Dynamics of Lake Michigan Plankton: A Model Evaluation of Nutrient Loading, Competition, and Predation[1]

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Scavia, D., G. A. Lang, and J. F. Kitchell. 1988. Dynamics of Lake Michigan plankton: a model evaluation of nutrient loading, competition, and predation. Can. J. Fish Aquat. Sci. 45: 165–177.

Lake Michigan's offshore ecosystem has been altered dramatically during the past decade. Summer zooplankton dominance has changed from calanoid copepods to *Daphnia* and the substantial contribution of filamentous blue-green algae to summer phytoplankton has been replaced by phytoflagellates. These changes occurred concurrently with reduced P load, P concentration, and abundance of the dominant zooplanktivore, the alewife (*Alosa pseudoharengus*). In this analysis we pose alternative hypotheses of nutrient loading and species interactions as determinants of zooplankton and phytoplankton species composition in the summer epilimnion. We evaluate these hypotheses with a food web model that was calibrated to measurements of the 1980s Lake Michigan plankton composition and algal production, sedimentation, and growth rates and literature estimates of zooplankton secondary production and nutrient excretion. The model simulates the influence of gradients of both P load and alewife abundance on predation–competition interactions. We conclude that summer plankton composition in Lake Michigan is controlled largely by predation. The model further predicts a return to a plankton community similar to that of the 1970s under a scenario of increasing invertebrate predation by a new zooplankton species for Lake Michigan, *Bythotrephes cederstroemi*.

Au lac Michigan, l'écosystème situé au large a changé de façon spectaculaire au cours des dix dernières années. Les copépodes calanoïdes, qui dominaient auparavant le zooplancton en été, ont fait place aux *Daphnia*, tandis que les cyanophycées filamenteuses, qui contribuaient de façon importante au phytoplancton en été, ont été remplacées par les phytoflagellés. Ces changements se sont produits en même temps que la réduction de la charge en P, de la concentration de P et de l'abondance du gaspareau (*Alosa pseudoharengus*), le zooplanctivore dominant. Dans cette analyse, nous proposons de nouvelles hypothèses concernant l'effet de la charge en éléments nutritifs et des interactions entre les espèces sur la composition spécifique du zooplancton et du phytoplancton dans l'épilimnion en été. Ces hypothèses sont évaluées à l'aide d'un modèle de réseau trophique calibré, d'une part, avec les mesures faites au lac Michigan en 1980 sur la composition du plancton ainsi que sur la production, la sédimentation et les taux de croissance des algues, et, d'autre part, avec les estimations publiées de la production secondaire et de l'excrétion d'éléments nutritifs chez le zooplancton. Le modèle simule l'effet de gradients de la charge de P et de l'abondance du gasparau sur les interactions prédation–compétition. Il ressort que la composition estivale du plancton dans le lac Michigan est en grande partie déterminée par la prédation. De plus, le modèle prédit un retour à une communauté planctonique semblable à celle des années 1970 suivant une prédation accrue des invertébrés par une espèce de zooplancton, *Bythotrephes cederstroemi*, nouvelle pour le lac Michigan.

Received February 6, 1987
Accepted September 24, 1987
(J9129)

Reçu le 6 février 1987
Accepté le 24 septembre 1987

Recent changes in Lake Michigan food-web structure (Wells 1985; Evans and Jude 1986; Evans 1986; Scavia et al. 1986; Fahnenstiel and Scavia 1987a) has stimulated discussion of whether plankton species composition is controlled from the top (food-web effects) or from the bottom (nutrient effects) of the ecosystem (Kitchell et al. 1988). These arguments developed because Lake Michigan has experienced (1) a major shift in the composition of its planktivorous fishes, presumably caused by environmental stress (Eck and Brown 1985) and predation by stocked salmonines (Stewart et al. 1981; Kitchell and Crowder 1986), and (2) reduced P loading (DePinto et al. 1986) and in-lake P concentrations (Lesht and Rockwell 1985; Scavia et al. 1986). While the mechanisms underlying these changes have not been defined indisputably, note the following:

[1]GLERL Contribution No. 542.

(1) Total phosphorus concentration during winter–spring isothermy has decreased gradually from approximately 7.5 $\mu g \cdot L^{-1}$ in 1975 to approximately 5.5 $\mu g \cdot L^{-1}$ in 1984 (Lesht and Rockwell 1985; Scavia et al. 1986).

(2) Abundance of alewife (*Alosa pseudoharengus*), the previously dominant planktivore, had decreased by about an order of magnitude since early 1970s and in 1983–84 was at its lowest level since its years of dominance (Wells 1985). The decrease represents a factor of 3–4 between the late 1970s and the early 1980s.

(3) Zooplankton total biomass in offshore waters did not change significantly during 1975–84; however, an abrupt change in summer species composition occurred between 1982 and 1983 (Scavia et al. 1986). The previously dominant calanoid copepods (*Diaptomus ashlandi, D. minutus, D. sicilis*) were replaced first by *Daphnia pulicaria* in 1983 and then by a complex of three daphnid species (*D. pulicaria, D. galeata mendotae, D. retrocurva*) in 1984 and 1985 (Evans and Jude 1986; Scavia et al. 1986; Scavia and Fahnenstiel 1987).

(4) Current summer epilimnetic phytoplankton species composition changed from that reported for the 1970s (Schelske and Stoermer 1972; Rockwell et al. 1980; Bartone and Schelske 1982). Using the assemblage scheme of Reynolds (1984) as a convenient summary, spring and early summer remain unchanged. Initially the system is dominated by diatoms characteristic of B and C assemblages (e.g. *Melosira* spp., *Tabellaria* spp., with lesser amounts of *Asterionella formosa, Fragilaria crotonensis*) and then by phytoflagellates of assemblage Y (*Cryptomonas, Rhodomonas*) and assemblage E (*Dinobryon, Mallomonas*). In the 1970s, the phytoflagellates were succeeded by a community dominated by colonial greens and blue-greens characteristic of Reynolds' H and M assemblages (e.g. *Anabaena* spp., *Microcystis*). However, these species abruptly disappeared after 1982 and the community of 3–30 μm phytoflagellates of assemblage Y continued to dominate through the summer (Fahnenstiel and Scavia 1987a). Thus, the 1970s Lake Michigan phytoplankton seasonal succession followed B/C ⟶ E/Y ⟶ H/M, while the early 1980s pattern followed B/C ⟶ E/Y ⟶ Y.

(5) Measures of summer water clarity (Secchi depth, transmissivity, photosynthetically active radiation) appear to have improved gradually between 1975 and 1982, but also have improved more abruptly after 1982 (Scavia et al. 1986). Summer Secchi depth averaged 7.0 ± 1.3 m between 1975 and 1982, but averaged 11.1 ± 1.4 m during 1983–86 (Scavia and Fahnenstiel 1988).

We believe that alterations in phytoplankton and zooplankton species composition were caused either by (1) reduced P loading and/or (2) reduced predation on large zooplankton due to declining alewife abundance (Scavia et al. 1986; Scavia and Fahnenstiel 1987; Fahnenstiel and Scavia 1987a). We tested these hypotheses by constructing a model of phytoplankton–zooplankton–nutrient interactions, calibrating it to conditions (concentrations and process rates) observed in the early 1980s (Scavia et al. 1986; Fahnenstiel and Scavia 1987a, 1987b, 1987c; Scavia and Fahnenstiel 1987), and subjecting it to a range of zooplanktivory under the influence of two P-loading scenarios. The simulation analysis tests whether the model, calibrated to conditions and species mixtures of the 1980s, could reproduce the trend (backward) of species changes representative of a summer complex comprising blue-green and colonial green algae and calanoid copepods under the relatively heavy alewife predation of the mid-1970s.

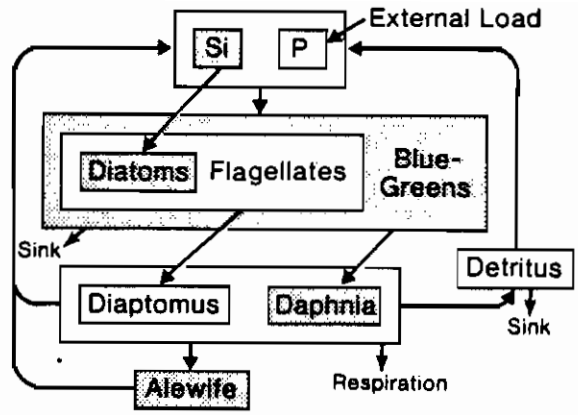

FIG. 1. Schematic of major pathways in model designed to simulate nutrient cycles and biomass flow among competing phytoplankton and zooplankton groups. Arrows represent major pathways; some are omitted for clarity. Nested boxes are used to show selective grazing pathways. For example, all algal groups are consumed by *Daphnia* whereas only flagellates and diatoms are consumed by *Diaptomus*.

Methods and Modeling Rationale

The Model

There is increasing evidence that pelagic models based on functional (e.g. Reynolds 1984) or size-grouped (e.g. Sheldon et al. 1982; Sprules et al. 1983) components offer advantages over traditional models of individual species (O'Neill et al. 1986). Changes that have occurred in Lake Michigan since the 1970s are adequately described by functional classes and we were intrigued by the possibility of exploring hypothesis on competition and predation with such an approach. Figure 1 details the functional categories of plankton used in the model.

Our approach incorporated both empirical principles correlated with size and biomass (Peters 1986) and experimentation that accounts for the specificity of functional groups expressed by parameters derived from species interactions (Lehman 1986). For example, cladoceran grazing rates and body size are related (e.g. Peters and Downing 1984); however, clear differences for cladocerans versus calanoid copepods (Knoechel and Holtby 1986a, 1986b) must be preserved. Hence, we separated zooplankton into these functional groups. Our algal functional groups were derived similarly from analysis of observed successions (Reynolds 1984) and growth rates (Sommer 1981) and from practical definitions for ecosystem models (Scavia 1979a).

In general, the model simulates competition among phytoplankton and zooplankton groups, each subject to differential grazing pressure. Algae and detritus are grazed and sedimented; algal growth is nutrient dependent. The zooplankton gain mass through food-dependent ingestion and lose mass through defecation, respiration, and fish predation. Inefficient alewife and zooplankton grazing provides input to detritus and available P pools. All ingested Si is routed directly to the detrital pool. Zooplankton P release is assumed proportional to respiration. Detrital Si settles and dissolves; detrital C and P settle and slowly decompose to available forms. Phytoplankton and zooplankton concentrations and fluxes are simulated in terms of C; associated nutrient fluxes are traced subject to a constant mass Redfield ratio (P:C = 0.024). Equations simulating these first-order processes leading to gains and losses of each modelled component are listed in Table 1. Some detailed aspects of those equations and their rationales follow.

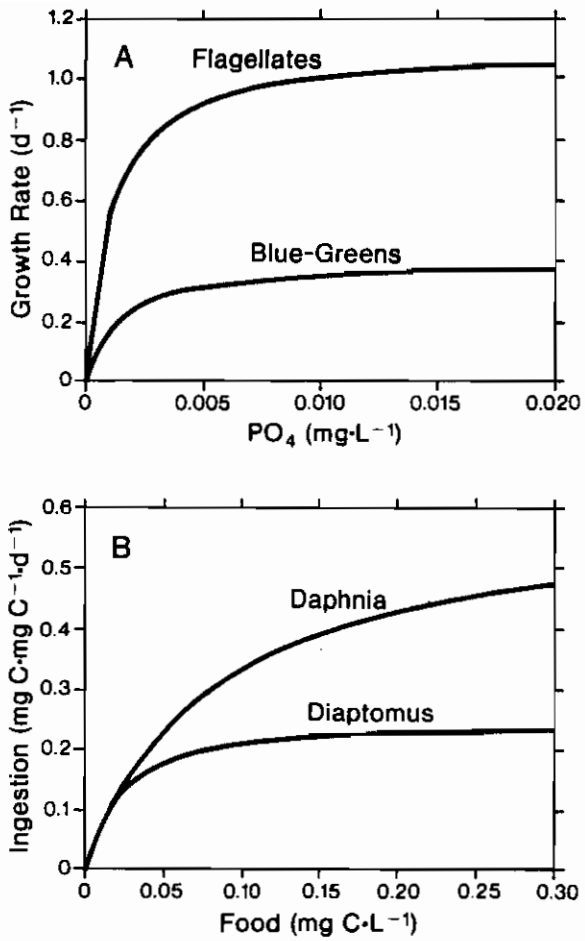

FIG. 2. Defining relationships for (A) phytoplankton and (B) zooplankton competition for resources. Both are represented as Monod responses to substrate or food concentration and the governing parameters are listed in Tables 2 and 3. For perspective, Lake Michigan summer epilimnion soluble reactive P concentrations are below 1.0 $\mu g \cdot L^{-1}$, total algal C is 20–40 $\mu g \cdot L^{-1}$, and particulate organic C is approximately 200 $\mu g \cdot L^{-1}$.

Our model of the offshore summer epilimnion assumes constant optimal light and temperature. Horizontal and vertical transport are not critical factors in the summer epilimnion (Scavia and Fahnenstiel 1987; Fahnenstiel and Scavia 1987b, 1987c); therefore, we ignore them.

During 1975–84, P loads decreased (DePinto et al. 1986). We included analyses for the high available-P load of the mid-1970s (0.0055 $\mu g\ P \cdot L^{-1} \cdot d^{-1}$) and the low load for 1981–82 (0.0035 $\mu g\ P \cdot L^{-1} \cdot d^{-1}$), based on estimates summarized by Rodgers and Salisbury (1981) and Lesht (1984) for a southern basin epilimnion volume of $4.28 \times 10^{11}\ m^3$.

Phytoplankton

Phytoplankton growth rate (μ) was modelled as a maximal rate (μ_m) scaled by the lesser of two growth-limiting factors, one for Si (diatoms only) and one for P (all groups);

$$(1) \quad \mu = \mu_m \cdot \mathrm{MIN}\{P/(K_p + P),\ Si/(K_{Si} + Si)\}.$$

Maximal growth rates and half-saturation constants (K) were generated from measured rate constants for species representative of our three modelled groups (Table 2). Diatoms are usually Si limited during summer both in the lake (Fahnenstiel and Scavia 1987a) and in our simulations. Competition for P between the two P-limited groups is illustrated in Fig. 2 for our kinetic constants. We used constant group-specific phytoplankton settling velocities, also drawn from several reviews (Table 2).

TABLE 1. Model equations.

State variable		Model equation
Phytoplankton	$\frac{dA}{dt}$	$= (\mu - s)A - gZ$
	A	= phytoplankton concentration
	μ	= growth rate (see text equation (1))
	s	= settling loss
		= sinking rate/epilimnion depth
	g	= zooplankton grazing (see text equation(2))
	Z	= zooplankton concentration
Zooplankton	$\frac{dZ}{dt}$	$= (g - r)Z - P$
	r	= respiration (see text equation(3))
	P	= fish predation
		= specific ration · alewife biomasses
Detrital C	$\frac{dC}{dt}$	$= B \cdot E - (d + s) \cdot C - gZ$
	C	= detrital C concentration
	B	= particulate fraction of unassimilated food
	E	= zooplankton egestion
		= (1 − assimilation efficiency)·ingestion
	d	= mineralization rate
Available P	$\frac{dP}{dt}$	$= PC \cdot [\Sigma rZ + (1 - B) \cdot E - \Sigma \mu A + d \cdot C]$
	P	= available P concentration
	ΣrZ	= zooplankton respiration
	$\Sigma \mu A$	= phytoplankton production
	PC	= P:C ratio
Available Si	$\frac{dSi}{dt}$	$= d_s \cdot S_d - SC \cdot \mu_d A_d$ *S
	Si	= available Si concentration
	S_d	= detrital Si concentration
	d_s	= dissolution rate
	μ_d	= diatom growth rate
	A_d	= diatom concentration
	SC	= Si:C ratio
Detrital Si	$\frac{dS_d}{dt}$	$= SC \cdot E_d - (d_s + s) \cdot S_d$
	E_d	= egested silica

Zooplankton

Zooplankton grazing rates (g) are based on saturation kinetics for feeding and the "effective food concentration" (EFC) construct of Vanderploeg et al. (1984):

$$(2) \quad g = g_m \cdot \mathrm{EFC}/(K + \mathrm{EFC})$$

where g_m is the maximal weight-specific ingestion rate and K is the half-saturation constant. The EFC is defined as $\Sigma W'_i X_i$,

TABLE 2. Properties of modelled algal groups. Each set of values from the literature represents the mean, standard deviation (in parentheses), and number of species included in the mean.

Parameter	Diatoms	Flagellates	Blue-greens	Source
Maximal growth rate (d^{-1})	1.09(0.42)6	0.82(0.01)2	0.79(0.46)10	Reynolds 1983
	0.73(0.23)28	—	0.57(0.22)5	Tilman et al. 1982
	1.47(0.37)17	0.79(0.11)4[a]	—	Sommer 1983
		1.18(0.27)6	—	Reynolds et al. 1982
	0.8–1.8	1.0–1.4	<0.7	Reynolds 1984
	1.5	*1.1*	*0.4*	Used in this study
Monod constants				
$\mu g\ P \cdot L^{-1}$	3.0(5.0)11	—	0.8(0.4)4	Tilman et al. 1982
	2.5	*1.0*	*1.3*	Used in this study
$mg\ Si \cdot L^{-1}$	0.11(.014)25	—	—	Tilman et al. 1982
	0.10	*0*	*0*	Used in this study
Sinking rates ($m \cdot d^{-1}$)	1.2(0.7)2	0.01(0.004)3	—	Fahnenstiel and Scavia 1987a
	1.0(0.4)7	0.0	0.04(0.004)	Sommer 1984
	0.5(0.3)9	0.0	—	Reynolds and Wiseman 1982
	1.0(1.3)37[b]	—	—	Wetzel 1983
	0.8	*0.05*	*0.05*	Used in this study

[a]Values are likely low due to mechanical hampering.
[b]Used minimal and maximal values to calculate averages when ranges were reported.

TABLE 3. Properties of modelled zooplankton groups.

Parameter	*Daphnia*	*Diaptomus*	Source
Maximal ingestion rate ($mg\ C \cdot mg\ C^{-1} \cdot d^{-1}$)	0.71	0.2	Muck and Lampert 1984
	0.86	—	Olsen et al. 1986
	0.61[a]	—	Peters and Downing 1984
	0.84[b]	—	Peters and Downing 1984
	0.2–0.3	—	Porter et al. 1982
	—	0.2	Vanderploeg et al. 1984
	—[c]	—[c]	Knoechel and Holtby 1986a
	—[c]	—[c]	Knoechel and Holtby 1986b
	0.60	*0.25*	Used in this study
Half-saturation constant ($mg\ C \cdot L^{-1}$)	0.12	0.01–0.05	Muck and Lampert 1984
	0.05–0.10	—	Porter et al. 1982
	—	0.02	Vanderploeg et al. 1984
	0.08	*0.02*	Used in this study

[a]From body weight regression assuming 10 μg dry weight and 1 $mg\ C \cdot L^{-1}$ food.
[b]From body weight regression assuming 30 μg dry weight and 5 $mg\ C \cdot L^{-1}$ food.
[c]Clearance rates on algae and bacteria were 5–10 times lower for calanoid copepods of the same size as comparable cladocerans in the cited report.

where W'_i is the selectivity coefficient for food source i with concentration X_i (Vanderploeg and Scavia 1979).

While the mathematical form of the relationshp between zooplankton ingestion and food concentration is arguable (Mullin et al. 1975; Porter et al. 1982), we use equation (2) which is similar to the Monod expression for phytoplankton growth. Maximal weight-specific ingestion rates and half-saturation constants, based largely on the works of Porter et al. (1982), Muck and Lampert (1984), Peters (1984), Peters and Downing (1984), Vanderploeg et al. (1984), and Olsen et al. (1986), are listed in Table 3 and are illustrated in Fig. 2.

Equation (2) estimates ingestion of all prey by a given predator. Loss rates for an individual prey item i are estimated from the product of equation (2) and the weighted diet portion attributable to prey i, $W'_iX_i/\Sigma W'_iX_i$. The rationale for selectivity coefficient (W'_i) values acknowledges that the phytoflagellates (3–30 μm) are within the size range of high preference for both calanoid copepods (Vanderploeg 1981; Vanderploeg et al. 1984) and *Daphnia* (Gliwicz 1980; Knisely and Geller 1986); thus, they are a most preferred prey ($W'_i = 1$). Both calanoids and *Daphnia* can ingest some diatoms (Knisely and Geller 1986; H. A. Vanderploeg, GLERL/NOAA, pers. comm.) and were thus assigned W'_i values of 0.5. The dominant calanoids (*Diaptomus* spp.) are highly selective against filamentous prey (Vanderploeg 1981; Hartmann 1985); *Daphnia* are not (Porter et al. 1982; Richman and Dodson 1983). We assigned a W'_i of 0.5 for colonial greens and blue-greens grazed by *Daphnia* and 0.1 for grazing by the calanoids.

Assimilation efficiencies were assumed to be 50% on all algal foods (48%, Comita 1972; 75%, Porter et al. 1982; 50%, Peters 1983; 50%, Parsons et al. 1984, 38%, Peters and Downing 1984) and 10% on detritus. Because zooplankton respiration rate is generally higher for well-fed animals than for starved ones (Porter et al. 1982; Lampert 1984; Parsons et al. 1984), we estimated respiration (r) as proportional to the ingestion function of equation (2):

(3) $r = r_1 + r_2 \cdot \mathrm{EFC}/(K + \mathrm{EFC})$.

Maximal respiration rates generally fall in the range of 0.1–0.4 mg C·mg $C^{-1} \cdot d^{-1}$ (Porter et al. 1982; Richman and Dodson 1983; Lampert 1984; Parsons et al. 1984; Lynch et al. 1986) with rates for well-fed animals typically 1.2–3.0 times higher than starved ones (Porter et al. 1982; Lampert 1984; Parsons et al. 1984). We use maximal rates of $0.25 \cdot d^{-1}$ for *Daphnia* and $0.11 \cdot d^{-1}$ for *Diaptomus*. The difference between *Daphnia* and *Diaptomus* respiration rates reflects different behavioral and feeding modes (Porter et al. 1982) as well as observations of body C loss under low food conditions (Muck and Lampert 1984).

Fish Predation

The functional underpinnings of alewife predation are not well understood. Nonetheless, we estimate, in a general way, the magnitude of alewife predation with a time-tested (Rice and Cochran 1984; Bartell et al. 1986) approach based on a bioenergetics model of alewife population structure and diets observed during 1976. The original energetics parameters were those developed by Stewart (1980) and modified by Stewart and Binkowski (1986).

From June through August of 1976, lake-wide mean feeding rates were estimated as 1.76×10^7 kg of zooplankton prey consumed per day. With summer alewife biomass of 7.6×10^7 kg (Stewart 1980) the mean daily ration becomes $(1.76/7.6) = 0.23 \cdot d^{-1}$, which is higher than that for other fishes, due to high feeding rates by juveniles (Stewart 1980; Kitchell 1983). We held this ration constant during simulations and varied alewife biomass to mimic its changing impact over time (see below).

Alewife prey selection was based on studies of prey preferences, foraging behavior, and optimal foraging theory (Morsell and Norden 1968; Webb and McComish 1974; Rhodes and McComish 1975; Janssen 1978; Janssen and Brandt 1980; Wells 1980; Crowder et al. 1981). The model treats alewife as a size-selective predator with preferences of major prey ordered as macroinvertebrates (*Mysis* and *Pontoporeia*) > cladocerans >> copepods. A biomass model such as ours can only include diet ontogeny by weighting selectivity coefficients. These coefficients can be derived as estimates of prey preference from forage ratios based on the fraction of prey *i* biomass in the summer diet (r_i) divided by the portion of prey *i* biomass in the available plankton (p_i) (Vanderploeg and Scavia 1979). From field studies conducted during the mid-1970s (Stewart 1980), diets of alewife (r_i) were 30% copepods, 20% cladocerans, and 50% hypolimnetic *Mysis* and *Pontoporeia*. During these survey years, *Daphnia* comprised only about 10–15% of the total zooplankton biomass (net hauls through top 40 m; Scavia et al. 1986); the remainder was dominated by calanoid copepods. Sufficient data are not available to estimate accurately the biomass concentration of *Mysis* and *Pontoporeia* available to alewife during those years; however, we can make certain estimates. *Pontoporeia* are likely not available to offshore (100-m depth contour) alewife during summer because the invertebrate is benthic and the alewife planktonic. Thus, the major macroinvertebrate prey is likely to be *Mysis*. Sell (1982) estimated its abundance to vary between 0.1 and 1.11 g dry weight·m^{-2} in Lake Michigan. Assuming a migratory behavior that places *Mysis* within a 15-m band available to alewife for about 6 h per day (Bowers and Grossenickle 1978) and a C : dry weight ratio of 0.5 yields a C concentration averaging 5.1 $\mu g \cdot L^{-1}$. This value is not unlike that for *Daphnia* during the mid-1970s (Scavia et al. 1986). If we assume that macroinvertebrate abundance ranged between being equal to the cladocerans and twice the cladocerans, then relative p_i estimates are 85–90, 5, and 5–10% for copepods, cladocerans, and the hypolimnetic invertebrates, respectively. Setting the largest W'_{ij} to 1.0 and scaling the rest for convenience results in values of 0.03–0.07, 0.4–0.8, and 1.0 for copepods, cladocerans, and *Mysis*; we used 0.05, 0.5, and 1.0 in the model.

TABLE 4. Lake Michigan summer epilimnion conditions measured in 1983–84 (Data from Scavia and Fahnenstiel 1987; Fahnenstiel and Scavia 1987a, 1987b, 1987c; Scavia et al. 1986).

Property	Concentration or rate
Algal growth rates	0.1–0.4 d^{-1}
Algal production	12.9 ± 2.2 $\mu g\ C \cdot L^{-1} \cdot d^{-1}$
Algal biomass	20–40 $\mu g\ C \cdot L^{-1}$
	Flagellate dominance
Algal sedimentation	0.02–0.45 $\mu g\ C \cdot L^{-1} \cdot d^{-1}$
Zooplankton grazing	8.7 ± 2.5 $\mu g\ C \cdot L^{-1} \cdot d^{-1}$
Zooplankton biomass	20–35 $\mu g\ C \cdot L^{-1}$
	Daphnia dominance

Simulated zooplankton loss rates were calculated from the product of alewife biomass, daily ration, and diet proportion ($W'_i X_i / \Sigma W'_i X_i$), where X_i is the concentration of prey *i*. We assume a constant pool of hypolimnetic prey equivalent to 5.0 $\mu g\ C \cdot L^{-1}$.

Nutrient Cycles

Available P concentration was determined by a balance between phytoplankton uptake, detritus mineralization ($0.01 \cdot d^{-1}$), and alewife and zooplankton release. A portion of food ingested but not assimilated by alewife and zooplankton was shunted to detritus, with the remaining portion shunted immediately to available nutrient pools. We assumed that 50% of egested P becomes available immediately to algae on the time scale of our simulations. Available Si concentration was determined by the balance between diatom uptake and detrital Si dissolution. In addition, all Si ingested by zooplankton was immediately placed in the detrital Si pool.

Calibration

For the calibration data set, we relied primarily on measurements made during the Lake Michigan Ecosystem Experiment of 1983–84 (Scavia et al. 1986; Scavia and Fahnenstiel 1987; Fahnenstiel and Scavia 1987a, 1987b, 1987c). The field experiment was designed to measure rates of phytoplankton growth and sedimentation and zooplankton grazing, as well as temporal and spatial variation of nutrients and phytoplankton and zooplankton species composition. The current state of southeastern Lake Michigan, based on the 1983–84 field seasons, is summarized in Table 4. For cases where comparable process rates were not determined empirically for Lake Michigan, we used published values from other lakes to establish bounds on model expectations.

Calibration consisted of varying coefficient values within ranges expected for Lake Michigan phytoplankton and zooplankton assemblages (Tables 2 and 3) until the model reproduced both measured state variables *and* process rates measured in the 1980s. Because coupled nonlinear differential equations such as the ones used here do not have unique solutions, it is possible to arrive at similar state-variable simulations with very

different sets of coefficient values, and thus, rates (Scavia 1979b, 1980, 1983). Therefore, requiring accurate reproduction of both state variables *and* process rates should minimize compensating rate-process errors and produce a reasonable model caricature of Lake Michigan ecosystem dynamics.

The nine differential, mass-balance equations describing ecosystem dynamics (Table 1) were solved numerically using a forward-difference Euler scheme with a time step of 2.4 h. Model output was stored every 25 d and simulations were run until competition results were clearly defined (usually 300 d, see below).

Alewife Impact Scenario

Lake Michigan alewife were first reported in 1949 (Smith 1970). The population expanded exponentially until a major overwinter mortality in 1966–67 and thereafter remained generally at less than half its peak abundance. Recently, alewife abundance has further decreased (Wells 1985). Although stock assessments and estimates of local variability exist, no unequivocal quantitative measures are available for lake-wide alewife abundance (Eck and Brown 1985). The alewife's distribution is highly patchy; they school, migrate vertically, and generally aggregate (vertically and horizontally) near the edges of the metalimnion during summer (Crowder et al. 1981). Abundance peaks near the 20 to 30-m depth contour and decreases exponentially offshore toward the region of the 100-m contour (Brandt 1980), the area we attempt to simulate. Hence, it is difficult to determine the absolute effective biomass impacting the epilimnion in our region of interest.

Initial model analyses demonstrated that we could not reproduce plankton dynamics observed at the 100-m contour under the grazing pressure imposed using the high lake-wide average alewife biomass estimates of the 1970s (75 000 Mt; Wells and Hatch 1985). For alewife biomasses above 15 000 Mt, simulated zooplankton and phytoplankton relative species composition remained constant; but total zooplankton biomass was reduced to unrealistically low levels, phytoplankton biomass increased to unrealistically high levels, and process rates were far below those observed. Given these results and the uncertainties on biomass impact estimates discussed above, we restricted our analyses to a range of lake-wide alewife biomasses from 0 to 15 000 Mt and explored species changes along the relative alewife biomass gradient.

Assuming an equal north–south distribution, an alewife C : wet weight ratio of 0.15 and a strictly epilimnetic existence, this range is equivalent to 0–2.64 $\mu g\ C \cdot L^{-1}$. Because it is difficult to assign an alewife biomass level to a particular set of years, we simulated the entire zooplanktivory gradient for each of the two P-loading scenarios: one reflecting conditions of the mid-1970s (0.0055 $\mu g\ P \cdot L^{-1} \cdot d^{-1}$) and one of the early 1980s (0.0035 $\mu g\ P \cdot L^{-1} \cdot d^{-1}$).

Uncertainty Analysis

We recognize the difficulty in justifying any one set of coefficient values used in the model, even though they fall within observed ranges and produce internally consistent and reasonably faithful reproduction of measured state variable and process rates. To explore the robustness of our simulations, we performed Monte Carlo analyses including 14 model coefficients as the random variables. We generated 300 sets of random and independent coefficient values, drawn from a 14-variate normal distribution (International Mathematical and Statistical Libraries subroutine GGNSM). Each coefficient was assigned a mean value equal to the value used in the deterministic simulation and a standard deviation equal to 10% of its mean. While 10% may not represent the true extent of coefficient variability, it is sufficient to use here to evaluate overall model sensitivity. A simulation was run for each set of coefficient values resulting in 300 time series for each state variable; we analyzed results at 300 d into the simulation, the same as for the deterministic model. Monte Carlo results were similar when more than 300 cases were used.

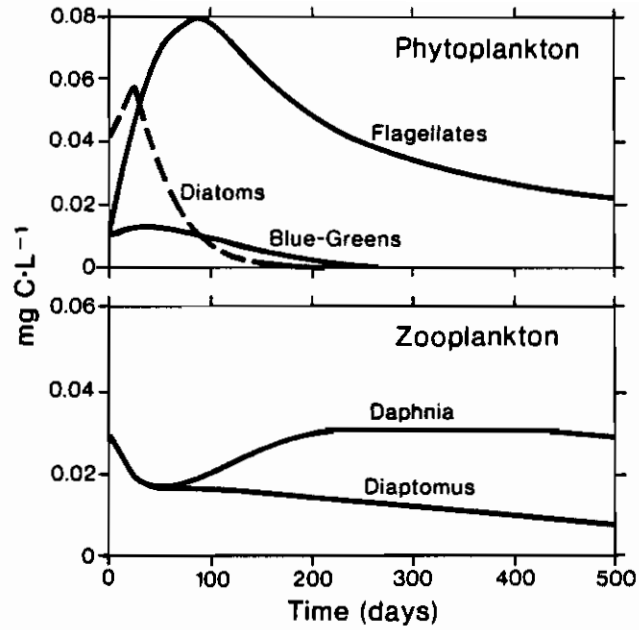

FIG. 3. Typical model output for simulation of competition among phytoplankton and zooplankton groups under low alewife abundance and low P load. Each simulation displays a transient response followed by slow development toward steady state. We use results at 300 d into the simulation throughout the analysis (see text).

Results

Deterministic Simulations

As expected for solution of differential equations with constant inputs, each simulation (Fig. 3) began with a transient response followed by a more stable period approaching steady state. While transient responses are influenced strongly by initial conditions, steady-state responses are independent of those starting values, depending only on the nature of the equations and values of the coefficients and inputs. Because very different transient responses can be effected with different starting values, and because we do not know starting values, we used simulation results clearly beyond the influence of the initial conditions (e.g. after 200 simulation days, Fig. 3).

In theory, as well as in continuous-culture competition experiments (e.g. Tilman 1982) with only one potentially limiting nutrient, one species will exist at steady state. While our analyses have two potentially limiting nutrients (P, Si), heavy sedimentary losses inflicted on the Si-limited diatoms essentially eliminate them from the summer competition. As a result, two species (modelled flagellate and blue-green groups in this case) are always left to compete for P and the model always predicts complete dominance by one of the two groups at steady state (usually after 400–500 simulation days). However, Lake Michigan is not a continuous culture and steady conditions rarely persist. It is not realistic therefore to expect

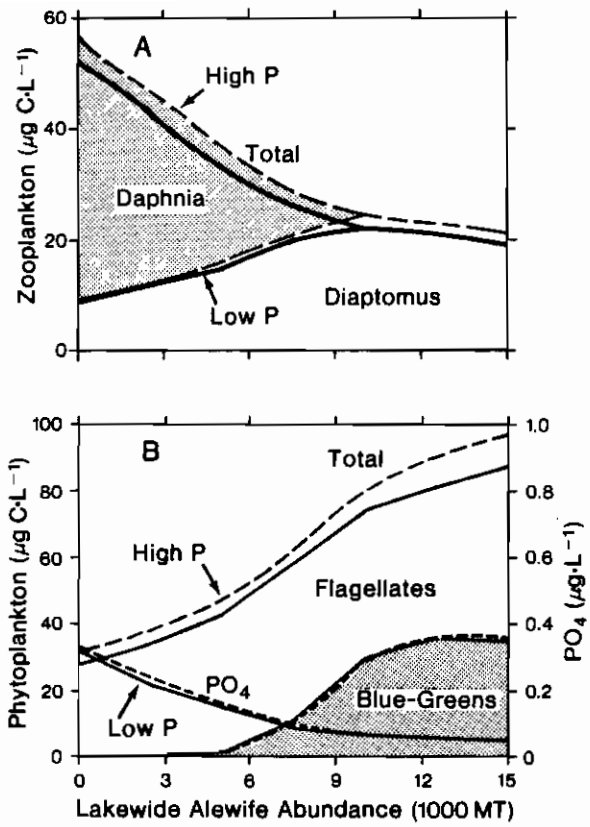

FIG. 4. (A) Simulated zooplankton biomass (total and groups) as a function of P load (high, broken line; low, solid line) and alewife abundance. The relative contribution of *Daphnia* to total biomass diminishes as alewife abundance increases. (B) Simulated total phytoplankton (total and groups) and PO_4 concentration as a function of P load (high, broken line; low, solid line) and alewife abundance. Flagellate concentration remains relatively constant, while blue-greens increase at higher alewife abundances.

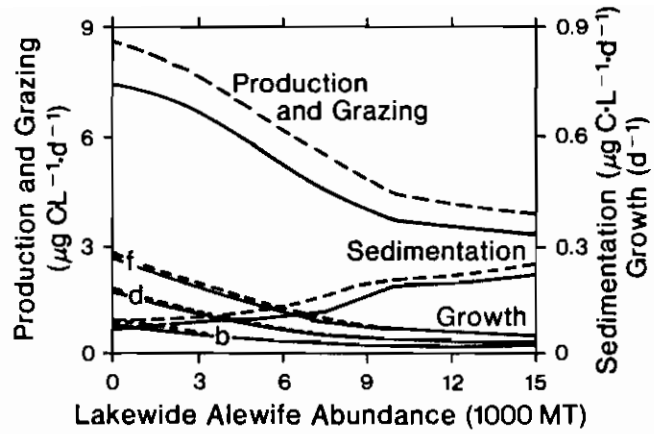

FIG. 5. Simulated phytoplankton production (≈ zooplankton grazing), sedimentation, and algal growth rates (f = flagellates, b = blue-greens, d = diatoms) as a function of P load (high, broken line; low, solid line) and alewife abundance. As alewife abundance increases, algal growth rates decrease and the importance of sinking, relative to grazing, increases.

the lake ever to be at steady state nor to run the model until those conditions prevail. We use 300 d into the simulation for our comparisons of alewife and P-load impacts. This is a reasonable compromise because, at this point in all simulations, the model is no longer under the influence of the transient response and the outcome of the competition is clear. Selecting time points further toward model steady state will only influence the abundance of total plankton; the overall trends in composition are unaffected.

Simulation days are not to be confused with actual days in the sense of time to reach steady state. The analysis does not suggest a time scale to steady state on the order of 1 yr (300 d) because the duration of the transient response is controlled by the extent to which the initial conditions deviate from steady state. For example, if we chose initial conditions exactly equal to the steady-state response, there would have been no transients.

Results of model runs for a range of zooplanktivory are summarized as response-surface plots (Fig. 4–7) of plankton abundances and process rates versus alewife abundance for the two P-load scenarios. Total zooplankton biomass is slightly higher under the higher P load for all levels of alewife abundance; however, the overall impact of alewife is much larger (Fig. 4A). As we increase alewife biomass, total zooplankton biomass decreases; more importantly, composition changes from *Daphnia* dominance to *Diaptomus* dominance.

Total phytoplankton biomass increases with increasing alewife biomass over this range of alewife abundance (Fig. 4B); the responses at both P loads are similar. Phytoplankton composition changes as well. The flagellate dominance under low alewife levels is replaced by an assemblage composed of flagellates (approximately 60%) and blue-greens (approximately 40%) under high alewife levels. Available P concentrations decrease at higher alewife levels (Fig. 4B), with the implication that more P is tied up in phytoplankton biomass.

As alewife abundance increases and P concentrations decrease, primary production and phytoplankton growth rates both decrease (Fig. 5). Although phytoplankton biomass increases, the lower growth rates controlled by lower P concentrations and the shift to slower growing blue-greens yield lower epilimnetic primary production rates. Growth rates decrease sevenfold over the full range of zooplanktivory; primary production decreases only twofold. Sedimentation loss rates increase from about 0.10 $\mu g\ C \cdot L^{-1} \cdot d^{-1}$ with no alewife predation to about 0.24 $\mu g\ C \cdot L^{-1} \cdot d^{-1}$ under maximal alewife biomass at the higher P load. Sedimentation increases from 0.07 to 0.22 $\mu g\ C \cdot L^{-1} \cdot d^{-1}$ for the low P load.

Because sedimentary losses are small during summer, model net primary production is nearly balanced by zooplankton grazing. Calculated ingestion minus defecation and respiration yield model estimates of zooplankton secondary production (Fig. 6A). Total zooplankton production increases as alewife abundance increases, but appears to level off at biomass levels above 5000 Mt. *Daphnia* production decreases as their contribution to total zooplankton biomass decreases. At low levels of zooplanktivory, *Diaptomus* is actually a negative contributor to secondary production (Fig. 6A). Under these conditions, *Daphnia* flourish and drive phytoplankton concentrations below the level that allow *Diaptomus* to survive. This result can be seen most readily in terms of relative production to biomass ratios (net growth) for the two groups at different levels of zooplanktivory (Fig. 6B). It is not until alewife abundance reaches approximately 5000 Mt and total phytoplankton C reaches approximately 40 $\mu g\ C \cdot L^{-1}$ that *Diaptomus* ingestion rates exceed egestion and respiration losses. Beyond that, they grow but still slowly relative to *Daphnia*.

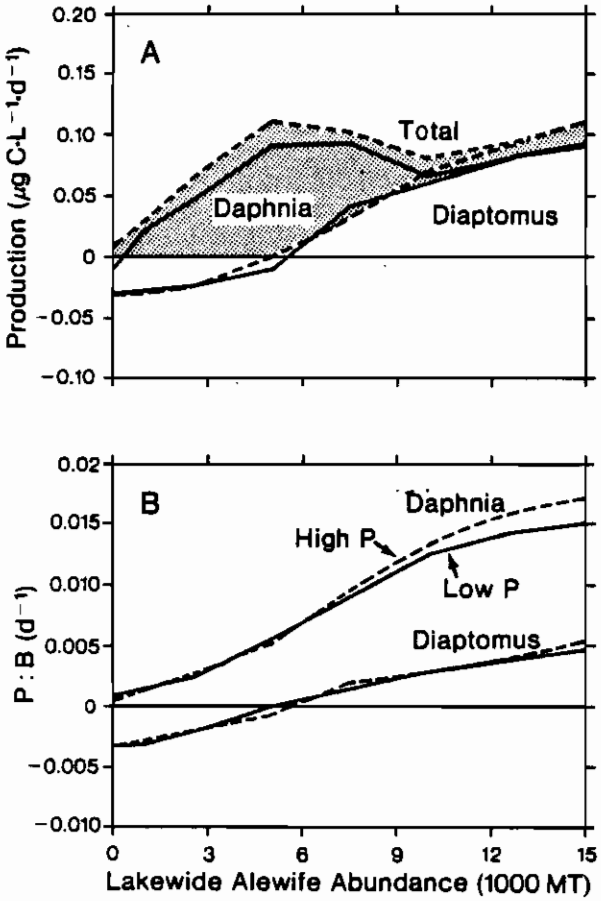

FIG. 6. Simulated zooplankton (A) secondary production and (B) production to biomass ratios as a function of P load (high, broken line; low, solid line) and alewife abundance. This suggests that during summer in Lake Michigan's epilimnion, *Daphnia* is always the superior competitor and only selective losses can shift the dominance toward *Diaptomus*.

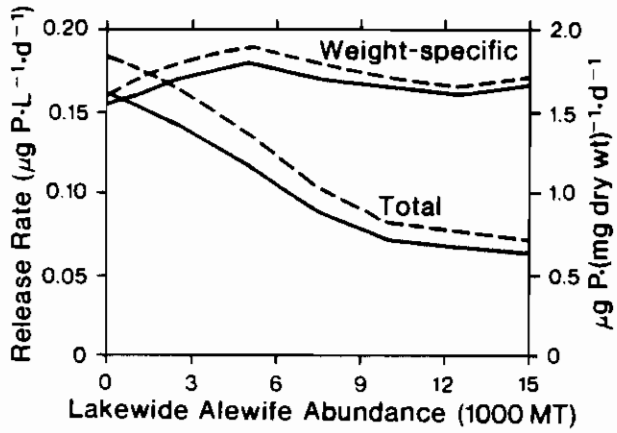

FIG. 7. Total and weight-specific zooplankton P regeneration rates as a function of P load and alewife abundance.

Phosphorus recycling by zooplankton is the major P supply supporting phytoplankton production. The decreased supply rate at higher alewife abundance (Fig. 7) reflects mostly decreased total zooplankton biomass (Fig. 4A). As excretion rates are tied to group-specific rates of grazing and respiration, however, weight-specific excretion rates also varied as the phytoplankton and zooplankton assemblage compositions changed (Fig. 7).

Summary of Model Results

In general, several ecosystem properties show dramatic changes along the predation gradient, whereas only small changes are evident when comparing results from the high and low P-load scenarios. As alewife abundance increases, (1) total zooplankton biomass decreases and the composition shifts from *Daphnia* dominance to *Diaptomus* dominance (Fig. 4A), (2) total phytoplankton biomass increases and the composition changes from dominance by flagellates to a mixture of flagellates and blue-greens (Fig. 4B), (3) primary production and zooplankton ingestion rates decrease and are nearly equal to each other (Fig. 5), (4) phytoplankton growth rates decrease more dramatically than production rates, (5) sedimentation rates increase but are never an important component of phytoplankton dynamics, (6) P regeneration by zooplankton (Fig. 7) and available P concentrations (Fig. 4B) decrease, and (7) zooplankton secondary production and growth rates increase (Fig. 6), with *Diaptomus* growth rates varying from negative to positive though always below *Daphnia* growth rates. These simulated changes are similar to those described for Lake Michigan during changing abundances of alewife. Thus, the model appears to reproduce the cascading influence of zooplanktivory on the Lake Michigan food web.

Uncertainty Analysis

For error analysis, we chose model coefficients considered to be most uncertain, most critical to the analysis, or both; phytoplankton maximal growth rates and half-saturation constants for P-limited growth; zooplankton maximal ingestion rates, half-saturation constants for ingestion, and respiration rates; and the selectivity coefficients for zooplankton on bluegreens and for alewife on zooplankton. We report medians (Fig. 8) for the Monte Carlo results because the distributions of model output were strongly skewed, as was the case in analysis of a similar model (Scavia et al. 1981). While the Monte Carlo medians differ from the deterministic projections described above (Fig. 4), the overall trends and shifts in plankton composition are the same. In 19 of the 20 cases (i.e. 4 state variables at 5 alewife abundances), the deterministic simulations fall within 12.5% of the medians. (Those ± 12.5% limits are shown in Fig. 8). We interpret the fact that the deterministic solutions are similar to the stochastic medians to mean that the deterministic simulations we presented above are rather robust.

However, to what extent are the deterministic simulations realistic representations of Lake Michigan ecosystem dynamics as opposed to simple mathematical exercises?

Discussion

Comparison with the 1980s

Our first task is to evaluate whether model results under conditions of low alewife abundance are similar to those observed during 1983–84 (Table 4). Lake Michigan summer phytoplankton concentrations ranged between 20 and 40 μg C·L⁻¹ (Scavia and Fahnenstiel 1987), averaging over 80% as phytoflagellates (range = 70–90%) (Fahnenstiel and Scavia 1987a). These conditions are reproduced by the model for alewife biomass levels below 5000–7500 Mt. Summer zooplankton concentrations ranged between 20 and 35 μg C·L⁻¹ (Scavia and Fahnenstiel 1987), with C assumed to be 50% of dry weight, although there has been little observable systematic variation over the past 10 yr (mean = 40 μg C·L⁻¹,

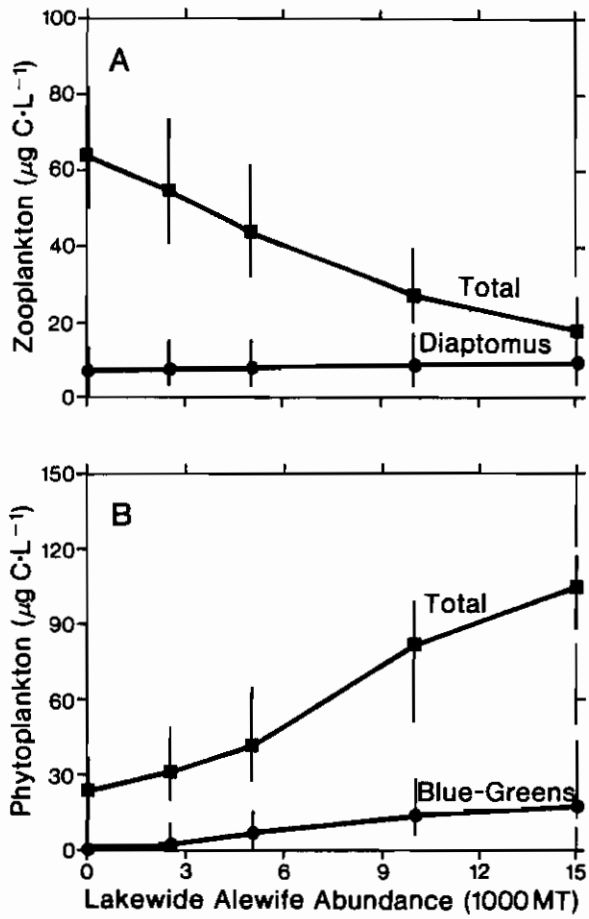

FIG. 8. Medians of Monte Carlo simulations of phytoplankton and zooplankton concentration as functions of alewife abundance at low P load. Deterministic simulations (see Fig. 4) generally fall within ±12.5% of the medians, shown here as error bars.

SD = 10.8; Scavia et al. 1986). During the early 1980s, however, *Daphnia* contributed about 70–90% to crustacean biomass. These conditions are reproduced by the model for alewife levels between 2500 and 5000 Mt.

Models can reproduce concentrations of ecosystem variables, yet severely under- and overestimate rates of material flow (Scavia 1980). As an example, summer phytoplankton dynamics are controlled by a balance between growth and grazing loss. Growth is controlled by the P supply, which is largely determined by zooplankton regeneration. Because P regeneration in the model (and likely in nature) is tightly coupled to zooplankton ingestion, both phytoplankton growth and loss rates are influenced strongly by zooplankton. It is easy to imagine situations where algal growth and zooplankton grazing both could be low or high and the resulting rate of algal biomass change be the same. Thus, we could get the right results (state-variable concentrations) for the wrong reasons (compensating rate processes). So, we must compare modelled and measured rates.

Measured production and loss rates from the 1983–84 field seasons are comparable in magnitude for much of the summer, although some unaccountable algal loss may have been evident (Scavia and Fahnenstiel 1987). Because the only loss included in the model (other than grazing) was sedimentation and because sedimentation rates were low (both in the model, 0.07–0.24 μg $C \cdot L^{-1} \cdot d^{-1}$, and in the field experiments, 0.02–0.45 μg $C \cdot L^{-1} \cdot d^{-1}$; Scavia and Fahnenstiel 1987), model estimates of phytoplankton net production and zooplankton grazing are in close balance. Net epilimnetic production averaged 12.9 μg $C \cdot L^{-1} \cdot d^{-1}$ (SE = 2.2, N = 8) and zooplankton grazing averaged 8.7 μg $C \cdot L^{-1} \cdot d^{-1}$ (SE = 2.5, N = 5) during 1983–84. These primary production estimates are somewhat higher than those simulated by the model, but the grazing rate estimates are similar to model results reproduced with alewife abundances less than 5000 Mt. Estimates of algal summer growth rates typically fall between 0.1 and $0.4 \cdot d^{-1}$ (Fahnenstiel and Scavia 1987b), consistent with predictions with alewife biomass below 5000 Mt.

Less is known specifically about Lake Michigan zooplankton processes. While our estimates of phytoplankton ingestion are similar to those determined in the field, we must rely on estimates from other environments for comparisons of secondary production, zooplankton growth, and P excretion. Secondary production is relatively constant (0.1 μg $C \cdot L^{-1} \cdot d^{-1}$) for model evaluations above 2500 Mt of alewife. Primary production varies between 3 and 6 μg $C \cdot L^{-1} \cdot d^{-1}$ over this range, yielding 1.7–3.3% transfer efficiencies for these herbivores. While these values appear somewhat low (5–15% might be expected, Wetzel 1983), they are within the ranges reported across several freshwater environments (13–15%, Blazka et al. 1980; 0.1–27.4%, Brylinsky 1980; 1.7–14%, Winberg 1980).

Production to biomass ratios (*P:B*) are another way to evaluate the validity of model calculations. Our daily *P:B* ratios range from -0.002 to $+0.003 \cdot d^{-1}$ for *Diaptomus* and from 0.003 to $0.013 \cdot d^{-1}$ for *Daphnia* between alewife abundances of 2500 and 10 000 Mt. These values, like the transfer efficiencies above, are similar to those at the lower end of recent summaries (0.003–0.30, Morgan et al. 1980; 0.001–0.17, Winberg 1980). Also, our simulated difference between *Daphnia* and *Diaptomus* is consistent with the generalization that *P:B* ratios for cladocerans are higher than those for calanoid copepods, even at cold temperatures (see Fig. 6.4e in Morgan et al. 1980).

Model analysis suggests that P recycling by zooplankton decreased with higher alewife abundance; however, because weight-specific rates were less variable, the trend was actually a reflection of decreased zooplankton abundance. Weight-specific rates varied between 1.6 and 1.9 μg $P \cdot mg\ dry\ wt^{-1} \cdot d^{-1}$ (assuming 0.5 g $C \cdot g\ dry\ weight^{-1}$). These values are well within the range expected for freshwater crustaceans (Lehman 1980; Wetzel 1983).

The above sets of comparisons between model and experimental results suggest that the model reasonably represents pelagic ecosystem structure and function in Lake Michigan. It reproduces observed state-variable concentrations and process rates using model equations and coefficients drawn from empirical studies. While the model does not contain the richness of the natural environment with respect to potential responses to variations in driving forces, it can be considered a caricature of the lake. In this respect, the simplified version of nature can be perturbed numerically with its responses being indications of the directions nature may take.

Top-down control

The above comparisons demonstrate that model simulations, with alewife equivalent to lake-wide abundance of 2500–5000 Mt, are consistent with measured ecosystem components and processes during the 1980s. The model also reproduced plankton composition changes consistent with those observed over

the period 1975–84 (Fig. 4). The simulated changes to the 1970s composition occurred for alewife equivalent to lake-wide abundance of 10 000 – 12 500 Mt, a three- to five-fold increase over the estimates used for simulation of the 1980s. While the absolute alewife abundances that we used are lower than current lake-wide assessments (see above), estimates from those assessments did change by about a factor of 4 during the period 1975–84 (Wells 1985). Thus, the model reproduces the conditions of the 1980s *and* the observed transitions over the previous decade within the confines of observed relative changes in alewife abundance. This result was accomplished with model constructs and coefficients drawn from empirical evidence (Tables 1–3). Because changes in species make-up was reproduced by varying alewife abundance only, we conclude that the transitions of the 1975–84 period were likely driven mainly from the top of the food web.

The nature of this top-down control can be dissected further by inspecting other model calculations. Analysis of *Daphnia* and *Diaptomus* growth rates (Fig. 6) under the conditions prescribed by modelled ingestion, egestion, and respiration (Table 3, above) suggests that Lake Michigan has always been a "*Daphnia* lake" with regard to competition for food; *Diaptomus* growth rates are always lower than those for *Daphnia*. This suggestion places Lake Michigan within the region of *Daphnia* dominance suggested by Richman and Dodson (1983) in their graphical model of *Daphnia*–calanoid competition along food quality/quantity gradients. We suggest that the transition from the 1970s to 1980s represents movement within that region rather than across its boundaries. The phytoplankton composition of the 1970s in Lake Michigan was not as low quality, for example, as that of inner Green Bay (Richman and Dodson 1983) nor of Lake Washington in its eutrophic state (Edmondson and Litt 1982). During the 1970s, Lake Michigan summer epilimnion chlorophyll concentrations were typically 1 $\mu g \cdot L^{-1}$ or less (Scavia et al. 1986) and blue-green and colonial green algae comprised 50–70% of total algal mass (Fahnenstiel and Scavia 1987a). This biomass is equivalent to approximately 20 $\mu g\ C \cdot L^{-1}$, calculated from data presented by Bartone and Schelske (1982). In contrast, summer chlorophyll concentrations were between 4 and 24 $\mu g \cdot L^{-1}$ in Lake Washington during the period (1965–75; Edmondson and Lehman 1981) when *Daphnia*'s major predator, *Neomysis mercedis*, was absent but *Daphnia*'s populations were limited by elevated blue-green abundance (Edmondson and Litt 1982). Total blue-green abundance during the summers of those years was likely between 400 and 800 $\mu g\ C \cdot L^{-1}$ (applying 1 g wet weight$\cdot cm^{-3}$ and a C : wet weight ratio of 0.1 to phytoplankton data reported in Edmonson and Litt 1982). In southern Green Bay, Lake Michigan, where blue-green algae dominate during summer and *Daphnia* appear to have difficulty competing with *Diaptomus* (Richman and Dodson 1983), summer average chlorophyll concentrations range between 20 and 80 $\mu g \cdot L^{-1}$ (Auer et al. 1986). These conditions are also more extreme than those found even in the 1970s in southern Lake Michigan. While excessive blue-green filament populations are apparently detrimental to *Daphnia*, we suggest that moderate concentrations are not as harmful; it is only when selective alewife predation increased *Daphnia* mortality compared with *Diaptomus* that the latter could succeed.

Why did Lake Michigan blue-greens decrease at lower alewife abudances? It is clear from the empirical evidence input to the model and from the literature (Table 2; Sommer 1981) that blue-green filaments have lower intrinsic growth rates than phytoflagellates (Fig. 5). Because both groups are subject to minimal sinking losses, it is only when grazing imparts selective losses against the flagellates that blue-greens outcompete them. During periods of *Diaptomus* dominance, the calanoids activity select against collecting the filaments and select for the competing flagellates. During periods of *Daphnia* dominance, grazing losses are more evenly distributed and the filaments lose ground to the faster growing flagellates. While the wider trophic niche (Infante and Edmondson 1985) for *Daphnia* could be either a disadvantage (Porter and Orcutt 1980; Infante and Abella 1985) or an advantage (Infante and Edmondson 1985), it is a disadvantage for the blue-green filaments, unless the filaments become so abundant that they interfere seriously with *Daphnia*'s food gathering (Gliwicz 1980) or increase its metabolic losses (Porter and McDonough 1984). As discussed above, with moderate filament population sizes in Lake Michigan, the cladoceran seems to effectively reduce the blue-green's success by increasing the alga's mortality rate over that imposed by the diaptomid community.

The future: potential impact of new invertebrate predator

A potential epilimnetic invertebrate predator, *Bythotrephes cederstroemi*, has been recently reported in Lakes Ontario, Erie, Huron, and Michigan (Bur et al. 1986; Lange and Cap 1986; G. L. Fahnenstiel and H. A. Vanderploeg, GLERL/NOAA, per. comm.). Invertebrate predation can have important consequences for plankton community structure. To evaluate potential invertebrate impacts for Lake Michigan, we added an invertebrate predator to the model. We used model coefficient values characteristic of *Bythotrephes*: a constant clearance rate (4 L$\cdot$mg dry weight$^{-1} \cdot d^{-1}$; H. A. Vanderploeg, unpubl. data) and a maximal respiration rate (0.2 mg C$\cdot$mg dry weight$^{-1} \cdot d^{-1}$) based on N and P excretion rates (0.9 μg N$\cdot$mg dry weight$^{-1} \cdot h^{-1}$, 0.2 μg P$\cdot$mg dry weight$^{-1} \cdot h^{-1}$; W. S. Gardner, GLERL/NOAA, unpubl. data) and assumed elemental mass ratios typical of zooplankton (C : dry weight = 0.5, C:N = 4.0, C:P = 75; Parsons et al. 1984). Respiration half-saturation constant was set to 0.12 mg C$\cdot L^{-1}$ and we assumed that *Bythotrephes* would be a favored fish prey (W'_i = 1.0). If *Bythotrephes* prefers *Daphnia* over *Diaptomus*, as preliminary data suggest (H. A. Vanderploeg, unpubl. data), the model predicts that increased *Bythotrephes* abundance will cause Lake Michigan's plankton to return to a community similar to that of the 1970s with *Diaptomus*-dominated zooplankton and a substantial filamentous blue-green component in the phytoplankton.

Conclusion

Our analysis suggests that, while Lake Michigan responded to the approximately 35% P-load reduction, the response to altered zooplanktivory was much greater. These results are important to Lake Michigan water quality management as well as to the larger context of a controversy currently emerging among ecologists and limnologists. As argued by McQueen et al. (1986), the trophic state of a lake system may play a role in the relative importance of food-web interactions. This conclusion derives from analysis based on comparative studies (i.e. regression analyses of among-lake variation) and is valid in that perspective, but it does not address questions often before the researcher or manager. Those questions pertain to the potential behavior of a particular lake and/or a subset of similar lakes. At that scale, the properties of dominant species and their inter-

actions appear to become critical. In Lake Michigan, the role of large *Daphnia* is the critical component. In fact, the relative abundance of large *Daphnia* is key to most theoretical and experimental food web studies reported to date (see Carpenter et al. 1985; McQueen et al. 1986; Carpenter et al. 1987).

Although we have evaluated the importance of nutrient loading and food-web interactions as a dialectic (i.e. as competing hypotheses), that approach may be less constructive than a hierarchical one (Allen and Starr 1984; Carpenter and Kitchell 1987). Nutrient loading obviously determines the basic trophic state of a system. Within the variation of annual nutrient loads, food-web interactions in Lake Michigan regulate nutrient cycling and the composition of the plankton community. Strong effects on community composition continue to cascade from fisheries management practices and the interactions among exotic species in Lake Michigan. While anthropogenic actions may evoke equally important and unexpected effects on food webs elsewhere, it is clear that we have only begun to develop the conceptual and analytical skills required to understand, anticipate, and effectively manage the role of food web interactions. These skills will only improve through aggressive, integrated experimental and theoretical research programs.

Acknowledgments

We thank our colleagues, B. J. Eadie, G. L. Fahnenstiel, T. D. Fontaine, W. S. Gardner, R. Knoechel, H. A. Vanderploeg, and an anonymous reviewer for their helpful comments and suggestions. J.F.K. was supported, in part, by grants from the Great Lakes Fishery Commission and the University of Wisconsin Sea Grant Program.

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