Trophic Relationships in Freshwater Pelagic Ecosystems

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Relative impacts of bottom-up (producer controlled) and top-down (consumer controlled) forces on the biomass and size structure of five major components of freshwater pelagic systems (piscivores, planktivores, zooplankton, phytoplankton, and total phosphorus availability) were estimated. Predictions that emerge are (1) maximum biomass at each trophic level is controlled from below (bottom-up) by nutrient availability, (2) this bottom-up regulation is strongest at the bottom of the food web (i.e. phosphorus → phytoplankton) and weakens by a factor of 2 with each succeeding step up the food web, (3) as energy moves up a food web, the predictability of bottom-up interactions decreases, (4) near the top of the food web, top-down (predator mediated) interactions are strong and have low coefficients of variation, but weaken with every step down the food web, (5) variability around the bottom-up regressions can always be explained by top-down forces, and (6) interplay between top-down and bottom-up effects changes with the trophic status of lakes. In eutrophic lakes, top-down effects are strong for piscivore → zooplankton, weaker for planktivore → zooplankton, and have little impact for zooplankton → phytoplankton. For oligotrophic lakes, the model predicts that top-down effects are not strongly buffered, so that zooplankton → phytoplankton interactions are significant.

Les incidences relatives des forces « ascendantes » (régies par les producteurs) et « descendantes » (régies par les consommateurs) sur la biomasse et la structure des tailles de cinq importants groupes ou paramètres des systèmes pélagiques d'eau douce (piscivores, planctonivores, zooplancton, phytoplancton et disponibilité du phosphore total) ont fait l'objet d'une modélisation. Selon ce modèle : (1) la biomasse maximale de chaque niveau trophique est régie par la disponibilité des matières nutritives des niveaux inférieurs; (2) cette régulation de type ascendant est la plus marquée à la partie inférieure de la chaîne alimentaire (phosphore → phytoplancton) et s'amoindrit par un facteur de 2 à chaque étape; (3) la possibilité de prévoir les interactions dans le sens ascendant diminue à mesure que l'énergie remonte la chaîne alimentaire; (4) près de la partie supérieure de la chaîne, les interactions vers le bas (par l'intermédiaire des prédateurs) sont importantes et de faible coefficient de variation, mais elles s'amenuisent avec chaque palier inférieur de la chaîne; (5) la variabilité annexe aux régressions ascendantes peut toujours s'expliquer par les forces agissant vers le bas; et (6) les relations entre les effets vers le bas et vers le haut se modifient en fonction de l'état trophique du lac. Dans les lacs eutrophes, les effets descendants sont importants pour la relation piscivores → zooplancton, moins importants pour la relation planctonivores → zooplancton et ont peu d'effets sur la relation zooplancton → phytoplancton. Dans les lacs oligotrophes, les effets descendants ne sont pas fortement tamponnés, de sorte que les interactions zooplancton → phytoplancton sont appréciables.

The limnological literature that deals with the biomass and abundance of organisms in pelagic food webs supports two apparently contradictory points of view. The first asserts that pelagic trophic level biomass is controlled from below by producers, and the second supports the conclusion that it is controlled from above by consumers. This is reminiscent of a general controversy that has long been part of the terrestrial literature (Hairston et al. 1960; Slobodkin et al. 1967; van Valen 1973) where at one extreme there are those (summarized by White 1978) who contend that biomass at all trophic levels is regulated by resource quantity and quality, and at the other extreme (exemplified by Mech et al. 1971; Simenstad et al. 1978) there are those who champion control by consumers (predators).

To date, the terrestrial literature has not yielded a consensus, because good empirical evidence has been extremely difficult to acquire; however, empirical data are now available for freshwater pelagic systems and support both the top-down and bottom-up hypotheses.

The evidence supporting the "producer-controlled" (bottom-up) model comprises empirically derived relationships based on data from many lakes. The relationships take the form of regression lines plotting the biomass of the dependent variable (consumer) as a function of the independent variable (producer). There are four basic sets of regressions that apply to freshwater pelagic ecosystems. The first is the relationship between total phosphorus (independent variable) and chlorophyll a (Sakamoto 1966; Dillon and Rigler 1974; Schindler

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TABLE 1. Summary of top-down regression lines. ZB = zooplankton biomass, PLB = planktivore biomass, CHLA = chlorophyll *a*, PHB = phytoplankton biomass, TP = total epilimnetic phosphorus, DAP > 1 = *Daphnia* > 1 mm, *n* = sample size, r^2 = coefficient of variation, ww = wet weight, dw = dry weight. An asterisk indicates a model II regression; all others are model I regressions.

Regression	*n*	r^2	Comments
Planktivores and zooplankton			
(1)* ZB (mg·L^{-1} ww) = 2.667 − 1.834PLB (mg·L^{-1} ww)	53	0.78	Each *n* represents one weekly sample (July, Aug., Sept. 1981)
(2) ZB (mg·L^{-1} ww) = 7.89 − 2.09PLB (mg·L^{-1} ww)	4	0.96	Each *n* is the average of eight weekly samples (May, June 1983)
(3)* $\log_{10}$ ZB (μg·L^{-1} dw) = 2.69 − 0.43 $\log_{10}$ PLB (μg·L^{-1} ww)	53	0.59	As above, all fish data
Zooplankton and phytoplankton (chlorophyll a)			
(4) $\log_{10}$ CHLA (μg·L^{-1}) = 2.27 − 1.08 $\log_{10}$ ZB (mg·L^{-1} ww)	18	0.21	Each *n* represents one weekly sample (May, June 1981) (Fig. 2)
(5) $\log_{10}$ CHLA (μg·L^{-1}) = 1.21 − 0.12 $\log_{10}$ ZB (mg·L^{-1} ww)	23	0.01	Each *n* represents one weekly sample (May, June 1983) (Fig. 2)
(6)* $\log_{10}$ PHB (μg·L^{-1} ww) = 7.82 − 1.96 $\log_{10}$ ZB (μg·L^{-1} ww)	54	0.07	Each *n* represents one weekly sample (July, Aug., Sept. 1982)
Cladocera ≥ *1 mm length and phytoplankton*			
(7) $\log_{10}$ CHLA (μg·L^{-1}) = 1.859 − 0.367 $\log_{10}$ DAP > 1 (μg·L^{-1} ww)	18	0.65	Each *n* represents one weekly sample, 1981 and 1983. May, June, only non-zero *Daphnia* samples are included
(8) $\log_{10}$ CHLA (μg·L^{-1}) = 1.52 − 0.367 $\log_{10}$ DAP > 1 (μg·L^{-1} dw)	18	0.64	Each *n* represents one weekly sample, 1981 and 1983. May, June, only non-zero *Daphnia* samples are included
Phytoplankton and mean epilimnetic TP			
(9) $\log_{10}$ TP (μg·L^{-1}) = 1.774 + 0.250 $\log_{10}$ CHLA (μg·L^{-1})	20	0.55	Each *n* represents one weekly sample (May, June 1981) (Fig. 4)
(10) $\log_{10}$ TP (μg·L^{-1}) = 1.758 − 0.090 $\log_{10}$ CHLA (μg·L^{-1})	30	0.02	Each *n* represents one weekly sample (May, June 1983) (Fig. 4)

1978; Janus and Vollenweider 1981; Hanson and Peters 1984; Pace 1984), the second relates phytoplankton biomass or chlorophyll *a* (independent variable) and zooplankton biomass (McCauley and Kalff 1981; Mills and Schiavone 1982; Hanson and Peters 1984; Canfield and Watkins 1984), the third relates zooplankton biomass (independent variable) and planktivore biomass (Mills and Schiavone 1982), and the fourth relates an index of planktivore biomass (independent variable) and an index of piscivore biomass (Mills and Schiavone 1982). When combined, these relationships suggest that the biomass of each of the major trophic levels (phytoplankton, zooplankton, planktivores, and piscivores) is resource limited, i.e. by the producer level immediately below.

The evidence supporting the "consumer-controlled" (top-down) model has spawned the theories of trophic "biomanipulation" (Shapiro et al. 1982; Shapiro and Wright 1984) and "cascading trophic interactions" (Carpenter et al. 1985). At the top of the food web is the negative relationship between piscivores (independent variable) and planktivores (Bonar 1977; Holčík 1977). One step down is the negative relationship between plantivore biomass (independent variable) and zooplankton biomass and species composition (Hrbáček 1962; Brooks and Dodson 1965; Galbraith 1967; Hall et al. 1970; Hutchinson 1971; Stenson 1972, 1976; O'Brien and de Noyelles 1974; Anderson et al. 1978). This relationship is almost entirely unquantified because most studies are based only on relative measures of fish biomass, but recent work

(Mills and Forney 1983; Post 1984; McQueen and Post 1984; Vijverberg and van Densen 1984) demonstrates negative relationships which are statistically significant ($p < 0.05$). Finally, the literature also shows that near the bottom of the food web, zooplankton (independent variable) can have a negative impact on phytoplankton biomass (Uhlman 1961; Burns 1968, 1969; Hurlburt et al. 1972; Porter 1977; Lynch 1979; Lynch and Shapiro 1981; Shapiro et al. 1982; Shapiro and Wright 1984; McCauley and Kalff 1981). Taken together, these data suggest that the biomass at each trophic level can be controlled from above by consumers.

In the analysis that follows, we will first present a series of empirically derived regressions which quantify top-down effects. These relationships are based on eutrophic lake enclosure experiments conducted at Lake St. George. The enclosures used are large enough (750 m³) and deep enough (15 m) to maintain normally growing fish populations for >18 mo (McQueen and Post 1984) and to maintain zooplankton and phytoplankton populations that are similar in terms of numbers and diversity to the communities found growing naturally in Lake St. George (Story 1982). These enclosures have allowed us to manipulate planktivore populations (0+ and 1+ *Perca flavescens* and 1+ *Notemigonus crysoleucas*) and then to monitor the subsequent effects on zooplankton, phytoplankton, and macronutrients. Our second step will be to review the literature and to derive average bottom-up regression lines which relate consumers (dependent variable) to producers (independent

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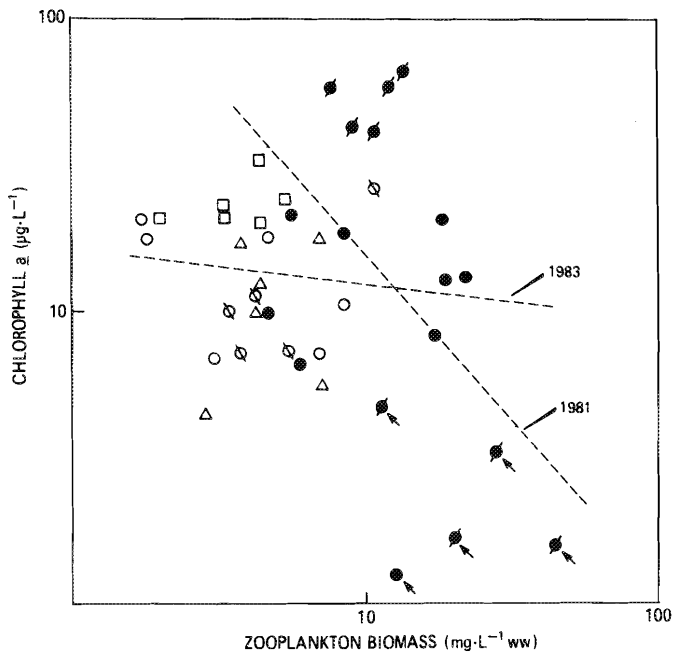*Can. J. Fish. Aquat. Sci., Vol. 43, 1986*

FIG. 1. Chlorophyll *a* biomass plotted with respect to total zooplankton biomass (ww = wet weight). The solid symbols represent 1981 data and the open symbols 1983 data. The 1981 and 1983 lines are given as lines 4 and 5 in Table 1. Arrows denote data points derived from samples containing more than 10% biomass of *Daphnia* >1 mm length. Enclosures described in McQueen and Post (1984) are denoted as follows: 1 = ◑, 2 = ●, 3 = ○, 4 = ◒, 5 = △, 6 = ☐.
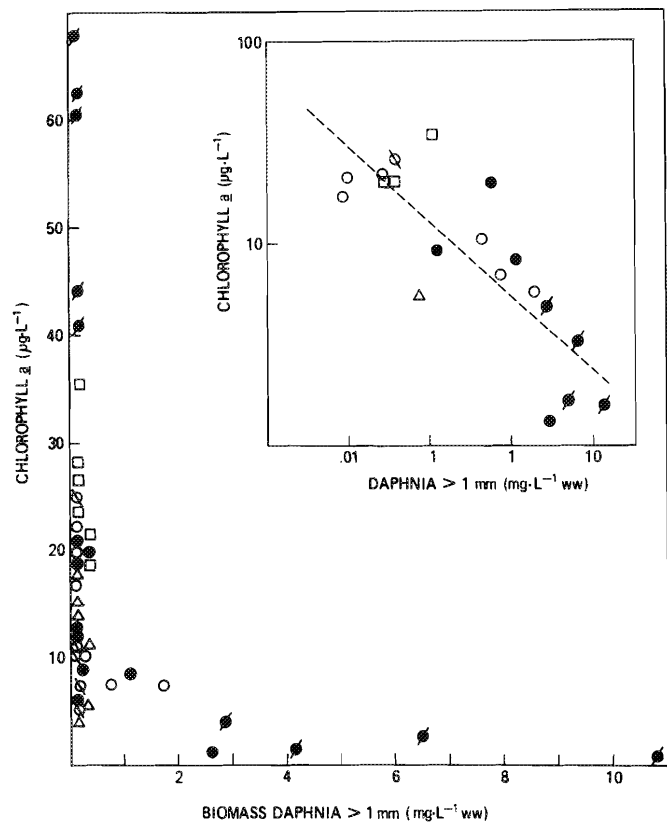

FIG. 2. Chlorophyll *a* biomass plotted with respect to the biomass of *Daphnia* > 1 mm in length (ww = wet weight). Enclosures described in McQueen and Post (1984) are denoted as follows: 1 = ◑, 2 = ●, 3 = ◒, 4 = ○, 5 = △, 6 = ☐. Inset: $\log_{10}:\log_{10}$ plot. The line is given as line 7 in Table 1.
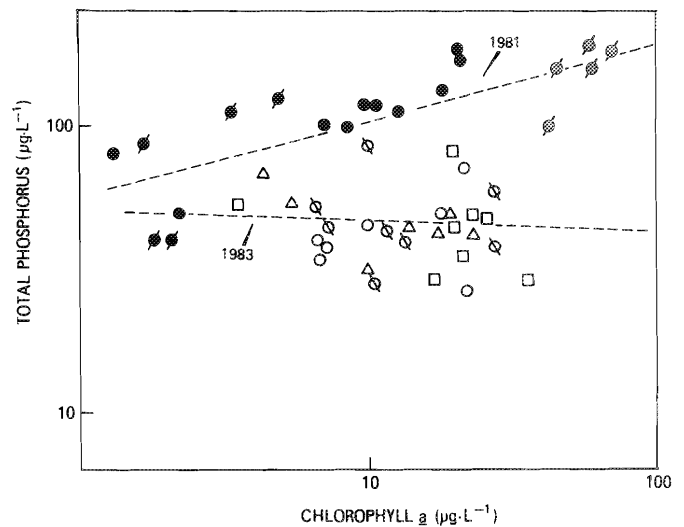

FIG. 3. Total phosphorus plotted with respect to chlorophyll *a*. Enclosures described in McQueen and Post (1984) are denoted as follows: 1 = ◑, 2 = ●, 3 = ○, 4 = ◒, 5 = △, 6 = ☐. The 1981 and 1983 lines are given as lines 9 and 10 in Table 1.

variable). The third step will be to test the hypothesis that bottom-up processes determine maximum biomasses at all trophic levels and that top-down processes are responsible for the observed deviations from each of the predicted relationships. The final step will be to estimate the impact of bottom-up and top-down forces at each level in the trophic food web and to investigate the effects of altered productivity levels.

Methods

Data for the top-down model were derived from enclosure experiments that were run during the spring (May and June) of 1981 and 1983 and the summer (July, August, and September) of 1982. The enclosures measured 8 m in diameter by 15 m deep and were open to the sediment–water interface. The same protocol was used for all the experiments. At ice-out, divers ensured that the weighted enclosure skirts were firmly fixed into the sediments. A high-capacity pump was used to add a minimum of 700 m^3 to each enclosure. During 1981, nutrients (10 g of 90% H_3PO_4 and 250 g of $NaNO_3$) were added to the epilimnion (1 m depth) on a weekly basis, and during 1982 and 1983 half of that amount was added. In the 1981 experiments, water samples were taken at 1, 3, 5, 8, and 12 m, and in the 1983 experiments, samples were taken at 2, 6, and 10 m. Samples were processed at the Canada Centre for Inland Waters using the methods described by Stainton et al. (1977). The mean epilimnetic total phosphorus (TP) concentrations were 118 and 113 $\mu g \cdot L^{-1}$ (two enclosures, 1981) and 45, 49, 56, and 47 $\mu g \cdot L^{-1}$ (four enclosures, 1983). TP was not measured during 1982.

Zooplankton were captured with a vertical haul net pulled between 0 and 12 m. During 1981 the mesh size used was 80 μm, and during 1982 and 1983 the mesh size was 150 μm. The count groups were nauplii, rotifers (excluding *Asplanchna*), *Asplanchna*, *Daphnia*, *Chydorus*, *Diaphanosoma*, *Bosmina*, *Skistodiaptomus oregonensis*, *Ceriodaphnia*, and cyclopoids. Counts were done at 25× or 50× magnification through a Wild stereo microscope. Subsample sizes were adjusted so that all major groups were represented by 40−500 individual counts. During the counts, samples were

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TABLE 2. Summary of published bottom-up regression relationships. n = sample size, r^2 = coefficient of determination, sb = standard error of the slope, S^2yx = error mean square. Regressions noted with an asterisk were calculated from published tables; all others were calculated by the original authors. MA = mean annual data, SO = spring overturn data, SM = summer mean, WS = weekly samples, dw = dry weight, ww = wet weight, SS = single samples, index = biomass index based on catch per unit effort, ps = pumpkin seed, bg = bluegill, p = perch, bc = black crappie, CHLA = chlorophyll a, TP = total phosphorus, ZB = zooplankton biomass, PLB = planktivore biomass, PISB = piscivore biomass.

	Regression	n	r^2	sb	S^2yx	Source(s)	Comments
	Phosphorus and phytoplankton						
(1)	$\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) = 1.583 $\log_{10}$ P ($\mu g \cdot L^{-1}$) − 1.34	30	0.975	—	—	Dillon and Rigler 1974; Sakamoto 1966	CHLA = SM, TP = SO
(2)	$\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) = 1.449 $\log_{10}$ P ($\mu g \cdot L^{-1}$) − 1.136	46	0.950	—	—	Dillon and Rigler 1974	CHLA = SM, TP = SO
(3)	$\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) = 1.213 $\log_{10}$ TP ($\mu g \cdot L^{-1}$) − 0.848	81	0.880	—	—	Schindler 1978	CHLA = MA, TP = MA
(4)	$\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) = 1.119 $\log_{10}$ TP ($\mu g \cdot L^{-1}$) − 0.676	29	0.670	—	—	Prepas and Trew 1983	CHLA = SM, TP = SO
(5)	$\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) = 1.250 $\log_{10}$ TP ($\mu g \cdot L^{-1}$) − 0.676	49	0.660	0.113	—	Hanson and Peters 1984	CHLA = SM, TP = SM
(6)	$\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) = 1.050 $\log_{10}$ TP ($\mu g \cdot L^{-1}$) − 0.530	57	0.760	—	—	Pace 1984	CHLA = WS, TP = WS
(7)	$\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) = 1.090 $\log_{10}$ TP ($\mu g \cdot L^{-1}$) − 0.560	12	0.93	—	—	Pace 1984	CHLA = SM, TP = SM
(8)	$\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) = 0.859 $\log_{10}$ TP ($\mu g \cdot L^{-1}$) − 0.446	140	0.77	0.040	0.066	Janus and Vollenweider 1981	CHLA = MA, TP = MA
(9)	$\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) = 1.010 $\log_{10}$ TP ($\mu g \cdot L^{-1}$) − 0.180	13	0.81	—	—	Stockner and Shortreed 1985	CHLA = SM, TP = SO
	Phytoplankton and zooplankton						
(10)	$\log_{10}$ ZB ($\mu g \cdot L^{-1}$ dw) = 0.53 $\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) + 1.44	49	0.57	0.064	—	Hanson and Peters 1984	ZB = SM, CHLA = SM
(11)	$\log_{10}$ ZB ($\mu g \cdot L^{-1}$ ww) = 0.511 $\log_{10}$ PB ($\mu g \cdot L^{-1}$ ww) + 1.807	207	0.63	0.044	0.45	McCauley and Kalff 1981	ZB = SS, CHLA = SS
(12)	$\log_{10}$ ZB ($\mu g \cdot L^{-1}$ ww) = 0.719 $\log_{10}$ BP ($\mu g \cdot L^{-1}$ ww) + 1.015	17	0.86	0.074	0.271	McCauley and Kalff 1981	ZB = SM, CHLA = SM
(13)*	$\log_{10}$ ZB ($\mu g \cdot L^{-1}$ dw) = 0.55 $\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) + 1.92	12	0.810	0.084	0.259	Pace 1984	ZB = MA, CHLA = MA
(14)*	$\log_{10}$ ZB ($\mu g \cdot L^{-1}$ dw) = 0.59 $\log_{10}$ CHLA ($\mu g \cdot L^{-1}$) + 1.355	11	0.377	—	—	Mills and Schiavone 1982	ZB = SM, CHLA = SM
(15)	$\log_{10}$ ZN (no.$\cdot$m^{-3}) = 0.50 $\log_{10}$ CHLA (mg$\cdot$m^{-3}) + 4.7	165	0.43	—	—	Canfield and Watkins 1984	ZB = SS, CHLA = SS
	Zooplankton and planktivores						
(16)*	$\log_{10}$ PLB (index) = 0.465 $\log_{10}$ ZB ($\mu g \cdot L^{-1}$ dw) + 0.893	10	0.24	0.276	0.398	Mills and Schiavone 1982	Data listed in Table 6
(17)*	$\log_{10}$ PLB (index) = 0.159 $\log_{10}$ ZB ($\mu g \cdot L^{-1}$ dw) + 2.10	11	0.08	0.179	0.258	Mills and Schiavone 1982	Table 5; ps, bg, p, bc
	Planktivores and piscivores						
(18)*	$\log_{10}$ PISB (index) = −0.395 $\log_{10}$ PLB (index) + 3.733	10	0.74	0.082	0.064	Mills and Schiavone 1982	Planktivores from Table 5; ps, bg, p, bc
(19)*	$\log_{10}$ PISB (index) = −0.143 $\log_{10}$ PLB (index) + 3.025	10	0.28	0.081	0.107	Mills and Schiavone 1982	Planktivores from Table 6

suspended in a circular counting chamber (Ward 1955) and projected on a television screen using a microscope-mounted Hitachi television camera. A caliper system (Sprules et al. 1981) was used to measure the length of every individual that was counted. This information was automatically recorded on a PET computer which converted lengths to biomasses using species-specific algorithms (W. G. Sprules, unpubl.) that had been stored as software. Knowing mesh size, net size, haul distance, and either species or group counts and lengths, the computer produced count group-specific length−frequency and weight−frequency tables and group-specific counts per litre and biomass (milligrams per litre).

During 1982, young of the year yellow perch (*P. flavescens*) were seined from Lake St. George and were stocked in densities of 600 (enclosure 1), 200 (enclosure 2), and none (enclosure 3). Plexiglas fish traps (Casselman and Harvey 1973), standard commercial minnow traps (40 × 25 cm), and Windermere traps (90 × 57 cm) were fished in the enclosures at 12 intervals during the experiment. Captured fish were measured for total length and weight and returned. During August, a multiple census mark−recapture experiment was conducted in the enclosures containing fish and those results were combined with weekly catch per unit effort data to produce estimates of fish biomass and numbers.

The relationships used for the development of the producer-controlled model were obtained directly from the literature or were calculated from published data. Conversions from wet to dry weight assumed a conversion ratio of 8:1 (Taguchi and Fukuchi 1975; McCauley and Kalff 1981).

Results and Discussion

Top-down Control

Two data sets yield regressions relating the effects of planktivores on zooplankton (Table 1). The first is based on 53 weekly samples taken from three enclosures and yields a negative slope (Table 1, line 1) which is statistically significant ($r^2 = 0.78$, $n = 53$, $p \ll 0.05$). This relationship is supported by the results of a separate experiment (involving four enclosures) which showed that the relationship between zooplankton biomass and an index of fish biomass is also linear negative and significant ($p \ll 0.05$) (Table 1, line 2).

The effects of zooplankton biomass on phytoplankton biomass were measured in three experiments involving nine enclosures (May and June 1981, $n = 2$; May and June 1983, $n = 4$; July, August, and September 1982, $n = 3$). The 1983 experiment (Fig. 1; Table 1, line 5) and the 1982 experiment (Table 1, line 6) both yield weak negative slopes (not different from zero) and r^2 values (0.1 and 0.07) which are not significant ($p \gg 0.05$). However, the 1981 experiment yielded a relationship (Fig. 1; Table 1, line 4) that was significant ($r^2 = 0.21$, $n = 18$, $p \ll 0.05$). Analysis of zooplankton size and species composition indicated that in the first two cases, large *Daphnia* (functionally defined as *Daphnia* > 1 mm, helmet to base of spine) were never abundant, but that in the third case, *Daphnia galeata mendotae* > 1 mm comprised more than 10% of the zooplankton biomass on five of the sampling weeks. These points are identified in Fig. 2 and suggest that the presence of these large cladocerans was associated with reduced phytoplankton biomass (measured as chlorophyll *a*). When these five points are removed from the 1981 data set the slope and r^2 are no longer statistically significant.

A linear plot of the spring data for chlorophyll *a* and large

D. galeata mendotae (Fig. 2) suggests that when the biomass of large *Daphnia* is greater than 0.5 mg·L⁻¹ wet weight (ww) (0.06 mg·L⁻¹ dry weight (dw)), chlorophyll *a* is consistently low, but when large *Daphnia* are absent, chlorophyll *a* values are unpredictable. A plot of chlorophyll *a* and biomass of large *Daphnia* (Fig. 2, inset) yields a significant (Table 1, line 7, $r^2 = 0.64$, $n = 18$, $p \ll 0.05$) negative relationship. The conclusion is that in eutrophic lakes, when large *Daphnia* (or perhaps this could be generalized to large cladocera) are absent, zooplankton cannot reduce phytoplankton biomass, but that when large *Daphnia* are present, a significant inverse relationship exists between large *Daphnia* biomass and phytoplankton biomass.

The relationship between phytoplankton (independent) and epilimnetic TP (Fig. 3) was monitored in two experiments (May and June 1981 and May and June 1983) (Table 1, lines 9 and 10). In one case there was no significant relationship, and in the other the slope was positive. The suggestion is that increased phytoplankton had no measurable impact on TP and that what little impact they might have had was obscured by the strong bottom-up relationship between TP and chlorophyll *a* biomass.

Bottom-up Control

Four groups of published regressions relate the biomass of pelagic phytoplankton, zooplankton, planktivores, and piscivores to the producer level one step down in the trophic food web. The relationship between TP (independent variable) and chlorophyll *a* has received the most attention in the literature (Nicholls and Dillon 1978) and is summarized in Table 2. Although the data sets deal with different lakes representing a variety of productivity levels, they all yield highly significant correlations and show some agreement with respect to slope. The relationship between phytoplankton biomass (usually chlorophyll *a*) and zooplankton biomass or numbers has also been documented in a number of published studies (Table 2), and again the regressions are statistically significant, although the r^2 values are lower than for TP and phytoplankton. The relationship between zooplankton biomass (independent variable) and planktivores (represented by an index of catch per unit effort) has been documented by Mills and Schiavone (1982), and regressions (Table 2) calculated from their original tabular values were either marginally significant or nonsignificant, which suggests that bottom-up control is weak. Finally, regressions of planktivore biomass indices (independent variable) and indices of piscivore biomass based on data published by Mills and Schiavone (1982) (Table 2) yield significant *negative* correlations, which suggests that the bottom-up effect of planktivore abundance on piscivore biomass has a weaker effect than the top-down effect of piscivores on planktivores.

The Model: Bottom-up vs. Top-down

The top-down and bottom-up models are supported by two very different data sets. The top-down data result from manipulations of predator populations that receive equal nutrient inputs, and the bottom-up regressions result from many measurements taken from different lakes that are all assumed to receive stable but different nutrient inputs. To investigate the interactions that are implied by these regressions, each of the four top-down and bottom-up relationships must first be represented by single "best-fit" (Fig. 4) regression lines. The four mean top-down lines follow directly from the experimentally derived data presented earlier. The mean effect of planktivo-

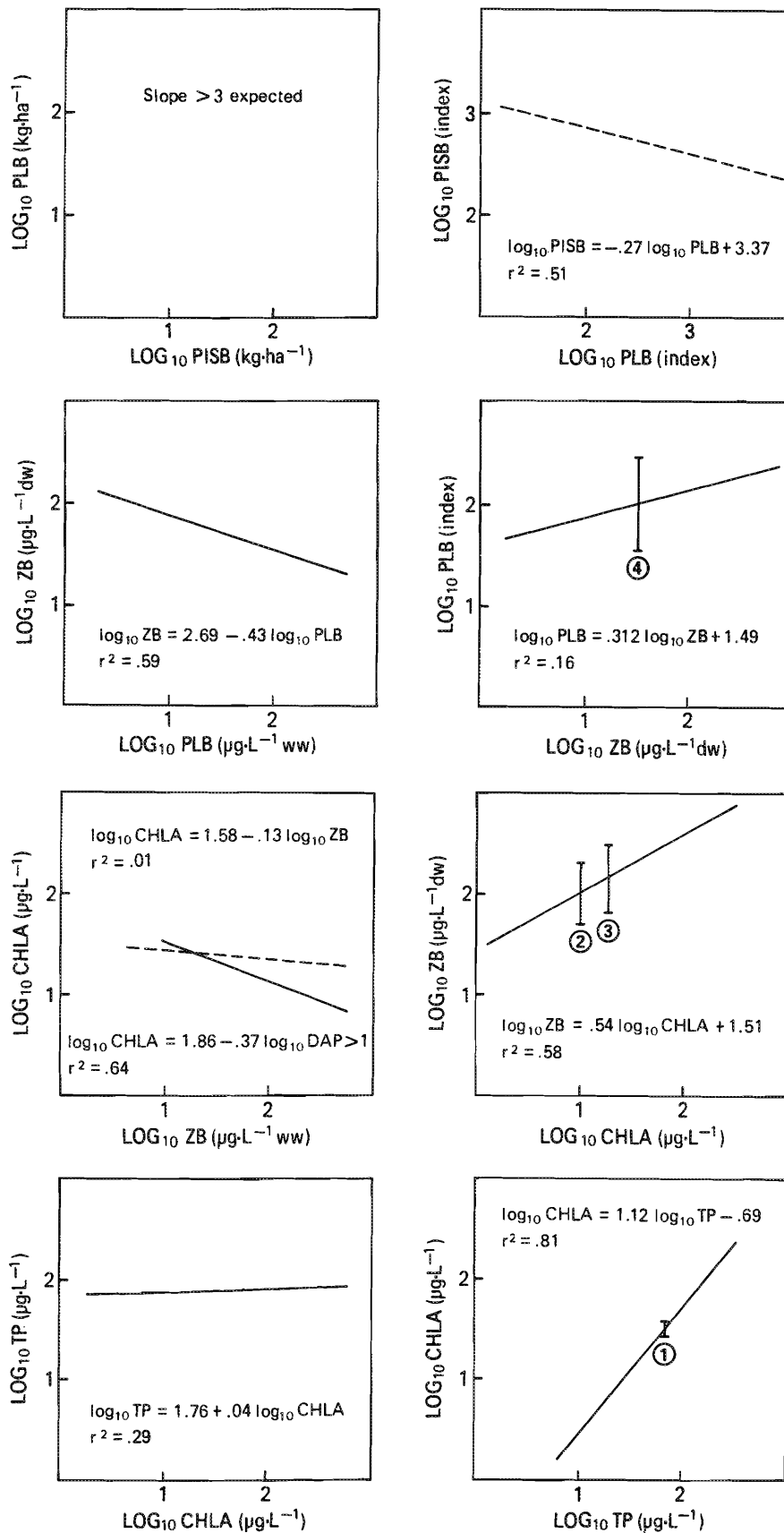*Can. J. Fish. Aquat. Sci., Vol. 43, 1986*

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FIG. 4. Mean regression lines for bottom-up relationships (right-hand panels) and top-down relationships (left-hand panels). Numbered 95% confidence intervals are based on data provided by (1) Janus and Vollenweider (1981), (2) and (4) Mills and Schiavone (1982), and (3) Pace (1984). Slopes of the broken lines are not statistically different ($\alpha = 0.05$) from zero.

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rous fish on zooplankton has the strongest negative slope and is statistically significant (Table 1, line 3). The effect of total zooplankton biomass on chlorophyll a (Table 1, lines 5 and 6) has a slope that is not different from zero and is not statistically significant; however, the effect of large *Daphnia* (Table 1, line 15) on phytoplankton biomass has a significant negative slope. Finally, the relationship between chlorophyll a and epilimnetic TP (Fig. 4, n weighted slope, intercept, and r^2 based on lines 9 and 10, Table 1) is not significant.

Average values for the producer-controlled regressions have been calculated from published relationships (Table 2). The slopes, intercepts, and r^2 values of the regressions linking TP and chlorophyll a were pooled with respect to sample size to produce the relationship shown in Fig. 4. The slopes and intercepts of the regressions linking chlorophyll a and zooplankton biomass were pooled with respect to the standard error of the slope, and the r^2 valeus were pooled with respect to sample size (Fig. 4). The same procedure was used to average the lines relating zooplankton biomass to planktivore biomass and planktivore biomass to piscivore biomass.

Inspection of the averaged regressions (Fig. 4) and the original data sets (Table 2) suggests that producer-controlled (bottom-up) regressions have two characteristics that tend to order the data set: (1) slopes are strong near the bottom of the food web and weak near the top and (2) explained variance (r^2) is large at the bottom and small at the top.

These generalizations require cautious analysis because slopes and r^2 could be influenced by the range over which mesurements are made. Fortunately, however, the data (Table 2) suggest that for most regressions, the X and Y variables have similar ranges. For example, the total TP versus chlorophyll a relationship has an average slope of $+1.26$, and the range for both TP and chlorophyll a extends from approximately 2 to 500 $\mu g \cdot L^{-1}$. Similarly, the phytoplankton biomass versus zooplankton biomass regression of McCauley and Kalff (1981) has a slope of $+0.511$, and the data sets range from approximately 30 to 20 000 $\mu g \cdot L^{-1}$ (fresh weight) for both zooplankton and phytoplankton. Because the range of TP equals the range of chlorophyll a and the range of planktivore biomass equals the range of zooplankton biomass, the slopes of the two lines can be compared, and such a comparison suggests that the effect of TP on chlorophyll a is more than twice the effect of chlorophyll a on zooplankton biomass. Similarly, the effect of chlorophyll a on zooplankton biomass is approximately twice as great as the effect of zooplankton biomass on planktivore biomass.

The second unifying characteristic that emerges from the plot of averaged lines is that the variability around the bottom-up regression lines increases by the power of approximately 3.3 (i.e. $r^2 = 0.84^{3.3} = 0.56$, $r^2 = 0.54^{3.3} = 0.13$) (Fig. 4) with every step up the food chain. This, combined with the fact that the variability and slope of the top-down lines (Fig. 4) shows the opposite trend, suggests that perhaps much of the variability in the bottom-up relationships can be explained by top-down effects. For example, the relationship between TP (independent variable) and chlorophyll a has variability that could perhaps be explained by zooplankton biomass. Similarly, the relationship between chlorophyll a (independent) and zooplankton biomass could perhaps be explained by planktivore biomass, and so on. In the following analysis, we have investigated these possibilities by comparing 95% confidence intervals for each of the average bottom-up regressions with the slopes and ranges of the top-down relationships and estimating the proportion of

unexplained variability that could be explained by the trophic level above (consumer or top-down control).

Beginning at the bottom of the food web, the variation around a chlorophyll a biomass of 31.6 is 28.0–35.5 $\mu g \cdot L^{-1}$ (95% confidence interval) based on $n = 140$ OECD and Canadian lakes (Janus and Vollenweider 1981). The next trophic level is zooplankton biomass, and the top-down data show that the relationship between zooplankton biomass and chlorophyll a is weak and that the slope is not significantly different from zero. It must be concluded, therefore, that zooplankton biomass does not influence chlorophyll a in any predictable way and cannot account for any of the variability in the TP $-$ chlorophyll a regression. However, the biomass of large *Daphnia* has a surprisingly strong effect on chlorophyll a biomass (Fig. 2), and over the range used in the enclosure experiments a change in the biomass of large *Daphnia* from 10 to 1000 $\mu g \cdot L^{-1}$ ww can change chlorophyll a from 31.6 to 5.5 $\mu g \cdot L^{-1}$, which is more than enough to explain all of the variability in the TP $-$ chlorophyll a regression. The 95% confidence interval derived from the data of Mills and Schiavone (1982) (Table 2) ranges from 48.9 to 204.2 $\mu g \cdot L^{-1}$ dw around a mean zooplankton biomass of 100 $\mu g \cdot L^{-1}$ dw, and the 95% confidence interval based on the data of Pace (1984) ranges from 66 to 295 $\mu g \cdot L^{-1}$ dw (Table 2) around a zooplankton biomass of 141 $\mu g \cdot L^{-1}$ dw. The trophic level above zooplankton is planktivore biomass, and the top-down data (Fig. 4) show that as planktivores range from 0 to 2000 $\mu g \cdot L^{-1}$ (0–100 kg·ha^{-1}), zooplankton biomass changes from 700 to 400 $\mu g \cdot L^{-1}$ dw in the spring and from 90 to 25 $\mu g \cdot L^{-1}$ dw in the summer (Post 1984). Such changes are enough to explain almost all of the variability around the empirical chlorophyll a $-$ zooplankton biomass regression. Finally, the variability around the zooplankton biomass $-$ planktivore biomass regression (based on Mills and Schiavone 1982) ranges from 35 to 287 planktivore units based on a mean of 100 units. Because there is no top-down regression (Fig. 4) that relates piscivores and planktivores, it cannot be shown that this variability can be explained in terms of piscivore biomass, but the expectation is that the top-down relationship is very strong and will explain the observed variability. This conclusion is supported by the relationship between fish yield (dependent variable) and percentage predatory fish ($r = -0.574$) observed in 43 Polish pikeperch lakes (Bonar 1977).

The Model: Eutrophic and Oligotrophic Systems

The model (Fig. 5) that emerges from this analysis bears some similarity to the HSS model proposed by Hairston et al. (1960) and Slobodkin et al. (1967). Like the HSS model, our treatment (Fig. 5) predicts that producers (chlorophyll a) are primarily regulated by nutrient supply and are only influenced by predators (zooplankon biomass) when large *Daphnia* are present. Both models (Fig. 5) also predict that zooplankton are strongly influenced by carnivores (planktivores) although the eutrophic pelagic (EP) model predicts that maximum attainable zooplankton biomasses are set from below and that divergence from this mean is controlled from above. Finally, the HSS model predicts that carnivore biomass is controlled from below. This is, in part, contrary to the predictions of the EP model which suggests that planktivores are strongly influenced by piscivore biomass, and that piscivore regulation is attained through a combination of self-regulation and regulation by resource (prey) availability based on the biomass of benthic organisms and benthivorous fish.

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PISCIVORE BIOMASS

PLANKTIVORE BIOMASS

DAPHNIA > 1 mm BIOMASS   ZOOPLANKTON BIOMASS

PHYTOPLANKTON OR CHLOROPHYLL BIOMASS

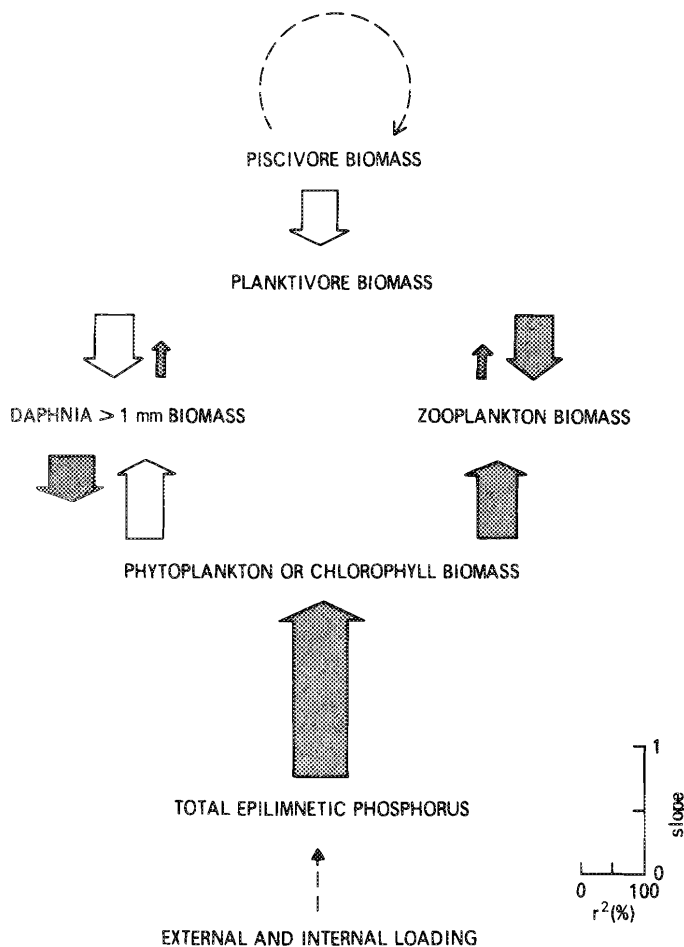TOTAL EPILIMNETIC PHOSPHORUS

EXTERNAL AND INTERNAL LOADING

FIG. 5. Flow diagram showing the relative influence of each trophic level on other trophic levels. The length of each arrow represents the magnitude of the effect (slope). The width of each arrow represents the proportion of variability accounted for by the regression (r^2). A scale for r^2 and slope is given in the lower right corner of the figure. The single broken line joining loading and TP is supported by many studies but has not been quantified in this model. The broken line joining piscivores to piscivores is hypothesized to be strong but the relationship cannot yet be supported by empirical data. The open arrow joining piscivores and planktivores represents a *minimum* estimate based on the empirical relationship between planktivores (independent) and piscivores (equations 19 and 20, Table 2). We hypothesize that experimental results will show that the relationship is stronger than indicated. The open arrows joining planktivores to *Daphnia* and phytoplankton to *Daphnia* are equal to the relationships obtained for planktivore biomass and zooplankton biomass and for chlorophyll *a* and zooplankton biomass, i.e. *Daphnia* are assumed to be no different than "average zooplankton." Subsequent analysis will be required before this estimate can be finely tuned.

The test of any model must lie in its ability to predict or perhaps even to explain field observations. In at least two cases the EP model fails to do this. The first involves a study by Yan et al. (1982) which shows that in Mountaintop Lake, there was a strong negative correlation between phytoplankton biomass and the biomass of *Diaptomus minutus* and *Bosmina longirostris*. Since neither are "large *Daphnia*," the EP model predicts that this should be impossible. The second example comes from Stenson et al. (1978) who showed that when roach (*Leuciscus rutilis*) were removed from Lake Lilla Stockelidsvatten, the dominant zooplankter changed from *B. longirostris* to *Eudiaptomus gracilis*, that *Chaoborus* increased, that water

clarity improved, and that primary production decreased. Again, without the presence of "large *Daphnia*," the EP model would not make this prediction.

The solution to this disagreement perhaps lies in the fact that both Mountaintop Lake and Lake Lilla Stockelidsvatten are oligotrophic and the EP model is based on top-down data from a eutrophic lake. Support for this possibility comes from the work of Brocksen et al. (1970) and Oksanen et al. (1981). Oksanen et al. (1981) showed that at low productivities, the effect of herbivores on producers (top-down) should be great, but that as productivity increases, the impact of herbivores on plant communities should decrease. In the case of Brocksen et al. (1970), the evidence which supports this model came from three lakes that contained sockeye salmon (*Oncorhynchus nerka*). In Lake Owikeno, productivity was low and the regression between sockeye biomass (independent) and zooplankton biomass was strongly negative. Data from the more productive Lake Babine—Nilkitkwa showed a similar negative relationship and a higher mean level of zooplankton biomass. Data from the most productive lake, Dalnee, showed little effect of fish on zooplankton and the highest zooplankton biomass. Brocksen et al. (1970, fig. 13) speculated that a similar relationship should exist between zooplankton biomass (independent variable) and phytoplankton.

Combining the Brocksen et al. (1970) and Oksanen et al. (1981) models with the EP model produces a more complete treatment (Fig. 6) which predicts that as productivity increases, top-down control at lower trophic levels weakens and that bottom-up control becomes more dominant. The Oksanen et al. (1981) model also suggests that as productivity increases, top carnivore (piscivore) diversity and biomass increases (Svärdson 1976; Arruda 1979). The conclusion is that increased productivity has two effects: (1) to increase biomass at all trophic levels and (2) to decrease the impact of top-down control. In oligotrophic systems, top-down effects are strong at the primary producer and herbivore level, but with increased nutrient loading and production, top-down control moves up the food web (Fig. 6) so that primary producers are only affected by substantial biomasses of large *Daphnia*.

The general conclusions of this analysis are that when the EP model is revised to account for lake productivity, the patterns commonly observed in both oligotrophic and eutrophic systems are consistent with the predictions made by the model. For both classes of lakes the model predicts that (1) maximum attainable trophic level biomasses are set by bottom-up effects (2) the top-down effects of piscivores on planktivores will always be strong, (3) planktivores will have a $\log_{10}$:$\log_{10}$ linear negative impact on zooplankton biomass and (4) a nonlinear production-dependent impact on zooplankton species composition and size selection, and (5) when planktivores are reduced or absent, invertebrate predators (McQueen 1969; Neill and Peacock 1980; Yan et al. 1982) will influence the structure and perhaps the biomass of the zooplankton community. The revised EP model also predicts that (6) in eutrophic lakes, only large-bodied zooplankton are efficient enough to have negative impacts on phytoplankton biomass, but (7) in oligotrophic systems, small-bodied zooplankton (Stenson et al. 1978; Yan et al. 1982) can reduce nutrient-limited phytoplankton populations. Finally, the model predicts that (8) algal biomass has no measureable effect on TP concentrations.

The Model: Implications for Lake Management

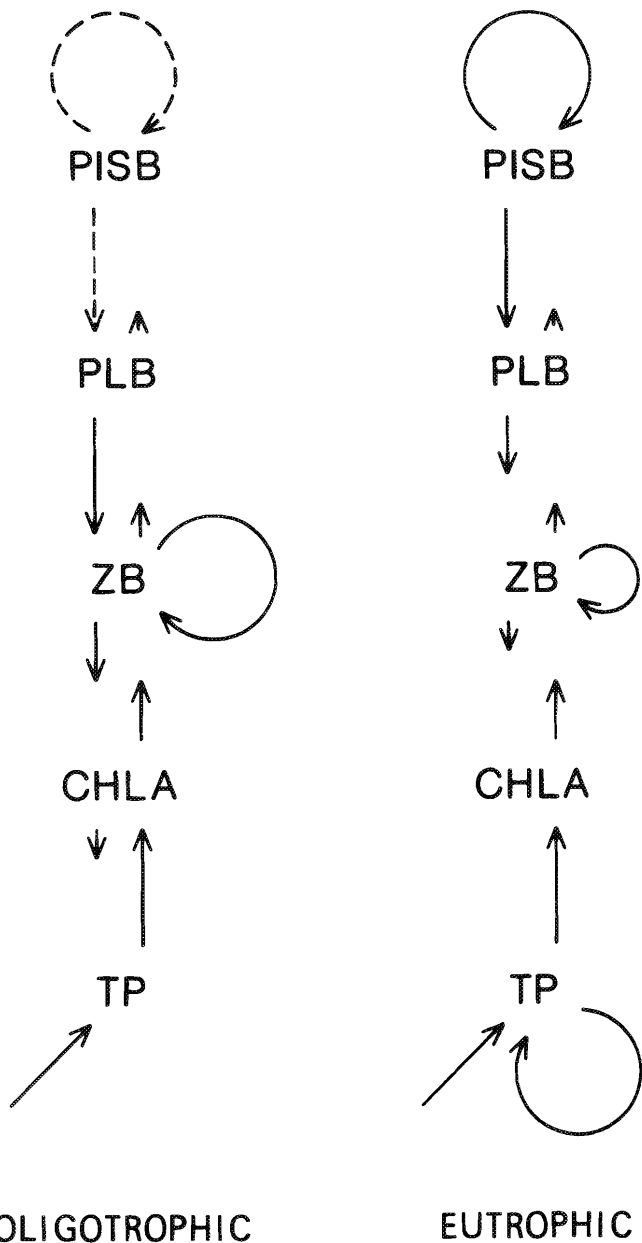The modified EP model makes two predictions that are appli-

FIG. 6. Comparison of trophic level dynamics in oligotrophic and eutrophic pelagic freshwater systems. The lengths of the arrows indicate the relative importance of the interactions. PISB = piscivore biomass, PLB = planktivore bimass, ZB = zooplankton biomass, CHLA = chlorophyll a, and TP = total epilimnetic phosphorus.

cable to biomanipulation and fish enhancement. The first is that increased nutrient additions will have a minimal impact on planktivore production. This prediction derives from the assumption that it is possible to model biomass enhancement using the average bottom-up regression lines (Fig. 4). For example, a 10-fold increase in TP yields a 12-fold increase in chlorophyll a which results in a 4-fold increase in zooplankton biomass and a 1.5-fold increase in planktivore biomass. It is important to recognize, however, that such multitrophic level cascading simulations can be misleading. For example, Hanson and Peters (1984) analyzed producer-controlled empirical relationships for 38 lakes and derived relationships for TP − chlorophyll a, chlorophyll a − zooplankton (crustacean) biomass, and chlorophyll a − zooplankton biomass. Using the

first two regressions, an increase in TP from 10 to 100 $\mu g \cdot L^{-1}$ increases zooplankton biomass from 55 to 253 $\mu g \cdot L^{-1}$ dw. Using the third relationship, a similar increase in TP increases zooplankton biomass from 46 to 371 $\mu g \cdot L^{-1}$ dw. The lack of agreement between the simulated outcomes could be due to either biological or statistical reasons. The statistical explanation derives from the fact that the standard errors on the slopes of the three regressions are large enough to explain the lack of agreement. The biological explanation involves the existence of alternate pathways (bacteria, protozoa) linking TP and chlorophyll a.

A similar analysis applies to the relationship between TP and planktivore biomass. Hanson and Peters (1984) have shown that a 5-fold increase in macrobenthos (dependent variable) is associated with a 10-fold increase in TP, and Hanson and Leggett (1982) have shown that a 3.5-fold increase in fish biomass is associated with a 5-fold increase in macrobenthos (independent variable). Finally, Hanson and Leggett (1982) have shown that a 5-fold increase in fish yield is associated with a 10-fold increase in TP (independent variable). In summary, a 10-fold increase in TP is directly associated with a 5-fold increase in fish yield, with most of the energy moving through the benthic pathway to benthivorous and piscivorous fish. There is also a growing literature which suggests that planktivores are strongly regulated by piscivores. Bonar (1977) showed a negative relationship between percent fish biomass comprising piscivores and total fish yield in 43 Polish pike-perch lakes ($r = -0.574$), and Holčík (1977) working in Klíčava reservoir showed similar negative relationships between percent piscivores and total yield ($r = -0.80$, 1968−72; $r = -0.99$, 1957, 1964, and 1967) and between percent piscivores and yield of forage fish ($r = -0.87$). These relationships all support the conclusion that obligate planktivores are doubly vulnerable. The cascading, bottom-up analysis implies that only about 30% of the potential energy that enters a lake as macronutrients moves directly through the pelagic pathway to planktivores and that about 70% of the potential energy cycles through the macrobenthos to obligate and facultative benthivores. This suggests that the maximum potential biomasses of planktivores should be determined by bottom-up forces, but that realized biomasses should be strongly controlled from above by stable populations of piscivores that can also prey on benthivorous fish and macrobenthos. The management implication is that lake fertilization may increase total fish biomass but will have little effect on planktivore biomass.

The second prediction from the revised EP model is that empirical regressions relating chlorophyll a (dependent variable) to epilimnetic TP should include a subset of eutrophic lakes which have chlorophyll a values that are much lower than expected and that these lakes should have populations of large *Daphnia* that are maintained either by a refuge or by planktivore biomasses that are less than some production-specific minimum biomass. Some limited support for this prediction comes from Osgood (1983) and Vanni (1983) who observed that large populations of large *Daphnia pulicaria* and *Daphnia pulex* were correlated with low algal biomasses. More convincing evidence comes from Hoyer and Jones (1983) and Pace (1984) who found that only "large zooplankton" biomasses could reduce the sum of squares in TP versus chlorophyll a regressions. Many authors have qualitatively shown that the presence of vertebrate predators is associated with reductions in the biomass of large herbivores (Hrbáček 1962; Brooks and

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Dodson 1965; Galbraith 1967; Hall et al. 1970; Hutchinson 1971; Stenson 1972, 1976; O'Brien and de Noyelles 1974; Hall et al. 1976; Anderson et al. 1978; de Bernardi and Giussani 1978; Gophen 1979, 1985). Recently, this relationship has been quantified by Mills and Forney (1983) who concluded that daphnid populations could not be sustained at fish populations $>20-40$ kg·ha^{-1}, by McQueen and Post (1984) who found that *D. galeata mendotae* could not survive at planktivore populations >40kg·ha^{-1}, and by Post (1984) who found that when juvenile perch attained biomasses of 20 kg·ha^{-1}, *D. galeata mendotae* populations declined. Together, these data suggest that when planktivore populations exceed a quantifiable production-dependent biomass, predation rates on large-bodied zooplankton exceed production rates and large-bodied forms are eliminated. This effect will certainly be important in eutrophic systems, but may be less so in oligotrophic lakes where both large and small herbivores can reduce algal standing stocks (Stenson et al. 1978; Yan et al. 1982). This suggests that there will not be a subset of oligotrophic lakes that have chlorophyll *a* concentrations that are lower than expected. The management implication is that in eutrophic lakes where large-bodied zooplankton are required for phytoplankton regulation, managers will have to ensure that production-specific planktivore biomasses are not exceeded. To date, there are no data which will allow us to predict the impact of this strategy on total fish yield, but it is possible that for eutrophic lakes, improved water quality will only be possible when planktivore yields are reduced to unacceptably low levels. In short, the use of biomanipulation for the control of algal standing stocks in eutrophic lakes must be approached with caution.

Acknowledgements

References

ANDERSON, G., H. BERGGREN, G. GRONBERG, AND C. I. GELIN. 1978. Effects of planktivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59: 9–15.

ARRUDA, J. A. 1979. A consideration of trophic dynamics in some tall grass prairie farm ponds. Am. Midl. Nat. 102: 259–264.

BONAR, A. 1977. Relations between exploitation, yield, and community structure in Polish pikeperch (*Stizostedion lucioperca*) lakes, 1966–71. J. Fish. Res. Board Can. 34: 1576–1580.

BROCKSEN, R. W., G. E. DAVIS, AND C. E. WARREN. 1970. Analysis of trophic processes on the basis of density dependent functions, p. 468–498. *In* J. H. Steele [ed.] Marine food chains. University of California Press, Berkeley, CA.

BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size and the composition of plankton. Science (Wash., DC) 150: 28–35.

BURNS, C. W. 1968. The relationship between body size of filter-feeding Cladocera and the maximum size of particle injested. Limnol. Oceanogr. 13: 675–678.

1969. Relation between filtering rate, temperature and body size in four species of *Daphnia*. Limnol. Oceanogr. 14: 693–700.

CANFIELD, D. E. JR., AND C. E. WATKINS. 1984. Relationships between zooplankton abundance and chlorophyll *a* concentration in Florida lakes. J. Freshwater Ecol. 2: 335–344.

CARPENTER, S. R., J. K. KITCHELL, AND J. R. HODGSON. 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634–639.

CASSELMAN, J. M., AND H. H. HARVEY. 1973. Fish traps of clear plastic. Prog. Fish-Cult. 35: 218–220.

DE BERNARDI, R., AND G. GIUSSANI. 1978. Effects of mass fish mortality on zooplankton structure and dynamics in a small Italian lake (Lago di Annone). Verh. Int. Ver. Limnol. 20: 1045–1048.

DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

GALBRAITH, M. G. 1967. Size selective predation of *Daphnia* by rainbow trout and yellow perch. Trans. Am. Fish. Soc. 96: 1–10.

GOPHEN, M. 1979. Extinction of *Daphnia lumholtzi* (Sars) in Lake Kinneret (Israel). Aquaculture 16: 67–71.

1985. Effect of fish predation on size class distribution of cladocerans in Lake Kinneret. Verh. Int. Ver. Limnol. 22: 3104–3108.

HAIRSTON, N. G., F. E. SMITH, AND L. B. SLOBODKIN. 1960. Community structure, population control and competition. Am. Nat. 94: 421–425.

HALL, D. J., W. E. COOPER, AND E. E. WERNER. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15: 839–929.

HALL, D. J., S. T. THRELKELD, C. W. BURNS, AND P. H. CROWLEY. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. Annu. Rev. Ecol. Syst. 7: 177–208.

HANSON, J. M., AND W. C. LEGGETT. 1982. Empirical prediction of fish biomass and yield. Can. J. Fish. Aquat. Sci. 39: 257–263.

HANSON, J. M., AND R. H. PETERS. 1984. Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. Can. J. Fish. Aquat. Sci. 41: 439–445.

HOLČÍK, J. 1977. Changes in fish community of Klíčava reservoir with particular reference to Eurasian perch (*Perca fluviatilis*), 1957–72. J. Fish. Res. Board Can. 34: 1734–1747.

HOYER, M. W., AND J. R. JONES. 1983. Factors affecting the relationship between phosphorus and chlorophyll *a* in midwestern reservoirs. Can. J. Fish. Aquat. Sci. 40: 192–199.

HURLBURT, S. H., J. ZEDLER, AND D. FAIRBANKS. 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*). Science (Wash., DC) 175: 639–641.

HUTCHINSON, B. P. 1971. The effect of fish predation on the zooplankton of ten Adirondack lakes, with particular reference to the alewife, *Alosa pseudoharengus*. Trans. Am. Fish. Soc. 100: 325–335.

HRBÁČEK, J. 1962. Species composition and the amount of zooplankton in relation to the fish stock. Rozpr. Cesk. Akad. Ved Rada Mat. Prir. Ved 72: 1–116.

JANUS, L. L., AND R. A. VOLLENWEIDER. 1981. Summary report. The OECD cooperation programme on eutrophication. Canadian contribution. Scientific Series No. 131. National Water Research Institute, Inland Waters Directorate, Canada Centre for Inland Waters, Burlington, Ont.

LYNCH, M. 1979. Predation, competition and zooplankton community structure: an experimental study. Limnol. Oceanogr. 24: 253–272.

LYNCH, M., AND J. SHAPIRO. 1981. Predation, enrichment and phytoplankton community structure. Limnol. Oceanogr. 26: 86–102.

MCCAULEY, E., AND J. KALFF. 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. Can. J. Fish. Aquat. Sci. 38: 458–463.

MCQUEEN, D. J. 1969. Reduction of zooplankton standing stocks by predaceous *Cyclops bicuspidatus thomasi* in Marion Lake, British Columbia. J. Fish. Res. Board Can. 26: 1605–1618.

MCQUEEN, D. J., AND J. R. POST. 1984. Effects of planktivorous fish on zooplankton, phytoplankton and water chemistry. Lake and Reservoir Management, Proceedings of the Fourth Annual Conference, NALMS, McAfee, NJ, October, 1984.

MECH, L. D., L. D. FRENZEL, SR., R. R. REAM, AND J. W. WINSHIP. 1971. Movements, behaviour, and ecology of timber wolves in northeastern Minnesota. *In* L. D. Mech and L. D. Frenzel, Jr. [ed.] Ecological studies of the timber wolf in northeastern Minnesota. USDA Forest Service Research Paper NC-52.

MILLS, E. L., AND J. L. FORNEY. 1983. Impact on *Daphnia pulex* of predation by young perch in Oneida Lake, New York. Trans. Am. Fish. Soc. 112: 154–161.

MILLS, E. L., AND A. SCHIAVONE, JR. 1982. Evaluation of fish communities through assessment of zooplankton populations and measures of lake productivity. N. Am. J. Fish Manage. 2: 14–27.

NEILL, W. E., AND A. PEACOCK. 1980. Breaking the bottleneck: interactions of invertebrate predators and nutrients in oligotrophic lakes, p. 715–724. *In* W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. University Press of New England, Hanover, NH.

NICHOLLS, K. H., AND P. J. DILLON. 1978. An evaluation of phosphorus chlorophyll–phytoplankton relationships of lakes. Int. Rev. Gesamten Hydrobiol. 63: 141–154.

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O'Brien, W. J., and de Noyelles, Jr. 1974. Relationship between nutrient concentration, phytoplankton density, and zooplankton density in nutrient enriched experimental ponds. Hydrobiologia 44: 105–125.

Oksanen, L., S. D. Fretwell, J. A. Arruda, and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. Am. Nat. 118: 240–261.

Osgood, R. A. 1983. Long term grazing control of algal abundance: a case history. In Lake and Reservoir Management. Proceedings of the Third Annual Conference of the North American Lake Management Society, 1983, Knoxville, TN.

Pace, M. L. 1984. Zooplankton community structure, but not biomass, influences the phosphorus – chlorophyll a relationship. Can. J. Fish. Aquat. Sci. 41: 1089–1096.

Porter, K. G. 1977. The plant animal interface in freshwater ecosystems. Am. Sci. 65: 159–170.

Post, J. R. 1984. Planktivorous fish and the structure of pelagic plankton communities. M.Sc. thesis, York University, Toronto, Ont.

Prepas, E. E., and D. O. Trew. 1983. Evaluation of the phosphorus–chlorophyll relationship for lakes off the Precambrian Shield in western Canada. Can. J. Fish. Aquat. Sci. 40: 27–35.

Sakamoto, M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. Arch. Hydrobiol. 62: 1–28.

Schindler, D. W. 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnol. Oceanogr. 23: 478–486.

Shapiro, J., B. Forsberg, V. Lamarra, G. Lindmark, M. Lynch, E. Smeltzer, and G. Zoto. 1982. Experiments and experiences in biomanipulation — studies of biological ways to reduce algal abundance and eliminate blue-green. EPA-600/3-82-096. Corvallis Environmental Research Laboratory, U.S. Environmental Protection Agency, Corvallis, OR.

Shapiro, J., and D. I. Wright. 1984. Lake restoration by biomanipulation. Round Lake, Minnesota — the first two years. Freshwater Biol. 14: 371–383.

Simenstad, C. A., J. A. Estes, and K. W. Kenyon. 1978. Aleuts, sea otters and alternate stable-state communities. Science (Wash., DC) 200: 403–411.

Slobodkin, L. B., F. E. Smith, and N. G. Hairston. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. Am. Nat. 101: 109–124.

Sprules, W. G., L. B. Holtby, and G. Griggs. 1981. A microcomputer-based measuring device for biological research. Can. J. Zool. 59: 1611–1614.

Stainton, M. P., M. J. Capel, and F. A. J. Armstrong. 1977. The chemical analysis of freshwater. 2nd ed. Fish. Mar. Serv. Misc. Spec. Publ. 25: 166 p.

Stenson, J. A. E. 1972. Fish predation effects on species composition of the zooplankton community in eight small forest lakes. Rep. Inst. Freshwater Res. Drottningholm 52: 132–148.
     1976. Significance of predator influence on composition of Bosmina sp. populations. Limnol. Oceanogr. 21: 814–822.

Stenson, J. A. E., T. Bohlin, L. Henrikson, B. I. Nilsson, H. G. Nyman, H. G. Oscarson, and P. Larson. 1978. Effects of fish removal from a small lake. Verh. Int. Ver. Limnol. 20: 794–801.

Stockner, J. G., and J. S. Shortreed. 1985. Whole lake fertilization experiments in coastal British Columbia Lakes: empirical relationships between nutrient inputs and phytoplankton biomass and production. Can. J. Fish. Aquat. Sci. 42: 649–658.

Story, V. A. 1982. Enclosure experiments on Lake St. George: phytoplankton response to manipulations. M.Sc. thesis, York University, Toronto, Ont.

Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Rep. Inst. Freshwater Res. Drottningholm 55: 144–171.

Taguchi, S., and M. Fukuchi. 1975. Filtration rate of zooplankton community during spring bloom in Akkeshi Bay. J. Exp. Mar. Biol. Ecol. 19: 145–164.

Uhlman, D. 1961. Uber den Einfluss von Planktonorganismen auf ihr Milieu. Int. Rev. Gesamten Hydrobiol 46: 115–129.

van Valen, L. 1973. Patterns and the balance of nature. Evol. Theory 1: 31–49.

Vanni, M. J. 1983. Biological control of nuisance algae by Daphnia pulex: experimental studies. In Lake and Reservoir Management. Proceedings of the Third Annual Conference of the North American Lake Management Society, 1983, Knoxville, TN.

Vijverberg, J., and W. L. T. van Densen. 1984. The role of the fish in the foodweb of Tjeukemeer, The Netherlands. Verh. Int. Ver. Limnol. 22: 891–896.

Ward, J. 1955. A description of a new zooplankton counter. Q. J. Microsc. Soc. 96: 371–373.

White, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia (Berl.) 3: 71–86.

Yan, N. D., C. J. Lafrance, and G. G. Hitchin. 1982. Planktonic fluctuations in a fertilized, acidic lake: the role of invertebrate predators, p. 137–154. In R. E. Johnson [ed.] Acid Rain/Fisheries. Proceedings of the Symposium on Acid Rain and Fishery Impacts in Northeastern North America.

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