transferring alewives from one stream to another for the development and maintenance of commercial runs (Rounsefell and Stringer 1943; Walton and Smith personal communication) have undoubtedly contributed to the spread of this disease and should be considered in the future management of this species. A case in point is the transfer, during the time of this study, of prespawning adults from the Damariscotta River fishery to Adams Pond in Boothbay for the initiation of a new spawning run. At the time of transfer, alewives from the Damariscotta fishery were exhibiting a 70% incidence of PEN.

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Comparison of an Ecological Model of Lake Ontario and Phosphorus Loading Models[1]

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SCAVIA, D., AND S. C. CHAPRA. 1977. Comparison of an ecological model of Lake Ontario and phosphorus loading models. J. Fish. Res. Board Can. 34: 286–290.

Predicted responses of Lake Ontario to phosphorus loads from two empirical relationships and an ecological model were compared. Predictions of annual average concentrations of total phosphorus and chlorophyll *a* by the ecological model were consistent with those predicted by the simpler models. We concluded that the use of a particular type of model is governed by the nature of the problems being addressed rather than an inherent superiority of either approach.

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Nous comparons les réponses du lac Ontario à des charges de phosphore prédites à partir de deux relations empiriques et d'un modèle écologique. Les prédictions des concentrations moyennes annuelles du phosphore total et de la chlorophylle *a* dérivées du modèle écologique

s'accordent avec celles dérivées des modèles plus simples. Nous en concluons que l'emploi d'un type de modèle particulier est dicté par la nature des problèmes étudiés plutôt que par une supériorité inhérente de l'une ou de l'autre approche.

THE use of mathematical models of lake eutrophication in environmental management has been strongly endorsed by the U.S. Environmental Protection Agency (1971) and is the basic reason for most modeling programs. These models generally have developed along two lines: phosphorus load models and ecosystem models. The former use empirical correlations to relate lake trophic state to simple expressions of hydrology, morphometry, and phosphorus loading and are most notably represented by the loading plots of Vollenweider (1968, 1975) and Dillon and Rigler (1974a, b). These empirical models typically employ macroscopic parameters, such as mean annual concentration of total phosphorus or summer concentration of chlorophyll *a*, to assess trophic state. Ecosystem models (Park et al. 1974; Thomann et al. 1975; Lehman et al. 1975), on the other hand, represent a more mechanistic approach designed to simulate the seasonal dynamics of various components of lake biology and chemistry. Since both approaches address the same processes, albeit on different scales, their predictions should be consistent. If this can be shown to be true, then the selection of the type of model to be used for a specific application is more a matter of the scope of the problems to be addressed than of an inherent superiority of either approach. The primary purpose of the present note is to show, by comparing the output of an ecological model (i.e. an ecosystem model built upon ecologically sound process formulations) of Lake Ontario with predictions from some phosphorus loading models, that within certain limits the approaches agree reasonably well.

The ecological model — The ecological model was developed originally by Scavia et al. (1976a) for Lake Ontario and has been applied successfully to other Great Lakes (Scavia et al. 1976b). It has been modified and improved for the present analysis and calculates the dynamics of the following state variables on a daily basis:

Available P	5 groups of phytoplankton
NH_3	6 groups of zooplankton
NO_3	Inorganic C system
Dissolved organic N	Sedimentary C
Soluble reactive Si	Benthic macroinvertebrates
Particulate Si	Detrital C

The model treats the lake as homogeneous in the horizontal plane and segments it vertically into two layers representing epi- and hypolimnion. A physical model is used to calculate changes in segment thickness, temperature, and transport in response to winds and temperature at the air–water interface.

Each state variable in the ecological model is described by a differential equation composed of the sum of important biological and chemical processes affecting the concentration of that substance (e.g. photosynthesis, grazing, respiration, remineralization, excretion, defecation). Physical processes are also simulated. Sedimentation, diffusion, and gas exchange at the air–water interface are all computed within the model as functions of the seasonal environmental conditions (i.e. temperature, wind). External loadings of the state variables are considered as constant throughout the year and added, as a lake-wide average, to either the epilimnion or the whole lake, depending upon whether or not the lake is stratified. Additional details of the model's mathematical structure and the interrelationships of the above variables are presented elsewhere (Scavia et al. 1976a).

Comparison with phosphorus loading models — The ecological model is compared below with two models representative of the phosphorus loading approach. The first, developed by Vollenweider (1969) and modified by Dillon and Rigler (1974b) to predict mean annual concentration of total phosphorus for a lake at steady state, is formulated as follows:

$$p = \frac{L(1 - R_p)}{\rho z} \qquad (1)$$

where p is the mean annual concentration of total phosphorus (milligrams per cubic metre), ρ is the inverse of the water retention time (per year), z is the mean depth (metres), L is the areal load of total phosphorus to the lake (milligrams per square metre per year), and R_p is the phosphorus retention coefficient. Chapra (1975) suggested the following relationship to calculate R_p:

$$R_p = \frac{v}{v + q_s} \qquad (2)$$

where v is the apparent settling velocity of total phosphorus (metres per year), and q_s (outflow divided by lake surface area) is the areal water

load (metres per year). Chapra (1975) evaluated v empirically, and his value of 16 m/yr is used in the following comparisons. Equations (1) and (2) can be combined to yield

$$p = \frac{L}{16 + q_s} \qquad (3)$$

since $q_s = \rho z$.

The ecological model was run for 5–20 yr to reach steady state under a variety of loading conditions for Lake Ontario. Mean annual total phosphorus was determined by summing the annual integrated concentrations of available phosphorus and phytoplankton, zooplankton, and detrital phosphorus. The latter three were calculated by assuming a fixed stoichiometric composition of organic matter of 41:7.2:1 for C:N:P on a weight basis (Redfield et al. 1963). A similar ratio (35–51:7.7:1) can also be determined by examining the relative fractions of particulate organic carbon, nitrogen, and phosphorus in Lake Ontario (Stadelmann et al. 1974; Stadelmann and Fraser 1974).

A comparison of the models (Fig. 1) shows that the predictions of p are quite consistent. This is particularly interesting considering there are large differences between Lake Ontario and the lakes used to derive equation (3). For example, the mean depth of Lake Ontario is 86 m, whereas the mean depth of the lakes used to derive equation (3) is 10 m. The consistency is also significant when one considers the vast differences be-

tween the models. For example, equation (3) uses a constant settling velocity for total phosphorus, whereas the ecological model calculates individual sinking rates for detrital phosphorus and each phytoplankton group based on size, shape, and the seasonal variations in temperature and phytoplankton "vigor."

The second comparison is between the ecological model and the following equation derived by Dillon and Rigler (1974a) relating the concentration of spring total phosphorus to that of summer chlorophyll a:

$$[\text{Chl } a] = 0.0731 \, [P_v]^{1.449} \qquad (4)$$

where [Chl a] is the mean epilimnetic concentration of chlorophyll a during summer (milligrams per cubic metre), and [P_v] is the concentration of total phosphorus in the spring (milligrams per cubic metre). [Chl a] values are determined from the ecological model by integrating epilimnetic values of phytoplankton carbon (C:Chl $a = 50$) for the period from mid-May to the beginning of September (Dillon and Rigler's definition of summer). The ecological model was again run under a variety of loading conditions. While steady state values are not required for Dillon and Rigler's correlation, the spring total N:P ratio must be > 12. This is an empirically defined threshold below which equation (4) breaks down. Sakamoto (1966) hypothesized that this is due to nitrogen taking precedence as the primary limiting nutrient at ratios < 12. This hypothesis was supported when results from the ecological model simulations were compared with equation (4). For points representing N:P > 12, the correlation between the ecological model prediction and equation (4) is good ($r = 0.85$), although the scatter increases at higher values of phosphorus (Fig. 2). For points representing N:P < 12 (not on Fig. 2), however, the agreement deteriorates, with the chlorophyll values falling below Dillon and Rigler's line as would be expected if something other than phosphorus were limiting.

Since the ecological model is a mathematical representation of the proposed mechanisms operating within the lake, the limitations of its dynamics can be determined directly. For N:P > 12, as phosphorus levels increase, first phosphorus and then phosphorus and light are the predominant factors limiting phytoplankton growth. Nitrogen never approaches levels at which it significantly influences seasonal phytoplankton dynamics. For N:P < 12, however, nitrogen gains importance to the point where, at very low N:P levels, phosphorus is no longer the major control of algal productivity in the model. This may seem self-evident, but it suggests a possible use of
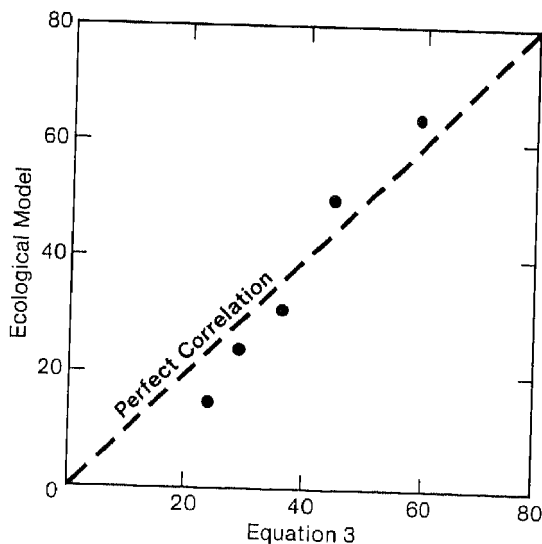
Fig. 1. Comparison of total phosphorus concentration (milligrams per cubic metre) as calculated by the ecological model and by equation (3).
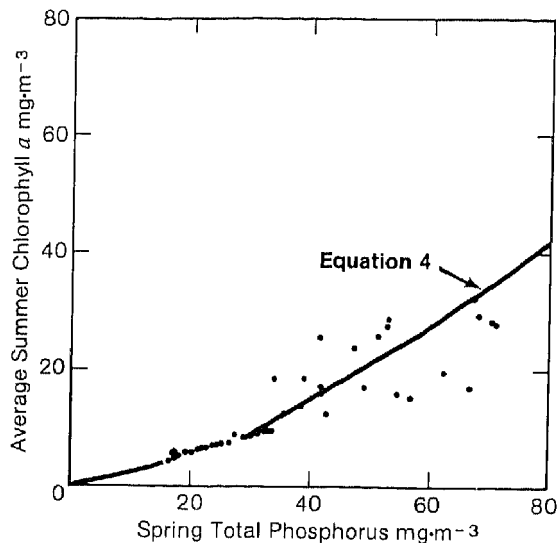
FIG. 2. Comparison of ecological model results (points) with Dillon & Rigler's (1974a) correlation (line) between average summer chlorophyll a and spring total phosphorus.

ecological models in elucidating the mechanisms of the more macroscopic modeling approaches.

When spring phosphorus concentrations are above approximately 75 mg/m³, the two approaches diverge. While Dillon and Rigler's correlation continues to show an exponential relationship of chlorophyll a to phosphorus, the ecological model levels off, with nutrient limitation becoming subsidiary to light as the major factor governing lake productivity. A possible explanation is that the ecological model was developed for a large mesotrophic lake — Lake Ontario (spring phosphorus ~ 20 mg/m³) — and certain mechanisms specific to hypereutrophic systems may not be included (e.g. heightened feedback of phosphorus from the sediments when the hypolimnion is anoxic). When Schindler (1976) compared two regression equations, developed from EPA-National Eutrophication Survey data and International Biological Program data, with equation (4) he observed a similar divergence at higher P concentrations. This anomaly should be investigated further.

At present the ecological model is being modified to include mechanisms describing more eutrophic processes and is being applied to several eutrophic lakes. When this is completed, the model will again be compared with phosphorus loading models to see if the modifications affect the consistency of the approaches for these hypereutrophic conditions.

The agreement between the model predictions indicates that model selection should be based

upon the scope of the problems to be addressed. That is, if one is interested in the effects of phosphorus loadings on the annual average concentration of total phosphorus or chlorophyll, the loading concept approach should be used. These models have been designed for that purpose and provide quick, inexpensive estimates of the loading impact. If one is interested in investigating the effects of external loads on seasonal dynamics of various components of a lake ecosystem, interactions among these components, or the nature of the components themselves, an ecological model should be used. These models generally represent mathematical aggregates of a number of aquatic biological and chemical processes and can provide more detailed predictions of the effects that will result.

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Factors in Interpreting Data Obtained by Diel Sampling of Fish Stomachs[1]

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A simple differential equation model describing the level of food in the stomach, incorporating simultaneous ingestion and gastric evacuation, is used to gauge the sensitivity of methods that utilize diel change in food level of the stomach to determine diel feeding activity of fish. Analysis of model behavior under different feeding regimes shows that diel pattern of food level in the stomach is less sensitive to feeding regime than many authors claim.

An expression is derived for the magnitude of bias associated with cessation of feeding and continuance of gastric evacuation while fish are retained by the fishing gear. This bias may be reduced by minimizing sampling time and accelerating preservation of captured fish in experiments to determine feeding chronology and daily ration.

Dans le but d'évaluer la sensibilité de méthodes utilisant le changement nycthéméral de la quantité de nourriture dans l'estomac pour déterminer le cycle alimentaire journalier des poissons, l'auteur se sert d'une simple équation différentielle décrivant le niveau de nourriture dans l'estomac et incorporant l'ingestion et l'évacuation gastrique simultanées. L'analyse du comportement du modèle sous différents régimes d'alimentation démontre que le cycle journalier du niveau de nourriture dans l'estomac est moins sensible au régime d'alimentation que ne le soutiennent plusieurs auteurs.

On obtient du modèle une expression de la grandeur du biais associé à l'arrêt de l'alimentation et à la continuation de l'évacuation gastrique pendant que les poissons sont retenus par l'engin de pêche. Un moyen de diminuer ce biais est de réduire au minimum le temps d'échantillonnage et de préserver le plus rapidement possible les poissons capturés lors d'expériences visant à déterminer la chronologie alimentaire et la ration quotidienne.

IT is a common practice to determine the diel timing of feeding for fish populations by observing daily variation in the level of food in the stomach (Darnell and Meierotto 1962; Girsa 1975; Gjösaeter 1973; Holton 1969; Merrett and Roe 1974; Narver 1970; Swenson and Smith 1973). The level of food in the stomach varies as a function of the rates of food ingestion and gastric evacuation. As these rates are simultaneous and interdependent, accurate description of diel variation in rate of food ingestion by the aforementioned methodology depends on consideration