The meaning of fish size spectra, the effects of fishing on them and the usefulness of their slope as indicator of fishing impacts

by
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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. Predation is size-dependent. 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 proven that linear size spectra are stationary solutions of the model. The slope of this size spectrum is 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. Exploited fish communities are simulated by adding a size-dependent fishing mortality to the model: it is found that realistic fishing pressures should not affect the slope of size spectra, but their shape and stationarity.

Keywords

Keywords: biomass size spectra; size-dependent processes; fishing effects; indicators.

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1. Introduction

Fish size spectra, the distribution of biomass over body size classes in a fish community, have a long time ago been reported as a regular and conservative characteristic of fish communities (Pope and Knights, 1982; Murawski and Idoine, 1992). The size spectrum is stationary within an exploited community, even when species composition changes, but vary between systems: the variations may be ascribed to fishing. Several authors have hypothesised that exploitation should decrease the slope of a fish size spectrum, and reported decreasing trends of this slope in exploited systems (Pope *et al.*, 1988; Anonymous, 1995; Anonymous, 1996; Greenstreet and Hall, 1996; Rice and Gislason, 1996), although this pattern is not consistent across systems (Bianchi *et al.*, 2000). In the modern quest for the tools necessary to an ecosystem approach to fisheries management, the slope of the size spectrum is hence scrutinised as a potential indicator of the impact of fishing on fish communities.

It makes sense that in most fisheries, exploitation will selectively remove large fish; consequently, there will be less large fish compared to the amount of small fish; hence the slope of the size spectrum should be steeper under exploitation. This effect might be enhanced if small fish benefit from the removal of large fish by being relaxed from predation. This is a general and qualitative prediction. Whether we can make a quantitative prediction is the subject of this paper. The first step is to have a quantitative model of the size spectrum: several such models have been developed in the past and they are briefly reviewed in section 2. Then a recently developed model with less restrictive assumptions is presented in section 3, and the predicted effects of fishing on it are reported in section 4. The predictable effects of fishing on size spectra are discussed in section 5.

2. Review of existing theories

2.1. Purely size-based models

In these size-based models, the rates ρ of processes like growth, assimilation, respiration or production are assumed to be allometric, *ie*, related to size (*eg* weight w) by $\rho=\alpha w^{\beta}$. Below we call β the allometric exponent.

2.1.1. Discrete models

A number of models considering discrete trophic levels have been developed. The first of these studies (Kerr, 1974) proved that the biomasses in two adjacent trophic levels will be in constant proportion if growth and metabolism rates respond similarly (allometrically) to changes in body size when averaged over entire trophic levels. If this constancy holds over the whole community, and if the ratio of sizes between adjacent trophic levels is constant, then biomass spectra will be linear on a log scale. Further developments considered additional processes such as production, respiration, predation and even reproduction and came to similar conclusions (Borgman, 1982; Borgman, 1983; Thiebaux and Dickie, 1992; Thiebaux and Dickie, 1993). Moreover, the "multispectrum" theory was developed by Dickie *et al* (1987; see also 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).

2.1.2. A generalised growth function

A first continuous biomass flow model was developed by Platt and Denman (1978; see also Silvert and Platt, 1978). In this model, energy flows through the ecosystem at a rate that

depends only on the size of the particles; it includes two allometric processes: loss (mainly by respiration), and a "generalised growth function", which implicitly includes predation. If the difference between the allometric exponents of these two processes is 1, then a linear biomass spectrum will be stationary. This model is the only size-based model where the biomass flow is continuous instead of jumping from the prey- to the predator- size class. Using this model to predict the impact of fishing on a fish community makes sense: most published fish size spectra hardly encompass more than two trophic levels, hence growth underlies the biomass flow in these communities at least as much as predation does. In an unpublished study (Rochet *et al.*, 1999), we simulated size spectra using this model and a realistic size-dependent fishing mortality (see section 4.2 below); we found that fishing creates a curvature downwards in the size spectrum, which increases with increasing fishing pressure.

2.1.3. Predation, growth and mortality

Silvert and Platt (1980) unified size-based theories of size spectra by developing a general equation for energy flow based on the amount of energy within discrete trophic levels. Some processes can fit into a continuous form of this general equation (see below). The model by Platt and Denman (1978) above is a particular case of this equation where growth is independent of the available biomass. On the other hand, if predation depends on the biomass of prey and generates both death of the prey and growth of the predator, assuming a fixed prey-predator size ratio results in a linear stationary biomass size spectrum. The present study will relax the latter assumption and show that linear size spectra can occur for any distribution of the prey-predator size ratio.

2.2. Other models

Several models assuming that processes based on size and other characteristics (*eg*, taxonomic) underlie size spectra have been developed.

2.2.1. MSVPA

Gislason and Rice (1998) were not seeking a theory for the size spectrum but rather trying to predict the impact of fishing on it. They used a Multi Species Virtual Population Analysis (MSVPA) model, where predation is both species- and age- (hence indirectly size-) based. MSVPA describes the age-structured dynamics of commercial species, assuming constant suitability functions of prey age-groups to predator age-groups; the less well known remainder of the food web is fixed. Gislason and Rice simulated quasi-linear size spectra under various fishing intensities, and found that the change in slope of the size spectrum in the North Sea would be proportional to the change in fishing intensity.

2.2.2. Simulation models (IBM...)

Shin and Cury (in press) developed a multispecies individual-based model where predation is a size-based opportunistic process. In this model predation is size-based only but the diversity in growth and life history parameters is fully accounted for. Simulated stationary size spectra are concave downwards, with oscillations in large sizes. Simulations show that fishing impacts the slope of the size spectrum if it is summarised by a linear equation, and its curvature if it is assumed quadratic.

3. A new size-based model

3.1. Assumptions

More details are to be found in Benoît and Rochet (In press). The fundamental independent variables are time t and x, the (natural) logarithm of the weight w of a fish. We focus on $u(x,t)$, the distribution of the number of fish with respect to x. The mass of a fish is $w=e^x$,

hence the biomass of all fish in the weight range $[w_1,w_2]$ is given by $\int_{x_1}^{x_2} e^x u(x,t)dx = \int_{w_1}^{w_2} u(\ln(w),t)dw$.

3.1.1. Balance

At time t, the number of fish in the weight range $[w_1,w_2]$ is $\int_{x_1}^{x_2} u(x,t)dx$.

During the time interval $[t,\ t+dt]$, some fish die and the remaining number of fish is $\int_{x_1}^{x_2}(1-\mu(x,t)dt)u(x,t)dx$ where $\mu(x,t)$ is the mortality rate of fish at weight e^x. In the same time, the remaining fish grow at the growth rate $g(x,t)$ until the weight range $[x_1+g(x_1,t)dt,$ $x_2+g(x_2,t)dt]$ and their number is: $\int_{x_1+g(x_1,t)dt}^{x_2+g(x_2,t)dt} u(x,t+dt)dx$. Equating the numbers and deriving with respect to dt and x_2, we get the fundamental equation:

$$\frac{\partial u}{\partial t} = -\frac{\partial(gu)}{\partial x} - \mu u \qquad\qquad \text{(1) (see Silvert and Platt, 1980).}$$

3.1.2. Predation, mortality and growth

Each predation event implies two individuals: the predator (weight e^y) will grow, the prey (weight e^x) will die. The volume searched is assumed to be an allometric function of weight: $Ae^{\alpha y}dt$ (Ware, 1978), hence the number of encounters with potential preys of weight in $[e^x,e^{x+dx}]$ is $Ae^{\alpha y}u(x,t)dtdx$. When two individuals meet, the probability that a predation happens is given by a function φ that depends only on the ratio of the weights $e^q=e^{y-x}$. We do not assume a particular shape for φ, it just has to be positive and dome-shaped. The distribution of predation events is given by $Ae^{\alpha y}\varphi(y-x)u(x,t)u(y,t)dxdydt$.

From the point of view of the prey, this gives the mortality rate by predation:

$$\mu(x,t) = Ae^{\alpha x}\int_{-\infty}^{\infty} e^{\alpha q}\varphi(q)u(x+q,t)dq \qquad\qquad (2)$$

If the biomass ingested is used to grow with a constant efficiency K, the growth rate of the predator is

$$g(y,t) = KAe^{\alpha y}\int_{-\infty}^{\infty} e^{-q}\varphi(q)u(x-q,t)dq \qquad\qquad (3)$$

Combining equations (1), (2) and (3), and allowing for an allometric non-predation density-dependent mortality rate $\mu_0 e^{\alpha x}u(x,t)$, we obtain the model

$$\frac{\partial u}{\partial t}(x,t) = \begin{aligned} &-\frac{\partial}{\partial x}\left[KAe^{\alpha x}\int_{-\infty}^{\infty} e^{-q}\varphi(q)u(x-q,t)u(x,t)dq\right]\\ &- Ae^{\alpha x}\int_{-\infty}^{\infty} e^{\alpha q}\varphi(q)u(x+q,t)u(x,t)dq - \mu_0 e^{\alpha x}u(x,t)^2 \end{aligned} \qquad (4)$$

3.2. Predictions

3.2.1. Stationary solution

Lemma There exists a unique real λ such that for any u_o, the function $u(x,t)=u_0 e^{\lambda x}$ is a solution of equation (4). This λ is the unique real solution of

$$(2\lambda+\alpha)K\int_{-\infty}^{\infty} e^{-(\lambda+1)q}\varphi(q)dq + \int_{-\infty}^{\infty} e^{(\alpha+\lambda)q}\varphi(q)dq + \frac{\mu_0}{A} = 0 \quad (5)$$

Moreover, $\lambda < -\alpha/2$ (see proof in Benoît and Rochet, In press).

3.2.2. Sensitivity analysis

The slope λ of the stationary size spectrum was computed from equation (5) for a variety of published parameters (Table 1). 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 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 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 w is related to body length L 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).

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.

Table 1: Values of the parameters used in the simulations below, and sensitivity of the slope of the stationary size spectrum to these parameters.

| Parameter	n	e^{q_0}	α	K	μ_0	λ
Definition	Inverse width of pred/prey size ratio distribution	Mode of pred/prey size ratio	Exponent of w in vol. searched	Growth efficiency	Non-predation mortality rate	Slope of the stationary size spectrum
Sources	C, D	C, D, V, W	W	B, P, W	(1)	
Baseline values	5	100	0.82	0.2	80	-1.050
	10	100	0.82	0.2	80	-1.059
	1	100	0.82	0.2	80	-1.012
	5	**1000**	0.82	0.2	80	-1.011
	5	**10**	0.82	0.2	80	-1.157
Sensitivity	5	100	**0.6**	0.2	80	-0.956
analysis	5	100	**0.9**	0.2	80	-1.085
of	5	100	0.82	**0.1**	80	-1.110
λ	5	100	0.82	**0.6**	80	-0.956
	5	100	0.82	0.2	**0**	-1.044
	5	100	0.82	0.2	**200**	-1.059
	10	**10**	**0.9**	**0.1**	**200**	-1.371
	10	**1000**	**0.6**	**0.6**	**0**	-0.838

Sources for the estimations: B (Buckel *et al.*, 1995), C (Cohen *et al.*, 1993), D (Daan, 1973), P (Paloheimo and Dickie, 1966), V (Vignes, 1998), W (Ware, 1978).

(1) μ_0 was set such that the non-predation mortality rate for a 500 g fish be 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) (Andersen and Ursin, 1977; Gislason and Helgason, 1985; Gislason, 1999; Anonymous, 2002).

4. Results: simulations and the effects of fishing

4.1. Effects of various "natural" perturbations

Size spectra were simulated using C++ on a Personal Computer with an order 4 Runge-Kutta method and log weight x discretised by an elementary method. The process parameters were selected in Table 1. A first series of simulations was run to check that the results conform to the theoretical expectations. Linear spectra $u_0 e^{\lambda x}$ were found to be stationary. 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 (Figure 1). 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 (Figure 2), and may result in infinite values if their amplitude is too large.
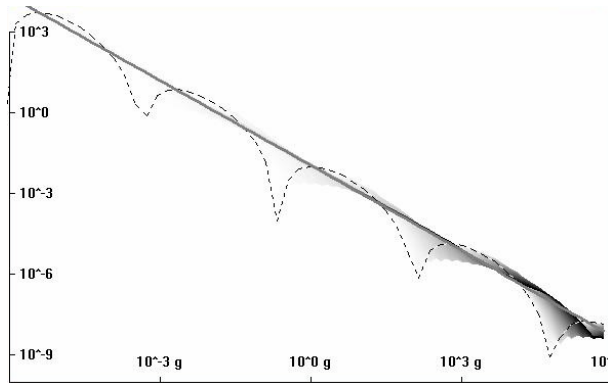
Figure 1: Simulated size spectrum using baseline parameters from Table 1, and an oscillatory initial spectrum. Dashed line: initial conditions. Grey bold line: stationary solution. The model solution for successive time steps is plotted with a grey shading from white (1st time step) to black (last time step).
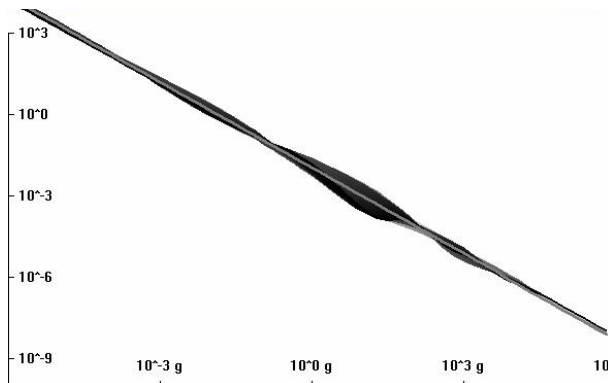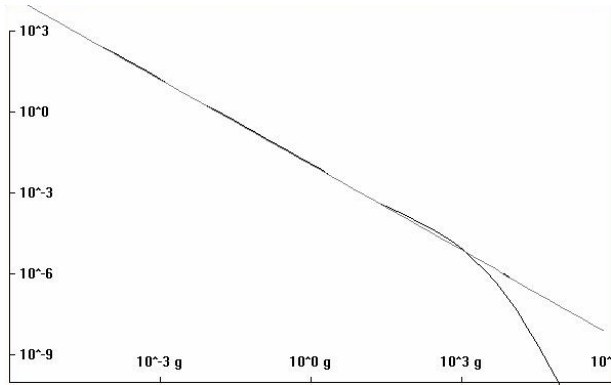

Figure 2: Simulated size spectrum using baseline parameters from Table 1, and an oscillatory plankton input.

4.2. Effects of fishing

We simulated exploitation by adding a size-dependent fishing mortality rate $\mu_f(x,t) = \max\left(0, a(x-b)\right)$ which is a linearly increasing function of log weight with recruitment to fishing at weight e^b. The parameters a and b were estimated by linear regression of the fishing mortality rate F at age versus log weight at age, combining all stocks assessed by the ICES Stock Assessment Working Groups in the North Sea and Bay of Biscay (Anonymous, 2000b; Anonymous, 2000a). The resulting estimates ($\hat{a} = 0.1y^{-1}, \hat{b} = \ln(10)$) were not found to differ significantly between the two ecosystems.

A strong fishing mortality starting at weight 1 g causes a change in slope for weights larger than 10 kg (Figure 3). However, a more realistic fishing mortality as estimated from real fisheries has no apparent effect on the slope of the spectrum, but rather on its curvature (Figure 4). This effect is not larger than the oscillations created by perturbations added to the model, which have a fairly large amplitude (Figure 5).

Figure 3: Simulated size spectrum using baseline parameters from Table 1, and a strong fishing mortality ($a = 0.5y^{-1}, b = \ln(1)$).
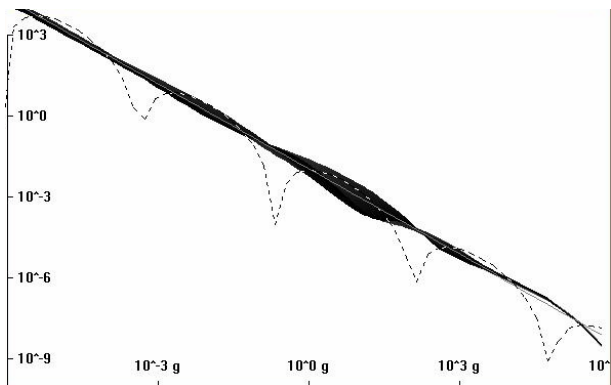
Figure 4: Simulated size spectrum using baseline parameters from Table 1, an oscillatory plankton input, oscillatory initial condition, and a realistic fishing mortality ($\hat{a} = 0.1y^{-1}, \hat{b} = \ln(10)$).
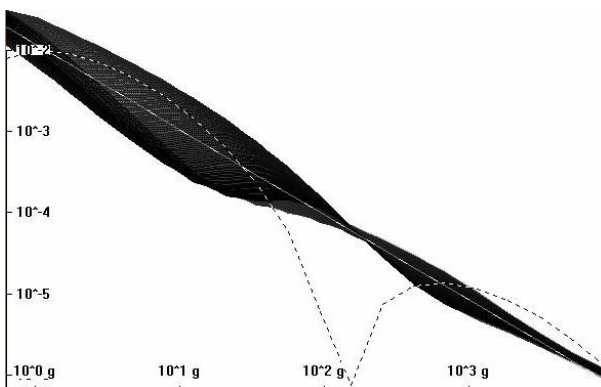
Figure 5: Same as Figure 4, focused on a fish-like size range.

5. Discussion

Generally, all studies reviewed here confirm the qualitative prediction about size spectra: fishing will make them steeper. A closer scrutiny reveals two types of quantitative predictions.

Purely size-based models' first purpose was to find the necessary conditions for the size spectrum to be regular, and, more specifically, linear. This can be met, assuming appropriate regularities in the processes that govern the flow of biomass up the food web. The progress from the initial models (Kerr, 1974; Platt and Denman, 1978) until the one presented here (Benoît and Rochet, In press) has been the continuous improvement of the realism of the assumptions. However, these assumptions remain quite general and extreme. Even if there is now a general agreement that predation in the marine environment is mainly opportunistic and that prey choice is guided by size and availability more than anything else, assuming that it is purely size-based is somewhat of a caricature. Moreover, assuming that the width of prey distribution is independent of predator size, that allometric exponents are similar for predation and non-predation mortalities and hold from plankton to whales are oversimplifying assumptions. However, these models help understand why size spectra might be regular. Given this regularity, simulating the effect of fishing gives consistent results for

continuous models: in a perfectly size-based world, exploitation would make size spectra curved instead of linear; fishing would decrease the linearity of size spectra.

On the other hand, more realistic models were developed with the objective of examining the effect of fishing on fish size spectra. In these models, predation or at least life history characteristics are not purely size-based but also include taxonomic differences. The exploitation-free size spectra simulated by these models are not exactly linear, but curved downwards, and may include oscillations. The predicted effect of fishing is to affect size spectra slope, if one is willing to see the spectrum as linear. However, this is less clear if the spectrum is assumed curvilinear, and fishing might well affect the curvature rather than the slope of the spectrum

The results of both types of models are thus consistent: in a perfectly size-based undisturbed world, size-spectra would be linear. Adding any kind of perturbation or diversity (*ie*, adding more realism) decreases their linearity and regularity. Among these perturbations, fishing is no exception. This is the reason why using size spectra slopes for monitoring fishing impacts is not necessarily a good idea: increased perturbation (fishing or other) will decrease the appropriateness of the linear model necessary to estimate the slope, hence will decrease the quality of the slope estimate.

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