CHAPTER 3

ASSESSING THE IMPACT OF ENVIRONMENTAL VARIABILITY ON TROPHIC SYSTEMS USING AN ALLOMETRIC FREQUENCY-RESOLVED APPROACH

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3.1 ABSTRACT

May (1976) suggested that populations are unlikely to be influenced by environmental fluctuations that occur more frequently than the reciprocal of their characteristic response time ($1/t_r = r$). Allometric relationships, which govern the body-size-dependence of many biological and ecological phenomena, can be used to predict this characteristic response time for a wide range of populations. However, when populations are embedded in a food web, the characteristic response time becomes a property of the food web rather than of the embedded populations. This study demonstrates that, for a range of pairings of body sizes in consumer-resource systems, the characteristic response time of the system can be entirely determined by resource body size while for other pairings, it can be predominantly determined by consumer body size. Using a recently developed framework to introduce temperature variability into consumer-resource models, this study evaluates the ability of

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the characteristic response time to predict the frequency at which populations are no longer influenced by environmental fluctuations. In contrast to May's (1976) results for an isolated population, the results demonstrate that the reciprocal of the characteristic response time often represents the frequency at which the variability of resource populations is most sensitive to environmental perturbation, suggesting that community processes must be considered when determining what scales of environmental variability are important to populations.

Keywords: population, variability, response time, frequency, environmental variability.

3.2 INTRODUCTION

Allometric relationships describe the relatedness of the body size of an organism to a wide variety of other characteristics occurring at both finer and broader scales of interest (e.g. from physiological to ecological processes). These characteristics scale as the bth power of body mass (m):

$$y = am^b \tag{3.1}$$

and there has been a great deal of literature devoted to the measurement of these scaling exponents (b) and the intercepts of these relationships (a; see Peters 1983; Calder 1996). Although there remains an ongoing debate about the ubiquitous application of scaling exponents across different taxa and processes (see Kozlowski and Konarzewski 2004), there are strong arguments to suggest that we should expect scaling exponents to occur as rational multiples of the fraction $1/4$ (West et al. 1997). Furthermore, those rates which are most important for the study of population dynamics, including per capita population growth, reproduction, and metabolism, all scale identically as $m^{0.75}$ (or as $m^{-0.25}$ per-unit-mass). The conservative nature of this exponent within and between taxa makes allometric relationships useful as a tool with which to provide general descriptions of the impact of body size on population dynamics (e.g. Yodzis and Innes 1992).

For many models of population dynamics, the population growth rate r, represents the reciprocal of a population's "characteristic response time" (t_r); the fraction $1/r$ describes the time required by a population to adjust to a perturbation introduced by a singular environmental fluctuation (e.g. climate or anthropogenic disturbance). May (1976) was first to note that environmental fluctuations occurring at frequencies higher than $1/t_r$ (or synonymously with a period smaller than t_r) should have little impact on population dynamics, because such frequencies of fluctuation do not provide adequate time for a population to adjust. Since populations are constantly bombarded by environmental fluctuations, occurring over a large range of frequencies, understanding which of these are of more or less consequence has an obvious importance for determining how environmental variability impacts populations.

One can arrive at May's (1976) conclusion through the analysis of the logistic equation

$$dN/dt = rN(1 - N/K) \tag{3.2}$$

which describes the rate of change of a population's density as a function of its density N, carrying capacity K, and intrinsic growth rate r. Under constant environmental conditions, and provided that enough time has passed since initializing the model, the population will be very near its equilibrium ($N^* = K$). However, if the carrying capacity K is constantly varied, as if driven by some periodic fluctuation in an environmental variable, the population will remain further from its equilibrium; it will track the variation in the equilibrium and express a fluctuation in its own density that is highly dependent upon the period of environmental fluctuation relative to its characteristic response time. Consider the following example which is taken from May (1976), where:

$$K(t) = K_0 + K_1 \cos(2\pi t/\tau) \tag{3.3}$$

and population dynamics are modelled using Eq. 3.2 (obviously $K_1 < K_0$ in order for the carrying capacity to remain positive). When the characteristic response time is greater than the period of environmental fluctuation ($t_r \gg \tau$) the population averages across the environmental fluctuations. However, when $t_r \ll \tau$ the population closely tracks the environmental fluctuations (Figure 3.1). Given that similar dependencies were found in models with stochastic fluctuations (e.g. Roughgarden 1975), May (1976) concluded that populations will average over the high frequency components of the environmental noise spectrum while tracking those at lower frequencies. The transition between the two behaviours occurs at a frequency on the order of r (i.e. when $t_r \approx \tau$). One way to visualize this is to vary the period of environmental forcing (τ) across a range of values and record the average distance between the population and its equilibrium (Figure 3.2). When the period (τ) is much larger than t_r this average distance is very small; when the period is only slightly larger than t_r (within an order of magnitude) the average distance grows substantially; and when the period is equal to or greater than t_r the average distance is at its maximum value. Conversely the variability of the population (measured as the coefficient of variation: CV = standard deviation/mean) is greatest when the period is much larger than t_r and least when the period is greater than t_r (Figure 3.2).

The simple relationship between the characteristic response time of a population t_r and its growth rate r allows a simple determination of the allometry of response time; since the rate of growth scales as $r \propto m^{-0.25}$, the response time must scale as $t_r \propto m^{0.25}$. Thus, populations comprised of smaller bodied individuals will have a lower response time than those comprised of larger bodied individuals. Furthermore, this relationship predicts that the frequency at which environmental fluctuations are no longer influential should be lower for larger bodied organisms – a surety given that variation at the per minute scale may be important for a population of single-celled organisms but inconsequential for one comprised of large-bodied mammals.

Despite the ease with which this prediction might be tested there have been few attempts at large-scale validation, possibly due to the wide variety of timescales that

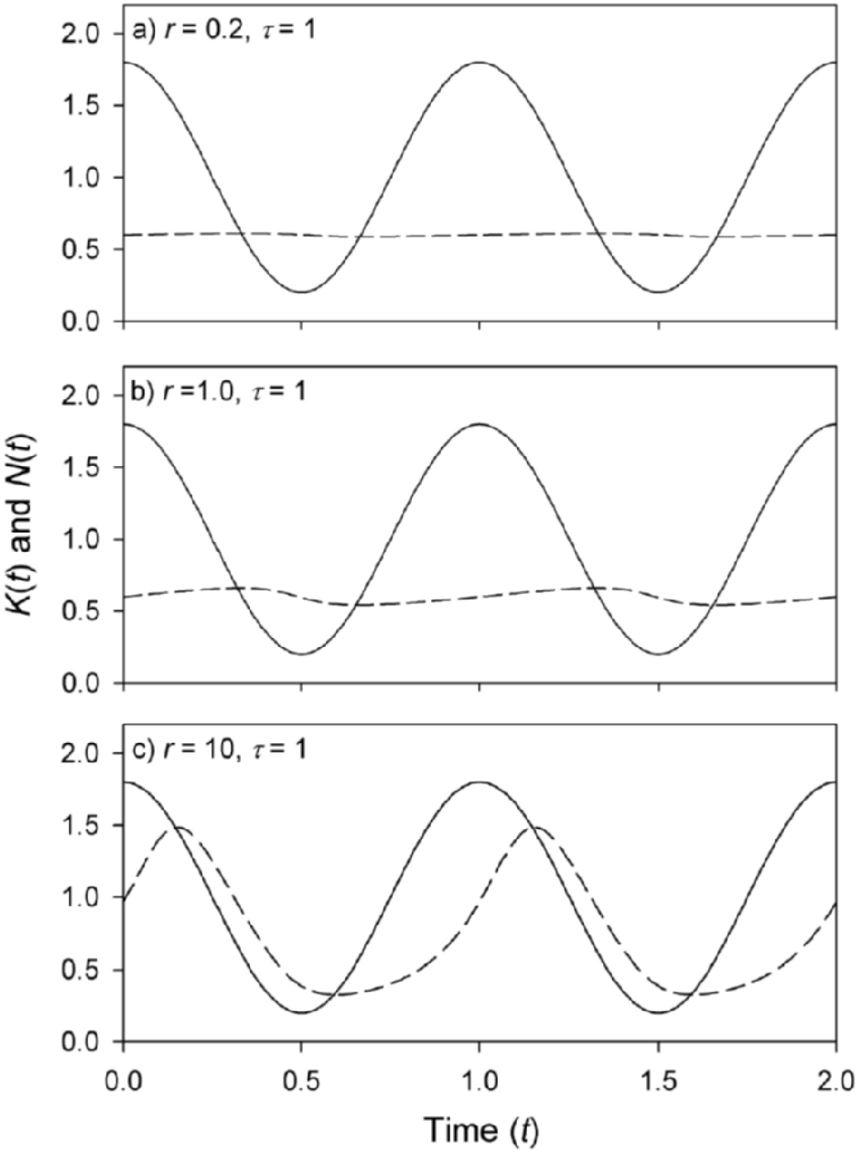

Figure 3.1. The equilibrium (solid line) and realized population density (dashed line) of the logistic model with sinusoidal variation in the carrying capacity. (From May 1976.) The three panels show examples where the frequency of environmental forcing is greater than (a), equal to (b), and less than (c) the characteristic response time.

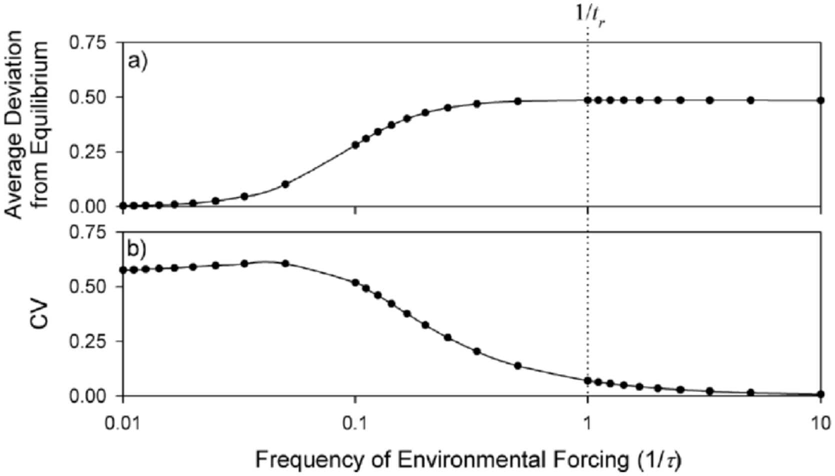

Figure 3.2. The relationship between the frequency of environmental forcing and the (a) average deviation from equilibrium (Mean Squared Error) and (b) the coefficient of variation (CV) for the logistic model with varying K (Eqs. 3.1 and 3.2). At low forcing frequencies the population density is usually near its equilibrium (cf. Figure 3.1c) and thus the mean squared error is low, while at high-forcing frequencies the population is usually far from equilibrium (cf. Figure 3.1a) resulting in a large (relative) mean squared error. The trend in the CV is opposite that of the equilibrium deviation. The dashed vertical line represents the frequency corresponding to $1/t_r$; above this frequency environmental forcing has little influence on population dynamics as evidenced by the near-zero slopes of the two curves in this region.

would be required. In perhaps the most comprehensive analysis of long-term animal population variability, Inchausti and Halley (2002) found that body size significantly influenced the spectral exponent (a measure of the expression of high relative to low frequency variability). But in contrast to theoretical predictions, they found that populations of larger-bodied primary and secondary consumers expressed more high (relative to low) frequency variation relative to their smaller-bodied counterparts (while herbivores behaved as predicted). While many factors may be responsible for the discrepancy between the allometrically based prediction and natural data, including differences in the environmental fluctuations which drive population variability and adaptations which buffer populations against environmental fluctuations, we cannot ignore the importance of ecological interactions in determining the response of populations to environmental variability. While each population in a food web has its own characteristic response time which is a function of its body size and characteristic of its internal renewal process, community processes (e.g. competition, predation) will ultimately determine a characteristic response time that is representative of the entire food web and which may depend, to varying extents, upon the body sizes and renewal processes of all the populations in the food web.

Through the analysis of a generalized allometric model for dynamic trophic systems, and using a recently developed extension of this model to include temperature, this study investigates how body size mediates the characteristic response times of small trophic communities to variability in the environment. In the first section below, I derive the relationship between body size and characteristic response time for a simple consumer-resource system using the Yodzis and Innes (1992) bioenergetic-allometric framework for dynamic trophic systems. Following this, I use numerical simulations to evaluate the utility of this measure to predict the frequencies of environmental variability that are important for population variability.

3.3 THE ALLOMETRY OF CHARACTERISTIC RESPONSE TIME IN CONSUMER-RESOURCE SYSTEMS

Yodzis and Innes (1992) pioneered the use of allometric relationships to provide logical bounds on the parameters of trophodynamic models (dynamic models of feeding relationships). For the simplest case, one consumer feeding upon one resource, they showed that although the body sizes of both populations are important determinants of the relative and total biomass in an ecological system, they do not influence the qualitative stability of the system (e.g. they have no bearing on whether the system exhibits stability, periodic oscillations, or chaos). Despite this, it has been shown that the ratio of consumer to resource body size influences the strength of interactions (Emmerson and Raffaelli 2004) and that theoretical food webs constructed from empirically plausible consumer/resource pairs, exhibit a much higher degree of stability than those with random interaction strengths (Williams and Martinez 2004; Brose and Berlow 2005). In addition to stability, body size is known to play an important role in the structuring of food webs (Cohen et al. 1993; Williams and Martinez 2000) and in their resultant dynamics (McCann and Hastings 1997; Law and Morton 1996).

The Yodzis and Innes (1992) model is a bioenergetic version of the consumer-resource system that was first proposed by Rosenzweig and MacArthur (1963). The model describes the rates of change of resource (R) and consumer (C) biomass (rather than individuals) per unit time, using the following pair of differential equations:

$$\begin{aligned} \frac{dR}{dt} &= rR\left(1-\frac{R}{K}\right) - JC\left(\frac{R}{R+R_0}\right) \\ \frac{dC}{dt} &= C\left[-M + (1-\delta)\,J\left(\frac{R}{R+R_0}\right)\right]. \end{aligned} \tag{3.4}$$

Here, resource biomass increases in the absence of consumers according to the logistic equation, which is governed by the rate of resource growth r and by the resource-carrying capacity K. The consumer population ingests resources at a rate governed by the type II functional response, where J is the maximum rate of ingestion, R_0 is the resource biomass required to realize an ingestion rate equal to $J/2$ (half-saturation density), and δ defines the fraction of biomass that is eaten but not assimilated. The consumer population loses biomass to metabolic processes at the rate M. This relatively simple model framework has three equilibria, only one of which is stable for a given set of parameters, and it can produce a variety of dynamical behaviours including stable nodes, foci, and oscillations (see Yodzis and Innes 1992; Vasseur and McCann 2005).

Body size enters the model through allometric scaling functions for the three parameters which describe per-unit-time rates of change, namely r, J, and M. Yodzis and Innes (1992) scaled these rates according to generally applicable power laws of the form of Eq. (3.1), where:

$$\begin{aligned} r &= f_r a_r m_R^{-0.25} \\ (1-\delta)J &= f_J a_J m_C^{-0.25}. \\ M &= a_M m_C^{-0.25} \end{aligned} \tag{3.5}$$

The parameters m_R and m_C represent the body sizes of resources and consumers respectively and the allometric intercepts a_r, a_J, and a_M are empirically derived constants for a "user-defined" species or set of species. Yodzis and Innes (1992) generalized these intercepts to the four metabolic classes defined by Robinson et al. (1983); endotherms, ectothermic vertebrates, ectothermic invertebrates, and unicells). Since the allometric intercepts used to represent resource growth and consumer ingestion (a_r and a_J) are usually measured under physiologically limited conditions, the fractional coefficients f_r and f_J can be used to impose ecologically limited conditions (see Yodzis and Innes 1992 for more detail).

The characteristic response time of this system can be determined, as it is for the logistic model of population growth, by calculating the eigenvalues (λ_i) of the system's Jacobian matrix. Equilibrium stability requires that all the system's eigenvalues be less than 0, but it is the most positive of the system's eigenvalues that determines the time required by the system to adjust to a change in environmental conditions. Specifically, the characteristic response time t_r is approximated by:

$$t_r = -1/\mathrm{Re}(\lambda_{\max}) \tag{3.6}$$

(Pimm and Lawton 1977). The eigenvalues of the model Eq. (3.4) and the corresponding response times are calculated for the model in Appendix 3A.

To visualize how body size influences the characteristic response time of the system, it is useful to parameterize the model and plot t_r across a range of consumer and resource body sizes. Table 3.1 provides a parameter set indicative of the interaction between a unicellular plant resource (e.g. algae) and a poikilothermic invertebrate consumer (e.g. zooplankton). The model's free parameters (R_0 and K) are chosen in the parameter space where the equilibrium is stable and approximately equidistant from the thresholds for system persistence and unstable dynamics (see Vasseur and McCann 2005). Figure 3.3 shows the characteristic response time plotted against a gradient of resource and consumer-body sizes.

Table 3.1. Model parameter descriptions and values

Parameter	Description	Value (units)	Source
Consumer-resource model			
R_0	Half-saturation density	$60\,\text{kg} \cdot \text{area}^{-1}$	
K	Carrying capacity	$10\,\text{kg} \cdot \text{area}^{-1}$	
Δ	Fraction of energy lost during ingestion and digestion	0.55	Yodzis and Innes (1992)
f_r, f_J	Realized fraction of maximum growth and ingestion rates	1	
Scaling function parameters			
a_r	Allometric intercept[1]	$0.386\,\text{kg} \cdot (\text{kg} \cdot \text{year}) \cdot \text{kg}^{0.25}$	Yodzis and Innes (1992) *in* Vasseur and McCann (2005)
a_J	Allometric intercept[1]	$9.7\,\text{kg} \cdot (\text{kg} \cdot \text{year}) \cdot \text{kg}^{0.25}$	
a_M	Allometric intercept[1]	$0.51\,\text{kg} \cdot (\text{kg} \cdot \text{year}) \cdot \text{kg}^{0.25}$	
E_r	Activation energy for resource growth	0.467 eV	Hansen et al. (1997) *in* Vasseur and McCann (2005)
E_J	Activation energy for consumer ingestion	0.772 eV	
E_M	Activation energy for consumer metabolism	0.652 eV	
k	Boltzmann's constant	$8.618\text{e}^{-5}\ \text{eV}\cdot\text{K}^{-1}$	
T	Temperature	varied (K)	
Body sizes (four sets)			
m_R	Resource body size	(A) 1.0e − 13 kg (B) 1.0e − 10 kg (C) 1.0e − 13 kg (D) 1.0e − 10 kg	
m_C	Consumer body size	(A) 1.0e − 8 kg (B) 1.0e − 8 kg (C) 1.0e − 5 kg (D) 1.0e − 5 kg	

[1] Allometric intercepts were measured at T_0 equals 20°C or 293 K.

There are a number of noteworthy properties that emerge from Figure 3.3. Firstly, the surface representing the characteristic response time shows two distinct zones which are separated by a vector of body-size combinations along which consumer body size is six orders of magnitude larger than resource body size ($m_C/m_R = 10^6$). This qualitative change in the system's characteristic response-time surface arises via changes in the nature of the system's eigenvalues. For combinations where $m_C/m_R > 10^6$ the system's two eigenvalues are real and distinct, generating a monotonic approach to equilibrium following perturbation. The dominant eigenvalue, and thus the characteristic response time, is strongly influenced by consumer body size, and only weakly influenced by resource body size in this region.

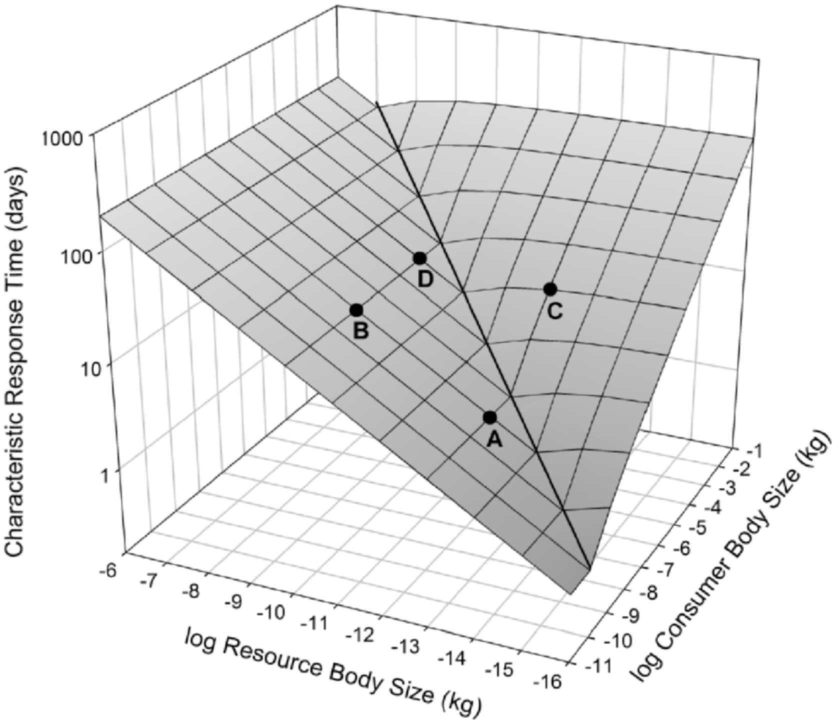

Figure 3.3. Characteristic response time surface of the body-size-dependent consumer-resource model (Eq. 3.3). The surface displays two distinct regions corresponding to different qualitative behaviours of the equilibria: when $m_C/m_R < 10^6$ the equilibrium is a focus and the response time is entirely determined by resource body size; when $m_C/m_R > 10^6$ the equilibrium is a node and the response time is determined by both resource and consumer body size. The four labelled points correspond to the four parameter sets A through D used in the analyses in later sections.

For combinations where $m_C/m_R < 10^6$ the eigenvalues are a complex conjugate pair, generating damped oscillations following perturbation. The real portion of this conjugate pair, which is used to determine the characteristic response time, is independent of consumer body size; it is determined only by the body size of the resource, through its effect on the growth rate r; $t_r \propto 1/r \propto {m_R}^{0.25}$. Although the characteristic response time of the system scales with resource body size in the same manner demonstrated by the population logistic model, the addition of a consumer to the system increases the characteristic response time by altering the intercept of the scaling function (see Appendix 3A). Pimm and Lawton (1977) were first to show that the response time of food webs quickly increases with the addition of each new trophic level to the system. This led them to the supposition that the maximum trophic level in ecological systems was limited by population dynamics rather than by the flow of energy. However, recent research has shown that decreasing the predator-prey body-size ratio at higher trophic levels can slow this increase, allowing longer chains to remain feasible (Jonsson and Ebenman 1998).

The result of this exercise leads to the rather obvious question: What body-size ratio typifies the consumer-resource interaction in natural systems? Cohen et al. (1993) provided a summary of predator and prey body sizes for 832 predator pairs from over 70 different ecological communities. Although they explain much of the variability in body-size ratios with habitat types and metabolic strategies they generally show that this ratio generally falls between $10^{1.5}$ and 10^3. In the extensive data set compiled by Brose et al. (2005), the average ratio for 16,807 consumer-resource pairs is $10^{1.74 \pm 3.06}$, including data from all habitats and from a variety of consumer-resource pairs (including host-parasitoid). In Figure 3.3 these ranges fall in the zone where the response time is entirely determined by resource body size and the return to equilibrium is typified by damped oscillations. However, it is worth noting that Figure 3.3 is parameterized to represent the interaction between algae and zooplankton and that alternative parameters will alter the location (but not the existence) of the boundary delimiting the two zones in Figure 3.3. Gaedke (1992) determined the size spectrum of the entire plankton community in Lake Constance, where plankton range from 2^{-6} to 2^{14} pg C and herbivorous zooplankton from 2^{13} to 2^{26} pg C. Obviously not all consumer-resource pairs falling within these ranges are valid; however, the ranges do provide conservative limits on the body-size ratios that may be possible ($10^{-0.3}$ to $10^{9.6}$). The median of this range ($10^{4.9}$) falls near the boundary in Figure 3.3 suggesting that both resource and consumer body sizes may influence the response times in natural systems.

Despite the frequency with which eigenvalues have, and continue to be used to infer the stability of an ecological system, they are an asymptotically biased measure whose error grows quickly as the system is moved further from its equilibrium. For large enough perturbations transient dynamics can be extremely important and endure for times on the order of the characteristic response time (Neubert and Caswell 1997). Although Yodzis and Innes (1992) suggested that the asymptotic approach to equilibrium appeared to be globally valid for the class of consumer-resource models described here, the characteristic response time may not adequately describe the response of the system to continued forcing at certain frequencies. For example, a perturbed system that has not returned to equilibrium before the subsequent perturbation occurs, may currently occupy a state that could excite or dampen the system's response to the subsequent perturbation. In the following sections I evaluate the ability of the characteristic response time to determine which frequencies of environmental forcing will influence population dynamics. However, before dealing with this issue, I describe some important and often overlooked assumptions which arise when considering exactly how the environment influences populations.

3.4 PARAMETRIC AND DEMOGRAPHIC PERTURBATIONS

Much of the theory surrounding the use of eigenvalues as predictors for the response of perturbed populations makes the assumption that perturbations are demographic in nature; that is, they reflect events which alter the density of the population without influencing its equilibrium, or the propensity of the population to return to its equilibrium. Such perturbations can arise from random variation among individuals in a population (e.g. quality or reproductive potential), by mass mortality events caused by extreme (rare) climatic conditions, or anthropogenic impacts. These perturbations are not directly akin to those imposed by "normal" (non-lethal) variation in environmental conditions, which is more likely to influence the parameters governing population dynamics than the population densities directly. For example the production, ingestion, and metabolic rates, which describe population dynamics in the Yodzis and Innes (1992) model are known to depend on temperature (Brown et al. 2004), and assumedly a variety of other environmental factors.

Parametric perturbations, through their effects on the parameters governing population dynamics, can indirectly influence population densities by altering the equilibrium density of the population. Recall the example presented in the introduction, where May (1976) varied the carrying capacity (K) of the logistic model through time. This perturbation influenced the population dynamics indirectly by varying the model's equilibrium; with the outcome depending upon the frequency of variation in K. However, there is an additional complication to consider when perturbing parameters – in addition to the equilibrium, the response time may itself vary with environmental conditions. Consider the dynamics of the logistic model under a new model of environmental variation which influences both r and K. Such variation will alter the equilibrium population density (K) and the characteristic response time (recall that $t_r = 1/r$) in concert. If the environmentally imposed variation in r and K is positively correlated then we expect the system to reach equilibrium faster at higher equilibrium densities. This implies that a unit increase in some environmental character (e.g. temperature, irradiance, pH) may have altogether different effects on populations than a unit decrease in the same character. Upon inspection of the equilibrium and eigenvalue equations for the Yodzis and Innes (1992) model of consumer-resource interactions (Appendix 3A) it is clear that r, K, and a number of other model parameters alter both the equilibrium and the eigenvalues of the system. This suggests that even simple model forcing (e.g. forcing of only one parameter) may produce complicated responses to perturbations, which are not predicted by determination of the eigenvalues, (and subsequently the response times) alone. Below I introduce a recent modification to the Yodzis and Innes (1992) model framework which incorporates temperature as a model parameter. Using this model I evaluate the utility of the characteristic response time to predict which frequencies of environmental forcing are important to populations.

3.5 CAN RESPONSES TIMES HELP DETERMINE HOW CONSUMERS AND RESOURCES VARY IN FLUCTUATING ENVIRONMENTS?

Any attempt to address the above question using theoretical models must make assumptions about how and where environmental variability enters the trophodynamic model. However, the risk of making such assumptions can be minimized by employing empirical relationships, which describe the dependence of model parameters, or their surrogates, on environmental conditions. Recently, the importance of temperature for a variety of biological and ecological processes including metabolic rate (Gillooly et al. 2001), developmental rate (Gillooly et al. 2002), and population growth rate (Savage et al. 2004), have been highlighted (see Brown et al. 2004 for a review). Already, these relationships have been used in theoretical models to predict temperature-induced changes in population ranges (Humphries et al. 2002), activity levels, (Humphries and Umbanhowar, Chapter 4 this volume), and energy usage (Ernest et al. 2003); and to describe gradients of global biodiversity (Allen et al. 2002) making temperature an obvious choice to address the issue at hand.

Vasseur and McCann (2005) merged the trophodynamic-allometric framework of Yodzis and Innes (1992) with the equations describing the temperature dependence of biological processes (e.g. Brown et al. 2004) to generate a trophic model that is capable of responding to environmental variability (temperature) in a mechanistic fashion. In this model, body size and temperature enter the model in the three rates r, J, and M as functions of the $-1/4$ power of resource or consumer body size (m_R, m_C) and as an exponential function of temperature (see Vasseur and McCann 2005):

$$\begin{aligned} r &= a_r(T_0)m_R^{-0.25}e^{E_r(T-T_0)/kTT_0} \\ (1-\delta)J &= a_J(T_0)m_C^{-0.25}e^{E_J(T-T_0)/kTT_0} \\ M &= a_M(T_0)m_C^{-0.25}e^{E_M(T-T_0)/kTT_0} \end{aligned} \tag{3.7}$$

where a_r, a_J,and a_M are the allometric intercepts of the body-size scaling relationships measured at the temperature T_0. The E_i are empirically estimated activation energies, k is Boltzmann's constant, and T is temperature in Kelvin. These equations follow the temperature-scaling laws developed to describe enzyme kinetics – which ultimately exert their influence upon population-level processes and are therefore suitable for biological and ecological models.

The dynamics of this model in response to long-term changes in temperature can be determined by assessing the equilibrium response to temperature. Vasseur and McCann (2005) showed that this response is governed by the differences $E_J - E_M$ and $E_r - E_M$, which control the energy requirements for the consumer and the energy budget for the system respectively. Based upon empirical estimates of the E_i, they suggested that the majority of pairings of consumers and resources would result in reduced equilibrium densities of both when the environmental temperature increased. I employ the same set of parameters used in Vasseur and McCann (2005) to describe the temperature-dependence of the interaction between unicellular algae and herbivorous zooplankton (Table 3.1) using four combinations of body sizes which fall within the range reported by Gaedke (1992) for phytoplankton and herbivorous zooplankton in Lake Constance (see Table 3.1 for parameter values).

The model provides a useful tool with which to test the influence of body size and environmental variability on the stability of consumer and resource dynamics and in addition, how the frequency of environmental forcing may influence these results. Figure 3.2 shows, using May's example for the logistic model, how the frequency of forcing influences the deviation of a population from its equilibrium values in relation to the response time. To obtain the same figures for the consumer-resource model above (Eqs. 3.4 and 3.7), the model was integrated through time, but perturbed by changes in the environmental temperature at regular intervals – to generate a specific frequency of forcing (f). Temperatures are drawn from a random normal distribution with a mean value of 20°C and a standard deviation of 5. The coefficient of variation (CV) of consumers and resources and their deviation from equilibrium conditions, were determined within each model iteration (which lasted 32,768 days) and averaged across 200 replicates at each of the frequencies tested.

For each of the four body-size combinations (Figures 3.4–3.7) it is apparent that the response of the system to different frequencies of forcing matches to some extent, the curve plotted in Figure 3.2; at low frequencies the dynamics are "at equilibrium", at intermediate frequencies the deviation from equilibrium is increasing, and at high frequencies the deviation from equilibrium is constant or decreasing. To test if May's (1976) prediction for isolated populations holds for consumer-resource pairs, the

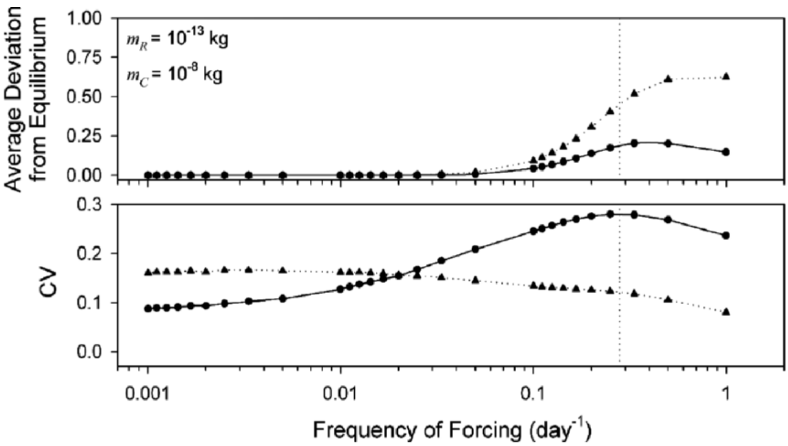

Figure 3.4. The observed relationship between the frequency of forcing and (a) the average deviation from equilibrium for resources (solid) and consumers (dotted), and (b) the CV. The vertical dotted line represents the frequency corresponding to $1/t_r$. The parameters used in this simulation are listed in Table 3.1 and body sizes are those of set A.

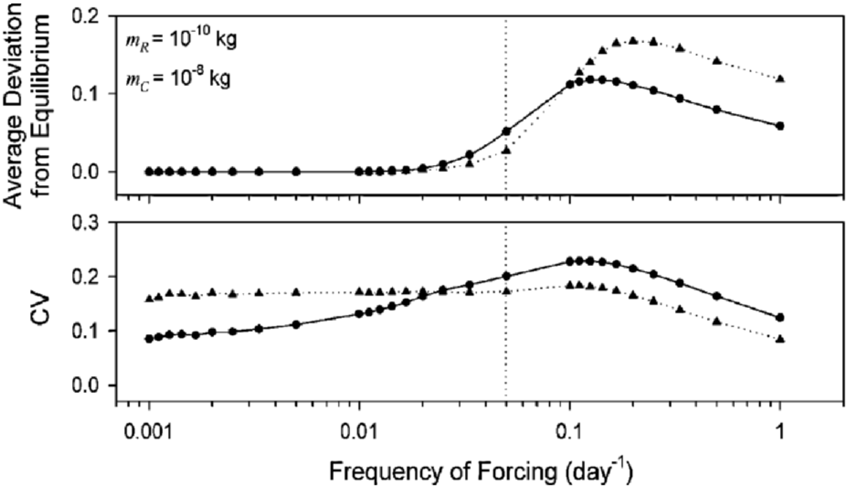

Figure 3.5. As in Figure 3.4 except body sizes are those of parameter set B.

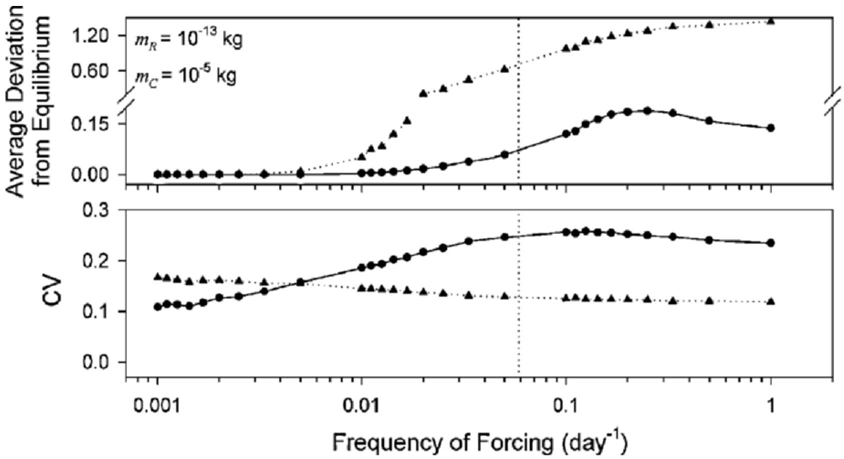

Figure 3.6. As in Figure 3.4 except body sizes are those of parameter set C.

frequency corresponding to $1/t_r$ (evaluated at 20°C) is plotted in Figures 3.3– 3.6. For all parameter sets this frequency lies within the zone where the deviation from equilibrium is increasing, suggesting that threshold frequency $1/t_r$ underestimates the importance of higher frequencies. However, there are distinct differences in the variability of the resource populations among the four body-size scenarios at, and nearby this frequency; $1/t_r$ is nearest to frequencies which produce the maximum equilibrium deviation for parameter sets A and D, but far below those for parameter sets B and C. Table 3.2 provides a summary of these results.

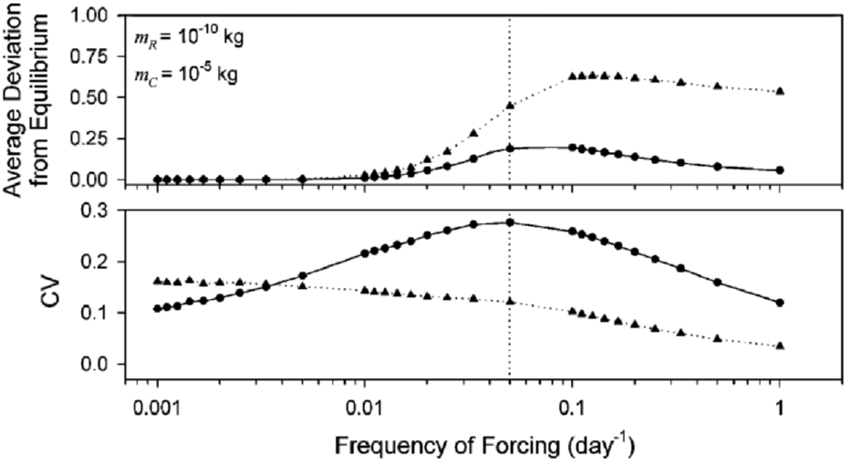

Figure 3.7. As in Figure 3.4 except body sizes are those of parameter set D.

Table 3.2. Characteristic dynamics of the four parameter sets A–D

Parameter set	Response rate ($1/t_r$) at 20°C	Largest deviation from equilibrium		Largest value of *resource* CV
		Resource	Consumer	
A	0.280 day^{-1}	0.20 @ f = 0.33 day^{-1}	0.62 @ f = 1.0 day^{-1}	0.280 @ f = 0.25 day^{-1}
B	0.050 day^{-1}	0.12 @ f = 0.13 day^{-1}	0.17 @ f = 0.20 day^{-1}	0.229@f = 0.11 day^{-1}
C	0.059 day^{-1}	0.46 @ f = 0.25 day^{-1}	3.28 @ f = 0.33 day^{-1}	0.317 @ f = 0.14 day^{-1}
D	0.050 day^{-1}	0.20 @ f = 0.10 day^{-1}	0.63 @ f = 0.13 day^{-1}	0.276 @ f = 0.05 day^{-1}

For the parameter sets A and D, the response rate $1/t_r$ denotes the (approximate) frequency at which the CV of resources is greatest and for parameter sets B and C, the peak in resource CV occurs at forcing frequencies 2–2.5 times larger than the response rate. These results are in direct contrast to those from the single population model – where the response rate $1/t_r$ denoted a frequency of forcing at and above which the population CV was relatively low (cf. Figure 3.2). The trend of having larger resource CVs at high-forcing frequencies is likely due to the ability of resources to overcompensate for changes in their equilibrium, a character that is not possible in the continuous-time logistic model. If we compare the magnitude of the equilibrium deviations and CVs among the four parameter sets, it is apparent that

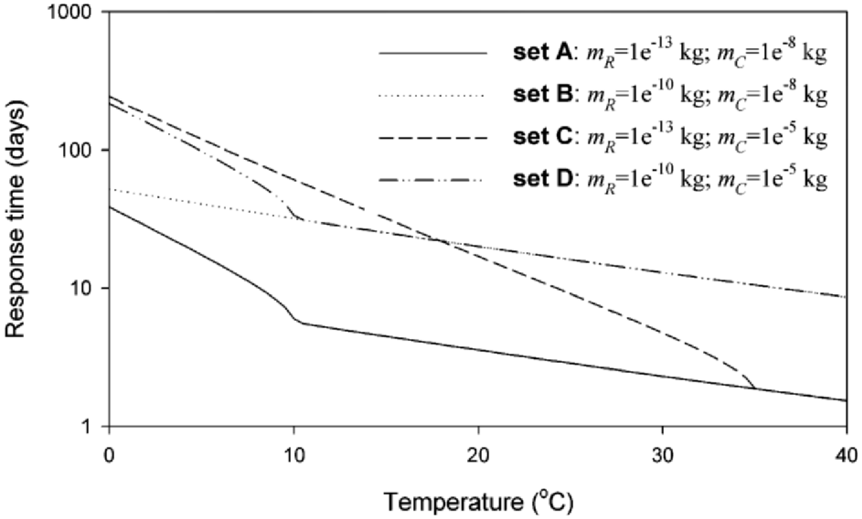

Figure 3.8. Response time of the model as a function of environmental temperature for each of the four parameter sets A through D. The curves for A, C, and D have a change in their slope corresponding to the temperature at which the system transitions from a node (at lower temperatures) to a focus (at higher temperatures).

lower absolute variability is expressed by systems whose body-size ratios are nearer to 1 (e.g. the CV for set B $<$ A $\approx$ D $<$ C).

Despite the similar response times for parameter sets B, C, and D plotted in Figure 3.1, there are evident differences in the way that these systems respond to fluctuations in environmental conditions, which arise from the underlying sensitivities of the systems' eigenvalues. As temperature varies over time, the equilibrium changes in concert with the response times of the system; at low temperatures equilibrium densities are relatively high but response times are relatively low. Figure 3.8 shows the relationship between response time and temperature for each of the four parameter sets. Over certain temperature ranges the scaling relationship between t_r and resource body size ($t_r \propto m_R{}^{0.25}$) is apparent in each curve; however, for sets A, C, and D there is a transition corresponding to a change in the fundamental properties of the equilibrium. One can envision temperature as effectively altering the body sizes of predators and prey; at low temperatures, response times are more likely to be strongly influenced by temperature and determined by both resource and consumer body size.

3.6 SUMMARY AND DISCUSSION

Characteristic response times have been cited as an important measure of the resilience of populations and trophic systems to perturbations in external conditions and given that external conditions vary continuously in most natural systems they are an important potential predictor of the level of variability these systems may express. For single populations, characteristic response times determine which frequencies of environmental variability will cause populations to themselves vary – depending on the body size of individuals in the population. Extending these results to consumer-resource models shows that when $m_C/m_R < 10^6$ response time is determined only by resource body size, and when $m_C/m_R > 10^6$ response time is mainly influenced by consumer body size (Figure 3.1). However, evaluating these results by forcing the rate parameters of the model via the Boltzmann factor shows that the characteristic response time should not be used to predict which frequencies of forcing will influence population dynamics. In fact, forcing at the frequency corresponding to $1/t_r$ often produces the largest variability one of the populations (resources).

Despite the results shown here, there are a myriad of other factors that can influence population dynamics at fixed temporal scales, or over a range of temporal scales. In practice, any population or food web will experience environmental fluctuations possessing a multitude of frequency components rather than a single frequency as I have modelled here in the latter section. While a few distinct frequencies may be responsible for the majority of environmental variation (e.g. ENSO cycles [see McPhaden, Chapter 1, this volume], seasonal cycles, lunar cycles, and diel cycles) many environmental variables are known to possess a distinct negative-scaling relationship between the frequency and magnitude of fluctuations ($f^{-\beta}$; Halley 1996; Vasseur and Yodzis 2004). This dictates that high-frequency noise has a lesser magnitude than low-frequency noise, an aspect that may lead to a reduction in resource variability at high frequencies.

Adaptive responses are also extremely important for determining the impact of environmental variability. For instance active thermoregulatory behaviours such as torpor can allow an individual to buffer environmental variability at a specific temporal scale. Humphries and Umbanhowar (Chaper 4, this volume) demonstrate that many populations traits can, under certain conditions, become decoupled from the environment through behavioural adaptations, and that this decoupling may be critical for the success of endotherms in cold climates.

Most studies examining the dynamical impacts of perturbations have remained isolated to examples involving single perturbations, in hope of being able to extrapolate their results to the more complicated cases where perturbations are not singular, but continual occurrences (Neubert and Caswell 1997). While this study provides only an example of how a consumer-resource system might respond to continually imposed environmental variability, it presents a technique whereby forcing frequencies, which excite the system can be isolated, and compared to linear measures of the forcing response (such as response time). Although I suggested earlier that communities provide a better "base" for the study of ecological variability, since populations rarely exist in isolation of others, they suffer the same criticism as they are most often embedded in larger food webs. While communities do provide a basis with which to begin understanding the importance of interspecific interactions for ecological variability, extrapolating these results to entire food webs can be highly inaccurate due to the existence of non-linear feedback mechanisms. We can project that the response times of food webs may scale predominantly with the body size of resources and that the period of forcing at which the system is most sensitive may be nearly equivalent to the response time, however, these projections are no substitute for more detailed theoretical and empirical experiments. Ultimately, ecologists need to derive a better understanding of how continual, press, and point perturbations interact to determine how ecosystems respond to environmental variability.

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APPENDIX 3A THE CHARACTERISTIC RESPONSE TIME OF THE TROPHODYNAMIC-ALLOMETRIC MODEL.

The Yodzis and Innes (1992) allometric model of consumer-resource dynamics is defined as:

$$\begin{aligned}\frac{dR}{dt} &= rR\left(1-\frac{R}{K}\right) - JC\left(\frac{R}{R+R_0}\right)\\ \frac{dC}{dt} &= C\left[-M+(1-\delta)\,J\left(\frac{R}{R+R_0}\right)\right]\end{aligned} \tag{3A.1}$$

where the model rates (per-unit-time parameters) are scaled with resource and consumer body size as follows:

$$
\begin{aligned}
r &= f_r a_r m_R^{-0.25} \\
(1-\delta)\,J &= f_J a_J m_C^{-0.25} \\
M &= a_M m_C^{-0.25}
\end{aligned}
\tag{3A.2}
$$

This model has three equilibrium points, two of which are trivial $[(\mathrm{R}_e, \mathrm{C}_e) = (0, 0), (\mathrm{K}, 0)]$ and the third which is defined as:

$$
\begin{aligned}
R_e &= \frac{R_0}{(1-\delta)J/M - 1} \\
C_e &= \left(1 - \frac{R_e}{K}\right)\left(\frac{(1-\delta)r}{M}\right) R_e
\end{aligned}
\; .
\tag{3A.3}
$$

The Jacobian matrix defines the matrix of partial derivatives of Eq. (3A.1) and is defined:

$$
J = \begin{bmatrix} \frac{\partial R}{\partial R} & \frac{\partial R}{\partial C} \\ \frac{\partial C}{\partial R} & \frac{\partial C}{\partial C} \end{bmatrix}.
\tag{3A.4}
$$

Solving for the eigenvalues of J, evaluated at Eq. (3A.3) gives:

$$
\lambda_{1,2} = \frac{\left.\frac{\partial R}{\partial R}\right|_{Eq_{A3}} \pm \sqrt{\left(\left.\frac{\partial R}{\partial R}\right|_{Eq_{A3}}\right)^2 - 4\left(-\left.\frac{\partial R}{\partial C}\right|_{Eq_{A3}} \left.\frac{\partial C}{\partial R}\right|_{Eq_{A3}}\right)}}{2}.
\tag{3A.5}
$$

It has been shown elsewhere (Vasseur and McCann 2005) that both $\lambda_{1,2} < 0$ when $\left.\frac{\partial R}{\partial R}\right|_{Eq_3} < 0$ which is true when $R_0/K < (1-\delta)J/M - 1$. Thus, the model is always stable when the consumer's perceived resource abundance (K/R_0) is sufficiently large enough to allow the consumer's realized ingestion rate to exceed its metabolic rate.

In the range of stable parameter space the two eigenvalues can be real and distinct (corresponding to an equilibrium node) or complex conjugates (corresponding to an equilibrium focus). In the latter case a noteworthy size invariance emerges in the characteristic response time, where $t_r = -1/Re\lambda_{\max}$. Here

$$
Re\lambda_{\max} = \frac{1}{2}\left.\frac{\partial R}{\partial R}\right|_{Eq_{A3}} = \frac{r}{2}\left[1 - \frac{2R_e}{K} - \left(\frac{(1-\delta)J}{M}\right)\left(1 - \frac{R_e}{K}\right)\left(\frac{R_e R_0}{(R_e + R_0)^2}\right)\right]
\tag{3A.6}
$$

is invariant to changes in consumer body size (m_C) since both $(1-\delta)J$ and $M \propto {m_C}^{-0.25}$. When the equilibrium is a node (two real distinct eigenvalues) $\lambda_{\max}$ is a function of both resource and consumer body sizes. The transition from focus to node is shown along a gradient of resource and consumer body sizes for a specific parameter set in Figure 3.2 and the algebraic form of this function can be found in Yodzis and Innes (1992).