LETTER

A unified treatment of top-down and bottom-up control of reproduction in populations

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Abstract

Generalizations describing how top-down and bottom-up processes jointly influence the production of offspring (recruitment) and the number of reproducing adults are lacking. This is a deficiency because (1) it is widely recognized that both top-down and bottom-up processes are common in ecosystems; and (2) the relationship between the number of individuals recruiting and number of reproductively active individuals present in that population is of fundamental importance in all branches of ecology. Here we derive a model to consider the joint effects of top-down and bottom-up forcing in any ecosystem. In general, during the lifetime of a cohort, bottom-up effects are likely to limit recruitment over longer periods of time than top-down effects. Top-down effects are likely to be most important early in the life history when potential recruits are small in size, and such effects will be more recognizable in small cohorts comprised of slowly growing individuals.

INTRODUCTION

Ecosystems are regulated by an array of biotic and abiotic factors that often are classified as either top-down or bottom-up processes (Roughgarden *et al.* 1994). A major focus of ecology is to measure the relative strengths of these top-down and bottom-up controls and attempt to disentangle the interactions between them (Hunter & Price 1992). Here we focus on the interplay between top-down and bottom-up controls over recruitment. In spite of drastic differences in fecundity, recruitment to populations of terrestrial and marine animals responds to exploitation in similar manners (Beddington & Basson 1994). Therefore, it should be feasible to apply existing knowledge about the recruitment process to establish a general theory describing how top-down and bottom-up controls interact.

We extend and adapt the theory of recruitment in fish populations (Beverton & Holt 1957) to a more general setting and show that top-down and bottom-up factors can be treated in a uniform way in the study of recruitment. This approach leads one to conclude that during the lifetime of a cohort, bottom-up effects are likely to limit recruitment over longer periods of time than top-down effects. Top-down effects are likely to be most important early in the life history when potential recruits are small in size, and such effects will be more recognizable in small cohorts comprised of slowly growing individuals.

MATERIALS AND METHODS

There is a large body of theory on the recruitment of fishes (Quinn & Deriso 1999), and we use that as the basis of our work. We begin with a description of the per capita change in abundance (N) over the life of a cohort

$$\frac{1}{N}\frac{\mathrm{d}N}{\mathrm{d}t} = -(T + B). \tag{1}$$

The first mortality coefficient (T) describes sources of top-down control while the second (B) describes sources of bottom-up control. We make the reasonable assertion that, broadly speaking, top-down control results from predation while bottom-up control stems from resource limitation. In general, we should expect that T is largely determined by the predator field to which cohort members are exposed, thus T should be a decreasing function of organism size (L); that is $(\mathrm{d}T/\mathrm{d}L) < 0$. Although there may be specific cases where increased size results in increased predation risk, generally speaking this is not the case. On the other hand, bottom-up controls result from resource limitation, which will become more severe as cohort biomass (M)

increases. Thus, we can reasonably assume that $B = B(M)$, and $(dB/dM) > 0$.

We first consider a specific, simple case to illustrate the connection between the concepts described in the previous paragraph and prior work. Under the simplifying assumption that the majority of top-down control is determined by predation risk, T should be inversely proportional to some power of length (L). That is, $T = \mu_T L^{-c}$ where μ_T is proportional to the number of predators, and the allometric parameter c describes the relationship between length and risk to top-down mortality. This formulation is consistent with numerous studies on the size spectrum of biomass as well as empirical observations of the size dependence of mortality (Holling 1992). Assuming that bottom-up control is determined primarily through competition among conspecifics for limited resources (e.g. food or space), we expect B to be proportional to the biomass of the cohort. Therefore, $B = \mu_B N L^b$, where μ_B is proportional to resource availability, and b the allometric parameter relating length to mass. Since B depends on N, mortality from density-dependent disease outbreaks may be considered a bottom-up process.

The initial number of recruits, $N(0)$, is a function of the current population size. Here we assume that $N(0) = \phi S$, where S is the biomass of the current population, and ϕ is the average fecundity per unit mass. [Stochastic effects on population dynamics can be easily treated at this point by assuming that $N(0) = \phi S e^{X_\sigma}$ where X_σ is normally distributed with mean $-\frac{1}{2}\sigma^2$ and variance σ^2]. Inserting these into eqn 1, and integrating while holding L constant provides an equation for predicting cohort abundance at time t (N_t).

$$N_t = \frac{\phi S \exp(-\mu_T L^{-c} t)}{1 + \phi S \frac{\mu_B}{\mu_T} L^{(c+b)}[1 - \exp(-\mu_T L^{-c} t)]} \quad (2)$$

To make this equation more interpretable, substitute $\alpha = \phi \cdot \exp(-\mu_T L^{-c} t)$ and $\beta = (\mu_B L^b)(\phi - \alpha)/(\mu_T L^{-c})$ to give

$$N_t = \frac{\alpha S}{1 + \beta S}, \quad (3)$$

which is a standard formulation of the Beverton–Holt stock recruitment relation (Beverton & Holt 1957; Quinn & Deriso 1999). Several things are apparent from this model. The number of recruits that can be produced at very low stock sizes ($\sim\alpha$) is strictly a function of top-down control and fecundity (which involves bottom-up control in the spawning generation). At the other extreme, as population size increases, the number of possible recruits reaches a limit determined by

$$N_{\max} = \frac{\alpha}{\beta} \quad (4)$$

so that both top-down and bottom-up effects in the current generation influence the maximum recruitment. However,

as we show below, the relative importance of each in determining maximum recruitment is a function of the time to recruitment.

We return to the general problem. For most species it is not likely that L is constant over time. Given our initial assumptions regarding T and B, we show that, as long as growth is positive (i.e. $\frac{dL}{dt} \geq 0$), cohorts will move through time from a region in which top-down processes dominate to a region dominated by bottom-up forces. To make this apparent, we define a new function z such that

$$z = T - B \quad (5)$$

when $z > 0$, top-down forces dominate, and when $z < 0$ bottom-up forces dominate. Thus, we ask whether z changes in a manner that highlights the way top-down and bottom-up forces act on the cohort as it develops. The total derivative of z with respect to L is

$$\frac{dz}{dL} = \frac{dT}{dL} - \frac{dB}{dM}\left[\frac{\partial M}{\partial L} + \frac{\partial M}{\partial N}\frac{dN}{dL}\right] \quad (6)$$

where $\frac{dN}{dL} = \frac{dN/dt}{dL/dt}$. Since we assume that $(dT/dL) < 0$, and $(dB/dM) > 0$, and, by definition, $(\partial M/\partial L) > 0$, and $(\partial M/\partial N) > 0$, dz/dL must always be more negative than dN/dL. Thus, a population starting at a point in the L–N plane that is inside the region where $z > 0$ will ultimately cross into the region where $z < 0$. Conversely, if the population starts in the region dominated by bottom-up control, it will remain there unless somatic growth becomes negative.

The general problem thus suggests coupling eqn 1 with an equation describing somatic growth, and, again, we provide a specific example. We assume that growth in length is given by a von Bertalanffy curve with growth rate k and asymptotic size L_∞ modified to account for the effects of biomass on growth. It is commonly observed in populations that growth rates of individuals in a cohort are reduced at high densities (e.g. Begon *et al.* 1996; Lorenzen & Engberg 2002). Since asymptotic size is related to the abundance of food in the environment, we scale it by a measure of biomass to account for depressed growth at high densities of biomass. The coupled dynamics of population number and individual size are then

$$\frac{1}{N}\frac{dN}{dt} = -(T + B)$$
$$\frac{dL}{dt} = k\left(\frac{L_\infty}{1 + \gamma N L^b} - L\right) \quad (7)$$

where γ measures the intensity of the decline in somatic growth with increasing biomass. The formulation in the second line of eqn 7 is analogous to Lorenzen & Engberg (2002) when $1/(1 + \gamma N L^b)$ is Taylor expanded. We choose this form because it is smoother than that of Lorenzen and Engberg.

RESULTS

Given a range of initial population sizes and constant μ_T, μ_B, b, k, and γ, numerical integration of eqn 7 produces population and length trajectories like those shown in Figure 1a,b. These trajectories are quite reasonable. The final population sizes may be plotted against initial size to produce a recruitment function (e.g. Fig. 1c) that is asymptotic and analogous to that which was originally produced by integrating eqn 2. By varying the parameters of eqn 7, a variety of population and length trajectories can be produced. Possible population trajectories range from nearly linear, to exponential, to nearly step-like. Possible growth curves range from nearly linear to strongly asymptotic. Regardless of these behaviours, however, the resulting recruitment function is always monotonic and decelerating, typically with an apparent asymptote.

Recruitment functions for fish, birds, and mammals are not stationary in time nor spatially invariant (Krebs 2002); therefore, the parameters in eqn 7 are not constants, and, in most populations, cohort strength will be determined from a family of recruitment functions whose shapes are themselves determined by temporal and spatial variations in the biotic and abiotic environments and the manners in which these environments determine T and B (Hunt *et al.* 2002).

Equation 7 provides a simple approach to visualizing the joint influences of top-down and bottom-up effects on recruitment previously presented in eqn 6. We divide the L–N plane into two regions: one in which T is the greater source of mortality, and one in which B is the greater source of mortality. These regions are separated by the curve $z = 0$, which is equivalent to the curve $N = \frac{\mu_T}{\mu_B} L^{-(c+b)}$ (Fig. 2). As individuals grow, regulation of cohort strength tends to move from the region where top-down processes dominate to the region where bottom-up processes dominate. Movement in the opposite direction is unlikely. Since both N and L are bounded by zero, the region in which B is the greater source of mortality occupies a substantially greater
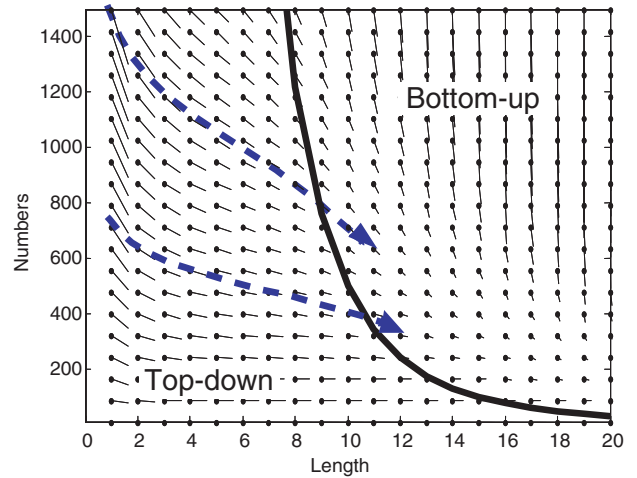

Figure 2 Vector field for eqn 7. Lines that emanate from each point in the L–N plane indicate the direction and magnitude of changes in length and numbers. The bold black line divides the L–N plane into regions where top-down and bottom-up forces dominate. The dashed blue lines are sample solution trajectories starting from $L = 1$ with $N = 1500$ and $N = 750$.

area than the region in which T dominates. Therefore, if cohort strength is measured after sufficient time, when organisms are relatively large, recruitment will appear to have been mostly determined by bottom-up processes. In contrast, if cohort strength is measured early, when organisms are relatively small, the effects of top-down forcing will be most apparent.

DISCUSSION

Figure 2 predicts that the attribution of recruitment variability to one source of control, top-down or bottom-up, depends on the snapshot in time when cohort strength is measured, with top-down processes predominating early and bottom-up processes predominating later. Empirical
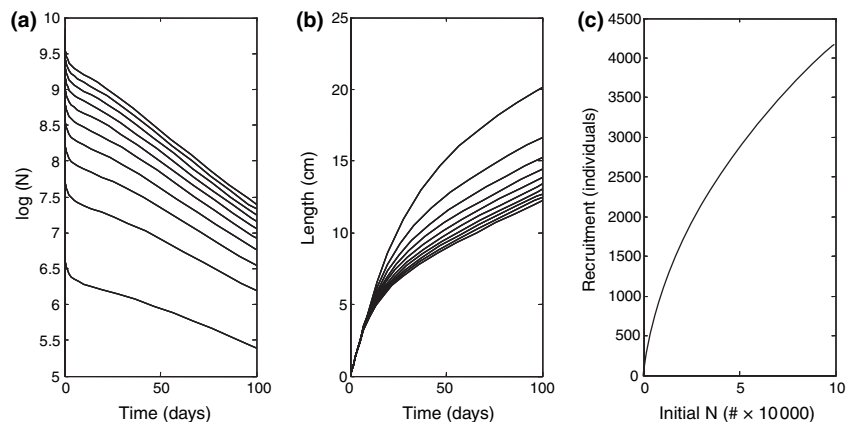
Figure 1 (a) Time courses of cohort dynamics for different initial population sizes. (b) Time courses of length dynamics for cohorts in (a). (c) Recruitment (final population size) plotted against initial cohort numbers. The numerical solutions were generated from $\mu_T = 0.05$; $c = 1$; $\mu_B = 5 \times 10^{-9}$; $b = 3$; $k = 0.005$; and $\gamma = 10^{-6}$.

evidence supporting this prediction can be found across a broad range of taxa and in many ecosystems. For example, in cod if egg survival is considered, top-down predation by clupeid species has been observed as a strong regulating mechanism (Köster & Möllmann 2000). Conversely, when recruitment to 1 year of age is considered, cod survival is regulated by bottom-up controls (Beaugrand *et al.* 2003). In birds, egg survival can be impacted by top-down mechanisms (Haemig 1999), while recruitment to the breeding population is better explained by bottom-up controls (Jenouvrier *et al.* 2003). An analogous relationship also occurs in plants. Seed and seedling (< 10 cm) survival is highly regulated by top-down predation (Green *et al.* 1997). However, while growth and survival of larger seedlings (> 1 m) are still impacted by browsing, at this size bottom-up control outweighs top-down control (Liang & Seagle 2002). Figure 2 also implies that organisms from relatively small or slow-growing cohorts will spend more time under top-down control. An example of such a phenomenon is commonly observed in studies of larval fish in which poor growth conditions result in extended larval period duration and consequently prolonged exposure to high predation risk (e.g. Houde 1997).

Given both the theory developed here and the empirical results discussed above, the generality of the predictions suggested by Figure 2 is likely not limited by the specific functional forms presented in our examples. Rather, the generality of our predictions is determined by the validity of our assumptions; $(dT/dL) < 0$, and $(dB/dM) > 0$. Although exceptions do exist, there is little doubt that these assumptions (respectively that predation mortality is likely to decrease as prey grow longer and competition is likely to increase as cohort biomass increases) apply to many taxa in many ecosystems. These assumptions are basic ecological paradigms and lead directly to the generality of our predictions.

The critical point is not whether top-down or bottom-up controls influence population dynamics, but rather understanding that both mechanisms play a role. The key is to identify where or when one control dominates more than the other. Here we present a model that considers top-down and bottom-up controls simultaneously, with population dynamics being impacted by both. In addition to bringing these components together, we also provide a means of weighing the importance of each control over the time to recruitment. The results of the model indicate that we should generally expect top-down sources of mortality to predominate in the early phases of recruitment. How long these mortality sources predominate depends on cohort size and growth rates, however, all trajectories shift from top-down control to bottom-up control. Attributing recruitment variability to only one source of control will depend on when cohort strength is measured and misses the point, because both top-down and bottom-up factors affect the relationship between adult numbers and the offspring that they produce.

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