Prépublications du Département de Mathématiques

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A continuous model of biomass size spectra governed by predation and the effects of fishing on them

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Mars 2003

Classification :
Mots clés :

2003/02

A continuous model of biomass size spectra governed by predation and the effects of fishing on them

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Résumé

A new time-dependent continuous model of biomass size spectra is developed. In this model, predation is the single process governing the energy flow in the ecosystem, as it causes both growth and mortality. The ratio of predator to prey is assumed to be distributed : predators may feed on a range of prey sizes. Under these assumptions, it is shown that linear size spectra are stationary solutions of the model. Exploited fish communities are simulated by adding fishing mortality to the model : it is found that resalistic fishing pressures should not affect the slope of the size spectrum.

1 Introduction

Biomass size spectra, the distribution of biomass over body size classes in a community, have been the subject of continuous interest since the first developments by Sheldon and colleagues [Sheldon et al., 1972, Sheldon et al., 1977]. This is both because it appears as a very conservative feature of marine communities, and because of the strong appeal of summarising complex communities, comprising numerous species with complex trophic interactions, within a simple plot and one or two numbers such as the slope and intercept of the spectrum.

Biomass size spectra have been widely used both in marine and freshwater ecosystems for estimating production at different trophic levels, especially fish production [Sheldon et al., 1977, Borgman, 1982, Leach et al., 1987, Sprules et al., 1991, Boudreau and Dickie, 1992, Cyr and Peters, 1996], predicting the effects of various human perturbations [Borgman and Whittle, 1983,

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Cottingham, 1999], and for more basic purposes such as analysing ecosystem structure [Schwinghamer, 1981, Sprules and Munawar, 1986] and dynamics [Denman et al., 1989], or estimating mortality rates [Peterson and Wroblewski, 1984]. Moreover, as the concern grows that fisheries management should consider ecosystems rather than isolated populations, there is increasing interest in using biomass size spectra as assessment tools for multispecies fisheries [Caddy and Mahon, 1996]. Pioneering works suggested that size spectra are regular and conservative within a fishery, but vary between systems [Pope and Knights, 1982, Murawski and Idoine, 1992]. These variations may be ascribed to fishing. Several authors have hypothesised that exploitation should decrease the slope of a fish community biomass size spectrum, and reported decreasing trends of this slope in exploited systems [Pope et al., 1988, Anonymous, 1995, Greenstreet and Hall, 1996, Anonymous, 1996, Rice and Gislason, 1996], although this pattern is not consistent across all systems ([Bianchi et al., 2000]).

These uses are mainly based on empirical observations. However, an underlying theory is needed to be fully able to predict and assess the effect of fishing on the size spectrum, and also to determine reference points (how steep should the size spectrum be or not be ?). This theory should explain why size spectra are regular.

Existing theories of the biomass size spectra rely on the flow of biomass from the smallest- to the largest-sized organisms through size-dependent processes. Some of them consider discrete trophic levels and the considered processes include growth, production, respiration, predation and even reproduction [Kerr, 1974, Borgman, 1982, Borgman, 1983, Thiebaux and Dickie, 1992, Thiebaux and Dickie, 1993]. However, applying them to real situations is complicated by the problem of defining trophic levels [Borgman, 1982]. A continuous biomass flow model avoiding this difficulty has been developed [Platt and Denman, 1978, Silvert and Platt, 1978]. In this model, the size-dependent processes governing the energy flow in the ecosystem are loss (mainly by respiration), and a "generalised growth function", which implicitly includes growth and predation. However, to predict the effect of additional mortality on a large community encompassing several size scales, it is desirable to explicitly describe predation processes. Silvert and Platt [Silvert and Platt, 1980] developed a continuous, time-dependent, non-linear model of the size spectrum where the energy flow is governed only by predation, and the associated growth and mortality. They predicted that biomass size spectra can be linear, assuming a fixed prey-predator size ratio.

In this paper, this assumption is relaxed and a continuous model of the size spectrum is developed, where the energy flow is governed by predation, with a distributed prey-predator size ratio. This means that predators may feed not only on preys of a given unique size, but on a range of prey sizes. In this model, reproduction is assumed constant and independent of the biomass present in the system. We first develop the model and establish some of its mathematical properties : it is predicted that size-spectra can still be linear. We then perform some numerical simulations to predict the effect of fishing on a fish community. The model is developed for fish in the broad meaning of "animals swimming and foraging in the open water".

2 The model

2.1 Notations

Symbol	Definition	Unit
w	weight of a fish	g
x	logarithm of w	$\ln(g)$
t	time	year$=y$
$u(x,t)$	number of fishes at time t by unit volume, by unit of x	m^{-3}
$\int_{x_1}^{x_2} u(x,t)dx$	number of fishes with weight in $[e^{x_1}, e^{x_2}]$, at time t, by unit volume	m^{-3}
$g(x,t)$	growth rate	y^{-1}
$\mu(x,t)$	mortality rate	y^{-1}
$\varphi(q)$	probability of predation when a predator size x meets a prey size $x-q$	

TAB. 1 – Definition of the mathematical variables

The fundamental independent variables are time t and x, where x is the (natural) logarithm of the weight w of a fish. The derivative with respect to x is related to the derivative with respect to w by

$$\frac{\partial}{\partial x} = w\frac{\partial}{\partial w}$$

The fundamental unknown is $u(x,t)$, the distribution of the number of fish with respect to x. Then, the number of fish on the weight range $[w_1, w_2]$ is given by the formula

$$\int_{\ln w_1}^{\ln w_2} u(x,t)dx$$

The mathematical change of variable $x = \ln w$ shows that this expression is equivalent to

$$\int_{w_1}^{w_2} \frac{1}{w} u(\ln(w), t)dw \tag{1}$$

The mass of a fish is $w = e^x$, so the biomass of all the fish the weight range in $[w_1, w_2]$ is given by

$$\int_{x_1}^{x_2} e^x u(x,t)dx \quad \text{or, equivalently} \quad \int_{w_1}^{w_2} u(\ln(w), t)dw \tag{2}$$

The function u can be considered either as the distribution in x of the number of fish or as the distribution in w of the biomass.

Consider a fish of weight $W(t)$, and $X(t) = \ln(W(t))$. The growth function g is given by

$$\frac{dX}{dt} = g(X(t), t) \tag{3}$$

or, using weight,

$$\frac{dW}{dt} = W(t)\ g(\ln(W(t)), t)$$

The function $\mu(x,t)$ is the mortality rate of fish at weight e^x.

2.2 Balance

At time t, the number of fish in the weight range $[e^{x_1}, e^{x_2}]$ is given by

$$\int_{x_1}^{x_2} u(x,t)dx$$

Some fish die and at time $t + dt$, the remaining number of fish is

$$\int_{x_1}^{x_2} (1 - \mu(x,t)dt)u(x,t)dx$$

Because, in the same time, they grow, these remaining fish are exactly the fish in the weight range $[e^{x_1+g(x_1,t)dt}, e^{x_2+g(x_2,t)dt}]$ at time $t + dt$. This number is

$$\int_{x_1+g(x_1,t)dt}^{x_2+g(x_2,t)dt} u(x, t+dt)dx$$

We equate these numbers and compute the derivative with respect to dt at the value $dt = 0$:

$$-\int_{x_1}^{x_2} \mu(x,t)u(x,t)dx = \int_{x_1}^{x_2} \frac{\partial u}{\partial t}(x,t)dx + g(x_2,t)u(x_2,t) - g(x_1,t)u(x_1,t)$$

Derive with respect to x_2 :

$$\frac{\partial u}{\partial t} = -\frac{\partial\,(gu)}{\partial x} - \mu u \tag{4}$$

2.3 Predation

In this model, predation is the unique driving force of growth and mortality. Each predation event implies two individuals. The larger one will grow, the smaller one will die. The ratio of the weights of the two individuals is supposed to be distributed independently of the weights of the individuals : when two individuals of weights e^x and e^y meet, the probability that a predation happens is given by a function φ which depends only on the ratio of the weights e^{y-x}. We will denote $y-x$ by q. The function φ (figure 2.3) will be dome-shaped, positive, defined only for q positive, having a unique maximum. For example, for numerical simulations,

$$\varphi(q) = e^n \left(\frac{q}{q_0}\right)^n e^{-n\frac{q}{q_0}} \tag{5}$$

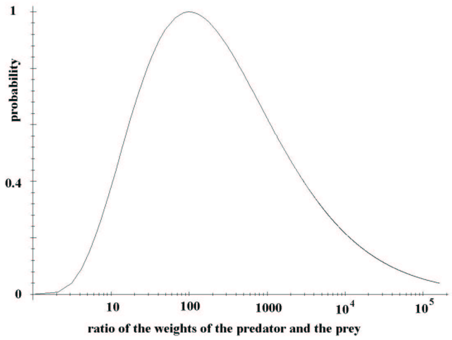

FIG. 1 – Graph of φ, the probability that a predator of weight e^y meeting a prey of weight e^{y-q} will eat it.

This function φ peaks at 1 for q_0. The parameter n determines the thickness of the peak of φ.

Let us consider a predator of weight e^y in a period of time dt. The volume searched is supposed to be an allometric function of weight ([Ware, 1978]) : it is given by $Ae^{\alpha y}dt$. Then the number of encounters with possible preys of weight in $[e^x, e^{x+dx}]$ is $Ae^{\alpha y}u(x,t)dtdx$. The number of preys eaten in the weight range $[e^x, e^{x+dx}]$ is $Ae^{\alpha y}\varphi(y-x)u(x,t)dtdx$. The distribution of predation events is given by

$$Ae^{\alpha y}\varphi(y-x)\, u(x,t)\, u(y,t)\, dx\, dy\, dt \tag{6}$$

2.4 Mortality

From the point of view of the prey, expression (6) gives the mortality rate by predation :

$$\mu(x,t) = \int_x^\infty Ae^{\alpha y} \varphi(y-x)\, u(y,t)\, dy$$

which is equivalent to

$$\mu(x,t) = Ae^{\alpha x} \int_0^\infty e^{\alpha q} \varphi(q)\, u(x+q,t)\, dq \tag{7}$$

In simulations, we will add the fishing mortality rate :

$$\mu_f(x,t) = \max(0, a(x-b))$$

where a and b are parameters. It is a linear increasing function of log weight with recruitment to fishing at weight $\exp(b)$.

2.5 Growth

From distribution (6), the mass of preys eaten by one predator is :

$$Ae^{\alpha y} dt \int_{-\infty}^y e^x \varphi(y-x)\, u(x,t)\, dx \tag{8}$$

(e^x is the weight of one prey).

The increase in weight of the predator is given by $e^y g(y,t)dt$ (confer section 2.1). If the biomass eaten is used to grow with a constant efficiency K, then

$$e^y g(y,t)dt = K \int_{-\infty}^y e^x Ae^{\alpha y} \varphi(y-x)\, u(x,t)\, dx$$

which is equivalent to

$$g(y,t) = KAe^{\alpha y} \int_0^\infty e^{-q} \varphi(q)\, u(y-q,t)\, dq \tag{9}$$

2.6 Conclusion

Combining equations (4), (7) and (9), we obtain the following model

$$\begin{aligned} \frac{\partial u}{\partial t}(x,t) \quad = \quad & -\frac{\partial}{\partial x}\left[KAe^{\alpha x} \int_0^\infty e^{-q} \varphi(q)\, u(x-q,t)\, u(x,t)\, dq\right] \\ & -Ae^{\alpha x} \int_0^\infty e^{\alpha q} \varphi(q)\, u(x+q,t)\, u(x,t)\, dq \\ & -\max(0, a(x-b))\; u(x,t) \end{aligned} \tag{10}$$

It is an equation of evolution, $\frac{\partial u}{\partial t} = \mathcal{A}(u)$, where $\mathcal{A}$ is an operator on the functions of one variable x. The difficulty lies in this operator being not local : it includes convolutions.

3 Some mathematical properties of the model without fishing

To allow a mathematical study, we first assume that the solution $u(x,t)$ is defined for all real x, *i.e.,* for all positive weights. Actually, it is not realistic : we need another model for lower levels (plankton or very small fish) in the ecosystem (see section 5.4).

For the sake of generality, φ is kept as a parameter-function with only one assumption : there exists a positive (maybe infinite) real γ such that the integral $\int_0^\infty \varphi(q)e^{\lambda q}dq$ is convergent if and only if λ is smaller than γ (with the explicit φ given, we have $\gamma = n/q_0$; if φ has a compact support, we have $\gamma = +\infty$). For technical reasons, we also assume that $\gamma > \alpha/2$ (with our fixed values of the parameters, this condition is satisfied).

3.1 Relationship between rate and concentration

As the operator $\mathcal{A}$ is homogeneous quadratic with respect to u, the following lemma is obvious :

Lemma 1 *If $u(x,t)$ is a solution of the model, and if c is a constant, then, $cu(x,ct)$ is also a solution of the model.*

The biological meaning of this lemma is : if the concentration of fish, biomass and nutrients is multiplied by a constant factor c, the biomass dynamics will be similar, at a rate multiplied by c. Another consequence of this lemma is that if we change the parameter A to cA, the solution $u(x,t)$ becomes $u(x,t/A)$, or $Au(x,t)$. Then, the parameters A and u_0 do not influence the qualitative behaviour of the model, they determine only the speed of the evolution.

3.2 Stationary linear spectrum

Lemma 2 *There exists a unique real λ such that for any u_0, the function $u(x,t) = u_0e^{\lambda x}$ is a solution of equation (10). This λ is the unique real solution of*

$$(2\lambda+\alpha)K\int_0^\infty e^{-(\lambda+1)q}\varphi(q)\,dq \;+\; \int_0^\infty e^{(\alpha+\lambda)q}\varphi(q)\,dq \;=\; 0 \qquad (11)$$

Moreover, λ *belongs to* $]-\gamma-1,-\alpha/2[$.

Proof The proof that a function $e^{\lambda x}$ is a solution of the model if and only if condition (11) is satisfied is easy.

To prove the existence and unicity of λ, we study the function

$$F(\lambda) = (2\lambda+\alpha)K\int_0^\infty e^{-(\lambda+1)q}\varphi(q)\,dq \;+\; \int_0^\infty e^{(\alpha+\lambda)q}\varphi(q)\,dq\ ,$$

and prove that

- the domain of F is $]-\gamma-1,\gamma-\alpha[$, and it contains $-\alpha/2$,
- for $\lambda \geq -\alpha/2$, the function F is nonnegative,
- for λ near $-\gamma-1$, the function F is negative,
- when $F(\lambda)=0$, and $2\lambda+\alpha<0$, the derivative $F'(\lambda)$ is strictly positive.

From this follows the existence and unicity of a real solution of $F(\lambda)=0$. ∎

Although this is not the only solution (even stationary solution : see below), this shows that a lineary decreasing size spectrum can appear, even if the predators are allowed to prey on a weight range rather than a single weight.

3.3 Other special solutions

3.3.1 Weak slope

Be C the constant

$$C = A\int_0^{+\infty}\left(1-\alpha K e^{-(1-\alpha)q}\right)\varphi(q)dq$$

(assuming that $\alpha<\gamma+1$, the integral is convergent). It is easy to show that

$$u(x,t) \;=\; \frac{u_0 e^{-\alpha x}}{1+Cu_0 t}$$

is a solution of equation (10) with $u(0,0)=u_0$.

If C is positive (which is consistent with parameters values plausible in real ecosystems), the solution is decreasing towards zero. It is a linear spectrum with a weaker slope than the stationary solution. This means that if for any reason the slope of the spectrum becomes less steep (*i.e.,* more large fish and less small fish), there is a risk of all biomass being washed out of the system by predators eating preys faster than they are created by growth. Only the input from the boundary condition (recruitment) could save the ecosystem.

If C is negative, the slope will be greater than the slope of the stationary solution, and the population will increase indefinitely and tend towards infinity.

This solution is mathematically correct, but the input of biomass in the small weights must also increase until infinity.

3.3.2 Gaps in the spectrum

Let us assume (for this section) that the function φ has a compact support, *i.e.*, $\varphi(q)$ is zero except for q in some range $[q_m, q_M]$. In this case, if u is a function which is zero except on some intervals of length less than q_m and with gaps of length at least q_M, then u is a stationary solution. It corresponds to size spectra where no predation can occur, because the weights of the fish do not match predators requirements. This solution illustrates a shortcoming of the model : there is no mortality except by predation, so, if a fish has no food and no predator, it stays at the same weight and never dies.

3.4 Total biomass

The total biomass in one cubic meter is :

$$B(t) = \int_{-\infty}^{+\infty} e^x u(x,t)dx$$

The integral is convergent only if the spectrum u is small enough for large x, which is not true for a spectrum linear on whole $\mathbb{R}$ (the integral $\int_{-\infty}^{+\infty} e^x e^{\lambda x} dx$ is infinite for all λ).

When the density u is given by $u_0 e^{-x}$ for x belonging to some range $[x_{\min}, x_{\max}]$ (it is almost the case for the stationary solution computed above), the biomass of fish of weight w in $[w_0, 2w_0]$ is $u_0 \ln 2$, independent of w_0 : the biomass is homogeneous with respect to the weight of fish. When $u = e^{\lambda x}$, with $\lambda < -1$, the concentration is higher in small weights.

To describe total biomass dynamics, we compute the derivative of B with respect to time, using equation (10) :

$$\frac{dB}{dt} = \int_{-\infty}^{+\infty} e^x \frac{\partial u}{\partial t}(x,t)dx =$$

$$= -\int_{-\infty}^{+\infty} \left[e^x \frac{\partial}{\partial x} \left(KAe^{\alpha x} I_1 \right) + Ae^x e^{\alpha x} I_2 \right] dx$$

with

$$I_1 = \int_0^\infty e^{-q} \varphi(q)\, u(x-q,t)\, u(x,t)\, dq$$

$$I_2 = \int_0^\infty e^{\alpha q} \varphi(q)\, u(x+q,t)\, u(x,t)\, dq$$

Integrating by parts, using $u(\pm\infty, t) = 0$, we obtain

$$\frac{dB}{dt} = \int_{-\infty}^{+\infty} [e^x K A e^{\alpha x} I_1 - A e^x e^{\alpha x} I_2] \, dx$$

Changing x to $y - q$ in the integral $\int e^x e^{\alpha x} I_2 dx$ gives

$$\iint e^{(\alpha+1)x} e^{\alpha q} \varphi(q) \, u(x+q,t) \, u(x,t) \, dq \, dx = \iint e^{(\alpha+1)(y-q)} e^{\alpha q} \varphi(q) \, u(y,t) \, u(y-q,t) dq \, dy$$

Then we conclude that

$$\frac{dB}{dt} = -A(1-K) \int_{y=-\infty}^{\infty} \int_{q=0}^{\infty} e^{(1+\alpha)y} e^{-q} \varphi(q) u(y-q,t) u(y,t) dq dy$$

From this result, it follows that, if $K = 1$, total biomass is invariant. This is a corollary of the model : if $K = 1$, the biomass is conservative, including for each individual predation event. In fact, there are losses when converting food into body mass, hence $K < 1$ and the biomass decreases towards zero. To avoid that, an external input of biomass in the small weights is needed : it is given by small fish food (e.g. plankton). This is related to the boundary condition for small x.

3.5 Individual life history

Here we give some consequences of the model for an individual fish : its growth curve, life expectancy (average time the fish will live, given it is alive at time t), and food ration.

We already defined the growth function $X(t)$ of an individual fish (equation (3)). Combining with g (equation (9)), this gives a differential equation for $X(t)$ which can be solved with the initial condition $X(0) = x_0$. It gives the weight $W(t) = e^{X(t)}$ as a function of time.

The food ration or instant amount of prey ingested is given by equation (8).

Equation (7) gives the function $m(t) = \mu(X(t), t)$ which is the mortality rate at time t for the individual fish. The probability of living until time t for a fish is given by $\exp \int_0^t -m(\tau) d\tau$.

The distribution of the random variable "age of death" is given by $p(t) = m(t) \exp\left(\int_0^t -m(\tau) d\tau\right)$.

Then classical formulae give the life expectancy : $E(x_0) = \int_0^\infty t p(t) dt$. An integration by parts makes the computation easier :

$$E(x_0) = \int_0^\infty \exp\left(-\int_0^t m(\tau) d\tau\right) dt$$

Let us apply this to compute the life expectancy in the case of the stationary exponential solution $u(x,t) = u_0 e^{\lambda x}$. We follow the procedure above : equation (9) gives :

$$g(x,t) \;=\; KAC_1 e^{(\alpha+\lambda)x}$$
$$\text{where} \qquad C_1 = u_0 \int_0^\infty e^{-(\lambda+1)q}\varphi(q)dq$$

Equation (3) is now :

$$\frac{dX}{dt} \;=\; KAC_1 e^{(\alpha+\lambda)X(t)}$$

and we can compute the solution with initial condition x_0 :

$$X(t) = -\frac{\ln(-C_1 KA\,(\alpha+\lambda)\,t + e^{-x_0\,(\alpha+\lambda)})}{\alpha+\lambda}$$
$$W(t) = (-C_1 KA\,(\alpha+\lambda)\,t + W_0^{-(\alpha+\lambda)})^{-1/(\alpha+\lambda)} \tag{12}$$

The mortality rate at time t for a fish of weigt $W(t)$ is given by equation (7)

$$m(t) \;=\; \frac{C_3}{C_4 t + C_0}$$
$$\text{where} \qquad C_3 = AC_2 \qquad C_4 = KAC_1(-\alpha-\lambda) \qquad C_0 = W_0^{-(\alpha+\lambda)}$$
$$\text{and} \qquad C_2 = u_0 \int_0^\infty e^{(\alpha+\lambda)q}\varphi(q)dq$$

Then, the life expectancy for a fish of weight W_0 is :

$$E(W_0) \;=\; \frac{C_0}{C_3 - C_4}$$

This is valid only if $C_3 > C_4$. It is easy to check this when λ is a solution of equation (11).

4 Parameters

The values of the parameters were set as follows (table 2), based on published literature. The parameters of the model are broad features of a food web and cannot be measured for a given community; rather, the values in table 2 are reasonable, given the available data on fish and marine organisms. The parameters a and b of the fishing mortality function were estimated by linear regression of fishing mortality rate F at age versus log weight at age, combining all stocks assessed by the International Council for the Exploration of the Sea in i) the North Sea and ii) the Ba of Biscay. Both sets of estimates were not found to differ significantly.

Parameter	Definition	see §	Unit	Ref. value	Lower limit	Upper limit	Sources
α	Exponent of weight in volume of water searched	(2.3)	—	0.82	0.6	0.9	[Ware, 1978]
A	Volume searched by unit weight	(2.3)	$m^3.y^{-1}$	640			[Ware, 1978]
e^{q_0}	Modal ratio of predator size to prey size	(2.3)	—	100	10	1000	[Daan, 1973, Ware, 1978, Silvert and Platt, 1980, Borgman, 1982, Cohen et al., 1993, Thiebaux and Dickie, 1993, Vignes, 1998]
n	An inverse measure of the width of the predator-prey size ratio distribution	(2.3)	—	5	1	10	guessed from the distribution of prey size in predator stomach from [Daan, 1973, Cohen et al., 1993]
K	Growth efficiency	(2.5)	—	0.2	0.1	0.6	[Paloheimo and Dickie, 1966, Ware, 1978, Borgman, 1982, Gurney et al., 1990, Buckel et al., 1995]
u_0	Intercept of the spectrum at time 0	(5.2)	m^{-3}	0.01			
	Slope of the plankton size spectrum	(5.4)	—	λ			
b	log weight at recruitment to the fishery	(2.4)	—	$ln(10)$	0		Estimated from [Anonymous, 1998b, Anonymous, 1998a]
a	Slope of the fishing mortality as a function of log weight	(2.4)	y^{-1}	0.1	0	0.5	Estimated from [Anonymous, 1998b, Anonymous, 1998a]

TAB. 2 – Values of the parameters used in model simulations. Lower and higher limits refer to the range of values used in the sensitivity analysis.

5 Numerical simulations

5.1 Slope of the stationary solution

The slope λ of the stationary size spectrum was computed from equation (11) with function φ given by (5), for different values of the parameters (table 3). The slope of the size spectrum is insensitive to the parameters of the model, especially to the ones determining the shape of function φ, n and q_0.

n	e^{q_0}	α	K	λ
5	100	0.82	0.2	-1.0439
10	100	0.82	0.2	-1.0499
1	100	0.82	0.2	-1.0146
5	1000	0.82	0.2	-1.0067
5	10	0.82	0.2	-1.1409
5	100	0.6	0.2	-0.9446
5	100	0.9	0.2	-1.0799
5	100	0.82	0.1	-1.1020
5	100	0.82	0.6	-0.9521

TAB. 3 – Numerical computation of the stationary slope λ

With any combination of the parameters, this slope is approximately -1, which is consistent with published data :

- slopes of log numbers *versus* log length class ranging from -4 to -10 for weakly to heavily exploited fish communities [Anonymous, 1996, Rice and Gislason, 1996, Bianchi et al., 2000]. Indeed, assuming that body weight is related to body length by $w \propto L^3$, the slope λ of the density of fish with respect to log weight is related to the slope σ of the log density of fish with respect to length by $3\lambda = \sigma + 1$.
- the slope of log biomass density *versus* log body mass in various aquatic ecosystems being very close to 0 [Boudreau and Dickie, 1992].
- the slope of normalized biomass spectra (log biomass per range of weight classes versus log weight) being close to -1 or steeper in various plankton communities as well as in benthic fish assemblages in the Benguela System [Macpherson and Gordoa, 1996, Zhou and Huntley, 1997].

5.2 Initial intercept of the spectrum

The intercept u_0 of the biomass spectrum at time $t = 0$ was estimated from average densities estimated from published size spectra (table 4). Fish densities are usually estimated from trawl surveys and reported in numbers or biomass per swept area, *i.e.* per m^2. Trawls usually have a vertical opening of a few meters, but considering that most fish are found close to the bottom, the density per m^2 can be considered very similar to the density in the first meter of the water column, *i.e.* per m^3.

For the stationary linear spectrum, the abundance of fish with weight in $[w_1, w_2]$ or length in $[L_1, L_2]$ is given by formula (1) *i.e.*, assuming that $w = 0.005L^3$,

$$u_0\left(\frac{{w_2}^{\lambda}}{\lambda} - \frac{{w_1}^{\lambda}}{\lambda}\right) \quad = \quad 0.005^{\lambda} u_0 \left(\frac{{L_2}^{3\lambda}}{\lambda} - \frac{{L_1}^{3\lambda}}{\lambda}\right)$$

and the biomass is given by formula (2) *i.e.*

$$u_0\left(\frac{{w_2}^{\lambda+1}}{\lambda+1} - \frac{{w_1}^{\lambda+1}}{\lambda+1}\right) \quad = \quad 0.005^{\lambda+1} u_0 \left(\frac{{L_2}^{3\lambda+3}}{\lambda+1} - \frac{{L_1}^{3\lambda+3}}{\lambda+1}\right)$$

Assuming that the values of the parameters are the reference values (and that $\lambda = -1.0439$), we can compute u_0 for each observation (table 4).

Spectrum	Source	Size range		Density		Estimated intercept
		Length (cm)	Weight (g)	Number (fish m^{-2})	Biomass (g m^{-2})	(g m^{-3})
Demersal fish	[Rochet and Lembo, 2003]	1-100		0.5		0.002
All fish	[Cyr and Peters, 1996]		0.2-790		1	0.13
Planktivorous fish	[Sprules et al., 1991]	5-20			6	1.5
Piscivorous fish	[Sprules et al., 1991]	30-80			0.2	0.09

TAB. 4 – Intercepts estimated from published size spectra.

5.3 Individual life history

The weight of a fish that would not die from predation would increase according to the equation

$$W(t) = (1.93\,t + 0.213)^{4.47}$$

if its initial weight is $W(0) = 10^{-3}g$, according to the results of section 3.5 and the reference values of the parameters (Table 2).

The annual food ration of a fish of weight W is

$$\frac{1}{K}\frac{dW}{dt} = \frac{1}{K}\frac{dX}{dt}e^X = AC_1W^{\alpha+\lambda+1}$$

Hence the life history of a hypothetical individual fish according to the model can be estimated in terms of growth, annual food ration and life expectancy (Table 5, Fig. 2). The growth is comparable to *e.g.* North Sea cod, which would reach 1 kg at 2 years and 10 kg at 5 – 6 years. According to Daan (1973), such an adult cod would ingest about 2% of its body weight daily, hence about 7 times its weight in a year. On the other hand, fish larvae with weight around 1 g ingest 30 to 70% of their body weight daily [Pepin and Penney, 2000]. The figures in table 5 are consistent with these data : the biomass spectrum model consists of realistic individual fish.

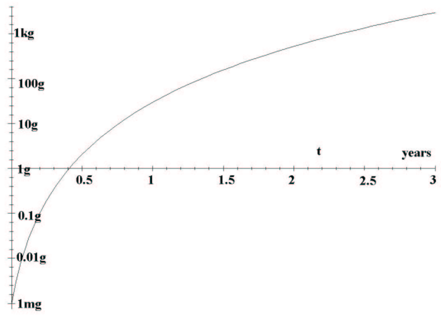

FIG. 2 – Growth curve of an individual fish.

Weight	1mg	1g	10g	100g	1kg	10kg
Age (from weight 1mg)	0	150d	277d	1y125d	2y120d	4y
Annual food ration	0.59g	43g	257g	1.53kg	9.17kg	54.7kg
Life expectancy	6d	26d	44d	74d	124d	208d

TAB. 5 – Life history of an individual fish, for reference values of the parameters (table 2)

5.4 Boundary conditions

As fish sizes have limits, the model has a biological interpretation only on a weight range $[w_{\min}, w_{\max}]$. Simulations also can be performed only on an interval $[x_{\min}, x_{\max}]$. Then equation (10) is not defined because of the convolution integrals. Therefore function φ is truncated and the model is changed at both ends of the interval. In addition, an input of biomass to the system is needed.

In the lower sizes, the input of prey into the system is simulated by a simple equation for plankton growth combined to equation (10). Symmetrically, in very large sizes, the loss of biomass is simulated by assuming that $u(t,x)$ is independent of time. Call $\mathcal{A}$ the operator describing the dynamics in the fish size spectrum u in equation (10) :

$$\begin{aligned} \mathcal{A}(u)(x) &= -\frac{d}{dx}\left[KAe^{\alpha x}\int_0^\infty e^{-q}\varphi(q)\,u(x-q)\,u(x)\,dq\right] \\ &\quad -Ae^{\alpha x}\int_0^\infty e^{\alpha q}\varphi(q)\,u(x+q)\,u(x)\,dq \end{aligned}$$

Similarly, $\mathcal{B}$ is the operator for plankton growth dynamics :

$$\mathcal{B}(u,t)(x) = \frac{1}{\tau_p}(u_p(x,t) - u(x))$$

where $u_p(x,t)$ is the equilibrium density of plankton and τ_p is the plankton characteristic time for going back to equilibrium after a perturbation. $\mathcal{C}$ is the operator for large sizes dynamics :

$$\mathcal{C}(u,t)(x) = \frac{1}{\tau_m}(u_m(x,t) - u(x))$$

with the characteristic time τ_m large (3 years) and $u_m(x,t)$ similar to the initial condition size spectrum. Transitions between the models $\mathcal{A}$, $\mathcal{B}$ and $\mathcal{C}$ are smoothed by simulating the equation

$$\frac{\partial u}{\partial t}(x,t) = \psi_p(x)\psi_m(x)\,\mathcal{A}(u)(x) + (1-\psi_p(x))\,\mathcal{B}(u,t)(x) + (1-\psi_m(x))\,\mathcal{C}(u,t)(x) \tag{13}$$

where ψ_p and ψ_m are smooth functions with :

$$\begin{cases} 0 \le \psi_p(x) \le 1 & \\ \psi_p(x) = 1 & \text{for} \quad x > x_2 \\ \psi_p(x) = 0 & \text{for} \quad x < x_1 \end{cases} \qquad \begin{cases} 0 \le \psi_m(x) \le 1 & \\ \psi_m(x) = 1 & \text{for} \quad x < x_3 \\ \psi_m(x) = 0 & \text{for} \quad x > x_4 \end{cases}$$

Hence the size spectrum governed by predation processes only is simulated in the size range $[x_2, x_3]$ only. For small sizes lower than x_1, model $\mathcal{B}$ is simulated, and model $\mathcal{C}$ for sizes larger than x_4. Over ranges $[x_1, x_2]$ and $[x_3, x_4]$ transition processes occur.

In addition, function φ is truncated in simulations to ensure that $\varphi(q) = 0$ while $q > x_1 - x_{\min}$ and $q > x_{\max} - x_4$. This makes sure that the composite operator in equation (13) is defined for all derivable functions over $[x_{\min}, x_{\max}]$.

5.5 Diffusion

From a strictly mathematical view, equation (13) may not have a solution at any time t. At some time t_0, the slope of the size spectrum may become infinite in some point, then the solution would not be defined any more. This is well known for the Burgers equation $\partial u/\partial t = u\partial u/\partial x$. As a consequence, in some simulations, the population of fish of weight e^{x_0} disappears at time t_0. This problem was counteracted by introducing diffusion in the model. This amounts to assume that two fish of similar weight, eating the same prey, will not grow exactly by the same amount. Hence this will add realism to the model. Mathematically, this introduces an additional term $\partial^2 u/\partial x^2$ in operator $\mathcal{A}$.

5.6 Simulated size spectra

Size spectra were simulated following equation (13) using **C**$^{++}$ on a Personal Computer with an order 4 Runge-Kutta method and log weight x discretized by an elementary method ($dx = dw/w = 0.5$). The process parameters were selected in table 2 and the boundary conditions parameters and limits were fixed according to table 6.

Parameter name	$w_{\min}$	w_1	w_2	w_3	w_4	$w_{\max}$
Value	10^{-12}g	10^{-6}g	10^{-3}g	10^{6}g	10^{9}g	10^{12}g

Parameter name	τ_p	$u_p(x,t)$	τ_m	$u_m(x,t)$
Value	3 days	$u_0 e^{\lambda x}$	3 years	$u_0 e^{\lambda x}$

TAB. 6 – Parameters and limits of the boundary conditions fixed for all simulations.

A first series of simulations was run to check that the results conformed to the theoretical expectations. Linear spectra $u_0 e^{\lambda x}$ were found to be stationary. A weaker slope initial spectrum decreased uniformly for all weights, conforming to section 3.3.1. An initial spectrum with appropriate gaps was stationary, conforming to section 3.3.2 as well.

Further simulations were run i) to study the stability of the stationary solution and ii) to predict the effect of fishing on the stationary solution (Fig. 3).

When the initial spectrum is perturbed by a sine function around the stationary slope, the peaks move downwards the spectrum and are rapidly damped, especially in small sizes (Fig. 3.a). On the other hand, if the plankton input to the spectrum oscillates in time following a sine function, the oscillations expand while propagating through the spectrum and may result in infinite values if their amplitude is too large (Fig. 3.b) . Note that the amplitude of the perturbations added is very large as the figures span 14 orders of magnitude (from 10^{-10} to 10^{+4}) on the y-axis. For example the input of plankton is assumed to double in summer as compared to winter, which is translated by the thickness of the size spectrum on the very left side of figure 3.b. Introducing diffusion stabilises the solution (not shown). A strong fishing mortality results in a steeper slope of the stationary solution in larger sizes. Introducing fishing mortality starting at weight 1g causes a change in slope for weights larger than 10kg, and oscillations between 1g and 10kg. Oscillations are damped when diffusion is added to the model (Fig. 3.c-d). However, a more realistic fishing mortality (as estimated from the North Sea and Bay of Biscay stocks) has no apparent effect on the slope of the spectrum, and merely results in oscillations beginning at the size at recruitment to fishing (Fig. 3.e). This holds when perturbations and diffusion are added to the model (Fig. 3.f).

6 Discussion

Relaxing the assumption of a constant predator-prey size ratio into a distributed size ratio still results in a linear size spectrum. Compared to the Silvert and Platt [1980] size spectrum model, the present model improves the regularity of the stationary solution. Adding a diffusion term into the growth term results in more stable stationary solutions. This means that improving the realism of the assumptions does not necessarily increase the complexity of the solution. We predict that an aquatic ecosystem where all processes are driven by predation, and predation is primarily size-dependent, can have a linear size spectrum, even if there is variability in prey sizes and in food assimilation. The slope of this size spectrum will be insensitive to the magnitude of processes in the food web, such as the width of prey size distribution, the volume of water searched while foraging or the assimilation efficiency. Moreover, perturbations that are likely to occur, such as seasonal primary production, can create oscillations in the spectrum. Size spectra observed from marine communities frequently show oscillations [Pope and Knights, 1982, Murawski and Idoine, 1992, Drgas et al., 1998, Saiz-Salinas and Ramos, 1999, Rochet and Lembo, 2003].

Introducing a simple model for fishing mortality as a function of size results in a steeper slope of the spectrum, as inferred a long time ago by fisheries scientists. However, this change of slope occurs in a range of sizes far larger than the size at recruitment to fishing. In addition, given the parameterisation of the model in the present study, a realistic fishing mortality as estimated from the North Sea and Bay of Biscay does not result in a detectable change in the slope of the spectrum. The North Sea and even the Bay of Biscay cannot be considered as lightly exploited systems, hence this means that given the assumptions of the model, even a high fishing pressure would not affect the slope of the spectrum. The present model is rather theoretical and its parameters could not be measured directly in the field. However, we put a large effort in getting as "realistic" orders of magnitude as possible from published literature, and we checked by various means that our predictions are comparable to broad ecosystem or individual observations (predicted slope, individual life history). Hence we predict that only unrealistically high fishing pressures would affect the slope of fish communities size spectra. This result differs from the study by Gislason and Rice [Gislason and Rice, 1998] who predicted based on a Multi Species Virtual Population Analysis (MSVPA) model that the change in slope of the size spectrum in the North Sea would be proportional to the change in fishing intensity. This might be due to the completely different assumptions of the models. MSVPA describes the age-structured dynamics of a few commercial species and the less well known remainder of the food web is fixed. In the MSVPA model, predation is mainly species-dependent, whereas it is exclusively size-dependent in the present model. Both assumptions are extreme and what happens in the field probably lies in between. What happens in a real community would depend on the validity of each assumption in the food web. This would explain why published evidences of fishing effects on size spectra are not consistent (see review in [Rochet and Trenkel, 2003]).

The main predicted effect of a realistic fishing pressure in the present model is to increase oscillations in the size spectrum in large sizes. These oscillations are caused by the depletion of large fish, allowing the numbers in the lower size-classes to increase due to decreased predation. This increased numbers in turn exert an increased predation on the next lower size-classes, etcetera. These effects then propagate backwards to large sizes as a depleted size class will cause food scarcity for the next larger size class. Indeed, many published size spectra from exploited fish communities show oscillations, but a comparison of the magnitude of these oscillations with less exploited communities or with the predictions of the model would hardly be feasible. An interesting feature of this model is that controls occur both top-down (predators controlling prey numbers) and bottom-up (preys limiting predator growth) and in this way may reflect the complexity of real food webs.

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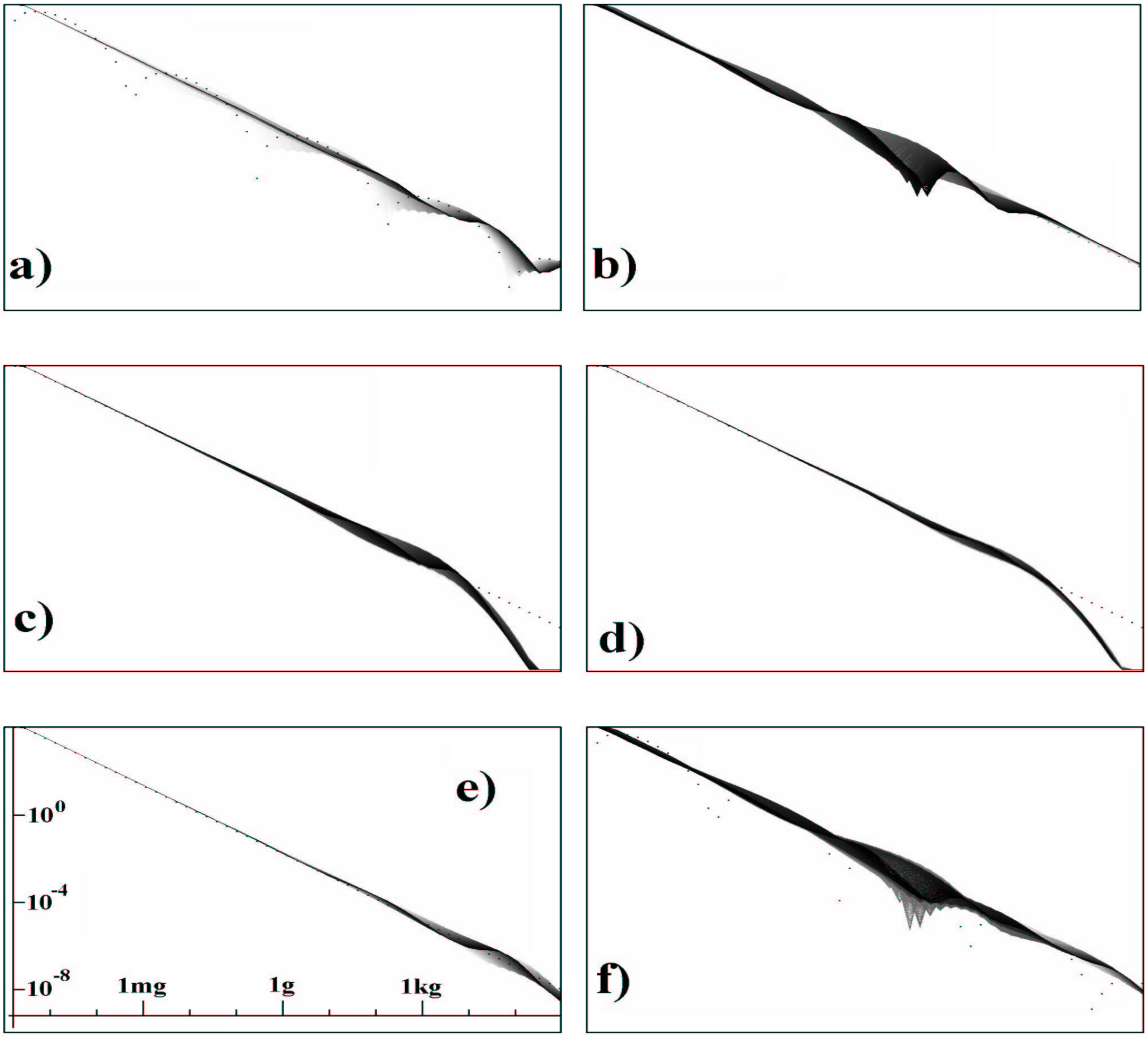
Panel	First time plotted (y)	Last time plotted (y)	Time step (d)	Diffusion	Initial condition	Left boundary condition	Fishing mortality parameters	
							a	b
a)	0	2	2	no	$u_0 e^{\lambda x}(1+\sin x)$	$u_0 e^{\lambda x}$	0	0
b)	0	2	1	no	$u_0 e^{\lambda x}$	$1 + 0.3\sin(2\pi t)$	0	0
c)	5	10	3	no	$u_0 e^{\lambda x}$	$u_0 e^{\lambda x}$	0.5	$\log 1$
d)	5	10	3	yes	$u_0 e^{\lambda x}$	$u_0 e^{\lambda x}$	0.5	$\log 1$
e)	5	10	3	no	$u_0 e^{\lambda x}$	$u_0 e^{\lambda x}$	0.1	$\log 10$
f)	5	10	3	yes	$u_0 e^{\lambda x}(1+\sin x)$	$1 + 0.3\sin(2\pi t)$	0.1	$\log 10$

TAB. 7 – Parameters for the simulations plotted in figure 3.

FIG. 3 – Simulated size spectra using reference parameters of Tables 2 and 6, unless otherwise specified in table 7.
The dynamics of the spectrum is represented by plotting the model solution for successive steps dt, $2dt$,..., Ndt with a grey shading from white at dt to black at Ndt.
Bold dotted line : initial condition.
a) Oscillatory initial spectrum.
b) Oscillatory plankton input.
c) Strong fishing effort.
d) Strong fishing effort with diffusion.
e) Realistic fishing effort.
f) Realistic fishing effort with diffusion, oscillatory initial condition and oscillatory plankton input.



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