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A mathematical derivation of size spectra in fish populations

Ovide Arino [a], Yunne-Jai Shin [b], Christian Mullon [a,c,*]

[a] *UR GEODES, IRD-Bondy, 32, av. Henri-Varagnat, 93143 Bondy, France*
[b] *IRD, Centre de recherche halieutique, av. Jean-Monnet, BP 171, 34203 Sète, France*
[c] *University of Cape Town, South Africa*

Abstract

Taking into account a predator/prey size ratio in a size-structured population model leads to a partial derivative equation of which we study the properties. By expliciting the structure of the attractor of this equation, it is shown that a simple mechanism, size-based opportunistic predation, can explain the stability in the shape of size spectra observed in various marine ecosystems. *To cite this article: O. Arino et al., C. R. Biologies 327 (2004).*
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Résumé

Une approche mathématique du spectre de taille des populations de poissons. La prise en compte, dans un modèle de populations structuré en taille, des rapports de taille entre proies et prédateurs conduit à une équation aux dérivées partielles dont nous étudions les propriétés. En explicitant la structure de l'attracteur de cette équation, nous montrons comment un mécanisme simple, la prédation opportuniste fondée sur la taille, peut conduire à la stabilité de la forme des spectres de taille observés dans différents écosystèmes marins. *Pour citer cet article : O. Arino et al., C. R. Biologies 327 (2004).*
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1. Introduction

The term 'size spectrum', or variants of it such as 'size distribution' or 'asynchronous steady state', can be met in a variety of contexts, from soil science to cell biology, and in almost all domains of science dealing with population dynamics.

The basic concept is as follows: consider a population described using a structure variable, which may be mono- or multi-dimensional, age, size, weight, concentration of a certain chemical element, or whatever. Then, in many situations, the population will behave in the long range in such a way that the proportion of a given size class within the total population approaches a fixed value independent on the initial state

* Corresponding author.
E-mail addresses: arino@bondy.ird.fr (O. Arino), shin@ird.fr (Y.-J. Shin), christian.mullon@bondy.ird.fr (C. Mullon).

of the population. In demography, it is the age pyramid, where a given age range represents a proportion of the total population, invariant through several census periods, provided that environmental conditions in a broad sense have not changed in the meantime; in cell biology, cells of a given line growing in a culture reach a state where the ratio of cells in any of the various stages (G_1, S, G_2, M) to the total population is approximately constant and again independent on the initial population; in oceanography, the particle-size spectrum describes the distribution of particles in a volume of water as a function of their size. The size of a particle is an important indicator of the physical processes that act on the particle: aggregated phytoplankton cells gain in density and may reach the sea bed more easily than isolated cells [1]. The present work focuses on fish size spectra in marine ecosystems. The most documented representation of the size spectra regarding the number of reported ecosystems is the logarithm of the fish numbers within each size class versus the logarithm of the median size of the size class (e.g., [2,3]). Using this representation, the size spectrum is usually a linear decreasing function of the size of the organisms. This shape is recurrent and is observed across various marine ecosystems. Furthermore, the shape of the size spectra is remarkably stable through time despite varying species composition in fish communities. Our goal is to study a possible mechanism accounting for the stability of size spectra in fish populations, namely, opportunistic predation of fish on smaller fish, independent on the species identity. To this aim, a modelling approach will be performed, using a representation of the population in terms of density functions and proceeding according to mathematical analysis. We start with some considerations on the ecological issues related to the size spectrum in fish populations and communities.

2. Ecological foundations of size spectra in fish populations

Fish have been successful on Earth, as over half of all described vertebrates are fish [4]. Despite this species richness, strong environmental constraints imposed by living in an aquatic environment have produced converging streamlined body forms for most fish species, without the development of prehensile appendices [5]. This underlines a common physical constraint for predation within fish communities: a predator must have a jaw large enough to swallow its prey as a whole. As the size of the jaw is linked to body diameter, which is in turn related to fish length, due to hydrodynamic constraints [6], fish size is considered as the prevailing factor involved in predation and for insuring successful capture of prey [7,8]. The feeding strategy of fish can then be considered to be opportunistic, the diet composition depending more on the ratio of the size of the predator versus its prey and on the relative abundance of prey, rather than on species preferences [9]. Strong patterns that are observed in marine food webs can be related to this size-based predation behaviour. Firstly, fish species have multiple predators and multiple prey, and omnivory is common. Indeed, fish larvae generally feed at the base of the food web and when they become adults, they feed at one or several trophic levels below their own [2]. Secondly, cannibalism is frequent in fish communities and can represent an important source of pre-recruit mortality (e.g., [10–12]). Finally, eggs and larvae are all located at the base of piscivorous trophic levels [13]. A peculiarity of teleost eggs is, indeed, their rather homogeneous size, of about 1 mm, whatever species is considered [14]. Consequently, two species can be simultaneously a predator or a prey of each other, according to the stage in their life cycle (i.e., their size). For instance, in the Baltic Sea, cod is known to be a predator of herring, but it is also its prey, since adult herrings feed on cod pre-recruits [15].

This suggests that a broad range of marine ecosystems may have been structured through evolutionary times by a rather basic mechanism, namely, bigger fish eat smaller ones, which might have driven and shaped current marine size spectra. Our goal in this work is to study, using a modelling approach, whether such a simple mechanism such as size-based opportunistic predation can lead to the type of size spectra that are observed in marine ecosystems. Based on ecological observations presented above, different assumptions are made: the community under consideration is structured by a single parameter, the size; predation of members of the community is only exerted from within the community and is governed solely by size. We leave the possibility for food to be partly provided from sources external to the community: in particular, it can be made in part of particles smaller than the min-

imal size. Besides, two other processes also responsible for the energy transfer up pelagic foodwebs to larger-sized fish are modelled: somatic growth, which increases biomass transfer through predation; and reproduction, which impedes biomass transfer by moving biomass down the foodweb to smaller sizes.

3. A density model

3.1. Presentation of the model

The equation we consider had been proposed in a very closely related context in [16] as an extension of an empirical model due to [17,18]. A previous size-structured model including cannibalism was due to J.M. Cushing [19]. However, the study that follows is original to the extent we performed it, that is, not only we show the existence of a non-trivial steady state, a candidate for the size spectrum, but we also show the convergence of the transients towards the steady state, which is an essential feature of observed marine size spectra.

$$\frac{\partial N}{\partial t} + \frac{\partial}{\partial s}\big(f(s)N(s,t)\big) = -m(s)N(s,t)$$
$$- N(s,t) \int\limits_{s}^{+\infty} l(s,u)\,N(u,t)\,\mathrm{d}u \tag{1}$$

$$N(0,t) = \int\limits_{0}^{+\infty} n(s)\,N(s,t)\,\mathrm{d}s \tag{2}$$

s is the size or the biomass of an individual, $N(s,t)$ is the density of the population biomass with respect to the individual biomass at size s.

$$\int\limits_{a}^{b} N(s,t)\,\mathrm{d}s$$

is the total biomass of the individuals whose weight lies between the values a and b.

$m(s)$ is the natural mortality rate at size s.

$n(s)$ is the fecundity rate of individuals of size s.

$f(s)$ is the somatic growth rate of the biomass at size s.

$l(s,u)$ is the rate of predation of individuals of size s by individuals of size u.

3.1.1. Assumptions on f, m, n

The functions m, n and f are assumed to be non-negative, continuous and bounded. $\underline{m}$, respectively $\underline{n}$, denotes the infimum of m, resp. n, over its domain, that will be generally supposed the set of non-negative reals; $\overline{m}$, resp. $\overline{n}$, is the supremum of m, resp. n.

3.1.2. About the kernel l

The term $l(s,u)$, $s < u$, is either a function or a generalized function (a Schwartz distribution) which models the predation of fish of size u on fish of size s. The expression

$$\int\limits_{0}^{+\infty} N(u,t)\left(\int\limits_{0}^{u} l(s,u)\,N(s,t)\,\mathrm{d}s \right)\mathrm{d}u$$

represents the time rate of the biomass taken out by predation. Since most of this loss is used to sustain physiological functions of the predator, it is logical to assume that it is proportional to the predator biomass. The kernel $l(s,u)$ accounts for several effects: it is dependent upon the food diet of the predator, it should reflect the range of prey sizes that the predator chooses; it may also reflect the effort it takes the predator to access the desired prey and how much food it can extract from the prey. These various specifications make the modelling of the right kernel a difficult task, out of the scope of the present work. We will just mention a few cases: for most of the study, we will assume the following: $l \geqslant 0$, is measurable and bounded; when dealing with the existence of an attractor, we will take l as: $l(s,u) = \underline{l}(s)$, where $\underline{l}$ is a function of s only, increasing, positive and bounded. One can also mention the case of a linear relationship between prey size and predator size, the predator looking for a prey whose size is a fixed fraction of its own size.

In this case, we have $l(s,u) = \underline{l}(s)\,\delta_0(s - u/\alpha)$, with $\alpha > 1$, where δ_0 is the Dirac distribution at zero.

At the level of the total biomass, the only growth term is the birth term. Integrating Eq. (1) in s, we obtain:

$$\frac{\mathrm{d}}{\mathrm{d}t}\left(\int\limits_{0}^{+\infty} N(s,t)\,\mathrm{d}s \right) = f(0)N(0,t)$$
$$- \int\limits_{0}^{+\infty} \Big[m(s)N(s,t)$$

$$+ N(s,t) \int_s^{+\infty} l(s,u)\, N(u,t)\, \mathrm{d}u \Bigg]\, \mathrm{d}s \qquad (3)$$

which is in accordance with the above remark.

The function $f(s)$ that models the time growth rate of the biomass should be expressed at least in part as a function of the prey that has been captured. This would introduce a non-linearity in the first-order term and complications that we want to avoid here.

3.2. The linear equation

If in Eq. (1), we take $l = 0$, then the problem becomes linear. It is also the expression obtained by linearizing the equation near $N = 0$, which is obviously a solution of the equation. In the sequel, we refer to the linear equation as Eq. (1)$_0$ or Eq. (1)$_0$–(2).

3.3. The steady-state equation

Before proceeding further, we consider the steady-state equation associated with system (1), (2), that is to say, the equation obtained by assuming that the solution does not depend on time. The general expression of the steady state equation is as follows

$$\begin{cases} \dfrac{\mathrm{d}}{\mathrm{d}s}\big(f(s)\overline{N}(s)\big) \\[2mm] \quad = -m(s)\overline{N}(s) - \overline{N}(s) \displaystyle\int_s^{+\infty} l(s,u)\, \overline{N}(u)\, \mathrm{d}u \\[2mm] \overline{N}(0) = \displaystyle\int_0^{+\infty} n(s)\, \overline{N}(s)\, \mathrm{d}s \end{cases} \qquad (4)$$

In the particular case where $l(s,u) = \underline{l}(s)\,\delta_0(s - u/\alpha)$, the system becomes

$$\begin{cases} \dfrac{\mathrm{d}}{\mathrm{d}s}\big(f(s)\overline{N}(s)\big) = -m(s)\,\overline{N}(s) - \overline{N}(s)\underline{l}(s)\,\alpha\,\overline{N}(\alpha s) \\[2mm] \overline{N}(0) = \displaystyle\int_0^{+\infty} n(s)\, \overline{N}(s)\, \mathrm{d}s \end{cases}$$

Such an equation belongs to the class of differential equations with deviated arguments. Showing the existence of a positive solution in the general case is not easy. We will consider two special situations: (1) we first assume that $l(s,u) = \bar{l} = const$, $m(s) = \overline{m} = const$ and $f(s) = \bar{f} = const$; (2) in the second

case, we still assume $m(s) = \overline{m}$, but this time $l(s,u) = \lambda(s)\,\zeta(u)$ and $f(s)$ is expressed in terms of $\overline{N}(s)$. In both cases, we will take for n a one-parameter family of functions

$$n(s) = q\, n_0(s), \quad q \geqslant 0 \qquad (5)$$

Moreover, we assume, for technical reasons, that $n_0(s) = \mathrm{O}(s^2)$, in the vicinity of $s = 0$.

3.3.1. First case

Under the above-mentioned conditions on l, m and f, Eq. (4) reads $\bar{f}\,\dfrac{\mathrm{d}}{\mathrm{d}s}\overline{N}(s) = -\overline{m}\,\overline{N}(s) - \bar{l}\,\overline{N}(s) \times \int_s^{+\infty} \overline{N}(u)\, du$.

Defining $y(s) = \int_s^{+\infty} \overline{N}(u)\, du$, the equation in y reads

$$-\bar{f}\,\frac{\mathrm{d}^2}{\mathrm{d}s^2}\, y(s) = \overline{m}\,\frac{\mathrm{d}y}{\mathrm{d}s} + \bar{l}\,\frac{\mathrm{d}y}{\mathrm{d}s}\, y(s)$$

We are looking for positive solutions of this equation that, moreover, approach zero at ∞. Integrating the equation on both members leads to:

$$-\bar{f}\,\frac{\mathrm{d}y}{\mathrm{d}s} = \overline{m}\,y + \frac{1}{2}\,\bar{l}\,y^2(s)$$

As a consequence of the zero condition at ∞, the constant of integration is zero. One obtains a Bernoulli equation that integrates to:

$$y(s) = \frac{1}{\exp(\overline{m}s/\bar{f})[C + l\bar{f}/(2\overline{m})] - l\bar{f}/(2\overline{m})}$$

The constant C is equal to $1/y(0)$. From $\overline{N}(s) = -\mathrm{d}y/\mathrm{d}s$, we get:

$$\overline{N}(s) = \frac{\exp(\overline{m}s/\bar{f})[C + l\bar{f}/(2\overline{m})]\overline{m}/\bar{f}}{(\exp(\overline{m}s/\bar{f})[C + l\bar{f}/(2\overline{m})] - l\bar{f}/(2\overline{m}))^2}$$

In order to complete the calculation of $\overline{N}$, a value must be assigned to C, which is done by taking the equation of the newborns into account, namely:

$$\overline{N}(0) = \int_0^{+\infty} n(s)\, \overline{N}(s)\, \mathrm{d}s$$

Note that $C = +\infty$ corresponds to $\overline{N} = 0$. It is a trivial solution of the equation for all $q \geqslant 0$. Denote by q_0 the number defined by unique value of q for which

$$q_0 = \frac{1}{\int_0^{+\infty} q\, n_0(s)\exp(\overline{m}s/\bar{f})\, \mathrm{d}s} = 1$$

Then, using the intermediate value theorem, one can see that, for each $q > q_0$, there exists $C > 0$ such that the above compatibility condition holds. While, for a given q, the equation in C may have two, possibly more than two, solutions, a given C leads, in contrast, to a single solution in q.

If we represent a solution $\overline{N}$ for a value q by the pair $(q, \overline{N}(0))$, the set of solution pairs comprises the straight line $\overline{N}(0) = 0$ and an unbounded curve crossing it at the point $(q_0, 0)$, contained in the set $\{(q, v): q > q_0, \ v > 0\}$.

3.3.2. Second case

The assumptions on m and l are now

$$m(s) = \overline{m}, \qquad l(s, u) = s^\alpha \zeta(u) \qquad (6)$$

for some $\alpha > 1$ and some function $\zeta(u)$ to be determined.

$\int_0^u l(s, u) \overline{N}(s) \, ds$ is the biomass consumed in the group of size u per unit of mass of the group, per unit of time.

In this example, we assume that a fraction γ of the food absorbed is transformed into increased biomass. So, the growth rate reads as follows: $f(u) = \gamma \int_0^u l(s, u) \overline{N}(s) \, ds$, which leads to the equation:

$$\frac{\mathrm{d}}{\mathrm{d}s}\left(\left[\int_0^s u^\alpha \overline{N}(u) \, \mathrm{d}u\right] \gamma \, \zeta(s) \, \overline{N}(s)\right)$$
$$= -\overline{m} \, \overline{N}(s) - \overline{N}(s) \, s^\alpha \int_s^{+\infty} \zeta(u) \, \overline{N}(u) \, \mathrm{d}u$$

where we have substituted for m and l their expressions given in (6).

Looking for a solution such that $\int_s^{+\infty} \zeta(u) \overline{N}(u) \, \mathrm{d}u = K/s^\alpha$, using standard algebra, we arrive at the following expressions for $\zeta(s)$ and $\overline{N}(s)$:

$$\zeta(s) = \frac{[(\overline{m} + K)s + \alpha \, \gamma \, K]^{\alpha+2}}{\alpha \, (\alpha + 1) \, \gamma \, K \, s^{\alpha+1}} \qquad (7)$$

$$\overline{N}(s) = \frac{\alpha^2 \, K^2 \, (\alpha + 1) \, \gamma}{[(\overline{m} + K)s + \alpha \, \gamma \, K]^{\alpha+2}} \qquad (8)$$

As for the first example, in order to ensure existence of $\overline{N}(s)$, it remains to verify the condition $\overline{N}(0) = \int_0^{+\infty} n(s) \overline{N}(s) \, ds$.

Keeping in mind that $n(s) = q \, n_0(s)$ then, for each given value of the parameters $(\alpha, \ \gamma, \ K, \ \overline{m})$, there is exactly one value of q,

$$q = q(\alpha, \gamma, K, \overline{m})$$

for which the above condition holds. If, on the other hand, one chooses the parameters q, α, γ, $\overline{m}$, then there may be zero, one or several values of K for which the equation has a solution satisfying formula (8). If, for example, one assumes n_0 to be integrable on the positive semi-axis, then there exists a threshold value for q below which the equation has no positive solution of the form (8), independently of $K > 0$. When the threshold is crossed, a positive solution emerges from the zero solution (and from $K = 0$).

3.4. Transient states

As soon as a steady-state solution is perturbed, even slightly, the corresponding solution becomes time-dependent, it goes through transient states to possibly come back to the previous steady state or approach another one or a more complex invariant subset. A complete understanding of what is going on is currently out of reach. The main result stated in Theorem 6.1 is just the easy part. The first step in the derivation of this result is to ensure that solutions of system (1), (2) do actually exist and are densities, namely, they remain non-negative all over their domain. This is the so-called Cauchy problem, which, in the present situation, is handled using a perturbation technique: the equation can in fact be decomposed into a sum of a linear and a non-linear part.

The linear part may be dealt with using a classical *semigroup* approach. The non-linear part is considered as a perturbation of the linear equation, making the whole problem a semilinear one. We refer the interested reader to the literature [20,21] for details about the treatment of such problems.

We summarize the relevant result as follows.

The work space is $X = L^1(0, +\infty)$, the space of Lebesgue integrable functions on the positive semi-axis. Given a non-negative function N_0 in X, system (1), (2) has a unique *integral* solution $N(s, t)$, defined and non-negative for all $t \geqslant 0$, such that the map $t \to N(\cdot, t)$ is continuous, with values in X and $N(0, \cdot) = N(0)$.

Solutions satisfy an integral form of the equation, obtained by applying a generalized variation of con-

stants formula, not the equation itself, unless the initial value is smooth enough. This is the reason for the expression *integral* in the above statement.

Our main interest is in looking at the qualitative features of the solutions. Again, we consider this issue using a perturbation approach. Indeed, the problem has $N = 0$ as a solution, and it is natural to start from this point: what happens if one takes an initial value close to 0? Will the solution go to 0? Answering this question requires investigating the stability of the linear equation. One would expect that in order to do so, we would just have to look at the spectrum of the operator defining the equation (which we occasionally call the *infinitesimal generator* or just the *generator* of the equation), as the characteristic polynomial of the matrix defining a linear o.d.e. provides the information about the asymptotic behaviour of the solutions of the o.d.e. However, the case is a little bit more intricate. First of all, the generator is not as simple as a matrix, and its spectrum is also rather wide.

Moreover, the solution operator does not have a property that would allow us to automatically translate information about the spectrum of the operator into the asymptotic behaviour of the solutions. In particular, the solution operator is not compact nor possibly compact. These problems have been overcome by using the notions of *quasi-compact* or *essentially compact* operators and *essential spectrum* [22,23]. We are not going into details of these issues here, it will be done elsewhere. We summarize in the next section results that are useful for application to the size spectrum.

4. Linear asynchronicity

The linear equation behaves asynchronically, which means that solutions tend to forget their past values and be distributed asymptotically according to the multiple of a distribution, the same for all the solutions. Mathematically, this corresponds to the fact that each solution can be written as a sum of a principal part and a remainder, where the principal part lives in a one-dimensional subspace of X. We first summarize in a proposition the main results regarding the spectrum of the generator.

Proposition 4.1. *The spectrum of the generator of Eq. (1)–(2)$_0$ is the union of a left complex half-plane*

and a finite collection of eigenvalues in the complementary half-plane with a leading real eigenvalue s_2, which is also an eigenvalue of the transposed operator. s_2 is the root with maximal real part of the characteristic equation:

$$\pi(\lambda)_{\text{def}} = 1 - \int\limits_0^{+\infty} n(s)\,\frac{f(0)}{f(s)}$$

$$\times \left(\exp - \int\limits_0^s \left[\frac{\lambda + m(\sigma)}{f(\sigma)} \right] d\sigma \right) ds = 0 \quad (9)$$

The function:

$$\phi_{s_2}(s) = \frac{1}{f(s)} \left(\exp - \int\limits_0^s \left[\frac{s_2 + m(\sigma)}{f(\sigma)} \right] d\sigma \right) \quad (10)$$

respectively,

$$\psi_{s_2}(s) = \exp \int\limits_0^s \frac{m(\sigma) + s_2}{f(\sigma)}\,d\sigma - f(0) \int\limits_0^s \frac{n(\sigma)}{f(\sigma)}$$

$$\times \exp \int\limits_\sigma^s \frac{m(r) + s_2}{f(r)}\,dr\,d\sigma \quad (11)$$

is an eigenvector of the generator, respectively its transposed operator, for the eigenvalue s_2. ϕ_{s_2} and ψ_{s_2} are positive $\forall s$. They are unique, up to the multiplication by scalars.

On occasion, we use the notation $\langle p, q \rangle$ to represent the integral over the interval $[0, +\infty[$ of the product of functions p and q.

Theorem 4.1. *Let ϕ be given in $L^1(0, +\infty)$, $\phi \geqslant 0$, $\neq 0$. Denote $N_\phi(s, t)$, or just $N(s, t)$, the solution of Eq. (1)$_0$–(2), starting from ϕ, that is, such that $N(s, 0) = \phi$. Then, the following asymptotic formula holds*

$$N(\cdot, t) = C \exp(s_2 t)\phi_{s_2} + o\big(\exp(s_2 - \varepsilon)t\big) \quad (12)$$

for some constant $C \geqslant 0$ where the expression $o(\exp(s_2 - \varepsilon)t)$ means that the quantity is infinitely smaller than $\exp(s_2 - \varepsilon)t$ near $t = +\infty$; $\varepsilon > 0$ can be chosen independently of ϕ. Finally, $C > 0$ if $\phi \geqslant 0$, $\neq 0$.

Suppose ϕ is a non-zero density. Integrating (12), the asymptotic formula can be extended to the total population:

$$\int\limits_0^{+\infty} N(s,t)\,\mathrm{d}s = C\exp(s_2\,t)\int\limits_0^{+\infty}\phi_{s_2}(s)\,\mathrm{d}s$$
$$+\,\mathrm{o}\big(\exp(s_2-\varepsilon)t\big)$$

Dividing the solution $N(s,t)$ by the total population at time t, using the asymptotic formulas of both N and the total population, one arrives at:

$$\frac{N(s,t)}{\int_0^{+\infty} N(\sigma,t)\,\mathrm{d}\sigma} = \frac{1}{\int_0^{+\infty}\phi_{s_2}(\sigma)\,\mathrm{d}\sigma}\phi_{s_2}(s)$$
$$+\,\mathrm{o}\big(\exp(-\varepsilon)t\big) \tag{13}$$

Formula (13) is the exact representation of the size-spectrum property, in the linear case, though it shows that all relevant solutions behave asymptotically so as to reach a fixed distribution, each of the various size classes converges to a fixed proportion of the total population, the same whatever the initial population was.

In addition, the formula for the total population shows that it grows or decays as $\exp(s_2 t)$. As long as $s_2 < 0$, the solutions vanish asymptotically. This property extends to small solutions of the non-linear equation. Of course, this situation is of little interest for the purpose of determining the size spectrum. In the real ecosystem, the situation has, at least at the scale of evolution, proved to be rather expanding, that is, $s_2 \geqslant 0$. It could be of some interest to use the characteristic equation (9) to determine whether s_2 being non-negative is indicative of any particular property satisfied by the parameters, which would, in turn, reflect some property of the real system. We are not going to address this issue here, or rather we consider it from a theoretical point of view: assuming that s_2 can be pushed up so that it crosses the value 0, we explore consequences of the change in the stability of 0 on the possible onset of a size spectrum in the non-linear model. Two approaches, a local and a global ones, are presented.

5. Local study

The local study is in the frame of the bifurcation theory: given a system of equations depending on one or several parameters, which has 0 as a solution for all values of the parameters, one looks for non-trivial steady states arising in the vicinity of 0. As parameters, here, we may consider the functions that enter the definition of the system, that is, the family (f,l,m,n). Non-trivial steady states will only emerge near parameter values for which $s_2 = 0$. Note that formula (9) does not depend on l, so we may discard l from the list.

Set

$$\tilde{p} = (f,m,n)$$

and define

$$\Gamma(\tilde{p})(\lambda)\underset{\mathrm{def}}{=}\pi(\lambda)$$

and

$$\gamma(\tilde{p})\underset{\mathrm{def}}{=}\Gamma(\tilde{p})(0)$$

Then, the values of interest are those for which

$$\gamma(\tilde{p}) = 0 \tag{14}$$

That we can restrict our attention to the points for which $\lambda = 0$ is a root is due to the linear solution operator being positive: so, there is only one (up to the multiplication by a scalar) positive eigenvector and the corresponding eigenvalue dominates the spectrum. Condition (14) is not sufficient to ensure existence. An additional condition (sufficient) for a bifurcation to take place at $\tilde{p}_0$ is that the following (transversality) condition holds

$$D_{\tilde{p}}\gamma(\tilde{p}_0) \neq 0 \tag{15}$$

The set of parameters $\tilde{p}$ is very large: it is in fact possible to restrict it to a finite dimensional space. Indeed, we could assume that the functions f,m,n depend on other *environmental* parameters, such as the average temperature, or the salinity, or whatever:

$$\tilde{p} = \tilde{p}(e_1,\ldots,e_k)$$

The reals e_i are environmental parameters. In most cases, it is enough to consider one parameter at a time, that is, $k = 1$.

Introducing the function

$$\beta(e_1,\ldots,e_k)\underset{\mathrm{def}}{=}\gamma\big(\tilde{p}(e_1,\ldots,e_k)\big) \tag{16}$$

in terms of β, the following is a sufficient condition for bifurcation at some value e^0:

$$\beta(e^0) = 0, \qquad \nabla\beta(e^0) \neq 0 \tag{17}$$

While the above condition entails existence of non-zero steady states, it leaves two open questions: are the steady states found this way positive, as they should be? Are they stable? In fact, the two questions are linked, somehow. In order to answer them, we use the centre manifold theorem that, roughly, states that the dynamical properties of the equation near 0, for a parameter value e^0 such that $\beta(e^0) = 0$, are the same as those of a low dimensional dynamical system, of dimension $k + 1$, filling up a $(k + 1)$th dimensional manifold Σ, and both systems have the same steady states in a small-enough neighbourhood of $(0, e^0)$. Σ is tangent at $(0, e^0)$ to the vector space sum of span$\{\phi_0\}$, where ϕ_0 is computed according to formula (10), with $\tilde{p} = (\tilde{e}^0)$, on the one hand, and, on the other hand, the space of parameters (e_i). A generic element in Σ reads (N, e), where e is a kth-fold parameter, close to e^0 and:

$$N = u\phi_0 + Q(u, e), \quad Q = o(|u| + \|e - e^0\|) \tag{18}$$

On Σ, system (1), (2) reduces to a scalar ordinary differential equation governing the variation of the component u of the generic element, rather a k-parameter family of o.d.es, which all have $u = 0$ as a trivial solution, and 0 changes from stable to unstable when the parameter e goes from one side to the other of the parameter plane passing through the point e^0 perpendicular to the vector $\nabla\beta(e^0)$. From this fact, it is possible to deduce the existence of a steady state other than 0 for the o.d.e. The nature of the non-linearity leads to the following theorem.

Theorem 5.1. *The non-negative solutions other than* 0 *arising near* 0 *occur for values of the parameter e for which $s_2(e) > 0$, therefore, they are stable.*

6. Global study

Prior to this, some comments about the nature of the solution operator are in order.

In part due to the framework chosen here, that is, the fact that the work space is made up of functions integrable over an unbounded domain, the solution operator lacks a standard property, namely, compactness for large t. A good part of the effort spent in the theoretical study has consisted in finding a substitute for the lacking compactness. For the linear equation, essential compactness was proved. Going back to the non-linear equation, the variation of constants formula together with some additional assumptions allows us to take advantage of the property of the linear equation and derive a general asymptotic result.

The next theorem collects two main features: ultimate boundedness of the solutions, on the one hand (that is to say, the fact that all the solutions are bounded above by a same finite number at $+\infty$) and a general description of their asymptotic behaviour, on the other hand.

Theorem 6.1. *Assume, in addition to the above-standing hypotheses on m, n and f, that there exists a function $\underline{l}(s)$ such that $l(s, u) \geqslant \underline{l}(s)$, where $\underline{l}$ is increasing and bounded and $\underline{l}(0) > 0$. Then,* (i) *each non-negative solution of system* (1), (2) *is bounded* (*in the sense that the integral in s is bounded uniformly in t*) *with ultimate bound R,*

$$R = \frac{2(f(0)\bar{n} - \underline{m})}{\underline{l}(0)} \tag{19}$$

if $R > 0$. All the solutions approach 0 if $f(0)\bar{n} \leqslant \underline{m}$
   (ii) *under the following condition*

$$\frac{4(f(0)\bar{n} - \underline{m})}{\underline{l}(0)} \sup_{u \geqslant s \geqslant 0} l(s, u) < \underline{m} \tag{20}$$

system (1), (2) *has a* (*unique*) *compact attractor, that is to say, a set $\mathcal{A}$, invariant, compact and connected, which is also maximal amongst sets having all these properties, such that, $\forall N_0 \geqslant 0$, the solution of the system starting from N_0 approaches asymptotically the set $\mathcal{A}$. Moreover, the convergence is uniform in each subset of uniformly bounded initial values.*

6.1. Nature of the attractor

The attractor is compact and connected: as long as $f(0)\bar{n} \leqslant \underline{m}$, it consists of a single point. Let us see how the situation changes as the parameter q entering the formula of n (5) is augmented.

The zero equilibrium becomes unstable past a certain value of q; beyond this value, the attractor

grows, a non-zero steady state arises in the vicinity of 0. Since the attractor is connected, it cannot be limited to a finite number of steady states: it is indeed infinite. One possibility is that apart from 0 and the non-trivial steady state, the equation has one or several curves connecting 0 to the other steady state; for example, it can be a solution that approaches 0 as $t \to -\infty$ and the non-trivial steady state as $t \to +\infty$. In this case, all non-negative solutions but 0 converge asymptotically to the non-trivial steady state, which corresponds to the size-spectrum property. Note that the emergence, near 0, of a non-trivial solution is indeed a consequence of 0 becoming unstable near some values of the parameters: using formula (9), the m, n, f where a change of stability occurs are given by

$$\int_0^{+\infty} n(s) \frac{f(0)}{f(s)} \left(\exp - \int_0^s \left[\frac{m(\sigma)}{f(\sigma)} \right] d\sigma \right) ds = 1 \qquad (21)$$

In particular, with $n = q\, n_0$, there is exactly one value of q for which formula (21) holds. We now discuss the issue of whether one can have at the same time the instability of 0 and the preservation of the attractor, which will ensure that the non-trivial equilibrium is stable. Instability of 0 is equivalent to the inequality:

$$\int_0^{+\infty} n(s) \frac{f(0)}{f(s)} \left(\exp - \int_0^s \left[\frac{m(\sigma)}{f(\sigma)} \right] d\sigma \right) ds > 1$$

and is implied by

$$\frac{\underline{n}}{\overline{m}} f(0) > 1$$

Combining the above inequality and (20), we obtain the following sufficient condition

$$\frac{\overline{m}}{\underline{n}} < f(0) < \frac{5m}{4\overline{n}}$$

Eliminating $f(0)$, we arrive at a condition involving m and n only:

$$\frac{\overline{m}}{\underline{m}} \frac{\overline{n}}{\underline{n}} < \frac{5}{4}$$

The condition looks somehow restrictive: this in fact is proportionate to the conclusion it allows, that is to say, global stability of the non-trivial solution in some parameter range. No condition is necessary for local stability.

7. Conclusion

In this paper, we discussed the existence of stable size spectra in fish populations. By means of mathematical analysis, we investigated a classical size-structured model of fish dynamics, which is mainly based on the hypothesis that predation is a size-based process. Depending on some estimates on the parameters and functions of the model, we showed that either the whole system collapses asymptotically or a non-trivial equilibrium emerges, which is at least a local attractor. Exact computation of that equilibrium, which is indeed the desired size spectrum is out of reach of the mathematical analysis, although we have provided examples where such a computation can be made. Numerical as well as computer approaches have been undertaken and simulations have been run. The analysis performed here explains some of the simulation findings and gives indications on what can be expected according to the location of the parameters: in some simulations, the population goes to extinction. This might reflect the fact that the parameters are in the range of stability of the zero equilibrium. Although we have restricted the study to the first bifurcation, a quick inspection of the linearization near a non-trivial equilibrium suffices to see that the situation is likely to become complicated, with unstable oscillations occurring most probably. Such complications do not seem to have been perceived by simulations and are, together with improving on the model, in our plans for future research.

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