

Modeling the effects of nutrient concentrations on ecosystem stability: Framework for a Great Lakes model

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ABSTRACT

The effects of nutrients on algal productivity are not transferred directly to production at higher trophic levels and can not be modelled as if they were. Rates of processes and time scales at different trophic levels require a modular approach to a comprehensive model of the Great Lakes. Predator growth is based ultimately on prey availability and life histories of predators. Factors that control availability of preferred prey (e.g. top-down vs. bottom up) are unresolved. Prey availability is ultimately controlled by C-flow from the base of the food web, but many factors besides nutrient loading influence C-flow to forage fish. Here we focus on factors at the base of the food web that influence C- and P-flow and the efficiency of energy transfer from phytoplankton to forage fish. Specifically, we consider a detailed model of the base of the food web that includes phytoplankton production, grazing interactions and processes in the microbial food web (MFW): bacterial production and bacterivory. The model is constructed from authentic field data and fit into an exact steady state model in a unique way. Phosphorus concentration is the major forcing in this model. The model is examined for ecosystem stability to loading perturbations. Examination of factors to which C- and P-flow is most sensitive indicates much more attention needs to be given to the significance of MFW, especially in offshore communities.

INTRODUCTION

Models are maps. As with any map, their value can be measured by the accuracy they deliver us at desired goals. But the best maps are those that do more than merely guide: they aid in their own refinement. Useful ecosystem models provide more than an accurate representation of our current views of ecosystem structure and function. The most useful ecosystem models allow us to explore the validity of the views on which they are based and to identify research most necessary for their improvement. For this reason ecosystem models need to be viewed as transitory products of a continuing iterative modeling process, useful not only for prediction of outcomes of ecosystem function and management scenarios but also for refinement of our views of the salient ecosystem features which provide those functions.

Ecosystems are those units of nature that control and regulate the efficiency of energy flow from the base of the food web to the highest trophic levels; they also regulate the efficiency of nutrient cycling, thereby regulating the availability of critical, "growth-limiting" nutrients (Margalef 1968). Energy flow into productive ecosystems is controlled by energy and nutrient availability and the efficiency of photosynthetic taxa to convert those resources into biomass. Not every Joule of energy fixed by primary production at the base of the food web is transferred with equal

efficiency to the highest trophic levels (Slobodkin 1959). Both the energy fixed by primary producers and the efficiency of trophic transfer from the base to the highest trophic levels is currently viewed as a function of the efficiency of the taxa and the food web nexus involved (Kerfoot, et al. 1988, deRuiter, et al. 1995). Ecosystem-level questions are those related to the overall function of energy transduction into biomass, efficiency of trophic transfers, efficiency of nutrient recycling and continued availability of critical or limiting nutrients.

Ecosystem management must necessarily be concerned with identification and regulation of those factors most important in controlling the efficiency of energy flow and nutrient cycling. Because ecosystems exist in a varying environment, their management must be particularly concerned with investigating their stability to perturbation and identifying those structures most important to their homeostatic regulation. Lake Erie communities are generally studied and modeled as a set of interacting populations rather than as an ecosystem, where matters of trophic efficiency or stability to nutrient perturbations are considered. Because Lake Erie is an incompletely understood ecosystem, management scenarios based on current knowledge likely will need revision. Models for management of the Lake Erie ecosystem need to provide more than a quantitative representation of ecosystem behavior giving reasonably accurate predictions of outcomes of potential management scenarios. They need to be constructed in such a way as to direct future research efforts directed at better descriptions of Lake Erie ecosystem function and those factors that control it.

Here we present a complex model of the base of the food web that explicitly addresses **ecosystem stability** to nutrient perturbation. We briefly discuss extension of this model to include exotic species (e.g. zebra mussels) and eutrophication issues. We especially address the necessity of considering nearshore and offshore communities separately. This model is an extension of an earlier modeling effort by Sturtevant and Heath (1995) to add portions of the base of the food web to the Lake Erie Ecosystem Model (LEEM) constructed by Prof. J. Koonce. Accordingly, we compare models at the base of the food web and higher trophic levels and consider C- and P-flow from the base of the food web to prey fish communities.

MODEL CONSIDERATIONS

Phosphorus loading does not translate directly to fish biomass. Models that implicitly take such a view are simplistic and likely to mislead if used in driving management decisions. Phosphorus availability has frequently been shown to constrain phytoplankton production (Schelske 1979, Hartig and Wallen 1984). Accordingly, management strategies to limit growth of noxious phytoplankton have sought to decrease P-loading to Lake Erie (GLWQA, IJC 1987). The success of this management strategy is evidenced both by decreased concentrations of detectable nutrient concentrations in Lake Erie and the expected response of phytoplankton communities. In the late 1980's the soluble reactive phosphorus concentrations (SRP = phosphate and possibly other readily available P-compounds) were very low in mid-to-late summer in Lake Erie, which is characteristic but not diagnostic of P-limited lake communities (Charlton, et al. 1993). There was a consistent decrease in phytoplankton biomass from 1958 through 1987 with dramatic decreases in the abundance of nuisance cyanophytes (Makarewicz 1993) that paralleled the decline in P-loading (Nichols and Hopkins 1993).

Effects of increased phytoplankton production on production at the highest trophic levels is unclear. Recent studies indicate there is little reason to presume that such effects would be direct and linear. Piscivore biomass in Lake Erie is affected not only by availability of prey fish, but also by their quality (Knight et al. 1984, Hartman and Margraf 1992, and Hartman 1998), and by factors which influence spawning success and recruitment, such as suitability of nursery habitat (Knight 1977), seasonal temperature (Kitchell and Stewart 1977, Madenjian 1991, and Madenjian et al. 1996), predation pressure (Hartman and Margraf 1993), and age at first reproduction which is controlled by food availability (Henderson and Nepszy 1994, Madenian et al. 1996). Factors controlling prey fish biomass and species composition are not as well studied. Whether prey fish are controlled primarily by food limitation (e.g. Hartman et al. 1992, Gopalan et al. 1998), or by predation pressure (e.g. Knight and Vondracek 1993), or by each of these at different seasons or places is unclear.

We see two different levels of concerns in Lake Erie management issues, necessitating two different levels of modeling efforts. One set of concerns are closely related to P-loading strategies (Input Strategies); the other set of concerns are related to game fish biomass, health and upper food web exploitation (Output Strategies). Shown in **Table 1** are the various concerns and variables best addressed by different models with different time scales; of course, the eventual modeling effort is to pull these together. Because much of the management strategy of Lake Erie has focused on Input Strategies and especially on control of P-loading, we believe a major modeling effort must be made to model the base of the food web, especially to explore the ecosystem consequences of nutrient perturbations to it.

Table 1. Lake Erie Management Issues, Ecosystem State Variables of Concern, and Modeling Needs

	INPUT STRATEGIES	OUTPUT STRATEGIES
Lake Erie Management Issues	Eutrophication and Primary Production Ecosystem Stability Exotic Species (affecting base of the food web) Contaminants (entering base of the food web)	Upper Food Web Exploitation Habitat Structure Exotic Fish Species Contaminants (entering fish directly)
State Variables of Interest	Nutrient Concentrations Total Algal Biomass Blue-Green Algal Biomass Zebra Mussel Biomass	Walleye Biomass Fish Community Richness and Evenness Fish Body Burdens of Bioaccumulative Chemicals
Modeling Needs	Base of Food Web (nutrients to zooplankton) Time Scale: hours -- days	Age Structured Population (prey and predator fish) Time Scale: months -- years

MICROBIAL FOOD WEB AND LAKE ERIE COMMUNITIES

The traditional view that transfer of phytoplankton fixed carbon can be determined (and modeled) simply by estimation of algivorous grazing rates of microcrustaceans is no longer tenable in Lake Erie. Advent of novel techniques (Sherr, et al. 1987) to observe the structure and function of the microbial food web (MFW) indicate its significance to C-flow in Lake Erie plankton communities, and especially, they point to the likelihood that C-flow in nearshore (NS) communities differs from that offshore (OS) in fundamental ways. This is important because theoretical considerations imply that as the MFW becomes a stronger "C-link", the energetic efficiency of C-flow from algae to higher trophic levels decreases (Pomeroy and Wiebe 1988).

Nutrient-rich nearshore areas are more productive of algae, bacteria, protozoans and macrozooplankton than nutrient-poor offshore regions. Both coastal and offshore sites in the central basin of Lake Erie are dominated by heterotrophic nanoflagellates, but the portion of plankton community C in protists was significantly greater in offshore communities (Hwang and Heath 1997a). Nearshore and offshore protist guilds differed taxonomically: *Chrysochromulina* dominated OS communities and *Dinobryon* occurred only at OS sites in association with colonial diatoms; ciliates were more diverse NS than OS (Hwang and Heath 1997a,b). The fraction of bacterial production grazed by protists was significantly greater OS, where protists grazed virtually the entire daily bacterial production, compared against generally grazing less than 25% of bacterial production at coastal sites (Hwang and Heath 1997b). These recent findings suggest that the MFW is more tightly coupled to phytoplankton production OS than NS and is more important in transfer of C to higher trophic levels than investigation of NS sites alone would indicate. Whether this is due to appearance of different bacterial taxa NS vs. OS or a relationship that depends on metabolic alterations within taxonomically similar microbial communities remains to be shown.

Whether bacterial abundance alone controls seasonal and spatial increases of bacterivore populations in the Great Lakes which are most important in the MFW is unresolved (Carrick and Fahnenstiel 1989, 1990). Recent studies indicate a considerably greater fraction of C is passed through the microbial loop OS than in coastal regions. Not only does this indicate the contribution of the MFW to overall C-flow to higher trophic levels may differ between NS and offshore OS communities, it also indicates that when OS communities are viewed as "dilute NS communities" the C-flow to higher trophic levels is likely to be underestimated. Bacterivorous rotifers dominated at both NS and OS sites, and all cladocerans (except *Leptodora kindtii*) grazed bacteria. Rotifers grazed between 40% (NS) to 75% (OS) of bacterial production, while cladocerans and calanoid copepods generally grazed less than 25% of daily bacterial production (Hwang and Heath 1999, in press).

A MODEL OF THE BASE OF THE FOOD WEB

A catenated P- and C- model of the base of the food web including elements of the microbial food web was constructed using field data from a study of P- and C-dynamics along a nearshore-to-offshore transect in Lake Erie. The transect ran from Sandusky Bay to the international boundary in the central basin. Study sites included a station in the Sandusky sub-basin as well as a station east of the Pelee-Lorain Ridge, encompassing a steep trophic gradient ranging from

hyper-eutrophic conditions in Sandusky Bay to mesotrophic conditions bordering on oligotrophic at those stations furthest offshore. Data were collected at monthly intervals from May through September in 1993 and 1994. Details of C- and P-dynamics have been reported elsewhere (Hwang 1995, Hwang and Heath 1997 a,b, Hwang and Heath 1999, and Sturtevant 1998).

Field observations included phytoplankton enumerated to species, bacterioplankton (counted as a single taxon), protists (enumerated to species where possible, and to genus otherwise), rotifers (enumerated to species), and microcrustaceans (enumerated to species). Field observations also included estimation of free CO₂, phosphate (detected as SRP and confirmed via Rigler bioassay; Rigler 1966), DOC (detected via the hot-dry combustion method with a Shimadzu TOC-200 Carbon Analyzer), and DOP (detected as the difference between total soluble P and SRP). Rates of processes were also measured at each station on each sampling date. Rate of photosynthesis was estimated from chlorophyll-corrected P-I curves and measured light intensity *in situ* (Fahnenstiel and Scavia 1987). Bacterial production was measured by rates of incorporation of ³H-leucine and ³H-thymidine (Reimann and Bell 1990). Bacterivorous grazers and grazing rates by protists, rotifers and microcrustaceans were estimated by the fluorescent-label technique (Sherr, et al. 1987). Impact and rate of grazing by microcrustaceans (cladocerans and copepods) was estimated in microcosms from which microcrustaceans had been removed vs. those amended with 1X, 2X and 4X quantities of microcrustaceans (Sorrick 1995).

Models were constructed from field observations for each site investigated and each sampling date. We considered phytoplankton, bacterioplankton, protists, rotifers, and microcrustaceans as single taxonomic units. Storages are shown in units of μmol/L, and rates are shown in units of μmol/L/hr. Models were constructed so that flows were expressed as pseudo-first order processes operating near steady state. Although each site-date model was constructed from data collected at that station on that date, **Table 2** shows means and standard deviations of all measurements taken at nearshore stations and all measurements taken at offshore stations. C- and P- models were catenated by considering that when grazers ingested prey, the ingestate contained the C:P ratio of their prey, even though they excreted different C:P ratios. Details of model construction and catenation of C- and P- models can be found in Sturtevant (1998).

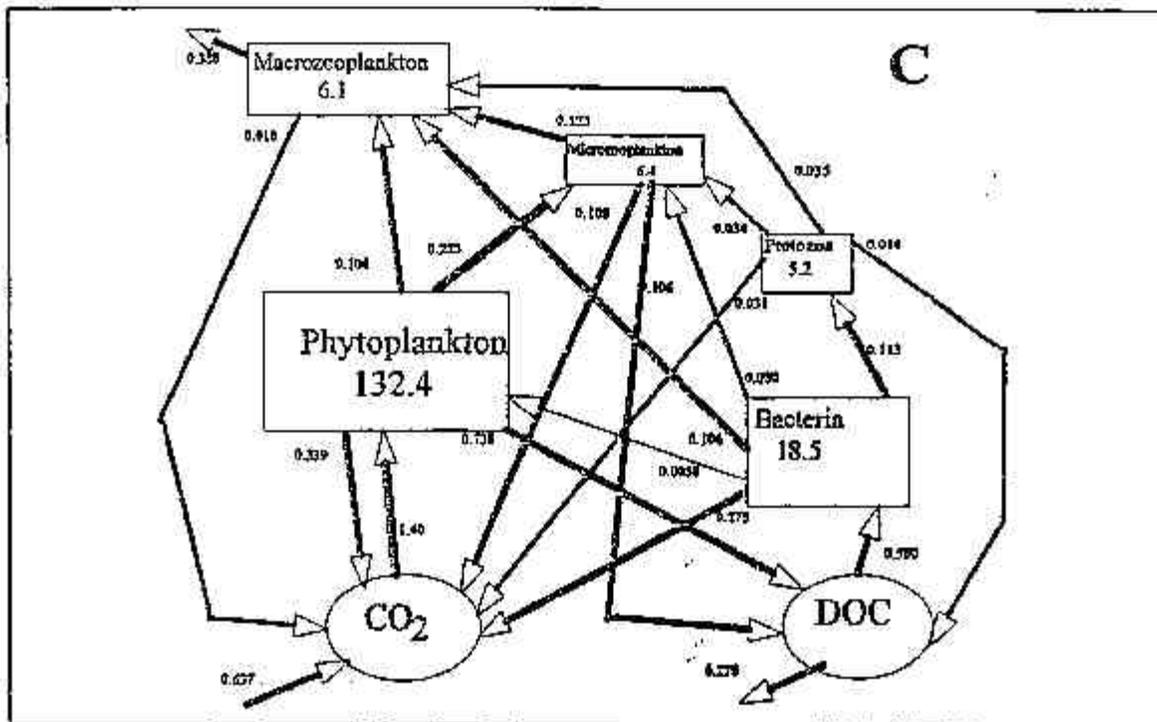
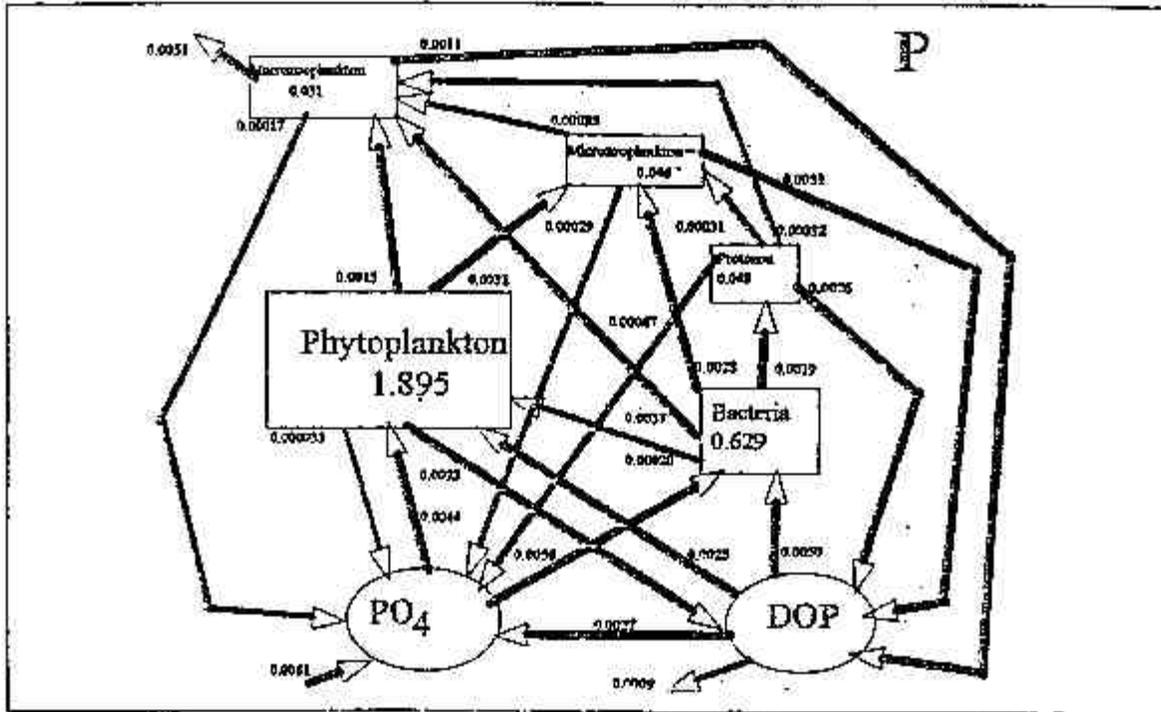
Table 2.
Average storage size and process rates in nearshore and offshore stations.

		Nearshore		Offshore	
		Mean	SD	Mean	SD
Carbon Pools (μmolC/L)	DIC	36	8	38	8
	DOC	497	327	291	284
	Algal C	124	89	5	4
	Bacterial C	14	4	6	1
	Protozoan C	4	2	1	1
	Microzooplankton C	4	3	2	2
	Macrozooplankton C	13	10	1	1
Carbon Flows (μmolC/L/hr)	Photosynthesis	0.44	0.49	0.03	0.03
	EOC Release	0.19	0.29	0.03	0.03

	Bacterial Production	0.46	0.58	0.02	0.04
	Algal Respiration	0.27	0.22	0.01	0.01
	Bacterial Respiration	0.19	0.05	0.05	0.02
	Protozoan Respiration	0.0079	0.0039	0.0024	0.0015
	Microz. Respiration	0.0021	0.0012	0.0007	0.0006
	Macroz. Respiration	0.0227	0.0196	0.0013	0.0013
	Bacteria -> Algae	0.001	0.002	0.002	0.002
	Bacteria -> Protozoa	0.05	0.03	0.02	0.03
	Bacteria -> Microz.	0.15	0.21	0.02	0.03
	Bacteria -> Macroz.	0.03	0.02	0.02	0.05
	Algae -> Microz.	0.119	0.123	0.031	0.034
	Algae -> Macroz.	0.030	0.057	0.006	0.008
	Protozoa -> Microz.	0.03	0.03	0.01	0.01
	Protozoa -> Macroz.	0.15	0.19	0.03	0.06
	Microz. -> Macroz.	0.07	0.11	0.0009	0.0009
	Macroz. -> Out	0.26	0.29	0.06	0.08
	Microz. -> DOC	0.001	0.004	0	0
	CO2 Input	0.121	0.268	0.005	0.014
	CO2 -> Out	0.158	0.140	0.075	0.152
	DOC Input	0.378	0.568	0.01	0.032
	DOC -> Out	0.118	0.271	0.019	0.032
Phosphorus Pools (nmolP/L)	PO4	300	300	300	300
	DOP	700	500	700	500
	Algal P	1700	1100	300	200
	Bacterial P	400	200	200	100
	Protozoan P	41	22	12	10
	Microzooplankton P	33	16	7	5
	Macrozooplanton P	92	88	8	7
Phosphorus Flows (nmolP/L/hr)	Phosphate -> Algae	99	213	5	8
	Phosphate -> Bacteria	33	51	10	23
	DOP -> Algae	83	129	18	35
	DOP -> Bacteria	3	6	18	44
	DOP -> Phosphate	6	10	2	4
	Bacteria -> Algae	0.03	0.07	0.09	0.10
	Bacteria -> Protozoa	1.4	1.1	0.7	1.1
	Bacteria -> Microz.	3.1	3.7	0.9	1.2
	Bacteria ->Macroz.	0.9	1.2	0.9	2.1
	Algae -> Microz.	2.4	3.6	4.2	7.4

Algae -> Macroz.	0.8	1.7	0.6	0.9
Protozoa -> Microz.	0.2	0.3	0.1	0.1
Protozoa -> Macroz.	1.4	1.8	0.3	0.6
Microz. -> Macroz.	0.461	0.689	0.005	0.006
Macroz. -> Out	1.9	2.4	0.4	0.6
Bacteria -> Phosphate	3	6	4	8
Bacteria -> DOP	2	3	3	5
Algae -> Phosphate	4	.5	4	9
Algae -> DOP	3	2	2	5
Protozoa -> Phosphate	0.5	0.4	0.3	0.6
Protozoa -> DOP	0.5	0.7	0.2	0.4
Microz. -> Phosphate	1.9	2.6	4.2	7.4
Microz. -> DOP	1.3	1.7	0.7	1.2
Macroz. -> Phosphate	0.9	1.3	0.8	0.9
Macroz. -> DOP	0.6	0.8	0.5	1.2
Phosphate Input	117	223	12	29
Phosphate Output	8	21	12	16
DOP Input	83	125	16	26
DOPd Output	3	4	5	9

Our aim was to analyze these models for total system throughput, average pathlength, cycling efficiency and stability using techniques requiring the model to be at steady state, *sensu strictu*. Although our observations provided "snapshots" of the pelagic plankton communities, which were likely to approximate a steady state closely, it was unlikely that any of these "snapshots" would be exactly at steady state. A steady state model for each site-date was derived from the corresponding "snapshot" model using a novel approach, based on the earlier work of Strong (1986 a,b). Each "snapshot" model was expressed as a point in 54-dimensional space, in which each dimension corresponded to a particular flow. Steady state and linkage constraints were used to define a region in the 54-D state space containing the set of all possible steady states. A series of MATLAB routines on a Maple V platform were used to calculate the nearest steady state point on the surface of the steady state region to the "snapshot" data point (outside the steady state region) as a least squares scalar fit (Sturtevant 1998). The "snapshot" models were then adjusted to this 54-D least squares best fit steady state model for analysis. In all cases examined, the "best fit steady state" model was closer to the "snapshot" model from which it was derived than to any other snapshot model, indicating that the "snapshot" models constructed from field data were internally consistent and close to steady state. **Figure 1 a and b** show July 1994 steady state models for Upper Sandusky Bay and central basin of Lake Erie, respectively.

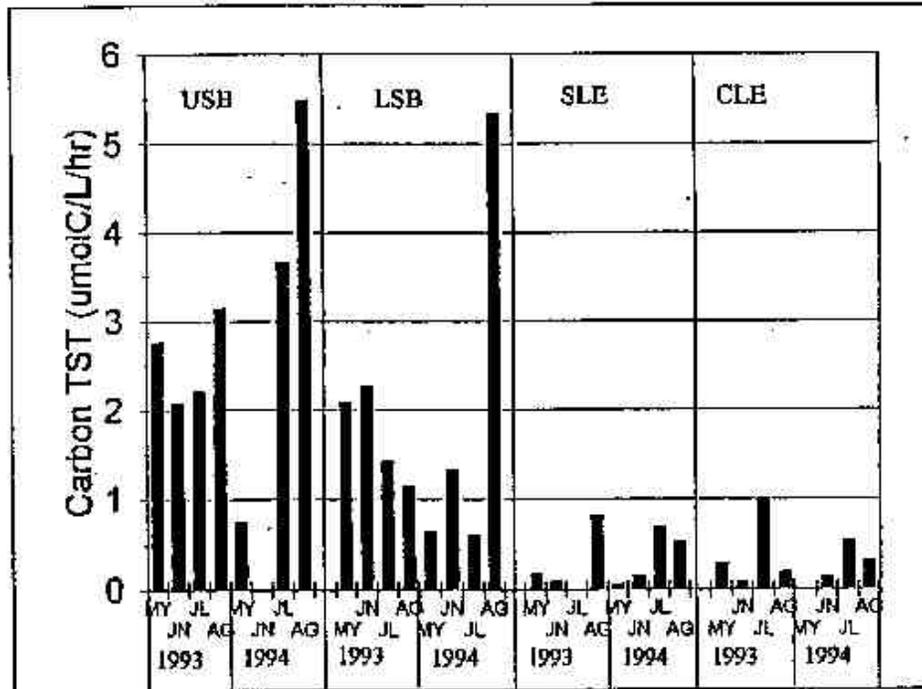


MODEL ANALYSIS

Flow analysis was conducted on the C- and P- steady state models separately using the methods of Finn (1976). The C-model was treated as a 6-compartment model (DOC, algal C, bacterial C, protist C, rotifer C, and microcrustacean C), whereas the P-model was treated as a 7-compartment model (phosphate P, DOP, algal P, bacterial P, protist P, rotifer P, and microcrustacean P) on the grounds that a release of phosphate followed by re-uptake constituted a recycling loop likely to occur, while respiration of CO₂ and re-uptake was unlikely due to relatively large concentrations of CO₂ in the water. Flow through each component was calculated from flow matrices for each compartment and Total System Throughflow (TST). TST was used as a scaling factor, to permit comparison of nearshore and offshore models with widely different absolute TST. Average path length (APL) was the average number of compartments through which a C or P atom passes between the time it entered and left the ecosystem. $APL = (TST)/Z$, where Z was the sum of all inflows. APL made no distinction between straight flows and flows lengthened through recycling. Separation of straight and recycled flows allowed calculation of a cycling index (CI), indicating increased residence pathlength an atom had because of recycling.

The roles of algae and bacteria in C- and P-models differed between coastal models and offshore models, indicating that although the NS and OS communities are structured similarly, they functioned differently. TST was significantly higher for coastal than offshore models (**Figure 2**). C- and P-models differed considerably in the significance of recycling processes. Only about 10 percent of C-TST was recycled, while greater than 40 percent of P-TST was recycled (Sturtevant 1998). The proportion of algal C flux lost through respiration declined slightly along the NS-OS gradient, while the fraction of nascent photosynthate released as DOC increased along the transect; these trends resulted in a greater portion of C transferred to higher trophic levels via grazing at intermediate stations along the transect (**Figure 3**). Bacterial C-flux was unchanged along the transect and equally apportioned between respiratory losses and transfer to bacterivores in both NS and OS steady state models. Steady state P-models indicated both algae and bacteria transferred more P to higher trophic levels in NS systems than OS. Cycling Indices (CI) for P-models were consistently higher than CI for C-models for the same station and date. Overall, C-models averaged CI = 0.11 and P-models averaged CI = 3.56 (Sturtevant 1998). This indicated P-recycling was more important than C-recycling, consistent with the view that nutrient cycles for the limiting nutrient should be more retentive. Cycling indices for C increased significantly as the season progressed and tended to increase more in OS systems than NS (**Figure 4**); no similar seasonal trend was noted for CI in P-models.

A



B

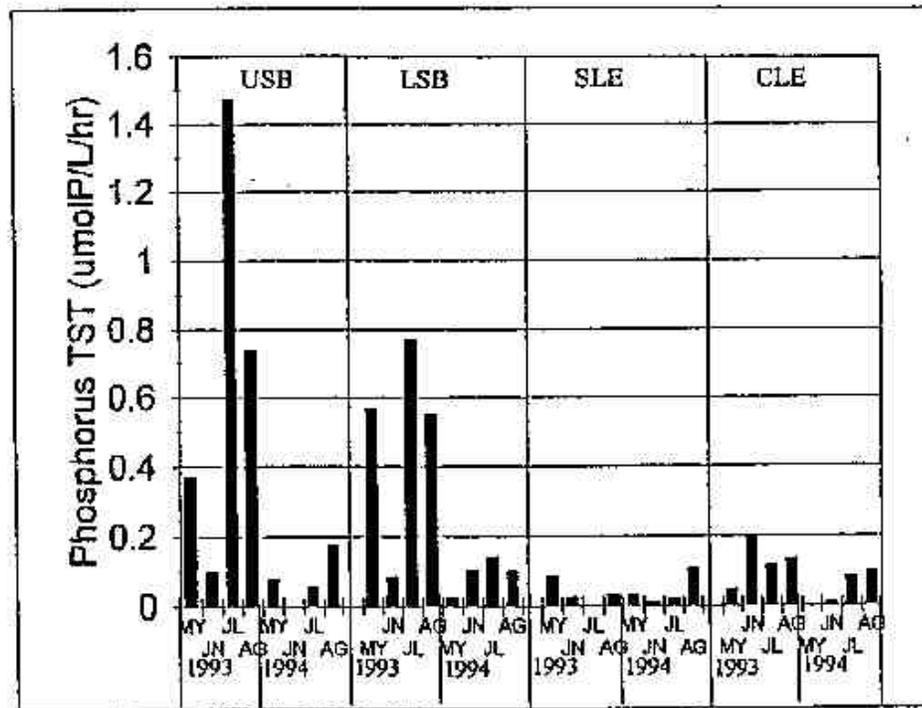


Figure 2 Total System Throughflows (TST) of Steady State models of the coastal stations USB and LSB and the offshore stations SLE and CLE. Dates are in May (MY), June (JN), July (JL) and August (AG) 1993 and 1994. All units are μmol per L per hour. (A) Carbon TST. (B) Phosphorus TST.

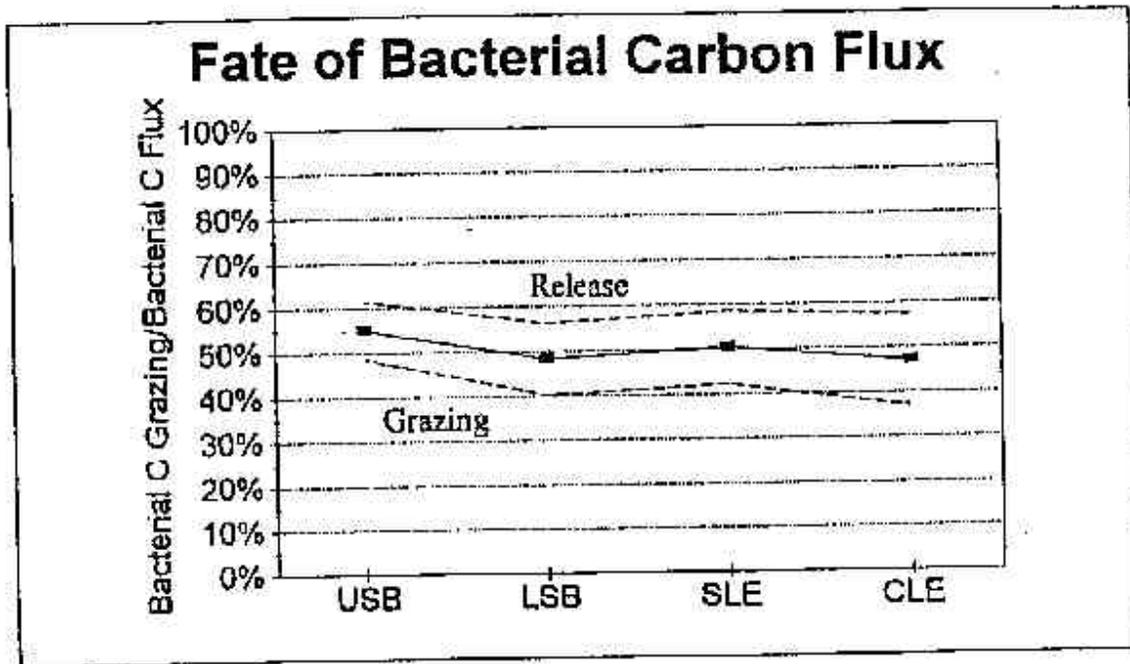
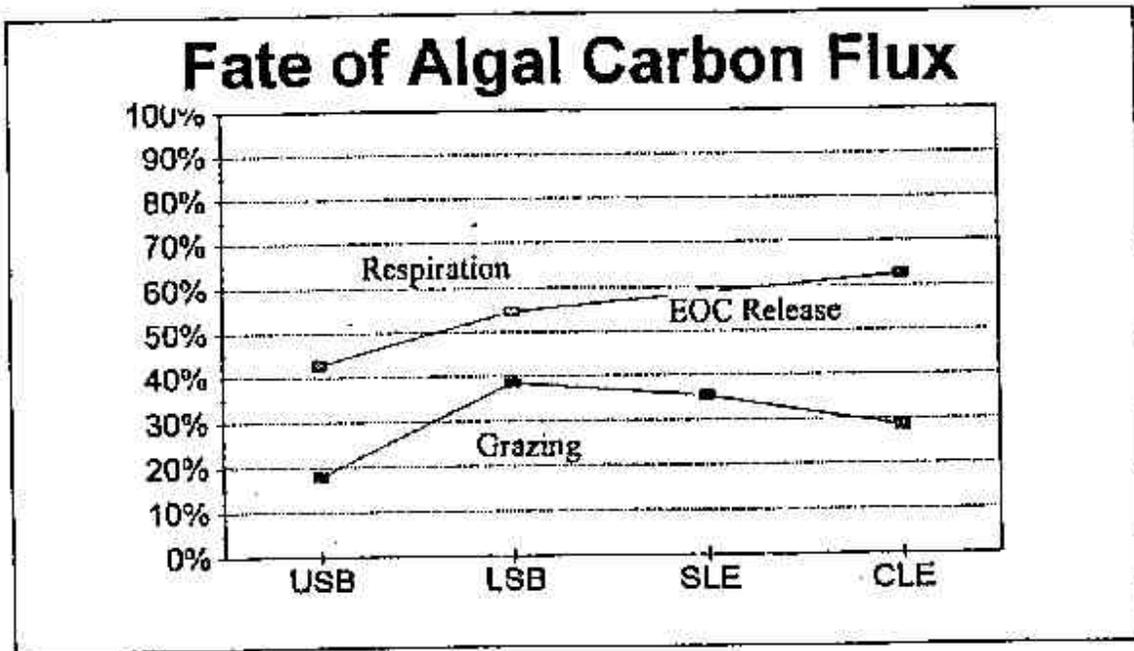


Figure 3a Fate of algal and bacterial C flux. Units are in stacked percentages of total flows out of algae and bacterial, respectively. Area above the top line indicates respiration, distance between lines represents extracellular organic carbon released (EOC), and distance below lower line is amount grazed.

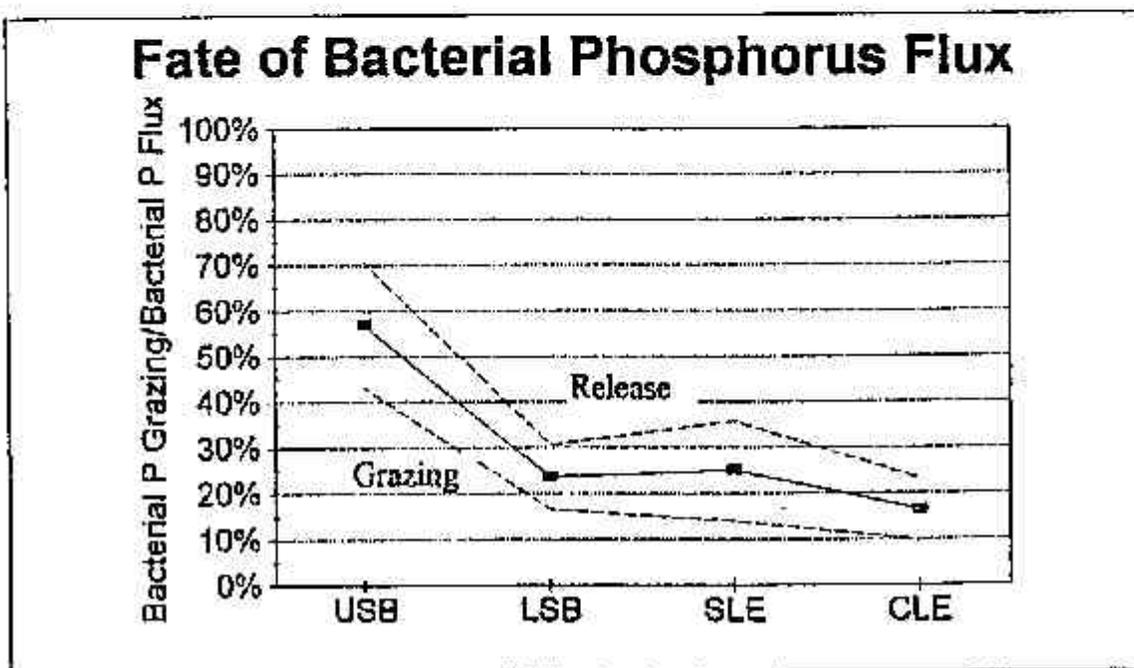
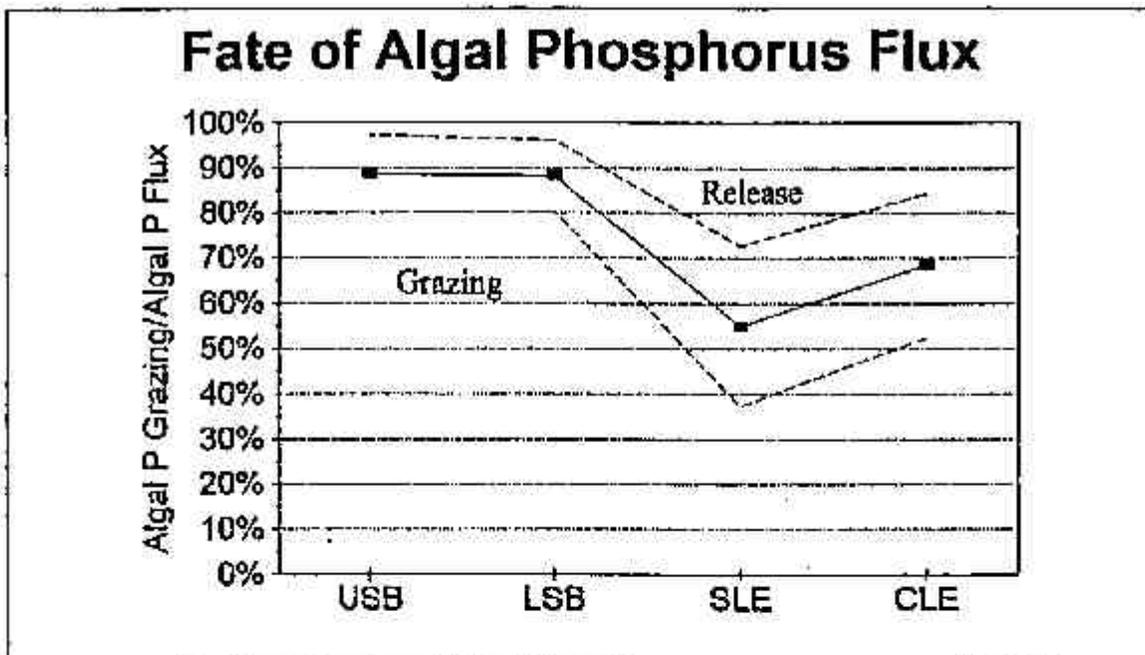


Figure 3b Fate of algal and bacterial P flux. Units are in stacked percentages of total flows out of algae and bacteria, respectively. Distance above solid line is flux due to release as phosphate or DOP; distance below line is percent total flux due to grazing.

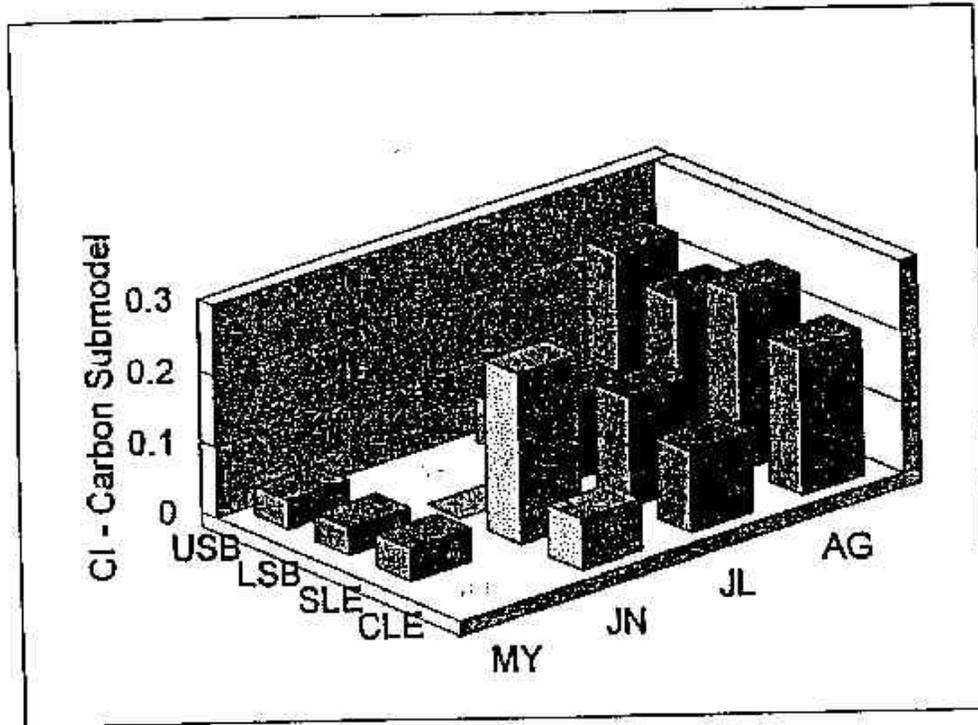
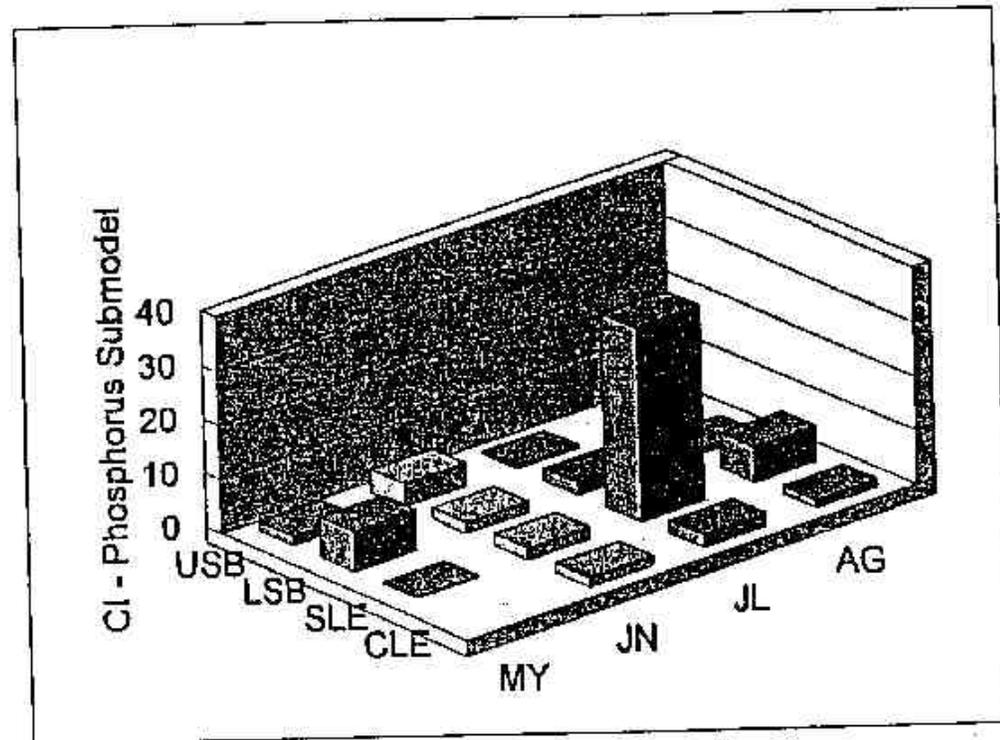
A**B**

Figure 4 Cycling Indices (CI) of Steady State models of the coastal stations USB and LSB and the offshore stations SLE and CLE. Dates are in May (MY), June (JN), July (JL) and August (AG) 1994. (A) Carbon CI. (B) Phosphorus CI.

We examined the stability of these NS and OS models to nutrient pulses (i.e. DOC, DIP, and DOP). Despite the importance of stability in ecological systems, there have been relatively few tests of its various facets using data from real ecosystems (Ives 1995). Deterministic stability analysis is difficult to apply to data (DeAngelis and Waterhouse 1987, Cottingham and Carpenter 1994). Analysis of the coefficients for equations used to generate steady state models derived from data, avoided many of the difficulties of the deterministic approach (Sturtevant 1998), following the approaches of Webster, et al. (1975). Margin of stability measured resistance to perturbation (i.e. the greater the margin of stability the more resistant the system is to a perturbation), and index of response time measured resilience (i.e. smaller indices implied greater resilience, expressed as shorter times required by "most" of the system to recover from a nutrient perturbation, Webster et al. 1976). Stability measures were calculated separately for each of the 29 site-date steady state models and correlated to measures of nutrient retention and recycling. In general, steady state models of systems with a high degree of P-recycling were less resistant but more resilient to P-pulse perturbations (**Figure 5**). As C- and P- retention increased in the steady state models, resistance of those systems to perturbation increased.

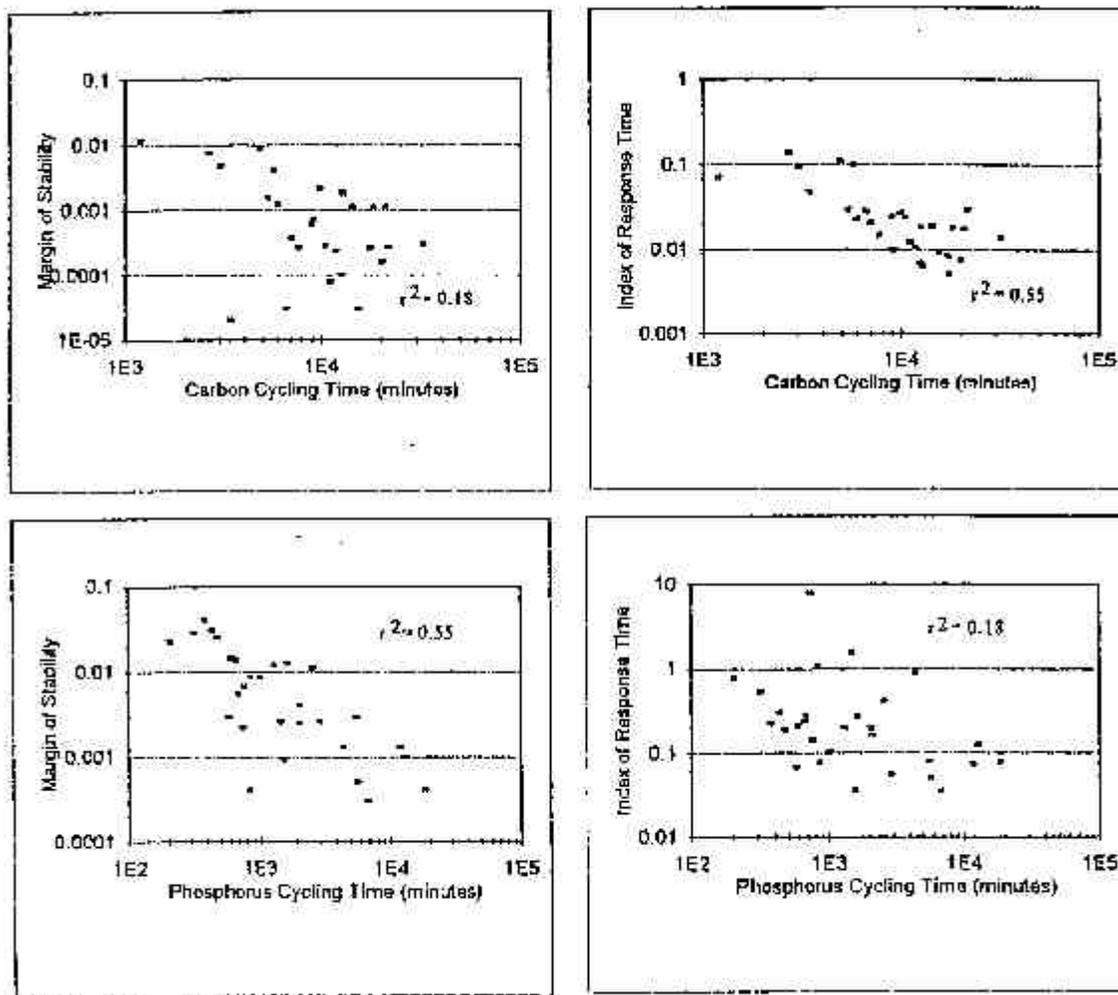


Figure 5 Comparison of Steady State stability indices, Margin of Stability (resistance, left column) and Index of Response Time (resilience, right column) for Carbon Models (top row) and Phosphorus Models (bottom row).

Correlation analysis and sensitivity analysis indicated the importance of bacterial activities and their role in the microbial food web (MFW). Correlation analysis of the flow coefficients was used to identify homomorphic regions as sub-structures within the context of the larger steady state models. Although the size of the compartments varied by greater than an order of magnitude from NS to OS ecosystems, the MFW behaved as a homomorphic subregion in both the C- and P-steady state models (**Figure 6**), having similar pseudo-first order transfer coefficients among the several compartments (i.e. the fraction transferred from one compartment to the next was uniform). Flows through the bacterial C compartment were linearly related to bacterial uptake of DOC; the transfer of C from microcrustaceans to higher trophic levels was predictable as a part of this homomorphic subregion and correlated most strongly with the rate of protozoan grazing on bacteria plus protist uptake of DOC, suggesting that the role of protists may be more important than bacteria as a direct link between DOC and microcrustaceans.

Sensitivity analysis further emphasized the possible importance of protistan bacterivory: as the protistan bacterivorous grazing coefficient was altered ± 10 percent, bacterial P varied by 88 percent, protist P by 233 percent, microcrustacean P by 78 percent, and bacterial P release by 87 percent (Sturtevant 1998). The significance of bacterioplankton to system stability was indicated by the finding that bacterial P retention was the only index of nutrient retention/recycling to correlate significantly with resilience of the system to respond to a perturbation of DOP (**Figure 7**).

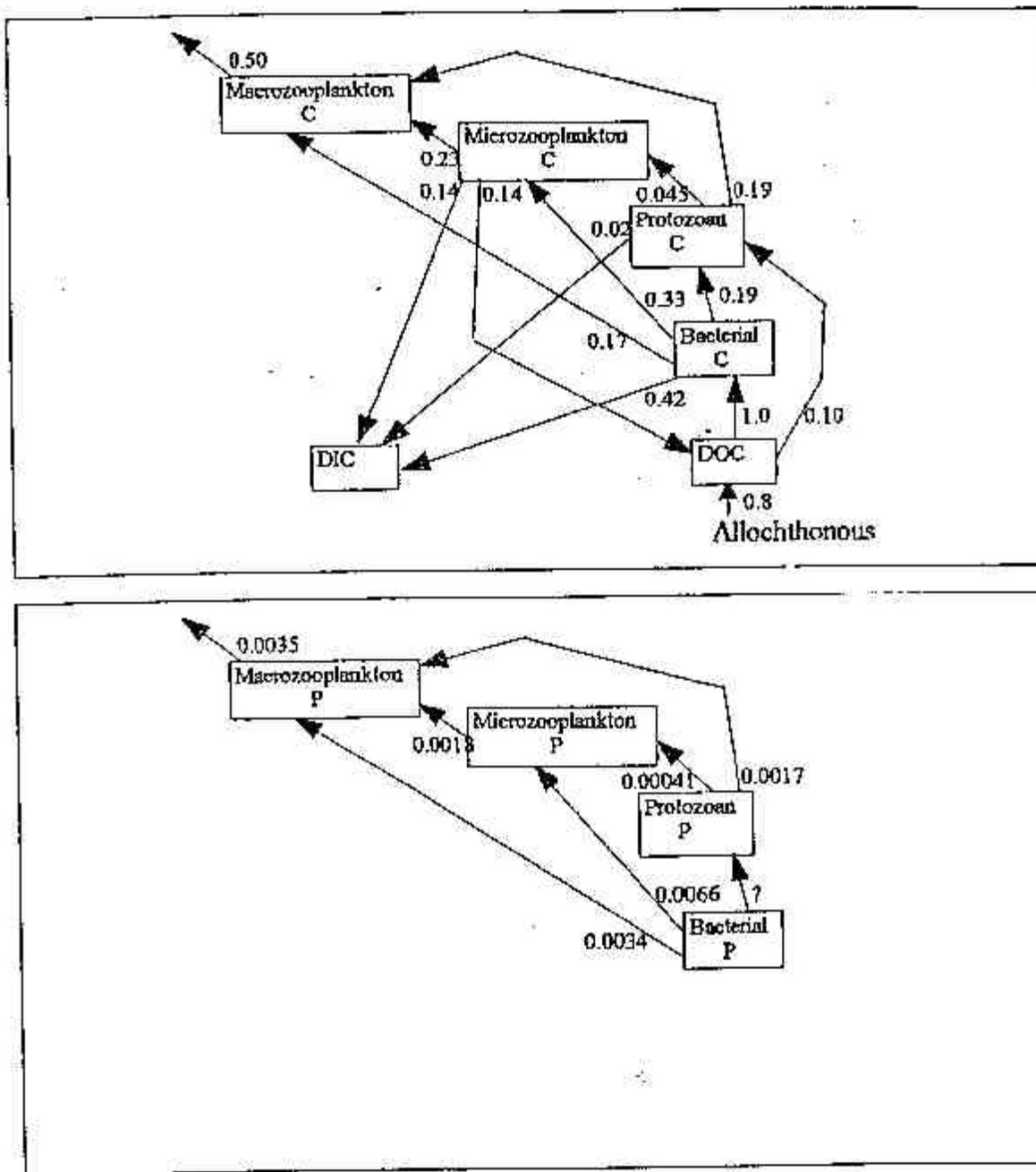


Figure 6 Microbial Food web homomorphic subregion of the planktonic ecosystem determined by correlation analysis of the steady state models (NS and OS models together). Fluxes are portion of donating compartment scaled per unit bacterial production.

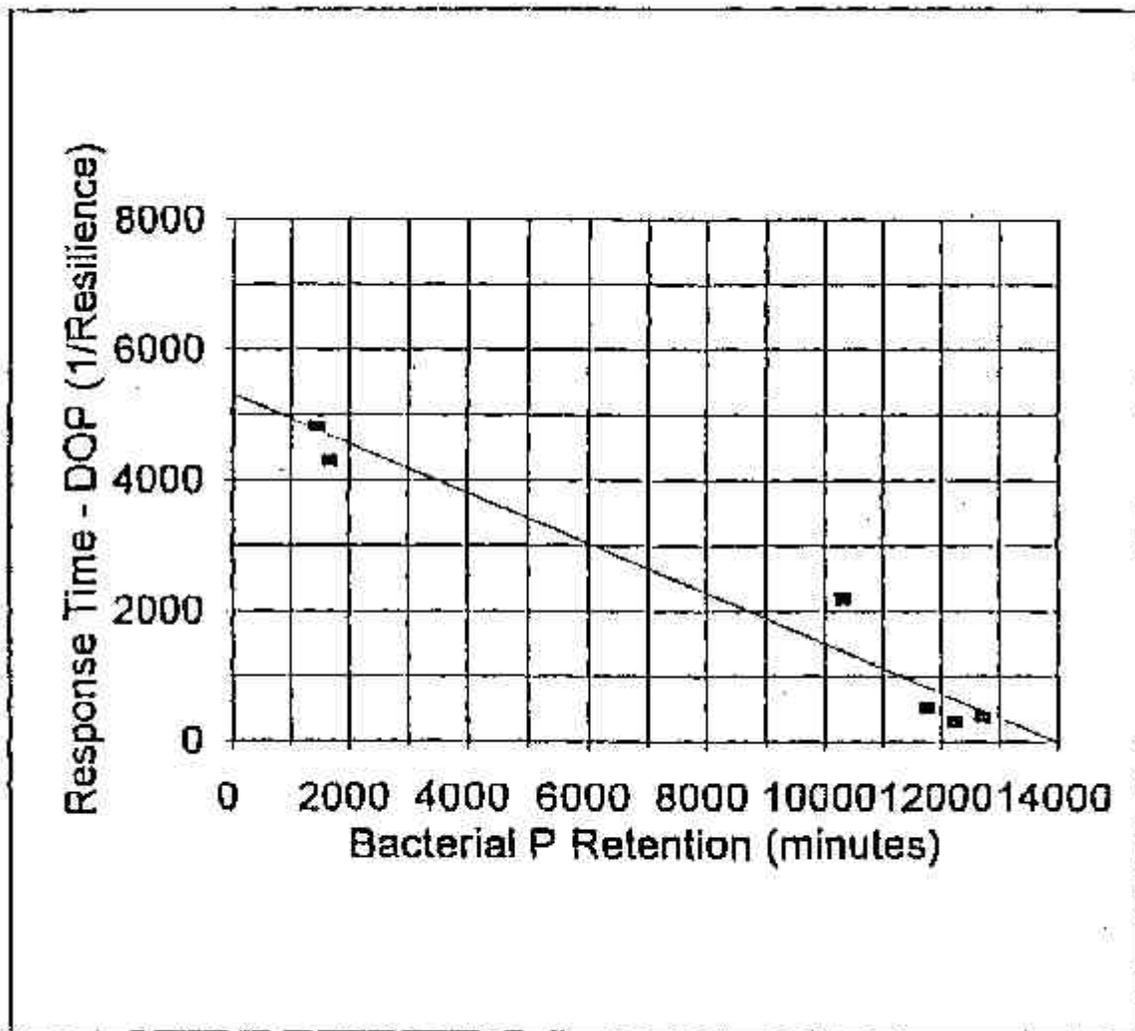


Figure 7 Correlation of system resilience (inverse Response Time) to systems perturbed by DOP pulses vs. Bacterial P Retention. Units are minutes.

MICROBIAL FOOD WEBS, OFFSHORE COMMUNITIES AND LAKE ERIE MODELS

We maintain that models are best used when they drive further investigation for scientific and practical purposes, rather than as ends in themselves. Models are tools useful for examining the consequences of complex arrays of data; they can't show novel findings beyond the data used to construct them. Our purpose here has been to consider the importance of the MFW to ecosystem functions of Great Lakes communities. Our approach has been to construct steady state models of nearshore and offshore communities in Lake Erie from field data collected using contemporary techniques designed to gather accurate information on the MFW, as well as those variables traditionally studied such as phytoplankton production and microcrustacean grazing. Analysis of these models for ecosystem functions such as regulation of C-flow and stability to

nutrient perturbations indicates the importance of the MFW, warranting its inclusion in models of the base of the food web. Behaviors of Lake Erie models that include the MFW must be viewed not merely as "more realistic" but as generators of testable hypotheses regarding the significance of the MFW to Lake Erie ecosystem functions.

The field studies and models of them presented here indicate two major conclusions that warrant further examination: (1) the MFW is considerably important for ecosystem level functions, especially the role of protists, and (2) offshore communities differ more in function than in structure from nearshore communities. Direct and indirect grazing of bacteria (indirect grazing = grazing of bacterivorous grazers) at times provided more than 80 percent of the C and more than half of the P to microcrustaceans. Protist activities often appeared to be the most sensitive activities in the model, as noted above. Sensitivity analyses also indicated that protozoa would be useful indicators of system behavior because they are likely to magnify small changes in other parts of the system, especially those related to bacterial standing crop and DOC concentrations. These models also indicated protists play a significant role in regeneration of dissolved P, based on mass-balance considerations. Whether this will be supported by further studies specifically designed to examine this issue remains to be seen, but similar findings have been made in other systems (Jugens and Gude 1990, Taylor and Lean 1991).

Although very similar in structure, nearshore and offshore communities functioned differently. Bacterial production was strongly correlated with allochthonous DOC input, so phytoplankton - bacterioplankton coupling was much stronger in OS communities, apparently due to the dependence of C-limited bacteria on DOC released from phytoplankton. Both bacteria and zooplankton appeared to retain C significantly longer in OS systems. NS and OS ecosystems differed in the degree of nutrient regeneration: nearshore bacterial P-release was generally around 10 percent of P-uptake, while in OS systems P-release by bacteria was often greater than 90 percent P-uptake. These observations taken together may indicate that bacteria were P-limited NS but C-limited in OS communities. Transfer of algal-C and bacterial-C was much more efficient in NS systems than OS. Likewise, a higher proportion of bacterial-P was transferred to bacterivores in NS systems. Such differences have been suggested previously in Great Lakes communities but without resolution (Moll and Brahe 1986, Scavia and Laird 1987).

IMPLICATIONS FOR LAKE ERIE MANAGEMENT

Traditionally, bacteria in the Great Lakes have been treated as a nuisance and their function only as a health hazard. Trophically, aquatic bacteria have been regarded as a C-sink, essential only as nutrient mineralizers (Ducklow, et al. 1986, Pomeroy and Wiebe 1988). Awareness of the structure and function of the MFW in marine and freshwater communities has increased over the past decade, and often the MFW has been shown to be a significant C-link to higher trophic levels, essential for many ecosystem processes (Sherr, et al. 1987, Sherr and Sherr 1988). Recent studies in the Great Lakes have increasingly indicated the significance of the MFW in the structure and function of plankton food webs. Our purpose here has been to provide reasons for inclusion of MFW components in Lake Erie models of the base of the trophic cascade and to suggest that those models be used to drive research inquiries. Especially, we suggest more attention be given to comparison of flows through the MFW vs. the traditionally considered flows through algae via microcrustacean grazing and those factors that influence the relative

contribution and efficiencies through each of those pathways. Exclusion of MFW from Lake Erie models could conceivably lead to management decisions that would lead to damage of the MFW and may mislead estimates of C-flux to higher trophic levels.

As an example of the need to include the MFW into research plans and models we mention briefly the effects of zebra mussels on the base of the food web. With the advent of the zebra mussel, *Dreissena polymorpha*, much attention has focused on loss of phytoplankton from the water column: zebra mussel damage to plankton communities has frequently been viewed exclusively as loss of phytoplankton and concomitant loss of C-flow to higher trophic levels. We see it otherwise. Zebra mussels graze bacterioplankton as well as phytoplankton (Cotner, et al. 1995); they also graze heavily on protists (Lavrentyev, et al. 1995), suggesting that zebra mussels could have a profound effect on processes that depend upon an intact MFW. Zebra mussels in Saginaw Bay, Lake Huron, excreted large amounts of ammonium to the water (Gardner, et al. 1995) and greatly increased ammonium regeneration and decreased community ammonium uptake rates. In some systems it has been shown that protistan bacterivory can control populations of nitrifying bacteria (Lavrentyev, et al. 1997), suggesting alteration of MFW by dreissenids could have profound effects on processing of ammonium released by zebra mussels. Zebra mussels also have a profound effect on P-dynamics at the base of the food web. Not only do these mussels release large amounts of phosphate, they also cause a great decrease of phosphate uptake by phytoplankton and bacterioplankton (Heath, et al. 1995). Phytoplankton uptake appears to slow due to alteration from P-limited to P-replete physiological conditions, but bacterial P-uptake may slow due to extreme C-limitation caused by loss of phytoplankton DOC release (Heath, et al. 1996).

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