Modeling environmental effects on the size-structured energy flow through marine ecosystems. Part 1: the model

Olivier Maury, Blaise Faugeras, Yunne-Jai Shin, Jean Christophe Poggiale, Tamara Ben Ari, Francis Marsac

PII: S0079-6611(07)00098-5
DOI: 10.1016/j.pocean.2007.05.002
Reference: PROOCE 718

To appear in: Progress in Oceanography


This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.
Modeling environmental effects on the size-structured energy flow through marine ecosystems. Part 1: the model.

Olivier Maury1*, Blaise Faugeras1, Yunne-Jai Shin1, Jean Christophe Poggiale2,
Tamara Ben Ari1, and Francis Marsac1

Abstract:
This paper presents an original size-structured mathematical model of the energy flow through marine ecosystems, based on established ecological and physiological processes and mass conservation principles. The model is based on a nonlocal partial differential equation which represents the transfer of energy in both time and body weight (size) in marine ecosystems. The processes taken into account include size-based opportunistic trophic interactions, competition for food, allocation of energy between growth and reproduction, somatic and maturity maintenance, predatory and starvation mortality. All the physiological rates are temperature-dependent. The physiological bases of the model are derived from the Dynamic Energy Budget theory. The model outputs the dynamic size-spectrum of marine ecosystems in term of energy content per weight class as well as many other size-dependent diagnostic variables such as growth rate, egg production or predation mortality.

In stable environmental conditions and using a reference set of parameters derived from empirical studies, the model converges toward a stationary linear log-log size-spectrum with a slope equal to -1.06 which is consistent with the values reported in empirical studies. In some cases, the distribution of the largest sizes departs from the stationary linear solution and is slightly curved downward. A sensitivity analysis to the parameters is conducted systematically. It shows that the stationary size-spectrum is not very sensitive to

1 IRD (Institut de Recherche pour le Développement) – UR 109 Thetis, CRH, av. Jean Monnet, B.P. 171, 34203 Sète cedex, France, * email : maury@ird.fr
2 LMGEM - UMR 6117 OSU - Case 901, Campus de Luminy, 13288 Marseille Cedex 9, France
the parameters of the model. Numerical simulations of the effects of temperature and primary production variability on marine ecosystems size-spectra are provided in a companion paper (Maury et al., this issue).

**Keywords:** size spectrum; mathematical model; predation; bioenergetics; Dynamic Energy Budget (DEB) theory; energy flow;

**List of content:**

1 INTRODUCTION

Trophic interactions between organisms are the main drivers of marine ecosystems dynamics. In particular, they allow the transfer and the dissipation of solar energy through ecosystems, along food chains, from primary producers to top predators. In marine systems, many species
interact within complex trophic networks where bottom-up as well as top down controls interfere continuously (e.g., Cury, Shannon & Shin, 2003). Understanding how environmental variability such as changes in primary production or temperature impacts ecosystems and ultimately fish stocks and reciprocally how fishing upper trophic levels impacts lower trophic levels requires reliable models based on realistic representations of energy fluxes through ecosystems. However, most marine ecosystems are extremely diverse, heterogeneous and poorly known. Modelling their dynamics explicitly down to the species level is challenging. Hence, most models of marine ecosystems rely on rough species and functional groups partitioning and use fixed predation rates between groups (e.g., Polovina, 1984, Walters, Christensen & Pauly, 1997; Pauly, Christensen & Walters, 2000). Alternatively, aggregated approaches based on size have been undertaken, taking into account allometric losses (respiration), predation and growth processes. In those approaches, phytoplankton is implicitly used as the source term of size-structured continuous mass-balance equations. The marine ecosystem is represented using a single aggregated state variable (e.g. a biomass) which experiences size-dependent growth and mortality (Platt and Denman, 1978; Silvert and Platt, 1978 and 1980; Dickie, Kerr & Boudreau, 1987; Cushing, 1992; Platt and Denman, 1997; Arino, Shin & Mullon, 2004; Benoit and Rochet, 2004). Those models rest on the fundamental assumption that size is the most structuring dimension of ecological systems along which their dynamics can be projected. Many ecological traits (including population abundance, growth rate and productivity, spatial niche, trophic, competitive and facilitative relationships between species) as well as metabolic processes are indeed well correlated with body size (Sheldon, Prakash & Sutcliffe, 1972; Blueweiss et al., 1978; Gillooly, Brown, West, Savage & Charnov, 2001; Brown and Gillooly, 2003; Marquet et al., 2005; West and Brown, 2005; Woodward et al., 2005). Furthermore, because most marine organisms are highly opportunistic feeders and because prey size is limited by the allometric diameter of predator’s
mouth (Bone, Marshall & Blaxter, 1999), predator-prey relationships are, in many marine systems, mostly determined by size (Lundvall, Svanbäck, Persson & Byström, 1999; Scharf, Juanes & Rountree, 2000; Jennings, Pinnegar, Polunin & Boon, 2001 and Jennings, Pinnegar, Polunin & Warr, 2002; Shin and Cury, 2004). For instance, Jennings et al. (2001) showed that body mass explained 93% of the variation in trophic level among 15 fish communities in the North Sea. Because it captures so many aspects of ecosystem functioning, body size can therefore be used to synthesize a suite of co-varying traits into a single dimension (Cousins, 1980; Woodward et al., 2005).

As Woodward et al. (2005) state, “the challenge now is for empiricists to produce highly resolved food webs that are quantified in terms of population dynamics, energetics and chemical fluxes, and for theoreticians to develop new and more realistic size-based models, so that emerging ideas can be explored and tested more rigorously”. Furthermore, “size-based models are easier and cheaper to parameterise than most food-web models” (Jennings et al., 2002). In this perspective, we model environmental influences on the dynamics of marine ecosystems with a size-spectrum approach. Primary producers are explicitly distinguished from consumer organisms and a mechanistic approach allows us to take into account various ecological and physiological processes supposed to be determining in the functioning of marine ecosystems:

- Size-structured opportunistic trophic interactions where producers are potential preys for consumers and where all consumer species are considered to be potentially prey and predator at the same time (Shin and Cury, 2004);
- Predators competition for preys;
- Allocation of energy between growth and reproduction;
• Somatic as well as maturity maintenance based on the Dynamic Energy Budget (DEB) theory (Kooijman, 1986, 2000 and 2001; Nisbet, Muller, Lika & Kooijman, 2000);
• Size-dependent nonpredatory mortality;
• Starvation mortality;
• Temperature-dependence of organism’s physiological rates.

It is expected that considering explicitly the physiological bases of metabolism, the main constraints which control trophic interactions and the size structured nature of those processes will help to better understand the various modes of energy transfer through marine ecosystems and their response to environmental forcing. Furthermore, a mass balanced formulation is used to represent the functioning of marine ecosystems in a quantitative way, assessing the actual energy flux from primary production to apex predators as well as the top-down effects that upper trophic levels have on the overall ecosystem. To keep consistency with bioenergetic studies and to avoid the complexity of explicit stoichiometric formulations based on chemical elements, our model is expressed in term of energy. Energy has to be understood as a currency measuring “the ability to do work” (Kooijman, 2000). It has to be noted that given homeostasis assumptions, all mass fluxes in organisms can be deduced from energy fluxes (Kooijman, 1995; Sterner & Elser, 2002). In our approach, energy is simply assumed to be proportional to biomass. This implies an assumption of strict homeostasis and constant chemical stoichiometry between organisms.

After a detailed presentation of the hypothesis and formulations of our model, a sensitivity analysis is undertaken to assess the impact of each parameter on the steady state size-spectrum. In a companion paper (Maury, Shin, Faugeras, Ben Ari & Marsac, this issue), we present
numerical simulations of our model focusing on the effects of primary production and temperature variability on the size-spectrum of marine ecosystem.

2 THE MODEL

2.1 Notations and state variables

The main state variable we are dealing with is \( \xi_{w} \), the distribution function of the energy content of the marine ecosystem (J.kg\(^{-1}\).m\(^{-3}\)) at time \( t \neq 0 \), \( +\infty \) and weight \( w \neq 0 \), \( w_{\text{max}} \) in 1 m\(^3\) of seawater. \( \xi_{w} \) is a density with respect to body weight and seawater volume. It can easily be converted into the more usual “normalized biomass size-spectrum” using the mean energetic content of one unit of biomass \( y \) (J.kg\(^{-1}\)) which is assumed to be a constant parameter. Hence, the quantity of energy in the weight range \([w_1, w_2]\) per m\(^3\) of seawater is given by

\[
\int_{x=w_1}^{x=w_2} \xi_{t,w} dx
\]

and \( \xi_{w} \) is related to \( N_{t,w} \), the distribution function of the number of individuals in terms of weight (kg\(^{-1}\).m\(^{-3}\)) at \((t, w)\) in 1 m\(^3\) of seawater, with \( \xi_{w} = yw . N_{t,w} \).

The symbols \( u, v, w, x \) are continuous indices which refer all to the weight dimension. Weight is supposed to be related to length with a fixed allometric function \( w = a t^{3} \).

According to basic ecological theory, marine ecosystems can be schematically divided into three distinct components using fundamentally different means to mobilize energy: producers, consumers and decomposers (Valiela, 1995). For the sake of simplicity, the present study ignores the third component and focuses on the two first components with a particular emphasis on the consumers group (Figure 1). Hence, our model has two main components:
• the primary producers (autotrophic organisms mostly composed of phytoplankton) which convert solar energy and mineral nutrients into biomass and whose weight belongs to \([0, w_1]\);

• the consumers (heterotrophic organisms encompassing numerous taxonomic groups of zooplankton and nekton) which gain energy solely by predation and whose weight belongs to \([w_{\text{egg}}, w_{\text{max}}]\). Consumers do reproduce, their eggs have a weight \(w_{\text{egg}} > 0\) and their maximal weight is \(w_{\text{max}} > w_f\).

**Figure 1**

The distribution function of the energy content of the producer and consumer groups are noted respectively \(\xi_{t,w}^p\) and \(\xi_{t,w}^c\) so that the distribution function of the energy content of the ecosystem is \(\xi_{t,w} = \chi_{[0,w_1]}\xi_{t,w}^p + \chi_{[w_{\text{egg}},w_{\text{max}}]}\xi_{t,w}^c\) with \(\chi_{[x_1,x_2]}\) being the characteristic function which is equal to one in the interval \([x_1, x_2]\) and to zero elsewhere.

### 2.2 Dynamics

To avoid an explicit modeling of phytoplankton growth and reproduction, the energy density of producer organisms is assumed to be uniformly distributed over \([0, w_1]\). Consequently, the size-dependent predatory mortality applied by all consumer organisms (see equation 8) is averaged over the producers size range \([0, w_1]\) to ensure that the producers size distribution remains constant at all time. The dynamics of phytoplanktonic organisms is then expressed as follows:

\[
\frac{d\xi_{t,w}^p}{dt} = \frac{1}{w_1} \left( \Pi_t - \frac{\xi_{t,w}^p}{\xi_{t,w}^p \int_{0}^{w_1} \lambda_{t,x} dx} - \frac{\xi_{t,w}^p}{\xi_{t,w}} M_t \right) \quad \forall w \in [0; w_1] \tag{1}
\]
With $\mathcal{H}(J.s^{-1}.m^{-3})$ the primary energy production which enters the system at time $t$, which constitutes the only external source of energy of the whole ecosystem, $M_t (s^{-1})$ the nonpredatory mortality rate affecting primary producers and $\lambda_t (s^{-1})$ the mortality rate due to predation at time $t$ and weight $x$.

The bio-ecological processes taken into account to model consumers are predation, mortality, assimilation and use of energy for maintenance, growth and reproduction. The basic equation used to describe the energy fluxes through the weight range of consumers combines a transport term for representing the growth process and three sink terms for predatory, nonpredatory and starvation mortality processes. It is based on the Mc Kendrick-Von Foerster equation which is usually used in population dynamics (e.g. Tuljapurkar & Caswell, 1997; Kot, 2001) and which is written as follows in the interval $[w_{egg}, w_{max}]$ assuming given initial conditions for $t=0$:

$$
\begin{align*}
\frac{\partial \xi_{t,w}}{\partial t} &= -\frac{\partial}{\partial w}\left(\gamma_{t,w} \frac{\xi_{t,w}}{\partial w}\right) - (\lambda_{t,w} + Z_{w} + M_{starv})\xi_{t,w} \\
\xi_{0,w} &= \xi_{w}^0
\end{align*}
$$

Where $\gamma (kg.s^{-1})$ is the growth rate, $\lambda (s^{-1})$ is the mortality rate due to predation, $Z (s^{-1})$ is the loss of energy from the system due to nonpredatory mortality and $M_{starv} (s^{-1})$ is the starvation mortality rate. For all those coefficients, the subscripts $t$ and $w$ refer to time and weight.

The input of eggs $R_t (J.s^{-1}.m^{-3})$ into the system due to reproduction is taken into account assuming a Dirichlet boundary condition in $w=w_{egg}$:

$$
\gamma_{t,w_{egg}} \xi_{t,w_{egg}} = R_t
$$

(3.)
The derivation of explicit expressions for all the coefficients of equations (2) and (3) ($\lambda_{w}$, $\chi_{w}$, $R_{b}$, $M_{t,w}^{star}$ and $Z_{t,w}$) are provided in the five subsections below.

- **The predation process: calculation of $\lambda_{w}$**

Predation can be viewed as a loss of energy for preyed weight classes and a gain of energy for predating weight classes. In the model, predation is supposed to be opportunistic and only controlled by the ratio of sizes between organisms. Hence, all organisms can be potentially predators and preys at the same time, depending on their relative weight (or size) (Figure 2).

**Figure 2**

To be able to calculate the quantity of food available to a predator, the size-based constraints on predation have to be specified. For that purpose, the selectivity $s_{u,w} \in [0,1]$ is defined as the capability for a consumer organism of weight $u$ to eat an encountered organism of weight $w$.

Assuming that predation can occur if the ratio of predator length over prey length is comprised between two $\rho$ and $\rho$ extreme values (Figure 3b), $s_{u,w}$ is a normalized function expressed as the product of two sigmoid functions which account for the limitation of ingestion when preys are either too small or too large (Figure 3a):

$$s_{u,w} = \left[ \frac{1}{1 + e^{\alpha_1 \left( \rho_1 - \left( \frac{u}{w} \right)^{1/3} \right)^{-1}}} \right] \left[ 1 - \left( 1 + e^{\alpha_2 \left( \rho_2 - \left( \frac{u}{w} \right)^{1/3} \right)^{-1}} \right) \right]^{R^+} \xrightarrow{s} \theta_{1}}\ ]$$  

(4.)
With \( \rho, \rho, \alpha \) and \( \alpha \), being constant positive parameters characterizing both the half saturation and the flatness of the sigmoid functions.

**Figure 3**

To take into account the basic physiological processes involved in the acquisition and use of energy by biological organisms, a simplified version of the DEB (Dynamic Energy Budget) theory is used (Kooijman, 1986, 2000 and 2001; Nisbet et al., 2000). In the DEB theory, the ingested energy is assimilated by organisms and stocked into reserves. A fixed fraction \( k \) of the energy utilized from reserves is then allocated to growth of structural material and somatic maintenance, the remaining fraction \( 1 - k \) being devoted to gonad development, maturity maintenance and egg formation. For the purpose of simplicity, neither the reserve dynamic nor the gonad development is considered explicitly in the present work. The ingested energy is supposed to be used in the same way by any organism: it is assimilated, and a fraction \( k \) is used for somatic growth and maintenance whereas a fraction \( 1 - k \) is allocated to reproduction and gonadic maintenance (Figure 4). A single set of mean physiological parameters (Table 1) is used to describe the mean energy fluxes through every consumer organisms of the ecosystem. From this perspective, the ecosystem is modeled as a “meta-organism” characterized by a mean life history.

**Figure 4**

According to the DEB theory, the maximum amount of preyed energy that can be ingested at time \( t \) during \( dt \) by a predator is supposed to be proportional to a body surface. It follows that
$E_{t,u} \ du \ dt$ (J.m$^{-3}$), the total amount of energy potentially preyed by all predators of weight comprised in the range $[u, u+du]$ at time $t$ during $dt$ in 1m$^3$ of water, can be expressed as follows:

$$E_{t,u}du\ dt \propto \left[\text{density of predators}_{t,u}du, \text{body surface}_{t,u}\right] \cdot \left[\text{functional response to preys}_{t,u}\right] dt$$

$$E_{t,u}du\ dt = \psi \omega \frac{\xi_{t,u}du}{u\psi} \ f_u(p_{t,u}) \ dt$$

$$f_u(p_{t,u}) = \frac{P_{t,u}}{c + P_{t,u}}, \ R^+ \rightarrow [0;1]$$

Where $\omega$ is the mean maximum surface-specific ingestion rate (kg.kg$^{-2/3}$s$^{-1}$) and $f_u$ is the functional response to the energy content of preys $p_{t,u}$

$$p_{t,u} = \int_{\text{max}}^{w_{\text{prey}}} \xi_{t,u}dv$$

of a weight $u$ predator. A size-dependent Holling type II functional response without predator interference is assumed with $c$ the half saturation constant (J.s$^{-1}$). $u^f$ is the volume of water explored by a predator of weight $w$ per unit of time (m$^3$.s$^{-1}$) which is supposed to be an allometric function of predator weight (it is assumed that the volume of water explored by a predator is proportional to its swimming speed which is proportional to its body size –Froese and Pauly, 2000- hence $c$ is taken equal to 0.33 cf. Table 1).

Then, according to the hypothesis of opportunistic predation (preys of a given weight are eaten in proportion to their selected biomass relatively to the biomass of all possible preys), the amount of preyed energy $E_{t,u/w} \ du \ dw \ dt$ (J.m$^{-3}$) that predators in the range $[u, u+du]$ take from preys in the range $[w, w+dw]$ at time $t$ during $dt$ is expressed as follows:
The total amount of energy preyed by all predators on preys in the range of weight \([w, w+dw]\) at time \(t\) during \(dt\) in 1 m\(^3\) of water is then calculated by integration over the weight range of predators:

\[
E_{t,w} \, dw \, dt = \int_{w_{\text{min}}}^{w_{\text{max}}} E_{t,w} \, du \, dw \, dt = \omega \xi_{t,w} \int_{v=0}^{w_{\text{max}}} s_{u,v} \xi_{t,v} \, dv \frac{\xi_{t,w} \xi_{t,v} \, dw \, dt}{u \xi_{t,w}^{1/3} s_{u,w}^{1/3}}
\]

(6.)

It follows that the instantaneous mortality rate exerted by all possible predators on \(\xi_w\) at time \(t\) is given by the following expression:

\[
\lambda_{t,w} = \frac{E_{t,w}}{\xi_{t,w}} = \omega \int_{u=\xi_{t,w}}^{w_{\text{max}}} \left[ \frac{\xi_{t,u} \xi_{t,w}^{1/3} s_{u,w}^{1/3}}{u^{1/3} + \xi_{t,u} \xi_{t,v}} \right] \, du
\]

(7.)

- **The growth process: calculation of \(\chi_w\)**

According to Figure 4, growth corresponds to the use of a fraction \(k\) of the assimilated energy diminished by a maintenance cost proportional to organism body volume and finally converted into structural material at an energy cost proportional to growth (Kooijman, 2000).
Following those simple rules for energy conservation, the growth of a mean consumer organism is expressed as follows:

\[
\frac{dw_{t,u}}{dt} = \frac{\kappa e_A E_{t,u}}{\psi N_{t,u}} - \frac{\mu u}{\psi} - \frac{E_g}{\psi} \frac{dw_{t,u}}{dt}
\]  \hspace{1cm} (9.)

Where \( e_A \in [0,1] \) is the mean fraction of the ingested energy which is assimilated, \( \kappa \in [0,1] \) is the mean fraction of this energy which is allocated to growth and somatic maintenance, \((1-\kappa)\) being allocated to reproduction, \( \mu \) is the mean amount of energy required for the somatic maintenance of one unit of weight during one unit of time \((J.kg^{-1}.s^{-1})\) and \( E_g \) is the mean weight specific cost of growth (Kooijman, 2000) \((J.kg^{-1})\).

We assume that growth in length cannot be negative for most marine organisms which have an exo- or an endo-skeleton such as vertebrates, most molluscs, crustaceans, etc… Because weight is assumed to be related to length with a fixed allometric function \((w=al^3, a>0)\), growth in weight cannot be negative either (see the paragraph on starvation mortality for the treatment of mass conservation). It follows that the instantaneous growth rate of organisms of weight \( u \) \((kg.s^{-1})\) can be expressed as:

\[
\gamma_{t,u} = \frac{dw_{t,u}}{dt} = \frac{\psi}{\psi + E_g} \left[ \frac{\kappa e_A E_{t,u}}{\psi N_{t,u}} - \frac{\mu u}{\psi} \right]^{+} = \frac{\psi}{\psi + E_g} \left[ \frac{\kappa e_A E_{t,u}}{\xi_{t,u}^{c}} u - \frac{\mu u}{\psi} \right]^{+} = \frac{\psi}{\psi + E_g} \left[ \frac{\kappa e_A E_{t,u}}{\xi_{t,u}^{c}} u - \frac{\mu u}{\psi} \right]^{+} = \frac{\psi}{\psi + E_g} \left[ \frac{\kappa e_A E_{t,u}}{\xi_{t,u}^{c}} u^{2/3} - \frac{\mu u}{\psi} \right]^{+}
\]

\]

\[
(10.)
\]
With \( f^+ \) is the function defined by
\[
\begin{align*}
[x]^+ &= 0 & \text{if } x < 0, \\
[x]^+ &= x & \text{if } x \geq 0.
\end{align*}
\]

At food saturation (when the functional response \( f=1 \)), this growth rate formulation is equivalent to a Von Bertalanffy (1969) formulation of growth where anabolism is proportional to a surface (weight at a power 2/3) and catabolism is proportional to body weight.

- **The reproduction process: calculation of \( R \)**

According to Figure 4, reproduction corresponds to the use of a fraction \( 1-k \) of the assimilated energy diminished by a maintenance cost proportional to \( (1-k) \) times body weight (Kooijman, 2000). All sizes of both sex are supposed to reproduce permanently but only female sexual products are re-injected into the system at \( w=w_{\text{egg}} \) (according to Cury and Pauly -2000-, egg size of marine fish is remarkably constant between species and approximately equals to 1mm).

As for the expression of the growth rate and because the contribution of the weight class \( w \) to the total eggs production cannot be negative, the function \( f^+ \) is used to express the egg input into the system (see the paragraph on starvation mortality for the treatment of mass conservation):

\[
R_t = \left(1 - M_{\text{egg}} \right) \phi \int_{w=w_{\text{egg}}}^{w_{\text{max}}} e_A \left(1 - \kappa\right) E_{t,w} - N_{t,w}^{c} \frac{1 - \kappa}{\kappa} \mu w \right]^+ dw
\]

\[
= \left(1 - M_{\text{egg}} \right) \phi \int_{w=w_{\text{egg}}}^{w_{\text{max}}} \left[ \left(1 - \kappa\right) e_A \omega_{k,w} w^{-1/3} \int_{v=0}^{w_{\text{max}}} s_{w,v} \xi_{t,v} dv - \left(1 - \kappa\right) \mu_{c_{t,w}} \right]^+ \frac{c}{w^2} + \int_{v=0}^{w_{\text{max}}} s_{w,v} \xi_{t,v} dv \right] d\psi
\]

(11.)
With \( R \ (J.s^{-1}.m^{-3}) \) being the reproductive flux (input of eggs at \( w=w_{egg} \)), \( \phi \in [0,1] \) the mean proportion of mature female in each size class, \( M_{egg} \) the fraction of the spawned eggs which are not fecundated \( (M_{egg} \in [0,1]) \), \( (1-\psi) \) the fraction of the assimilated energy which is allocated to reproduction and \( w_{egg} \), the weight of eggs.

- **The starvation mortality: calculation of** \( M_{starv}^{t,w} \)

When starvation occurs, i.e. when the food ration is not sufficient to meet organism’s needs, growth and/or reproduction cease and structural materials of the body are lysed and used for maintaining the most important physiological functions necessary for survival (Kooijman, 2000). The starvation process leads to a quick weakening of organisms which increases mortality. At the ecosystem level, starvation is a net dissipation of energy. To conserve the mass in a consistent way when growth and/or reproduction cease due to insufficient food intake (cf. equations 10 and 11), it is considered that the quantity of energy which is needed for maintenance but which cannot be provided by food intake is removed from the ecosystem. In this perspective, starvation acts as a mortality term at the level of the ecosystem and the starvation mortality coefficient can be expressed as follows using equations (10) and (11):

\[
M_{starv}^{t,w} = \left[ \frac{\mu}{\psi} - \frac{c}{w_{max}^2} \int_{v=0}^{w_{max}} s_{w,v} \xi_{v,t,v} \, dv \right] + \left[ \frac{(1-\kappa) \mu}{\psi} - \frac{c}{w_{max}^2} \int_{v=0}^{w_{max}} s_{w,v} \xi_{v,t,v} \, dv \right]
\]

(12.)

- **The nonpredatory mortality: calculation of** \( Z_{t,w} \) :
The mortality for other causes than predation includes diseases, parasites, ageing, etc. Since large organisms exhibit much longer life span than small organisms (e.g., Speakman, 2005), it is simply supposed to be a decreasing allometric function.

\[
Z_w = M l^\nu = M \left( \frac{w}{a} \right)^{\nu/3}
\]  

(13.)

With \( M \) being the nonpredatory mortality rate for a 1m long organism (s\(^{-1}\)), \( l \) being body size (m), \( a \) (kg.m\(^{-3}\)) being the coefficient linking weight to cubed length (\( w = al^3 \)) and \( \nu \) a parameter.

### 2.3 Conservation of energy

In our model, primary production is the only supply of energy to the system. This is appropriate in open ocean ecosystems where phytoplankton is the only energy input at the basis of the food chain. Energy is injected into producer size classes which do not grow. It is only transferred to consumers through predation. The model formulation is energy conservative and losses from the system occur only through nonpredatory mortality (\( M > 0 \)), loss of male sexual products (\( f < 1 \)) and dissipation processes such as imperfect efficiency of the assimilation process (\( e_A < 1 \)), maintenance expenditures (\( m > 0 \)) and energetic cost of growth (\( E_g > 0 \)). If \( H \neq M = E_g = 0 \) and \( e_A = f = 1 \), the total quantity of energy in the system is conserved and kept constant (even if its distribution in the weight spectrum changes through time).
2.4 Temperature effect on physiological rates

Due to its major importance in controlling chemical reactions, temperature strongly influences metabolic rates of living organisms (Clarke et al., 1999; Kooijman, 2000; Pörtner, 2002; Clarke, 2004; Speakman, 2005). Despite its purely molecular basis, the description of Arrhenius (Figure 5) based on the van’t Hoff equation \( k(T) = k_a e^{-\frac{E_a}{RT}} \) with \( k \) a reaction rate, \( k_a \) the frequency factor, \( E_a \) the activation energy, \( R \) the gas constant and \( T \) (°K) the ambient temperature fits well temperature effects on the physiological rates of organisms at the intra-specific level (Kooijman, 2000, Clarke and Fraser, 2004). Such effects are especially important to take into account given that most marine organisms are poikilotherms and hence their internal temperature equals ambient water temperature which is potentially variable. The Arrhenius equation does not keep a mechanistic meaning at the inter-specific level (Clarke, 2004; Clarke and Fraser, 2004). However, it still provides a good statistical description of temperature effects on metabolic rates at the ecosystem level, even if purely chemical effects are altered by complex eco-evolutionary processes acting at this scale (Clarke and Johnston, 1999; Gillooly et al., 2001 and 2002; Enquist et al., 2003; Clarke, 2004; Clarke and Fraser, 2004). In our model, the Arrhenius temperature-dependent correction factor \( A(T) \) is used to correct ingestion rate, maintenance rate, nonpredatory mortality rate and swimming speed.

\[
rate(T) = rate(T_{ref}) A(T) \quad \text{with} \quad A(T) = e^{\left(\frac{T - T_{ref}}{E_a / R}\right)}
\]  

(14.)

With \( T_{ref} \) (°K), the reference temperature and \( \tau_i \), a parameter (the “Arrhenius temperature” which equals \( \frac{E_a}{R} \)).
Combining Equations. (1), (2), (3), (8), (10), (11), (12) (13) and (14) gives the full model which is presented in a compact form in Appendix A.

2.5 Numerical approximation

Marine ecosystems encompass very different organisms ranging from very small organisms such as phytoplankton cells ($10^{-6} \text{ m}, 10^{-16} \text{ kg}$) to very large organisms such as adult fish predators (4 m and more than 650 kg for giant bluefin tuna or swordfish for instance). To account accurately for growth and predation processes over such a large range of size would require numerically approximating the model with an extremely small resolution over an extremely high number of size intervals. Alternatively, a base log scale can be used to ensure that processes are considered at the proper resolution whatever the size of organisms is and to keep a limited number of weight classes. Using such a length-based log scale can be done by defining

\[
\sigma = \frac{\ln(l - \beta)}{\ln(\alpha)} - \gamma = \frac{\ln\left(a^{-\frac{1}{2}}w^{\frac{1}{2}} - \beta\right)}{\ln(\alpha)} - \gamma \iff w = a^{(\alpha^{\sigma} + \beta)} \quad \text{with} \quad \alpha \text{ and } \beta
\]

being fixed parameters and $\sigma = \{1, 2, 3, \ldots, n\}$. To be able to choose easily the grid characteristics, the parameters $\beta$ and $\gamma$ are expressed in terms of $l_{\text{min}}$ and $l_{\text{max}}$ which are fixed so that the grid depends only on $\alpha$ (Figure 6). Because the present study focuses mostly on large consumer organisms such as fish or large mesozooplankton ranging from 1mm to 2m, $\alpha$ is set at 1.04 which corresponds to grid cells varying from 1.5mm for the smallest size class to 75mm for the largest class. An irregular grid is derived calculating weight steps $\delta_i$ so that
each grid point \( w_i \) is placed at the middle of its associated grid cell (Figure 6a). The first grid point which represents producers is placed at \( 1.24 \times 10^{-3} \) m which corresponds to the \( 10^{-5} \) m, \( 1.56 \times 10^{-3} \) m size range. This size range obviously exceeds the phytoplankton size range (which roughly extends from \( 10^{-6} \) m to \( 10^{-4} \) m) and covers also microzooplankton and small meso-zooplankton sizes. However, it has to be kept in mind that our paper aims at representing the behaviour of a generic size-spectrum model formulated independently from the size range considered. To optimize computation time, the discretization used here focuses mostly on large organisms, as an illustration. Using our model to represent specifically small organisms such as small copepods would require refining the discretization used for small sizes. Such a grid refinement would not change the qualitative behavior of the model (but would be more costly in terms of computing time, allowing less simulations to be made). In this perspective, two coupled size-spectrum could profitably be used, one for small zooplankton and one for larger organisms such as fish and large zooplankton.

The model is integrated numerically along 101 length/weight classes from \( l_{\text{min}} = 10^{-5} \) m to \( l_{\text{max}} = 2 \) m (Figure 6b). Producers are assumed to occupy only the first length/weight class and consumers to range from the second to the 101\(^{\text{th}}\) class (no overlap between their respective ranges).

**Figure 6**

Integrals are evaluated using first order approximations. Since the growth rate cannot be negative, a usual first order upwind finite difference scheme explicit in time is used to integrate equation (2). Most of the parameters used in the model have a clear physiological or ecological significance and are well documented in the literature, in both experimental and theoretical studies. The values used for simulations are given in Table 1 with the
corresponding references of the literature. The maximum surface specific ingestion rate $\alpha$, as well as the maintenance rate $\mu$, are estimated given mean von Bertalanffy (1969) parameters (growth rate $K$ and asymptotic size $L$) of fish (cf. Appendix A). The estimation of nonpredatory mortality rate (parameters $M$ and $\varphi$) is based on assumptions about the size-dependent mean life duration of marine organisms (Appendix B). The value of $\mathcal{P}$, the primary energy production which enters the system is calculated so that the stationary concentration of phytoplankton in the reference simulations matches the value of 3144.225 J per m$^3$ of seawater which is approximately equivalent to $10^{-3}$ N-mole.m$^{-3}$ and that we use as the reference concentration for producers (multiplying the redfield ratio C:N=106:16 by the biomass free energy which is 474.6 kJ.C-mol$^{-1}$ - Kooijman, 2000- gives 3144225 joules per mole of N). This value is then divided by the weight range of producers in the model $[1.5.10^{-14}$ kg, $5.72.10^{-8}$ kg] to obtain the value for the distribution function of the energy content of the producers $\xi_{p, w}^{\text{m}} = 549.10^8$ J.kg$^{-1}$m$^{-3}$. This value is obtained in the reference simulation using $\mathcal{P}$=1177 J.day$^{-1}$m$^{-3}$.

Table 1

2.6 Simulation experiments

In a first set of simulations, the existence of a linear steady state is tested by running the model during fifty years. The sensitivity of the steady state to the individual value of the model parameters is then explored systematically. For that purpose, the parameters $\omega \mu M_{eg}$,
\( M, \nu c, \kappa \rho, \rho, e_A, E_g \) are varied individually in a large range around their reference values (Table 1) and the influence of their variations on the stationary size-spectrum is considered.

3 MODEL BEHAVIOUR

3.1 Steady state

The first set of numerical experiments was conducted using the reference values of the parameters (Table 1). In stable environmental conditions (constant primary production and constant temperature), the distribution of energy in the ecosystem converges from any positive initial distribution to a stationary quasi-linear size-spectrum (Figure 7a). Only the first point (the primary producers) departs from the linear spectrum as well as the largest length classes for which the spectrum is slightly curved downward due to the slowdown of growth for large sizes close to the asymptotic length.

Figure (7b, c, d, e) provides the reader with the time evolution of the functional response function, the growth coefficient, the nonpredatory, predatory and starvation mortality coefficients and the egg production per size classes at steady state and during the transition phase. At steady state, the functional response increases with organism size from the highly food-limited small sizes to the less limited large sizes (Figure 7b). The growth rate (in weight) as a function of organism size is dome-shaped, reaching a maximum for intermediate to large sizes and then decreasing down to zero for length equal to \( L_\infty \) (Figure 7c). The log-log predatory mortality curve at steady state shows a linearly decreasing trend for organisms between 2mm and 11cm (Figure 7d) with higher mortality rates for producers. For larger organisms, the predation mortality decreases sharply down to zero for length above 70 cm. The log-log contribution of each size class to egg production \( R_i \) at steady state (Figure 7e)
exhibit a linearly decreasing trend with a downward curvature for sizes above 1.4m, when maintenance processes are becoming to be non-negligible in equation (11).

**Figure 7**

When the reference values of the parameters (Table 1) are used, the slope of the stationary length-spectrum equals -3.175 which is equivalent to a slope equal to -1.058 for the weight-spectrum (Figure 8).

**Figure 8**

### 3.2 Sensitivity to the parameters

The slope of the stationary size spectrum is not sensitive to the value of the maximum surface specific ingestion rate ($\omega$) but its intercept decreases when $\omega$ increases (the size spectrum is translated vertically, cf. Table 2 and Figure 9a). The stationary size spectrum is not sensitive to the value of the maintenance rate $m$ (Table 2 and Figure 9b). It has to be noted, however, that for length classes close to $L_\infty$ (biomass is null for length greater than $L_\infty$, cf. appendix B), the stationary size-spectrum may depart from its linear shape and be curved downward. This is the case for low $\omega$ values or for high $\mu$ values (Table 2 and Figure 9a and b).

Varying the value of the fraction of the spawned eggs which are not fertilized ($M_{\text{egg}}$) does not change the size spectrum over medium and large size classes (Table 2 and Figure 9c). Only small size classes are sensitive to $M_{\text{egg}}$ and depart from the linear solution when $M_{\text{egg}}$ is smaller than 0.4. Conversely, the nonpredatory mortality coefficient $M$ only influences the
large classes of the size-spectrum, leading to a spectrum curved downward for high $M$ values (Table 2 and Figure 9d). Over the explored range, the exponent $\nu$ of the nonpredatory mortality length-dependence has almost no effect on the size-spectrum (Table 2 and Figure 9e).

The Holling type II half-saturation constant $c$ has only a weak effect on the stationary size spectrum slope. However it has to be noted that decreasing its value leads to lower phytoplankton and small organism biomass which departs from the linear size spectrum. Conversely, high values of $c$ lead to smaller $L_\infty$ (Table 2 and Figure 9f).

The fraction of the assimilated energy which is allocated to growth and somatic maintenance ($\kappa$ slightly influences the curvature of the spectrum for small lengths (Table 2 and Figure 9g). $\kappa$ also influences positively the $L_\infty$ value (and hence the curvature of the spectrum for large lengths). For high values of $\kappa$ the model produces unstable oscillations (waves propagating from small to large size classes cf. Figure 9g). This unstable oscillatory phenomenon does not appear when $M_{\text{egg}}$ is set equal to 0 (Figure 9h).

Increasing the size of the smallest prey that can be eaten by a given predator (decreasing $r_2$ and increasing $a_2$) decreases substantially the slope of the stationary size-spectrum (Table 2 and Figure 9i). Increasing the size of the largest prey that can be eaten by a given predator (increasing $r_1$ and decreasing $a_1$) increases the slope of the stationary size-spectrum (Table 2 and Figure 9j).

Decreasing the fraction of the ingested energy which is assimilated ($e_A$) slightly decreases both the slope of the size spectrum and $L_\infty$ (Table 2 and Figure 9k). On the contrary, an increase of the weight specific cost of growth $Eg$ decreases both the slope of the size spectrum and $L_\infty$ (Table 2 and Figure 9l).
4 DISCUSSION

4.1 Our model in the context of previous studies

The development of continuous size spectrum models based on allometric growth and mortality processes is a long lasting story in quantitative marine ecology (e.g.: Platt and Denman, 1978; Silvert and Platt, 1978 and 1980; Dickie et al., 1987; Cushing, 1992; Duplisea and Kerr, 1995; Arino et al., 2004; Benoit and Rochet, 2004). Models first dealt with constant growth rate. Later, Silvert and Platt (1980) assumed a constant size ratio between a predator and its prey. More recently, Arino et al. (2004) incorporated reproduction to the model and Benoit and Rochet (2004) linked explicitly the growth rate to the actual quantity of food being eaten and extended the predation process to any distribution of prey selectivity. In the model of Benoit and Rochet (2004), a given predator is supposed to eat all the potential preys swimming in a searched volume which increases allometrically with predator size. Like previous models, their model is built on a “supply system” vision of the ecosystem: all the selected preys supplied in the “hunting volume” of the predator are eaten. Consequently, the growth rate of predators is not limited: if the biomass of prey tends to infinity, the growth rate of predators will also tend to infinity. Such a characteristic is not realistic and is furthermore likely to generate instability as reported by Benoit and Rochet (2004).

Conversely, our approach is based on a symmetrical “demand system” vision of the ecosystem: any organism in the ecosystem targets a maximal amount of energy proportional to its squared length to meet its growth, reproduction and maintenance needs and cannot eat more than this demand. Consequently, the growth rate of predators is limited: if the biomass
of prey tends to infinity, the growth rate of predators tends to a maximum. Hence, in our
model, a predator generates a mortality rate proportional to its maximal needs (and related to
the biomass of prey with a Holling type II functional response) which is distributed over its
prey range. Energy from prey is then shared between all their possible predators,
proportionally to the mortality they exert. If predator needs for growth and/or reproduction are
not satisfied, a starvation mortality coefficient is applied, which is proportional to the
maintenance needs not fulfilled by assimilated energy. Our approach allows to take into
account more biological and ecological processes (opportunistic size-structured predation,
predators competition, allocation of energy between growth and reproduction, somatic and
gonadic maintenance, starvation mortality) in a rigorous mass-balanced physiologically-based
formulation derived from the Dynamic Energy Budget theory (Kooijman, 2000).

4.2 Stationary solutions

Numerical simulations show that the model produces stable solutions which do not need to be
stabilized using diffusion or complex boundary conditions. In most cases with constant
environmental conditions, the model converges toward a stationary log-log linear size-
spectrum which is independent of initial conditions (Figure 7). Numerically, 20 years are
most of the time sufficient to approximate the stationary solution with a good precision. It is
theoretically well established that size-structured predator-prey models admit a linear log-log
size-spectrum as a stationary solution (Silvert and Platt, 1980, Arino et al., 2004, Benoit and
Rochet, 2004) as far as the smallest sizes are put apart (Shin and Cury, 2004). Our simulations
corroborate previous studies and show that this important property still holds when size-
dependent opportunistic predation, predator competition, energy allocation between growth
and reproduction, nonpredatory mortality and starvation mortality are explicitly taken into
account as key processes governing energy flow through marine ecosystems.
From an ecological perspective, the distributed nature of predation over a large size range multiplies the weak links in ecosystems, and hence is likely to dampen oscillations between consumers and resources and enhance persistence and stability (McCann, Hastings & Huxel, 1998; McCann, 2000). In other respects, the stationary state can be considered as the “ultimate state of maturity” of an ecosystem as defined by Odum (1969). Being always submitted to perturbations, ecosystems are actually in a never-ending transient state of “maturation” toward their steady state “maturity”.

Using our reference set of parameters, the slope of the simulated log-log biomass spectrum equals -1.06. This value matches fairly well with the values reported in empirical studies (e.g. MacPherson and Gordoa, 1996; Zhou and Huntley, 1997; Quinones, Platt & Rodriguez, 2003; Marquet et al., 2005). For the first size class of the spectrum however (the size class of the producers), the model departs from the linear solution. This is likely to be due to the poor representation of producers in the model, in particular to the lack of representation of phytoplankton growth and division. Furthermore, our numerical simulation grid, which focuses on consumer dynamics, has only one size-class for representing producers which likely leads to potential irregular solutions when approximating the integrals over small sizes. It has furthermore to be noted that for large sizes close to $\mathcal{L}_e$, the size spectrum is curved downward. This phenomenon corresponds in our model to the slowdown of growth around the maximum size.

4.3 Sensitivity of the simulated size-spectrum to the parameters

The slope, intercept and curvature of the stationary size-spectrum are generally not very sensitive to the parameters of the model, at least in the explored ranges (Table 2 and Figure 9). The parameters can be classified according to their qualitative effect on the size spectrum.
Some parameters, such as the size of the smallest prey that can be eaten by a given predator ($\varrho$), act only on the slope of the spectrum (cf. Figure 9 i and j) when others, such as the maximum surface specific ingestion rate ($\dot{a}$) act only on its intercept (Figure 9 a). Other parameters, such as the nonpredatory mortality coefficient ($M$), modify the curvature of the spectrum (Figure 9 d) when some others, such as the fraction of the spawned eggs which are not fertilized ($M_{egg}$), have only a local influence on the very small sizes of the spectrum (Figure 9 c). Finally, most parameters modify slightly the $L_\infty$ value and hence influence the linearity of the spectrum for large sizes.

It has furthermore to be noted that, as suspected by Arino and al. (2004), for certain combinations of extreme values of the parameters, the stationary solution becomes unstable and oscillatory solutions appear, even in the case of stable phytoplankton production and constant temperature (Figure 9 g).

5 CONCLUSION

The proposed model improves previous studies by incorporating processes playing an important role in the energy fluxes through marine systems. It is furthermore based on a “demand system” approach which leads to more stable solutions than previously developed “supply system” models. Despite its simple ecological assumptions, the model seems to represent adequately the main qualitative and quantitative characteristics of marine size-spectra which have been reported in empirical studies and enables testable insights regarding the effect of environmental variability and changes on ecosystems. Those effects are explored through simulations in a companion paper (Maury et al., this issue) which focuses on temperature and primary production effects on the size spectrum.
However it has to be kept in mind that marine ecosystems encompass a large number of zoological groups which exhibit very different eco-physiological and behavioral characteristics. Each zoological group is in turn composed of a large number of species, each having various life histories (various growth rates, longevities and sizes at maturity). Hence, in real ecosystems, small organisms comprise adults of various small short-living species as well as juveniles of various large long-living species. Despite this obvious diversity, our model assumes constant physiological parameters and rules for any consumer organisms in the ecosystem. That could constitute a limitation of our approach since biodiversity plays important functional roles in ecosystems. This furthermore leads us to use simplified hypothesis about the reproduction process since all size classes are supposed to contain the same proportion of mature individuals. Formalizing and quantifying the effects of biodiversity in size-spectrum models is indeed critical and will be an important goal of our future work.

Acknowledgements

We thank Bernard Cazelles, Philippe Cury, Michel langlais, Alain Menesguen, Frédéric Ménard and Christian Mullon for their constructive criticisms of an earlier version of the manuscript and for their kind encouragements.

6 APPENDIX

A) Full model equation

Combining Eqs. (1), (2), (7), (9), (10), (11), (12) and (13) gives the full model equation:
\( \forall w \in [0; w_1] \)

\[
\frac{d\xi^c_{r,t}}{dt} = \frac{\prod_{l} A(T_l) \xi^c_{r,t}}{w_1} \omega^w_{\max} \int_{x=0}^{w_\max} \left( \frac{\xi^c_{r,t} u^{-\frac{1}{3}} s_{u,v}}{u^2} + \int_{v=0}^{w_\max} s_{u,v} \xi^c_{r,t,v} dv \right) du + M_t
\]  

(15.)

\( w = w_{\text{egg}} \)

\[
\gamma_{t,w_{\text{egg}}} \xi^c_{r,t} = (1 - M_{\text{egg}}) \gamma_{A(T_r)} \gamma_{t,w_{\text{egg}}} \int_{u=w_{\text{egg}}}^{\max} \left( \frac{(1 - \kappa) \kappa \omega \xi^c_{r,t} u^{-\frac{1}{3}} \int_{v=0}^{w_\max} s_{u,v} \xi^c_{r,t,v} dv}{u^2 A(T_r)} + \int_{v=w_{\text{egg}}}^{w_\max} s_{u,v} \xi^c_{r,t,v} dv \right) du
\]

(16.)

\( \forall w \in [w_{\text{egg}}; w_{\max}] \)

\[
\frac{\partial \xi^c_{r,t}}{\partial t} = -\frac{\psi A(T_t)}{\psi} \frac{\partial}{\partial w} \left( \left( \frac{\xi^c_{r,t} u}{w_{\max} A(T_r)} \right)^{\frac{2}{3}} - \frac{\mu}{\psi} \xi^c_{r,t} \left( \frac{u}{w_{\max} A(T_r)} \right) + \frac{c}{w_{\max} A(T_r)} \int_{v=0}^{w_\max} s_{u,v} \xi^c_{r,t,v} dv \right) + \left( \frac{(1 - \kappa) \kappa \omega \xi^c_{r,t} u^{-\frac{1}{3}} \int_{v=0}^{w_\max} s_{u,v} \xi^c_{r,t,v} dv}{w_{\max} A(T_r)} + \int_{v=0}^{w_\max} s_{u,v} \xi^c_{r,t,v} dv \right)
\]

(17.)

Where \( [x]^+ \) is the function defined by \( [x]^+ = x \) if \( x \geq 0 \) \( [x]^+ = 0 \) if \( x < 0 \),

\[
s_{u,w} = \left( 1 + e^{-a_1 \left( \frac{\rho_1 - \left( \frac{u}{w} \right)^{1/3} \right)} \right)^{-1} - \left( 1 + e^{-a_2 \left( \frac{\rho_2 - \left( \frac{u}{w} \right)^{1/3} \right)} \right)^{-1}
\]

is the size-dependent selectivity.
function of preys of weight \( w \) by predators of weight \( u \); and \( A(T) = e^{\left(\frac{T_u - T}{T_o}\right)} \) is the Arrhenius temperature-dependant correction factor.

**B) Calculation of \( w \) and \( m \) as a function of the Von Bertalanffy growth parameters \( K \) and \( L_x \)**

At food saturation, our growth equation (eqs. 9) is related as follows to the Von Bertalanffy growth equation:

\[
\frac{dw}{dt} = Aw^{2/3} - Bw \quad \text{with} \quad \begin{cases} A = \frac{\psi}{\psi + E_A} \\ B = \frac{\mu}{\psi + E_A} \end{cases}
\]

(18.)

This well known equation can be rewritten in length and integrated between \( l=0 \) and \( l=l_t \) to get \( l_t \) as a function of time:

\[
\frac{d(lt^3)}{dt} = 3al^2 \frac{dl}{dt} = A(lt^3)^{2/3} - Bal^3 \quad \Leftrightarrow \quad \frac{dl}{dt} = \frac{Aa^{-\frac{3}{2}}}{3} - \frac{Bl}{3}
\]

(19.)

Which, after integration gives:

\[
l_t = Aa^{-\frac{3}{2}} \left( 1 - e^{-\frac{B(l-l_0)}{3}} \right)
\]

(20.)

This expression is used to express \( \omega \) and \( \mu \) as a function of the Von Bertalanffy growth parameters \( K \) and \( L_x \).
\begin{align*}
L_\infty &= \frac{A \alpha^{-\frac{\gamma}{3}}}{B} = \frac{\kappa \alpha \psi a^{-\frac{\gamma}{3}}}{\mu} \\
K &= \frac{B}{3} = \frac{\mu}{3(\psi + E_g)} \\
\omega &= \frac{3K L_\infty (\psi + E_g)}{\kappa \alpha \psi a^{-\frac{\gamma}{3}}} \\
\mu &= 3K(\psi + E_g)
\end{align*}
\tag{21}

For the numerical applications presented in the present paper, an asymptotic length $L = 2.2 \text{ m}$ is assumed with a corresponding growth rate $K = 0.2 \text{ year}^{-1}$ deduced from the mean statistical relationships observed between $K$ and $L$ by Froese and Pauly (2000).

C) Estimation of the mortality parameters $M$ and $\nu$

To estimate the parameters $M$ and $\nu$ which determine the length-dependent nonpredatory mortality, 5 groups of organisms having very different mean length are considered (diatoms, copepods, and three fish of 0.1m, 0.8 m and 1.7m). For each group an arbitrary life span is attributed and the corresponding mortality is estimated assuming that the life span corresponds to the age at which only 10\% of a cohort remains (Table 3). The parameters $M$ and $\nu$ are estimated by fitting the modeled mortality curve to the estimated mortality curve (Table 3).

Table 3: Estimation of the nonpredatory mortality parameters $M$ and $\nu$(see text).

<table>
<thead>
<tr>
<th>species</th>
<th>Mean size</th>
<th>Estimated life span</th>
<th>Estimated mortality</th>
<th>Modeled mortality $M \nu$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diatoms</td>
<td>$5 \times 10^{-3}$ m</td>
<td>90 days</td>
<td>$2.56 \times 10^{-2}$ day$^{-1}$</td>
<td>$2.56 \times 10^{-2}$ day$^{-1}$</td>
</tr>
<tr>
<td>Copepods</td>
<td>$5 \times 10^{-3}$ m</td>
<td>180 days</td>
<td>$1.28 \times 10^{-2}$ day$^{-1}$</td>
<td>$1.28 \times 10^{-2}$ day$^{-1}$</td>
</tr>
<tr>
<td>Fish size</td>
<td>Length</td>
<td>Width</td>
<td>Days</td>
<td>Day^{-1}</td>
</tr>
<tr>
<td>-----------</td>
<td>--------</td>
<td>-------</td>
<td>------</td>
<td>----------</td>
</tr>
<tr>
<td>0.1m</td>
<td>0.1m</td>
<td>730</td>
<td></td>
<td>3.15.10^{-3}</td>
</tr>
<tr>
<td>0.8m</td>
<td>0.8m</td>
<td>1825</td>
<td></td>
<td>1.26.10^{-3}</td>
</tr>
<tr>
<td>1.7m</td>
<td>1.7m</td>
<td>2555</td>
<td></td>
<td>9.01.10^{-4}</td>
</tr>
</tbody>
</table>

7 REFERENCES


8 TABLES

Table 1: Parameters used for numerical simulations (ranges are given when several studies are available). The values are derived from the literature or from estimations detailed in the Appendix.

<table>
<thead>
<tr>
<th>parameter</th>
<th>Designation and unit</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A$</td>
<td>Shape coefficient $w=aL^2$ (kg.m$^{-3}$)</td>
<td>15</td>
<td>Data from Froese and Pauly (2000)</td>
</tr>
<tr>
<td>$\phi$</td>
<td>Sex ratio (no dimension)</td>
<td>0.5</td>
<td>Arbitrary</td>
</tr>
<tr>
<td>$M$</td>
<td>Nonpredatory mortality for $l=1$m $(s^{-1})$</td>
<td>$1.524 \times 10^{-8}$</td>
<td>See Appendix C</td>
</tr>
<tr>
<td>$\nu$</td>
<td>Allometric coefficient of $M$ (no dimension)</td>
<td>-0.2995</td>
<td>See Appendix C</td>
</tr>
<tr>
<td>$M_{egg}$</td>
<td>Fraction of the spawned eggs which are not fecundated</td>
<td>0.4</td>
<td>Arbitrary</td>
</tr>
<tr>
<td>$\psi$</td>
<td>Energetic content of one unit of biomass (J.kg$^{-1}$)</td>
<td>$4 \times 10^6$</td>
<td>Daan (1975), Edwards, Finlayson &amp; Steele (1972), Krohn, Reidy &amp; Kerr(1996), Kitchell, Neill, Dizon &amp; Magnuson (1978)</td>
</tr>
<tr>
<td>$\omega$</td>
<td>Maximum Surface specific ingestion rate (kg.kg$^{-2/3}$.s$^{-1}$)</td>
<td>$5.459 \times 10^{-7}$</td>
<td>See Appendix B</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>Fraction of the assimilated energy allocated to growth and somatic maintenance (no dimension)</td>
<td>[0.65, 0.88]</td>
<td>Estimations from Brill (1978) and Van Der Veer (2003)</td>
</tr>
<tr>
<td>$\epsilon_A$</td>
<td>Fraction of the ingested energy</td>
<td>[0.65, 0.99]</td>
<td>Data and estimates from</td>
</tr>
<tr>
<td>Symbol</td>
<td>Description</td>
<td>Value</td>
<td>Source</td>
</tr>
<tr>
<td>--------</td>
<td>-------------</td>
<td>-------</td>
<td>--------</td>
</tr>
<tr>
<td>$E_g$</td>
<td>Weight specific cost of growth (Kooijman, 2000) ($J.kg^{-1}$)</td>
<td>$7 \times 10^6$</td>
<td>van der Veer, Kooijman &amp; van der Meer (2003)</td>
</tr>
<tr>
<td>$\mu$</td>
<td>Amount of energy required for the somatic maintenance of one unit of weight during one unit of time ($J.kg^{-1}.s^{-1}$)</td>
<td>0.20949</td>
<td>See Appendix B</td>
</tr>
<tr>
<td>$\rho$</td>
<td>Minimum ratio of predator size over prey size</td>
<td>3</td>
<td>Floeter and Temming, 2003; Juanes, 2003; Menard, Labrune, Shin, Asine &amp; Bard (in review);</td>
</tr>
<tr>
<td>$\beta$</td>
<td>Maximum ratio of predator size over prey size</td>
<td>100</td>
<td>Floeter and Temming, 2003; Juanes, 2003; Menard et al., 2006;</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Shape parameter for the selectivity curve</td>
<td>5</td>
<td>(see text)</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Shape parameter for the selectivity curve</td>
<td>0.05</td>
<td>(see text)</td>
</tr>
<tr>
<td>$C$</td>
<td>Holling type II half-saturation constant ($J.m^3.s^{-1}$)</td>
<td>117.7</td>
<td>Tuned</td>
</tr>
<tr>
<td>$\chi$</td>
<td>$w'$ is the volume of water explored by a predator of weight $w$ ($m^3.s^{-1}$)</td>
<td>0.33</td>
<td>Fixed so that $w'$ is proportional to length</td>
</tr>
<tr>
<td>$\tau_i$</td>
<td>Arrhenius temperature-dependent correction factor (°K)</td>
<td>$[2 \times 10^3, 16 \times 10^3]$</td>
<td>Brett and Groves (1979), van der Veer et al., (2003)</td>
</tr>
</tbody>
</table>
Table 2: Qualitative summary of the sensitivity analysis of the model (slope, intercept and curvature of the stationary size spectrum) to the value of its main parameters. 0=no effects, +=positive effect and -=negative effect. Corresponding figures are provided in Appendix D.

<table>
<thead>
<tr>
<th>parameter</th>
<th>Designation</th>
<th>Slope</th>
<th>Intercept</th>
<th>Curvature</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M$</td>
<td>Nonpredatory mortality for l=1m</td>
<td>0</td>
<td>0</td>
<td>++</td>
</tr>
<tr>
<td>$v$</td>
<td>Exponent of the M length-dependence</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>$M_{egg}$</td>
<td>Fraction of the spawned eggs which are not fecunded</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>$\omega$</td>
<td>Maximum Surface specific ingestion rate</td>
<td>0</td>
<td>--</td>
<td>-</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>Fraction of the assimilated energy allocated to growth and somatic</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>maintenance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$e_A$</td>
<td>Fraction of the ingested energy which is assimilated</td>
<td>+</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>$E_g$</td>
<td>Weight specific cost of growth</td>
<td>-</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>$\mu$</td>
<td>Maintenance rate</td>
<td>0</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>$\rho$ and $\alpha$</td>
<td>Minimum ratio of predator size over prey size</td>
<td>+</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>$\beta$ and $\gamma$</td>
<td>Maximum ratio of predator size over prey size</td>
<td>+</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
9 LEGEND OF FIGURES

Figure 1: Schematic representation of the weight structured ecosystem distinguishing primary phytoplanktonic producers from predatory consumers (log-log).

Figure 2: Schematic representation of weight (size) structured energy flow through the ecosystem.

Figure 3: (a) Limitation curves for preys too large to be ingested (black dots), preys too small to be ingested (open circles) and resulting prey selectivity function $s_{2,w}$ as a function of prey length $\left(\frac{w}{a}\right)^{1/3}$ for a 2m long predator ($\beta=3$, $\rho=100$, $\alpha=5$ and $\phi=0.05$).

(b) Selectivity function $s_{u,w}$ versus prey length $\left(\frac{w}{a}\right)^{1/3}$ and predator length $\left(\frac{u}{a}\right)^{1/3}$ with $\beta=3$, $\rho=100$, $\alpha=5$ and $\phi=0.05$.

Figure 4: Schematic representation of energy flow through organisms (simplified from Kooijman, 2000).

Figure 5: Arrhenius correction factor for temperatures ranging from 10 °C to 30 °C ($T_A=8000$ and $T_{ref}=298.15$ K=25 °C). Each biological rate in the model is multiplied by the Arrhenius correction factor.
Figure 6: (a) First 10 grid points (black dots) of the discretization used to approximate numerically the model and their associated size classes (vertical bars) used to calculate the integrals. (b) Full length/weight grid used for numerical simulations of the model. Each point represents the mean weight and the corresponding size of each of the 101 grid cells.

Figure 7: Simulation of the transition toward the stationary state. (a) Size spectrum, (b) functional response, (c) growth rate, (d) starvation mortality and nonpredatory mortality (e) predatory mortality, (f) contribution of each size class to egg production. Triangles correspond to the initial energy distribution in the ecosystem (end of day 0), dotted lines correspond to the energy spectrum every 30 days except for starvation mortality where they are drawn every 3 days and continuous lines are drawn every 2 years after the first year. Black circles correspond to the steady state size-spectrum (after 50 years).

Figure 8: Stationary size-spectrum and associated regression line as a function of weight (circles) and length (triangles).

Figure 9: Systematic sensitivity analysis of the steady state to the parameters. Different values of $Q, \mu, M_{\text{egg}}, M, \psi, c, \kappa, \beta, \rho, eA$ and $Eg$ varying in a large range around their reference values are considered respectively in (a), (b), (c), (d), (e), (f), (g), (h), (i), (j), (k) and (l). The sensitivity of the steady state to the parameter $\kappa$ is considered in the case where $M_{\text{egg}}=0.4$ (g) and $M_{\text{egg}}=0$ (h).
Figure 1:

Graph showing the weight distribution between primary producers and consumers, with weight axes labeled as $w$, $w_{\text{max}}$, and $w_{\text{egg}}$. The shaded regions represent different categories within the weight spectrum.
Figure 2:

Predation energy fluxes
Figure 3a:

Figure 3b:
Figure 4:
Figure 5:
Figure 6 a and b
Figure 7
Figure 8
Figure 9