Modeling inverted biomass pyramids and refuges in ecosystems

Hao Wang [a,*], Wendy Morrison [b], Abhinav Singh [c], Howard (Howie) Weiss [a]

[a] School of Mathematics, Georgia Institute of Technology, Atlanta, GA 30332, USA
[b] School of Biology, Georgia Institute of Technology, Atlanta, GA 30332, USA
[c] School of Physics, Georgia Institute of Technology, Atlanta, GA 30332, USA

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ABSTRACT

Although the existence of robust inverted biomass pyramids (IBPs) seems paradoxical, they are well known to exist in planktonic communities, and have recently been discovered in pristine coral reefs and in a reef off the North Carolina coast. Understanding the underlying mechanisms which produce inverted biomass pyramids provides new ecological insights. Some ecologists hypothesize that "the high growth rate of prey and low death rate of predators" causes IBPs. However, we show this is not always the case (see Sections 3.1 and 4). We devise predator–prey models to describe three mechanisms that can lead to IBPs: (1) well-mixed populations with large prey turn-over rate, (2) well-mixed populations with prey immigration, and (3) non-mixed populations where the prey can hide in refuges. The three models are motivated by the three ecosystems where IBPs have been observed. We also devise three refuge mediated models, with explicit refuge size, which incorporate different prey responses in the refuge, and we discuss how these lead to IBPs.

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1. Introduction

The biomass structure is a fundamental characteristic of ecosystems (Odum, 1971). The shape of biomass pyramids not only encodes the structure of communities, but also integrates functional characteristics of communities, such as patterns of energy flow, transfer efficiency, and turnover of different components of the food web (Odum, 1971; Reichle, 1981; Del Giorgio et al., 1999).

A trophic pyramid is a graphical representation showing the energy or biomass at each trophic level in a closed ecosystem. Energy pyramids illustrate the production or turnover of biomass and the energy flow through the food chain, while biomass pyramids illustrate the biomass or abundance of organisms at each trophic level. When energy is transferred to the next higher trophic level, typically only 10% is used to build new biomass (Pauly and Christensen, 1995) and the remainder is consumed by metabolic processes. Hence, in a closed ecosystem, each trophic level of the energy pyramid is roughly 10% of the level below it, and thus inverted *energy* pyramids cannot exist. A standard biomass pyramid is found in terrestrial ecosystems such as grassland ecosystems or forest ecosystems, where a larger biomass of producers support a smaller biomass of consumers (Dash, 2001). For inverted biomass pyramids (IBPs), the biomass of primary producers is low, with increasing biomass at each trophic level (Odum, 1971). Even

though it is common for IBPs to be mentioned in introductory ecological textbooks (Odum, 1971; Campbell et al., 2007; Cain et al., 2008), they seem to have received little experimental and theoretical attention. Usually the energy and biomass pyramids are highly correlated, but this manuscript studies examples where they are strikingly different.

Previous research has documented the presence of IBPs in freshwater plankton (Odum, 1971; Del Giorgio et al., 1999; Moustaka-Gouni et al., 2006), marine plankton (Buck et al., 1996; Gasol et al., 1997), and marine coral reefs (Friedlander and Martini, 2002; Sandin et al., 2008). Some ecologists hypothesize that "the high growth rate of prey and low death rate of predators" leads to IBPs (Odum, 1971; Cho and Azam, 1990; Del Giorgio et al., 1999); however, we show this is not always the case. While multiple hypotheses exist to explain these IBPs, we could find no theoretical model in the literature demonstrating how these hypotheses can lead to an IBP. This paper fills that void by presenting theoretical models illustrating three mechanisms that lead to an IBP. The three models are motivated by the three ecosystems where IBPs have been observed.

Odum (1971) proposed that a high turn-over rate and metabolism of planktonic algae can produce an IBP. Other hypotheses include low turn-over rate of heterotrophs (Cho and Azam, 1990; Del Giorgio et al., 1999), and allochthonous input of organic matter which act as food for heterotrophs (Del Giorgio et al., 1999). The first observation of IBPs occurred in oligotrophic plankton communities (Odum, 1971; Buck et al., 1996; Gasol et al., 1997; Del Giorgio et al., 1999; Moustaka-Gouni et al., 2006). Recently, IBPs

* Corresponding author. Tel.: +1 404 894 3949; fax: +1 404 894 4409.
E-mail address: wanghao@math.gatech.edu (H. Wang).

have also been observed in pristine coral reefs (Friedlander and Martini, 2002; Sandin et al., 2008), where the benthic coral cover provides refuge for prey fish. At least one prominent researcher suspects that an IBP exists on a reef off the North Carolina coast, which is caused by significant immigration of prey fish into the reef (Hay, 2008). This paper introduces three classes of predator–prey models to study how IBPs can arise in the three cases where they have been observed. Throughout the paper we will refer to the coral reef example (Friedlander and Martini, 2002; Sandin et al., 2008), as it is the only documented example involving higher trophic levels and refuges, and as such, it has intrigued and inspired this research.

Some ecologists believe that refuges provide a general mechanism for interpreting ecological patterns (Hawkins et al., 1993). Most experimental and theoretical studies of prey refuges have focused on the impact of refuges on the abundance of prey and how refuges add stability to the system (Huffaker, 1958; Berryman and Hawkins, 2006). Few studies have analyzed the impact of refuges on predator abundance (but see Persson and Eklov, 1995 for discussions on predator growth). In this paper, we study this question using mathematical models. We introduce and study a family of predator–prey models with explicit refuge size. We group these models into three classes with different mechanistic dependence of prey availability for predators as a function of the refuge size. We also discuss how these different responses lead to IBPs.

2. Planktonic well-mixed mechanism

Most predator–prey models implicitly assume that predators and prey are well mixed, and many incorporate a Holling-type predation response (Holling, 1959a, b). Although the "well mixed" assumption is usually far from being satisfied when prey are animals, it appears to be a reasonable assumption for phytoplankton–herbivore interactions in aquatic ecosystems, and we first discuss the existence of inverted biomass pyramids in this setting.

We begin by considering the standard Lotka–Volterra predator–prey model with mass-action predation response (Lotka, 1925; Volterra, 1926), described by the system:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = ax - bxy, \tag{1}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = cbxy - dy, \tag{2}$$

where x, prey biomass density; y, predator biomass density, a, prey growth rate, b, per capita predation rate; c, biomass conversion efficiency; d, predator death rate.

The interior equilibrium point $(x^*, y^*) = ((d/cb), (a/b))$ is neutrally stable (a center), at which the predator:prey biomass ratio is

$$\frac{y^*}{x^*} = \frac{ac}{d}. \tag{3}$$

A straightforward calculation shows that the mean values of x and y along each periodic trajectory correspond to the coordinates of the interior equilibrium point. Thus, we can use the biomass ratio at the interior equilibrium point to represent the averaged ratios of all trajectories. The biomass ratio at the interior equilibrium point is greater than 1 if and only if $ac > d$. We obtain our first result in biomass pyramid theory:

Result 1. For the model (1)–(2), if $ac > d$ (the prey growth rate multiplied by the conversion efficiency is greater than the predator death rate), the biomass pyramid is inverted; otherwise, the biomass pyramid is standard.

Result 1 provides a rigorous foundation for the belief expressed by some biologists that IBPs result from the high growth rate of

prey and low death rate of predators (Del Giorgio et al., 1999). Result 1 further suggests that the biomass conversion efficiency can significantly influence the shape of the biomass pyramid.

We now incorporate a general well-mixed predation response into the predator–prey model, which is described by the system:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = ax - f(x)y, \tag{4}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = cf(x)y - dy, \tag{5}$$

where $f(x)$ is the predation response function. It is continuously differentiable and strictly increasing. At the interior equilibrium point $(\hat{x}, \hat{y})$, the ratio $\hat{y}/\hat{x} = a/f(\hat{x})$, where $f(\hat{x}) = d/c$. Thus the predator:prey biomass ratio is

$$\frac{\hat{y}}{\hat{x}} = \frac{ac}{d}. \tag{6}$$

This interior equilibrium point is attracting when the system (4)–(5) is eventually bounded and has no stable limit cycles. The system is eventually bounded if there is a bounded region where all solutions eventually enter into and stay. Result 1 remains valid for this extended model whenever the interior equilibrium point is stable. Stability is closely linked to the properties of the functional response. Result 1 is robust to variations in refuge-dependent predation patterns when the prey grow exponentially and the interior equilibrium point is stable.

We now incorporate logistic prey growth into the preceding predator–prey model, which is described by the system:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = ax\left(1 - \frac{x}{K}\right) - f(x)y, \tag{7}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = cf(x)y - dy, \tag{8}$$

where K is the prey carrying capacity and the predation functional response $f(x)$ is a strictly increasing function. Any reasonable predation function must satisfy this monotone condition, which all three Holling-type functions do. The monotonicity implies that the inverse function f^{-1} exists (Stewart, 2002), and thus the x-component of the interior equilibrium point can be solved from $cf(x) = d$ as $\tilde{x} = f^{-1}(d/c)$. The biomass ratio at the interior equilibrium point $(\tilde{x}, \tilde{y})$ can be written as

$$\frac{\tilde{y}}{\tilde{x}} = \frac{ac}{d}\left[1 - \frac{f^{-1}(d/c)}{K}\right]. \tag{9}$$

This formula modifies the biomass ratio in models (1)–(2) and (4)–(5) by the factor $1 - f^{-1}(d/c)/K$. This interior equilibrium point is attracting when the predator-extinction equilibrium $(K, 0)$ is unstable and there exist no stable limit cycles. For instance, if $f(x) = bx/(\eta + x)$ is a Holling type II functional response, then the interior equilibrium point is globally attracting whenever $\eta d/(bc - d) < K < \eta(bc + d)/(bc - d)$. Using this stability condition, we obtain the new result:

Result 2. For the model (7)–(8), if $(ac/d)[1 - f^{-1}(d/c)/K] > 1$, the biomass pyramid is inverted; otherwise, the biomass pyramid is standard.

The new condition for the IBP depends additionally on the prey carrying capacity K and the form of f^{-1}. We see that the predator:prey biomass ratio is an increasing function of the prey growth rate (a), the conversion efficiency (c), and the prey carrying capacity (K), while the biomass ratio is a decreasing function of the predator death rate (d). As a conclusion, we have the following result:

Result 3. The increase of prey growth rate, the conversion efficiency, the prey carrying capacity, or the predator life span facilitates the occurrence of inverted biomass pyramids.

Result 3 is robust whenever the predation function is an increasing function of prey density. We will see in the next section that the same relations hold for refuge-dependent predation functions.

3. Refuge mechanism

Seeking refuge from predators is a general behavior of most animals in *natural* ecosystems (Cowlishaw, 1997; Sih, 1997) where the refuge habitats can include burrows (Clarke et al., 1993), trees (Dill and Houtman, 1989), cliff faces (Berger, 1991), thick vegetation (Cassini, 1991), or rock talus (Holmes, 1991). Some ecologists even believe that refuges provide a general mechanism for interpreting ecological patterns (Hawkins et al., 1993), specifically the extent of predator–prey interactions (Huffaker, 1958; Legrand and Barbosa, 2003; Rossi et al., 2006). Aquatic ecologists have recently observed inverted biomass pyramids in pristine coral reefs, where the benthic coral cover provides the refuge for prey fish (Friedlander and Martini, 2002; Sandin et al., 2008).

In Singh et al. (2008), we needed to introduce a refuge with explicit size. Although the Holling type III functional response offers the prey a refuge at low population density (Murdoch and Oaten, 1975), the refuge is only implicit, and one cannot specify the size of the refuge. Some authors include an explicit refuge size into their models by multiplying the prey density by $1 - r$, where $0 \le r < 1$ is a proxy of the refuge size (McNair, 1986; Sih, 1987; Hausrath, 1994; Kar, 2005, 2006; Huang et al., 2006; Ko and Ryu, 2006). This procedure has two fundamental drawbacks. The first is that for these modified predation response functions, the switch point, where the predation rate starts to quickly increase, critically depends on both the proxy refuge size and the proxy half-saturation constant (independent of the refuge size). The latter dependence is undesirable. For our model, it is important that the switch point be a function of only the refuge size. The second drawback is that, unlike the Holling-type functional responses which are mechanistically derived from basic biological principles, we have seen no derivation in the literature and we are unable to mechanistically derive these functional forms from basic biological principles to incorporate a refuge.

We now introduce a family of predator–prey models with explicit refuge size, which we call refuge-modulated predator–prey (RPP) models. An important feature of this family is that the switch points for the functional responses depend solely on the size of the refuge. We group these models into three classes, RPP Types I, II, and III, depending on the mechanistic dependence of prey availability for predators on the refuge size. All previous refuge models assume the mechanism behind our Type I class.

3.1. Refuge-modulated predator–prey models

In our recent work (Singh et al., 2008), we modeled the biomass of fish in coral reefs. Small fish find refuge in coral reefs by hiding in holes where large predators cannot enter (Hixon and Beets, 1993). This field observation led us to incorporate a refuge into the standard predator–prey model, where the coral reef refuge size influences the pattern of predation response. We introduced the following family of models:

$$\frac{dx}{dt} = ax\left(1 - \frac{x}{K}\right) - f(x, r)y, \tag{10}$$

$$\frac{dy}{dt} = cf(x, r)y - dy, \tag{11}$$

where r is the refuge size. The function $f(x, r)$ is the refuge-dependent predation response and it is a strictly increasing function of prey biomass density x. For each fixed r, the function $f_r(x) = f(r, x)$ is strictly increasing in x, and thus its inverse f_r^{-1} exists. We

solve for the x-component of the interior equilibrium point from $cf(x, r) - d = 0$ as $\bar{x} = f_r^{-1}(d/c)$. The biomass ratio at the interior equilibrium point $(\bar{x}, \bar{y})$:

$$\frac{\bar{y}}{\bar{x}} = \frac{ac}{d}\left[1 - \frac{f_r^{-1}(d/c)}{K}\right]. \tag{12}$$

This ratio shows that $ac > d$ is a necessary, but not sufficient, condition for an IBP. For each fixed refuge size r, the relationships between the biomass ratio and other parameters are the same as in the well-mixed predator–prey models. This provides the robustness of Result 3. Additional hypotheses are needed to determine the relationship between the biomass ratio and the refuge size. Although the field observation in Hixon and Beets (1993) suggests that prey fish hide in refuges from predators, it is still unclear how the refuge regulates the prey availability for predators. In the next subsection, we propose three hypotheses all motivated from biological considerations.

3.2. Hypotheses on refuge effects

We model three biological hypotheses on how prey availability for predators depends on the refuge size (Fig. 1). We call these models RPP (refuge-modulated predator–prey) Type I, Type II, and Type III. All predation functions depend on the maximum predation rate b, the refuge size r, the minimum predation rate regulator β, and the slope regulator ξ.

RPP Type I: This model assumes that the prey available for predators decreases as the refuge size increases. Prey hide in the refuge, but trade-off protection (i.e. increased survival) for a decrease in growth or reproduction due to lower quality resources within the refuge (Persson and Eklov, 1995; Gonzalez-Olivares and Ramos-Jiliberto, 2003; Reaney, 2007). Thus an increase in the size of the refuge protects more of the prey and results in less prey available to the predator. Hence, the prey available for predators is the prey density outside the refuge and $f(x, r)$ is a decreasing function of refuge size r. We choose the following representative function that lends itself to being fitted to empirical data:

$$f(x, r) = \frac{b}{1 + \beta e^{-\xi(x-r)}}. \tag{13}$$

The variable x is the total prey density (per unit area) and thus the prey available for predators is $x - r$.
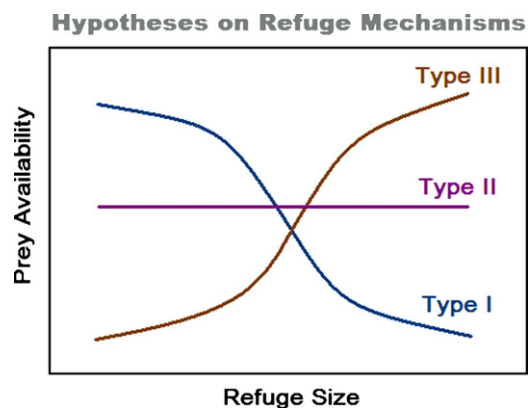

Fig. 1. Three biological hypotheses for the effects of the refuge size on the prey availability for predators. Type I: the prey available for predators is a decreasing function of the refuge size, because the refuge provides places for prey to hide from predators. Type II: the prey available for predators is independent of the refuge size in the sense of density (per unit area), because in a number of cases prey biomass is proportional to the refuge size. Type III: the prey available for predators is an increasing function of the refuge size, because the refuge both provides prey to predators and stores prey for latter consumption by predators.

The parameter β captures the minimum predation rate as follows: when no prey and no refuge are available, the predation rate is $b/(1+\beta)$, which is the minimum predation rate. We should choose β sufficiently large such that $1/(1+\beta) << 1$, since it is reasonable to have a small predation rate when no prey are available. The parameter ξ determines the slope of the predation curve when x is close to r. The prey density at the interior equilibrium point is $\bar{x} = f_r^{-1}(d/c) = r - (1/\xi)\ln[(1/\beta)(bc/d - 1)]$. The interior equilibrium point only exists when $bc > d$. To understand this, if $bc \le d$ and $\beta > 0$, then $dy/dt < (bc - d)y \le 0$, and thus predators go extinct since all solutions tend to the boundary equilibrium point $(K, 0)$. Biologically, when the maximum predation rate multiplied by the conversion efficiency is less than the predator death rate, one would expect that predators cannot persist. Under the conditions that β is sufficiently large and $bc > d$, the term $(1/\xi)\ln[(1/\beta)(bc/d - 1)]$ is negative. Hence, $\bar{x} = f_r^{-1}(d/c) =$

$$r - (1/\xi)\ln[(1/\beta)(bc/d - 1)] = \boxed{r + (1/\xi)\ln[\beta d/(bc - d)] > 0}$$

for sufficiently large β.

RPP Type II: This model assumes that the prey available for predators is independent of the refuge size (in the sense of density, per unit area), i.e. $f(x, r)$ is a constant function of r. Prey biomass within the refuge may increase, but the amount available to the predators remains the same. We choose our representative RPP Type II predation function:

$$f(x, r) = \frac{b}{1 + \beta e^{-\xi x}}. \tag{14}$$

The variable x is the prey density, and the parameters b, β, and ξ have the same meanings as in RPP Type I. The x-component of the interior equilibrium point is $\bar{x} = f_r^{-1}(d/c) = \boxed{(1/\xi)\ln[\beta d/(bc - d)] > 0}$ for $bc > d$ and sufficiently large β.

RPP Type III: This model assumes that the prey available for predators increases as the refuge size increases. This may occur when resources such as food and mating sites are available within the refuge, allowing the prey to increase in numbers until some limiting resource forces a number of the prey to emigrate from the refuge in search for new habitat. The number of emigrants should be positively related to refuge size. Thus, $f(x, r)$ is an increasing function of r. Our representative RPP Type III predation function looks quite similar to our Type I predation function, but the parameters require different interpretations:

$$f(x, r) = \frac{b}{1 + \beta e^{-\xi(x+r)}}. \tag{15}$$

The variable x is the exterior (out of refuge) prey density (per unit area), and $x + r$ is the total prey density (per unit area). This model assumes that the refuge stores a substantial amount of prey and constantly provides food to predators, and thus the prey availability is the total prey density (per unit area), i.e. $x + r$.

For $bc > d$ and β sufficiently large such that $(1/\xi)\ln(\beta d/(bc - d)) > 0$, the x-component of the interior equilibrium point is $\bar{x} = f_r^{-1}(d/c) = \boxed{-r + (1/\xi)\ln[\beta d/(bc - d)] > 0}$ for $r < \bar{r}$. The threshold refuge size $\bar{r} = (1/\xi)\ln[\beta d/(bc - d)] > 0$ for $bc > d$ and sufficiently large β. Because the refuge size in the model is measured by density (per unit area), it is biologically reasonable to assume a threshold maximum value for the refuge size.

We now make a couple of general remarks about the RPP-type functional responses. We always assume that $f(0, r) > 0$ and small, i.e. for each fixed r, the predation rate at zero prey density is positive, but minimal. For Holling-type responses, $f(0, r) = 0$. We believe our choice is reasonable, since when the main prey species are no longer available, predators may temporarily switch to alternative lower

quality food sources (Warburton et al., 1998; Ohizumi et al., 2000; Kjellander and Nordstrom, 2003; Elliott, 2004). Mathematically, this can lead to negative prey population, and we must stipulate that this means prey extinction. In addition, one must choose β sufficiently large such that $1/(1+\beta) << 1$. If we fit this predation function to empirical data, ξ may need to be chosen large, depending on the size of β. When the prey availability is high, $f(x, r)$ is close to the maximum predation rate b. Mathematically, the refuge size r solely determines the shift of the predation curve.

3.3. Dependence of biomass ratio on the refuge size

In this subsection, we use Eq. (12) to analyze the effects of the refuge size on the predator:prey biomass ratio. It is evident that the biomass ratio in Eq. (12) is a decreasing function of $f_r^{-1}(d/c)$.

For RPP Type I, the term $f_r^{-1}(d/c) = r + (1/\xi)\ln[\beta d/(bc - d)]$ is an increasing function of the refuge size r. Thus, the predator:prey biomass ratio at the interior equilibrium point is a decreasing function of the refuge size r.

For RPP Type II, the predator:prey biomass ratio is independent of the refuge size.

For RPP Type III, the term $f_r^{-1}(d/c) = -r + (1/\xi)\ln[\beta d/(bc - d)]$, is decreasing as the refuge size r increases. Thus, the predator:prey biomass ratio at the interior equilibrium point is an increasing function of the refuge size r.

The following results immediately follow from these observations:

Result 4. For the model Eqs. (10) and (11), if $(ac/d)[1 - f_r^{-1}(d/c)/K] > 1$, the biomass pyramid is inverted; otherwise, the biomass pyramid is standard.

Result 5. For RPP Type I, the decrease of the refuge size facilitates the occurrence of inverted biomass pyramids. For RPP Type II, the refuge size has no effects on biomass pyramids. For RPP Type III, the increase of the refuge size facilitates the occurrence of inverted biomass pyramids.

As an illustrative example, data from Kingman and Palmyra (Sandin et al., 2008) suggests that the predator–prey biomass ratio is an increasing function of the refuge size (equivalent to the benthic coral cover), and thus the appropriate predation response function is RPP Type III. RPP Type III may be biologically appropriate if increases in refuge size either increase recruitment or increase the survival of recruits (Shulman, 1984; Doherty and Sale, 1985). After the surviving recruits grow into juveniles or adults, they leave the refuge and provide an increase in the food available to the predators.

4. Immigration mechanism

Reef ecologists observed significant immigration of prey fish in a North Carolina reef (Hay, 2008). We consider two types of immigration: (i) immigrating prey fish stay in the coral reef and adapt to survive in the new habitat; (ii) immigrating prey fish leave the coral reef if they are not eaten by hungry predators, i.e. they provide additional food to predators but do not add to the local prey population. In this section, we incorporate both types of immigration into the Lotka–Volterra predator–prey model:

(i)
$$\frac{dx}{dt} = ax - bxy + \theta, \tag{16}$$

$$\frac{dy}{dt} = cbxy - dy; \tag{17}$$

(ii)
$$\frac{dx}{dt} = ax - bxy, \tag{18}$$

$$\frac{dy}{dt} = cb(x + \hat{\theta})y - dy; \tag{19}$$

where θ, $\hat{\theta}$ are indicators for the immigration. For case (i), the predator:prey biomass ratio at the interior equilibrium point $(\tilde{x}, \tilde{y})$ is

$$\frac{\tilde{y}}{\tilde{x}} = \frac{ac}{d} + \theta \frac{c^2 b}{d^2}. \tag{20}$$

For case (ii), the predator:prey biomass ratio at the interior equilibrium point $(\hat{x}, \hat{y})$ is

$$\frac{\hat{y}}{\hat{x}} = \frac{ac}{d - \hat{\theta}cb}. \tag{21}$$

In both immigration cases, the biomass ratios are increasing functions of the immigration indicators θ and $\hat{\theta}$. This remains true when we incorporate these two immigration effects into Holling type or RPP type models. As a conclusion, we obtain the following robust result:

Result 6. The immigration of prey facilitates the occurrence of inverted biomass pyramids.

In addition, the biomass ratios in Eqs. (20) and (21) show that $ac > d$ is a sufficient, but not necessary, condition for an IBP.

5. Discussion

We develop a mathematical theory of biomass pyramids. Our major contributions can be summarized as follows. First, when prey grow exponentially, the biomass pyramid is inverted if the prey growth rate multiplied by the conversion efficiency is greater than the predator death rate. Second, the increase of prey growth rate, the conversion efficiency, the prey carrying capacity, or the predator life span facilitates the development of inverted biomass pyramids. Third, based on plausible biological hypotheses, we devise a new series of predator–prey models (called RPP type models) which explicitly and naturally incorporates a prey refuge. Fourth, depending on the nature of the refuge, the occurrence of inverted biomass pyramids can be positively or negatively related to, or independent of, the refuge size. Fifth, the immigration of prey facilitates the occurrence of inverted biomass pyramids.

Our conclusions are valid for a linear food chain with two trophic levels. Biomass pyramids usually consist of more trophic levels and species on each trophic level can feed on several trophic levels simultaneously. Even though our results are only valid for two trophic levels, the results are robust for any two sequential levels and are not limited to primary producers and herbivores (i.e. see Singh et al., 2008). There are extensive discussions in the ecological literature about the relative importance of bottom-up and top-down regulations (Micheli, 1999). Since our models use only two-levels, these discussions are not applicable to this model. We do not discuss omnivory, intra-guild predation, or ontogenetic diet shifts. Obviously these behaviors would influence the results of our model and the intricacies of trophic pyramids.

Prey animals seek refuges to hide from predators and thus it is sometimes necessary to explicitly incorporate the refuge mechanism into the predation function of predator–prey models. Our family of RPP-type models explicitly incorporating the refuge size can more accurately describe realistic predator–prey interactions in ecosystems. We propose three new refuge-dependent predation functions with explicit refuge size, which capture the three essential biological hypotheses on how the refuge impacts the availability of prey to the predator (Fig. 1). The three can be combined into one function:

$$f(x, r) = \frac{b}{1 + \beta e^{-\xi[x-(2-i)r]}}, \tag{22}$$

where i is the index of RPP type, that is, $i = 1$ for RPP Type I, $i = 2$ for RPP Type II, and $i = 3$ for RPP Type III. Some, but not all, of the prey that hide in the refuge are available to predators. Thus, there should be a discount rate for the refuge size in the predation function of either RPP Type I (assume no prey in the refuge are available) or RPP Type III (assume all prey in the refuge are available). We incorporate this discount rate into the general refuge-dependent predation function:

$$f(x, r) = \frac{b}{1 + \beta e^{-\xi(x + \eta r)}}, \tag{23}$$

where $-1 \le \eta \le 1$. This model is close to RPP Type I if $-1 \le \eta < 0$, close to RPP Type II if $\eta = 0$, and close to RPP Type III if $0 < \eta \le 1$. We call η as the refuge-effect parameter.

RPP type functional responses $f(x, r)$ have a mathematical defect: the first quadrant is not invariant. To guarantee invariance, such a function must satisfy the following conditions: (i) $f(x, r)$ are continuously differentiable in x and r; (ii) $f(0, r) = 0$; (iii) $\partial f / \partial x > 0$; (iv) $\partial^2 f / \partial x^2 < 0$ for sufficiently large x; (v) the refuge size r solely determines the shift of the predation curve. We are unable to find a closed-form expression for such a function.

Many of our results are based on the existence of a globally attracting interior equilibrium point. However, extremely small or extremely large refuge sizes may destabilize the equilibrium. Conclusions are only true on a bounded interval of the refuge size (see Singh et al., 2008 as an example). Local stability analysis shows that Hopf bifurcations can occur in RPP-type models.

The results from our models support previous hypotheses regarding inverted biomass pyramids. Odum (1971) hypothesized that the high turn-over rate of the prey created inverted biomass pyramids, while Cho and Azam (1990) mentioned alternatively that the low turn-over rate of the predator was important. We show that it is a combination of these two hypotheses that are essential (i.e. prey growth rate times conversion efficiency must be greater than predator death rate, $ac > d$). In addition, we show that the presence of appropriate turn-over rates is not a sufficient explanation to explain all inverted biomass pyramids. Other factors, such as the refuge size, the immigration rate, the conversion efficiency, and the prey carrying capacity, can also be important determinants. Field observations support this claim since similar turn-over rates for autotrophs and heterotrophs exist in oligotrophic and eutrophic conditions, the former which supports inverted biomass pyramids and the latter which supports traditional biomass pyramids (Del Giorgio et al., 1999). Del Giorgio et al. (1999) suggested that inverted biomass pyramids in oligotrophic lakes are due to the input of organic materials from outside the system. This is analogous to our model incorporating immigration of prey into the area; both provide food subsidies for the predator (heterotrophs).

In addition to these previous hypotheses, we propose two new hypotheses here: (1) as mentioned above, inverted biomass pyramids exist when prey growth rate times conversion efficiency is greater than prey death rate ($ac > d$). This suggests that high conversion efficiencies in addition to appropriate predator and prey turnover rates could create the conditions necessary for inverted biomass pyramids; (2) our incorporation of refuge into the discussion of inverted biomass pyramids is new. Until recently, all examples of inverted biomass pyramids have been in planktonic communities that are for the most part well mixed (Odum, 1971; Buck et al., 1996; Gasol et al., 1997; Del Giorgio et al., 1999; Moustaka-Gouni et al., 2006). The coral reef examples (Friedlander and Martini, 2002; Sandin et al., 2008) are the first examples of a situation that incorporates prey refuge. The presence of refuges could increase either the number or survival of recruits (Shulman, 1984; Doherty and Sale, 1985), increasing the prey available to the predators when these recruits have grown into juveniles and left the refuges, creating the conditions necessary for inverted biomass

pyramids (i.e. RPP type III). In practice, the immigration scenario and the RPP Type III are incorporating the same mechanism. The Type III refuge creates a prey source population which emigrates out of the refuge and subsidizes the predator population.

Through creation of the model, we realized that the behavior of prey within the refuge was not obvious, and different behavior could lead to drastically different impacts on the availability of the prey to the predator (i.e. RPP Types I, II and III). What characteristics of the prey might lead to RPP Type I versus RPP Type III? RPP Type I will occur when the use of the refuge results in strong trade-offs between survival and reproduction. The evidence for the presence of trade-offs (survival versus reproduction) with the use of refuges is plentiful (Lima and Dill, 1990; Persson and Eklov, 1995; Reaney, 2007). However, we are aware of no experiments that show a decrease in predator abundance with the introduction of refuges (but see Persson and Eklov, 1995 for an example that shows a decrease in the growth rate of the predator in response to the use of a refuge by the prey). We know of no biological examples of RPP Type II. However, we believe that RPP Types I and III are the extremes of a continuum, suggesting that condition can exist where the prey available to predators is not affected by the area within the refuge. Most previous theoretical models assume that the hypothesis for RPP Type I is the case; however, we hypothesize that RPP Type III will occur when the prey have the ability to reproduce within the refuge and/or when the refuge increases prey survival through a population bottleneck (i.e. decreasing the bottleneck). The Elk Refuge in Yellowstone National Park is one example of a RPP Type III. The Elk Refuge provides protection (and food) to the elk during winter increasing survival to 97% (Lubow and Smith, 2004). The surviving elk migrate out of the refuge and provide a source of food for predators in Yellowstone National Park and surrounding areas (Smith, 2008). Our RPP Type III is also analogous to spillover and larval export hypotheses in marine protected areas (MPA) (Ward et al., 2001). MPAs are areas of the ocean that are protected from fishing (i.e. man is the predator). The fish within these MPAs are hypothesized to increase the number of fish (prey) available outside the protected area through two mechanisms. The first, spillover, occurs when adult fish become crowded within the MPA and immigrate into the surrounding area. The second occurs when the fish within the MPA increase their reproductive output, increasing the number of recruits available to surrounding areas (larval export). While support for the spillover hypothesis is present (though limited spatially), it is much harder to prove the benefits of larval export (Ward et al., 2001).

In summary, we return to the widely accepted hypothesis that "the high growth rate of prey and low death rate of predators" causes an inverted biomass pyramid. Our refuge-dependent models show that $ac > d$ is a necessary, but not sufficient, condition for an inverted biomass pyramid (see the biomass ratio in Eq. (12)). Our immigration models show that $ac > d$ is a sufficient, but not necessary, condition for an inverted biomass pyramid (see the biomass ratios in Eqs. (20) and (21)).

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