

The Effect of Nutrient Recycling on Ecosystem Stability

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The term ecosystem structure has been variously defined in the ecological literature. I prefer to use the definition proposed by Margalef (1963) "Ecosystems have a structure, in the sense that they are composed of different parts or elements, and these are arranged in a definite pattern. For the purposes of this study, I define ecosystem structure as including the elements of the system (Odum 1962), the structure of their interactions (network design - Hill and Wiegert 1980), and the particular form of the interactions (instantaneous flow rates - Hill and Wiegert's form). The structure of an ecosystem determines its behavior and functional attributes, including both nutrient recycling and ecosystem stability. Based on Odum's 1969 tabular model of ecosystem maturity, I hypothesized that certain ecosystem characteristics tend to co-occur based on similar causal factors in the underlying ecosystem structure. **The purpose of this study was to test the hypothesis that tightening of the phosphorus and carbon cycles increases the stability of pelagic ecosystems to nutrient perturbation.**

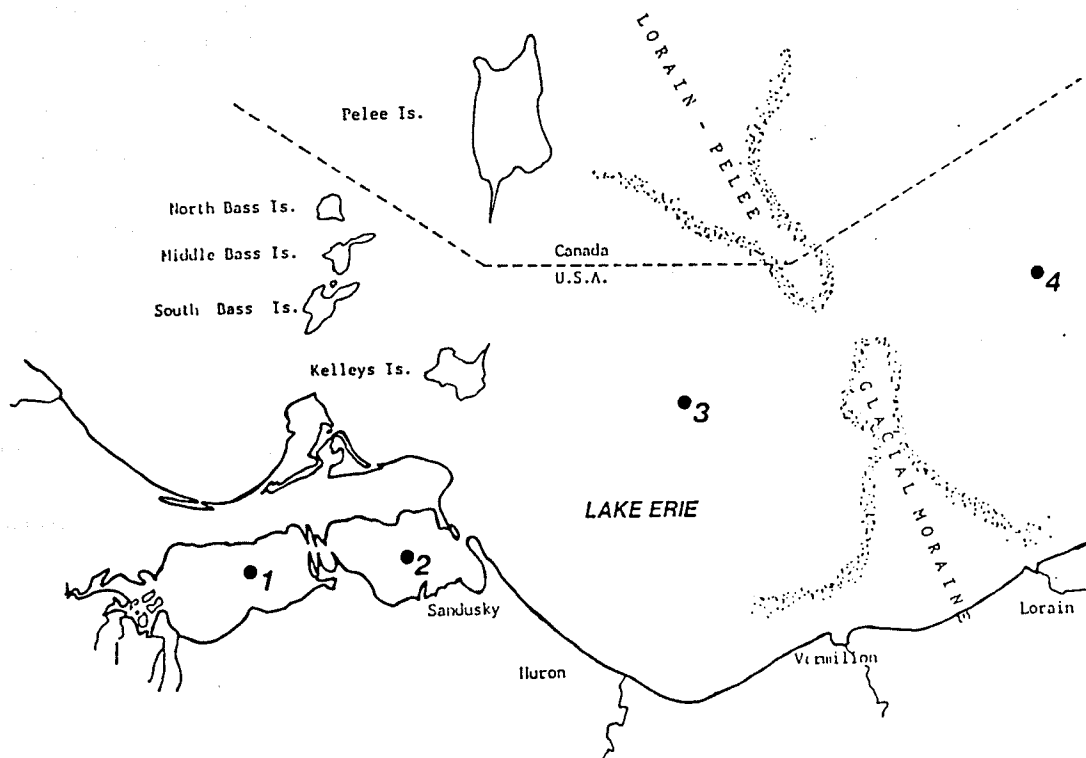
The relationship between nutrient cycling characteristics and the stability of natural ecosystems is not well understood. Although nutrient cycling characteristics have frequently been cited as causative factors for ecosystem stability (Odum 1963, Ganf and Viner 1973) studies of the nature of this relationship have been few and generally incomplete. Steady state analyses are quite common (e.g. McIntire 1968, Rosensweig 1971, deAngelis et al 1989), but generally look only at a single nutrient, missing the potential for interactions between nutrient cycles influencing the behavior of the system.

One factor which has greatly confused this effort is the proliferation and confusion of terms associated with both 'nutrient cycling' and 'stability'. Both terms have developed 'concept clusters' with an associated array of operational definitions, not all of which are compatible. Most studies of the relationship between nutrient recycling use only a narrow definition of each concept and so yield conflicting results and may miss the subtleties of the relationship between these two ecosystem characteristics. In this study I have tried to retain the broadest definition and have used a suite of indices for each. Tightening of the nutrient cycles here refers to the tendency of nutrients to remain within the biotic components of the ecosystem, whether through increased retention by a particular species, increased efficiency of transfers between species (for example decreases in 'sloppiness' of feeding) or increased path length. Stability here refers to the tendency of the ecosystem structure to return to a steady state (or nominal trajectory) following a disturbance. The disturbance of interest in this study is a perturbation in the allochthonous nutrient supply. Stability of the ecosystem to other types of perturbation (heat stress or toxics, for example) would not necessarily be expected to be directly related to the nutrient cycling characteristics. In this study, I consider the effects only of pulse perturbations, though other types likely exist in nature.

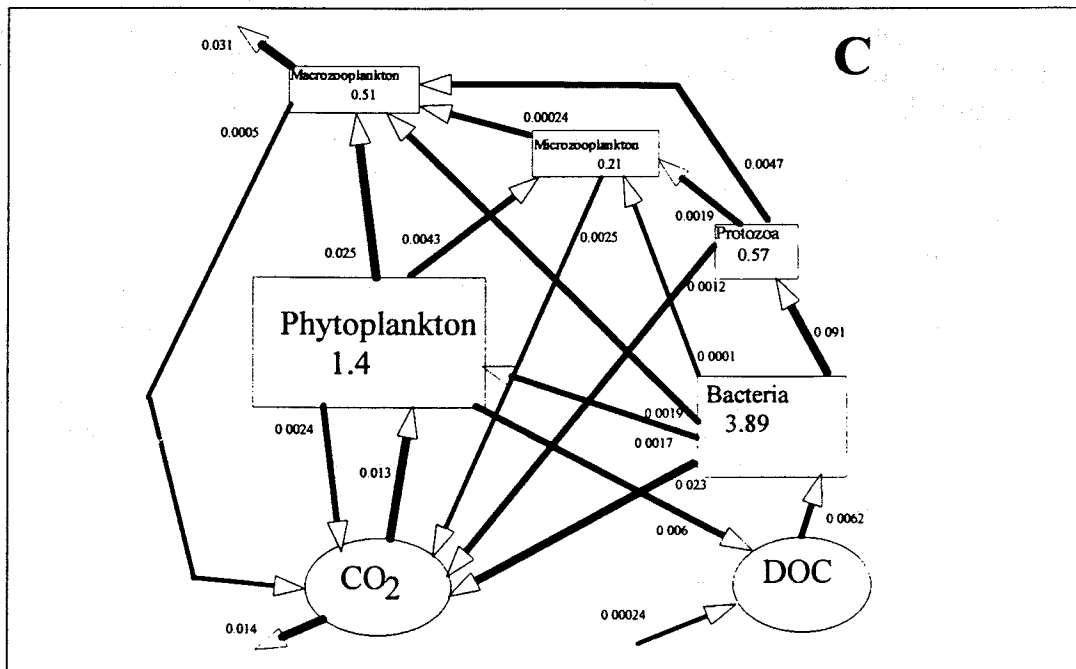
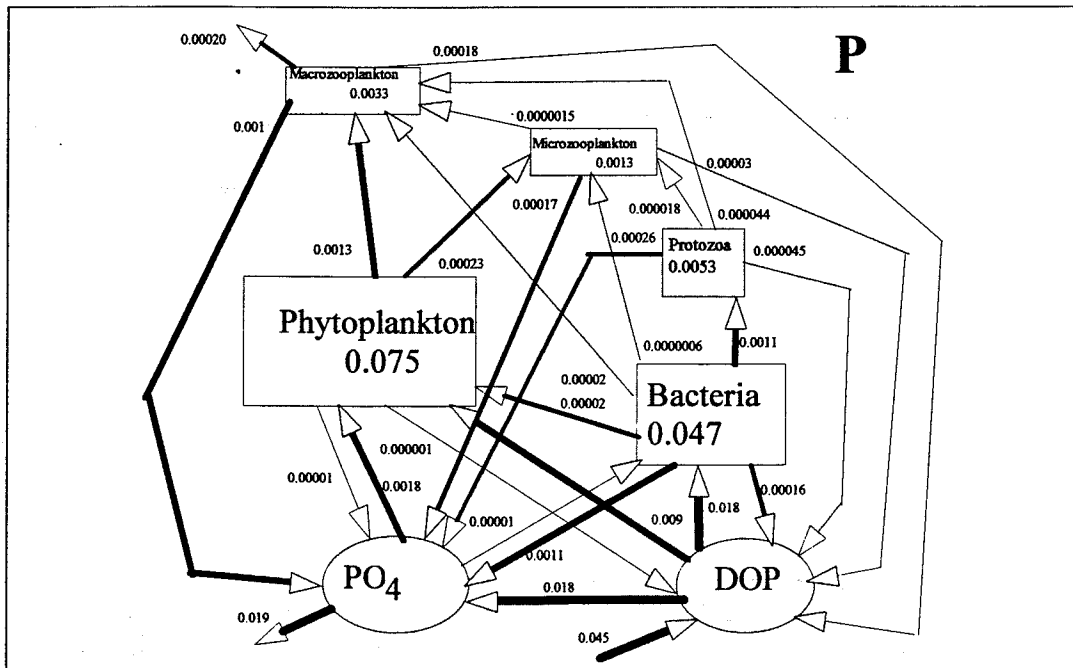
This study takes advantage of a unique opportunity to study a continuum of nutrient availability along a transect extending from upper Sandusky Bay to the central basin of Lake Erie (See Map). Each of the four study sites was visited at approximately monthly intervals during the summers of 1993 and 1994 for a total of 29 site-dates. The approach is unique in combining a broad range of field and laboratory analyses with computer modelling and contemporary systems analysis. Ecosystem structure (consisting of both components and flows) was determined for each of the 29 site-dates through the use of contemporary field and lab techniques (See sample data set for ecosystem structure).

Ecosystem structures as determined for each site-date were used to construct a series of models of increasing complexity. First level models are simple steady state models constructed by using a Matlab-based search protocol to find the steady state model nearest to the data set in 54 dimensional space (See 2-D representation of the steady state protocol). All higher modelling levels were constructed on a STELLA II for Windows platform. Second-level models were donor controlled models, primarily linear using steady state coefficients but with the addition of sufficient non-linear functions to mimic the diurnal rhythms of the system. Third level models link the dynamics of the phosphorus and carbon cycles, for example, predation occurs at the P:C ratio of the prey. Fourth level models change the donor-controlled dynamics (production controlled) to flow controlled (productivity controlled) dynamics for several of the key transfers in the microbial loop in order to better match the trends observed in the field data and laboratory experiments. Fifth level models explicitly couple bacterial productivity to the release of EOC by algae by making the algal-released EOC more palatable than allochthonously-derived DOC.

Sampling sites in Lake Erie

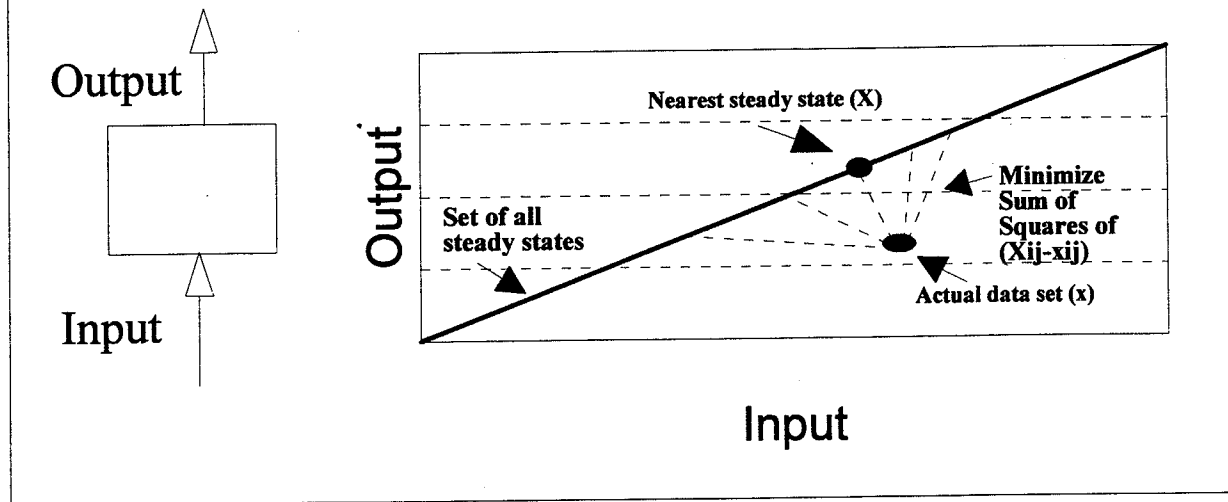


Sandusky sub-basin of Lake Erie - May 1993



* Units are $\mu\text{mol/L/hr}$. Arrow width reflects order of magnitude.

2-D Representation of the MATLAB Protocol



Each model was examined for several nutrient cycling characteristics including retention of C and P within the biota, uptake and transfer efficiencies, average path length, total cycling time, and Finn's cycling index. Nutrient cycling characteristics are largely independent of the level of model complexity since these characteristics are determined from the baseline simulation for which the models are calibrated. The transfer efficiencies for carbon are higher than for phosphorus as are the turnover times, indicating that all trophic levels are excreting more phosphorus than carbon. Although average path lengths for straight throughflow are similar, the phosphorus cycle has a much higher cycling index than does the carbon cycle. The individual biota do not appear to be adapted to obtain or retain phosphorus at high efficiencies (as would be expected from phosphorus-limited organisms) but the ecosystem structure does appear to retain phosphorus by rapid recycling.

Each model was examined for several system stability characteristics including Lyapunov boundaries, amplitude, resistance, resilience, margin of stability, and response time. Stability characteristics are dependent on the model complexity, indicating that more precise measurements of the mechanisms underlying the observed flow rates are necessary for thorough understanding of the relationship between nutrient recycling and ecosystem stability. Within the steady state modelling level (least complex), the systems with the highest cycling indices generally have the greatest margin of stability but the longest response time. This result matches those of previous studies indicating that resistance increases with nutrient recycling but resilience decreases.