

APPLICATION OF A MODEL OF ZOOPLANKTON
COMPOSITION TO PROBLEMS OF FISH INTRODUCTIONS
TO THE GREAT LAKES

BY

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APPLICATION OF A MODEL OF ZOOPLANKTON COMPOSITION TO PROBLEMS OF FISH INTRODUCTIONS TO THE GREAT LAKES

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INTRODUCTION

Size-selective predation by fishes on zooplankton, as well as the species composition of both herbivores and algae, has recently drawn the most attention in discussions of biological control of algal production. Current papers have regarded changes involving the succession toward smaller forms as an adjustment to fish predation (Allan 1974, Dodson 1974). Such a strategy includes high probability for small adult size at age of first reproduction as a developmental factor of major importance (McNaught 1975). However, little attention has been given to the seasonality of predatory intensity in determining the relative abundance of zooplankton prey over a growing season. The relative importance of size-selection by fishes as well as the effects of the nonuniform seasonal inshore distribution of fish predators both upon zooplankton composition and abundance will be examined using a simple two-equation model.

Size-selective feeding by zooplankton upon phytoplankton, in contrast, may determine species success in an oligotrophic environment. In low nutrient situations where small nannoplankton dominate, those calanoid copepods that are small-particle specialists may likewise dominate (McNaught 1975), chiefly because they have a high efficiency for removing

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small algal cells (Bogdan and McNaught 1975). Within such a genus (*Diaptomus*) of small-cell specialists characteristic of the Great Lakes, those which give birth at the smallest size (*Diaptomus minutus*) may be most successful. In some instances zooplankton production, but not species composition, may be correlated with food abundance, as in fishponds (Hall, *et al.* 1970). In other instances zooplankton production may be tied to fish predation, while species composition is related chiefly to fish predation and then to algal food composition, as we suspect to be true in the Great Lakes and in most aquatic environments.

THE MODEL

As we have suggested, the availability of phytoplankton and detrital food resources (R_i), the selectivity or preference of the zooplankton for these foods (WZ_{ji}), and size-selective predation by fishes (fish biomass times selectivity) are some of the inputs necessary to simulate zooplankton succession. Predation by fishes (Figure 11.1) dominates, especially in determining which species of zooplankton succeed, while algal productivity influences how many of each species are present. The real-time output of the model is easily used by the modeler to determine when the system has reached steady-state, the principal criterion in determining when to examine community composition (the output provides estimates of zooplankton and resource numbers at predetermined intervals), as readily observed in Figure 11.2. Both in nature, and in these mathematical simulations, steady-state conditions occur when the birth rate is equal to the death rate of a species, where both natural and predation related deaths are considered.

In our simulations, once steady-state has been reached, it persists indefinitely (Figure 11.2, day 121-day 601 for the copepod) because food resources and predation are fixed. In nature, changing food production and predatory pressures, as well as natural cycles of reproduction, limit steady-state conditions to brief periods. Likewise, in nature maximum standing crops of zooplankton usually occur at the time of steady-state. Thus we have used simulated densities at steady-state (Figure 11.2) to simulate the standing crop of a species.

The following equations have been used to model zooplankton dynamics (Equation 11.1) and the production of algal and detrital food resources (Equation 11.2).

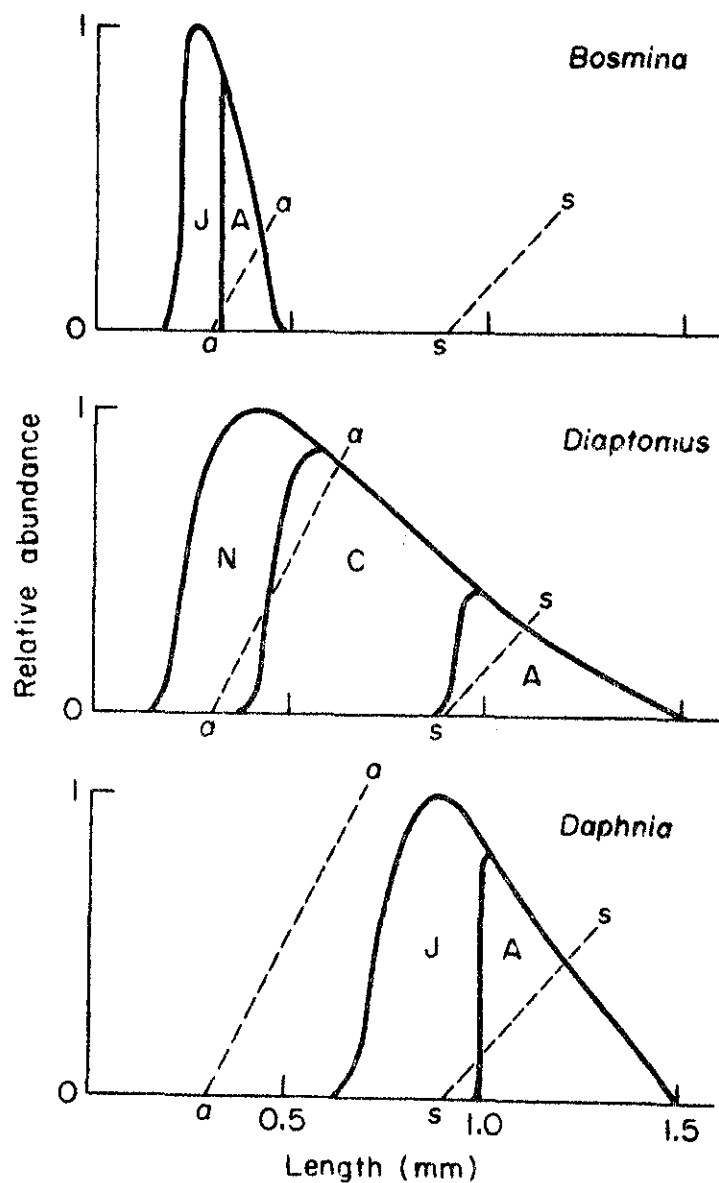


Figure 11.1 Pictorial representation of size structure of populations of *Bosmina longirostris*, *Diaptomus minutus* and *Daphnia galeata*, and relative number and size of each available to fine-filtering alewife (to right line a-a) and coarse filtering salmonids (right line s-s). (J = juveniles, A = adult, N = nauplii, C = copepodites).

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MODEL PARAMETERS

BZ= .500 .500 .500 .500 .500 .500 .500 .500 .500 .500
WZ= .40 .33 .33 .17 .33 .33 .47 .01 .01 1.00 1.00 1.00
E= .400 .170 .470
DZ= .140 .140 .140 PZ= .13+002 .13+002 .13+002
BEZ= .18-007 .36-008 .18-007 .36-008 .18-007 .36-008
PSZ= .070 .030 .100
MDA= .200+004 .200+004 .200+004 MR= .560+009 .212+010 .230
+011
RMIN= .15+005 .75+005 .75+005 .30+003 .15+004 .15+004
.30+003 .30+003 .30+003 .00 .00 .00
QZ= .100+008 .100+008 .100+008 .100+003 .100+003
PCHIN= .140 .090 .900
CMAX= 7. ALPHA= .999 PE= .35000 .35000 .35000
INPUT:
>PRI
INITIAL CONDITIONS
BIDMIC= .100+004 .100+004 .100+004
.100+009 .100+009 .100+009 .165-001
TFIRST= 1.00 TLAST=601.00 STEP=30.000 ACCUPC=.00500 IMAX=10
INPUT:
>INT

TIME	COPE	CLAD1	CLAD2	NANNO	NET	PDM
1	.100+004	.100+004	.100+004	.100+009	.100+009	.100+009
31	.434+003	.252+003	.417+003	.358+009	.230+009	.185+010
61	.416+003	.200+003	.357+003	.324+009	.488+009	.147+011
91	.418+003	.202+003	.376+003	.355+009	.399+009	.224+011
121	.420+003	.214+003	.420+003	.359+009	.137+010	.230+011
151	.420+003	.227+003	.483+003	.360+009	.173+010	.230+011
181	.421+003	.239+003	.564+003	.360+009	.194+010	.230+011
211	.421+003	.248+003	.663+003	.360+009	.204+010	.230+011
241	.421+003	.254+003	.792+003	.360+009	.209+010	.230+011
271	.421+003	.259+003	.923+003	.360+009	.211+010	.230+011
301	.421+003	.261+003	.109+004	.360+009	.211+010	.230+011
331	.421+003	.263+003	.129+004	.360+009	.212+010	.230+011
361	.421+003	.264+003	.152+004	.360+009	.212+010	.230+011
391	.421+003	.265+003	.180+004	.360+009	.212+010	.230+011
421	.421+003	.265+003	.181+004	.360+009	.212+010	.230+011
451	.421+003	.265+003	.181+004	.360+009	.212+010	.230+011
481	.421+003	.266+003	.181+004	.360+009	.212+010	.230+011
511	.421+003	.266+003	.180+004	.360+009	.212+010	.230+011
541	.421+003	.266+003	.191+004	.360+009	.212+010	.230+011
571	.421+003	.266+003	.180+004	.360+009	.212+010	.230+011
601	.421+003	.266+003	.181+004	.360+009	.212+010	.230+011

Figure 11.2 Simulation for Lake Michigan for inshore alewife biomass of 414 kg/ha during May 1972, producing simulations shown in Table 11.4.

Zooplankton Equations

$$\frac{dN_j}{dt} = \text{births}_j - \text{deaths}_j - \text{predatory deaths}_j - \text{metabolic costs}_j \quad (11.1)$$

where

$$\text{births}_j = \sum_i BZ_j \cdot N_j \left(\frac{WZ_{ji} (R_i - RMIN_{ji})}{QZ_j + \sum_i WZ_{ji} (R_i - RMIN_{ji})} \right) \quad (11.1a)$$

$$\text{deaths}_j = DZ_j \cdot N_j \quad (11.1b)$$

$$\text{deaths}_{\text{predatory}_j} = CMAX \cdot N_f [WZ_{fj} (N_j - NMIN_{fj})] \cdot \text{size} \quad (11.1c)$$

$$\text{size} = \begin{cases} 1 & \text{where } N_j/MDA_j > 1 \\ 0 & \text{where } N_j/MDA_j < PCMIN_j \\ \text{or } 1 - \left[\frac{\alpha}{1-PCMIN} \right] \left[1 - \frac{N_j}{MDA_j} \right], & \text{in all other cases} \end{cases} \quad (11.1d)$$

$$\text{metabolic costs} = (S_j + E_j)N_j \quad (11.1e)$$

Abbreviations for Zooplankton Equations

- N_j = zooplankton standing crop (no/m³)
- N_f = fish standing crop (no/m³)
- $RMIN_{ji}$ = minimum level of resource i for feeding by consumer j (cells/m³)
- WZ_{ji} = selectivity index for consumer j upon food resource i
- QZ_j = half-saturation constant for feeding by consumer j (cells/m³)
- BZ_j = intrinsic birth rate of zooplankter j (ind/ind/day)
- DZ_j = intrinsic death rate of zooplankter j (ind/ind/day)
- $CMAX$ = maximum foraging area of fish per day (m²/fish/day)
- $NMIN_{fj}$ = minimum level of zooplankton j for feeding by fish f (no/m³)
- MDA_j = density of zooplankton j population at which all organisms are mature (no/m³)
- $PCMIN$ = per cent of MDA necessary to originate feeding by fish f
- S_j = respiratory rate for zooplankter j (l/day)
- E_j = excretory rate for zooplankter j (l/day)
- α = per cent of CMAX not achieved when fish consumption begins at PCMIN

Resource Equations

$$\frac{dR_i}{dt} = \text{growth}_i - (\text{grazing}_{\text{clad}} + \text{grazing}_{\text{cope}}) \quad (11.2)$$

where

$$\text{growth}_i = \text{PSZ}_i \cdot R_i \cdot \left\{ 1 - \frac{R_i}{\text{MR}_i} \right\} \quad (11.2a)$$

$$\text{grazing}_{\text{clad}} = \sum_j \text{BEZ}_j \cdot N_j \cdot (R_i - \text{RMIN}_{ji}) \quad (11.2b)$$

$$\text{grazing}_{\text{cope}} = \sum_j \text{FZ}_j \cdot N_j \cdot \frac{\text{WZ}_{ji}(R_i - \text{RMIN}_{ji})}{\text{QZ}_j + \sum_i \text{WZ}_{ji}(R_i - \text{RMIN}_{ji})} \quad (11.2c)$$

Abbreviations for Resource Equations

R_i	= resource standing crop (cells/m ³)
N_j	= zooplankton standing crop (no/m ³)
PSZ_i	= turnover rate of resource i (1/days)
MR_i	= maximum resource level in temperate eutrophic lake (cells/m ³)
BEZ_j	= filtering rate of cladocerans (m ³ /ind/day)
RMIN_{ji}	= minimum level of resource i for feeding by consumer j (cells/m ³)
FZ_j	= feeding rate of copepods (cells/ind/day)
WZ_{ji}	= selectivity index for consumer j upon food resource i
QZ_j	= half-saturation constant for feeding by consumer j (cells/m ³)

Zooplankton population growth by species and thus relative community composition is controlled by instantaneous rates of birth, natural death, metabolic costs and above all by fish predation. Birth rates are maximum only with high food levels (R_i); at lower food concentrations food controls birthing. Below minimum food levels (RMIN), the individual species cannot harvest the relatively rare resource and birthing does not proceed. We have assumed that the relation between food and birth rate can be described by a modified Michaelis-Menton expression (Equation 11.1a). Food does not stimulate birthing unless it is plentiful (exceeds RMIN_{ji}), and is preferred by the grazer (high WZ_{ji}). The assumption that increased amounts of food stimulate birthing has been demonstrated for *Daphnia galeata* by Hall (1964) and others.

Fish predation is proportional to the population density of fishes (N_f), and a function of zooplankton species and density. Size selective predation

is the major control factor (Equation 11.1d). This construct is based on the following assumptions: (1) the percentage of young in a population is proportional to the ratio of the observed density (N_j) to an all adult density (MDA_j), and (2) when the population reaches a certain percentage ($PCMIN$) of MDA_j , the organisms are large enough for predation to begin at some low rate, where $N_j/MDA_j > PCMIN$, and increase until the zooplankton density reaches MDA_j and consumption reaches $CMAX$. Since size-selective fish predation is based upon the percentage ($PCMIN$) of the ultimate adult population that must be achieved before predation commences, $PCMIN$ is a particular characteristic of each species of fish predator relative to zooplankton composition. Since the model, and hopefully the real aquatic world, is controlled chiefly by predation from the top of the trophic pyramid, this parameter deserves further attention.

The susceptibility of populations of zooplankton to predation can be visualized with regard to $PCMIN$ (Figure 11.1). This vital parameter, describing size-selection by alewife and trout, was determined by plotting the size distributions (McNaught, unpublished) of the three common crustacean zooplankters being simulated, considering the selectivity by alewife (Allan 1974) and trout (Galbraith 1967), and calculating graphically the *per cent* of the adult population of appropriate size-structure unavailable to alewife (14, 9 and 90%) and trout (94, 89 and 99%) of the three crustaceans, *Diaptomus*, *Daphnia* and *Bosmina*, respectively. As depicted in Figure 11.1, selectivity begins with zooplankters 0.3 mm in length and is maximum at lengths greater than 0.7 mm in the case of the alewife (Allan 1974), while the onset is at 0.9 mm and the maximum begins at 1.6 mm in the case of trout (Galbraith 1967). Thus the slope of lines a-a and s-s (Figure 11.1) indicates the increased efficiency at which both predators capture larger animals.

The resources, nanoplankton, netplankton and detritus, are controlled by turnover rates (PSZ), which drive these standing crops toward preset maximum levels (MR). In addition, these resources are controlled by grazing. Copepods (PZ) and cladoceran plankters (BEZ) have been modeled to filter and ingest food rather differently to simulate their described feeding behavior. Each has a food preference (WZ_{ji}) and a minimum food level ($RMIN_{ji}$) at which feeding commences. The term WZ_{ji} thus represents the palatability and susceptibility to capture of a particular resource by a consumer (O'Neill 1969). This concept is particularly useful in describing zooplankters that exhibit selective feeding, but could also be employed to provide a (mathematical) sanctuary for distasteful or otherwise unavailable prey from fish predators. In a similar fashion, fish-feeding commences at a minimal zooplankton level ($NMIN_{jf}$) and is linear with abundance. For further details of the constructs of this model consult the detailed description (McNaught and Scavia 1975).

Calibration of the Model

This resource allocation-predation model for zooplankton community composition has been calibrated (Table 11.1) for a large inland lake (McNaught and Scavia 1975). The details of the experiments and observations involved in calibration can be found elsewhere. However, it is vital for the reader to understand the extent to which we went to either find or make original determination of parameters describing zooplankton physiology and behavior. This initial calibration has not been altered for either the Lake Ontario or Lake Michigan simulations. Thus results of these simulations, compared to observed densities of zooplankton, have enabled us to *validate* a previously *calibrated* model.

The necessary parameters may be divided into two groups. The first includes system parameters, which describe the maximum biotic potential of a species. These are presented in Table 11.1; it must be understood that these are maximum estimates for the rate functions involved as well as the parameters describing submaximum behavior. The second group is the lake parameters, which vary by degree of eutrophication and include the turnover rate of the food resources (*PSZ*) and the abundance or biomass of fish predators (*BIOMIC*).

VALIDATION USING LAKE MICHIGAN PARAMETERS

Once the model had been calibrated to produce reasonable simulations of zooplankton density by species for a large inland lake (Lake George, New York) (McNaught and Scavia 1975), the organismic characteristics, such as maximum birth rate, ingestion rates, and natural death rates, were held constant. That is, once calibration was completed, these characteristics of the biotic potential of *Diatomus*, *Daphnia galeata*, and *Bosmina longirostris* should describe these species under all environmental conditions. Simulations of zooplankton composition in various ecosystems thus require only a knowledge of the turnover times for food resources (nannoplankton, netplankton and detritus) and the biomass (*BIOMIC*) and characteristics of size selectivity (*PCMIN*) of the major fish predators.

Turnover Rates for Algal and Detrital Food Resources

Limited estimates for the rate of primary productivity ($\text{mgCm}^{-3} \text{day}^{-1}$) and the standing crop of algae in terms of carbon (mgCm^{-3}) are available for Lake Michigan. The most extensive seasonal study of primary productivity is that of Fee (1973), while the best seasonal estimates of algal carbon are those of Robertson, *et al.* (1971). From such shipboard estimates of primary productivity, made during 1970, and corresponding

Table 11.1 Values and Sources of Parameters used in Calibration of Zooplankton Model^a

Parameter	Units	Genera of Zooplankton			Source
		Diaptomus	Daphnia	Bosmina	
BZ	ind ind ⁻¹ day ⁻¹	0.5	0.5	0.5	Hall 1964, McNaught unpublished
DZ	ind ind ⁻¹ day ⁻¹	0.14	0.14	0.14	Allan 1974
PZ	cells anim ⁻¹ day ⁻¹	0.13 x 10 ²	—	—	Bogdan and McNaught 1975
BEZ	m ³ anim ⁻¹ day ⁻¹	—	0.18 x 10 ⁻⁷	0.36 x 10 ⁻⁸	Bogdan and McNaught 1975
WZ	—	(nanno) 0.40	0.33	0.33	Bogdan and McNaught 1975
	—	(net) 0.17	0.33	0.33	Bogdan and McNaught 1975
	—	(detritus) 0.47	0.01	0.01	Bogdan and McNaught 1975
RE	ind ind ⁻¹ day ⁻¹	0.35	0.35	0.35	LaRow 1973
RMIN	cells m ⁻³	(nanno) 0.15 x 10 ⁵	0.75 x 10 ⁵	0.75 x 10 ⁵	Richman 1966, McMahon & Rigler 1963
	cells m ⁻³	(net) 0.3 x 10 ³	0.15 x 10 ⁴	0.15 x 10 ⁴	Richman 1966, McMahon & Rigler 1963
	cells m ⁻³	(detritus) 0.7 x 10 ³	0.3 x 10 ³	0.3 x 10 ³	Richman 1966, McMahon & Rigler 1963
NMIN	no. m ⁻³	0	0	0	this chapter
PCMIN	%	(alewife) 14	09	90	this chapter
	%	(trout) 94	89	99	this chapter
CMAX	m ³ anim ⁻¹ day ⁻¹	7	7	7	calculated from stock
QZ	cells m ⁻³	1 x 10 ⁷	1 x 10 ⁷	1 x 10 ⁷	Hall 1964
MDA	no. m ⁻³	2000	2000	2000	from literature
MR	cells m ⁻³		nannoplankton 5.6 x 10 ⁸		from literature
	cells m ⁻³		net plankton 2.1 x 10 ⁹		from literature
	cells m ⁻³		detritus 2.3 x 10 ¹⁰		from literature

^aFor abbreviations of parameters see text.

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standing crops of algal carbon (C) made in 1969, we have estimated resource turnover rates for the entire algal assemblage (Table 11.2). These doubling-times ranged from 8 to 22 days during May and August. From these estimates of turnover time (days) we calculated the instantaneous rates (days^{-1}) shown in Table 11.2. In running all simulations, we then assumed that nanoplankton turnover more rapidly than netplankton (ca. 2:1). We have also assumed that rates of primary productivity in Lake Michigan were unchanged between 1966 and 1972 and identical to those measured by Fee (1973) in 1970.

Table 11.2 Estimates of Forcing Functions for Simulation of Zooplankton Composition of Lake Michigan^a

Month and Location	Rate of Primary Productivity		Algal Carbon (mgC m^{-3})	Turnover (T) (days)	1/T (day^{-1})
	($\text{mgC m}^{-2} \text{d}^{-1}$)	($\text{mgC m}^{-3} \text{d}^{-1}$)			
May 1970					
Inshore	1188 ^b	29.7	222 ^c	7.5	0.134
Offshore	450 ^b	11.2	210 ^c	18.8	0.053
August 1970					
Inshore	425 ^b	10.6	181 ^c	17.1	0.059
Offshore	317 ^b	7.9	172 ^c	21.8	0.046

^aTurnover rates for phytoplankton and detrital resources (PSZ)

^bFee 1973.

^cRobertson, et al. 1971.

Biomass of Predatory Alewife

The alewife, *Alosa pseudoharengus*, is the specific planktivore whose effect upon zooplankton has been modeled simply because of its overwhelming impact on the Lake Michigan ecosystem (Wells 1970). But because of our general knowledge concerning the dominance of salmonids and especially coregonines prior to 1954 (Beeton 1969), we have also attempted to arrive at biomass estimates for salmonids characteristic of pre-1954 levels. We have not attempted to calibrate the model for the coregonidae, as the model will currently accept only one predatory fish. However, a common coregonid, the bloater (*Coregonus hoyi*) is chiefly a nonplanktonic feeder as an adult (Wells and Beeton 1963).

Fortunately the Great Lakes Fishery Laboratory of the U.S. Fish and Wildlife Service has made yearly estimates of alewife abundance, utilizing a standard series of trawls off Saugatuck, Michigan, to arrive at an estimate of lakewide biomass, which has ranged from 191 kg/ha at the peak abundance during the spring of 1967 (lakewide = 1.1 billion kg) to a low of 23 kg/ha following the massive die-off in late 1967 and 1969 (Brown 1972). In addition, the horizontal distribution of alewives is beginning to be understood. Age-classes III-VII move inshore in April (Wells 1968) in Lake Michigan, certainly inside the 54.7 m (30 fathom) contour, whereas age-classes I-II remain more uniformly distributed. Later in August, the younger alewife (I) prefers inshore waters, but the bulk of the population is more uniformly dispersed. Based on these observations of Wells (1968), we have made estimates of the biomass of alewives inshore (<54.7 m) and offshore (> 54.7 m) during May and August, because such inshore spawning aggregations most likely have a profound effect on the relative numbers of zooplankton selectively cropped. Thus, as with zooplankton, standing crops of the alewife are well documented in Lake Michigan, especially with regard to inshore abundance, but with limited knowledge of open water populations. Unfortunately, we have only records of commercial catches for the salmonids.

Biomass of Predatory Salmonids Prior to 1954

Accurate lakewide estimates of salmonid standing stocks prior to 1954 are not currently available. Approximately 7.7×10^6 kg of lake herring, lake trout and whitefish were harvested commercially from Lake Michigan in 1949. By 1960, the commercial yield of these three salmonids had decreased to 0.08×10^6 kg (Beeton 1969). In simulating the predatory pressures of salmonids upon the zooplankton, we have arbitrarily assigned a biomass of 100-145 kg/ha, certainly crude at best. This is based upon the fact that standing crops of phytoplankton in 1954 were 43% of those in 1958 (Damann 1960) and 31% of those in 1963 (Damann, unpublished).

Results of Simulation of Species Composition for Lake Michigan

Using available estimates of algal productivity (Table 11.2) and predatory alewife biomass (Table 11.3), we have simulated the relative abundance of the dominant crustaceans *Diaptomus* spp, *Daphnia galeata* and *D. retrocurva*, and *Bosmina longirostris*, for the four major periods in which alewife abundance varied greatly. The alewife appeared in Lake Michigan in 1949 (Smith 1972). The pre-1954 simulation (Table 11.4) is characteristic of this period, during which salmonid predators prevailed.

Table 11.3 Estimates of Forcing Functions for Simulation of Zooplankton Composition of Lake Michigan^a

Month and Year	Biomass Inshore kg/ha	Biomass Offshore kg/ha	Mean Lakewide Biomass kg/ha
May 1966	423	93	220
August 1966	286	132	191 ^b
May 1969	49	11	26
August 1969	34	16	23 ^b
May 1972	462	100	240 ^c
August 1972	313	145	210 ^c

^aAlewife biomass estimates (BIØMIC).^bBrown 1972.^cEdsall, *et al.*, M.S.

The simulation for May and August of 1966 permits validation of the model and understanding of the importance of alewife predation, especially at the maximum period of alewife abundance in the 1960s. The 1968-69 simulation examines the effect of reduced alewife predation, and the 1972 simulation again verifies the general species composition expected under very heavy alewife predation.

Changes in Zooplankton Composition

For the Great Lakes the most comprehensive documentation of changes is available for Lake Michigan. The large cladocerans (*Daphnia retrocurva* and *D. galeata*) were abundant in 1927 (Brooks 1969) and 1954 (Wells 1960). They gave way to the smaller more predation-free *D. longiremis* by 1966, with a return by 1968 to the larger *D. retrocurva*, along with other larger cladocerans like *Leptodora kindtii* and the calanoids *Limnocalanus macrurus*, *Epischura lacustris* and *Diaptomus sicilis* (Wells 1960, Wells 1970). The abrupt return of larger zooplankton during 1968 has been linked with the alewife die-off in 1966 (Wells 1970).

As of 1972, the zooplankton composition of Lake Michigan is similar to that of Lake Ontario, with *Bosmina longirostris* and *Cyclops bicuspidatus* most abundant (Roth and Stewart 1973). Fortunately, this careful historical documentation of changes in species composition of zooplankton communities of the Great Lakes will enable us to perform a variety of validations of our model.

Table 11.4 Results of Simulation of Zooplankton Standing Crops (no/m³) in Lake Michigan, Compared to Observed Densities for 1954, 1966, 1968, 1972^a

Month and Location	Fish Biomass (kg/ha)	Zooplankton Standing Crop (no/m ³)					
		<i>Diaptomus</i> spp (4)		<i>Daphnia galeata + retrocurva</i>		<i>Bosmina longirostris</i>	
		Predicted	Observed	Predicted	Observed	Predicted	Observed
Pre 1954 - Salmonid Community							
May-June - lakewide	100	1930	2534	1830	430	1980	250
August - lakewide	145	1910	2282	1810	2600	1980	26
1966 - Alewife Maximum							
May-June - inshore	423	433	1167	273	8	1810	320
- offshore	93	991	-	615	-	1850	-
August - inshore	286	509	579	319	16	1810	100
- offshore	132	779	-	483	-	1830	-
1968-69 Alewife Crash							
May-June - inshore	49	1580	-	913	-	1890	-
- offshore	11	52400	-	4370	-	5500	-
August - inshore	34	2840	3206	1220	2100	1930	32
- offshore	16	20700	-	2100	-	2730	-
1972 Alewife Buildup							
May-June - inshore	462	421	7650	266	45	1810	7500
- offshore	100	931	-	579	-	1840	-
August - inshore	313	492	8360	309	1700	1810	2500
- offshore	145	731	-	454	-	1840	-

^aObserved densities: 1954 (Wells 1960), 1966 (Wells 1970), 1968 (Wells 1970), 1972 (Roth and Stewart 1973).

Comparison Between Predicted (Simulated) and Observed Changes

Results of simulations for four years are summarized with respect to observed values of relative zooplankton abundance (Table 11.4). As McNaught (1975) suggested, the large calanoid *Diaptomus* is especially sensitive to predation, while the small, early reproducing cladoceran *Bosmina* is least sensitive both in results of simulations and as observed in nature. Under salmonid predation before 1954, we have predicted (1910-1930 m^{-3}) only slightly fewer *Diaptomus* than observed (2282-2534 m^{-3}). Under intense predation by alewife (1966), we have predicted 433 and 509 m^{-3} in inshore waters, with 1167 and 579 m^{-3} observed. The model properly simulated decreases in *Diaptomus* under heavy (93-423 kg/ha) alewife predation in 1966. Following the alewife crash in 1967 (Brown 1972), we simulated increases in *Diaptomus* to about 2840 m^{-3} inshore during August. Approximately 3206 *Diaptomus* m^{-3} were observed (Wells 1970). Again, with the alewife increase on the upswing in 1972 (Edsall, *et al.* 1972), the abundance of *Diaptomus* decreased (Table 11.4).

Daphnia (*galeata* and *retrocurva*) also responded in the results of simulations as expected. Predictions of abundance in pre-1954 years and 1968-69 were confirmed by field observations (Wells 1970), as we have summarized (Table 11.4). Generally, the least impressive relationship between predicted and observed densities occurred in the case of *Bosmina*. Only in 1972 were the high densities observed (Roth and Stewart 1973) that would be expected under heavy alewife predation (Table 11.4).

Since this model has been constructed to simulate interrelationships between the herbivorous zooplankton and their food resources and predators, we have not attempted to simulate the abundance of *Cyclops bicuspidatus*. This common cyclopoid copepod is chiefly predatory as an adult, and even the copepodites exhibit low feeding rates on algae in the Great Lakes (McNaught, unpublished). Thus this model is not appropriate for predicting the abundance of *Cyclops*.

Clearly, our simulations of zooplankton abundance based on available foods and predatory pressure by the alewife are of the proper order of magnitude and in proper relationship to changes in predatory pressure (Figure 11.3). While the model is useful for careful investigation of the interactions between fish predator and zooplankton prey, more detail could be developed to focus upon the relationship between species composition of zooplankton, especially *Bosmina*, and algal species diversity. Alternatively, it may be that *Bosmina* abundance is not a function of predator density because it is essentially predator-free in the Great Lakes.

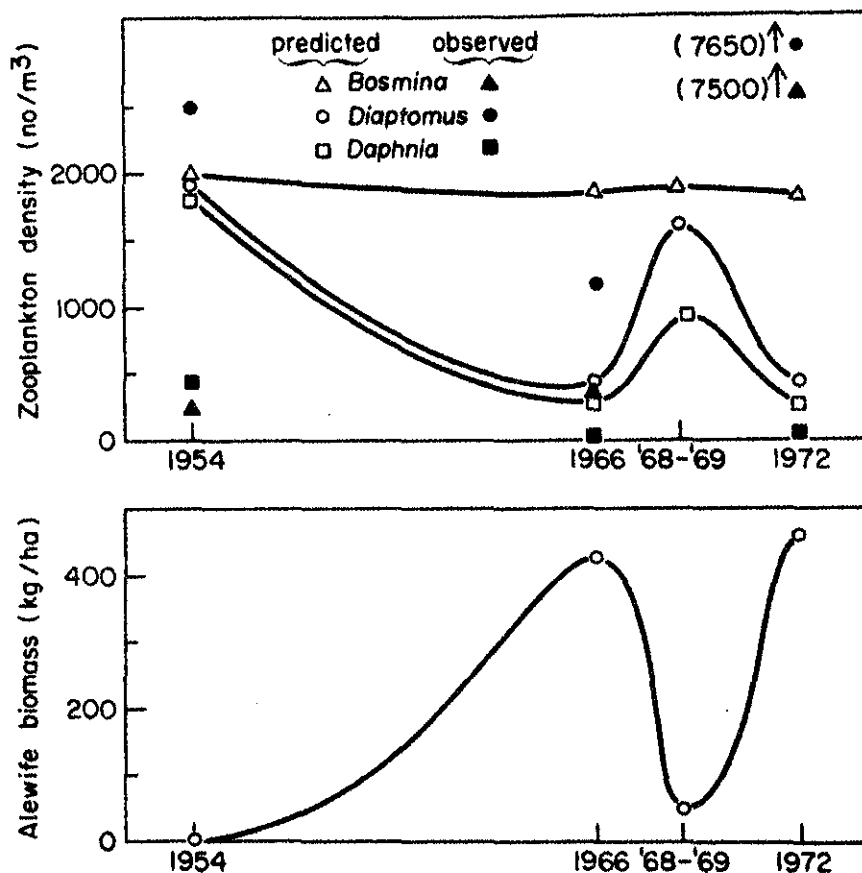


Figure 11.3a Simulated and observed changes in abundance of *Bosmina longirostris* (simulated Δ , observed \blacktriangle), *Daphnia* (\square , \blacksquare), and *Diaptomus* spp. (\circ , \bullet) with regard to biomass of alewife, during May-June in inshore waters of Lake Michigan.

VALIDATION FOR LAKE ONTARIO PARAMETERS

Intensive study of Lake Ontario during the IFYGL program has provided excellent information on primary productivity (Stadelmann, *et al.* 1974) and zooplankton abundance (McNaught, *et al.* 1975), although in contrast to Lake Michigan little is known of the alewife populations. Generally turnover rates during May of the primary producers in Lake Ontario (0.10) are higher than in Lake Michigan (0.09) (Tables 11.2 and 11.5). Inshore phytoplankton populations doubled in about 10 days

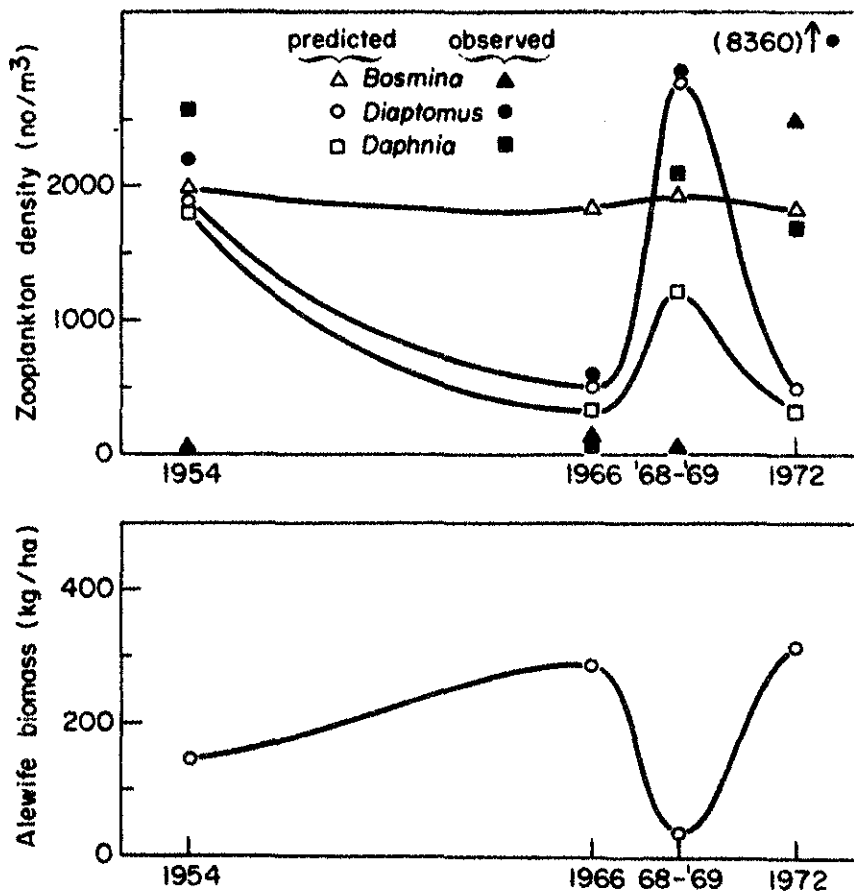


Figure 11.3b Simulated and observed changes (as in Figure 11.3a) during August in inshore waters of Lake Michigan.

during 1972. The alewife was less abundant inshore and generally less abundant lakewide than in Lake Michigan, probably because it has been in equilibrium with its predator for much longer.

Detailed Observations of Historical Abundance of Alewife and Zooplankton

The alewife has had access to Lake Ontario since the end of the Pleistocene. However, it did not become abundant there until 1873, following the loss of its major fish predator, the Atlantic salmon (Smith 1972). Currently, the spring months (April-June) find the alewife inshore

spawning, at which times their population density is 100-268 kg/ha (personal communication, A. Larsen, Bureau of Sports Fisheries). While detailed estimates of these populations after they have moved offshore (July) are not available, a simple calculation based on the surface area of Lake Ontario outside of the 40 meter contour (70% area) would indicate open water populations of approximately 11 kg/ha (Table 11.5).

In Lake Ontario rather limited evidence has indicated that zooplankters of the genera *Diaptomus* and *Daphnia* were abundant during the summer of 1939; *Bosmina* was clearly not observed. By 1969, *Bosmina longirostris* and *Cyclops bicuspidatus* were most abundant (McNaught and Buzzard 1973). *Bosmina longirostris* is especially abundant in nearshore waters.

Comparison Between Predicted and Observed Zooplankton Composition

Since our model is most sensitive to fish predation upon zooplankton, it is not surprising that our results for Lake Ontario, where little is known of alewife abundance, are less precise than those for Lake Michigan. Where estimates are available for alewife biomass (May-June inshore, Larsen, personal communication) we have predicted similar zooplankton composition as we ourselves observed. For May-June inshore, with an alewife biomass of 185 kg/ha, we predicted 420 *Diaptomus* m⁻³, 405 *Daphnia* m⁻³, and 4020 *Bosmina* m⁻³ and observed 719, 300 and 6800 m⁻³ respectively, a very good relationship indeed. Calculation of an offshore biomass of alewife of 11 kg/ha from crude inshore densities did not provide enough predation to get our simulated abundance down to observed levels (Table 11.6). The model does suggest that openwater alewife biomass is greater than 11 kg/ha. Possibly simulations, using known zooplankton composition, could be used to predict fish biomass.

USE OF MODEL IN MANAGEMENT OF GREAT LAKES

The idea that aquatic ecosystems are controlled in a large degree from atop the pyramid—the predatory fishes controlling the abundance of planktivorous alewives, these small fishes in turn controlling the turnover and standing crop (~ grazing) of herbivorous zooplankton, and these grazers the type of algae—is not a new idea. However, simulations presented for Lake Michigan and Lake Ontario are strong evidence for such control.

Table 11.5 Estimates of Forcing Functions for Simulation of Zooplankton Composition of Lake Ontario

Month and Location	Turnover Rates for Phytoplankton Resources (PSZ)				Alewife Biomass Estimates (BIØMIC) (kg/ha)
	Rate of Primary Productivity (mg Cm ⁻³ d ⁻¹)	Algal Carbon (mg Cm ⁻³)	Turnover (T) (days)	1/T (days ⁻¹)	
May-June					
Inshore	54.2 ^a	550 ^a	10.1	0.10	185 ^b
Offshore	18.5 ^a	183 ^a	9.9	0.10	11

^aStadelmann, *et al.* 1974.^bLarsen, personal communication.Table 11.6 Results of Simulation of Zooplankton Standing Crops (no/m³) in Lake Ontario

Month and Location	Fish Biomass (kg/ha)	Zooplankton Standing Crop (no/m ³)					
		<i>Diaptomus spp.</i>		<i>Daphnia galeata + retrocurva</i>		<i>Bosmina longirostris</i>	
		Predicted	Observed	Predicted	Observed	Predicted	Observed
May-June							
Inshore	185	420	719 ^a	405	300 ^a	4020	6800 ^a
Offshore	11	56,000	697 ^{a,b}	5670	32 ^a	8420	290 ^a

^aMcNaught, *et al.* 1975.^bDoes not include abundant nauplii.

Suppose that a commission with power to regulate these magnificent bodies of water decided that we should attempt to restore the oligotrophic zooplankton fauna as a first step in returning the lakes to an earlier trophic state, or at least controlling the increased rate of eutrophication. This is not ecologically a bad idea, since most herbivores associated historically with oligotrophic periods in the Great Lakes were large. Larger herbivores are more efficient filtrators (filtering capacity is proportional to the cube of the length ($L^{3.02}$) (Burns and Rigler 1967). A large calanoid 1.5 mm in length as an adult should filter about 8.1 times as much as a smaller calanoid species of 0.75 mm, although for populations of equal biomass the difference will be less. One method would be to add a large salmonid predator like the Coho salmon, *Oncorhynchus kisutch*, or the Chinook salmon, *Oncorhynchus tshawytscha*, as has been done in Lake Michigan. As these salmonid predators reduced the alewife standing stock, the percentage of composition of the zooplankton would shift toward dominance by the calanoids (Figure 11.4).

A detailed examination of this series of simulations for Lake Ontario is of interest from a management point of view. They were run using constant turnover rates as one forcing function. The instantaneous rate of resource turnover was held at a constant characteristic of offshore waters > 40 m) during August [$1/T$ (nannoplankton) = 0.15, $1/T$ (net-plankton) = 0.05], as in Table 11.5. At an alewife biomass of 11 kg/ha, *Diaptomus* ($52,000 \text{ m}^{-3}$) is dominant, followed distantly by the more eutrophic *Bosmina longirostris* ($7,200 \text{ m}^{-3}$) and *Daphnia* ($4,700 \text{ m}^{-3}$). With increased predation by the alewife, which as we remember becomes progressively more efficient for zooplankters between 0.3 and 0.7 mm in length, the standing crops of the larger *Diaptomus* and *Daphnia* drop rapidly, reaching a sharp break to an asymptote at approximately 33 kg/ha. Thereafter increased alewife predation, equated to increased standing crop of these fishes, has little effect upon zooplankton composition. Thus, to increase the proportion of oligotrophic *Diaptomus* in the community requires holding the alewife lakewide below 33 kg/ha.

Unfortunately, we do not presently have a good offshore estimate of alewife stocks for the open waters of Lake Ontario. We realize that the alewife has been in this lowest of the Great Lakes for a long time, and in abundance since 1873 (Smith 1972). Thus alewife stocks may be in equilibrium and likely lower than in Lake Michigan. Yet changes in the historical past point to an increased incidence of *Bosmina longirostris* (McNaught and Buzzard 1973), itself evidence for increased fish predation in the system. One way to control alewife stocks is by introducing predatory salmon. The introduction of salmonids has an additional ecological advantage, since they are coarse filter feeders

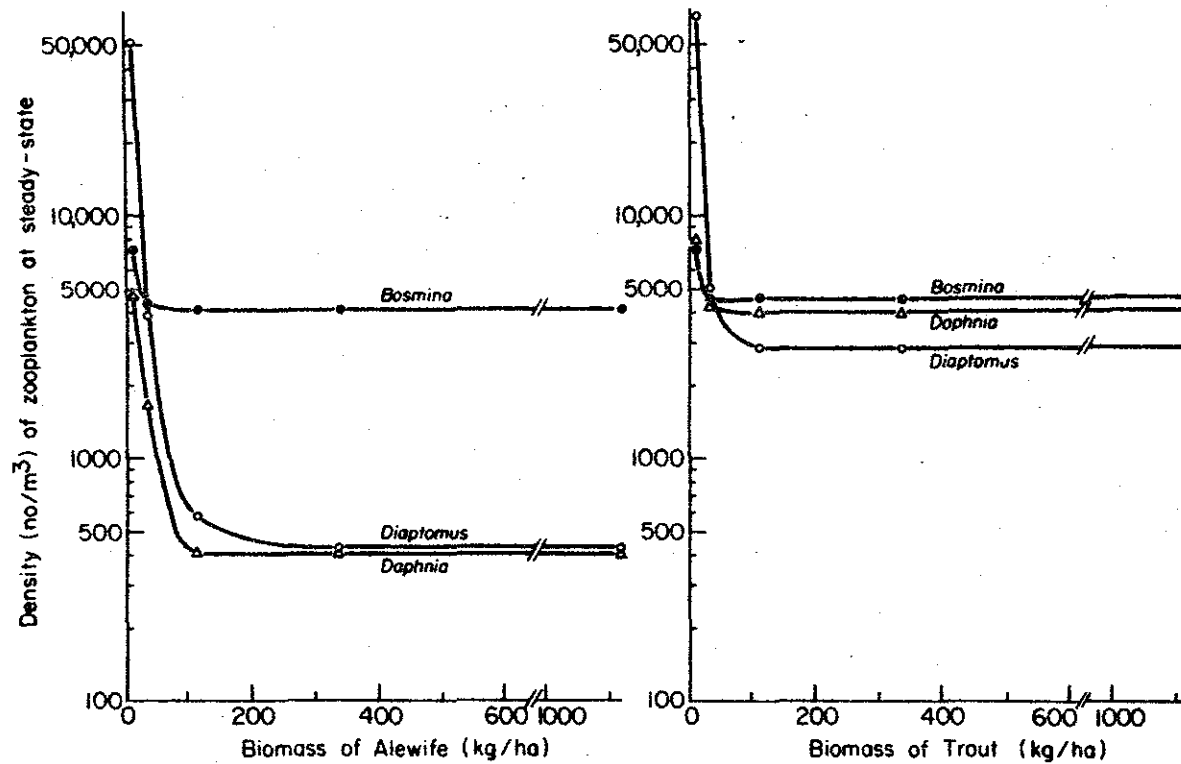


Figure 11.4 Simulated densities (no/m³) of *Diaptomus* (○), *Daphnia* (△) and *Bosmina longirostris* (●), with varying biomass of (left) alewife (kg/ha) and (right) trout, in Lake Ontario at levels of primary productivity corresponding to inshore waters during May.

(*PCMIN* is large). Thus the young salmon should act more like the oligotrophic planktonphage fishes (coregonines) that originally occupied this lake in large numbers. The commercial yield of coregonines, especially the lake herring and whitefish, did not drop markedly until 1945-1955 in Lake Ontario (Beeton 1969).

Salmonids like the rainbow trout, *Salmo gairdneri*, about which a good deal is known concerning size-selective feeding (Galbraith 1967) would permit the original oligotrophic zooplankton fauna to persist. Remnants of relict populations still exist in deeper water, such as small populations of *Limnocalanus macrurus* and *Diaptomus sicilis*, but as relatively low (0.2 and 0.1%) components of the crustacean zooplankton in 1972 (McNaught and Buzzard 1973). With the reestablishment of salmonid-like planktivorous fishes, standing crops of *Bosmina longirostris* would be expected to increase slightly (8.8%), but those of the large calanoid *Diaptomus* (384%) and the large cladoceran *Daphnia galeata* (885%) would increase markedly at a salmonid biomass of 100 kg/ha, according to our simulation (Figure 11.4). In terms of simulated composition of zooplankton community, the dominant calanoid (*Diaptomus*) would comprise 13% of the standing crop (numbers) under predation by 100 kg/ha of alewives, but would constitute a larger fraction of the standing crop (34%) under the same biomass of salmonids. From the standpoint of zooplankton biomass, these differences would be even larger, since *Diaptomus* is one of the largest genera.

From a management viewpoint, the introduction of salmonid predators upon the exotic alewife, concomitant with the reestablishment of coregonine populations, makes considerable ecological sense. But we are dealing with simulations. Whether they can be directly converted to management recommendations is unknown and untested. The challenge, however, is clear; biological control of the alewife in Lake Michigan is certainly desirable.

THEORETICAL IMPLICATIONS

Two basic theoretical implications of these simulations are evident: the first suggests that fish predation is the principal factor controlling zooplankton composition. Second, these simulations clearly indicate that the often-used eutrophic indicator, *Bosmina longirostris*, is an indicator of *predatory pressure* and not solely of advanced eutrophication or shifts to larger algal species. In suggesting that selective fish predation controls zooplankton species composition, we agree with recent conclusions of others (Allan 1974, Dodson 1974).

The conclusion that inshore *spawning* populations of the alewife during May and June in effect largely determine summertime zooplankton composition is both stimulating and surprising. This new and basic observation may negate previous statements concerning interpretation of shifts from *Eubosmina coregoni* to *Bosmina longirostris* during cultural eutrophication. This conclusion was drawn from the observations that inshore spawning runs of alewives are followed by rapid growth of *Bosmina longirostris* populations and the independent simulation of large *Bosmina* populations with high predatory density. Thus the seasonality of predation related to spawning may influence zooplankton composition. We suggest that an exotic predator, like the alewife, in addition to nutrient enhancement and concomitant changes in algal composition, may be responsible for such shifts from larger to smaller *congeneric* species.

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