USE OF GROWTH MODELS OF FISH AND ZOOPLANKTON FOR TOP-DOWN CONTROL IN SUCCESSFUL BIOMANIPULATION

トップダウン方式によるバイオマニピュレーションのための 魚類一動物プランクトン成長モデルの検討

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ABSTRACT
A fish biomass growth model is developed based on the bioenergetics which is then combined with the zooplankton biomass growth model to form a prey predator relationship. The mortality of zooplankton is linked with the food consumption of fish through the energy content of the food and the caloric value of zooplankton, thus quantifying the zooplankton biomass depletion. These models were combined with the phytoplankton model to observe the phytoplankton variation in the lake. All parameters for fish model were implemented for the bluegill and single species of zooplankton (cladocerans) representing the total biomass was assumed. The simulated results were compared with the laboratory data collected from the published literatures. The simulation results of fish and zooplankton biomass were fairly compatible with the laboratory and field data. The total amount of food, in terms of zooplankton, that the fish required during the summer was found to be much less than the existing zooplankton concentration showing significantly low predation pressure. However the food requirement was much higher in spring, depleting the zooplankton concentration severely.

Keywords: Bioenergetics; biomanipulation; fish; lake ecosystem; numerical model

1. INTRODUCTION
The term ‘biomanipulation’ was originally defined as management of aquatic communities by controlling natural populations of organisms aimed at water quality improvement (Shapiro et al., 1975). In a broad sense, biomanipulation term is similar to top-down-forces, trophic cascade interactions or food-web manipulation; these terms refer to manipulation of secondary or tertiary aquatic producers and its impact on the community structure (Gophen, 1990). Earlier the limnologists had focussed on the lake systems consisting of unidirectional control through the nutrients, phytoplankton, zooplankton and the fish. Hurlbert et al., (1972) suggested that manipulation of fish populations, especially through artificial enhancement of piscivore populations could be a potential method of reduction of phytoplankton levels in lakes. This idea was supported by the observations of Zaret and Paine, (1973) and further experimental work by Shapiro et al., (1975) who emphasized, removing or stocking fish can be a promising tool for biomanipulation. Hosper and Jagtman, (1990) supplemented, a drastic reduction of the planktivorous and benthivorous fish stock may induce a shift from the turbid water state to clear water state. Most of the further approaches have focused on manipulation of zooplanktivorous fish and zooplankton population to increase grazing pressure on phytoplankton (Shapiro and Wright, 1984).

The focus of our study is to study the changes in phytoplankton concentration as a result of decreased fish stock by developing a simple fish and zooplankton biomass growth model and applying them with the phytoplankton model. The fish biomass model is based on the bioenergetics model developed by Kitchell et al., (1974), Kitchell and Stewart (1977). The use of bioenergetics model is an economical, reasonably accurate and feasible method for simulating growth. These models offer much potential for ecosystem analysis. By quantifying the consumption rates of predators, critical links in the trophic structure and critical periods of interaction can be located (Kitchell et al., 1977; Stewart et al., 1983), which can be of tremendous help for the lake managers.
2. MODEL
The model has three main components, planktivorous fish, zooplankton and the phytoplankton with the necessary nutrient components. The modeling approach for fish is based on the bioenergetics principle. Zooplankton model is developed at this stage as a single constituent representing the total zooplankton. Phytoplankton model developed by Asaeda and Bon (1997) has been used.

2.1 Fish
The change in biomass of fish is defined by the energy budget equation with all units expressed as biomass equivalents and on a per day basis. Fish means zooplanktivorous fish in our model and all the parameters have been used for bluegill fish as available as possible. In some cases where the data for bluegill was not available, data from the other fishes close to bluegill have been used. A bioenergetics model essentially accounts for the energy intake by fish (Elliot, 1979; Ursin, 1979; Kitchell, 1983). The basic equation is:

\[
\frac{dB}{Bdt} = C - (R + F + U)
\]

Energetic equations used are described below. The calculations are based on specific consumption rates, equivalents in biomass, on a per day basis. The total rates can be calculated as the product of specific rates and fish weights.

\[
C = C_{\text{max}} \cdot P \cdot r_e
\]

\[
C_{\text{max}} = a_1 w^{b_1}
\]

\[
r_e = (V^{x})(e^{x(1-v)})
\]

\[
V = \frac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}}
\]

\[
F, U = C_o T^{b_2} e^{b_3}
\]

Consumption, the rate of feeding, C is defined as a function of the maximum rate for an individual fish of a given size at a specified temperature. Cmax is the maximum weight specific ration at the optimum temperature, Topt, for consumption and a, and b, are regression constants. P is a proportionality constant having values between 0 and 1.0 used to adjust the ration. r_e is a temperature dependent proportional adjustment (i.e. 0 to 1.0) of consumption rate. The value of r_e reaches a maximum of 1.0 at the optimum temperature and declines rapidly to zero at the maximum temperature, T_{\text{max}}. The consumption is the equivalent of fish weight in grams, which is later converted to equivalent of zooplankton biomass by the energy content (caloric values of fish and zooplankton). Respiration rate is dependent on weight, ambient temperature and the amount of food eaten. Rmax is the maximum weight specific respiration rate at optimum temperature and a, and b, are regression constants and r_R is similar to r_e with temperature values for respiration. S is the specific dynamic action coefficient and depends on consumption. F and U are waste losses due to egestion and excretion respectively.

2.2 Zooplankton
Zooplankton have been modeled as a single constituent representing total zooplankton. Cladocerans are considered to be the one representing total zooplankton hence all the parameters used in the model are for cladocerans. Zooplankton dynamics are governed by the general process of growth, respiration and excretion. The general zooplankton equation which forms the basis for the model is (EPA, 1985; Matsuka and Goda et al., 1986):

\[
\frac{dz}{dt} = (G_z - R_z - M_z)z - Pm_z
\]
Where,

\[ G_z = I_{z_{\text{max}}} I_z I_z e F A z (1 - \frac{z}{C_z_{\text{max}}}) \]
\[ I_z = \frac{F_T - F_o}{Kz + (F_T - F_o)} \]
\[ M_z = M_z R \theta^{T-20} \]
\[ I_T = \theta z \theta^{(T-23)} \]

\( Z \) is the zooplankton biomass (g/m³); \( G_z \) is the growth rate of zooplankton which is dependent on nominal maximum grazing rate, \( I_{z_{\text{max}}} \), temperature, \( I_T \), assimilation coefficient, \( F A z \), and concentration of edible phytoplankton, \( I_z \). \( F_T \) is the total edible food available and \( F_o \) is the threshold food concentrations. \( C_{\text{abs}} \) and \( C_{\text{bg}} \) are the concentrations of non-blue green and blue green biomass and \( P_f \) and \( P_f \) are the preference ratios. Respiration and non-predatory mortality have been treated as the simple function of temperature. The predatory mortality is a function of temperature, fish biomass and light intensity etc. The predatory mortality fluctuates greatly as the fish stock decreases and increases allowing the zooplankton to grow and graze on phytoplankton. We have calculated the predatory mortality, \( P_m \), based on the food consumption of fish in the fish model.

2.3 Phytoplankton

We did not develop the indigenous phytoplankton model because there are many such models already developed and tested with satisfactory results. We have used one such model developed by Asaeda and Bon (1997). The details of this model are beyond the scope of this paper, however we have listed the main state equation for the phytoplankton growth. For the details of the model, readers are referred to Asaeda and Bon (1997).

\[ \frac{d Chl_i}{dt} = G_m \theta^{T-20} Chl_i \left[ f(I_i) f(IP_i) f(IN_i) f(S_i) \right] - k_i \theta^{T-20} Chl_i - k_m \theta^{T-20} Chl_i - k_z \theta^{T-20} Chl_i \]

Where \( Chl_i (i=1,2,3) \) is the chlorophyll-a concentration of diatom, green and blue green (mg/m³), \( IP_i \) and \( IN_i \) are the internal phosphorus and Nitrogen concentration (P mg or N mg per Chl mg), \( k_r, k_m, k_z \) are the coefficients of respiration, mortality and zooplankton grazing on phytoplankton (per day), respectively. \( z \) is the zooplankton biomass, \( Chl_{\text{ini}} \) is min Chl-a level for zooplankton grazing (mg/m³), \( G_m \) is the maximum rate of phytoplankton growth. \( \theta \) is the temperature multiplier for growth, respiration and mortality and \( P_f \) is preference factor. Internal phosphorus, internal nitrogen, phosphate, nitrate, ammonium, silica and BOD are other state variables of the model.

3. RESULTS AND DISCUSSION

The computational period started from the beginning of January for 365 days. The time interval was kept to be one day to account for the daily biomass change of fish and zooplankton. In the calculation, length:depth:width ratio of 8:2:1 for fish and 4:1:1 for zooplankton and density of 1 g/cm³ were assumed which gives \( W=0.01L^3 \) for fish and \( W=0.03L^3 \) for zooplankton as length and weight relationship (Gerritsen, 1984). The dry to wet weight ratio of zooplankton was taken as 0.20 (Peters, 1984). Each model was run separately and together to obtain various results. The lake was considered to be shallow and hence no temperature stratification was considered. Since the temperature constitutes a major determinant of growth, the model is restricted to the sites where temperature data have been available. We have used the temperature data reported from the shallow lakes in Netherlands.

Fig. 1 shows the simulation of bluegill biomass compared with observed data over a period of 365 days. The simulation compared favourably with the data from the laboratory conditions. Starting with 2.5 g/m³, it reached nearly 45 g/m³ at the end. The simulated value did not exceed the observed value. The increase in
biomass was slower at the beginning due to the lower temperature regime and higher in June to August with highest feeding level at optimum temperature and slower again towards the end of the year.

We simulated the biomass with various initial biomass concentrations (0.1, 0.5, 2.5, 12.5 g/m³) to observe the changing pattern of increase or decrease at the end of the year (Fig.2). The maximum biomass observed with initial concentration of 12.5 g/m³ was around 55 g/m³ and tended to decrease after reaching a maximum threshold value whereas for 0.1 g/m³, it was around 35 g/m³ and tended to increase further. The difference in changing pattern was similar with uniform change for the 0.1, 0.5 and 2.5 g/m³. The differences in the total biomass after a year were considerably small. This may highlight the point that the appropriate time at which the reduction of fish stock needs to be done. Also, the reduction of initial biomass concentration from 12.5 gm³ to 0.1 g/m³ did not result in a very high reduction in the increasing pattern and the total biomass concentration which may explain the reason why some of the lakes, such as, Sonderleijen, and Breukeleveense plas did not show any improvement after >75% fish reduction.

Fig. 3 is a simulation result of zooplankton biomass without the predation pressure of planktivorous fish. The data for zooplankton biomass for a year without the fish predation is difficult to find, however we compared the simulation result with the observed zooplankton biomass of the lake Zwemlust in 1987 after refilling the lake in March when the fish stock was reduced by 98% to 10 kg/ha. The simulated result matches fairly well in the increasing period and the maximum biomass, however the decreasing rate was more rapid in the observed value mainly because there were still some fish remaining in the lake. Fig 4. Shows the simulated zooplankton biomass in the presence of fish. The simulation results show the depletion of zooplankton biomass quite rapidly; by the middle of June, the initial zooplankton of 1 g/m³ drops to a very low level. We also simulated the threshold fish biomass for zooplankton to sustain until the summer when they could grow exponentially, but the value obtained was quite low (>2 g/m³ which is equivalent to 20 kg/ha considering the lake is approximately 1 m deep).
This low value could be because fish food was only limited to zooplankton and also the effect of piscivorous fish was not taken into account. With this, we can roughly say that the fish stock reduced to less than 2 g/m³ at the beginning of the year can reduce the predation pressure on zooplankton even without the presence of piscivorous fish. It is documented in the literature, for a successful restoration by biomanipulation the initial planktivorous fish should usually be reduced to a value less than 150 kg/ha (Hosper, 1986) but it is not clearly mentioned whether it is with piscivorous fish or without it. However the value of 150 kg/ha seems more reasonable in the presence of piscivorous fish.

Fig. 5 is the comparison of cumulative zooplankton biomass of predation pressure free environment and the equivalent biomass required by fish (for initial biomass of 2.5 g/m³) for their food. The result shows the demand for food clearly exceeding supply until the summer but zooplankton abundance could be several orders of magnitude higher in the peak period without the predation pressure. Fig 6 shows the simulation of phytoplankton biomass compared with the observed values in lake Bleiswijkse Zoom in Netherlands (without fish means the reduced fish predation pressure i.e., after manipulation). Before manipulation the phytoplankton concentration (Bleiswijkse Zoom mainly consisted of greens and blue greens) ranged from 20 to 140 mg/m³ that is the fish pressure on zooplankton was intense. After the removal of fish (84% removal was done from 760 kg/ha to 120 kg/ha) the phytoplankton biomass was very low. It was obviously due to the reduced predation pressure on zooplankton.

4. CONCLUSIONS

Model simulations show that the growth of planktivorous fish is an important issue to be dealt with; only the drastic reduction of such fish stocks do not help in the long run. We also observed that, amount of zooplankton, the fish used for food in the month of May until August was much less than the potential zooplankton biomass in the lake, however, the fish food requirement before the beginning of summer was higher than the available zooplankton during which the zooplankton got suppressed. Control of phytoplankton with reduced fish predation pressure was also simulated well by the model. It was clearly seen from the simulated results that the reduction of planktivorous fish or natural winter kill is not sufficient for the long term clearing of lakes because planktivorous fish stock will grow quite rapidly making it unsuitable for the following year. This emphasises the need for other means to be taken together with planktivorous fish reduction such as introducing the piscivorous fish and enhancing the appropriate condition for aquatic vegetation. The role of vegetation is also highly important as they help reduce the phytoplankton by competing for nutrients, by providing shelter for zooplankton and by reducing wind induced resuspension of the sediments.

We attempted to compute the desirable level of planktivorous fish and the quantitative relationships with zooplankton for the application of biomanipulation through the bioenergetics models, although this requires...
further knowledge of the prey predator relationship of planktivorous fish and zooplankton for more accuracy. Bioenergetics models are a practical way to achieve such information with reasonable effort (Hewett and Stewart, 1989). The model presented here, obviously, has many shortcomings such as the uncertainty and the errors of field and laboratory data, uncertainty in the inputs used as forcing functions to the model. Also, the influence of numerous other biological activities other than the ones used in the model add up to the complexities. This type of modelling is connected with a lot of uncertainties coming from different phases of model development (Meyer and Jorgenson, 1983; Van Straten, 1983). Nonetheless, development of such modelling tools as an aid to the research and management strategies seems to be of considerable interest because the trivial knowledge obtained from such simple modelling works could lead to a solution of much larger problems later.

REFERENCES