How optimal life history changes with the community size-spectrum

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This paper derives optimal life histories for fishes or other animals in relation to the size spectrum of the ecological community in which they are both predators and prey. Assuming log-linear size-spectra and well known scaling laws for feeding and mortality, we first construct the energetics of the individual. From these we find, using dynamic programming, the optimal allocation of energy between growth and reproduction as well as the trade-off between offspring size and numbers. Optimal strategies were found to be strongly dependent on size spectrum slope. For steep size spectra (numbers declining rapidly with size), determinate growth was optimal and allocation to somatic growth increased rapidly with increasing slope. However, restricting reproduction to a fixed mating season changed optimal allocations to give indeterminate growth approximating a von Bertalanffy trajectory. The optimal offspring size was as small as possible given other restrictions such as newborn starvation mortality. For shallow size spectra, finite optimal maturity size required a decline in fitness for large size or age. All the results are compared with observed size spectra of fish communities to show their consistency and relevance.

Keywords: fisheries; predator–prey; size at maturity; offspring size

1. INTRODUCTION

In this paper we show how the distribution of organism sizes in an ecological community strongly affects the optimal life history strategy of any member species. This effect is intuitive but has not previously been investigated or quantified. It is important to understanding phenomena such as the effect of size-selective harvesting (e.g. trawl fishing) on exploited populations, the population effects of invading species and the evolution and character of life history strategies. The study of both life-history evolution and size spectra each have a long and distinguished past (Roff 1992; Kerr & Dickie 2001) but have never previously been brought together.

Both the survival of organisms (Sogard 1997) and the rate at which they can accumulate resources (Hjelm & Persson 2001) depend on their position in the size spectrum of the community. This is because body size relative to the community generally determines the number of potential predators faced and the number and size of potential prey available. An organism's position within a community size-spectrum depends on the allocation of resources to somatic growth, which is a life history decision variable. Meanwhile, the size of the population to which the organism belongs depends on the lifetime reproductive success (LRS) of its species in the context of the community size-spectrum. This is the product of the number of offspring produced and their individual probabilities of survival to reproductive maturity. Both of these quantities depend on growth and on the allocation of resources for reproduction, which is usually

assumed to be mutually exclusive to the allocation for growth (Law 1979; Charnov 2001b).

Denoting ψ as the fraction of resources allocated to reproduction as a function of mass or age (ζ), $(1 - \psi(\zeta))$ is devoted to growth. Since natural selection acts through LRS, which, for the above reasons, depends on $\psi(\zeta)$, we can expect evolutionary pressures to drive $\psi(\zeta)$ towards an optimal function of organism mass (or age) and can expect there to be an evolutionary stable strategy for $\psi(\zeta)$, given a particular community size-spectrum. This is also expected for the size–number trade-off (Smith & Fretwell 1974), described here by the optimal offspring size, m_0 , for a given reproductive allocation. Optimal offspring size sets the initial position in the community size-spectrum and will depend on the predation risk and food availability set by the spectrum.

Previous efforts to understand the evolution of life-histories under age or size-specific mortality have used arbitrary (Law 1979), quasi-empirical (Taborsky *et al.* 2003) or explicit predator–prey functions (Chase 1999) for mortality. Using a size-spectrum improves realism by generalizing the explicit predator–prey function. The community size-spectrum also gives an explicit account of resource abundance not previously seen in life-history models, enabling realistic calculations of growth rates and reproductive allocations.

In what follows, we take a size-spectrum model and use it to calculate size-dependent food intake and predation–mortality risk for a focal species. From these we find the optimal life history traits using dynamic programming (Houston & McNamara 1999; Bertsekas 2001) in a non-dimensional transformation of the model. This leads to a quantitative prediction of an evolutionary pressure exerted

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Table 1. The quantities and functions in the model with their dimensions, range and typical values (mass is designated 'M', length 'L' and time 'T').

	description	dimension	range	typical
κ	dimensional magnitude of the number spectrum	$M^{k-1} L^{-3}$	$\kappa > 0$	
β	ratio between prey mass and predator mass	—	$0 < \beta < 1$	0.01
γ	coefficient in clearance volume	$L^3 M^{-q} T^{-1}$	$\gamma > 0$	
k	exponent governing community spectrum	—	$k < q + 2$	
q	exponent governing clearance volume	—	$q > 0$	1
r	exponent governing maintenance cost	—	$r > 0$	0.7
δ	scaling constant for maintenance costs	$M^{1-r} T^{-1}$	$\delta > 0$	
m_p	pivot mass	M	$m_p > 0$	
m_+	characteristic mass-scale: stagnation mass	M	$m_+ > 0$	
t_+	characteristic time-scale	T	$t_+ > 0$	
$e(m)$	available energy to an individual of size m	$M T^{-1}$	$e(m) > 0$	
$p(m)$	density of individuals with regard to mass and volume	$M^{-1} L^{-3}$	$p(m) > 0$	
$v(m)$	encounter kernel (clearance volume)	$L^3 T^{-1}$	$v(m) > 0$	
$\mu(m)$	mortality of an individual of size m	T^{-1}	$\mu(m) > 0$	
α	intake efficiency	—	$0 < \alpha < 1$	0.3
ϕ	dimensionless intake/mortality coefficient	—	$\phi > 1$	
$V(m)$	fitness, assuming no growth in future	M	$V(m) > 0$	
$W(m)$	fitness, assuming optimal growth	M	$W(m) > 0$	

by changes in community size spectra (e.g. through size-selective harvesting or species introduction or removal).

2. MODEL DESCRIPTION

We take our inspiration from the marine environment but the principles derived are general, given some basic assumptions.

We take the independent variable describing the state of an individual to be its mass (m). (Since we assume deterministic growth, that is, a one-to-one relationship between age and mass, the same results would be obtained with age as with the independent variable, but with slightly less elegance). Throughout, we assume a well-mixed environment so the model is essentially non-spatial. For simplicity, we shall refer to a three-dimensional space, though the model is equally valid in zero, one or two dimensions.

The model is founded on the assumption of an ecological community described by a log-linear size spectrum (Silvert & Platt 1978; Benoit & Rochet 2004),

$$p(m) = \kappa(m/m_p)^{-k}, \quad (2.1)$$

that gives the number of individuals per size group. Such power-law spectra form the null hypothesis in most fisheries studies (Bianchi *et al.* 2000; Jennings & Mackinson 2003; Shin & Cury 2004). The pivot mass m_p is included so that we can later let the slope k of the spectrum vary; the spectrum then stays constant at the mass $m = m_p$. Note that we take this community spectrum and its parameters as externally given; we do not aim to derive it.

(a) Growth and mortality of the individual

Given the community spectrum described by equation (2.1), the growth of an individual is determined by predation on smaller individuals while mortality stems from predation by larger ones.

We assume that individuals with mass m prey on individuals in the size range from βm to $\beta m + \Delta \beta m$. Here β is the prey/predator mass ratio, typically between 0 and 1

as animals tend to feed on smaller prey. The parameter Δ is the relative width of the size selection; a larger Δ implies a less discriminate or less size-specialized predator. We have chosen a square selection function of small width ($\Delta \ll 1$) for technical simplicity; other shapes would lead to similar results but at greater effort (see Benoit & Rochet 2004).

Predators are assumed to eat all encountered prey in their selected size range, so their intake is governed by the clearance volume

$$v(m) = \gamma m^q, \quad (2.2)$$

with dimensions volume per time, which may be derived from perception radius and relative speed of movement. A predator of size m then encounters prey with the rate

$$v(m)p(\beta m)\Delta\beta m + o(\Delta). \quad (2.3)$$

Here $o(\Delta)$ represents terms in a Δ of second order or higher and may be ignored when we assume $\Delta \ll 1$.

Thus, the energy (measured in units of mass) absorbed by the individual per unit of time is

$$E(m) = \alpha v(m)p(\beta m)\Delta\beta^2 m^2, \quad (2.4)$$

where α is the intake efficiency, a parameter independent of mass which specifies the ratio of assimilated matter to ingested matter. Next, we assume that the cost of maintenance (equivalent to respiration loss) is approximated by the metabolic rate, which scales as

$$M(m) = \delta m^r. \quad (2.5)$$

By combining the previous equations we obtain the energy (measured in mass per time) which may be allocated between growth and reproduction

$$e(m) = E(m) - M(m) = \alpha \Delta \gamma \kappa m_p^k \beta^{2-k} m^{q-k+2} - \delta m^r. \quad (2.6)$$

For an individual of size m , mortality $\mu(m)$ results from predators in the size range $[m/(\beta(1+\Delta)), m/\beta]$. Consistency requires that the mortality of an individual equals

the total search volume of its predators

$$\mu(m) = v(m/\beta)p(m/\beta)\Delta m/\beta + o(\Delta). \quad (2.7)$$

This completes the dynamics of an individual. The parameters and other quantities in the model are listed in table 1 for convenience.

(b) Non-dimensionalization

We non-dimensionalize the equations by rescaling mass and time. As characteristic mass we take the stagnation mass m_+ , where all the energy is used for maintenance, that is, $E(m_+) = M(m_+)$ or

$$m_+ = \left(\frac{\alpha \gamma \kappa m_p^k \Delta \beta^{2-k}}{\delta} \right)^{1/(r-q+k-2)}. \quad (2.8)$$

This is well defined except when $r-q+k-2=0$. Among several obvious choices for the characteristic time, we make use of the mean expected future life time of an individual at mass m_+

$$t_+ = \frac{1}{\mu(m_+)} = \frac{\beta^{1+q-k}}{\Delta \gamma \kappa m_p^k} m_+^{k-q-1}. \quad (2.9)$$

We now introduce dimensionless mass $\tilde{m} := m/m_+$, time $\tilde{t} = t/t_+$ and energy

$$\tilde{e}(\tilde{m}) = \frac{t_+}{m_+} \tilde{e}(\tilde{m} \cdot m_+) \quad (2.10)$$

Similarly, $\tilde{E}$, $\tilde{M}$ and $\tilde{\mu}$ are now considered dimensionless. All quantities are dimensionless for the remainder of the paper and for the convenience of notation we drop the tilde so that, for example, $e(m)$ now means dimensionless available energy as a function of dimensionless mass. The final model consists of the non-dimensional available energy

$$e(m) = E(m) - M(m) = \phi(m^{q-k+2} - m^r) \quad (2.11)$$

and mortality

$$\mu(m) = m^{q-k+1}, \quad (2.12)$$

where the dimensionless coefficient ϕ , obtained by dividing the specific absorption rate $E(m)/m$ by the mortality, is

$$\phi = \alpha \beta^{q+3-2k}. \quad (2.13)$$

(c) Parameter values

The remaining parameters of the model are the scaling of the community spectrum k , the scaling of the clearance volume q , the scaling of the metabolism r and the dimensionless coefficient ϕ .

The precise value of maintenance scaling is a matter of debate, with values between 2/3 and 1 being suggested. We take $r=0.7$ (Peters 1983).

The scaling of clearance volume can be estimated by considering a fish cruising with velocity v and having a perception range r : $v(m) \propto v(m)r(m)^2$. Peters (1983) shows a scaling of swimming speed with mass for fishes between 0.136 and 0.35. If the perception range scales with length, then $r \propto m^{1/3}$ and we get the scaling of the clearance volume $q=0.8 \dots 1$. We use the upper limit, $q \approx 1$, as it fits with the generally used relation that swimming speed is proportional to the length of the fish.

The coefficient ϕ depends on the intake efficiency α and the prey/predator mass ratio β . Among organisms,

α ranges between 0.1 and 0.8 (Begon *et al.* 1996, pp. 731–738); our default value is $\alpha=0.3$. Prey to predator size ratios β have been extensively studied among fishes (Scharf *et al.* 2000). Most values lie between 0.001 and 0.1 in mass terms; cod (*Gadus morhua*) is a typical piscivore with half its diet being less than 0.01 body mass (Andersen & Ursin 1977), though it predate up to around 0.1 its body mass. Members of the intensively studied Ythan Estuary community (which includes most important body-cavity phyla) show an enormous range of preferred prey-to-predator mass ratios: between 10^{-8} and 0.1 (Leaper *et al.* 2001). However, there is a large cluster around 0.01, with the arthropod Crangon being typical as it takes prey between 0.1 and 0.001 (Emmerson & Raffaelli 2004). We shall use the value $\beta=0.01$ as a default.

Trenkel *et al.* (2004) show that estimates of community spectrum slope vary with season and sampling 'gear'. Jennings & Blanchard (2004) found k for fishes (only) in the North Sea to be close to 1.0, while Floeter & Temming (2003) reported values of k between 1.2 and 3.5, with a mean of 2.7, from large-scale North Sea surveys. Bianchi *et al.* (2000) report length spectrum slopes from other marine systems as between -4 and -7 , giving k from between 1.3 and 2.3. The spectra simulated by Shin & Cury (2004) implied k was between 1.36 and 2.33. Theoretical arguments for spectra that have not been fished suggest k is from 1 (Brown & Gillooly 2003) to 2 (Silvert & Platt 1980), although fishing is generally considered to steepen the spectrum (Gislason & Rice 1998).

As mentioned earlier, the stagnation mass m_+ has a singularity when $k=2-r+q=2.3$ for the chosen parameter values. At the singularity, the energy uptake has the same scaling with mass as the maintenance, that is, m^r . For k larger than this value, m_+ sets the maximally attainable size and the energy rate $e(m)$ will decelerate as it approaches m_+ . For shallow spectra ($k < 2-r+q$) m_+ sets the smallest size at which the intake exceeds the maintenance and the growth will accelerate from there on. This latter region of k is also lower bounded (see §3b) leaving only the narrow range $2.13 < k < 2.3$, so we will focus on the range $k > 2.3$ in what follows. We briefly consider the shallow slopes in §3e.

When we let slope k of the community spectrum vary, the spectrum stays constant at the pivot mass m_p . How a species is affected by variation thus depends on how this pivot mass compares to the characteristic mass of the species. We present below two situations: one in which the pivot mass is small ($m_p = 10^{-2.5} m_+$), so that a steeper spectrum implies less prey available, and one where the pivot mass is relatively larger ($m_p = 10^{-1.5} m_+$) so that a steeper spectrum implies more prey.

3. OPTIMAL LIFE HISTORY STRATEGIES

(a) Optimal life histories for general size-structured models

For now, we take the available energy e and the mortality μ to be general functions depending on individual body mass only. We first consider the classic question (Law 1979) of optimal size at maturity as the problem of optimal allocation of energy between growth and reproduction, assuming that the objective is to maximize individual fitness. Assuming a steady-state population, each newborn

female must expect to have exactly one female offspring during the course of her life. For the species to be impervious to invasion, no other life history strategy can result in a greater number of female offspring (Mylius & Diekmann 1995). Using energy allocation as a proxy for the number of offspring, the appropriate fitness measure is the expected total energy allocated to reproduction during the entire remaining lifespan (Houston & McNamara 1999; Charnov *et al.* 2001), denoted as $W(m)$.

In Appendix A we determine the optimal strategy and the resulting fitness using dynamic programming (Houston & McNamara 1999; Bertsekas 2001). The optimal strategy is to allocate all energy to growth until a certain mass m_* is reached, after which all energy is devoted to reproduction: that is, determine growth where the somatic growth ceases upon sexual maturation.

To characterize the size at maturity m_* , we first introduce $V(m)$ for the expected future reproductive effort, assuming all future energy is allocated to reproduction

$$V(m) = \frac{e(m)}{\mu(m)}. \quad (3.1)$$

With this, the size at maturity m_* is found from the condition (Taylor *et al.* 1974; Perrin & Sibly 1993)

$$V'(m_*) = 1, \quad (3.2)$$

which expresses a trade-off between large reproduction, given survival to maturation (suggesting that V should be maximized) and large probability of survival to maturation (suggestion that m_* should be minimized). The resulting fitness W is

$$W(m) = V(m_*) \exp\left(-\int_m^{m_*} \frac{1}{V(\xi)} d\xi\right), \quad m \leq m_*, \quad (3.3)$$

while $W(m) = V(m)$ holds when $m \geq m_*$. The latter term appearing in equation (3.3) is the probability of surviving to mass m_* , given (i) all energy is allocated to growth and (ii) survival to mass m . A sufficient technical requirement for these results is that V be concave with m .

Next, we turn to the offspring size to number trade-off, following Smith & Fretwell (1974) and considering the total fitness of the offspring. Letting the total mass of offspring be M and individual mass m_0 , then the number of offspring is M/m_0 and the total fitness of the offspring is $MW(m_0)/m_0$. It follows that the optimal recruit size solves the maximization problem

$$\sup_{m_0} \frac{W(m_0)}{m_0}. \quad (3.4)$$

Equation (3.4) is solved by finding a stationary point in the growth phase. Such a point is characterized by (Appendix A)

$$V(m_0) = m_0. \quad (3.5)$$

When V is concave, there can be at most one such point in the growth phase; this will then be the optimal offspring size.

We can now combine the results regarding optimal size at maturity and optimal offspring size. Together, they state that the function V must have the characteristics shown in figure 1 for an optimal life history to exist. It must start

Figure 1. Optimal life histories derived from a general function V . The optimal offspring size is where $V(m) = m$. The optimal size at maturity is where $V'(m) = 1$. The resulting life history displays an initial growth phase (thick solid line) that is terminated at the onset of reproduction when mass m_* is reached. The specifics of V outside the growth phase (thin solid line) are not important, as long as other locally optimal strategies are not introduced. Concavity of V would ensure this.

at a well-defined stationary offspring size, exhibit a growth phase and finally end with a reproductive phase.

(b) Life histories derived from the ecosystem size spectrum

We now insert the specific expressions for $e(m)$ and $\mu(m)$ from §2b that arise from the size spectrum of the ambient ecosystem, that is, equations (2.11) and (2.12), to obtain

$$V(m) = \phi(m - m^{k-q+r-1}). \quad (3.6)$$

It is important to note that if $\phi < 1$ then $V(m) < m$, except when $m=0$, in which case V cannot resemble figure 1. Thus, if $\phi < 1$, offspring size can never satisfy the stationarity condition (3.5): bigger will always be better. Although there may exist a point m_* with $V'(m_*) = 1$ such that, in principle, the criterion for optimal size at maturity is met, the resulting strategy will lead to a collapsing population. Thus, an individual with $\phi < 1$ is too inefficient to persist in this ecosystem model. Accordingly, we restrict our attention to the case $\phi > 1$ in the remainder of the paper. With equation (2.13), this implies a lower limit on slope k of the size spectrum, which for the chosen parameters is $k > 2.13$.

(c) Spectra with steep slopes, $k > 2 + q - r$

In this case m_+ represents the maximum attainable mass, so we only consider individuals with dimensionless mass in the interval $(0, 1)$. As figure 2a shows, the optimal size at maturity is well defined by the criterion $V'(m_*) = 1$, where

$$m_* = \left(\frac{\phi - 1}{\phi(k + r - q - 1)} \right)^{1/(k-q+r-2)}. \quad (3.7)$$

Figure 2. (a) an individual's fitness as a function of its mass for $k=2.8$ and $\phi=5$ (parameters chosen for clarity). To the left of the switching point, in the growth phase, the fitness is given by equation (3.3) (thick line). Also plotted is $V(m)$ (dashed line). To the right of the switching line, the fitness is $W=V$ (thin solid line); note that an individual behaving optimally never enters this region but stays at the switching point. (b) the dimensional size at maturity m_+/m_+ (normalized with m_+ , the stagnation mass corresponding to $k=2.5$), as a function of slope k for standard parameters, for two values of the pivot mass m_p . In the first case (solid line), the pivot mass $m_p=10^{-2.5}m_+$ when $k=2.5$. In this case, a steeper spectrum implies fewer prey and fewer predators during the growth phase and the result is maturation at smaller sizes. In the second case (dashed line), the pivot mass $m_p=10^{-1.5}m_+$ when $k=2.5$. In this case, a steeper spectrum implies more prey and fewer predators during the growth phase and the result is maturation at larger sizes. Also included is the corresponding results for the seasonal model of §3d (grey shaded zone); see the main text for explanation.

Figure 2b shows the dimensional mass at maturity, m_+/m_+ , as a function of k for two choices of the pivot mass m_p .

Finally, we can calculate the fraction of total energy used by a mature organism on reproduction (as opposed to maintenance)

$$\frac{e(m_*)}{E(m_*)} = 1 - \frac{\phi - 1}{\phi(k + r - q - 1)}. \quad (3.8)$$

For reference parameters, this becomes 0.43; that is, the resources are roughly equally divided between maintenance and reproduction.

Inserting the specific expressions for $e(m)$ and $\mu(m)$ into the optimization of offspring size, the objective function $W(m)/m$ in equation (3.4) tends to infinity as $m \rightarrow 0$, indicating that offspring mass should be minimal (zero in the theoretical limit). Clearly, there is a minimum offspring size given by physiological limits but it is also plausible that the feeding rate and mortality scaling laws break down for very small body mass. For instance, mortality due to starvation may be significant for the smallest individuals and even dominate the predation mortality, particularly in heterogeneous environments. Permitting these additional effects, a well-defined optimal offspring size m_0 is obtained as the solution to $\mu_s(m_0) = (\phi - 1)\mu_p(m_0)$, where μ_s is starvation mortality, μ_p is the predation mortality obtained with equation (2.12) and maintenance is assumed negligible for very small mass.

(d) Optimal recruitment strategies in a seasonal environment

Despite the determinate growth pattern obtained in the §3c, many species continue to grow after maturity, especially fishes (Takada & Caswell 1997).

There are several possible modifications of the model, which will result in a gradual shift from somatic growth to reproduction, seasonal variation over the year being a particular good example. Previous formulations have involved modifying mortality or growth during seasons (Heino & Kaitala 1996; Kozłowski & Teriokhin 1999;

Taborsky *et al.* 2003) or have assumed a maximum-allowed allocation to gonads, proportional to somatic mass (Lester *et al.* 2004). Here, we show that it is sufficient to consider a minimal model of seasonality, where mortality and intake rates remain unchanged but reproduction occurs only once a year at mating time. Hence, the only extra parameter in the model is the length T of the year, measured in units of the characteristic time-scale t_+ .

Appendix B conducts the mathematical analysis of such a model in the steep domain ($k + r - q > 2$), predicting that the animal uses the first part of the year for somatic growth and, if large enough, switches the allocation to reproductive tissue at some point during the year (figure 3). Furthermore, the larger the animal the earlier this switch, so the greater the fraction of the year spent growing gonads. Annual growth rates therefore decline, so that mass converges geometrically to a stagnation mass from which the entire year is spent growing gonads. The overall growth produced is well approximated by the von Bertalanffy model.

The same qualitative pattern arises if seasonal variations in mortality and energy uptake are included, as argued in Appendix B. However, we find it appealing that the effect of indeterminate growth arises even in this minimal model of an annual reproduction cycle.

We can now investigate how the reproduction timetable varies with slope k of the community spectrum. In figure 2b the grey shaded zone displays the onset of reproduction for each slope k , as well as the maximum attainable mass. This is for the larger choice of pivot mass m_p only, that is, corresponding to the dashed line in the graph. Note the fairly close correspondence between the variation in the aseasonal and seasonal settings.

(e) Spectra with shallow slopes, $k < 2 + q - r$

In this final case, m_+ represents the minimum sustainable mass, so we only consider individuals with dimensionless mass greater than 1. These, in turn, may grow to arbitrarily large sizes, so the interval of mass in

Figure 3. Growth and reproduction in a seasonal environment. (a) switching from growth to reproduction during the year takes place at $(t_s(m), m)$ (solid line). Growth trajectories (dashed line) displaying the somatic mass, excluding gonads, are also included. (b) the resulting growth curve (solid line, with steps). Also included is a smoothed growth curve (thin line) where we take the average ψ at each m , that is, $\psi(m) = 1 - t_s(m)/T$, and the approximating von Bertalanffy growth curve (dotted line) at each m . Finally, the growth curve in the corresponding aseasonal environment (dash-dot line).

consideration is $(1, \infty)$. The optimal offspring size is well defined as the solution to equation (3.5)

$$m_0 = \left(\frac{\phi - 1}{\phi} \right)^{1/(k+r-q-2)}.$$

However, there is no optimal size at maturity; it will always be advantageous for the individual to postpone reproduction. This is because lack of mortality among larger, older organisms distorts the optimization so that the inclusion of some realistic decline in fitness V at large body sizes becomes necessary. Biological ageing processes or oxidative stress could be incorporated to produce such an effect and such processes would then be determining for the optimal size at maturity. Similarly, if the population is in a state of growth, rather than in a steady state, then earlier reproductive efforts have greater value than later efforts and the conclusions may be different. In the context of the present work, any such additions may be thought rather arbitrary and so are not pursued.

4. DISCUSSION

We have proposed a minimal framework for investigating evolution against size-structured communities and shown that optimal life histories may derive from the size spectrum of the ambient community. This implies that size spectrum models possess an internal consistency, which is an important justification of these models.

We have shown that the optimization of life histories and the resulting size at maturity strongly depend on the slope of the community size spectrum. The direction of the effect is different between large and small species. For the former, a steeper spectrum implies less food and leads to maturation at smaller size, whereas for the latter a steeper spectrum implies more food but smaller mortality and leads to maturation at larger sizes. These results are relevant to fisheries science because fishing not only imposes extra mortality on larger individuals, leading to earlier maturation (Grift *et al.* 2003; Engelhard & Heino 2004; Olsen *et al.* 2004), but also changes the community size spectrum (Gislason & Rice 1998). Therefore, we

predict that the exploitation of a community should lead to an evolutionary pressure, even on unharvested species.

Our prediction of determinate growth coincides with most previous models (Perrin & Sibly 1993), though they usually assumed a fixed or simple heuristic for size-dependent mortality (Abrams & Rowe 1996), predator's intake rate (Taborsky *et al.* 2003) and competition (Chase 1999). Here, optimality of determinate growth arose directly from the linearity of the objective function in ψ (upper and lower bounds define the optima in all linear models). This linearity does not depend on any particular form for the energy intake rate $e(m)$ or mortality function $\mu(m)$, but results from assuming a linear relation between growth rate and allocation to growth, and between reproductive product and allocation to reproduction. Thus, wherever these (rather standard) assumptions are made, determinate growth patterns should be expected. Taking into account, for example, costly reproductive behaviours, or physiological limits to reproductive allocation of resources, would therefore lead to indeterminate growth predictions (Charnov 2001b).

Introducing seasonal spawning predicted indeterminate growth that matched the von Bertalanffy model (figure 3). This qualitatively agrees with earlier models which indicate that von Bertalanffy growth results from life history choices (Kozłowski 1996; Czarnoleski & Kozłowski 1998; Lester *et al.* 2004). Seasonality is an established explanation for indeterminate growth (Kozłowski & Uchmński 1987) and may be expected from periodicities in the fundamental rates. Here, we have shown that the same pattern emerges, even when seasonality only affects the parents by fixing reproduction time.

We also demonstrated that offspring size should generally be minimized (maximizing numbers) within a log-linear size spectrum. This prediction results from the initial linearity of the fitness function V , in contrast with the classical Smith–Fretwell (Smith & Fretwell 1974) model, which assumes a diminishing marginal return for offspring survival with size. Physiological limits (e.g. to protein digestion), size-dependent anoxia and early predation performance may overrule the optimal extreme. As effects such as size-dependent starvation (see Threlkeld

1976; Beyer 1981) are admitted, the fitness function becomes initially convex leading to finite, but small, optimal offspring.

Recalling that the optimal life history strategies were found assuming a population near equilibrium, we may ask if the model can lead to a constant population size, that is, if a newborn offspring is expected to generate one offspring itself. From our results on offspring size, we found that $W(m_0) > V(m_0) \geq m_0$. Taking into account energy-consuming activities associated with reproduction, for example, migration and courtship, the strict inequality $W(m_0) > m_0$ is a *necessary* condition for equilibrium. Although the condition is necessary (not sufficient), and although density dependent effects are required to stabilize an equilibrium, this serves as a check on consistency.

Our model is quite sensitive to variations in slope k . Assuming that energy uptake increases with size while mortality decreases, this restricts k to the interval $[2, 3]$ and efficiency requires $k > 2.13$ (§3b). Although this range is not inconsistent with observed spectra (§2c), our findings naturally lead one to ask if a stabilizing mechanism allows the species in real ecosystems to display greater robustness towards variations in community size spectra than our model predicts.

While we chose a minimalist model, the main results are independent of most parameter values and robust towards changes in model structure. For example, we assumed that the size selection of predators was independent of scale, allowing a fixed predator/prey body mass ratio to be used. It is known (see Benoit & Rochet 2004) that any selection function that is independent of scale will lead to non-dimensional equations of the forms (2.11) and (2.12). Thus, without significant change, one could replace the fixed ratio β with a more realistic smooth selection function, for example, the lognormal-like function used by Andersen & Ursin (1977) and Beyer (1981). Similarly, random variations in the available energy would lead to a diffusive term in the generator L_ψ but would not change the main findings.

Our basic models can be expanded in several directions. First, we assumed that the functional response of predators is in the approximately linear region, corresponding with the classical Lotka–Volterra formulation used by Chase (1999) and many others. Although Silvert & Platt (1980) derived size-spectrum dynamics with hyperbolic (type II) and linear feeding rates, they concentrated on the latter and more recent works (Benoit & Rochet 2004; Shin & Cury 2004) have assumed linear feeding rates. A natural continuation of our work would be to investigate the effects of a functional response; preliminary findings (not presented here) suggest that the conclusions are not qualitatively altered. Second, we did not include any non-predation (natural) mortality, other than for very small (supposed larval) organisms. Taborsky *et al.* (2003) previously demonstrated discontinuities in optimal strategy resulting from the combined effects of predation and size-independent (natural) mortality. Such discontinuities may distract from our focus on size-spectrum slope and were excluded in our analysis; however, natural and harvesting mortality are easily included in the model. Finally, like most life-history models, we have focused on the female, whose investment in offspring is generally much larger. Since the fitness function may be qualitatively different for males (e.g. dependence on body size through aggressive

competition for mates), a study of sex differences could be based on a modification of our model.

In this paper we have focused on the general effect of community structure on the life history of an individual. It would be an interesting pursuit to compare our findings with observations from a specific system, such as a fish community undergoing structural changes imposed by fishing. Another interesting subject would be when power-law spectra emerge in a community of species which each follow optimal life histories.

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APPENDIX A: OPTIMAL STRATEGIES IN AN ASEASONAL ENVIRONMENT

To solve the maximum fitness problem of §3a, we apply the technique of dynamic programming, according to which the fitness W satisfies Bellman’s equation

$$\forall m : \sup_{\psi \in [0,1]} (L_\psi W(m) + \psi e(m)) = 0, \quad (\text{A } 1)$$

in which ψ is the instantaneous fraction of the available energy devoted to reproduction. L_ψ is the differential operator

$$L_\psi W(m) = W'(m)(1 - \psi)e(m) - W(m)\mu(m), \quad (\text{A } 2)$$

which gives fitness W ’s expected rate of change, for a given ψ . The first term arises from the chain rule $dW/dm(t) = W'(m(t))m'(t)dt$ while the second term $W(m)\mu(m)$ is the loss of fitness resulting from mortality. The optimization in (A 1) can be seen as a trade-off between an immediate gain ψe and an investment in growth leading to higher future gains, $L_\psi W$. Moreover, the equation (A 1) states that, with the optimal strategy ψ , any current reproductive effort ψe must deduct from the future expected effort.

Since the objective function (A 1) is linear in the decision variable ψ , a maximum point is always found on the boundary, that is $\psi = 0$ or $\psi = 1$. It follows that for each m , one of the following three options must be true:

- (i) $W' < 1$. In this case, $\psi = 1$ maximizes (A 1), that is, all energy is allocated to reproduction. Then (A 1) reduces to $W = V$.
- (ii) $W' > 1$. Now all energy is allocated to growth, that is, $\psi = 0$. Then (A 1) reduces to the differential equation in the fitness $W(m)$

$$W' = W/V. \quad (\text{A } 3)$$

- (iii) $W' = 1$. In this case ψ vanishes from the maximization problem in (A 1) and is undetermined. The equation reduces to $W = V$.

To combine these pieces, assume that V is strictly concave for brevity. More substantially, assume that there exists one point m_* such that $V'(m_*) = 1$. Then m_* represents the unique point of switching, that is, for $m < m_*$ the animal will allocate all energy to growth ($\psi = 0, W' > 1$) while for $m \geq m_*$ the animal will allocate

all energy to reproduction ($\psi = 1$, $W = V$ and hence $W' < 1$). This defines the optimal strategy.

To also derive the fitness W in the growth phase, it is sufficient to verify that equation (3.3) satisfies the differential equation (A 3).

Remark 1

If we take for granted that the optimal strategy is indeed a switching strategy, we may derive the switching criterion $V'(m_*) = 1$ by direct optimization, that is, by differentiating with regard to the decision variable m_* (Charnov 2001a). The dynamic programming approach, though more involved, has the advantage of not making the prior assumption of determinate growth.

Turning to optimal offspring size, we differentiate the objective function (3.4)

$$\frac{d}{dm_0} \frac{W(m_0)}{m_0} = \frac{W(m_0)}{m_0} \left(\frac{1}{V(m_0)} - \frac{1}{m_0} \right). \quad (\text{A } 4)$$

Here we have assumed that the offspring starts in the growth phase; thus (A 3) applies. The derivative vanishes only when $V(m_0) = m_0$.

APPENDIX B: OPTIMAL GROWTH AND REPRODUCTION WITH SEASONAL REPRODUCTION

Assume that reproduction takes place in discrete events at times: $\dots, -T, 0, T, \dots$; between these events the individual may invest its surplus energy into somatic growth or into gonad growth. At the reproduction event the entire gonad is released. At any time during the year, the state of an individual is its body mass m excluding gonads and the mass x of its gonads. Its fitness will then be a function, $W(m, x, t)$, of state and time.

The dynamic programming equation governing W between reproductive events is

$$\sup_{\psi \in [0,1]} \partial_t W + L_\psi W = 0 \quad \text{where} \quad (\text{B } 1)$$

$$L_\psi W = \partial_x W \psi e + (1 - \psi) \partial_m W e - \mu W,$$

(cf. Houston & McNamara 1999, p. 155). Here, the subscripts in $\partial_t W$, $\partial_x W$ and $\partial_m W$ indicate partial derivatives. The boundary condition to complete this equation is

$$\lim_{t \nearrow T} W(m, x, t) = x + U(m) \quad \text{where} \quad (\text{B } 2)$$

$$U(m) = \lim_{t \searrow 0} W(m, 0, t),$$

that is, pre-spawning fitness is the mass of the gonads plus the post-spawning fitness. Note that the framework could easily be modified to include, for example, an instantaneous mortality immediately before or after spawning, or a fixed cost associated with reproduction.

This completes the model and we turn to its analysis. Since the optimization in ψ is linear, we obtain a switching strategy where the growth is somatic at the start of the year and perhaps switches to gonadic during the year, when $\partial_m W = \partial_x W$. If the energy e and the mortality μ do not depend on the gonad size x , then W is affine in x for given t and m . This reduces the dynamic programming equation (B 1) to a set of coupled ordinary differential equations. The terminal condition for these involve the function

$U(m)$; the value function is then constructed by backwards iteration in $U(m)$.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.