Consumption Driven Population Dynamics (CDPD): Further Explorations

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ABSTRACT

The consumption driven population dynamics (CDPD) model, described and demonstrated in my previous paper (Bentley, 2006), suggests a fundamental structure connecting all life produced by simple, independent mechanisms for mass gain and loss that are determined by those constraints of natural law governing transfers of mass and energy. This basic system may be modified to a greater or lesser degree by additional mechanisms that account for living and nonliving elements of the environment, much of which is stochastic. Collectively, this accounts for the broad range of population dynamics we observe within the web of linkages connecting all living things.

CDPD implies that mortality has a much greater influence on the dynamic than previously considered. While this is certainly no surprise to those doing field research, mortality has not been properly addressed in prior population models. A population subject to hard times, very low consumption or extreme environmental conditions, can suffer losses at rates that are orders of magnitude greater than rates of gain under the most favorable conditions. CDPD exhibits this dynamic under harsh conditions.

The '*CDPD response*', a biologically derived model of consumption functional response that may be used in conjunction with the CDPD model, introduced but never exercised in the previous paper, is demonstrated to show the effects of past consumption. The '*CDPD response*' is explored in the effort to more completely understand how past consumption may help explain certain observations.

While scenarios driven by consumption appear to explain single peak events and seasonal oscillations, environmental effects aside from consumption produce stable aperiodic oscillations with characteristics highly similar to the great majority of extended time series data contained in the NERC database.

Keywords: Birth, death, population, consumption, environment, model.

INTRODUCTION

This paper continues the exploration of the consumption driven population dynamics (CDPD) model (Bentley, 2006).

Population gains and losses are driven by environmental conditions. Those aspects of environment explicitly defined in CDPD as contributing directly to a population's level of consumption, specifically a resource population, constitute an essential component of environment with a dynamic of its own that CDPD deals with separately from all other impacts of environment. Consumption is dependent both upon resource level and upon a population's 'predation proficiency' which in large part is contingent upon the predation environment. Consumption, or more precisely level of consumption, can produce an overall population dynamic anywhere from rapid growth to an even more rapid population decline. This is why I use the words 'consumption driven' in the title of both papers.

The concept of 'predation proficiency' introduced by CDPD, the ability of a population to acquire its sustenance, and which can change in value subject to a wide range of mechanisms, is an element not offered in previous models. One might argue that the effects of predation proficiency can be emulated by 'predator efficiency', and by other variables used in previous models. But this does not provide the gain in understanding that results from an explicit proposal of predation proficiency, and the definition of Rp in terms of biological mechanism, and corresponding use of Rp in the formulary describing each population within a system. Predation proficiency in the CDPD model plays a pivotal role in population dynamics when combined with proper mechanism for mortality. It produces a dynamic closely matching the dynamic observed in nature, and does so for reasons concluded from the data of Beschta (2003), Ripple (2004), Nelson et al. (2004), and others.

While loss of resource can be devastating, changes in those elements of a population's environment that do not contribute directly to consumption can have an equally dramatic impact upon a population and do so in a manner equivalent to the effects generated by consumption. Mortality for many populations increases under conditions of extreme weather events or disease, and may increase in spectacular form in the face of a volcanic eruption, asteroid impact, or the simple draining of a wetland.

Population increase proceeds at a reproductive rate consistent with the level of consumption currently available *and* whatever environmental conditions currently exist. While a population under favorable conditions may increase at seemingly alarming rates, that same population faced with *extremely* adverse conditions will drop precipitously. This rate of decrease, an aspect of the natural dynamic frequently observed, can be orders of magnitude greater than any possible rate of increase, proceeding rarely even to extinction.

This strongly suggests that mortality, rather than fecundity, dominates the natural dynamic. A correct model of population dynamics must include a mechanism that replicates this response.

The CDPD inverse dependence of mortality upon consumption *and* upon other environmental factors emulates just such an accelerating response to degenerating conditions with mortality rising rapidly if consumption approaches zero or environmental conditions turn lethal. This is a fundamental property of CDPD.

This marks a clear difference between CDPD and earlier models, compiled in such works as *Population Ecology: First Principles* by John H. Vandermeer and Deborah E. Goldberg (2003). Most models treat loss as a simple constant fraction of population, in good times and in bad. A few models, Anderson-May (1978), Hanski et al. (1991), and others use an inverse of the resource population in their mortality functions, but generate abnormally low mortality in the presence of excess resource.

The CDPD Population Model Reiterated

(See Bentley, 2006, for a full definition of all variables and constants.)

CDPD is a logical construct enabling a comprehensive accounting of all forces acting upon individual life forms, and upon those aggregates of individuals we call populations, whether considered in their entirety upon the planet, or local as delineated in any manner natural or otherwise.

CDPD is implemented as a difference equation where all functions are evaluated at discrete time intervals [$\Delta\mathbf{t}$ = 1 time increment]. The following well known simple relationship accounts for all possible gains and losses.

$$\mathbf{N_{t+1} = N_t + B - D}$$ …where all terms have units of ***mass***.

$$\mathbf{N_{t+1} = N_t + B - D + IE}$$ …for an unbounded system

Gains **B** and losses **D** are summed to establish change in **N** for the next iteration. Mechanisms for **B** and **D** are quite different. In a bounded system, gain under constant conditions of consumption and environment as defined below will be a constant fraction of the population **N**. In that same bounded system, loss as defined below is composed of two mechanisms, losses in the absence of predation **Q** which I term natural losses, and losses due to predation **P**. In CDPD, using this discrete time approach, losses during a time increment are each calculated separately, but then must be combined using an overlap function to calculate **D** because predation losses will replace some natural loss over the course of a time increment.

Aside from immigration minus emigration **IE** in an unbounded system, *there are no other mechanisms for gains and losses* additional to those just stated.

At its base the CDPD model requires 5 parameters, Rb, Rq, Rc, Rp, and Kd. If one wishes to introduce the effects of environment and stochastic forces then one needs to add E. To differentiate the environment for gain, loss and consumption then you need to replace E with Eb, Eq, and Ec. However, throughout both the original paper and this current paper I have used E only for stochastic runs of the model by inserting random values for E. Deterministic runs set E to a value of 1 thus removing E from the model.

You will find in the relationships below a much greater number of parameters and this can be a source of confusion. For example, Rp is represented as a product of terms Ec, Kp/Ka, Rs, and Ri, offered as elements of the system that may be useful to those making a more detailed study. It could easily be argued that Rs and Ri should simply be included in Ec, or perhaps some even greater number of environmental aspects should be dissected out for special treatment. However, in this work I have simply used singular values for Rp to represent the product of all elements that collectively produce Rp.

Parametric analysis shows the nature of the model dynamic hinges upon the value of Rp. Above a threshold the dynamic changes from steady state to collapse. While the other parameters change equilibrium populations, or peak values in the case of collapse, and while they can also shift the threshold for collapse, they do not otherwise fundamentally change the nature of the dynamic.

Another potential source of confusion is my additional model for a biologically derived consumption functional response I call the *CDPD response*. My first CDPD paper introduced this model which allows the inclusion of time lagged past consumption. Portions of this paper demonstrate how the *CDPD response* affects the dynamic for both steady state and collapse scenarios. However, this additional complexity is unnecessary to demonstrate a full range of the CDPD dynamic from equilibrium to collapse and the validity and usefulness of CDPD does not depend upon its inclusion.

Within all populations of living things, just as within individual organisms and human infrastructure, there exist concurrent processes of building up and tearing down. These processes are quite different. Growth is directly driven by the amount of resource applied to growth, and further affected, for better or worse, by all other elements in the environment.

Within a bounded system there is only a single mechanism for mass gain.

FECUNDITY – mechanism for *ALL* mass gain in a bounded system

B = (total ***mass gain*** during time increment)

$B = N_t \cdot Rb \cdot (C \cdot Eb)$

Rb=(fractional gain at (C·Eb)=1. Rb is a *constant*.)

Eb=(environment for births)

In nature B may not be a linear function, nor Q a simple inverse. But likely values for B and Q at C=0 and C=1 make B and Q a good place to start.

Non-predation MORTALITY

Q = (non predation ***mass loss*** due to natural causes during time increment)

$Q = N_t \cdot Rq/(C \cdot Eq)$ ...conditional to [If $(C \cdot Eq)=0$ then $N_{t+1}=0$]

Rq=(fractional loss at $(C \cdot Eq)=1$. Rq is a *constant*.)

Eq=(environment for deaths)

CONSUMPTION – current fraction of satiation [0≤C≤1] (Unitless)

$C = (Rp \cdot Neaten)/(Rc \cdot Neater)$ ...conditional to [if $C>1$ then $C=1$]

Rp=(predation proficiency) (Unitless)

$Rp = Ec \cdot Rs \cdot Ri \cdot (Kp/Ka)$ (Unitless)

Ec=(environment for predation) (Unitless)

Rs=(food source quality) (Unitless)

Ri =(predator interference) (Unitless)

(Kp/Ka) variables described under *CDPD response* further on.

Rc=(satiation consumption ratio in units of Prey/Predator)

CORRECTION (Bentley, 2006): Rs and Rp are unitless. Rc has units of Nprey/Npredator (a simple mass ratio). This does NOT change the results presented in that paper.

The CDPD model provides for easy incorporation of environmental mechanisms, both biotic and abiotic, affecting gain [Eb], loss [Eq], and the predation environment [Ec] thus allowing the modeling of the great multitude of scenarios found in nature.

[Eb, Eq] All elements of Environment Other Than for Consumption

[Ec] All elements of Predation Environment EXCEPT Neaten

E = 1 in a *nomina*l environment, but can range from E=0 to E>1

E = *f*(environmental factors of interest) (Unitless)

Predation MORTALITY

P = (***mass loss*** during time increment due to predation)

$P = Cp \cdot Rcp \cdot Npredator$ …where Cp and Rcp are predator C and Rc

In a bounded system there are two mechanisms for loss. There is natural mortality Q, a function of species and environment, and there is predation P, a function of the predator. Natural mortality Q can change precipitously under conditions of a very bad environment ($Eq<<1$) or low consumption ($C<<1$). Even a run of middling consumption combined with an equal span of less than ideal environment can have a devastating effect on a population.

Total MORTALITY – *ALL* mass loss in a bounded system

D = (total mortality, ***mass loss*** during time increment)

$D = (1-Kd) \cdot (P+Q) + Kd \cdot (P+Q+|P-Q|)/2$ ...for $[0 \le Kd \le 1]$ (Kd is Unitless)

Kd = (predator propensity to kill prey close to a natural death)

Within the CDPD model total mass loss D is calculated using a function that accounts for the *overlap* of predation loss P with natural loss Q; loss that, would, absent predation, otherwise have occurred during the time increment, such that the *overlap* of these two sets is not counted twice. Kd sets the amount of overlap.

IMMIGRATION minus EMIGRATION (*unbounded* mass gain or loss)

IE = (Immigration – Emigration) = IM–EM

$IE = IE_1+IE_2+IE_3+IE_4+\ldots+IE_i$ ...mass flow to or from connected populations N_i

$IE_i = Z\cdot(C-C_i)\cdot([C>C_i]\cdot W_{IMi}\cdot N_i+[C_i>C]\cdot W_{EMi}\cdot N)$ …for TRUE=1, FALSE=0

Z =(Unitless scaling factor specific to population)

W=(Unitless scaling factor specific to environment for IM or EM)

The function for calculating IE based on relative consumption $(C-C_i)$ has been described in detail in my preceding CDPD paper (Bentley, 2006). Z is the population's nominal movement in response to $(C-C_i)$. W_{IMi} and W_{EMi} are factors of difficulty for movement to or from a particular adjoining area.

Subdividing the Time Increment

One may wish to change the model time increment to some subdivision of the original increment. This allows one to enter effects that occur at a finer scale, perhaps seasonal change or other mechanism that would not be observed at the original increment size. This is accomplished as follows:

$B = FRACTION \cdot N_t\cdot Rb\cdot(C\cdot Eb)$

$Q = FRACTION \cdot N_t\cdot Rq/(C\cdot Eq)$

$P = FRACTION \cdot Cp\cdot Rcp\cdot Npredator$

$IE = FRACTION \cdot (IE_1+IE_2+IE_3+IE_4+\ldots+IE_i)$

FRACTION = 1/(number of increment subdivisions)

This simple approach does not take into account the effect of compounding rates of increase and decrease and this may be observed in the approach to a steady state. However, the deterministic steady state produces exactly the same final population values.

R versus Consumption *See *Footnote.*

When one wishes to examine some process causing changes in a variable over time, population for example, one may present the problem using a difference equation as shown below. This simple approach, often in the form of a differential equation, has been used in most attempts to model populations prior to CDPD.

$$\mathbf{N_{t+1} = r\cdot N_t}$$ where **r** = (multiplier at each *time increment*).

For r=1 the population neither increases nor decreases. Setting **r=(1+R)** the above equation may be rewritten as:

$$\mathbf{N_{t+1} = N_t + R\cdot N_t}$$ …Compare this to the CDPD form:

$$\mathbf{N_{t+1} = N_t + B - D}$$ …where $B=N_t\cdot Rb\cdot(C\cdot Eb)$ and, ignoring predation for the moment, $D=N_t\cdot Rq/(C\cdot Eq)$.

Ignoring also Eb and Eq [by setting Eb=1 and Eq=1], we can write:

R = Rb·C – Rq/C …This is $R_{CDPD}=f(C)$ for CDPD.

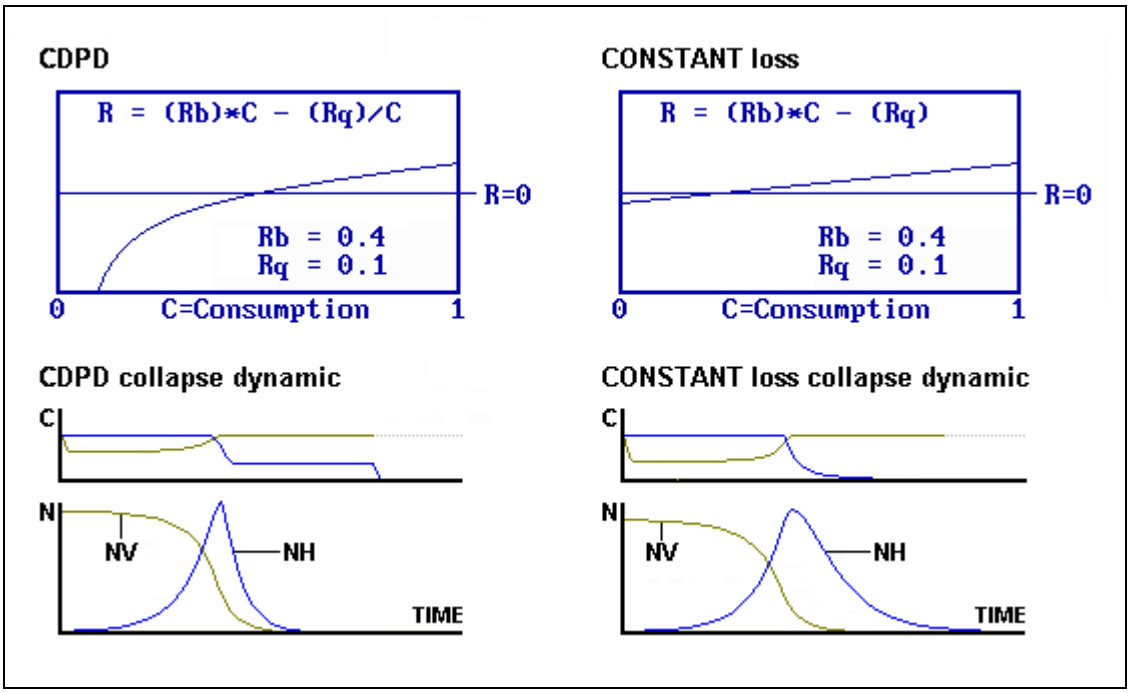
The functions for R in most prior population models (see *Turchin, 2003; Vandermeer and Goldberg, 2003*) assume mortality to be a constant fraction of population ($Rq_{nonCDPD}$) similar to the function below.

R = Rb·C – $Rq_{nonCDPD}$ …This is $R_{nonCDPD}=f(C)$ for most prior models.

Applying either of these functions to a steady state scenario will produce very similar results; equilibrium. With stochasticity even the initial rise or fall to the steady state makes the two approaches indistinguishable.

But, if you apply both of these functions to the single peak collapse (high Rp) with its consequent greater consumption C, the dynamic is quite different:

Figure 1



In CDPD the second trophic level population drops to zero when resource is totally consumed. In the 'constant loss' function used in most prior models the second trophic level population persists long after both resource and consumption have dropped to zero. Constant loss is a very bad simplifying assumption, unsupported by observation and in violation of thermodynamics.

Vertical axis labeled C represent population consumption levels between 0 and 1 (satiation). Vertical axis labeled N represent population levels in units of mass. Populations NV (vegetation), NH (herbivore), and NP (predator), a trophic cascade, are scaled independently to clearly show the relational dynamic between populations, the subject of interest in this generic study of the fundamental interactions between all living things.

Parametric Analysis

Logic dictates that Rq (the minimum fractional mass decrease during a time increment) must be *less* than Rb (the maximum fractional mass increase during a time increment). A violation of this necessarily leads to collapse and would not be a property of any viable population. Thus, we can say with certainty that Rq<Rb. And, Bpredator(mass)<Pprey(mass) due to losses that go to maintenance. A bit of algebraic manipulation using the CDPD relationships yield Rb<Rc, therefore Rq<Rb<Rc.

The following parameters were examined at the second level of a 3 trophic cascade (V,H,P), thus all variables have an extension of H.

Rb (0.5 - 5.0)

At RpH=0.3 the CDPD model produces a steady state dynamic over the entire range. The NH steady state population mass goes from 275.5 to 1133.8, but over that same range steady state consumption drops from CH=0.93 to CH=0.20. Rc was set to 10 at all trophic levels to remain consistent with Rb<Rc.

At RpH=0.7 the CDPD model produces a collapse dynamic in which populations NH and NP rapidly drop to zero. NHmax, the peak height of NH, goes from 363 at RbH=0.5 to 3549 at RbH=5. Despite the higher peak as RbH goes from 0.5 to 5, the NH population reaches peak in fewer and fewer time increments.

Rq (0.2 – 0.02)

At RpH=0.3, model runs at Rq=0.2 and Rq=0.02 display a steady state dynamic, the difference appearing as much higher population mass levels at RqH=0.02 due to the drop in mortality. Populations would have climbed to even higher levels if not for the fact that these higher population masses lower the relative availability of resource, lowering consumption levels as revealed by the values for CV, CH, and especially CP because NP has no losses to higher trophic level predation in this limited 3 level cascade.

At RpH=0.7, runs at Rq=0.2 and Rq=0.02 both display a collapse scenario. RpH=0.7 is a value sufficiently higher than the actual threshold for collapse to clearly demonstrate a sharp break. Once again there were higher peak population mass levels due to decreased mortality at Rq=0.02.

Rp over total range (0<Rp<1)

Examination of the other 4 parameters makes it is very clear that the CDPD dynamic transitions from stability to collapse when Rp exceeds a threshold between 0 and 1. This threshold generally resides in the area of Rp=0.35, but can be higher or lower depending on parameters.

Kd over total range (0≤Kd≤1)

At RpH=0.3 the CDPD model produces a steady state dynamic for KdH=0 to KdH=1. As Kd goes from 0 to 1 all steady state population masses increase, but over this same range consumption for NV and NH drops to 0.63.

At RpH=0.7 the CDPD model produces a collapse dynamic in which all populations rapidly drop to zero. As Kd goes from 0 to 1 all peak maximums increase. As KdH approaches 1 the peak maximums not only increase, but do so in far fewer time increments.

For both the steady state and collapse phase, the transition from KdH=0 to KdH=1 results in increasingly greater population equilibrium levels for the steady state and peak levels in collapse. This is particularly apparent at the NH trophic level. The difference between the NH level and the NP level is the absence of predators at the NP level in this limited cascade.

Rc (1 - 100)

RcH was examined at RpH=0.33 which generated the steady state over the entire 2 order of magnitude range for RcH. At RpH=0.7 the dynamic consistently collapsed in a single peak event for all values of RcH.

Rc determines the ratio of maximum mass transfer from one trophic level to the next during a given time increment and any change in the value of Rc must be reflected in the viable range of values that may be assigned NA, the base mass available to the primary producer which accounts for base input of mass and energy to the system during each time increment. Increase in Rc is directly reflected as an increase in mass differences between trophic levels.

E (Eb,Eq,Ec) (with values from 0 to something greater than 1)

E values act within the CDPD model much like the value of C. E has not been used in this or the previous paper *except* to introduce stochasticity into specified model runs. While environment is extremely important in ecological scenarios, it does *not* alter the *fundamental* nature of the underlying consumption driven dynamic.

The *CDPD response* **(Consumption Functional Response according to CDPD)**

The *CDPD response* is derived from biology as described in my previous paper (Bentley, 2006). It is a model separate from and not required by the CDPD model of population dynamics.

For any level of prey, predators, and Rc, predation proficiency Rp sets the level of consumption C. And, $Rp=Ec\cdot Rs\cdot Ri\cdot(Kp/Ka)$ where (Kp/Ka) contains the terms for time lagged past consumption by predator (Kp) and prey (Ka). $Kp=Gp\cdot CP$ and $Ka=Ga\cdot CA$ where CP represents the effect of predator's past consumption on ability to predate, and CA represents the effect of prey's past

consumption on ability to avoid predation. Rk=Gp/Ga represents the base ratio of predator to prey ability, thus (Kp/Ka)=Rk·(CP/CA).

CP=CPlow·CPhigh, where CPlow represents predator's decreased ability to predate due to a relatively long period of insufficient past consumption (starvation), while CPhigh represents the combined effect of predator's decreased ability (physical effects of gorging) and motivation to predate under conditions of recent high consumption (satiety). CPhigh produces the gradual approach to C=1 characteristic of a Type-II response.

CPlow = $1/(1+SPlow\cdot((1/CpredatorPrior_1)-1))$

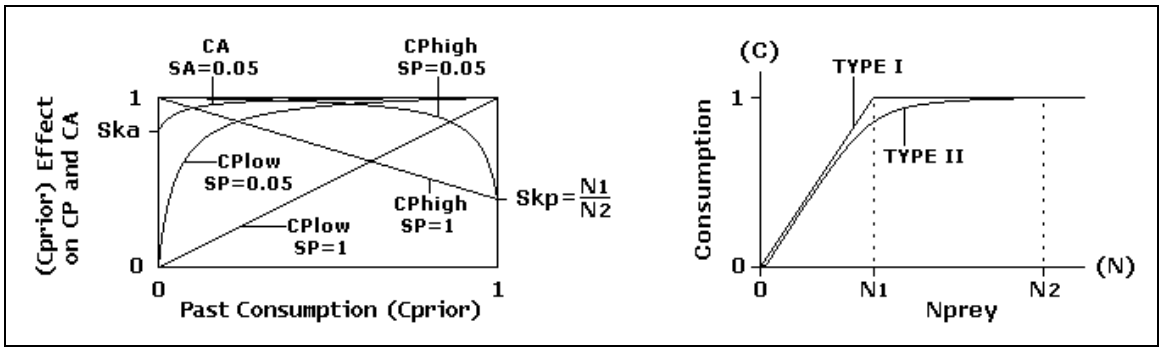
CPhigh = $SKp+(1-SKp)/(1+SPhigh\cdot((1/(1-CpredatorPrior_2/1))-1))$

Subject to the condition that **CPhigh=SKp** *when* **$CpredatorPrior_2=1$**.
And where **$SKp=(N_1/N_2)$ = Nprey[type I]/Nprey[type II]** at C=1.

CA = $SKa+(1-SKa)/(1+SA\cdot((1/CpreyPrior_1)-1))$
where **SKa** must be determined by observation or experiment.

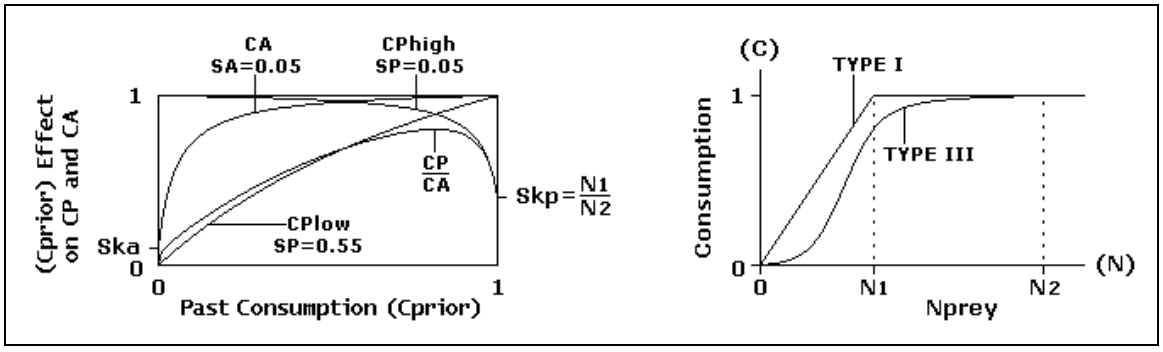
Rp = Ec·Rs·Ri·Rk·(CPlow·CPhigh)/CA

Figure 2 - SPlow, SPhigh, and SA produce a primarily Type-II response



Functions offered for CPlow, CPhigh, and CA may be modified in the light of observed data, but endpoints at Cprior=0 and Cprior=1 must hold.

Figure 3 - Increase in SPlow and lower Ska produce a Type-III response



You may reproduce these curves by calculating consumption versus prey for Np predators using C as the independent variable.

Plot $N=C\cdot N_1\cdot CA/(CPlow\cdot CPhigh)$ over the range $[0\leq C\leq 1]$ while N goes from zero to N_2. $N_1=Rc\cdot Np/Rp_0$ where Rp_0 is the base Rp before factoring in the effects of prior consumption. (*ONLY for CpreyPrior=CpredatorPrior*)

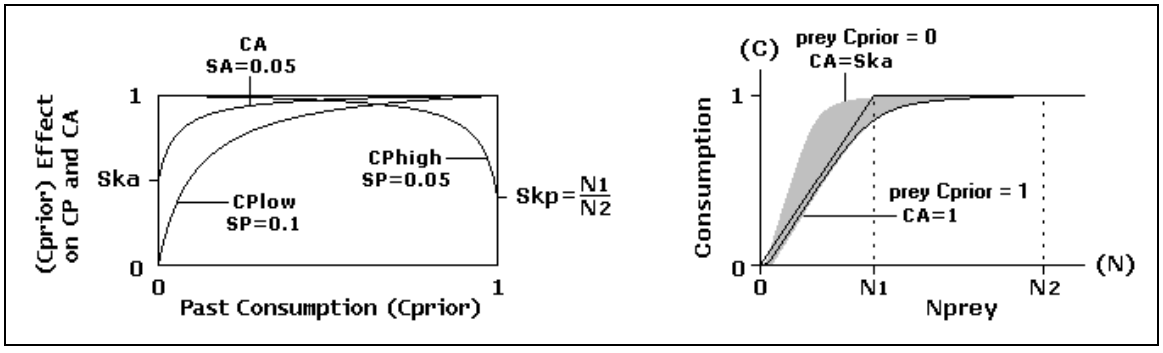
Figures 2 and 3, especially figure 3 which includes a curve designated CP/CA, might be a bit misleading. CP, effect of past consumption on predator ability to predate, and CA, the effect of past consumption on prey ability to avoid predation, are both plotted on the same graph. However, predator past consumption and prey past consumption are unlikely to be the same. While a calculation of CP/CA for the purpose of establishing a level of predation proficiency within the CDPD model is correct, the CP/CA curve would be valid only if predator and prey populations experience identical past consumption.

There is a mechanism that will tend to roughly link predator and prey consumption. If predator consumption has been high, this implies a higher loss of prey population. Surviving prey will have a greater share of their own resource and thus a higher level of consumption. If predator consumption has been low for reasons other than low numbers of prey, the prey will increase in number reducing individual share of resource, lowering prey consumption level. This comes with its own attendant time lag.

Under steady state conditions, consumption levels for both predator and prey seek constant levels, perturbed only by stochastic events and the small oscillations generated by time lagged past consumption.

Figure 4 shows a shaded area surrounding the rise to satiation representing the range of possible consumption response to increase in Nprey depending on past prey consumption between prey Cprior=0 and prey Cprior=1.

Figure 4 – Range of *CDPD response* curves depending upon Prey Cprior



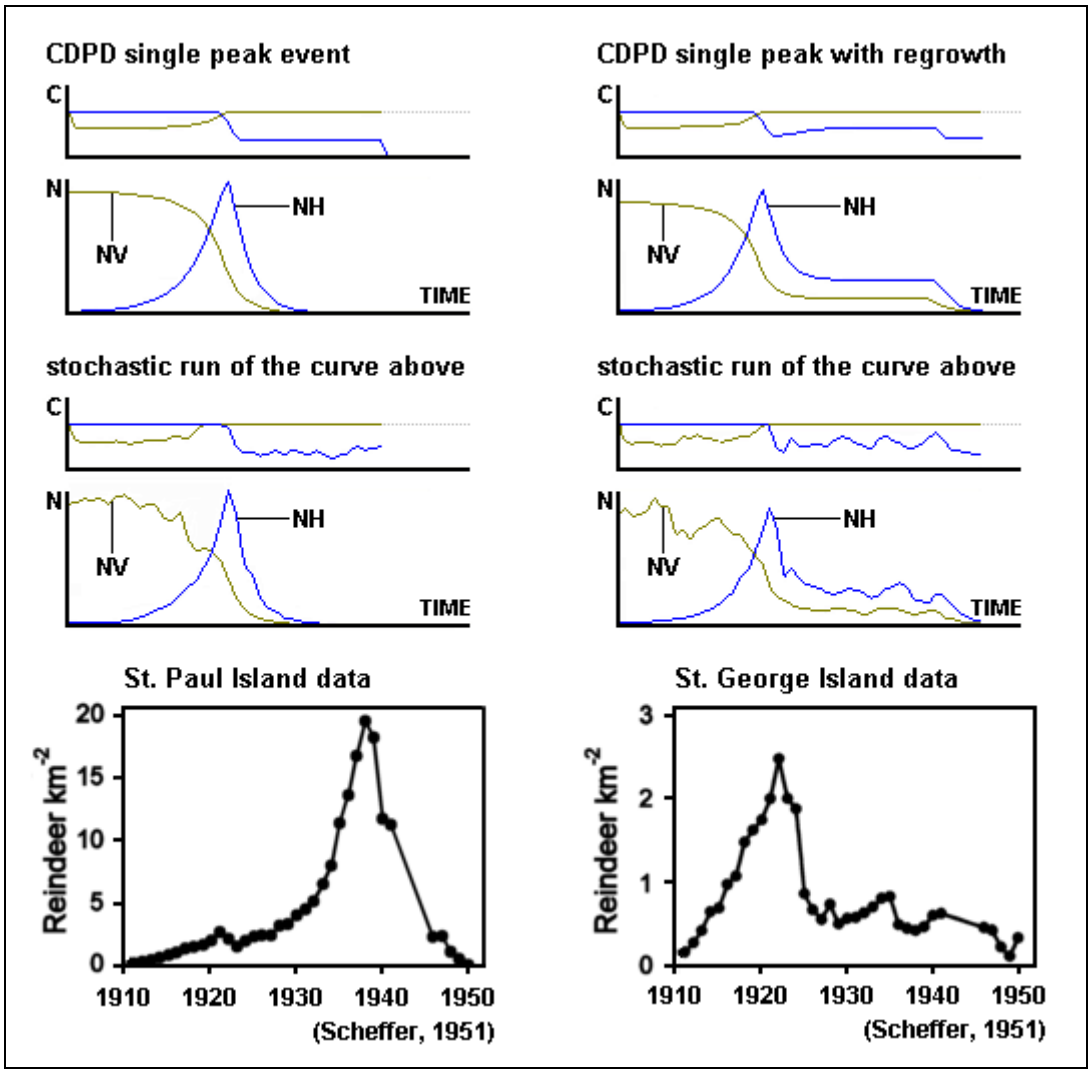
Thus, the *CDPD response* offers a biologically based explanation for the observed spectrum of consumption functional response. This is quite different from the response embodied in the oft used hyperbolic consumption functional response, a mathematical structure offering only the visual appearance of the functional response. The *CDPD response* proposes to actually explain why such a response is observed based upon sound physical and biological principles. Moreover, the *CDPD response* offers a hypotheses from which one may be able to make testable predictions regarding why the

response differs among predator-prey interactions, and how it may change in response to varying environmental conditions including the loss or introduction of other species into a specific predator-prey environment.

Variations on Single Peak Events

The first CDPD paper (Bentley, 2006) examined the CDPD dynamic in response to the single peak event scenario wherein it was found that increase in predation proficiency Rp beyond a threshold leads to collapse within CDPD. Figure 5 shows the deterministic and stochastic CDPD responses which may be compared with the observed data of the St. Paul Island and St. George Island data.

Figure 5 – CDPD Single Peak Events *versus* Observed Single Peak Events



Both CDPD runs were generated using the same parameters, the only difference being a presumption that the vegetation in the second run possessed a small amount of regrowth capacity, as might be the case if the resource included grasses and shrubs, rather than being totally consumed as would a resource consisting of mosses and lichens in the first scenario. While calculating vegetation increase in the second run, 10 percent of the original vegetation was added at each iteration to account for regrowth.

It would appear the above explanation for this variation on single peak events deserves further study. However, one should first consider the *CDPD response* to past debilitation or satiation.

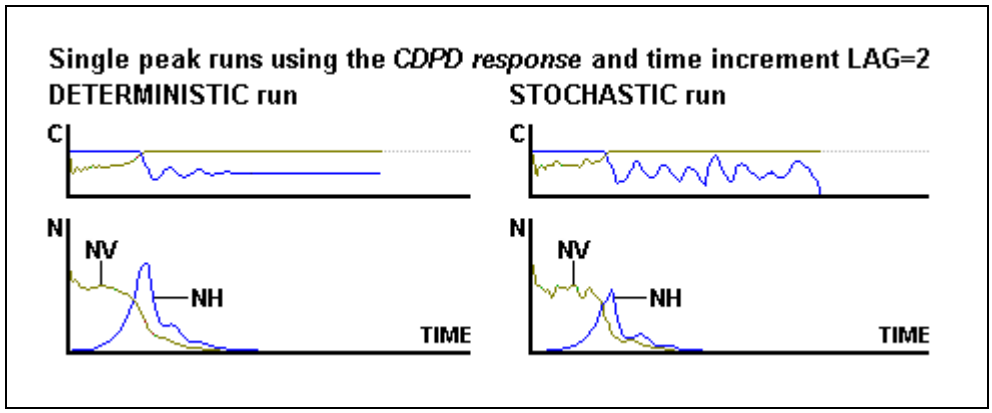
Effects of Past Consumption on Single Peak Events (High Rp)

A single peak scenario that includes the effects of past consumption shows oscillations in both consumption and population for all populations when modeled deterministically. These oscillations vary depending upon rates of increase (Rb) and decrease (Rq) for all populations, and upon the time lags chosen for the effects of consumption on ability to predate.

When the capricious effects of environmental stochasticity are added, the model demonstrates a broad spectrum of forms. Some of these are abrupt, similar to the St. Paul event. Others show the lingering plateau (figure 6) seen in the St. George event. Many possess the double peaks (figure 7) of the Lapland data. It would seem that the CDPD model when implemented using the *CDPD response* could go a long way toward explaining the differing observations without a need to invoke additional mechanism.

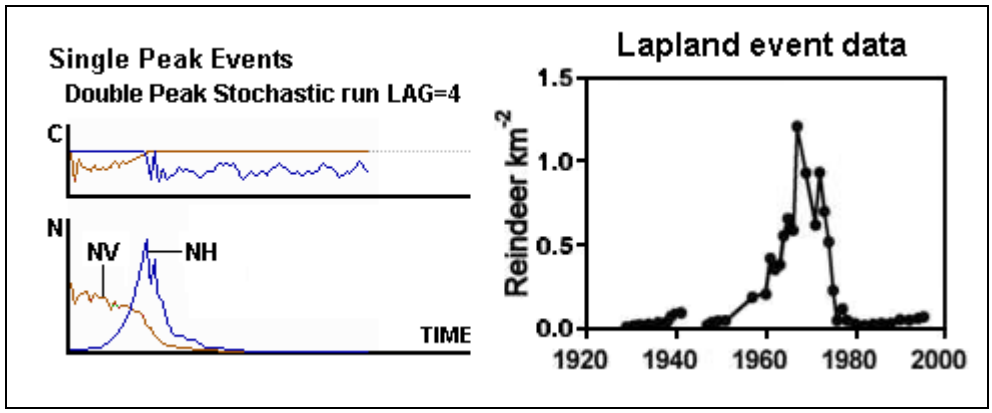
Parameters for Figure 6 and 7	**VEGETATION**	**HERBIVORE**
(Rb) Mass gain per increment	**0.5**	**0.5**
(Rq) Mass loss per increment	**0.2**	**0.2**
(Kd) calculate (D)	**0.2**	**0.8**
(Rc) prey/predator	**1**	**1**
(Rp) Predation Proficiency	**1**	**0.7**
***CDPD response* parameters with LAG=2 and LAG=4**		
(SPlow) low PRED past Cpred	**0.5**	**0.5**
(SPhigh) high PRED past Cpred	**0.05**	**0.05**
(SKP) effect on PRED at Cpred=1	**0.75**	**0.75**
(SA) low PREY past Cprey	**1**	**0.5**
(SKA) effect on PRED at Cprey=0	**0.5**	**0.5**

Figure 6 – Lingering Plateau result of past consumption



Between approximately 1950 and 1975 a single peak event was observed in the Lapland Wildlife Refuge on the Kola Peninsula in Russia. This event was examined by Lopatin and Abaturoy (2000), and more recently discussed in "Complex Population Dynamics" by Peter Turchin (2003).

Figure 7 – Double Peak result of past consumption

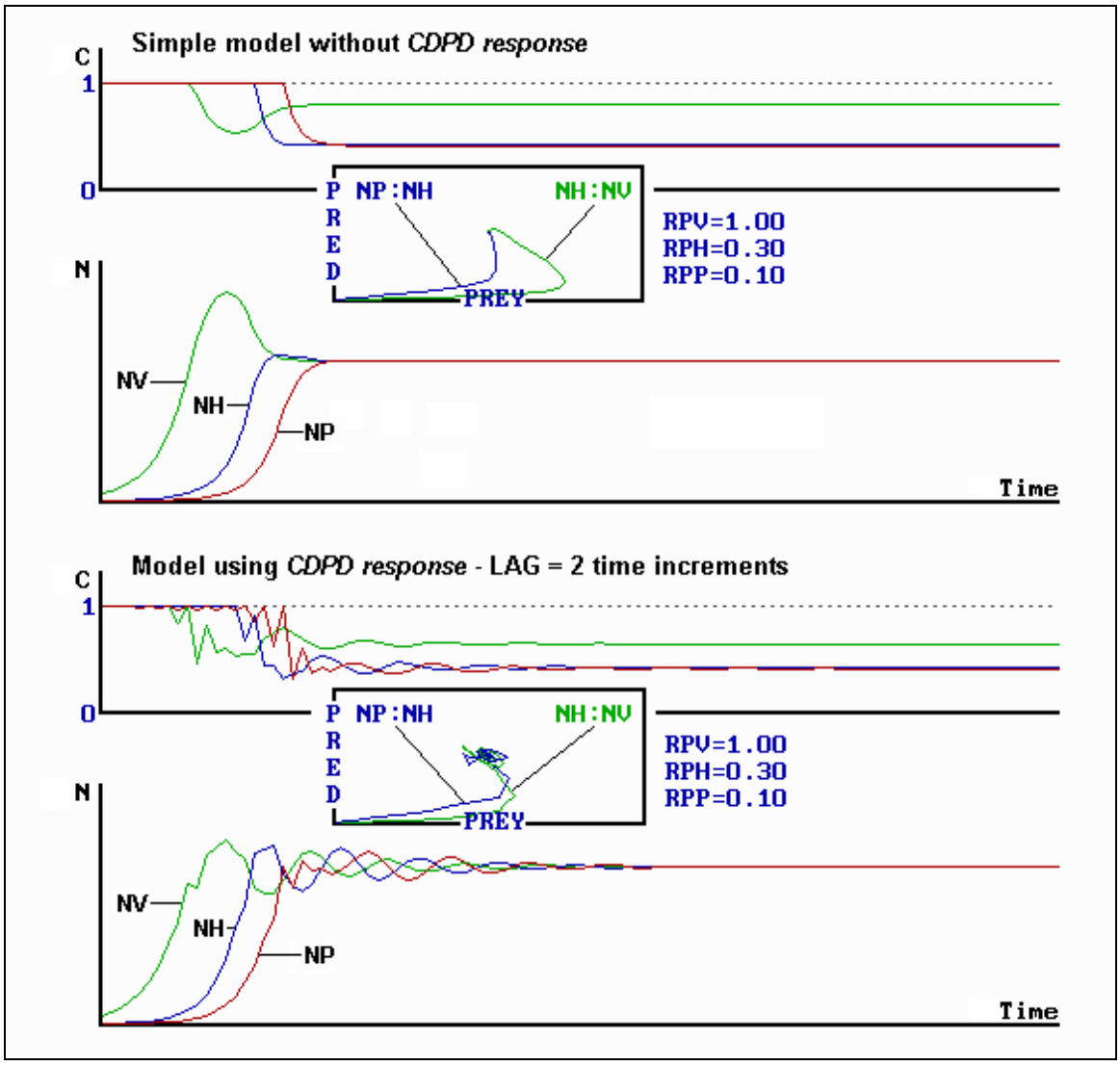


The single peak curve shown in Figure 7 was generated stochastically using the same parameters for both the primary CDPD dynamic, and for the *CDPD response* as used for the curves in Figure 6. The model run differs only in that it was run with LAG=4 and produces the double peak that appears to be a defining feature of the Lapland event. This double peak appears in the majority of stochastic runs made at LAG=4. It is more than possible that Lag time is not the only factor that can influence this dynamic. Measuring biological response to past consumption should be a subject of further study. I have calculated Cprior as an average value of past consumption over the LAG time period. The actual value of Cprior may more likely depend on a weighted average of past consumption, that is, most recent past consumption carrying more weight than consumption further past. The manner of weighting past consumption should be a subject of study. The findings of such a study would most likely be species specific.

Effects of Past Consumption on the Steady State (Low Rp)

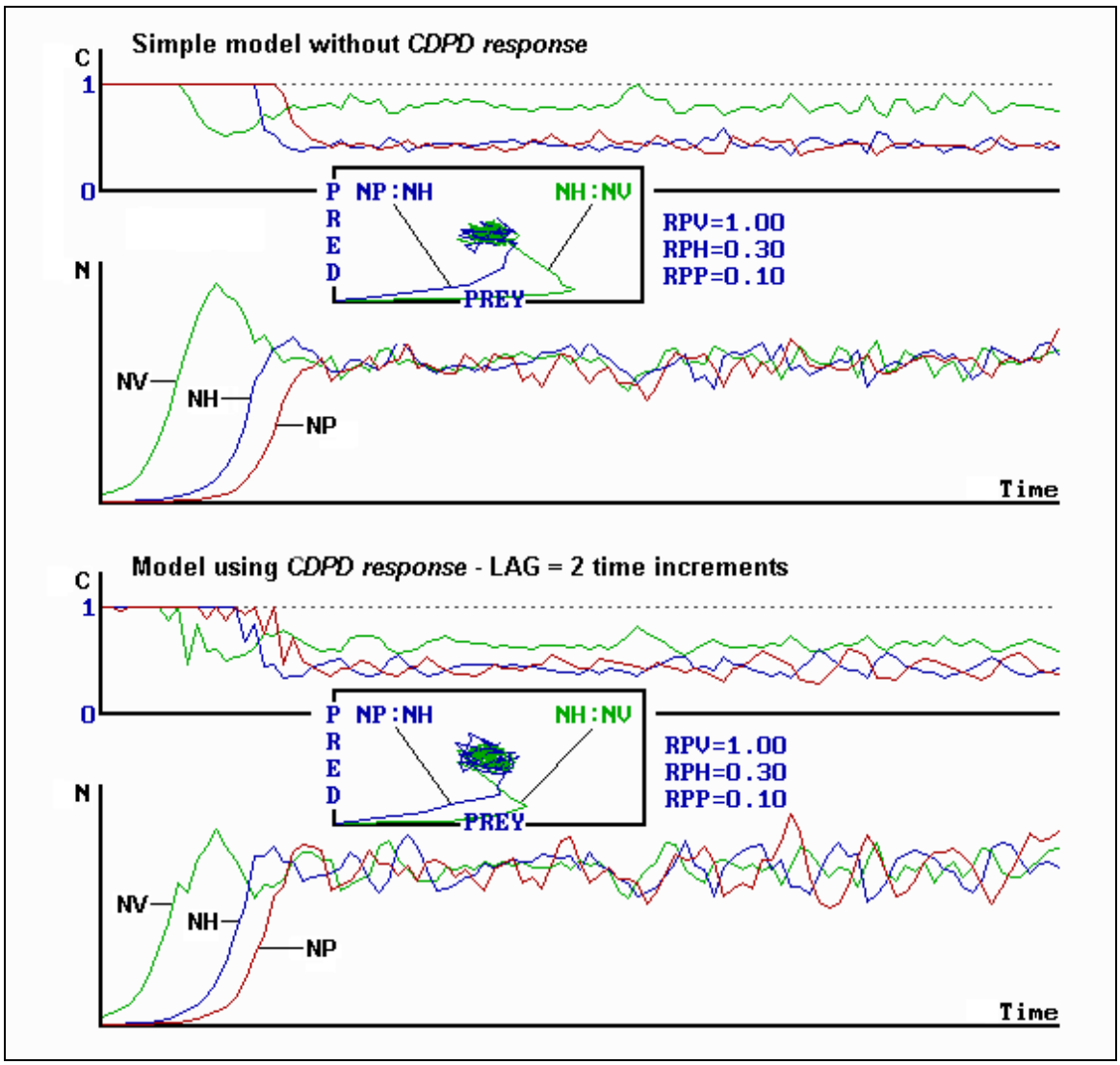
Parameters for Figures 8-9	VEGETATION	HERBIVORE	PREDATOR
(Rb) Mass gain per increment	0.5	0.6	0.6
(Rq) Mass loss per increment	0.1	0.1	0.1
(Kd) calculate (D)	0.2	0.8	0.8
(Rc) prey/predator	0.5	0.5	0.5
(Rp) Predation Proficiency	1	0.3	0.1
CDPD response parameters with LAG=2			
(SPlow) low PRED past Cpred	0.5	0.5	0.5
(SPhigh) high PRED past Cpred	0.05	0.05	0.05
(SKP) effect on PRED at Cpred=1	0.5	0.5	0.5
(SA) low PREY past Cprey	1	0.5	0.5
(SKA) effect on PRED at Cprey=0	0.5	0.5	0.5

Figure 8 - Deterministic Dynamic



Compare the deterministic model runs shown in figure 9, noting the oscillations due to the influence of time lagged past consumption in the model using the *CDPD response*.

Figure 9 - Stochastic Dynamic



Comparing the stochastic runs in figure 9 shows that under steady state conditions past consumption in the model using the *CDPD response* increases the amplitude *difference* by around a factor of two. However, *total* population change is no where near as great, thus leading me to conclude that the effects of past consumption have only a small effect on the steady state dynamic. This is in contrast to the collapse scenario described earlier in figures 5, 6 and 7 where past consumption can significantly affect the shape of the event curve. As Rp increases up into the range of Rp=0.38 to Rp=0.42, the model exhibits far greater population swings.

The effects of past consumption always reduce the value of Rp, pushing the dynamic in the direction of greater stability. If one is measuring the average Rp of a *real* population, be aware that such a measurement *includes* the moderating effects of past consumption on that specific population.

LAG represents the number of past time increments contributing to prey and predator Cprior which in turn produce the *CDPD response*. LAG as used here is LAGlow for low end effects that cause debilitation. LAGhigh has been set to one time increment, and even this may be too great insofar as satiation effects depend upon very recent past consumption.

I have used LAG as a universal parameter applied to all of the populations in a single system only for the sake of simplicity at this stage of investigation. LAG should be specific to each population since metabolic function varies among species and especially between plants and animals.

This study using the *CDPD response* has thus far demonstrated that regardless of any perturbations caused by the influence of past consumption, *the primary dynamic of stability or collapse remains little changed*. The basic 5 parameter CDPD model controls the dynamic.

Oscillations, if they do not lead to collapse, should be considered a form of stability. Whether the dynamic is stable or unstable depends, primarily upon consumption as controlled by Rp. If predation proficiencies for all populations are below a level that would lead to collapse we find that environmental fluctuations, either regular as driven by planetary cycles, or sporadic, have great influence upon the overall dynamic.

Deeper layers of mechanism within the dynamic certainly have influence as can be seen in model output for single peak events showing a greater range of forms, many reminiscent of what has been observed. But the primary dynamic remains stability or collapse. Contributions to the dynamic from the finer nuances of mechanism have less effect as one gets further from the primary factors. This is not to say the fine details may be disregarded. If the main action is taking place close to the threshold between stability and collapse, a mechanism at a lower level may push the dynamic one way or the other. And, may potentially offer explanation for perturbations observed in the natural dynamic. Within the *CDPD response* model, even large changes in parameter value at this depth of mechanism appear to have little effect on the primary dynamic in model runs so far conducted.

Presence of Predators and other Environmental Influences

CDPD has invoked the mechanism of predator presence upon prey behavior to explain changes in 'predation proficiency' Rp by means of Ec to account for erratic population changes, including single peak events. Thus it is not too much of a stretch to extend such a behavior changing mechanism in the predation environment to the environment affecting births Eb and deaths Eq.

Nelson, Matthews, and Rosenheim (2004) measured the effect that behavioral changes in prey pea aphids (*Acyrthosiphon pisum*) induced by the presence of predator damsel bugs (*Nabis* spp.), had upon prey survival and reproduction. Their results compare rates of pea aphid increase in the absence of damsel bugs, in the presence of surgically altered damsel bugs that could not kill or consume pea aphids, and in the presence of unaltered damsel bugs. Rates of pea aphid increase in the presence of disarmed damsel bugs, while greater than pea aphids among unaltered damsel bugs, was significantly lower than for pea aphids with no damsel bugs present in their environment.

Predators, even when they are intentionally handicapped to the extent that they cannot harm prey, will induce avoidance behavior in their prey which can reduce prey survival and reproduction. This can take the form of missed mating opportunities and potentially lethal avoidance actions. Pea aphids have been observed jumping off the leaf on which they are feeding when a damsel bug appears. If such action lands them in a bad place, for instance on the hot, dry ground below rather than on another leaf, they are more likely to perish. Even if they make it back to their food supply, environmental stress and interruption to feeding can be debilitating. This work of Nelson et al. followed predictions of such behavior by others (Spitze 1992, McPeek and Peckarsky 1998, and Kuhlmann et al. 1999). Tamaki et al. (1970) demonstrated predator-induced suppression of prey population growth in laboratory experiments, also using pea aphids.

Interactions with the environment other than predation, including interactions with other species such as the above described predator-prey interaction investigated by Nelson et al., are implemented in CDPD by the insertion of appropriate functions into E variables (Eb, Eq, Ec). When some *condition* such as the presence of other populations or abiotic state makes the environment better or worse for a particular population, and when the effect of an increasing *condition* asymptotically approaches a LIMIT, the appropriate function expressing this interaction will take the following form:

$$E_{interaction} = LIMIT + (1 - LIMIT)/(1 + CONSTANT \cdot (condition))$$

When *condition* makes things *worse* for a population then LIMIT<1 and LIMIT is the maximum degradation that *condition* will cause to a population's environment E. If it is possible for a *condition* to approach a point where that *condition* becomes lethal one would set LIMIT=0.

When *condition* makes things *better* for a population then LIMIT>1 and LIMIT is the maximum improvement that *condition* can make to a population's environment E.

In either case, *condition* represents either an absolute magnitude or a deviation from a norm. A function to properly profile the magnitude or deviation may also stand in the place of *condition*. Examples of a *condition* could be a population mass or count, foliage density or terrain complexity enumerated on some scale, turbidity of water, humidity, or any other factor

that may affect the well being of a population but for which there is diminishing impact for each increment of additional *condition*.

CONSTANT is a constant of proportionality scaling the numerical value of a measured *condition* to a measured effect upon the subject population with units that are the inverse of whatever units are associated with *condition*.

When the range of a possible environmental *deviation* X (difference between benign value and observed value) can reach or exceed a lethal *deviation* X_{LIMIT} such as a pollution level or temperature that is too hot or cold for the continued survival of a population, the appropriate function that expresses this interaction would take the following form:

$$E_{interaction} = 1/(1+SKEW\cdot((1/(1-X/X_{LIMIT}))-1)) \quad \text{…for } 0 \le X < X_{LIMIT}$$
$$E_{interaction} = 0 \quad \text{…for } X \ge X_{LIMIT}$$

SKEW is a unitless number that describes the manner in which a population reacts to a change in X as X approaches X_{LIMIT}. If SKEW=1 the effect on the population will be linear as X goes to X_{LIMIT}. Values of SKEW<1 model a mild reaction to increasing X at small values of X, but a rapidly increasing reaction to X when X gets close to X_{LIMIT}.

Eb for increase, Eq for decrease, and Ec for the predation environment may all respond quite differently. And, E variables (Eb, Eq, Ec) may be composed of multiple Einteraction factors.

Considering the manner in which environment impacts the system, Eb for mass gain and Eq for mass loss that act exactly like changes in C, and Ec, a building block for Rp making it a factor in the level of C, most environmental interactions, aside from perhaps introducing oscillations, appear to do little to force the CDPD dynamic very far off course. The exception to this would be environmental occurrences of great intensity, deforestation for example, that force E toward 0, which will cause a direct population drop just as occurs when C approaches 0.

Oscillations

Oscillations of every cause may be observed using CDPD. Firstly, there is stochasticity – changes in environmental conditions of a random nature. One could argue that these changes are not truly random, each change the effect of an underlying cause and thus all part of a more complex dynamic. While true up to a point, this is like the weather, an element of the environment responsible for much stochasticity in and of itself. One can strengthen the validity of a weather prediction only at a cost of greatly increased measurement. This pursuit rapidly leads to diminishing returns and would, were the effort even possible, eventually bring us up against the fuzziness of quantum mechanics which for all that tremendous effort would still leave us with uncertainty. As science continues to explore the vast arena of life scenarios we shall continue to uncover mechanisms accounting for many

interesting and surprising phenomena. At the same time there will remain a background of stochasticity.

CDPD applies stochasticity through environment variables Eb, Eq, and Ec. Stochasticity is the application of both positive and negative forces according to some pattern of probability for the occurrence of effects at different magnitudes. I have used for demonstration a 'normal distribution' of effects whereby large effects have a smaller frequency of occurrence than do effects of a lower magnitude. After deciding on a frequency of distribution, one must determine impact upon a population caused by effects of a particular magnitude so that one may properly scale such random effects within a model to emulate an observed dynamic.

Stochasticity occurs over time periods that are both greater and lesser than whatever time increment may have been chosen for a model. Application of stochasticity for multiple increments is a simple programming task. Stochasticity occurs at all time scales and may impact *your* choice of time increment.

The CDPD model of 'consumption functional response' (the *CDPD response* discussed above) employs time lagged effects of past consumption as they are likely to affect current consumption. Such time lags produce oscillations as seen in the above discussion of 'Effects of Past Consumption'. Depending upon rates of fecundity, mortality and time LAG, CDPD shows oscillation around a stable point that may persist or die out under deterministic conditions. This is difficult if not impossible to observe in nature because stochasticity forces displacements that keep the oscillations going.

Rp is constantly in flux in the natural world, changing not just in response to past consumption but in response to the weather and all the seasonal changes in flora and fauna. The CDPD model thus far demonstrated, with the exception of those instances where the *CDPD response* has been employed, treats Rp as a constant that may be considered an average of fluctuations over time. Model correspondence to population time series thus far appears to validate this approach, but one should keep this in mind.

As Rp increases, population swings become more pronounced. Beyond a certain point, even with stochasticity and the effects of past consumption included in the model, the dynamic turns to collapse. Approaching extinction, a population may be saved from that fate within a refuge from which it can later recover in the event that environmental changes lower Rp. Thus, the stable range of Rp may be greater than indicated by CDPD model runs without refuges.

Beyond stochasticity and in addition to time lagged past consumption affecting current consumption, there are likely to be a great number of other mechanisms that generate time lagged negative feedback to fecundity, mortality, and consumption. Many plants express toxins in their edible parts,

not on a constant basis but seemingly in response to predation. Generation of toxins represents a metabolic load on the organism. Producing toxins only in response to need is an efficient way to utilize available resources.

Surviving members of a population under a heavy predation load have access to a greater share of their resource, likely increasing consumption. Greater consumption makes production of metabolically expensive toxins more affordable allowing the plant to increase production of these substances. Other mechanisms may involve the surviving portion of the prey plant, and perhaps even neighboring plants, responding to released chemical agents that are unique to the predators or to the tissue damage of predation. This response could be the generation of chemicals or structures that inhibit the predator or attracts predators of the predator, or perhaps, emulates a signal that alerts a predator to the presence of their own predator. Much of this has been observed (Karban 2009).

There are a great many events in nature, some large portion of which are quite regular in period, and others which occur often but which may be aperiodic. These events are sufficient in and of themselves to produce oscillations, often of a dramatic nature, changing populations by several orders of magnitude. Such drivers would include seasonal swings in temperature, moisture, and sunlight. Others will include periodic, or aperiodic infestations of predators, parasites, and disease vectors.

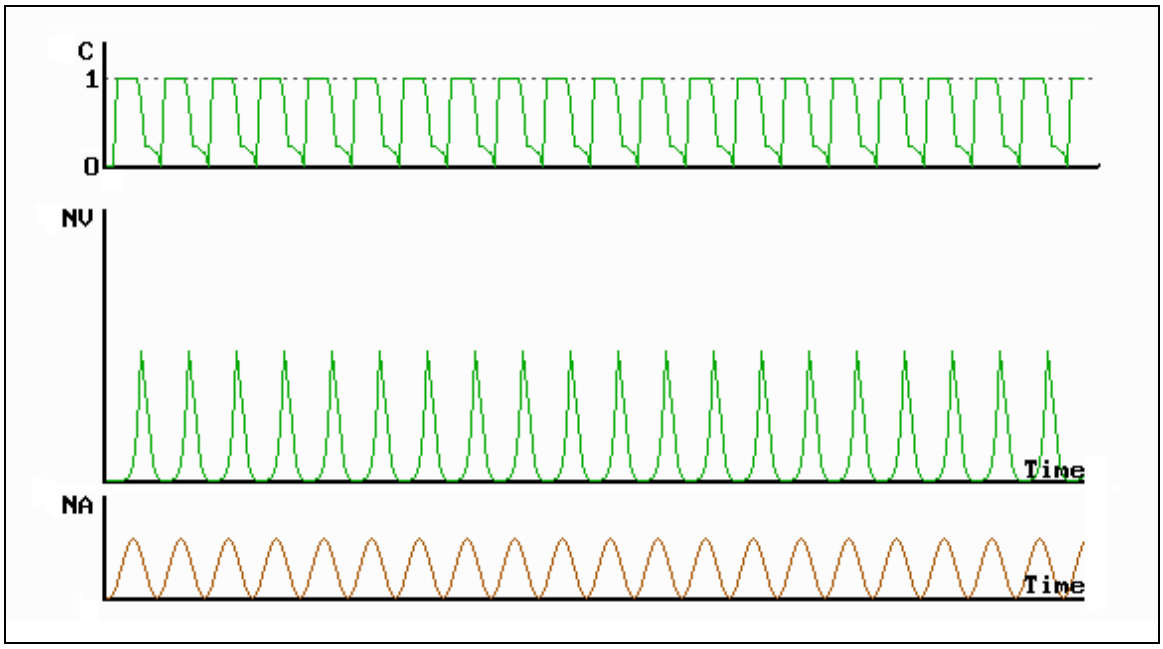
Periodic Oscillations

Figures 10-11 demonstrate a CDPD model of response to seasonal resource availability where the resource (NA) for a rapidly reproducing population is implemented as a simple sine wave. This model assumes that as the resource approaches its minimum the population supported by that resource will not drop to zero but will instead drop into a refuge that will maintain the population, in the form of active individuals, spores, eggs, or seeds at a level that for the parameters used in this model turns out to be less than 0.0014 of maximum population mass for the deterministic run shown in Figure 10.

Figures 10 and 11 were run at 12 increments per year using the following parameters:

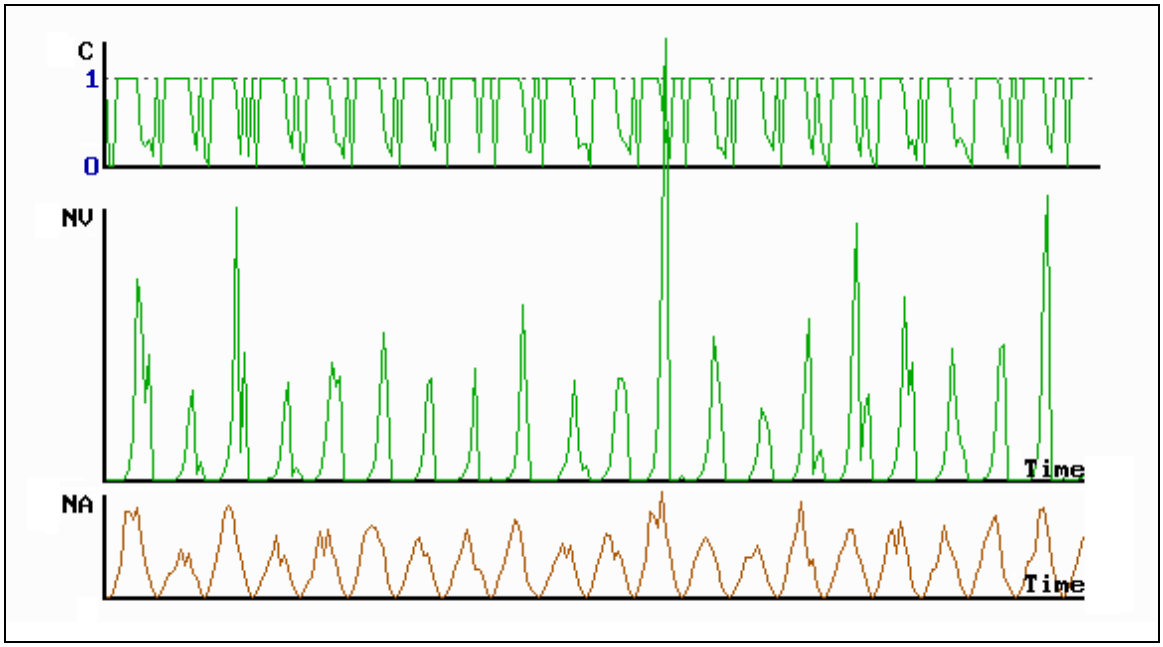
Parameters for Figures 10-11	**Organism supported by seasonal resource**
(Rb) Mass gain per increment	**2.5**
(Rq) Mass loss per increment	**0.2**
(Kd) calculate (D)	**0.2**
(Rc) prey/predator	**5**
(Rp) Predation Proficiency	**0.2**
Refuge (mass units)	**0.1**

Figure 10 - CDPD oscillation – seasonally triggered deterministic run



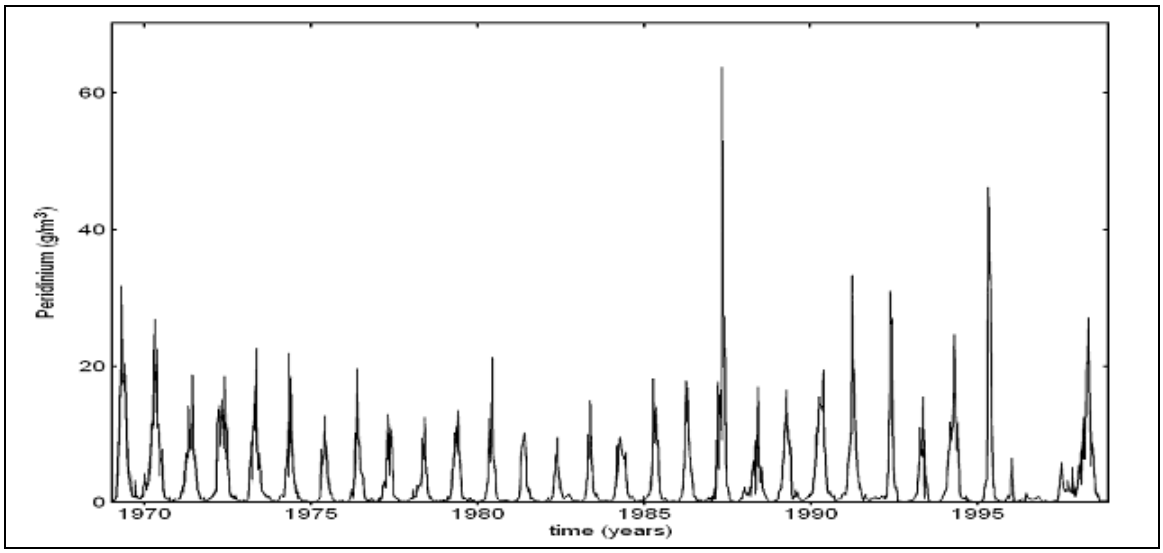
Stochasticity occurs at all scales. The model run in Figure 11 is subject to random displacement at the increment level, 12 per year, the average value of which will vary little from year to year, and additional stochasticity on a yearly scale (every 12 increments), the period over which resource (NA) completes 1 cycle. This more closely emulates a natural dynamic of change from year to year.

Figure 11 - CDPD oscillation – seasonally triggered stochastic run



An example of a seasonally driven population oscillation may be seen in Figure 12, a time series graph of observed *Peridinium gatunense* phytoplankton density from 1970-1999 in the waters of Lake Kinneret (Sea of Galilee), Israel, made by Utza Pollingher and Tamar Zohary (Huppert et al, 2002, and also Berman et al, 1995).

Figure 12 - Lake Kinneret time series (Utza Pollingher and Tamar Zohary data)



This is only a demonstration offered to show the ability of the CDPD model to readily produce oscillations in response to a seasonal fluctuation. This paper makes no claim that the dynamic observed in the Lake Kinneret data is totally explained by the simple assumptions of the above demonstration.

I refer here to a *seasonal fluctuation* and began this exercise by providing a resource NA that fluctuates in the form of a sine wave subjected to a stochastic environment E. I could just as easily have calculated B and Q by providing NA in a constant manner while allowing the environment E to fluctuate in the form of a sine wave, overlaid by stochasticity. This would have produced a similar result. The situation in Lake Kinneret is likely to be some combination, resource fluctuation and environmental fluctuation. A careful evaluation of *Peridinium gatunense* to determine its sensitivity to the many aspects of its environment along with a careful measurement of those environmental factors and availability of resource in Lake Kinneret should more fully explain the observed dynamic.

Aperiodic Oscillations - 2-trophic level system

Parameters for Figures 13-16	VEGETATION	HERBIVORE
(Rb) Mass gain per increment	0.5	0.5
(Rq) Mass loss per increment	0.2	0.2
(Kd) calculate (D)	0.2	0.8
(Rc) prey/predator	1	1
(Rp) Predation Proficiency	1	0.42 (0.33 Fig. 16)
CDPD response parameters with LAG=1 (Figures 14-15 only)		
(SPlow) low PRED past Cpred	0.5	0.5
(SPhigh) high PRED past Cpred	0.05	0.05
(SKP) effect on PRED at Cpred=1	0.75	0.75
(SA) low PREY past Cprey	1	0.5
(SKA) effect on PRED at Cprey=0	0.5	0.5

Figure 13, run deterministically and generated without time lagged past consumption, shows an unstable system where populations collapse to zero.

Figure 13 - High RpH 2-trophic level system run deterministically and (LAG=0)

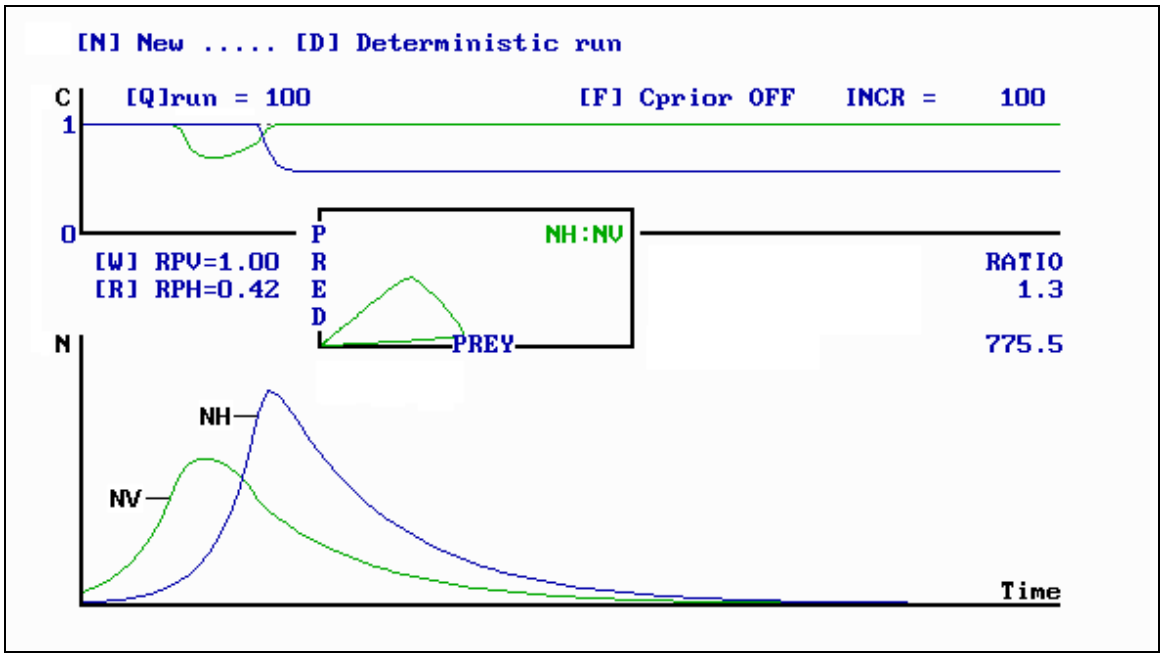
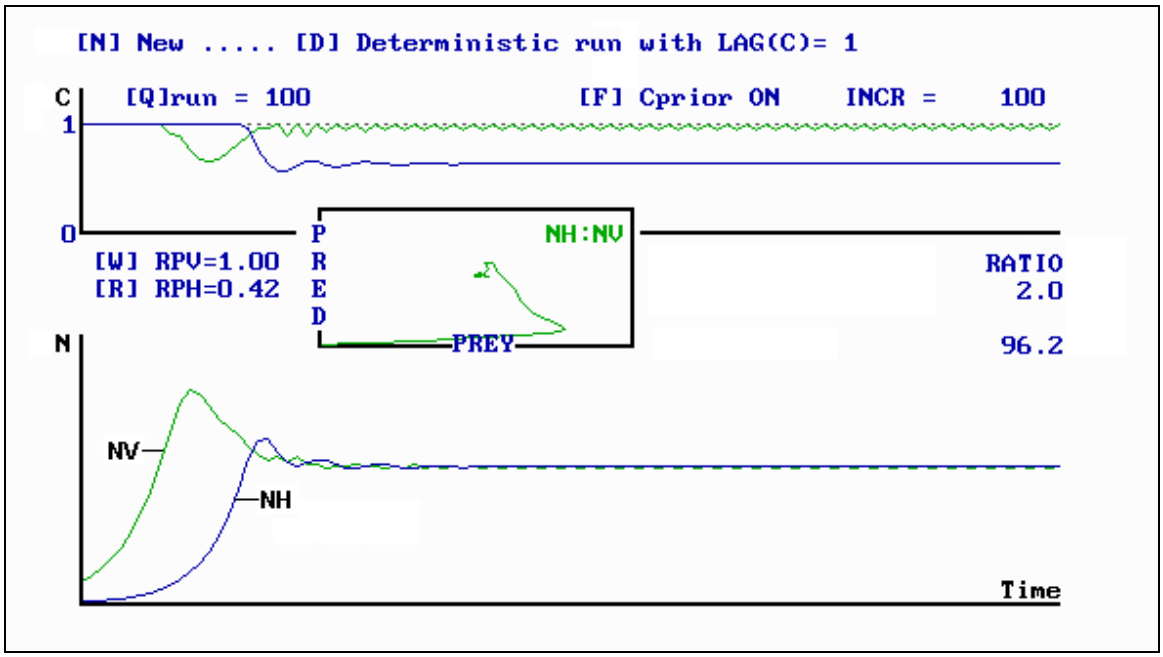


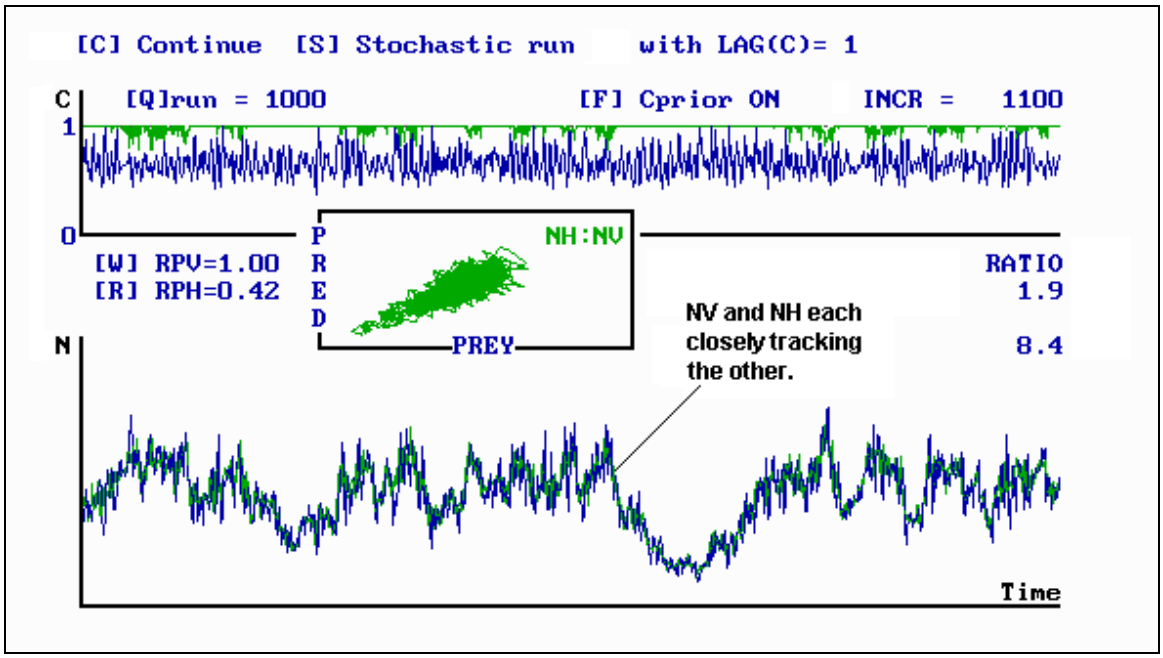
Figure 14 below, a deterministic run incorporating the effects of time lagged past consumption, shows a stable system because effects of past consumption lower the effective Rp.

Figure 14 - High RpH 2-trophic level system run deterministically with (LAG=1)



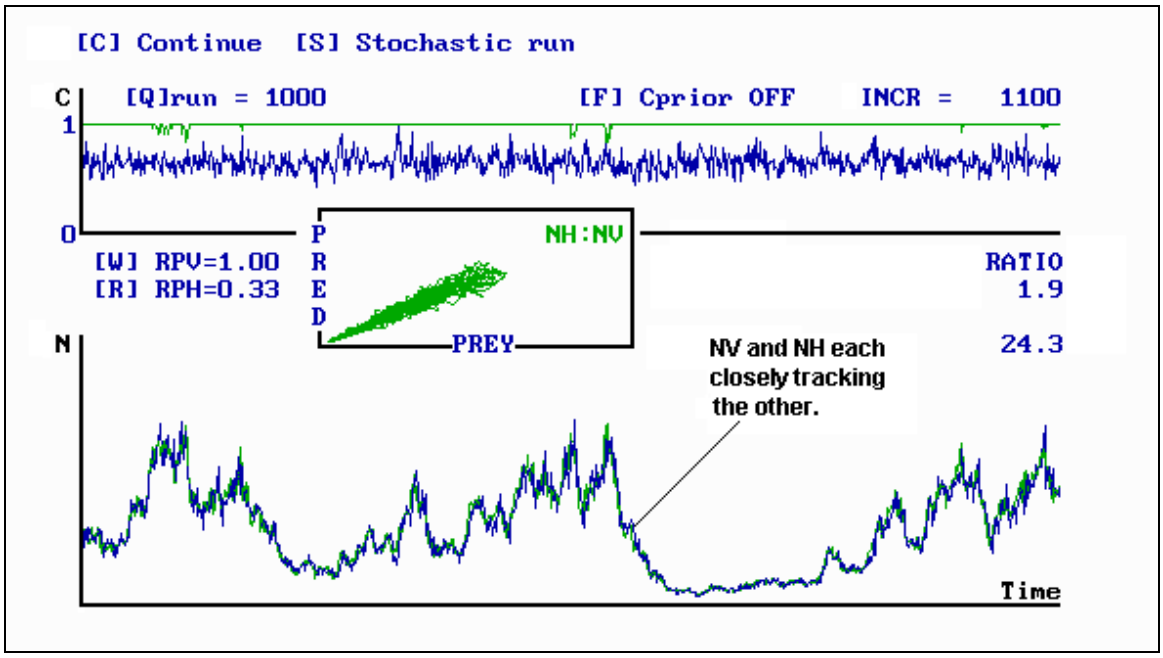
Figures 15-16 introduce stochasticity and increase the run length to 1000 time increments. Introduction of stochasticity generates an aperiodic oscillation that is quite different to the slight oscillation seen in the deterministic run of figure 14.

Figure 15 - High RpH 2-trophic level system run stochastically with (LAG=1)



Removing the *CDPD response* (LAG=0) and compensating for this removal by reducing RpH from 0.42 to 0.33, thus returning to the simple 5 parameter model, produces a similar aperiodic oscillation in figure 16. Population shifts occur less rapidly, and as seen in the trajectory plots of figure 16, coupling between predator and prey is tighter when time lagged past consumption is not included in the model, but the dynamic retains largely the same quality as the results with time lagged past consumption seen in figure 15.

Figure 16 - High RpH 2-trophic level system run stochastically with (LAG=0)



The only parameter change between figures 15 and 16 is a decrease in predation proficiency from RpH=0.42 to RpH=0.33 in compensation for removing the effects of past consumption (LAG=0). Population shifts occur with less vigor, and as seen in the trajectory plots of figure 16, coupling between predator and prey is tighter when time lagged past consumption is not included in the model, but the dynamic retains the same quality as the run with time lagged past consumption seen in figure 15.

You will notice in figures 15 and 16 that when the predatory population exceeds a certain point, consumption by the resource population drops below C=1 sharply limiting further population increase by either population. Below this maximum the resource population experiences full consumption (C=1). But at high RpH, the predatory population places such a high downward pull on the resource population that both populations remain tightly coupled, moving up and down proportionally. This tight coupling is seen in predator consumption which tracks a level of approximately C=0.65, for the parameters used, independent of population size. Consequently, below the upper limit set by the resource population, forces for population increase are only slightly greater than forces to decrease.

This places exogenous forces in control. Below the upper limit the common path taken by both populations resembles a random walk very similar to the random runs demonstrated in figure 20. However, during a run of adverse conditions a population does not easily 'walk' to extinction. This is because environmental forces act proportional to population size. A large population will see larger absolute losses than a small population and this can also be seen in figure 20. An environmental insult causing a population loss of ten percent in a population numbering 1000 would be 100 individuals. But, if the population had been 100, the proportional loss would be only 10 individuals. *Please remember that CDPD works with population mass rather than a count of individuals, but the idea is exactly the same.*

This proportional effect tends to make recovery from a drop slower than the drop. A population of 1000 encountering a condition causing a 50 percent loss drops it to 500. Improved conditions during the next time increment that cause a 50 percent increase bring it back to only 750. Populations may encounter a further difficulty. Bad conditions can drop a population precipitously, but even under extremely good conditions that population will be limited by a maximum reproduction capability.

Aperiodic Oscillations - 3-trophic level system

Figures 17-19 demonstrate another interesting interaction producing extreme oscillations *only* when subject to stochasticity. This system is unstable deterministically or when perturbed only by a regular oscillation. The system displays great persistence taking the form of sustained aperiodic oscillation only under conditions of random perturbations.

The following analysis describes the dynamics observed in this 3-trophic level system where RpH for the herbivore and RpP for the predator have been pushed to the collapse threshold. This dynamic may be observed in model runs that are stable or unstable deterministically. Deterministically unstable systems slowly collapse until one observes extinction of first the predator and then the herbivore. The run in Figure 17 shows a deterministically unstable 3-trophic level system.

Parameters for Figures 17-19	VEGETATION	HERBIVORE	PREDATOR
(Rb) Mass gain per increment	0.5	0.5	0.5
(Rq) Mass loss per increment	0.2	0.2	0.2
(Kd) calculate (D)	0.2	0.8	0.8
(Rc) prey/predator	1	1	1
(Rp) Predation Proficiency	1	0.35	0.45

Figure 17 - 3-trophic level system at high RpH and RpP – deterministic run

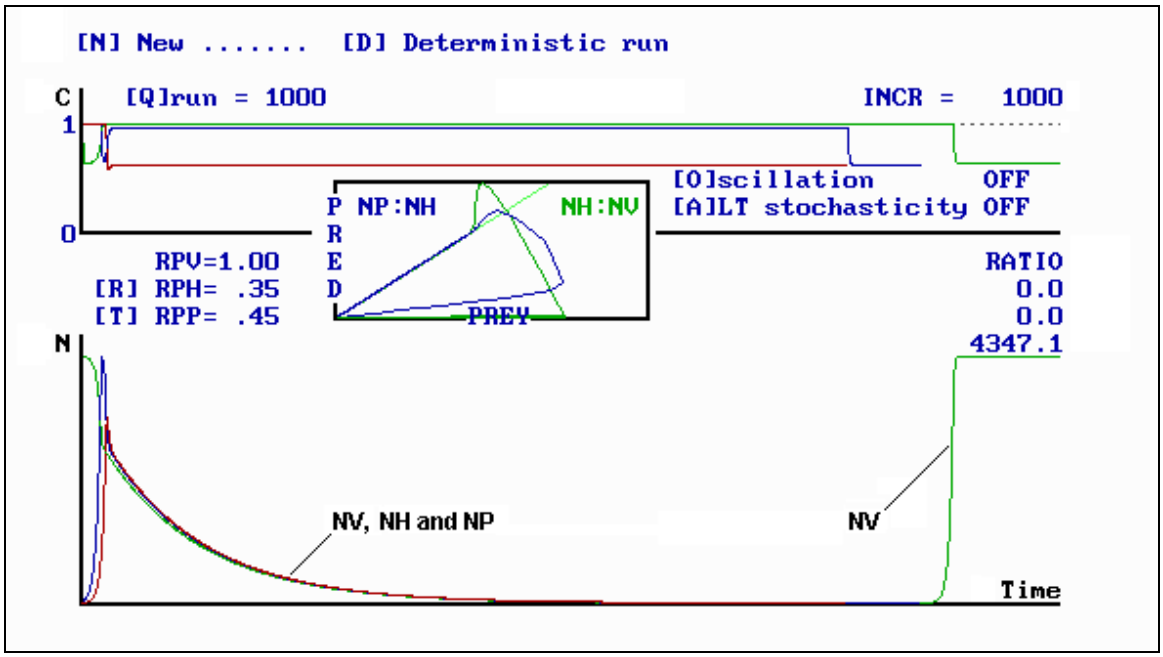
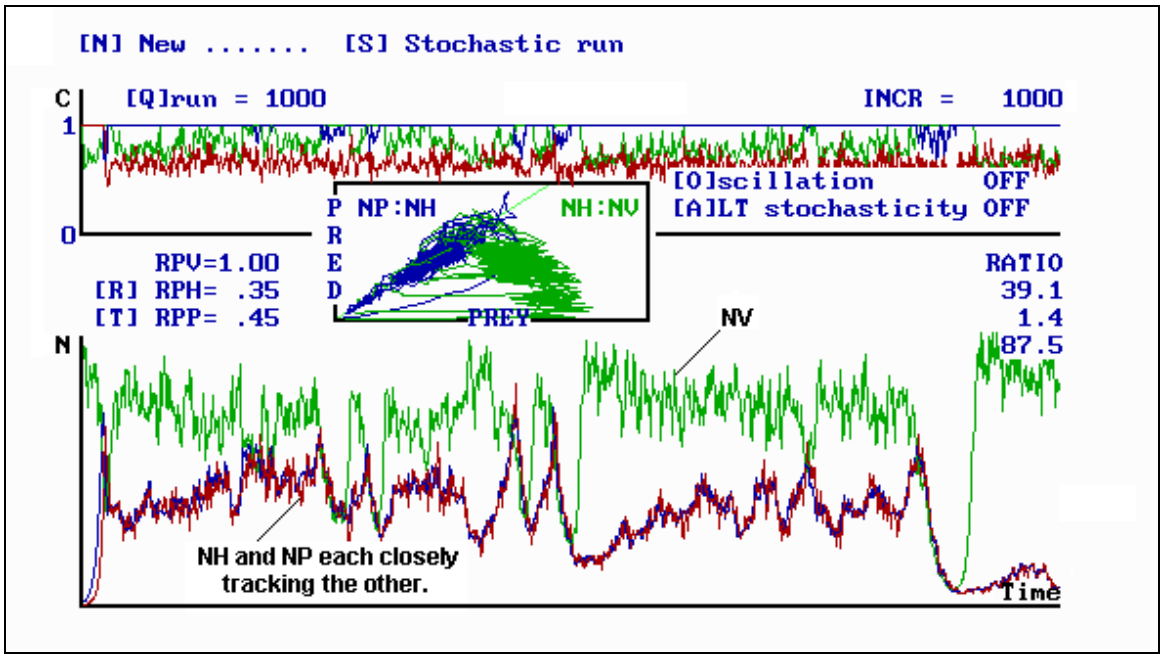


Figure 18 represents an initial run of the same system where stochasticity has been introduced at all three trophic levels. The run displays 1000 time increments, same as in the deterministic run in Figure 17, but it is evident that the system has not collapsed.

Figure 18 - 3-trophic level system at high RpH and RpP – stochastic run



The second notable feature of figure 18 is the similarity of the 2nd and 3rd trophic levels in both population dynamic and consumption to the 2-trophic

level system in figures 15-16. However, trophic level-1, the resource for this system, possesses an interesting dynamic of its own.

Figure 19 - 3-trophic level system continuation (increments 3000-4000)

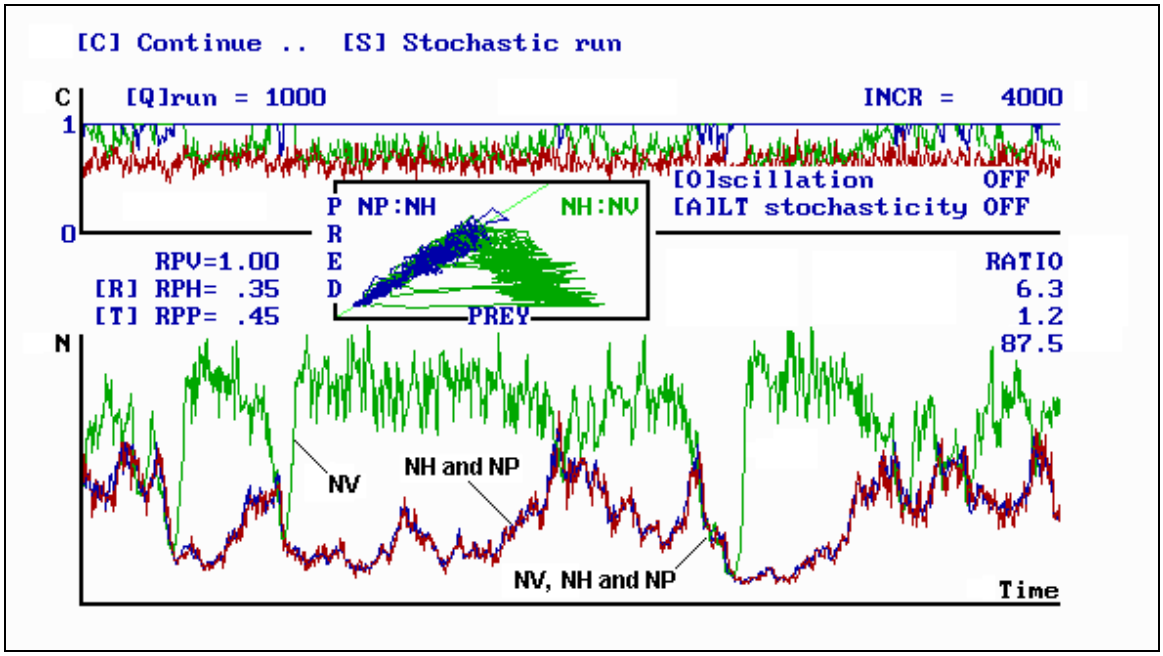


Figure 19 continues the stochastic run begun in figure 18 showing increments from 3000 to 4000. Swings in population level are large and aperiodic. The third trophic level population tracks the second level closely and the heavy load it imposes upon the second level, high enough to drag the level-2 population to extinction under deterministic conditions when consumption drops just a little below satiation, is necessary to the emergent dynamic illustrated here. Model runs (*not displayed*) introducing the effects of past consumption using the *CDPD response* do not alter the observed dynamic qualitatively.

This system appears to randomly transition between two phases when stochasticity is introduced. I have found stochasticity need only be imposed upon level-2, while the top and bottom trophic levels continue to be modeled deterministically. However, the system appears most robust when there is stochasticity at every trophic level. During the first of these two phases, and the phase of shortest duration, all three trophic levels tend to track together proportionate to each other, generally dropping in a fairly steady manner, and at a rate much faster than if there were no stochasticity.

Populations can drop to very low levels before any transition to the alternate phase, and there is the possibility that level-3 will go to extinction causing level-2 to follow if populations drop too low before a phase change occurs. This has been observed in the model, but only when stochasticity has been reduced to a coin toss of two values. It is only during this phase that level-2 consumption becomes erratic, tending to drop below C=1.

At some point in this downward course, with all populations heading toward extinction, the level-2 population, subject to stochasticity, will during some random interval experience a string of bad luck unrelated to the level of resource and due only to stochastic forces. Such negative environmental misfortunes may be one, or a combination of things, and not necessarily the same things at each occurrence. Examples would be anything from extreme weather conditions to disease or parasitism. When such a misfortune appears to affect a widely distributed population, where local weather conditions vary significantly from one portion of the population to another, a likely cause might be communicable disease. This could tend to 'synchronize' the observed dynamic over large distances.

During this interval of misfortune the level-2 population will encounter negative environmental influence of such strength and for sufficient duration that level-2 population drops, lowering the weight of predation upon level-1 that has up to this point been holding the level-1 population in thrall to the downward pull of level-2 consumption. This gives the level-1 population opportunity to rise, and to continue to rise above that point where level-2 predation had kept level-1 population in check. This is the point where phase change occurs. Level-1 population climbs to high levels pushing level-2 consumption to C=1. The level-1 population continues to grow until it becomes limited by its own finite resources. In the brief interval before level-1 population encounters limitation, level-2 and level-1 consumption both go to C=1 with level-1 consumption dropping to C<1 at limitation.

While this is going on, level-3 population continues to take the same heavy toll on level-2 population. From the beginning of this phase, level-2 and level-3 populations enter a dynamic identical to the aperiodic 2-trophic level system previously described; a random walk that sooner or later brings the level-2 population to a point where its consumption of the level-1 population becomes great enough to once again enthrall that population, and it is at this point where phase change transitions back. Level-1 consumption jumps to C=1, level-2 consumption drops below C=1, level-3 consumption remains about where it was at C<1, and all three populations begin the sharp, lockstep descent characteristic of this phase of the dynamic.

It is easy to think about this dynamic in terms of the level-1 population being 'captured' by the level-2 population. The level-1 population wins 'release' when level-2 falls on hard times, but after 'release' level-2 and level-3 begin their largely lockstep random walk that sooner or later brings the level-2 population to a point where it once again is able to pull the level-1 population back into its clutches.

The above description of level-2 predation holding level-1 population to a low, proportionate level within one phase of the dynamic sounds like top-down control which I have shown in my previous paper (Bentley, 2006) to be a self-eliminating scenario and thus not viable as a population control

mechanism. This continues to be true because if this phase persists, the dynamic will definitely run to extinction. Fortunately for the persistence of this dynamic there is a very strong tendency, enabled by stochasticity, to quickly transition back to the alternate phase where top down forces are no longer pulling populations toward extinction, thus bringing stability to the overall dynamic.

***

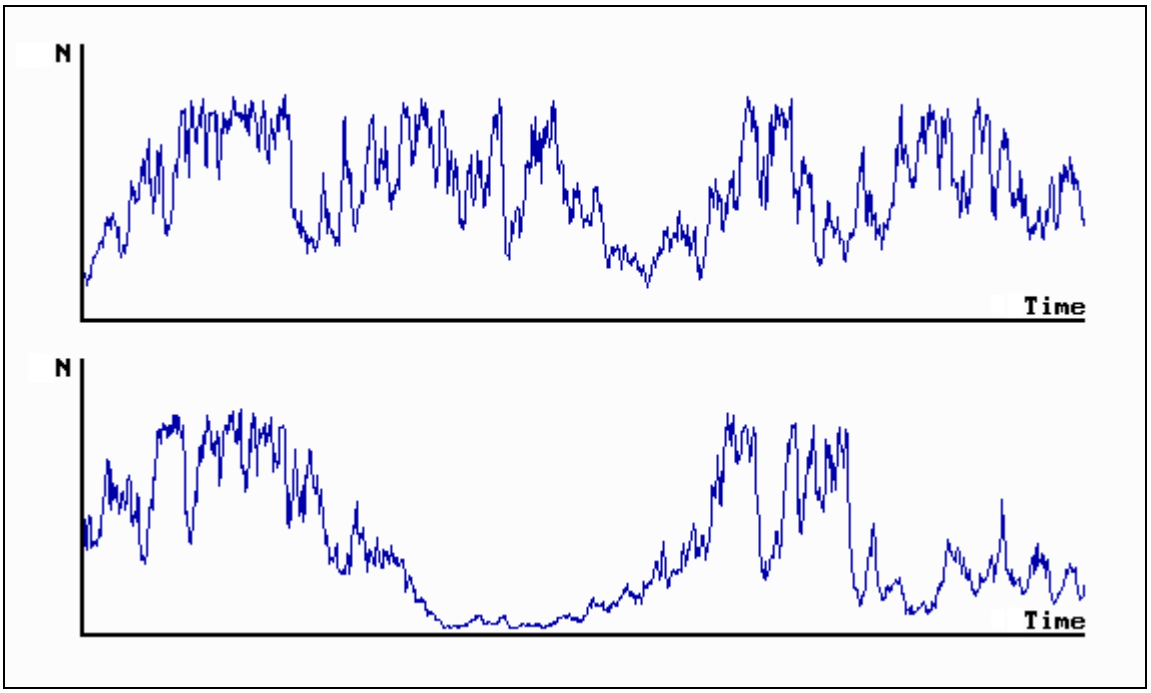
The scenarios demonstrated in figures 15-16 and figures 18-19 show a dynamic that is constrained by resource limitation at the top and resistant to extinction at the bottom where hard winters, dry spells, windfalls of resource, episodes of disease or parasites, fortuitous confluences of nutrients and sunlight, drops or increases in competitor or predator populations, and all the other uncountable exogenous forces to which a population is subject produce a wandering aperiodic oscillation with remarkable similarity to a great many populations observed in nature (NERC Centre for Population Biology, 1999).

Demonstration of a random dynamic

After examining the dynamic of the systems demonstrated in figures 15-16 and figures 18-19 it appears random forces dominate the dynamic between population levels of zero up to the limiting point where resource consumption drops from C=1 to C<1. Exploring this, I removed the code for the CDPD mechanism emulating living populations and substituted code for a mechanism to examine the dynamic resulting from random forces.

This mechanism, over the entire range of N at each incremental evaluation, subjects N to a slight upward force expressed as N=N+(0.015·N). Above a level of Nlimit, N is subject to a downward force on the growth of N expressed as N=N-((N-Nlimit)/2). Below Nlimit, N is subject only to the previously described slight upward force, *similar to a living population when C=1*, and to up or down forces of a random value that act proportional to N.

Figure 20 - Random Runs

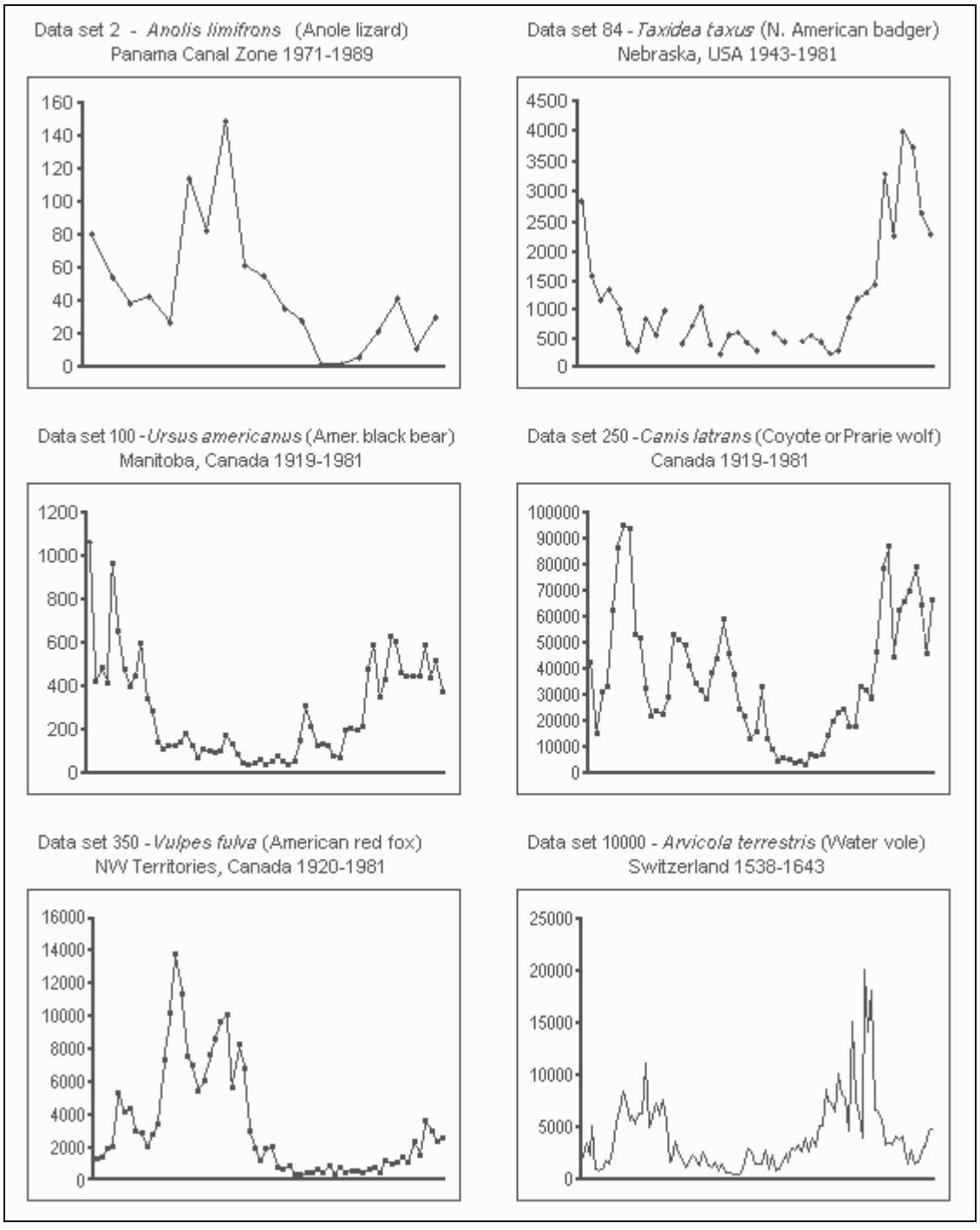


These random runs produce a range of aperiodic oscillations that look very similar to the dynamic seen in figures 15-16 and figures 18-19.

Returning to the CDPD model, the behavior of stochastic runs at high Rp, both with and without taking into account time lagged effects of past consumption, shows a remarkable similarity to a great many of the time series data sets that may be found in the NERC database (NERC Centre for Population Biology, 1999).

Some of the NERC studies show population numbers dropping closer to zero than shown in the CDPD runs. Population studies in the wild are not as simple as counting eggs in a carton. A study area may account for only a small portion of the actual population range. Also, immigration and emigration to and from a study area may push population counts to both greater and lesser densities within the study area than would be true for the total population as has been observed in metapopulation dynamics.
The NERC Centre for Population Biology in the UK has established a global population database with over 5000 time series data sets. I have examined only a small portion of this database but have found a very significant number resemble the CDPD aperiodic oscillations shown above. Figure 22 offers a few of these NERC data sets for comparison. You may note, as evidenced by my choice of largely common species, I have not chosen examples based on what best fits my thesis.

Figure 21 – NERC Data Sets



Summation

The foregoing presents a single model and the predictions of that model when applied to the broad range of conditions found in the natural world. As demonstrated, CDPD displays great fidelity replicating natural populations under conditions where one would expect to observe collapse, steady state, or periodic oscillations. In the course of this investigation there also came to light the aperiodic oscillations demonstrated above as the model prediction for the dynamic under conditions of predation proficiency close to the threshold of collapse, a likely condition under the pressure of evolution. This dynamic, or at least the appearance of this dynamic, may be observed in the NERC data base.

While gathering data is an essential part of ecological study it is equally important to make sense of that data. Ecology needs a robust unifying theory of fundamental population dynamics, and the insight that comes with such a theory. Data by itself, no matter how much one massages that data with statistical analysis, will not produce such a theory.

Data on the positions of the planets constituted a substantial data base several thousand years ago leading to a theory of epicycles that was highly predictive for the future motions of those studied astronomical bodies. But this approach consisted of a separate little model for each planet. Aside from structural similarities, there was no overall mechanism that explained and tied this approach together, thus no real understanding and no predictive ability for any newly discovered heavenly body. A change in perspective, and rather deep insight by Isaac Newton finally brought understanding and great predictive power with the theory of gravitation.

Population ecologists, when pressed on the issue of a unifying theory, often speak words to the effect that, "we have many models for different things." Unless we wish for epicycles, that is not good. Instead, I believe we need to search for a fundamental unifying theory underlying the interactions of all living things.

CDPD is such an attempt.

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***Footnote** (see **R versus Consumption** above):*

Proposal of an experiment to measure Rate (R), an organism's increase or decrease, as a function of Consumption:

This is not meant to be a formal experimental protocol, just a brief outline from which an experimental protocol might be developed that should be able to demonstrate the response of an organism to consumption level for births and deaths.

Total mass of the experimental population is the variable of concern and it must be possible to make regular measurements of this variable. Processes of both gains and losses will be going on simultaneously. The organism should probably be large enough that actual counts of live and dead individuals may easily be made, photographically or otherwise. However, I would certainly not discount the use of microorganisms if one can figure out a way to determine population mass, be able to distinguish living from nonliving individuals, figure out how to remove and measure the nonliving on some regular schedule, and do all this without changing the test population's normal rates of increase and decrease.

Insects might be useful except for the complication of several life stages, each of which has its own set of parameters for gains and losses and thus complicates measurement since measuring those parameters would be part of the experiment. Also, most insects have a very limited adult lifespan.

I originally had guppies in mind, but I am not an experimentalist. In any case, guppies are omnivores and because of the measurements that one need make, I believe one should rather choose an herbivore. I would expect that anyone thinking about performing such an experiment would likely work with an organism with which they already have experience, and know what is necessary to maintain a healthy population.

In any case, during the experiment one must be able to remove dead individuals in a regular and timely manner and be able to make a measurement of the mass of such individuals undistorted by the presence of waste products or uneaten food. I expect there will be many problems of a similar nature in the design of such an experiment. For instance, one would not want to choose an organism that eats its own kind or its own dead.

Population mass calculations must be made at regular intervals. This is necessary to calculate the amount of food the experimenter must provide during each feeding interval to maintain a constant level of consumption. The experimenter must take into account the consumption functional response of the population and adjust the amount so that the mass of food actually 'consumed' by the population remains at a set fraction of population mass.

All the above needs be considered in the choice of experimental organism.

DETERMINATION OF SATIATION LEVEL

Determination of satiation level does not appear to lend itself to easy measurement due to the effect of 'consumption functional response', another unknown. However, it should not be too difficult to determine several related data points. The experiment proposed, sketched out above, should allow the experimenter to measure rates of gain (addition of new mass) and rates of loss (mass contained in the death of individuals) at specific levels of sustained consumption (set ratio of available food mass per total population mass). Each change in this ratio should provide new data points for both 'rate of gain' and 'rate of loss', and, of course, for the combination of these, the overall rate of absolute gain or loss. During the conduct of preliminary runs, the feeding ratio that delivers zero net gain should become apparent. Appropriately chosen feeding ratios above and below this point should disclose a line of points that CDPD predicts should begin to drop sharply as the feeding ratio approaches zero.

Steady increases in the feeding ratio above the point of zero net gain should reveal a gradual tapering off in gain rate and death rate to the point of no change in these rates regardless of how far the feeding ratio is increased indicating that available resource has exceeded satiation level.

Throughout this procedure one should note the difference between amount of food provided, and amount actually consumed during a feeding interval. Depending on the physical nature of the food provided, it may be possible to separate uneaten food from the population's waste products and thus make a measurement of this difference for different feeding ratios. The point where consumption no longer increases despite an increase in the amount of food provided reveals satiation.

PROCEDURE

Rates calculated for gains and losses would be as a fraction of population mass at the beginning of the '*rate* period' rather than '*run* period'. Rate period should start at a point in time later than the beginning of the '*run* period' (run time at a constant consumption level) to avoid transition error due to change from previous consumption level.

Each '*rate* period' would be composed of a number of '*feeding* periods'. Feeding period intervals would be dependent upon the physiological needs of our chosen experimental organism. And as described above, each feeding period would be preceded by the removal and recording of mass of dead individuals from the previous period, and a measurement of remaining population mass to determine amount of food to be administered.

N0 = (population mass at the start of 'rate period')
N1 = (population mass at the end of 'rate period')

Nq = (total mass of dead individuals during 'rate period')

RATEb = (mass gain rate) = (Nq+N1-N0)/N0
RATEq = (mass loss rate) = Nq/N0

RATE = (combined effect of gains and losses at a specific level of C)
RATE = RATEb - RATEq = (N1-N0)/N0

Rb (as used in CDPD) = (RATEb measured at C=1) satiation level
Rq (as used in CDPD) = (RATEq measured at C=1) satiation level

Naturally, to the extent that resources permit, multiple runs should be conducted in parallel or sequentially to minimize error.

RATE as a function of consumption C should be the result of greatest confidence. RATEq and thus RATEb will be more difficult to measure as I expect there to be problems determining mass of very young offspring, dead offspring that become lost among waste products, and mass loss from debilitated living individuals, to name a few of the problem areas.

Implicit in the above, and openly stated in my paper (Bentley, 2006), are the assumptions that maximum mass increase and minimum mass loss will both coincide with consumption at satiation. While the concept of CDPD does not loose validity if these assumptions are wrong, an exploration of these assumptions in the above experiment should help to clarify the issue.

Computer programs for the dynamics shown in the figures, plus many more, are available from the author.

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