Temporal variation in resource levels is a fundamental component of the dynamics of many biological systems. Resource pulses and allochthonous inputs play as essentially insurance in allowing species to persist. Persistence of species with lifetimes short relative to the timescale of resource variability is determined by the arithmetic mean of resource levels, while the persistence of species where resources vary on a much shorter time scale (or with exponential survivorship) are determined by the geometric mean of resource levels. Models that incorporate features of time-varying resources and explicit life histories dramatically change our understanding of how fluctuations in resource availability through time and space will affect population persistence and community dynamics.

**Keywords:** resource pulses; allochthonous inputs; persistence; life histories

1. INTRODUCTION

Pulses [1–14] and allochthonous inputs [7] are dramatic examples of temporally varying resource availability in ecological systems, which can have large impacts on the temporal and spatial abundances of species. However, theoretical understanding of the impact of these influences on population dynamics is limited [2,10,15] since simple population dynamic models typically ignore time-dependent aspects of reproduction, survival and resource availability. Although the study of age- and stage-structured populations through detailed models has progressed greatly [16], these models are typically too complex to incorporate resource variability in time and simultaneously to allow for general understanding. The role of resource variability is a large and complex subject so here I focus on the specific case of the interaction between allochthonous inputs and pulses. Note however that there are many other ecological and evolutionary areas where the life history of consumers plays a significant role, and the approach developed here could be applied to those.

The classical models in ecology include die-off of consumers with exponentially distributed waiting times in the absence of resources. This does not lead to difficulties if resources do not vary on time scales that would influence the survival of individuals, but it will lead to difficulties if the time scale of variability of resources is comparable to that of the lifetime of individuals. Temporal variation of resources has only been considered in specific cases [17,18]. Dramatically, pulsed input of resources [1–14] is a key component of the dynamics of many biological systems with resources coming from within the system owing to seasonal or annual or irregular fluctuations. Specific examples include resources from outside the system owing to allochthonous input [6,7], or in marine systems from upwelling. Other dramatic cases include plant masting or the emergence of periodical cicadas or other insect outbreaks [3]. Key biological questions that arise are what controls persistence of species that consume these irregular resources, and how do pulses affect population dynamics.

A minimal model must incorporate the appropriate time scales of the interaction between life histories of consumers and temporal dynamics of resource availability. Including explicitly the effects of resources on persistence of individuals is essential for scaling up the role of resource pulses and allochthonous input on the dynamics of populations as well as communities. As the focus here is on the simplest models that can be used to understand these issues, it is important to identify the minimal biological issues that must be included. In particular, the model must include the possibility of death of all individual consumers in the absence of resources. The second essential ingredient that must be included is the time-dependent availability of resources, including the possibility that there are times where resources may be completely unavailable.

The key principles already emerge in simple models where the availability of resources is periodic in time, as in a seasonal environment, and the role of the resources is implicit and appears through their impact on fecundity and survival. More complex models would treat resource pulses that arise stochastically through time with large fluctuations and follow the impact of the consumer on the resources.

2. METHODS AND RESULTS

The basic aspects of the modelling approach and the consequences for understanding population dynamics can easily be seen in the simplest setting of a single resource and a single consumer species. Even for the first model, I make a number of important simplifying assumptions. I assume that although the resource may last only a finite time (it disappears or becomes unavailable or unusable even if not consumed by the species of interest), the quality of the resource is independent of the time since it was created (its 'age'). I ignore any issues of density dependence other than those mediated through the resource.

The dynamics discussed here are those of a single consumer and a single time-varying resource. A simple model can be constructed for this system using McKendrick–von Foerster equations. The model is described by the following system of coupled

\[
\frac{dN}{dt} = \alpha N - \beta N^2 - \gamma N R,
\]

where \(N\) is the population density, \(R\) is the resource density, \(\alpha\) is the reproduction rate, \(\beta\) is the density-dependent survival rate, and \(\gamma\) is the consumption rate.
equations:

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu_n(R(t))n(t, a),$$

$$n(t, 0) = \int_0^A n(t, a)m(R(t), a)da,$$

$$N(t) = \int_0^A n(t, a)da,$$

$$\frac{\partial r}{\partial t} + \frac{\partial r}{\partial a} = -\mu_rN(t)r(t, a) - \mu_r(t, a)r(t, a),$$

$$r(t, 0) = I(t)$$

and

$$R(t) = \int_0^B r(t, a)da,$$

where $n(t, a)$ is a density function on age for the population at time $t$, $N(t)$ is the total population size of the consumer at time $t$, $r(t, a)$ is a density function on age for the resource at time $t$, $R(t)$ is the total resource at time $t$, $\mu_{a2}$ is the age-dependent death rate of the consumer which depends on the total resource level, $m$ is the age-dependent birth rate and $A$ is the maximum age of the consumer. The resource is removed by the consumer (linear functional response) at a rate $\mu_{rs}$ and the resource disappears due to other factors at a rate $\mu_{rs}$ which can depend on the ‘age’ of the resource.

In the body of the paper, simpler versions of this model are analysed which can be derived from the more complete model under a variety of assumptions.

To understand issues of persistence, the first model can be further simplified greatly, since, for persistence, the consumer population would be small and the effect on the resource could be ignored (essentially linearizing about the solution where the consumer population level is zero). Recall that $N(t)$ is the consumer population, $R(t)$ is the resource level, and let $m(t, R(\cdot))$ be the per capita reproduction as a function of the resource level, all at time $t$. This assumes that reproduction depends only on the instantaneous level of the resource. These assumptions mean that in the McKendrick–von Foerster equations only the consumer need be considered. Integrate the partial differential equation for $n(a, t)$ to find an explicit expression for $n(a, t)$, and substitute the answer and the boundary condition for $n(0, t)$ into the equation for $N(t)$. Then the description of the consumer population dynamics reduces to the single equation

$$N(t) = \int_{-\infty}^t N(s)m(s, R(s))l(t - s, R(\cdot))ds,$$  \hspace{1cm} (2.1)

where the survival to age $t - s$, $l(t - s, R(\cdot))$, depends on the ongoing level of resources. The notation indicates that the survivorship may depend explicitly on resources available to the organism at all ages.

The easiest setting in which to analyse this simple model is where the resource varies in time and the dependence of the birth rate on the resource level is linear. By scaling the resource level, we can assume that the per capita birth rate is the resource level $R(s)$. I make the further simplifying assumption that the consumer species has a fixed lifespan independent of the resource level (resources affect only the birth rate), i.e. $l$ is one for ages less than 1 and 0 for ages greater than 1. Then replacing $m$ by $R(s)$, setting $l$ to one for ages less than 1 and 0 for larger ages which can be represented by changing the limits of integration, we arrive at the model

$$N(t) = \int_{t-1}^t N(s)R(s)ds.$$  \hspace{1cm} (2.2)

A complete analysis of model (2.2) is still not straightforward, but two extreme cases are easy. If the time scale over which the resource level varies is very short, then $R(s)$ in (2.2) can be replaced by its average $R_{ave}$ and the persistence condition simply is $R_{ave} > 1$. (This can be confirmed by replacing $N(s)$ in (2.2) by $ae^N$ and finding $\lambda$). Conversely, if the resource level changes on a long time scale only (i.e. $R$ is fixed over times much longer than 1), then the persistence condition is essentially the geometric mean, i.e. that $[\log(R)]_{ave} > 0$.

The result in (2.3) follows from observing that in this case equation (2.2) reduces to essentially a discrete time model with $R$ chosen randomly; this is the classic result [19] for discrete time models.

In contrast, the analogous model with an exponentially distributed lifetime can be found from equation (2.1) by setting $l(t - s) = e^{t-s}$, $m = R$, assuming the mortality rate is one, and differentiating equation (2.1) producing

$$\frac{dN}{dt} = R(t)N - N.$$ \hspace{1cm} (2.4)

which has the solution

$$N(t) = N(0)e^{\int_0^t (R(s)-1)ds}.$$ \hspace{1cm} (2.5)

From equations (2.3) and (2.5), we see the key result that if the lifetime is exponentially distributed, persistence depends only on the average resource level independent of the time scale of the variability in the resource, while if there is a fixed lifetime both the magnitude and the time scale of variability in the resource matters.

A different model would be needed to examine the importance of the resource for survival, rather than fecundity. Assuming that the instantaneous survival depends on the resource, if the resource level ever drops completely to zero, the population goes extinct. This reflects the observation that a period with no births that is shorter in duration than the maximum age span does not produce certain extinction, but any period with no survival certainly leads to extinction.

3. DISCUSSION

The model framework developed here provides important insight into the general role of the dynamics of resource pulses in population biology. This can be used to understand the impact of alternative food sources of varying kinds. As demonstrated here, the role of allochthonous inputs, such as inputs into islands [6,7], can be far more important than would be suggested by considering the mean level of input.
[15], as even small levels of input can greatly change the geometric mean of resource levels available to consumers when the in situ resource levels fluctuate and can reach very low levels. This can explain the observations [6,7] of the dramatic effect of allochthonous input on the recipient community, and is in contrast to the role of allochthonous input described in previous models [15] that do not include the temporal aspects considered here.

Similarly, the survey [13] of the role played by pulses and allochthonous inputs in general demonstrates the dramatic influence on community dynamics. The results from even the simplest models that incorporate both life histories with finite age spans and temporally varying resources are dramatically different from models that incorporate only one or the other factor (or neither). Incorporation of explicit temporal aspects will be key to understanding the influence of temporal and spatial variation, and changes in these, for population dynamics. For example, variability may affect the dynamics of apparent competition [20]. The results here are clearly consistent with the classic results [19] that the geometric mean of the population growth rate determines the long-term growth rate in a discrete time model with non-overlapping generations, but the extension to the continuous time case is only possible with the explicit inclusion of consumer life histories which have not typically been included in ecological models. Although the results here are derived under explicit extreme assumptions about the dynamics of resources, the results clearly indicate behaviour under less extreme assumptions as well. Understanding the evolution of life-history characteristics, such as senescence [21], will certainly require including the role of time scales and variable resources. This interaction between temporal resource dynamics and consumer life histories has been underappreciated.

I thank Carl Boettiger for helpful discussions and the referees for very helpful comments. This research was supported by US National Science Foundation grant EF-0742674.