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Utricularia's secret: the advantage of positive feedback in oligotrophic environments

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Abstract

An interesting example of positive feedback in ecosystems centers around the carnivory exhibited by various species of submerged aquatic plants belonging to the genus *Utricularia*. The autocatalytic loop of processes engendered by plant carnivory can be modeled by a very simple, but nonlinear system of 5 coupled differential equations. The stationary states of the model reveal how *Utricularia* harnesses the production of its own periphyton via intermediary zooplankton grazers. This subsidy to the plant apparently allows it to thrive in oligotrophic environments that would stress other macrophytes with similar direct uptake rates. As ambient nutrient levels rise, however, the advantage gained by positive feedback wanes, until a point is reached where the system collapses. For certain parameter values the model exhibits a Hopf bifurcation, which might help to explain dramatic differences in the composition of communities associated with different species of *Utricularia*. The results suggest that the role of positive feedback in ecosystems might be confined largely to oligotrophic environments.

Keywords: Oligotrophic environments

1. Introduction

The fundamental, burning question in ecosystems research is what, if anything, accounts for the perceived organization of ecological systems? While there is some justification to the criticism that ecosystem science should relate better to evolutionary theory, it is not at all clear that the fault lies entirely with the ecologists. As the noted developmental biologist, Gunther Stent (1981) opined, "The regularity of [ecological] phenomena is obviously not the consequence of an ecological program encoded in the genome of the participating taxa." If neo-Darwinian theory is insufficient to describe fully the development of

ecological communities, what is its legitimate complement?

There appears to be scant enthusiasm on the part of most ecologists to embrace the organicist expositions of Clements and Shelford (1939), or later Lovelock (1979). However, many ecosystems researchers remain open to the possibility that cybernetic behavior is somehow inherent in the phenomenon of ecological succession. G.E. Hutchinson (1948) was a participant in the Macy conferences that gave birth to the modern cybernetic movement. His ideas on "circular causality" resound in the descriptions of "reward loops" by his student, H.T. Odum (1971) and are discernible even in later expositions of positive feed-

back (De Angelis et al., 1986) and formal causality (Ulanowicz, 1986, 1989, 1990, 1991).

There is notable speculation that positive feedback imparts structure to aquatic communities (Bianchi et al., 1989). Recently, Stone and Weisburd (1992) have pointed to the microbial loop as constituting the nexus of positive feedback that structures open ocean ecosystems. They cite work demonstrating that grazing tends to stimulate algal productivity and suggest the “grazing, together with the positive feedback it generates, can be viewed as a keystone mechanism.” Elsewhere, the work on mutualism in coral reef communities is voluminous. Yet, despite these very interesting observations, it does not appear to most ecologists that their systems could be described as engaging in (to use Robert May’s colorful phrase) an “orgy of mutual benefaction.”

A useful tool for exploring the role of positive feedback in structuring ecosystems might be a model of a particular community wherein positive feedback is believed to exert major influence. One very obvious manifestation of positive feedback in ecology is the process of carnivory as exhibited by certain plants. Usually carnivory by plants is viewed as a very isolated phenomenon that plays only a minuscule role in overall system trophic dynamics. Occasionally, however, carnivorous plants may comprise a significant portion of the biomass of autotrophs in an ecosystem. Such is the case in some softwater oligotrophic lakes and marshes, where species of the genus *Utricularia* are a dominant or subdominant member of the macrophyte community. These plants are usually associated with copious amounts of periphyton. The plants are often separated from the substrate, the major source of nutrients for most aquatic plants (Wetzel, 1975).

Of particular interest concerning *Utricularia* is the presence of utricles, or bladders that vary in length from 0.2 to 5 mm and can trap rotifers, small molluscs, cladocera and other small animals (Wallace, 1978). Each bladder is a small hollow sac with an inwardly swinging trap door surrounded by trigger hairs. The plant sets its trap by creating a negative osmotic pressure within the bladder. When an animal trips a trigger hair, it springs the trap door, and the animal is sucked

into the bladder (Knight and Frost, 1991). The animal is not digested, but decomposes within the bladder. It takes approximately 20 minutes to reset the trap.

Exactly how *Utricularia* benefits from carnivory is a matter of contention; however, it is reasonably established that there is an energetic cost of producing and operating the utricles, and that in order to persist the plant must receive some net return on its investment (Knight, 1992). It should be emphasized that this investment is by no means small. As much as 40–50% of the plant biomass may consist of utricles (Friday, 1992). Whenever species of *Utricularia* form a major component of any macrophyte community, the potential for positive feedback to impart structure to the overall ecosystem looms large!

Bosserman (1979) has shown that the *Utricularia*–periphyton assemblage behaves as a self-organizing unit. Efforts to separate the plant itself from the accompanying periphyton and epiphytic invertebrates have proved futile. The system always tends to regenerate itself. Unfortunately, Bosserman did not attempt to specify the pathways for feedback in the system, nor model the component interactions. What follows is an attempt to describe at least one pathway for positive feedback in the *Utricularia* community and to explore the response of this feedback configuration to changes in environmental conditions.

Briefly, I will assume that the *Utricularia* serves as an areal substrate for periphyton growth, which in turn is grazed by a “zooplankton” population. The feedback loop is closed by the zooplankton, which provide nourishment to the *Utricularia*. Because the P/B ratios of periphyton are usually higher than those of most macrophytes (Bohr and Lucinska, 1975), *Utricularia*, through carnivory, subsumes periphyton production to persist in nutrient-poor environments. By contrast, macrophytes with comparable uptake rates but exhibiting no feedback would starve. This could explain the prevalence of *Utricularia* species in many oligotrophic freshwater environments.

The model presented below might be described as minimalistic. The object here is not to strive for realistic detail, but rather to draw the

simplest caricature of the system possible that will demonstrate the nonlinear peculiarities of the feedback. Thus, bilinear kinetics (e.g., Lotka–Volterra) are used to represent trophic feeding, instead of the more realistic Michaelis–Menten or Ivlev functions. The consequent loss of realism appears to be more than compensated by a gain in analytical detail (i.e., the ability to pursue analytical solutions and solid inferences, rather than search laboriously, and often futilely, through copious output from numerical simulations). Besides, the simplest models are often surprisingly powerful in predicting qualitative behavior (e.g., Ulanowicz and Tuttle, 1992).

2. Model variables

As with many such analyses, we develop a model for macrophyte growth in a “continuous, stirred-tank reactor”. Such a model would pertain most readily to *Utricularia* communities in quiescent karst lakes, such as Lake Annie in Highlands County, Florida. Lake Annie is a 37-ha sinkhole in the Florida scrub. It is fed almost entirely by seepage inflows from the nutrient-starved sands surrounding the lake, and has a small stream outflow to lakes downstream. Nutrient levels are low, and the littoral regions are heavily populated by two species of *Utricularia*.

The model consists of five components. Each variable is quantified by its content of some crucial nutrient. The amount of nutrient dissolved in the aqueous phase will be denoted by N ; the amounts incorporated into mesoheterotrophs and detritus by Z and D , respectively.

The nutrients in the *Utricularia* and periphyton will be expressed in a way that emphasizes the tight areal connection between these two compartments. To begin with, *Utricularia* presents a surface area, U , which supports the periphyton. We shall assume that the instantaneous biovolume of *Utricularia* can be represented as the product of this changing surface area times a constant “width” factor, w . Furthermore, we assume one can calculate the total amount of nutrient incorporated in the *Utricularia* by multiplying its biovolume, Uw , by a constant density function,

η . Thus, the nutrient pool for the macrophyte will be represented by the double product, $Uw\eta$, wherein the only variable is U .

The assumptions of constant w and η are supported by a linear-like growth habit on the part of *Utricularia*. This plant is not a rooted macrophyte in the conventional sense. It can grow entirely detached from the bottom, but more often it sends occasional branches into the bottom to anchor itself. The microphyte, however, does not appear to draw sustenance from the sediments via these connections. Growth occurs at the terminal end of various branches, and the growing bud quickly reaches mature proportions. Far back along its axis the tissue eventually senesces. The simplest way to visualize the growth pattern is to imagine a long string uniformly thick with filamentous leaflets that grow radially from the stem. This axis grows at one end and disappears as it senesces at the opposite end in “conveyor-belt” fashion. The picture is complicated only by occasional branching.

Finally, the film of periphyton covers the *Utricularia* surface, U , to a (variable) thickness, l . Multiplying the periphyton biovolume, Ul , by its (constant) nutrient density, ψ , yields the total amount of nutrient in the periphyton biomass.

To summarize the treatment of plants in the model, the size of the *Utricularia* population is characterized by its total surface area U and that of the periphyton film by its thickness, l . The nutrients present in each compartment are represented by $Uw\eta$ and $Ul\psi$, respectively.

3. Nutrient balances

Utricularia acquires nutrients both via normal uptake from the dissolved phase as well as through carnivory on mesoheterotrophs. As mentioned earlier, nutrient uptake will be represented in Lotka–Volterra, or bilinear form. It will be proportional to the product of the existing biomass ($Uw\eta$) times the available nutrients (N), with the constant of proportionality being denoted by α .

The growth of *Utricularia* slows down as the periphyton film thickens. This interference will be represented in the model by multiplying the

normal uptake rate by the factor $e^{-\beta l}$, where l is the thickness of the periphyton growth and β is the effective coefficient of transmission of light to the macrophyte surface.

The capture of heterotrophs also will be represented in bilinear form as a constant, ϕ , times the product of the heterotroph biomass, Z , with the *Utricularia* density, $Uw\eta$.

Finally, mortality of the macrophyte is assumed to occur at a linear rate, m . That is, *Utricularia* is lost (off the end of the “conveyor belt”) at the rate $m(Uw\eta)$. The balance of nutrient in macrophyte thus becomes:

$$\begin{aligned} \frac{d(Uw\eta)}{dt} \\ = e^{-\beta l} \alpha (Uw\eta) N + \phi Z (Uw\eta) - m(Uw\eta). \end{aligned} \quad (1)$$

The nutrient balance for the periphyton is cast in similar fashion. The bilinear coefficient of nutrient uptake is called γ , while that for grazing by heterotrophs is ρ . Periphyton is assumed to perish at the same rate as the macrophyte, i.e., when its areal substrate disappears. The nutrient balance for periphyton thus appears as

$$\frac{d(Ul\psi)}{dt} = \gamma (Ul\psi) N - m(Ul\psi) - \rho Z (Ul\psi). \quad (2)$$

Mesoheterotrophs gain sustenance from the periphyton and are lost to carnivory by *Utricularia*. Mortality due to other factors is assumed to occur at the linear rate, ξ . The ensuing nutrient balance for the epizoids is

$$\frac{dZ}{dt} = \rho Z (Ul\psi) - \xi Z - \phi Z (Uw\eta). \quad (3)$$

The mortalities of macrophyte, periphyton and zooplankton add detritus to the system. The detrital pool itself is remineralized at a linear rate, r .

$$\frac{dD}{dt} = m(Uw\eta) + m(Ul\psi) + \xi Z - rD. \quad (4)$$

Finally, dissolved nutrients are added to the system at the rate n_0 . They appear also from the breakdown of detritus. Nutrient sinks include up-

take by macrophyte and periphyton as well as advection out of the system at a rate e . The balance for N is

$$\begin{aligned} \frac{dN}{dt} \\ = n_0 + rD - e^{-\beta l} \alpha (Uw\eta) N - \gamma (Ul\psi) N - eN. \end{aligned} \quad (5)$$

4. Model solution

Eqs. 1–5 form a set of coupled, first-order differential equations representing the nutrient kinetics of the system. Rather than try to solve them analytically or simulate them numerically, we instead will inquire about the feasibility of steady-states. That is, we ask the question (as is traditional in stirred-tank analyses), “Does there exist a quintuple of positive values U_0 , l_0 , Z_0 , D_0 and N_0 , such that the right-hand sides of Eqs. 1–5 all vanish identically?” Then, instead of solving a system of differential equations, the task becomes one of searching for solutions to coupled quadratic, algebraic equations.

The algebra involved in solving the five simultaneous nonlinear equations is tedious. Fortunately, the ensuing solution is relatively compact. It is

$$l_0 = -\frac{1}{\beta} \log \left[\frac{em}{n_0 \alpha} \left(1 + \frac{\phi}{\rho} \right) - \frac{\gamma}{\alpha} \frac{\phi}{\rho} \right] \quad (6a)$$

$$U_0 = \xi / (\rho l_0 \psi - \phi w \eta) \quad (6b)$$

$$Z_0 = \frac{m}{\rho} \left(\frac{n_0 \gamma}{em} - 1 \right) \quad (6c)$$

$$N_0 = n_0 / e \quad (6d)$$

$$\begin{aligned} D_0 = \frac{m\xi}{r\rho} \left[\rho(l_0\psi + w\eta) / (\rho l_0\psi - \phi w\eta) \right. \\ \left. + \left(\frac{n_0 \gamma}{em} - 1 \right) \right] \end{aligned} \quad (6e)$$

Study of the solution (Eqs. 6a–e) reveals that there are three conditions which must be met in order for all five variables to remain positive: (1) the argument of the logarithm in Eq. 6a must fall

between 0 and 1; (2) the denominator in Eq. 6b must be positive; and (3) the quotient $(n_0\gamma/em)$ in Eq. 6c must be greater than 1.

The meaning of the second condition is obvious. The intake of periphyton by the mesoheterotrophs must remain greater on average than their rate of capture by *Utricularia*.

The third condition is one frequently encountered in such “stirred tank” analyses. The numerator $n_0\gamma$ characterizes the rate of supply of nutrients to the periphyton stock. Conversely, the denominator, em , sets the rate of nutrient loss to the periphyton. Requiring that the ratio $(n_0\gamma/em)$ remains greater than one is another way of saying that the rate of nutrient uptake by periphyton must exceed its losses. Should such condition fail to be satisfied, the periphyton population will starve. In engineering parlance this failure is known as “washout”, because it occurs whenever the advection rate out of the system (e) is too high to allow the population in the tank to build. The uptake rates by periphyton are usually quite high in comparison to those of macrophytes (Bohr and Luscinska, 1975), making it unlikely that washout of periphyton will limit the system.

It appears most likely that this analysis will turn upon the first requirement, namely, that the argument of the logarithm in Eq. 6a be a positive fraction. To see exactly what this condition means, we first consider what happens when $\phi = 0$, i.e., when there is no feedback. We then see that $(em/n_0\gamma)$ must be less than 1, or equivalently that $(n_0\gamma/em)$ be greater than 1. We immediately recognized this latter ratio as the “washout” parameter for the macrophyte. If nutrient supply and/or macrophyte uptake are insufficient, or if the losses to mortality and advection are too great, the macrophyte population potentially would be unable to sustain itself.

It is near this limit of potential macrophyte washout that the survival value of feedback via carnivory becomes manifest. The fact that the uptake rate by periphyton, (γ) , well exceeds that by macrophytes (α) , makes it possible for the last term in the logarithmic argument in Eq. 6a to compensate for a “washout” parameter that is dangerously close to, or even below one! Such numerical compensation attests to the fact that

positive feedback builds a niche for *Utricularia* to persist and thrive in oligotrophic environments that otherwise provide marginal or inadequate sustenance to non-carnivorous macrophytes.

One can quantify the breadth of this niche in terms of the range of allowable values for the feedback parameter, ϕ . At one extreme, the logarithmic argument in Eq. 6a must remain greater than zero. This translates into the condition that ϕ must remain below the quantity $\rho/[(n_0\gamma/em) - 1]$. Too heavy a predation rate upon the zooplankton would allow the periphyton to grow to inordinate proportions. The *Utricularia* would then be suffocated by the periphyton, and the entire system would collapse—a condition that might best be described as “choke-off” (see Kemp et al., 1983).

One might think that the other bound on ϕ occurs when the argument of the logarithm approaches 1. However, a glance at Eq. 6b reveals that the periphyton thickness cannot shrink to infinitesimal dimensions. By substituting Eq. 6a into the denominator of Eq. 6b, it is possible to show that the entire system has a singular point when the value of ϕ satisfies the transcendental equation

$$\frac{em}{n_0\alpha} \left(1 + \frac{\phi}{\rho} \right) - \frac{\gamma}{\alpha} \frac{\phi}{\rho} = e^{-\beta w \frac{\phi}{\rho} \frac{\eta}{\psi}}. \quad (7)$$

Call the solution to Eq. 7 ϕ_{\min} . At values of ϕ only slightly greater than ϕ_{\min} the *Utricularia* and detrital populations grow to unrealistically high levels. Similarly, nutrients recycle at exceedingly fast rates. This unnatural behavior of the model can likely be ascribed to not including saturation phenomena into the scheme of things. It seems reasonable to assume that the system assumes a configuration as close to ϕ_{\min} as other limits (not included in this model) will allow.

It is further evident from Eq. 7 that the dimensionless grouping βw in the exponent of Eq. 7 regulates the “niche breadth” as measured in terms of $(\phi_{\max} - \phi_{\min})$. This breadth will be widest when βw is as small as possible. Because β is more or less fixed by the optical properties of the periphyton, the most advantageous response by *Utricularia* is to minimize w . It does so by adopt-

ing a branched filamentous morphology that provides a very high surface area per unit volume.

5. Model calibration

Insufficient data currently exist to “calibrate” the solution Eqs. 6a–e. That is, not enough independent measurements can be assembled to determine if they are consistent with the model structure and thus pin down the values of the model parameters. However, the few observations that do exist can be applied to the model to see if it is capable of conforming at least to the scales represented in those measurements.

Ulanowicz et al. (1993) recently measured the density of *Utricularia floridana* (without periphyton) in Lake Annie at 11.4 g dry weight m^{-2} . Periphyton on nearby *Myriophyllum laxum* constituted 50% of macrophyte biomass. Due to a lapse in communications in the field, the periphyton on *U. floridana* was not weighed. It was somewhat lighter than that on *M. laxum*, and an estimate of 25% of macrophyte biomass should not be far from the mark. Dry weight for most plants consists of about 50% carbon, and the C:N ratios (by weight) of macrophyte and periphyton are about 17 and 5, respectively (W. Boynton, pers. commun.). The depth of the macrophyte stand was about 0.5 m above the bottom, so that the standing stocks of nitrogen work out to 671 mg N m^{-3} for the *Utricularia* and 570 mg N m^{-3} for the associated periphyton.

The morphometric parameters U_0 , w and l_0 are readily estimated. The characteristic width, w , of the *U. floridana* in Lake Annie is about 2 mm. Whence 0.5 mm would be an estimate of the periphyton film thickness. The high surface to volume ratio of the *Utricularia* probably means that it enhances the effective surface area of one square meter by several-fold, say 4. Under these assumptions U_0 works out to be $4 \text{ m}^2/\text{m}^3$, and η and ψ become 83 900 and 285 000 mg N m^{-3} , respectively.

Given an estimate of 14.25 g C m^{-3} for total plant mass, it would seem reasonable to assume that the “zooplankton” might constitute about 1% of this figure. Assuming a C:N ratio of 4 for

the heterotrophs, a value for Z_0 of 35.6 mg N m^{-3} results.

Total dissolved nitrogen concentration over the *Utricularia* beds was measured at 89 mg N m^{-3} . This figure is all that is needed for the model, because the nutrient addition rate, n_0 , and the flushing rate, e , always appear together in the solution as the quotient $N_0 = n_0/e$.

Values for the uptake parameters, α and γ , are not easy to establish. Kim et al. (1992) reported that the quantity $0.185 \mu\text{g N s}^{-1}$ (g dry weight) $^{-1}$ was a good estimate of the maximum rate of nitrogen uptake by periphyton. To account for diel periodicity, we use one-half of this value, which when combined with the total biomass of periphyton and the previously-estimated parameters U_0 , l_0 , ψ , n_0 and e yielded a value of $\gamma = 0.000449 \text{ m}^3 \text{ d}^{-1} (\text{mg N})^{-1}$.

These observations and estimates, taken collectively, are still insufficient to determine all the parameters in the model. Thus, I made some arbitrary assumptions to complete the balance. To obtain the mortality constant, m , and the zooplankton grazing parameter, ρ , I have assumed that natural periphyton mortality and grazing by zooplankton are roughly equal. Furthermore, I set the direct uptake rate by *Utricularia* to be twice as large as the subsidy it obtains via carnivory. I guessed that the nitrogen in the detrital pool was about 2/3 of that in the plant

Table 1
Nominal parameter estimates

| Process/quality | Symbol | Value | Dimensions |
|-------------------------------------|----------|-----------------------|---|
| <i>Utricularia</i> uptake | α | 0.000173 | $\text{m}^3 \text{ d}^{-1} \text{ mg}^{-1}$ |
| Periphyton shading | β | 290 | m^{-1} |
| <i>Utricularia</i> mortality | m | 0.02 | d^{-1} |
| <i>Utricularia</i> width | w | 0.002 | m |
| <i>Utricularia</i> nitrogen density | η | 83 851 | mg N m^{-3} |
| <i>Utricularia</i> carnivory | ϕ | 1.87×10^{-4} | $\text{m}^3 \text{ d}^{-1} \text{ mg}^{-1}$ |
| Periphyton uptake | γ | 0.000449 | $\text{m}^3 \text{ d}^{-1} \text{ mg}^{-1}$ |
| Periphyton nitrogen density | ψ | 285 095 | mg N m^{-3} |
| Zooplankton feeding | ρ | 5.61×10^{-4} | $\text{m}^3 \text{ d}^{-1} \text{ mg}^{-1}$ |
| Zooplankton mortality | ξ | 0.1944 | d^{-1} |
| Detrital decomposition | r | 0.0384 | d^{-1} |
| Nutrient input | n_0 | 0.9889 | $\text{mg m}^{-3} \text{ d}^{-1}$ |
| Flushing | e | 0.01111 | d^{-1} |

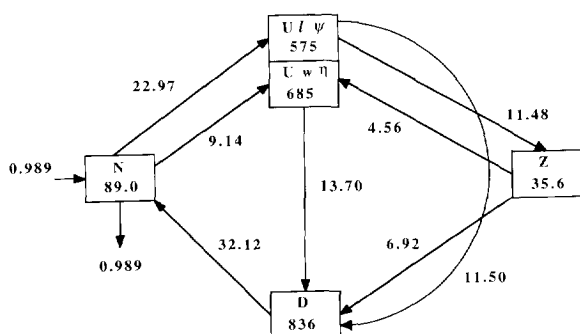


Fig. 1. Nitrogen fluxes in a hypothetical *Utricularia*–periphyton complex. All flows in $\text{mg N m}^{-3} \text{ d}^{-1}$. Standing stocks (numbers inside boxes) in mg N m^{-3} . Components are dissolved inorganic nitrogen (N), *Utricularia* ($Uw\eta$), periphyton ($UI\psi$), zooplankton (Z) and non-living organic nitrogen (D).

biomass. Under these assumptions the characteristic turnover time (stock/throughput) for *U. floridana* works out to about 50 days, that for the periphyton and dead organic matter (some of which is dissolved) to 25 days, and the zooplankton to about 3 days. These appear to be reasonable values. The suite of parameters is arrayed in Table 1 and the resulting system flows are depicted in Fig. 1.

Under this scenario one sees that direct uptake by *Utricularia* is insufficient to avoid washout ($n_0 \propto /me = 0.75$). The macrophyte is being maintained by the 33% subsidy it acquires through carnivory. Clearly, a systematic field and laboratory program for measuring transfers within the *Utricularia* system (preferably one that employs stable isotopes) is necessary before more precise parameter values for this model can be obtained.

6. A Hopf bifurcation

To emphasize the remaining ambiguities and to demonstrate the richness of even this simplistic model, one need only make adjustments to two of those parameters listed in Table 1 about which we are least certain. For one, the *Utricularia* uptake rate, α , is increased to $0.00023 \text{ m}^3 \text{ d}^{-1} \text{ mg}^{-1}$ so as to increase the macrophyte washout parameter to 1.024. Secondly, the periphyton shading parameter, β , is increased to 2100 m^{-1} .

The reader is invited to verify that after these changes, the solution to Eq. 7 is no longer unique. In place of one solution, ϕ_{\min} , there are now two positive solutions, call them $\phi_1 = 8.65 \times 10^{-5}$ and $\phi_2 = 1.28 \times 10^{-4} \text{ m}^3 \text{ d}^{-1} \text{ mg}^{-1}$.

What has happened is that these changes have translated the former interval of allowable feedback which had extended from $\phi_{\min} = 1.484 \times 10^{-4}$ to $\phi_{\max} = 5.619 \times 10^{-4}$ into one that now extends from ϕ_2 to ϕ_{\max} . Throughout this range of feedback values the periphyton mats are generally thick in comparison to the characteristic macrophyte thickness, w , and the feedback flow constitutes a significant input to the macrophyte.

The situation is quite different in a new zone now defined as ranging from zero to ϕ_1 . There periphyton film thicknesses are quite small, and the carnivory flow appears as a minor supplement to the macrophyte nutrient that is taken up directly from the water phase. It remains an open question as to whether *Utricularia* species exhibit both modes of behavior. By way of anecdote, the *U. floridana* studied in Lake Annie was not heavily overgrown with periphyton, the biomass of which was visually inferior to that of its supporting vegetation. By contrast, Bosserman (1979) and others report that species such as *U. inflata* that dominate wetland plains of the Okefenokee and the Everglades support copious overgrowths of periphyton, the mass of which was roughly double that of its support. The contrast is striking to observe and suggests that bimodality in the feedback kinetics may be a factor behind speciation in the genus *Utricularia*.

7. Discussion

Given the manifold uncertainties regarding the parameters used in this model, it would be premature to undertake serious discussion regarding the quantitative results just presented. A coordinated field and laboratory program should be undertaken to quantify the individual processes that comprise this community.

Furthermore, the model remains incomplete in many respects. For example, it would be interesting to explore the changes in model behavior

once feeding saturation were introduced into the scheme. It is also possible that key processes were not incorporated into this model. Wallace (1978), for instance, noted that the leaves of *Utricularia* often secrete “copious” quantities of mucopolysaccharides that possibly bind periphyton and attract bacteria. Bosserman (1979) even presents his own evidence that bacteria in the assemblage are fixing nitrogen, so that our model may not account for all nutrient sources.

These shortcomings notwithstanding, this model may help to elucidate the foundations of many oligotrophic aquatic ecosystems. For the opinion is growing that the role of periphyton in supporting higher trophic levels has been hitherto underestimated. Periphyton production can exceed macrophyte production, even when the thickness of the periphyton cover is small (Kitting et al., 1984). Macrophytes are rarely consumed while they are alive, and the processing of detrital biomass by microbiota is exceedingly inefficient. All of which has led Porter et al. (1988) to declare, “...grazing food chains based on photosynthetic carbon fixation by periphyton or phytoplankton could be more important to animal production than food chains based on microbial conversion of detrital organic carbon derived from vascular plants....”

Although simplistic, the current model nonetheless exhibits qualitative behavior that is thought-provoking. Certainly, it was interesting to see the model illumine how carnivory could supplement macrophyte nutrition. But this behavior of the system near washout was largely anticipated. More surprising was the appearance of a chokeoff point in response to rising nutrient inputs. That is, with increasing n_0 , the advantages of positive feedback appear to wane, until a point is reached where the system “self destructs”. (All other things remaining equal, this occurs at $n_0 = 1.97951 \text{ mg N m}^{-3} \text{ d}^{-1}$ in the current version.)

One often reads and hears talk about “fragile” ecosystems. Yet so many of our sophisticated models behave in an uninteresting and elastic fashion. Only infrequently does one encounter models that exhibit well-defined breakpoints that weren’t built into them a priori. Such “brittleness” (Holling, 1986) or inelasticity has practical

ramifications as well. In the SE United States several of the large oligotrophic wetlands dominated by *Utricularia* mats, including the renowned Everglades ecosystem, soon may be receiving increased nutrient loadings from domestic and industrial sources. The results of this model warn that their extensive *Utricularia* communities could vanish as a consequence.

Finally, there is the question of how far the results of this exercise might be extrapolated. In this particular model, the domain of positive feedback is confined to oligotrophic conditions only. As regards other ecosystems wherein positive feedback and mutualism are obvious, mid-ocean picoplankton communities and coral reefs jump first to mind. Is it a coincidence that all three systems occur in resource-poor environments, or is there some generic property of positive feedback that makes it less likely to appear in systems with access to abundant resources?

One possible lead toward answering this question is the observation (Timothy Allen, pers. commun.) that counter to every autocatalytic cycle runs a loop of negative feedbacks. For example, in the system just described periphyton shades *Utricularia*, which captures zooplankton, which in their turn crop periphyton. Is there something about abundant resources that allows one of the negative counterlinks to grow suddenly and disrupt the cycle of positive influences? This is grist for the modelling mill!

In the event one believes that ecosystem dynamics are somehow analogous to those of the human economy, our results portend even wider consequences, albeit of ambiguous social impact. On the one hand, the prospect that autocatalytic processes might help to sustain global production in a world of ever diminishing resources is comforting. On the other, the draconian rigidity that autocatalytic configurations impose upon their constituents looms most frightening. But, of course, such questions are bound to arise whenever an ecological modeller gazes into the lake!

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