

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

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Abstract

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 realistic fishing should affect the curvature and stability of the size spectrum rather than its slope.

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1. Introduction

Biomass size spectra, the distribution of biomass across body size classes in a community, have been the subject of continuous interest since the first developments by Sheldon and colleagues (1972), Sheldon et al. (1977). This is both because it appears to be a very conservative feature of marine communities, and because of the strong appeal of summarizing 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 and colleagues, 1972, 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; 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, there is growing concern that fisheries management should consider ecosystems rather than individual populations, and biomass size spectra are considered a potentially powerful tool for assessing human impacts on exploited aquatic communities (Kerr and Dickie, 2001; 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 hypothesized 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, 1996; Greenstreet and Hall, 1996; Rice and Gislason, 1996), although this pattern is not consistent across all systems (Bianchi et al., 2000).

These studies 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 also explain why size spectra are regular.

Existing theories of biomass size spectra rely on the flow of biomass from the smallest- to the largest-sized

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organisms through size-dependent processes. Some of them consider discrete trophic levels and the processes considered include growth, production, respiration, predation and even reproduction (Kerr, 1974; Borgman, 1982, 1983; Thiebaut and Dickie, 1992, 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 “generalized 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 (1980) developed a continuous, time-dependent, nonlinear 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; other ecological consequences of the model are also examined to appraise the consistency and realism of the assumptions. 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

The fundamental independent variables are time t and x , where x is the (natural) logarithm of the weight w of a fish (Table 1). 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 in the weight range $[w_1, w_2]$ is given by

Table 1
Definition of the mathematical variables

Symbol	Definition	Unit
w	Weight of a fish	g
x	Logarithm of w	$\ln(\text{g})$
t	Time	year = yr
$u(x, t)$	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	yr^{-1}
$\mu(x, t)$	Mortality rate	yr^{-1}
$\varphi(q)$	Probability of predation when a predator size x meets a prey size $x - q$	

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

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

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

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

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

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

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 $dt = 0$:

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

Derive with respect to x_2 :

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

This equation is well known in hydrodynamics (mass-balance in a transport equation) and in population dynamics (see Silvert and Platt, 1978, 1980, and Mc Kendrick–von Foerster equation, see e.g. Kot, 2001).

2.3. Predation

In this model, predation is the unique driving force of growth and mortality. Each predation event implies two individuals. One (with weight e^y) will grow, the other (with weight e^x) 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 denote $y - x$ by q . The function φ (Fig. 1) is chosen dome-shaped, positive, having a unique maximum which implies an effective search for a preferred prey size. Because preys are generally smaller than predators, the function φ is almost zero for negative values of q . But we

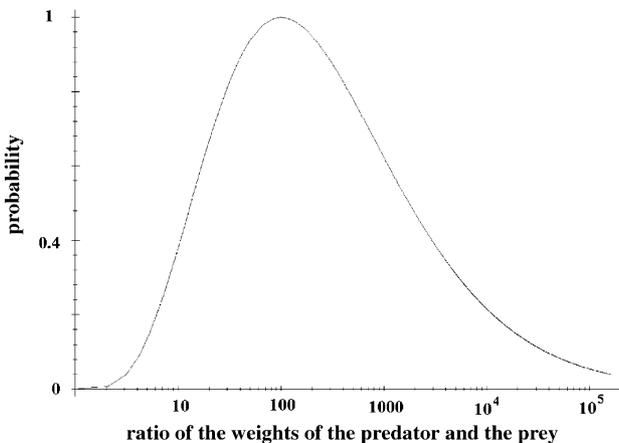


Fig. 1. Graph of φ , the probability that a predator of weight e^y meeting a prey of weight e^{y-q} will eat it.

do not need that φ is exactly zero for negative q . For numerical simulations, we take

$$\varphi(q) = \begin{cases} e^n \left(\frac{q}{q_0}\right)^n e^{-nq/q_0} & \text{if } q \geq 0, \\ 0 & \text{if } q \leq 0. \end{cases} \tag{5}$$

This function φ peaks at 1 for q_0 . The parameter n determines the width 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: it is given by $Ae^{zy} dt$. This allometry was derived by Ware (1978) based on considerations about the bioenergetics of fish. Then the number of encounters with possible preys of weight in $[e^x, e^{x+dx}]$ is $Ae^{zy} u(x, t) dt dx$. The number of preys eaten in the weight range $[e^x, e^{x+dx}]$ is $Ae^{zy} \varphi(y - x) u(x, t) dt dx$. The distribution of predation events is given by

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

2.4. Mortality

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

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

which is equivalent to

$$\mu(x, t) = Ae^{zx} \int_{-\infty}^{\infty} e^{zq} \varphi(q) u(x + q, t) dq. \tag{7}$$

Non-predation mortality is accounted for by an additional mortality rate

$$\mu_0 e^{zx} u(x, t),$$

which increases allometrically with body size and also increases with the number of animals in the ecosystem (density-dependent mortality). The allometric coefficient was chosen to allow the mathematical analysis in Section 3.

In simulations, we will add a fishing mortality rate $\mu_f(x, t)$.

2.5. Growth

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

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

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

The increase in weight of the predator is given by $e^y g(y, t) dt$ (cf. Section 2.1). If the biomass eaten is used

to grow with a constant efficiency K , then

$$g(y, t) = KAe^{zy} \int_{-\infty}^{\infty} e^{-q} \varphi(q) u(y - q, t) dq. \quad (9)$$

2.6. Conclusion

Combining Eqs. (4), (7) and (9), we obtain the following model:

$$\begin{aligned} \frac{\partial u}{\partial t}(x, t) = & -\frac{\partial}{\partial x} \left[KAe^{zx} \int_{-\infty}^{\infty} e^{-q} \varphi(q) u(x - q, t) u(x, t) dq \right] \\ & - Ae^{zx} \int_{-\infty}^{\infty} e^{zq} \varphi(q) u(x + q, t) u(x, t) dq \\ & - \mu_0 e^{zx} u(x, t)^2 - \mu_f(x, t). \end{aligned} \quad (10)$$

Eq. (10) is an equation of evolution, $\partial u / \partial t = \mathcal{A}(u)$, 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) in the ecosystem (see Section 5.4).

For the sake of generality, φ is kept as a parameter function. Let D_φ be the set of real numbers ℓ such that the integral $\int_{-\infty}^{\infty} \varphi(q) e^{\ell q} dq$ is convergent. For the explicit φ given above, $D_\varphi = (-\infty, n/q_0)$; if φ has a compact support, $D_\varphi = (-\infty, +\infty)$.

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 , consistently with the findings by Silvert and Platt (1980) for a fixed prey–predator size ratio. Another consequence of this lemma is that if we change the parameter A to cA and μ_0 to $c\mu_0$, 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 behavior of the model, they determine only the rate of biomass flow.

3.2. Stationary linear spectrum

Lemma 2. *If $\varphi(q)$ is zero for negative values of q , there exists a unique real λ such that for any u_0 , the function $u(x, t) = u_0 e^{\lambda x}$ is a solution of Eq. (10). This λ is the unique real solution of*

$$(2\lambda + \alpha)K \int_{-\infty}^{\infty} e^{-(\lambda+1)q} \varphi(q) dq + \int_{-\infty}^{\infty} e^{(\alpha+\lambda)q} \varphi(q) dq + \frac{\mu_0}{A} = 0. \quad (11)$$

Moreover, $\lambda < -\alpha/2$.

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

$$\begin{aligned} F(\lambda) = & (2\lambda + \alpha)K \int_{-\infty}^{\infty} e^{-(\lambda+1)q} \varphi(q) dq \\ & + \int_{-\infty}^{\infty} e^{(\alpha+\lambda)q} \varphi(q) dq + \frac{\mu_0}{A}. \end{aligned}$$

With the hypothesis on φ , the domain D_φ has no lower bound. We can then prove that

- the domain of F is

$$\{\lambda \text{ such that } -1 - \lambda \in D_\varphi \text{ and } \alpha + \lambda \in D_\varphi\}$$

and it contains $(-\infty, -\alpha/2)$,

- for $\lambda \geq -\alpha/2$, the function F is nonnegative,
- the derivative $F'(\lambda)$ is positive for all $\lambda < -\alpha/2$,
- when λ decreases towards $-\infty$ the second integral in F goes to 0, and F goes to $-\infty$.

From this follow the existence and unicity of a real solution of $F(\lambda) = -\mu_0/A$, because $-\mu_0/A < 0$. \square

When φ takes positive values for some negative q (when small predators can eat large preys) the lemma above is not valid (the sign of $F'(\lambda)$ becomes not obvious). In some cases, F can have a global negative minimum, so both existence and unicity can be wrong. For example, it is the case for

$$\varphi(q) = \begin{cases} q \exp(-q) & \text{if } q > 0, \\ 1/10 |q| \exp(-q) & \text{if } q < 0. \end{cases}$$

Although this is not the only solution (nor the only stationary solution: see below), Lemma 2 shows that a linearly decreasing size spectrum can appear, even if the predators are allowed to prey on a weight range rather than a single weight, and whatever the shape of the predator–prey size ratio distribution.

3.3. Other special solutions

3.3.1. Weak slope

Be C the constant

$$C = \mu_0 + A \int_{-\infty}^{+\infty} (1 - \alpha K e^{-(1-\alpha)q}) \varphi(q) dq$$

(assuming that $0 \in D_\varphi$ and $\alpha - 1 \in D_\varphi$ the integral is convergent). If both $\alpha < 1$, $K < 1$, and the probability of eating large preys is negligible, then $C > 0$. It is easy to show that

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

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

Because C is positive, the solution is decreasing towards zero. It is a linear spectrum with a slope weaker 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) can keep some biomass in the ecosystem. This solution can appear unrealistic, but would it happen, it would be transient and hence not easy to observe.

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 towards 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 positive range $[q_m, q_M]$. In this case, if $u(0, x)$ 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 the solution of the system is

$$u(t, x) = \frac{u(0, x)}{1 + \mu_0 e^{\alpha x} t u(0, x)}$$

It corresponds to size spectra where no predation, hence no growth, can occur, because the weights of the fish do not match predators requirements. The only process ongoing is mortality due to the term $\mu_0 e^{\alpha x} u^2$.

3.4. Total biomass

The total biomass in 1 m^3 is

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

This integral is divergent, but from an ecological point of view it is not a problem: there is a maximum and a minimum size in any ecosystem. 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.

For a spectrum u which is zero outside a bounded interval, we can compute the variation of the biomass. Using Eq. (10)

$$\begin{aligned} \frac{dB}{dt} &= \int_{-\infty}^{+\infty} e^x \frac{\partial u}{\partial t}(x, t) dx \\ &= - \int_{-\infty}^{+\infty} \left[e^x \frac{\partial}{\partial x} (K A e^{\alpha x} I_1) + A e^x e^{\alpha x} I_2 \right. \\ &\quad \left. + \mu_0 e^{(\alpha+1)x} u(x, t)^2 \right] dx \end{aligned}$$

with

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

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

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

$$\frac{dB}{dt} = \int_{-\infty}^{+\infty} [e^x K A e^{\alpha x} I_1 - A e^x e^{\alpha x} I_2 - \mu_0 e^{(\alpha+1)x} u(x, t)^2] dx.$$

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

$$\begin{aligned} &\int \int e^{(\alpha+1)x} e^{\alpha q} \varphi(q) u(x + q, t) u(x, t) dq dx \\ &= \int \int e^{(\alpha+1)(y-q)} e^{\alpha q} \varphi(q) u(y, t) u(y - q, t) dq dy. \end{aligned}$$

Then we conclude that

$$\begin{aligned} \frac{dB}{dt} &= - A(1 - K) \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} e^{(1+\alpha)y} e^{-q} \varphi(q) u(y - q, t) \\ &\quad \times u(y, t) dq dy - \mu_0 \int e^{(\alpha+1)x} u(x, t)^2 dx. \end{aligned}$$

From this result, it follows that, if $K = 1$ and $\mu_0 = 0$, total biomass is invariant. This is a corollary of the model: if $K = 1$, the biomass is conservative for each individual predation event. In fact, there are losses when converting food into body mass, hence $K < 1$ and the biomass decreases with time. 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. All this quantities can be computed for an

individual fish in a given environment $u(x, t)$. We first assume that this environment is a solution of Eq. (10); then we make effective computations for the stationary solution of Eq. (10).

We already defined the growth function $X(t)$ of an individual fish (Eq. (3)). Combining with g (Eq. (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 Eq. (8).

Eq. (7) gives the function $m(t) = \mu(X(t), t) + \mu_0 e^{\alpha X(t)} u(X(t), t)$ 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 $p(t) = m(t) \exp(\int_0^t -m(\tau) d\tau)$.

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 $u(x, t) = u_0 e^{\lambda x}$. Following the procedure above, Eq. (9) gives

$$g(x, t) = KAC_1 u_0 e^{(\alpha+\lambda)x}$$

where

$$C_1 = \int_{-\infty}^{\infty} e^{-(\lambda+1)q} \varphi(q) dq.$$

Eq. (3) is now

$$\frac{dX}{dt} = KAC_1 u_0 e^{(\alpha+\lambda)X(t)}$$

and we can compute the solution with initial condition x_0 :

$$X(t) = -\frac{\ln(-C_1 K A u_0 (\alpha + \lambda)t + e^{-x_0(\alpha+\lambda)})}{\alpha + \lambda},$$

$$W(t) = (-C_1 K A u_0 (\alpha + \lambda)t + W_0^{-(\alpha+\lambda)})^{-1/(\alpha+\lambda)}. \quad (12)$$

The mortality rate at time t for a fish of weight $W(t)$ is given by Eq. (7)

$$m(t) = \frac{C_3}{C_4 t + C_0},$$

where

$$C_3 = AC_2 u_0, \quad C_4 = KAC_1 u_0 (-\alpha - \lambda), \quad C_0 = W_0^{-(\alpha+\lambda)}$$

and

$$C_2 = \frac{\mu_0}{A} + \int_{-\infty}^{\infty} e^{(\alpha+\lambda)q} \varphi(q) dq.$$

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

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

It is easy to check that $C_3 > C_4$ if we remember that λ is a solution of Eq. (11).

4. Parameters

For numerical analyses below, we used values of the parameters based on published literature (Table 2). 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 published knowledge on marine organisms and food webs. Both experimental and theoretical sources are reported, as previous theoretical studies performed valuable compilations of former experimental results.

The value of μ_0 is set such that the non-predation mortality rate for a 500 g fish is 0.2, an assumption in the range of residual mortality rates usually assumed in multispecies models e.g. for the North Sea and Baltic Sea (0.1–0.2) (Gislason and Helgason, 1985; Gislason, 1999; Anonymous, 2002; Andersen and Ursin, 1977).

5. Numerical simulations

5.1. Slope of the stationary solution

The slope λ of the stationary size spectrum was computed from Eq. (11) with function φ given by Eq. (5), for different values of the parameters (Table 3).

The slope of the size spectrum is not sensitive to individual variations in the parameters, especially the width of the predator–prey size ratio distribution. Predators eating larger preys, searching in volumes increasing steeper with size, and having a lower growth efficiency result in steeper spectra than the opposite settings. A higher non-predation residual mortality rate also results in a steeper slope. Keeping all but one of the parameters to their reference value results in slopes of approximately -1 , which is consistent with published data:

- slopes of log numbers vs. 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 vs. 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 vs. log weight) being close to -1 or steeper in various plankton communities as

Table 2
Values of the parameters used in model simulations

Parameter	Definition	Section	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 yr ⁻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; Thiebaut and Dickie, 1993; Vignes, 1998
n	An inverse measure of the width of the predator–prey size ratio distribution	(2.3)	—	5	1	10	Gessed 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
μ_0	Natural mortality rate	(2.4)	m ³ yr ⁻¹	80	0	200	Gislason and Helgason, 1985; Gislason, 1999; Anonymous, 2002; Andersen and Ursin, 1977

Lower and higher limits refer to the range of values used in the sensitivity analysis.

Table 3
Numerical computation of the stationary slope λ

n	e^{q_0}	α	K	μ_0	λ
5	100	0.82	0.2	80	-1.0500
10	100	0.82	0.2	80	-1.0589
1	100	0.82	0.2	80	-1.0117
5	1000	0.82	0.2	80	-1.0105
5	10	0.82	0.2	80	-1.1569
5	100	0.6	0.2	80	-0.9558
5	100	0.9	0.2	80	-1.0847
5	100	0.82	0.1	80	-1.1099
5	100	0.82	0.6	80	-0.9560
5	100	0.82	0.2	0	-1.0439
5	100	0.82	0.2	200	-1.0589
10	10	0.9	0.1	200	-1.3710
10	1000	0.6	0.6	0	-0.8376

well as in benthic fish assemblages in the Benguela System (Macpherson and Gordo, 1996; Zhou and Huntley, 1997).

Simultaneous changes in the parameters result in wider variations in the slope. However, combining extreme values of all parameters still results in consistently slowly decaying size spectra. The reference value $\lambda = -1.0500$ was taken for the simulations below.

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 m². Trawls usually have a vertical opening of a few meters, but considering that most fish are found close to the bottom, the density per m² can be considered very similar to the density in the first meter of the water column, i.e. per m³. The estimated intercepts vary by three orders of magnitude, depending on ecosystems: it is determined both by primary production and food web structure (Sprules et al., 1991; Cyr and Peters, 1996).

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 $w = 0.005L^3$,

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

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

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

Assuming that the values of the parameters are the reference values (hence $\lambda = -1.0500$), u_0 was computed for each observation (Table 4).

Table 4
Intercepts estimated from published size spectra

Spectrum	Ecosystem	Source	Size range Length (cm)	Weight (g)	Density Number (fish m ⁻²)	Biomass (g m ⁻²)	Estimated intercept (g m ⁻³)
Demersal fish	Mediterranean Sea	Rochet and Lembo, 2003	1–100		0.5		0.002
All fish	Lakes	Cyr and Peters, 1996		0.2–790		1	0.14
Planktivorous fish	Lake Michigan	Sprules et al., 1991	5–20			6	1.56
Piscivorous fish	Lake Michigan	Sprules et al., 1991	30–80			0.2	0.09

Table 5
Life history of an individual fish, for reference values of the parameters (Table 2)

Weight	1 mg	1 g	10 g	100 yr g	1 yr kg	10 yr kg
Age (from weight 1 mg)	0	142 day	266 day	1 yr 112 day	2 yr 106 day	3 yr 349 day
Annual food ration	0.22 g	45 g	262 g	1.55 kg	9.10 kg	53.6 kg
Life expectancy	8 day	39 day	66 day	113 day	191 day	324 day

For all simulations below, $u_0 = 0.01$ was taken as reference value.

5.3. Individual life history

The life history of a hypothetical individual fish with initial weight $W(0) = 10^{-3}$ g was estimated in terms of growth, annual food ration and life expectancy (Table 5). The predicted growth and life expectancy were checked against the data in Pauly (1980), who compiled the parameters of the von Bertalanffy growth model and natural mortality rate estimates for 175 fish species encompassing a wide range of taxonomic groups and environmental conditions. We partitioned the species into 10 groups of increasing natural mortality rate. Based on the growth parameters, the weight at age for each group was then computed, as well as the life expectancy for fish near their asymptotic weight. The growth curves compare satisfactorily, except in ages below one year (Fig. 2). This is partly due to the von Bertalanffy growth model not being appropriate to describe early growth of fish. Similarly, the life expectancy predicted by the model fits rather well the data for large fish, but overestimates it in small sizes. This is due to small fish in the model being a mix of small short-lived adult fish and young longer-lived animals. Furthermore, the food ration estimated by the model is consistent with the range of published data, from 30%–70% of the body weight daily for fish larvae (Pepin and Penney, 2000) to 1–7% for adult fish of various species (Gislason and Helgason, 1985; Daan, 1973; Essington et al., 2001). Hence the model individual fish seem to have a reasonable life history.

5.4. Boundary conditions

Eq. (10) cannot be used for numerical computations: sizes have to be discretized, hence x is bound in an

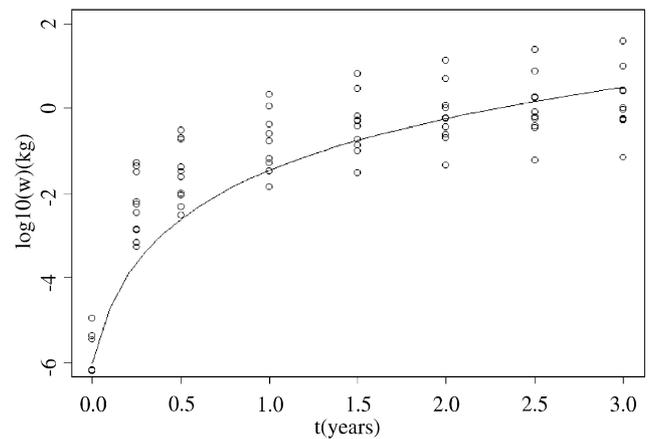


Fig. 2. The model growth curve of an individual fish (line), compared with estimated weights at age derived from the data compiled by Pauly (1980) (circles) (for explanations see text).

interval $[x_{min}, x_{max}]$. Subsequently, Eq. (10) has no meaning because of the convolution integrals. To circumvent this difficulty, 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 small size, the population of plankton $u_p(x, t)$ is assumed to control the system. In large size, the biomass should be almost independent of time. This is described by two simple models, the differential equation \mathcal{B} for plankton, and \mathcal{C} for very large animals.

$$\frac{\partial u}{\partial t} = \mathcal{B}(u) \quad \text{where } \mathcal{B}(u) = \frac{1}{\tau_p}(u_p - u) \quad \text{with } \tau_p \text{ small,}$$

$$\frac{\partial u}{\partial t} = \mathcal{C}(u) \quad \text{where } \mathcal{C}(u) = \frac{1}{\tau_m}(u_m - u) \quad \text{with } \tau_m \text{ large.}$$

The parameters τ_p (resp. τ_m) is the characteristic time to return to equilibrium after a perturbation, for plankton (resp. large animals).

Table 6
Values of the parameters of fishing mortality used in model simulations

Parameter	Definition	Unit	Ref. value	Sources
b	Log weight at recruitment to the fishery		$\ln(10)$	Estimated from Anonymou (1998a,b)
a	Slope of the fishing mortality as a function of log weight	yr^{-1}	0.1	Estimated from Anonymou (1998a,b)

Call \mathcal{A} the operator describing the dynamics in the fish size spectrum u in Eq. (10):

$$\begin{aligned} \mathcal{A}(u)(x) = & -\frac{d}{dx} \left[K A e^{ax} \int_{-\infty}^{\infty} e^{-q} \varphi(q) u(x-q) u(x) dq \right] \\ & - A e^{ax} \int_{-\infty}^{\infty} e^{aq} \varphi(q) u(x+q) u(x) dq \\ & - \mu_0 e^{ax} u(x, t)^2. \end{aligned}$$

Models \mathcal{B} and \mathcal{C} were chosen similar to \mathcal{A} to allow a smooth transition between the populations of plankton, fish and big fish. The complete model is then

$$\begin{aligned} \frac{\partial u}{\partial t}(x, t) = & \psi_p(x) \psi_m(x) \mathcal{A}(u)(x) + (1 - \psi_p(x)) \mathcal{B}(u, t)(x) \\ & + (1 - \psi_m(x)) \mathcal{C}(u, t)(x), \end{aligned} \quad (13)$$

where ψ_p and ψ_m are smooth functions with

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

The functions ψ_p and ψ_m used in simulations are cubic spline.

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 ensures that the composite operator in Eq. (13) is defined for all derivable functions over $[x_{min}, x_{max}]$.

5.5. Fishing mortality

For simulations, fishing mortality rate $\mu_f(x, t)$ is given by

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

where a and b are parameters. It is a linearly increasing function of log weight with recruitment to fishing at weight $\exp(b)$. The parameters a and b were estimated by linear regression of fishing mortality rate F at age vs. 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 Bay of Biscay. The resulting estimates did not to differ significantly (Table 6).

5.6. Diffusion

From a strictly mathematical view, Eq. (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 circumvented 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} .

Simulated size spectra with non-predation mortality ($\mu_0 > 0$) are more regular than those without non-predation mortality ($\mu_0 = 0$). When $\mu_0 > 0$, diffusion is not needed to obtain a solution defined for all positive t . Unfortunately, we have no mathematical explanation for this observation.

5.7. Simulated size spectra

Size spectra were simulated following Eq. (13) using \mathbf{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 size and time steps were determined by trial and error, small enough so that the observed patterns be independent of the value of the steps, and large enough to allow simulation of some years within a reasonable computing time. The process parameters were selected in Table 2 and the boundary conditions parameters and limits are reported in Table 7.

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. For $\mu_0 = 0$, 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. 3a). 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 (Fig. 3b) and may result in infinite values if their amplitude is too large. This confirms a conjecture of Silvert and Platt (1980) that small oscillations in the food supply can drive large swings in populations. 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. Introducing either diffusion or larger non-predation mortality stabilizes 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 1 g causes a change in slope for weights larger than 10 kg (Fig. 3c). 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, but rather on its curvature (Fig. 3d). This effect is not larger than the oscillations

Table 7

Parameters and limits of the boundary conditions fixed for all simulations. (see Section 5.4 for explanations)

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	10 days	$u_0 e^{\lambda x}$	3 yr	$u_0 e^{\lambda x}$

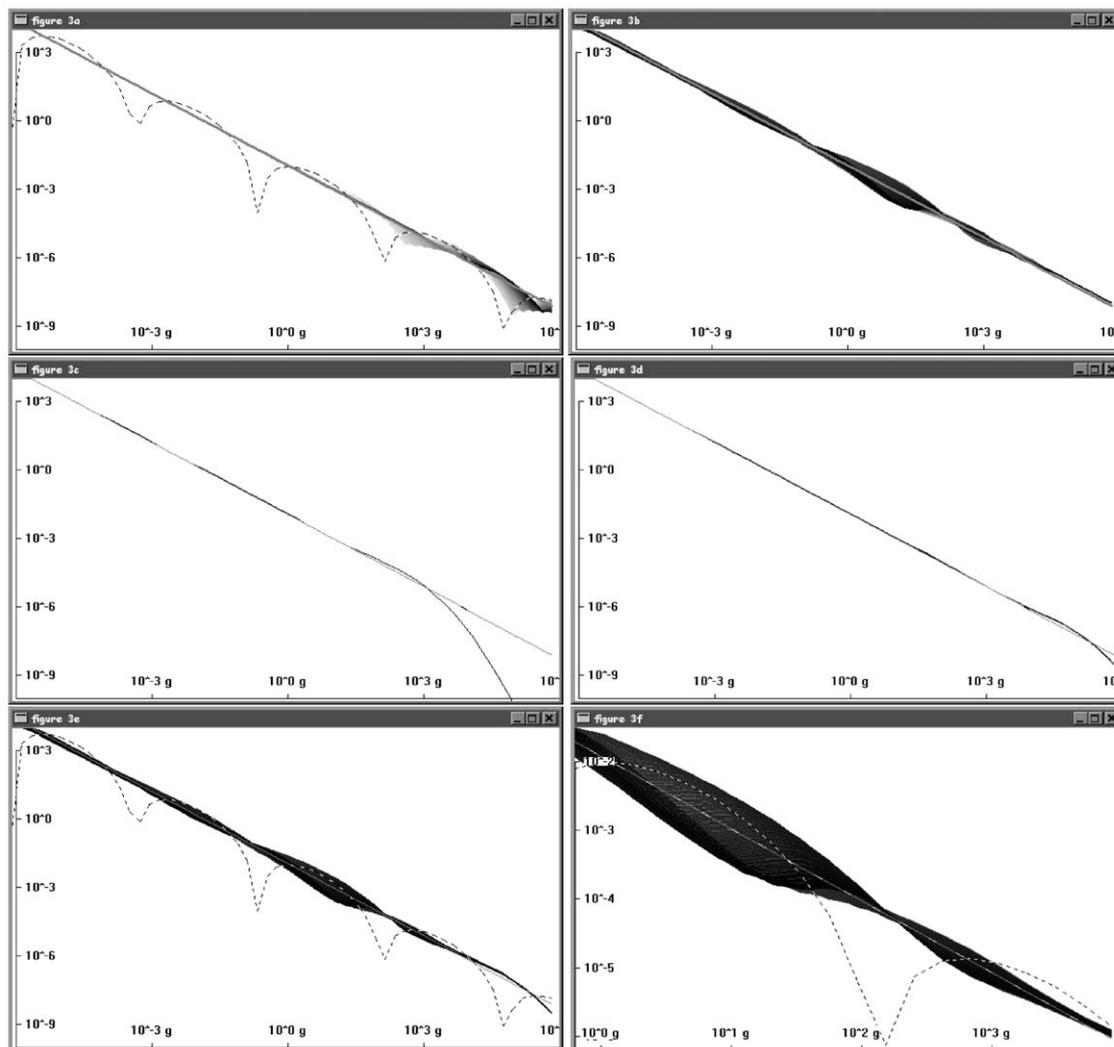


Fig. 3. Simulated size spectra using reference parameters of Tables 2–7, unless otherwise specified in Table 8. The dynamics of the spectrum is represented by plotting the model solution for successive steps $dt, 2dt, \dots, N dt$ with a grey shading from white at dt to black at $N dt$. Dashed line: initial condition. Gray bold line: stationary solution: (a) oscillatory initial spectrum; (b) oscillatory plankton input; (c) strong fishing effort; (d) realistic fishing effort; (e) realistic fishing effort with oscillatory initial condition and oscillatory plankton input; (f) the same as (e) focused on a fish-like size range.

Table 8
Parameters for the simulations plotted in Fig. 3

Panel	First time plotted	Last time plotted	Time step	Initial condition	Left boundary condition	Fishing mortality parameters	
	(yr)	(yr)	(day)			a	b
(a)	0	3	2	$u_0 e^{\lambda x} (1 + \sin x)$	$u_0 e^{\lambda x}$	0	0
(b)	0	3	2	$u_0 e^{\lambda x}$	$u_0 e^{\lambda x} (1 + 0.3 \sin(2\pi t))$	0	0
(c)	10	15	3	$u_0 e^{\lambda x}$	$u_0 e^{\lambda x}$	0.5	log 1
(d)	5	10	3	$u_0 e^{\lambda x}$	$u_0 e^{\lambda x}$	0.1	log 10
(e, f)	5	10	3	$u_0 e^{\lambda x} (1 + \sin x)$	$u_0 e^{\lambda x} (1 + 0.3 \sin(2\pi t))$	0.1	log 10

created by perturbations added to the model, which can have a fairly large amplitude (Fig. 3e and f).

6. Discussion

That a regular size spectrum can be the result of regularity in the predation processes along the food web was suspected by Beyer (1989), who found that if the size spectrum is linear and if growth and mortality rates are allometric, then mortality rate has to be proportional to growth rate (i.e. they should have the same allometric exponent). Silvert and Platt (1980) formally started from the processes to prove that given allometric growth and mortality and a constant predator to prey size ratio, a linear size spectrum is stationary. In an unpublished paper, Beyer further proved that his result is still valid when predators select their preys according to a log-normal (symmetric) suitability rather than a single size (Beyer, 1990. Size spectrum theory and multispecies assessment: basic concepts and perspectives. Working paper No 21 to the ICES Multispecies Working Group held in Woods Hole, dec. 1990). The present study still relaxes this assumption and proves that a linear spectrum can be stationary for any distribution of prey size suitability, provided this distribution is consistent throughout the whole size spectrum. This is an important contribution as field data show that there is a wide variability in predator to prey size ratio, and that predator size–prey size distributions are asymmetric (Scharf et al., 2000). Furthermore, we demonstrate that a linear spectrum is still possible while taking account of non-predation mortality, provided the latter has an appropriate allometric exponent. Thus improving the realism of the assumptions does not necessarily increase the complexity of the solution.

Under the same assumptions, size spectra can also be oscillating, both in time and along the size axis. Perturbations that are likely to occur in the real world, such as seasonal primary production, can result in oscillations in the spectrum. Size spectra observed from various 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). On the other hand, solutions oscillating in size can also be stationary. This has to do with the “multispectrum” theory developed by Dickie et al. (1987) and Boudreau et al. (1991). They assumed discrete jumps of energy between relatively fixed size ranges of prey and predator, resulting in a secondary structure of the body size spectrum consisting of a series of stationary biomass domes periodically spaced. The data from several ecosystems verify this theory (see review of theory and data in Kerr and Dickie, 2001). Our results show that there is no need to assume discrete trophic levels to obtain periodic spectra.

Although assuming a variable rather than fixed predator to prey size ratio improves the regularity of the size spectrum model, it is still unstable. Simulations frequently resulted in ecosystem crash and this is justified theoretically (see Section 5.6). However, introducing diffusion in the model stabilized the solution: once again, the more realistic assumption that all fish are not similar but have a variable efficiency in food assimilation improves the realism of the solution. Moreover, this is a contribution to the never-ended debate about biodiversity and ecosystem stability (Johnson et al., 1996). In this model, introducing biodiversity (although a small amount of it) improves the stability of the system. Surprisingly, the non-predation mortality term also improves the stability of the solution. This may be due to the density-dependence introduced thereby, providing a weak feedback control of numbers in the spectrum.

Introducing a simple size-dependent fishing mortality results in a steeper slope of the spectrum, as inferred a long time ago by fisheries scientists. This change of slope occurs in a range of sizes larger than the size at recruitment. Given the parametrization 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 change in the slope of the spectrum. Rather, its curvature and regularity are affected by fishing. These impacts are expected to be larger if

diffusion and oscillations in primary production are assumed. Moreover, it might be underestimated in the simulations, due to assuming a process that keeps the biomass invariant in large sizes (Section 5.4). Hence we conclude that realistic fishing pressures could cause disruptions in the size spectrum, consistently with the increasing awareness that fishing depletes large predators in world fisheries (Myers and Worm, 2003; Pauly et al., 1998).

Our result differs from the study by 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 by a factor of -1.3 to -3 . This might be due to the completely different structures of the models. MSVPA describes the age-structured dynamics of a few commercial species; the less well-known remainder of the food web is fixed. Hence compensations and species replacements in diets assumed to occur in any case in the present model are completely neglected in MSVPA. This hypothesis is confirmed by the results by Shin and Cury (in press). These authors developed a multispecies individual-based model where predation is a size-based opportunistic process. Their simulations show that fishing impacts the slope of the size spectrum if it is assumed linear, and its curvature if it is assumed quadratic. This would explain why published evidences of fishing effects on the slope of size spectra are not consistent (see review in Rochet and Trenkel, 2003). If, as shown by our work, the main effects of fishing on size spectra are to increase their curvature and to make them vary through time, the linearity assumption would result in erroneous and variable slope estimates that would not be straightforward to interpret. This would be an argument not to use the slope of size spectra, but rather some other characteristic, if we are to monitor fishing impacts.

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. These increased numbers in turn exert an increased predation on the next lower size-classes, and so on. 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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