higher in more impacted systems.
The average size (figure 7(c)) shows a different pattern than what was observed with the fathead minnow. In the present case, the average size is not very different between the two types of system.
Regarding the number of eggs per female versus population size change (figure 7(d)), it shows that females in less impacted system produce less eggs compared to systems that will be impacted. This is similar to what was observed with the fathead minnow.

3.2.2 Effect on food availability:

When considering a decrease of food availability, the population-level effects are limited (figure 9(a)). The maximum decrease is about 6 percent. It appears that in this case, the effects are the same whatever the considered system. As the population size effects are limited, we can not give any interpretation to the patterns observed for the Fulton's condition index (figure 9(b)), the average individual size (figure 9(c)) or the reproduction rate (figure 9(d)).

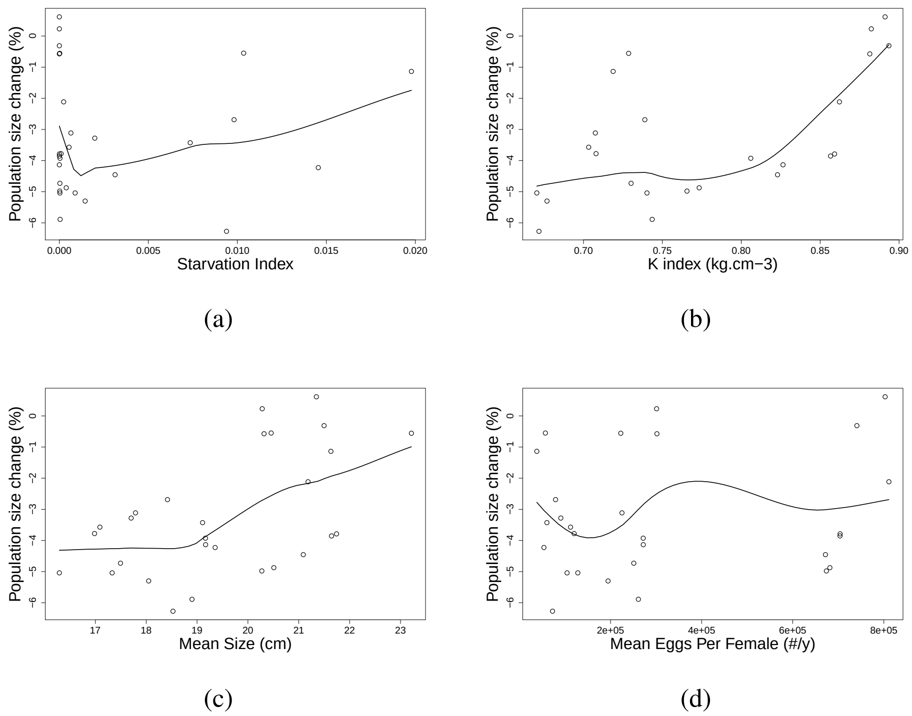


Figure 9: Relative population decline (in percent) after 5 year exposure to estrone as function of the starvation index (a), the Fulton's condition index (noted K index) before exposure to estrone (b), the mean individual size before exposure to estrone (c) and the reproduction rate before exposure to estrone (d). Considered effect is a 25 percent decrease of the environmental food carrying capacity. Each point represents the average population decline for 20 simulations of one particular system. The line is a non-parametric regression of the points (LOESS).

3.2.3 Combined effects on larval survival rate to predation and food availability:

When a decrease of the food availability and a decease of the larval survival rate to predation are simultaneously considered, population-level effects are very similar to the case when only exposure effect on larval survival rate was considered (figure 8(a)). The intensity of the population decline is the same, as well as how much a system is impacted considering his own properties.
The pattern of Fulton's condition index versus population size change is similar to what was previously observed with effects on larval survival rate (figure 8(b)).
It is also the case of the average size versus population size change (figure 8(c)) and the number of eggs per female versus population size change (figure 8(d)).

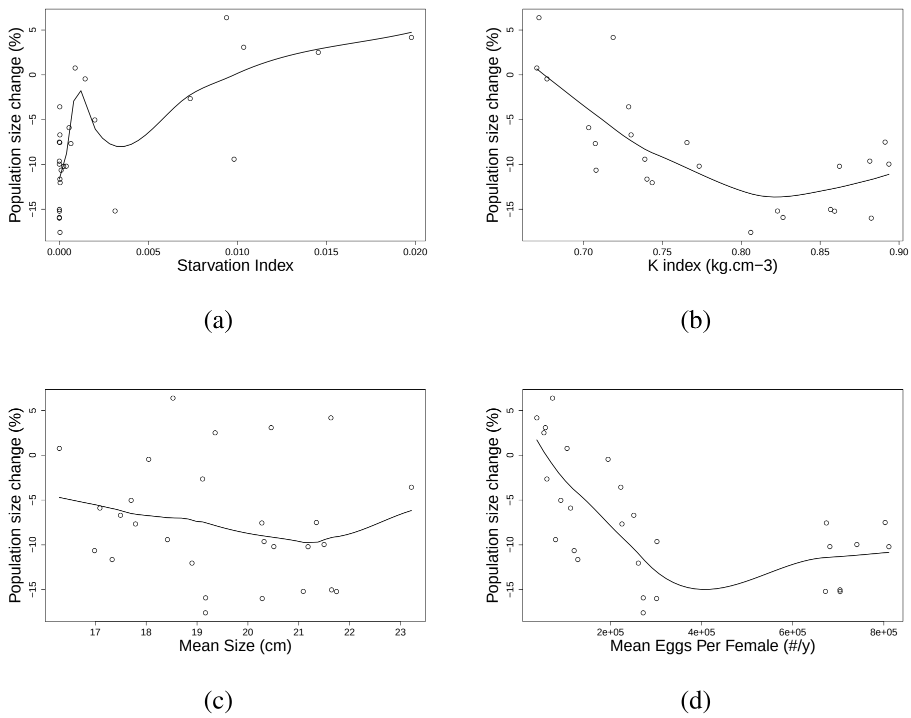


Figure 10: Relative population decline (in percent) after 5 year exposure to estrone as function of the starvation index (a), the Fulton's condition index (noted K index) before exposure to estrone (b), the mean individual size before exposure to estrone (c) and the reproduction rate before exposure to estrone (d). Considered effects are a 25 percent decrease of the environmental food carrying capacity and a 25 percent decrease of the larval survival rate to predation. Each point represents the average population decline for 20 simulations of one particular system. The line is a non-parametric regression of the points (LOESS).

4 Conclusions

River systems are not all equals when facing exposure to a stressor. Some of them are more vulnerable than the others. When a population is exposed to a stressor, all the individuals are impacted at the same level. However, the impact at the population scale can be more or less important. In the present work, we showed how different river systems can be impacted after 5 years exposure to estrone.

What makes the difference in how a fish population will be impacted is the properties of the river system in which individuals live. In the wild, the observed fish density results of the interactions between many processes. Basically, you can have two populations of the same size in two systems driven by different processes. In this work we only focused on two of them, the intra-specific competition for food and the predation by other species. We first showed that a realistic population pattern can be reproduced by different types of system. Actually, the population density can either be controlled by the food availability and the strength of intra specific competition for food or by the predation pressure exercised by other species.

The overall response of the system to a stressor will thus depends on the system properties. In systems in which population density is more controlled by predation, individuals are more likely to grow without limitation of food. Because of the high predation, the system almost never reach the environmental carrying capacity. Therefore, on average, individuals will grow and reproduce at their optimal capacity. The population will show a higher average size, a higher Fulton's condition index and a shorter spawning interval (*i.e.* higher reproduction rate). On the other side, in a system in which individuals are limited in food, individuals will struggle for feeding. Consequently, their growth and reproduction will not be optimal. The population will show a low average size, a lower Fulton's condition index and a larger spawning interval (*i.e.* shorter reproduction rate).

When facing a stressor like estrone, those two types of population will show a very different response. In the system in which population size is more controlled by food availability, individuals are not reproducing and growing at their best. Increasing mortality due to predation on egg or larval stage will result in a reduction of the number of individuals that will escape predation. Individuals surviving predation will be less numerous and the competition for food will be less important. Consequently, juveniles and adults will grow and reproduce slightly more. In some cases, this higher *per capita* reproduction rate will fully compensate the increased predation loss due to estrone exposure. In other cases, it will not be compensated at all. This corresponds to system in which population size is more controlled by predation pressure. In those types of system, increasing the predation pressure on egg or larvae will result in a population decrease, as the individuals in the population are not able to increase their reproduction and growth. In between these two extreme cases, there are other ones in which the compensation effect will only partially counterbalance the effects of exposure to estrone.

Exposing a system to a stressor will result in a modification of its equilibrium. The process that had the most control over the system before the exposure could lose some of its hold for the benefit of another process. With exposure to estrone, we can say that if it is only some systems that are negatively impacted, none of them is positively impacted.

Depending on the considered effect and its intensity at the individual scale, the population scale impacts will be more or less important. For instance, when considering effect on larval survival rate to predation, a 25 percent impact showed a significantly higher population decrease. Also, when comparing a 25 percent effect on larval survival rate with a 25 percent effect on egg survival rate, we showed that the impact on the population size is more intense when considering effect on egg survival rate to predation. Moreover, we also showed that more system types are in danger when considering the effect on egg survival rate. These results suggest that more experiments are needed regarding the impact on egg survival rate due to predation. So far, experiments showed that male aggressiveness are affected when exposed to estrone. Nevertheless, how this decrease in aggressiveness relates to egg survival rate to predation remains to be determined.

We conclude that measuring effects of stressors (*e.g.*, estrone) on individuals is not sufficient to determine whether or not such stressor causes impacts at the population scale. Intra-specific and inter-specific interactions are responsible for the emergence of the population dynamics. Individuals of the same species can respond very differently to a stressor depending on their environment. Also, populations of the same species living in two different systems can show very different impacts of exposure to a stressor. This indicates that accurately predicting impacts of chemicals on populations in natural systems requires incorporation of key ecological properties of the system. When considering a potential impact on any river system, this one should be extensively investigated.

References

R. O. Anderson. Length, weight, and associated structural indices. *Fisheries techniques*, 1996.

G. T. Ankley, K. M. Jensen, M. D. Kahl, J. J. Korte, and E. A. Makynen. Description and evaluation of a short-term reproduction test with the fathead minnow (pimephales promelas). *Environmental toxicology and chemistry*, 20(6):1276–1290, 2001.

M. A. Bozek, D.A. Baccante, and N. P. Lester. Walleye and sauger life history. *Biology, management, and culture of Walleye and Sauger*, pages 233–301, 2011.

T. A. Cichosz. Wisconsin department of natural resources 2005-2006 ceded territory fishery assessment report. *Wisconsin Department of Natural Resources, Bureau of Fisheries Management, Administrative Report*, 63, 2009.

N. Dumoulin. Simaqualife: un cadriciel pour la modelisation de la dynamique spatiale d'organismes aquatiques. *TSI. Technique et science informatiques*, 26(6):701–721, 2007.

W. F. Gale and G. L. Buynak. Fecundity and spawning frequency of the fathead minnowâĂŤa fractional spawner. *Transactions of the American Fisheries Society*, 111(1): 35–40, 1982.

V. Grimm, U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J.n Goss-Custard, T. Grand, S. K. Heinz, G. Huse, et al. A standard protocol for describing individual-based and agent-based models. *Ecological modelling*, 198(1):115–126, 2006.

V. Grimm, U. Berger, D. L. DeAngelis, J. G. Polhill, J. Giske, and S. F. Railsback. The odd protocol: a review and first update. *Ecological modelling*, 221(23):2760–2768, 2010.

K. M. Jensen, J. J. Korte, M.D. Kahl, M. S. Pasha, and G. T. Ankley. Aspects of basic reproductive biology and endocrinology in the fathead minnow (pimephales promelas). *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, 128 (1):127–141, 2001.

M. Jusup, T. Sousa, T. Domingos, V. Labinac, N. Marn, Z. Wang, and T. Klanjšček. Physics of metabolic organization. *Physics of Life Reviews*, 2016.

S. A. L. M. Kooijman. *Dynamic energy budget theory for metabolic organisation*. Cambridge university press, 2010.

S. A. L. M. Kooijman, N. Van der Hoeven, and D. C. Van der Werf. Population consequences of a physiological model for individuals. *Functional Ecology*, pages 325–336, 1989.

S. A. L. M. Kooijman, T. Sousa, L. Pecquerie, J. Van der Meer, and T. Jager. From food-dependent statistics to metabolic parameters, a practical guide to the use of dynamic energy budget theory. *Biological Reviews*, 83(4):533–552, 2008.

V. Korn. Effects of estrone and temperature on the predator-prey relationship between bluegill sunfish and fathead minnows. 2018.

B. T. Martin, E. I. Zimmer, V. Grimm, and T. Jager. Dynamic energy budget theory meets individual-based modelling: a generic and accessible implementation. *Methods in Ecology and Evolution*, 3(2):445–449, 2012.

N. A. Nate, M. J. Hansen, L. G. Rudstam, R. L. Knight, and S. P. Newman. Population and community dynamics of walleye. *Biology, management, and culture of walleye and sauger. American Fisheries Society, Bethesda, Maryland*, pages 321–374, 2011.

R. M. Nisbet, E. B. Muller, K. Lika, and S. A. L. M. Kooijman. From molecules to ecosystems through dynamic energy budget models. *Journal of animal ecology*, 69(6): 913–926, 2000.

Y.J. Shin, M.J. Rochet, S. Jennings, J.G. Field, and H. Gislason. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of marine Science*, 62(3):384–396, 2005.

T. Sousa, T. Domingos, J. C. Poggiale, and S. A. L. M. Kooijman. Formalised deb theory restores coherence in core biology. *Phil. Trans. R. Soc. B*, 365:3413–3428, 2010.

J. van der Meer. An introduction to dynamic energy budget (deb) models with special emphasis on parameter estimation. *Journal of Sea Research*, 56(2):85–102, 2006.

J.L. Ward, M.K. Cox, and H. Schoenfuss. Thermal modulation of anthropogenic estrogen exposure on a freshwater fish at two life stages. *Hormones and behavior*, 94:21–32, 2017.

K. H. Watanabe, K. M. Jensen, E. F. Orlando, and G. T. Ankley. What is normal? a characterization of the values and variability in reproductive endpoints of the fathead minnow, pimephales promelas. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, 146(3):348–356, 2007.