

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

Olivier Maury^{a,*}, Blaise Faugeras^a, Yunne-Jai Shin^a, Jean-Christophe Poggiale^b,
Tamara Ben Ari^a, Francis Marsac^a

^a *Institut de Recherche pour le Développement (IRD) – UR 109 Thetis, CRH, av. Jean Monnet, B.P. 171, 34203 Sète Cedex, France*

^b *LMGEM – UMR 6117, OSU – Case 901, Campus de Luminy, 13288 Marseille Cedex 9, France*

Available online 13 May 2007

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 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, O., Shin, Y.-J., Faugeras, B., Ben Ari, T., Marsac, F., 2007. Modeling environmental effects on the size-structured energy flow through marine ecosystems. Part 2: simulations. *Progress in Oceanography*, doi:10.1016/j.pocean.2007.05.001]. © 2007 Elsevier Ltd. All rights reserved.

Keywords: Size spectrum; Mathematical model; Predation; Bioenergetics; Dynamic energy budget (DEB) theory; Energy flow

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

* Corresponding author.

E-mail address: maury@ird.fr (O. Maury).

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 et al., 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 et al., 1997; Pauly et al., 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, 1980; Dickie et al., 1987; Cushing, 1992; Platt and Denman, 1997; Arino et al., 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 et al., 1972; Blueweiss et al., 1978; Gillooly et al., 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 et al., 1999), predator–prey relationships are, in many marine systems, mostly determined by size (Lundvall et al., 1999; Scharf et al., 2000; Jennings et al., 2001 and Jennings et al., 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, 2001; Nisbet et al., 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 bioener-

getic 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 and 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 et al., 2007), 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 $\xi_{t,w}$, the distribution function of the energy content of the marine ecosystem ($\text{J kg}^{-1} \text{m}^{-3}$) at time $t \in [0, +\infty[$ and weight $w \in [0, w_{\max}]$ in 1 m^3 of seawater. $\xi_{t,w}$ 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 ψ (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 $\int_{x=w_1}^{x=w_2} \xi_{t,x} dx$ and $\xi_{t,w}$ is related to $N_{t,w}$, the distribution function of the number of individuals in terms of weight ($\text{kg}^{-1} \text{m}^{-3}$) at (t,w) in 1 m^3 of seawater, with $\xi_{t,w} = \psi \cdot w \cdot N_{t,w}$.

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 $w = al^3$.

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 (Fig. 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 $[w_{\text{egg}}, w_{\max}]$. Consumers do reproduce, their eggs have a weight $w_{\text{egg}} > 0$ and their maximal weight is $w_{\max} > w_1$.

The distribution function of the energy content of the producer and consumer groups are noted respectively $\xi_{t,w}^{\text{P}}$ and $\xi_{t,w}^{\text{C}}$ so that the distribution function of the energy content of the ecosystem is $\xi_{t,w} = \chi_{[0,w_1]} \xi_{t,w}^{\text{P}} + \chi_{[w_{\text{egg}},w_{\max}]} \xi_{t,w}^{\text{C}}$ 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.

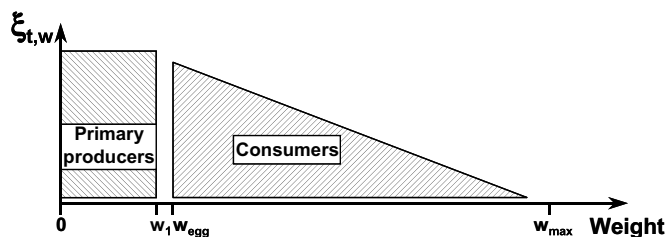


Fig. 1. Schematic representation of the weight structured ecosystem distinguishing primary phytoplanktonic producers from predatory consumers (log–log).

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 Eq. (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:

$$\frac{d\xi_{t,w}^p}{dt} = \frac{1}{w_1} \left(\Pi_t - \xi_{t,w}^p \int_{x=0}^{x=w_1} \lambda_{t,x} dx \right) - \xi_{t,w}^p M_I \quad \forall w \in [0; w_1] \tag{1}$$

With Π_t ($J s^{-1} m^{-3}$) the primary energy production which enters the system at time t , which constitutes the only external source of energy of the whole ecosystem, M_I (s^{-1}) the nonpredatory mortality rate affecting primary producers and $\lambda_{t,x}$ (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 and Caswell, 1997; Kot, 2001) and which is written as follows in the interval $]w_{egg}, w_{max}]$ assuming given initial conditions for $t = 0$:

$$\begin{cases} \frac{\partial \xi_{t,w}^c}{\partial t} = -\frac{\partial(\gamma_{t,w} \xi_{t,w}^c)}{\partial w} - (\lambda_{t,w} + Z_w + M_{t,w}^{starv}) \xi_{t,w}^c & \forall w \in]w_{egg}; w_{max}] \\ \xi_{0,w}^c = \xi_w^0 \end{cases} \tag{2}$$

where γ ($kg s^{-1}$) is the growth rate, λ (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 $w = w_{egg}$:

$$\gamma_{t,w_{egg}} \xi_{t,w_{egg}}^c = R_t \tag{3}$$

The derivation of explicit expressions for all the coefficients of Eqs. (2) and (3) ($\lambda_{t,w}$, $\gamma_{t,w}$, R_t , $M_{t,w}^{starv}$ and $Z_{t,w}$) are provided in the five subsections below.

2.2.1. The predation process: calculation of $\lambda_{t,w}$

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) (Fig. 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 ρ_1 and ρ_2 extreme values (Fig. 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 (Fig. 3a):

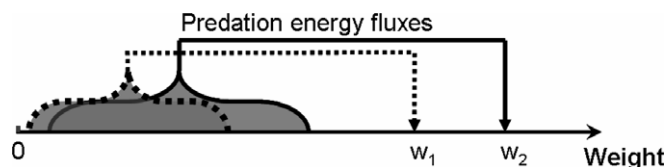


Fig. 2. Schematic representation of weight (size) structured energy flow through the ecosystem.

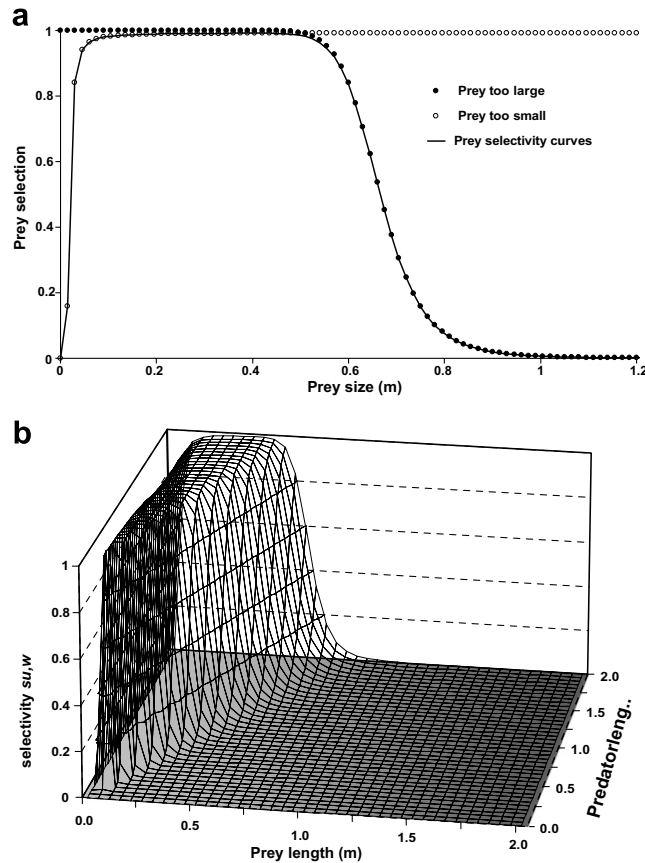


Fig. 3. (a) Limitation curves for preys too large to be ingested (black dots), preys too small to be ingested (open circles) and resulting prey selectivity function $s_{2,w}$ as a function of prey length $(\frac{w}{a})^{1/3}$ for a 2 m long predator ($\rho_1 = 3, \rho_2 = 100, \alpha_1 = 5$ and $\alpha_2 = 0.05$). (b) Selectivity function $s_{u,w}$ versus prey length $(\frac{w}{a})^{1/3}$ and predator length $(\frac{u}{a})^{1/3}$ with $\rho_1 = 3, \rho_2 = 100, \alpha_1 = 5$ and $\alpha_2 = 0.05$.

$$s_{u,w} = \left(1 + e^{\alpha_1 \left(\rho_1 - \left(\frac{w}{a} \right)^{1/3} \right)} \right)^{-1} \left(1 - \left(1 + e^{\alpha_2 \left(\rho_2 - \left(\frac{u}{a} \right)^{1/3} \right)} \right)^{-1} \right) R^{+*2} \xrightarrow{s}]0; 1[\quad (4)$$

With ρ_1, ρ_2, α_1 and α_2 , being constant positive parameters characterizing both the half saturation and the flatness of the sigmoid functions.

To take into account the basic physiological processes involved in the acquisition and use of energy by biological organisms, a simplified version of the dynamic energy budget (DEB) theory is used (Kooijman, 1986, 2000, 2001; Nisbet et al., 2000). In the DEB theory, the ingested energy is assimilated by organisms and stocked into reserves. A fixed fraction κ of the energy utilized from reserves is then allocated to growth of structural material and somatic maintenance, the remaining fraction $1 - \kappa$ 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 κ is used for somatic growth and maintenance whereas a fraction $1 - \kappa$ is allocated to reproduction and gonadic maintenance (Fig. 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: the ecosystem is modeled as a “meta-organism” characterized by a mean life history.

According to the DEB theory, the maximum amount of prey 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

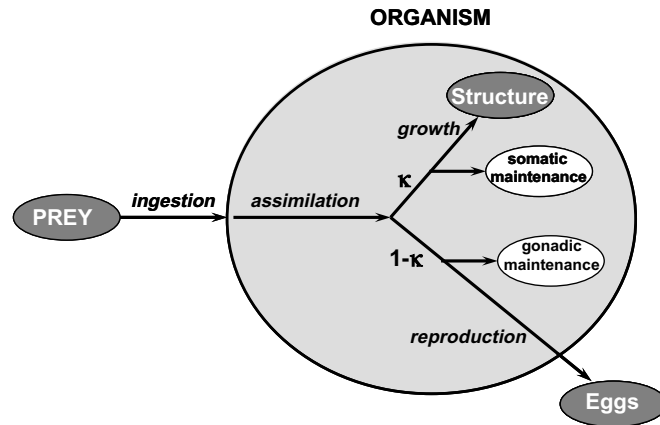


Fig. 4. Schematic representation of energy flow through organisms (simplified from Kooijman, 2000).

Table 1

Parameters used for numerical simulations (ranges are given when several studies are available)

Parameter	Designation and unit	Value	Source
A	Shape coefficient $w = a^3$ (kg m^{-3})	15	Data from Froese and Pauly (2000)
ϕ	Sex ratio (no dimension)	0.5	Arbitrary
M	Nonpredatory mortality for $l = 1$ m (s^{-1})	1.524×10^{-8}	See Appendix C
v	Allometric coefficient of M (no dimension)	-0.2995	See Appendix C
M_{egg}	Fraction of the spawned eggs which are not fecunded	0.4	Arbitrary
ψ	Energetic content of one unit of biomass (J kg^{-1})	4×10^6	Daan (1975), Edwards et al. (1972), Krohn et al. (1996) and Kitchell et al. (1978)
ω	Maximum surface-specific ingestion rate ($\text{kg kg}^{-2/3} \text{s}^{-1}$)	5.459×10^{-7}	See Appendix B
κ	Fraction of the assimilated energy allocated to growth and somatic maintenance (no dimension)	[0.65, 0.88] 0.65	Estimations from Brill et al. (1978) and van der Veer et al. (2003)
e_A	Fraction of the ingested energy which is assimilated (no dimension)	[0.65, 0.99] 0.8	Data and estimates from Essington et al. (2001), Andersen and Riis-Vestergaard (2003), Krohn et al. (1996), Kitchell et al. (1978) and Brett and Groves (1979)
E_g	Weight specific cost of growth (Kooijman, 2000) (J kg^{-1})	7×10^6	van der Veer et al. (2003)
μ	Amount of energy required for the somatic maintenance of one unit of weight during one unit of time ($\text{J kg}^{-1} \text{s}^{-1}$)	0.20949	See Appendix B
ρ_1	Minimum ratio of predator size over prey size	3	Floeter and Temming, 2003; Juanes, 2003 and Ménard et al. (2006);
ρ_2	Maximum ratio of predator size over prey size	100	Floeter and Temming, 2003; Juanes, 2003 and Ménard et al., 2006
α_1	Shape parameter for the selectivity curve	5	(See text)
α_2	Shape parameter for the selectivity curve	0.05	(See text)
C	Holling type II half-saturation constant ($\text{J m}^3 \text{s}^{-1}$)	117.7	Tuned
χ	w^χ is the volume of water explored by a predator of weight w ($\text{m}^3 \text{s}^{-1}$)	0.33	Fixed so that w^χ is proportional to length
τ_A	Arrhenius temperature-dependent correction factor (K)	$[2 \times 10^3,$ $16 \times 10^3]$ 8×10^3	Brett and Groves (1979) and van der Veer et al. (2003)

The values are derived from the literature or from estimations detailed in Appendix.

amount of energy potentially preyed by all predators of weight comprised in the range $[u, u + du]$ at time t during dt in 1 m^3 of water, can be expressed as follows:

$$\begin{aligned}
 E_{t,u} du dt &\propto [\text{density of predators}]_{t,u} du \cdot \{\text{body surface}\}_u \cdot \{\text{functional response to preys}\}_{t,u} \cdot dt \\
 E_{t,u} du dt &= \psi \omega \frac{\xi_{t,u}^c du}{u \psi} u^{2/3} f_u(p_{t,u}) dt \\
 &= \omega \xi_{t,u}^c u^{-1/3} f_u(p_{t,u}) du dt \\
 f_u(p_{t,u}) &= \frac{p_{t,u}}{\frac{c}{u^\chi} + p_{t,u}}, \quad R^+ \xrightarrow{f} [0; 1[
 \end{aligned}
 \tag{5}$$

where ω is the mean maximum surface-specific ingestion rate ($\text{kg kg}^{-2/3} \text{ s}^{-1}$) and f_u is the functional response to the energy content of preys $p_{t,u}$ ($p_{t,u} = \int_{v=0}^{w_{\max}} s_{u,v} \xi_{t,v} dv$) 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^χ is the volume of water explored by a predator of weight w per unit of time ($\text{m}^3 \text{ s}^{-1}$) 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 χ 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:

$$\begin{aligned}
 E_{t,u/w} du dw dt &= E_{t,u} du dt \frac{s_{u,w} \xi_{t,w} dw}{\int_{v=0}^{w_{\max}} s_{u,v} \xi_{t,v} dv} = \omega \xi_{t,u}^c u^{-1/3} f_u \left(\int_{v=0}^{w_{\max}} s_{u,v} \xi_{t,v} dv \right) \frac{s_{u,w} \xi_{t,w} dw}{\int_{v=0}^{w_{\max}} s_{u,v} \xi_{t,v} dv} du dt \\
 &= \omega \xi_{t,u}^c u^{-1/3} \frac{s_{u,w} \xi_{t,w}}{\frac{c}{u^\chi} + \int_{v=0}^{w_{\max}} s_{u,v} \xi_{t,v} dv} du dw dt
 \end{aligned}
 \tag{6}$$

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:

$$E_{t,/w} dw dt = \int_{u=w_{\text{egg}}}^{w_{\max}} E_{t,u/w} du dw dt = \omega \xi_{t,w} \int_{u=w_{\text{egg}}}^{u=w_{\max}} \left[\frac{\xi_{t,u}^c u^{-1/3} s_{u,w}}{\frac{c}{u^\chi} + \int_{v=0}^{w_{\max}} s_{u,v} \xi_{t,v} dv} \right] du dw dt
 \tag{7}$$

It follows that the instantaneous mortality rate exerted by all possible predators on $\xi_{t,w}$ at time t is given by the following expression:

$$\lambda_{t,w} = \frac{E_{t,/w}}{\xi_{t,w}} = \omega \int_{u=w_{\text{egg}}}^{w_{\max}} \left[\frac{\xi_{t,u}^c u^{-1/3} s_{u,w}}{\frac{c}{u^\chi} + \int_{v=0}^{w_{\max}} s_{u,v} \xi_{t,v} dv} \right] du
 \tag{8}$$

2.2.2. The growth process: calculation of $\gamma_{t,w}$

According to Fig. 4, growth corresponds to the use of a fraction κ 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:

$$\frac{dw_{t,u}}{dt} = \frac{\kappa e_A E_{t,u}}{\psi N_{t,u}} - \frac{\mu u}{\psi} - \frac{E_g}{\psi} \frac{dw_{t,u}}{dt}
 \tag{9}$$

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, μ is the mean amount of energy required for the somatic maintenance of one unit of weight during one unit of time ($\text{J kg}^{-1} \text{ s}^{-1}$) 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 ($w = a l^3$, $a > 0$), 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:

$$\begin{aligned} \gamma_{t,u} &= \frac{dw_{t,u}}{dt} = \frac{\psi}{\psi + E_g} \left[\frac{\kappa e_A E_{t,u}}{\psi N_{t,u}^c} - \frac{\mu}{\psi} u \right]^+ = \frac{\psi}{\psi + E_g} \left[\frac{\kappa e_A E_{t,u}}{\xi_{t,u}^c} u - \frac{\mu}{\psi} u \right]^+ \\ &= \frac{\psi}{\psi + E_g} \left[\kappa e_A \omega f_u(p_{t,u}) u^{2/3} - \frac{\mu}{\psi} u \right]^+ = \frac{\psi}{\psi + E_g} \left[\frac{\kappa e_A \omega \int_{v=0}^{w_{\max}} s_{u,v} \xi_{t,v} dv}{\frac{c}{w^z} + \int_{v=0}^{w_{\max}} s_{u,v} \xi_{t,v} dv} u^{2/3} - \frac{\mu}{\psi} u \right]^+ \end{aligned} \quad (10)$$

Where $[x]^+$ is the function defined by

$$\begin{cases} [x]^+ = x & \text{if } x \geq 0 \\ [x]^+ = 0 & \text{if } x < 0 \end{cases}$$

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.

2.2.3. The reproduction process: calculation of R_t

According to [Fig. 4](#), reproduction corresponds to the use of a fraction $1 - \kappa$ of the assimilated energy diminished by a maintenance cost proportional to $(1 - \kappa)/\kappa$ 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 1 mm).

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 $[\]^+$ is used to express the egg input into the system (see the paragraph on starvation mortality for the treatment of mass conservation):

$$\begin{aligned} R_t &= (1 - M_{\text{egg}}) \phi \int_{w=w_{\text{egg}}}^{w_{\max}} \left[e_A (1 - \kappa) E_{t,w} - N_{t,w}^c \frac{1 - \kappa}{\kappa} \mu w \right]^+ dw \\ &= (1 - M_{\text{egg}}) \phi \int_{w=w_{\text{egg}}}^{w_{\max}} \left[\frac{(1 - \kappa) e_A \omega \xi_{t,w}^c w^{-1/3} \int_{v=0}^{w_{\max}} s_{w,v} \xi_{t,v} dv}{\frac{c}{w^z} + \int_{v=0}^{w_{\max}} s_{w,v} \xi_{t,v} dv} - \frac{(1 - \kappa) \mu \xi_{t,w}^c}{\kappa \psi} \right]^+ dw \end{aligned} \quad (11)$$

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

2.2.4. The starvation mortality: calculation of $M_{t,w}^{\text{starv}}$

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. Eqs. (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 Eqs. (10) and (11):

$$M_{t,w}^{\text{starv}} = \left[\frac{\mu}{\psi} - \frac{\kappa e_A \omega w^{-1/3} \int_{v=0}^{w_{\max}} s_{w,v} \xi_{t,v} dv}{\frac{c}{w^z} + \int_{v=0}^{w_{\max}} s_{w,v} \xi_{t,v} dv} \right]^+ + \left[\frac{(1 - \kappa) \mu}{\kappa \psi} - \frac{(1 - \kappa) e_A \omega w^{-1/3} \int_{v=0}^{w_{\max}} s_{w,v} \xi_{t,v} dv}{\frac{c}{w^z} + \int_{v=0}^{w_{\max}} s_{w,v} \xi_{t,v} dv} \right]^+ \quad (12)$$

2.2.5. The nonpredatory mortality: calculation of $Z_{l,w}$

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.

$$Z_w = Ml^v = M \left(\frac{w}{a} \right)^{v/3} \tag{13}$$

With M being the nonpredatory mortality rate for a 1 m 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 v 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 ($\phi < 1$) and dissipation processes such as imperfect efficiency of the assimilation process ($e_A < 1$), maintenance expenditures ($\mu > 0$) and energetic cost of growth ($E_g > 0$). If $\Pi = \mu = M = E_g = 0$ and $e_A = \phi = 1$, 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 and Johnston, 1999; Kooijman, 2000; Pörtner, 2002; Clarke, 2004; Speakman, 2005). Despite its purely molecular basis, the description of Arrhenius (Fig. 5) based on the van't Hoff equation ($k(T) = k_\infty e^{(-\frac{E_a}{RT})}$) with k a reaction rate, k_∞ 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, 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.

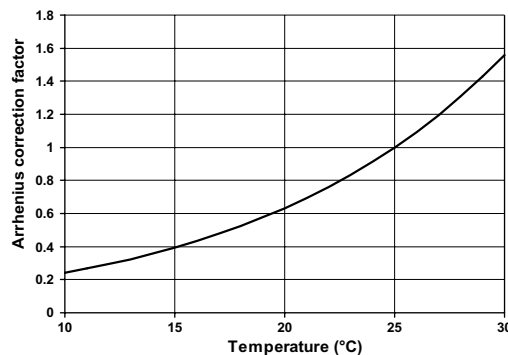


Fig. 5. Arrhenius correction factor for temperatures ranging from 10 °C to 30 °C ($T_A = 8000$ and $T_{ref} = 298.15K = 25\ ^\circ C$). Each biological rate in the model is multiplied by the Arrhenius correction factor.

$$\text{rate}(T) = \text{rate}(T_{\text{ref}}) \cdot A(T) \quad \text{with } A(T) = e^{\left(\frac{\tau_A}{T_{\text{ref}}} - \frac{\tau_A}{T}\right)} \tag{14}$$

With T_{ref} (K), the reference temperature and τ_A , a parameter (the ‘‘Arrhenius temperature’’ which equals $\frac{E_a}{R}$).

Combining Eqs. (1)–(3), (8) and (10)–(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} m, 10^{-16} 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 α 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 $\varpi = \frac{\ln(l-\beta)}{\ln(\alpha)} - \gamma = \frac{\ln(\alpha^{-1/3}w^{1/3}-\beta)}{\ln(\alpha)} - \gamma \iff w = a(\alpha^{\varpi+\gamma} + \beta)^3$ with α and β being fixed parameters and $\varpi = \{1, 2, 3, \dots, n\}$. To be able to choose easily the grid characteristics, the parameters β and γ are expressed in terms of l_{min} and l_{max} which are fixed so that the grid depends only on α (Fig. 6). Because the present study focuses mostly on large consumer organisms such as fish or large meso-zooplankton ranging from 1 mm to 2 m, α is set at 1.04 which corresponds to grid cells varying from 1.5 mm for the smallest size class to 75 mm for the largest class. An irregular grid is derived calculating weight steps δw_i so that each grid point w_i is placed at the middle of its associated grid cell (Fig. 6a). The first grid point which represents producers is placed at 1.24×10^{-3} m which

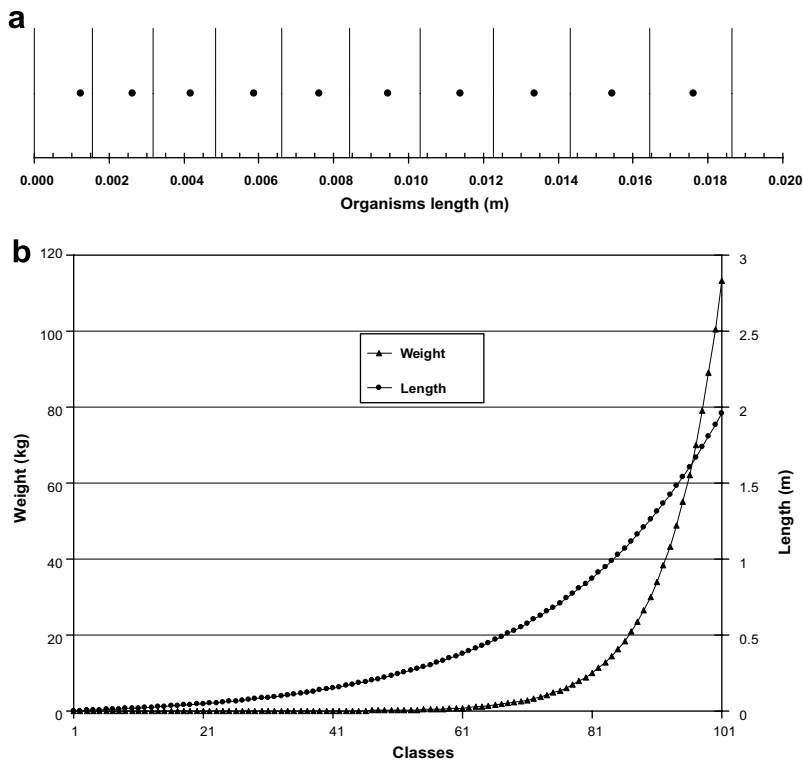


Fig. 6. (a) First 10 grid points (black dots) of the discretization used to approximate numerically the model and their associated size classes (vertical bars) used to calculate the integrals. (b) Full length/weight grid used for numerical simulations of the model. Each point represents the mean weight and the corresponding size of each of the 101 grid cells.

corresponds to the $]10^{-5} \text{ m}, 1.56 \times 10^{-3} \text{ m}]$ 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 $l_{\min} = 10^{-5} \text{ m}$ to $l_{\max} = 2 \text{ m}$ (Fig. 6b). Producers are assumed to occupy only the first length/weight class and consumers to range from the second to the 101th class (no overlap between their respective ranges).

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 Eq. (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 ω as well as the maintenance rate μ 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 ν) is based on assumptions about the size-dependent mean life duration of marine organisms (Appendix B).

The value of Π_t , 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/m^3 of seawater which is approximately equivalent to $10^{-3} \text{ N mol m}^{-3}$ 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 $474.6 \text{ kJ C mol}^{-1}$ – Kooijman, 2000 – gives $3,144,225 \text{ J/mol of N}$). This value is then divided by the weight range of producers in the model [$1.5 \times 10^{-14} \text{ kg}$, $5.72 \times 10^{-8} \text{ kg}$] to obtain the value for the distribution function of the energy content of the producers $\xi_{l,w}^p = 549.10^8 \text{ J kg}^{-1} \text{ m}^{-3}$. This value is obtained in the reference simulation using $\Pi_t = 1177 \text{ J day}^{-1} \text{ m}^{-3}$.

2.6. Simulation experiments

In a first set of simulations, the existence of a linear steady state is tested by running the model during 50 years. The sensitivity of the steady state to the individual value of the model parameters is then explored systematically. For that purpose, the parameters ω , μ , M_{egg} , M , ν , c , κ , ρ_1 , ρ_2 , 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 (Fig. 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.

Fig. 7b–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 (Fig. 7b). The growth rate

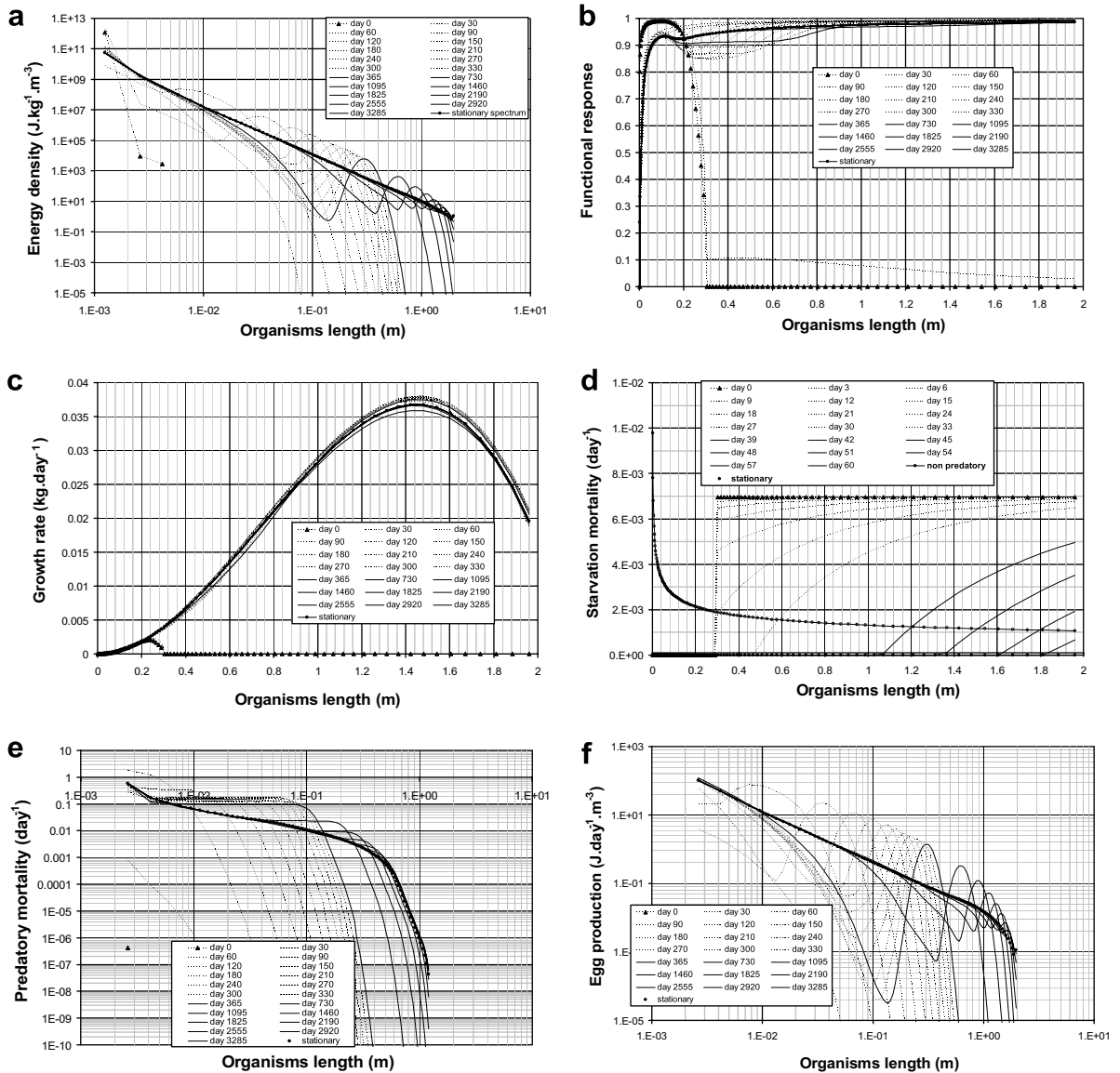


Fig. 7. Simulation of the transition toward the stationary state. (a) Size spectrum, (b) functional response, (c) growth rate, (d) starvation mortality and nonpredatory mortality (e) predatory mortality and (f) contribution of each size class to egg production. Triangles correspond to the initial energy 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).

(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_{∞} (Fig. 7c). The log-log predatory mortality curve at steady state shows a quasi-linear decreasing trend for organisms between 2 mm and 20 cm (Fig. 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 (Fig. 7e) exhibit a linearly decreasing trend with a downward curvature for sizes above 1.4 m, when maintenance processes are becoming to be non-negligible in Eq. (11).

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 (Fig. 8).

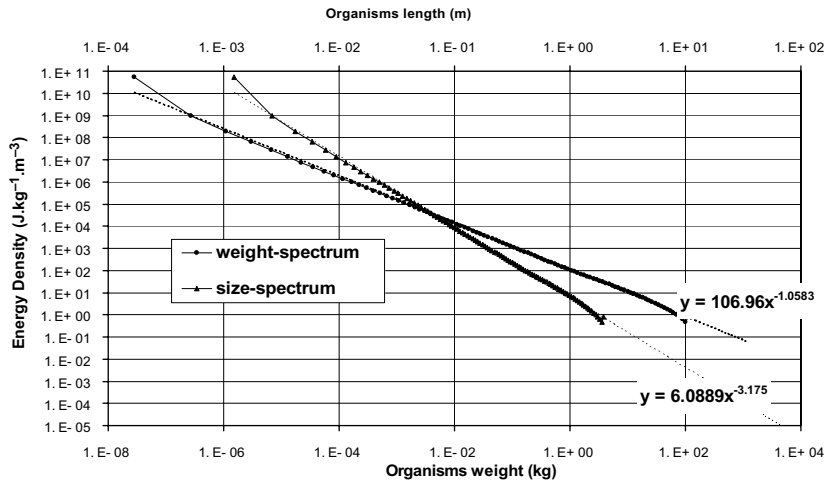


Fig. 8. Stationary size-spectrum and associated regression line as a function of weight (circles) and length (triangles).

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 (ω) but its intercept decreases when ω increases (the size spectrum is translated vertically, cf. Table 2 and Fig. 9a). The stationary size spectrum is not sensitive to the value of the maintenance rate μ (Table 2 and Fig. 9b). It has to be noted, however, that for length classes close to L_∞ (biomass is null for length greater than L_∞ , cf. Appendix B), the stationary size-spectrum may depart from its linear shape and be curved downward. This is the case for low ω values or for high μ values (Table 2 and Fig. 9a and b).

Varying the value of the fraction of the spawned eggs which are not fertilized (M_{egg}) does not change the size spectrum over medium and large size classes (Table 2 and Fig. 9c). Only small size classes are sensitive to M_{egg} and depart from the linear solution when M_{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 Fig. 9d). Over the explored range, the exponent ν of the nonpredatory mortality length-dependence has almost no effect on the size-spectrum (Table 2 and Fig. 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_∞ (Table 2 and Fig. 9f).

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

Parameter	Designation	Slope	Intercept	Curvature
M	Nonpredatory mortality for $l = 1$ m	0	0	++
ν	Exponent of the M length-dependence	0	0	0
M_{egg}	Fraction of the spawned eggs which are not fecunded	0	0	0
ω	Maximum Surface specific ingestion rate	0	–	–
κ	Fraction of the assimilated energy allocated to growth and somatic maintenance	0	0	–
e_A	Fraction of the ingested energy which is assimilated	+	0	–
E_g	Weight specific cost of growth	–	0	+
μ	Maintenance rate	0	0	+
ρ_1 and α_1	Minimum ratio of predator size over prey size	+	0	0
ρ_2 and α_2	Maximum ratio of predator size over prey size	+	0	0
C	Holling type II half-saturation constant	0	++	+

0 = no effects, + = positive effect and – = negative effect.

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

Increasing the size of the smallest prey that can be eaten by a given predator (decreasing ρ_2 and increasing α_2) decreases substantially the slope of the stationary size-spectrum (Table 2 and Fig. 9i). Increasing the size of the largest prey that can be eaten by a given predator (increasing ρ_1 and decreasing α_1) increases the slope of the stationary size-spectrum (Table 2 and Fig. 9j).

Decreasing the fraction of the ingested energy which is assimilated (e_A) slightly decreases both the slope of the size spectrum and L_∞ (Table 2 and Fig. 9k). On the contrary, an increase of the weight specific cost of growth E_g decreases both the slope of the size spectrum and L_∞ (Table 2 and Fig. 9l).

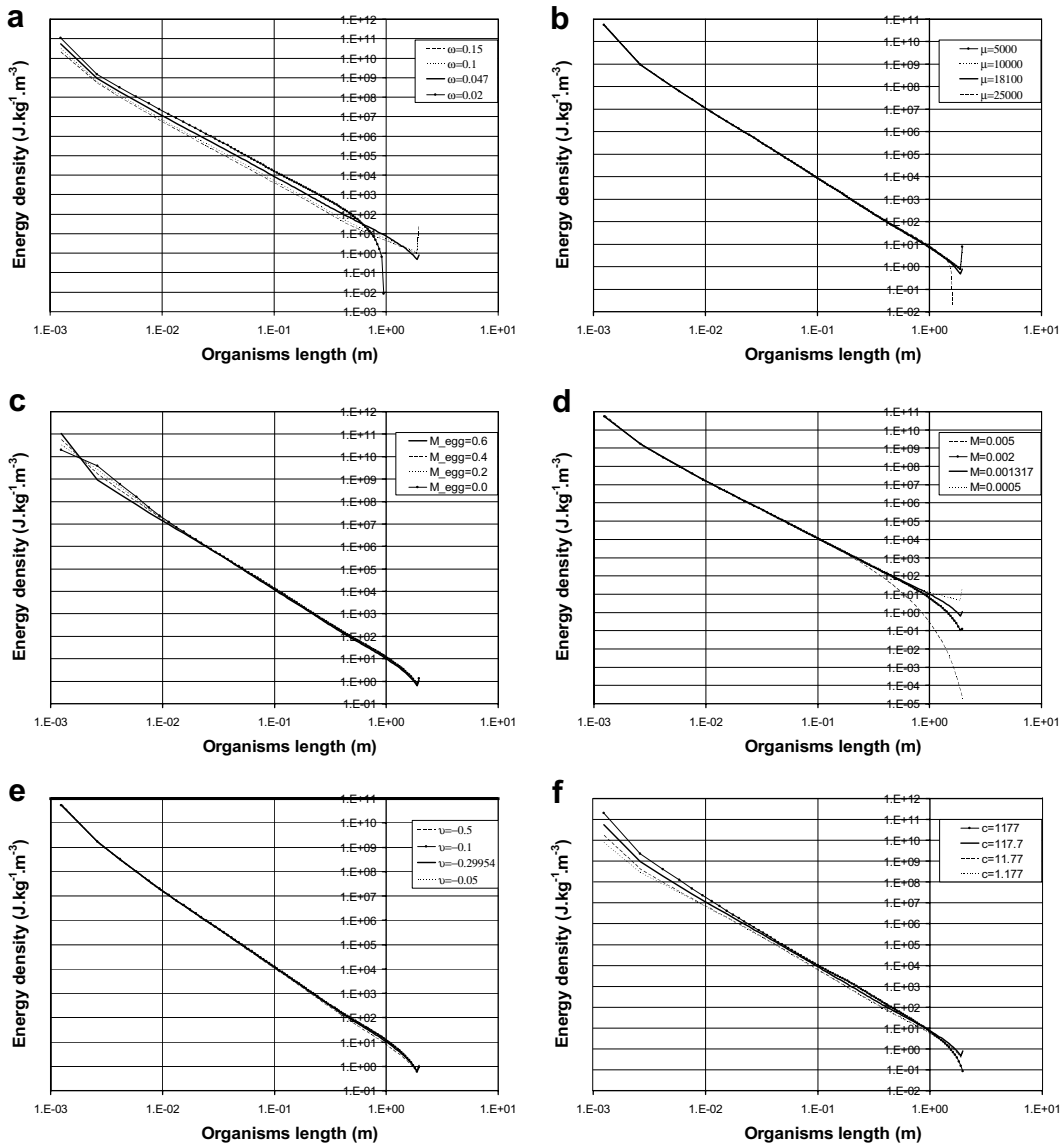


Fig. 9. Systematic sensitivity analysis of the steady state to the parameters. Different values of ω , μ , M_{egg} , M , v , c , κ , ρ_2 , ρ_1 , e_A and E_g varying in a large range around their reference values are considered respectively in (a)–(l). The sensitivity of the steady state to the parameter κ is considered in the case where $M_{egg} = 0.4$ (g) and $M_{egg} = 0$ (h).

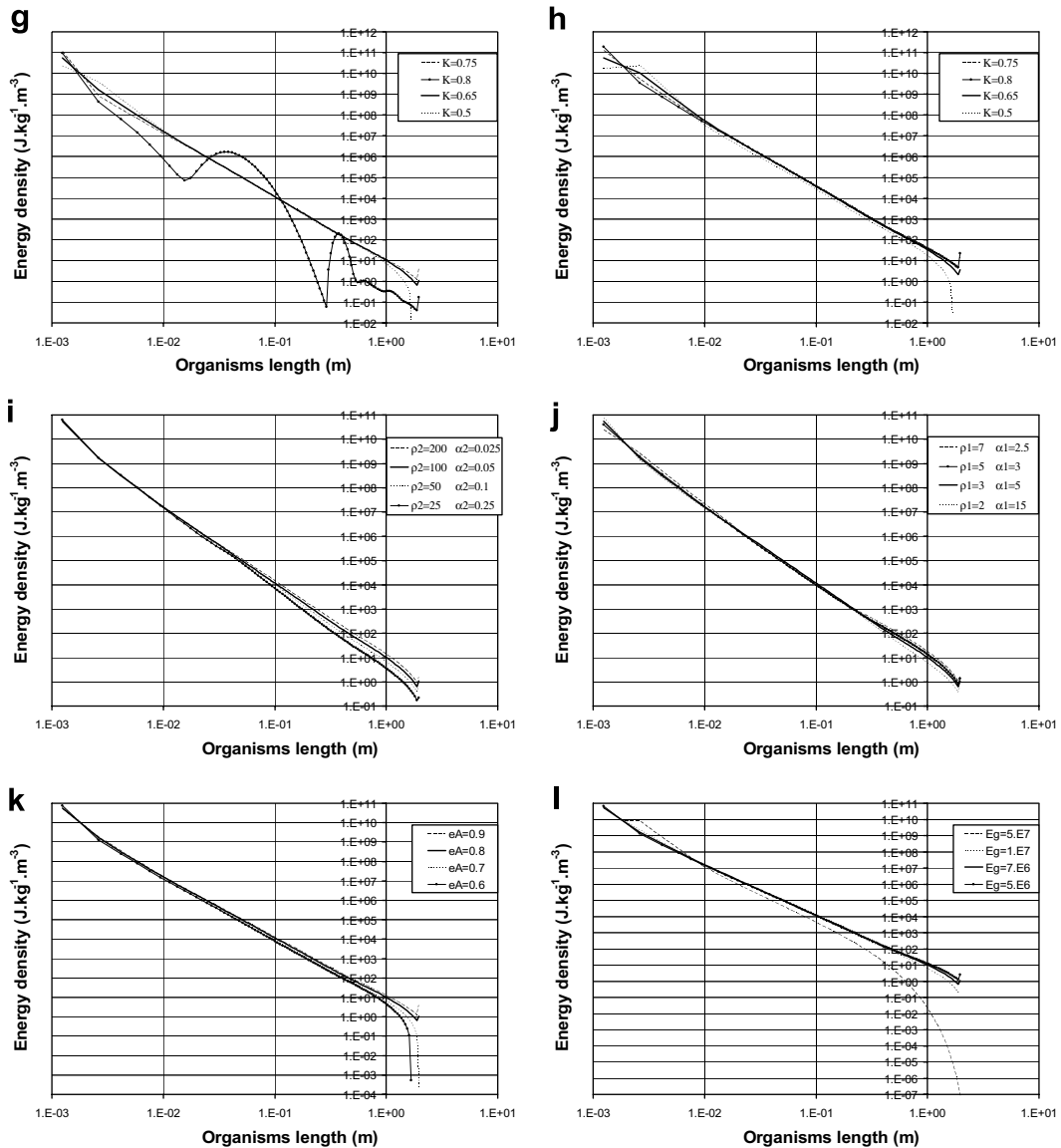


Fig. 9 (continued)

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, 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 ([Fig. 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 et al., 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 Gordo, 1996](#); [Zhou and Huntley, 1997](#); [Quinones et al., 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 L_{∞} , 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 [Fig. 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 (ρ_2), act only on the slope of the spectrum (cf. Fig. 9i and j) when others, such as the maximum surface specific ingestion rate (ω), act only on its intercept (Fig. 9a). Other parameters, such as the nonpredatory mortality coefficient (M), modify the curvature of the spectrum (Fig. 9d) 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 (Fig. 9c). Finally, most parameters modify slightly the L_∞ value and hence influence the linearity of the spectrum for large sizes.

It has furthermore to be noted that, as suspected by Arino et 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 (Fig. 9g).

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., 2007) 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.

Appendix A. Full model equation

Combining Eqs. (1), (2), (7) and (9)–13 gives the full model equation:

$$\forall w \in [0; w_1]$$

$$\frac{d\xi_{t,w}^{\text{P}}}{dt} = \frac{\Pi_t}{w_1} - A(T_t)\xi_{t,w}^{\text{P}} \left(\frac{\omega}{w_1} \int_{x=0}^{w_1} \int_{u=w_{\text{egg}}}^{w_{\text{max}}} \left[\frac{\xi_{t,u}^{\text{C}} u^{-1/3} s_{u,x}}{\frac{c}{u^\lambda} + \int_{v=0}^{w_{\text{max}}} s_{u,v} \xi_{t,v} dv} \right] du dx + M_t \right) \quad (15)$$

$$w = w_{\text{egg}}$$

$$\gamma_{t,w_{\text{egg}}} \xi_{t,w_{\text{egg}}}^{\text{C}} = (1 - M_{\text{egg}})\phi A(T_t) \int_{u=w_{\text{egg}}}^{w_{\text{max}}} \left[\frac{(1 - \kappa)e_A \omega \xi_{t,u}^{\text{C}} u^{-1/3} \int_{v=0}^{w_{\text{max}}} s_{u,v} \xi_{t,v} dv}{\frac{c}{u^\lambda A(T_t)} + \int_{v=w_{\text{min}}}^{w_{\text{max}}} s_{u,v} \xi_{t,v} dv} - \frac{(1 - \kappa)}{\kappa} \frac{\mu \xi_{t,u}^{\text{C}}}{\psi} \right]^+ du \quad (16)$$

$\forall w \in]w_{\text{egg}}; w_{\text{max}}]$

$$\begin{aligned} \frac{\partial \xi_{t,w}^c}{\partial t} = & - \frac{\psi A(T_t)}{\psi + E_g} \frac{\partial}{\partial w} \left(\left[\frac{\kappa e_A \omega}{w^{\lambda A(T_t)}} + \int_{v=0}^{w_{\text{max}}} s_{u,v} \xi_{t,v}^c \, dv \right] w^{2/3} - \frac{\mu}{\psi} w \right) \xi_{t,w}^c \\ & - \omega A(T_t) \int_{u=w_{\text{egg}}}^{w_{\text{max}}} \left(\frac{\xi_{t,u}^c u^{-1/3} s_{u,w}}{\frac{c}{w^{\lambda A(T_t)}} + \int_{v=0}^{w_{\text{max}}} s_{u,v} \xi_{t,v}^c \, dv} \right) du \xi_{t,w}^c \\ & - A(T_t) \left(M \left(\frac{w_1}{a} \right)^{v/3} + \left[\frac{\mu}{\psi} - \frac{\kappa e_A \omega w^{-1/3} \int_{v=0}^{w_{\text{max}}} s_{w,v} \xi_{t,v}^c \, dv}{\frac{c}{w^{\lambda A(T_t)}} + \int_{v=0}^{w_{\text{max}}} s_{w,v} \xi_{t,v}^c \, dv} \right] \right)^+ \\ & + \left[\frac{(1-\kappa)\mu}{\kappa\psi} - \frac{(1-\kappa)e_A \omega w^{-1/3} \int_{v=0}^{w_{\text{max}}} s_{w,v} \xi_{t,v}^c \, dv}{\frac{c}{w^{\lambda A(T_t)}} + \int_{v=0}^{w_{\text{max}}} s_{w,v} \xi_{t,v}^c \, dv} \right]^+ \xi_{t,w}^c \end{aligned} \tag{17}$$

where $[x]^+$ is the function defined by

$$\begin{cases} [x]^+ = x & \text{if } x \geq 0 \\ [x]^+ = 0 & \text{if } x < 0 \end{cases}, \quad s_{u,w} = \left(1 + e^{\alpha_1 \left(\rho_1 - \left(\frac{u}{w} \right)^{1/3} \right)} \right)^{-1} \left(1 - \left(1 + e^{\alpha_2 \left(\rho_2 - \left(\frac{u}{w} \right)^{1/3} \right)} \right)^{-1} \right)$$

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

Appendix B. Calculation of ω and μ as a function of the Von Bertalanffy growth parameters K and L_∞

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

$$\frac{dw}{dt} = Aw^{2/3} - Bw \quad \text{with} \quad \begin{cases} A = \frac{\psi}{\psi + E_g} \kappa e_A \omega \\ B = \frac{\mu}{\psi + E_g} \end{cases} \tag{18}$$

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:

$$\frac{d(al^3)}{dt} = 3al^2 \frac{dl}{dt} = A(al^3)^{2/3} - Bal^3 \iff \frac{dl}{dt} = \frac{Aa^{-1/3}}{3} - \frac{B}{3}l \tag{19}$$

which after integration gives:

$$l_t = \frac{Aa^{-1/3}}{B} \left(1 - e^{-\frac{B}{3}(t-t_0)} \right) \tag{20}$$

This expression is used to express ω and μ as a function of the Von Bertalanffy growth parameters K and L_∞ :

$$\begin{cases} L_\infty = \frac{Aa^{-1/3}}{B} = \frac{\kappa e_A \omega \psi a^{-1/3}}{\mu} \\ K = \frac{B}{3} = \frac{\mu}{3(\psi + E_g)} \end{cases} \iff \begin{cases} \omega = \frac{3KL_\infty(\psi + E_g)}{\kappa e_A \psi a^{-1/3}} \\ \mu = 3K(\psi + E_g) \end{cases} \tag{21}$$

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

Appendix C. Estimation of the mortality parameters M and v

To estimate the parameters M and v which determine the length-dependent nonpredatory mortality, five groups of organisms having very different mean length are considered (diatoms, copepods, and three fish of 0.1 m, 0.8 m and 1.7 m). For each group an arbitrary life span is attributed and the corresponding mortality

Table 3
Estimation of the nonpredatory mortality parameters M and ν (see text)

Species	Mean size	Estimated life span	Estimated mortality	Modeled mortality M'
Diatoms	5×10^{-5} m	90 days	2.56×10^{-2} day ⁻¹	2.56×10^{-2} day ⁻¹
Copepods	5×10^{-4} m	180 days	1.28×10^{-2} day ⁻¹	1.28×10^{-2} day ⁻¹
Fish 0.1 m	0.1 m	730 days	3.15×10^{-3} day ⁻¹	2.63×10^{-3} day ⁻¹
Fish 0.8 m	0.8 m	1825 days	1.26×10^{-3} day ⁻¹	1.41×10^{-3} day ⁻¹
Fish 1.7 m	1.7 m	2555 days	9.01×10^{-4} day ⁻¹	1.12×10^{-3} day ⁻¹

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 ν are estimated by fitting the modeled mortality curve to the estimated mortality curve (Table 3).

References

- Andersen, N.G., Riis-Vestergaard, J., 2003. The effects of food consumption rate, body size and temperature on net food conversion efficiency in saithe and whiting. *Journal of Fish Biology* 62, 395–412.
- Arino, O., Shin, Y.-J., Mullon, C., 2004. A mathematical derivation of size spectra in fish populations. *Comptes Rendus de l'Académie des Sciences. Section Biologies* 327, 245–254.
- Benoit, E., Rochet, M.J., 2004. A continuous model of biomass size spectra governed by predation and the effects of fishing on them. *Journal of Theoretical Biology* 226, 9–21.
- Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R., Sams, S., 1978. Relationships between body size and some life history parameters. *Oecologia* 37, 257–272.
- Bone, Q., Marshall, N.B., Blaxter, J.H.S., 1999. *Biology of Fishes*. Stanley Thornes, p. 332.
- Brett, J.R., Groves, T.D.D., 1979. Physiological energetics. In: Hoar, W.S., Randall, D.J., Brett, J.R. (Eds.), *Fish Physiology*. Academic press.
- Brill, R.W., Guernsey, D.L., Stevens, E.D., 1978. Body surface and gill heat loss rates in restrained Skipjack Tuna. In: Sharp, G.D., Dizon, A.E. (Eds.), *The Physiological Ecology of Tunas*. Academic Press, p. 277.
- Brown, J.H., Gillooly, J.F., 2003. Ecological food webs: high-quality data facilitate theoretical unification. *Proceedings of the National Academy of Sciences (USA)* 100, 1467–1468.
- Clarke, A., 2004. Is there a universal temperature dependence of metabolism? *Functional Ecology* 18, 252–256.
- Clarke, A., Fraser, K.P.P., 2004. Why does metabolism scale with temperature? *Functional Ecology* 18, 243–251.
- Clarke, A., Johnston, N.M., 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology* 68, 893–905.
- Cousins, S.H., 1980. A trophic continuum derived from plant structure, animal size and a detritus cascade. *Journal of Theoretical Biology* 82, 607–618.
- Cury, P., Pauly, D., 2000. Patterns and propensities in reproduction and growth of marine fishes. *Ecological Research* 15, 101–106.
- Cury, P., Shannon, L., Shin, Y.-J., 2003. The functioning of marine ecosystems a fisheries perspective. In: Sinclair, M., Valdimarsson, G. (Eds.), *Responsible Fisheries in the marine Ecosystem*. FAO, Cabi, 462 pp.
- Cushing, J.M., 1992. A size-structured model for cannibalism. *Theoretical Population Biology* 42, 347–361.
- Daan, N., 1975. Consumption and production in north sea cod: an assessment of the ecological status of the stock. *Netherlands Journal of sea research* 9, 24–55.
- Dickie, L.M., Kerr, S.R., Boudreau, P.R., 1987. Size-dependent processes underlying regularities in ecosystem structure. *Ecological Monograph* 57 (3), 233–250.
- Duplisea, D.E., Kerr, S.R., 1995. Application of a biomass size spectrum model to demersal fish data from the Scotian Shelf. *Journal of Theoretical Biology* 177, 263–269.
- Edwards, R.R.C., Finlayson, D.M., Steele, J.H., 1972. An experimental study of the oxygen consumption, growth and metabolism of the cod. *Journal of Experimental Marine Biology and Ecology* 8, 299–309.
- Enquist, B.J., Economo, E.P., Huxman, T.E., Allen, A.P., Ignace, D.D., Gillooly, J.F., 2003. Scaling metabolism from organisms to ecosystems. *Nature* 423, 639–642.
- Essington, T.E., Kitchell, J.F., Walters, J.C., 2001. The von bertalanffy growth function, bioenergetics, and the consumption rates of fish. *Canadian Journal of Fishery and Aquatic Science* 58, 2129–2138.
- Floeter, J., Temming, A., 2003. Explaining diet composition of North Sea cod (*Gadus morhua*): prey size preference vs. prey availability. *Canadian Journal of Fishery and Aquatic Science* 60, 140–150.
- Froese, R., Pauly, D., (Eds.), 2000. *FishBase 2000: concepts, design and data sources*. ICLARM, Los Baños, Laguna, Philippines, 344 pp.
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of size and temperature on metabolic rate. *Science* 293, 2248–2251.

- Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M., Brown, J.H., 2002. Effects of size and temperature on developmental time. *Nature* 417, 70–73.
- Jennings, S., Pinnegar, J.K., Polunin, N.V.C., Boon, T., 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology* 70, 934–944.
- Jennings, S., Pinnegar, J.K., Polunin, N.V.C., Warr, K.J., 2002. Linking size-based and trophic analyses of benthic community structure. *Marine Ecology Progress Series* 226, 77–85.
- Juanes, F., 2003. The allometry of cannibalism in piscivorous fishes. *Canadian Journal of Fishery and Aquatic Science* 60, 594–602.
- Kitchell, J.F., Neill, W.H., Dizon, A.E., Magnuson, J.J., 1978. Bioenergetic spectra of skipjack and yellowfin tunas. In: Sharp, G.D., Dizon, A.E. (Eds.), *The Physiological Ecology of Tunas*. Academic Press, p. 357.
- Kooijman, S.A.L.M., 1986. Energy budgets can explain body size relations. *Journal of Theoretical Biology* 121, 269–282.
- Kooijman, S.A.L.M., 1995. The stoichiometry of animal energetics. *Journal of Theoretical Biology* 177, 139–149.
- Kooijman, S.A.L.M., 2000. *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press.
- Kooijman, S.A.L.M., 2001. Quantitative aspects of metabolic organization: a discussion of concepts. *Philosophical Transactions of the Royal Society of London B356*, 331–349.
- Kot, M., 2001. *Elements of Mathematical Ecology*. Cambridge University Press, Cambridge, p.453.
- Krohn, M., Reidy, S., Kerr, S., 1996. Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod. *Canadian Journal of Fishery and Aquatic Science* 54, 113–121.
- Lundvall, D., Svanbäck, R., Persson, L., Byström, P., 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Canadian Journal of Fishery and Aquatic Science* 56, 1285–1292.
- Macpherson, E., Gordo, A., 1996. Biomass spectra in benthic fish assemblages in the Benguela system. *Marine Ecology Progress Series* 138, 27–32.
- McCann, K.S., Hastings, A., Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. *Nature* 395, 794–798.
- McCann, K.S., 2000. The diversity–stability debate. *Nature* 405, 228–233.
- Marquet, P.A., Quiñones, R.A., Abades, S., Labra, F., Tognelli, M., Arim, M., Rivadeneira, M., 2005. Scaling and power-laws in ecological systems. *The Journal of Experimental Biology* 208, 1749–1769.
- Maury, O., Shin, Y.-J., Faugetas, B., Ben Ari, T., Marsac, F., 2007. Modeling environmental effects on the size-structured energy flow through marine ecosystems. Part 2: simulations. *Progress in Oceanography* 74 (4), 500–514.
- Ménard, F., Labrune, C., Shin, Y.-J., Asine, A.-S., Bard, F.-X., 2006. Opportunistic predation in tuna: a size-based approach. *Marine Ecology Progress Series* 323, 223–231.
- Nisbet, R.M., Muller, E.B., Lika, K., Kooijman, S.A.L.M., 2000. From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology* 69, 913–926.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262–270.
- Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science* 57, 697–706.
- Platt, T., Denman, K., 1978. The structure of pelagic marine ecosystems. *Rapp. Procès-Verbaux des Réunions du Conseil International d'Exploration de la Mer* 173, 60–65.
- Platt, T., Denman, K., 1997. Organisation in the pelagic ecosystem. *Helgol. Wiss. Meeresunters* 30, 575–581.
- Polovina, J.J., 1984. Model of a coral reef ecosystem. I: the ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* 3, 1–11.
- Pörtner, H.O., 2002. Physiological basis of temperature-dependent biogeography: trade-offs in muscle design and performance in polar ectotherms. *The Journal of Experimental Biology* 205, 2217–2230.
- Quiñones, R.A., Platt, T., Rodríguez, J., 2003. Patterns of biomass size-spectra from oligotrophic waters of the Northwest Atlantic. *Progress in Oceanography* 57, 405–427.
- Scharf, F.S., Juanes, F., Rountree, R.A., 2000. Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series* 208, 229–248.
- Sheldon, R.W., Prakash, A., Sutcliffe, W.H.J., 1972. The size distribution of particles in the ocean. *Limnological Oceanography* 17 (3), 327–340.
- Shin, Y.-J., Cury, P., 2004. Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Canadian Journal of Fishery and Aquatic Science* 61, 414–431.
- Silvert, W., Platt, T., 1978. Energy flux in the pelagic ecosystem: a time-dependent equation. *Limnological Oceanography* 23, 813–816.
- Silvert, W., Platt, T., 1980. Dynamic energy flow model of the particle size distribution in pelagic ecosystems. In: Kerfoot, W. (Ed.), *Evolution and Ecology of Zooplankton Communities*. University Press of New England, Illanover, NH, pp. 754–763.
- Speakman, J.R., 2005. Body size, energy metabolism and lifespan. *The Journal of Experimental Biology* 208, 1717–1730.
- Sterner, R.W., Elser, J.J., 2002. *Ecological Stoichiometry*. Princeton University Press, Princeton, p. 439.
- Tuljapurkar, S., Caswell, H. (Eds.), 1997. *Structured-population models in marine, terrestrial, and freshwater systems*. Chapman & Hall, p. 643.
- Valiela, I., 1995. *Marine Ecological Processes*. Springer-Verlag, New York, p. 686.
- van der Veer, H.W., Kooijman, S.A.L.M., van der Meer, J., 2003. Body size scaling relationships in flatfish as predicted by Dynamic Energy Budgets (DEB theory): implications for recruitment. *Journal of Sea Research* 50, 255–270.
- von Bertalanffy, L., 1969. Basic concepts in quantitative biology of metabolism. *Helgolander Wissenschaft Meeresunters* 9, 5–34.
- Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic massbalance assessments. *Review in Fish Biology and Fisheries* 7 (2), 139–172.

- West, G.B., Brown, J.H., 2005. The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure. *The Journal of Experimental Biology* 208, 1575–1592.
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., Warren, P.H., 2005. Body size in ecological networks. *Trends in Ecology and Evolution* 20 (7), 402–409.
- Zhou, M., Huntley, M.E., 1997. Population dynamics theory of plankton based on biomass spectra. *Marine Ecology Progress Serie* 159, 61–73.