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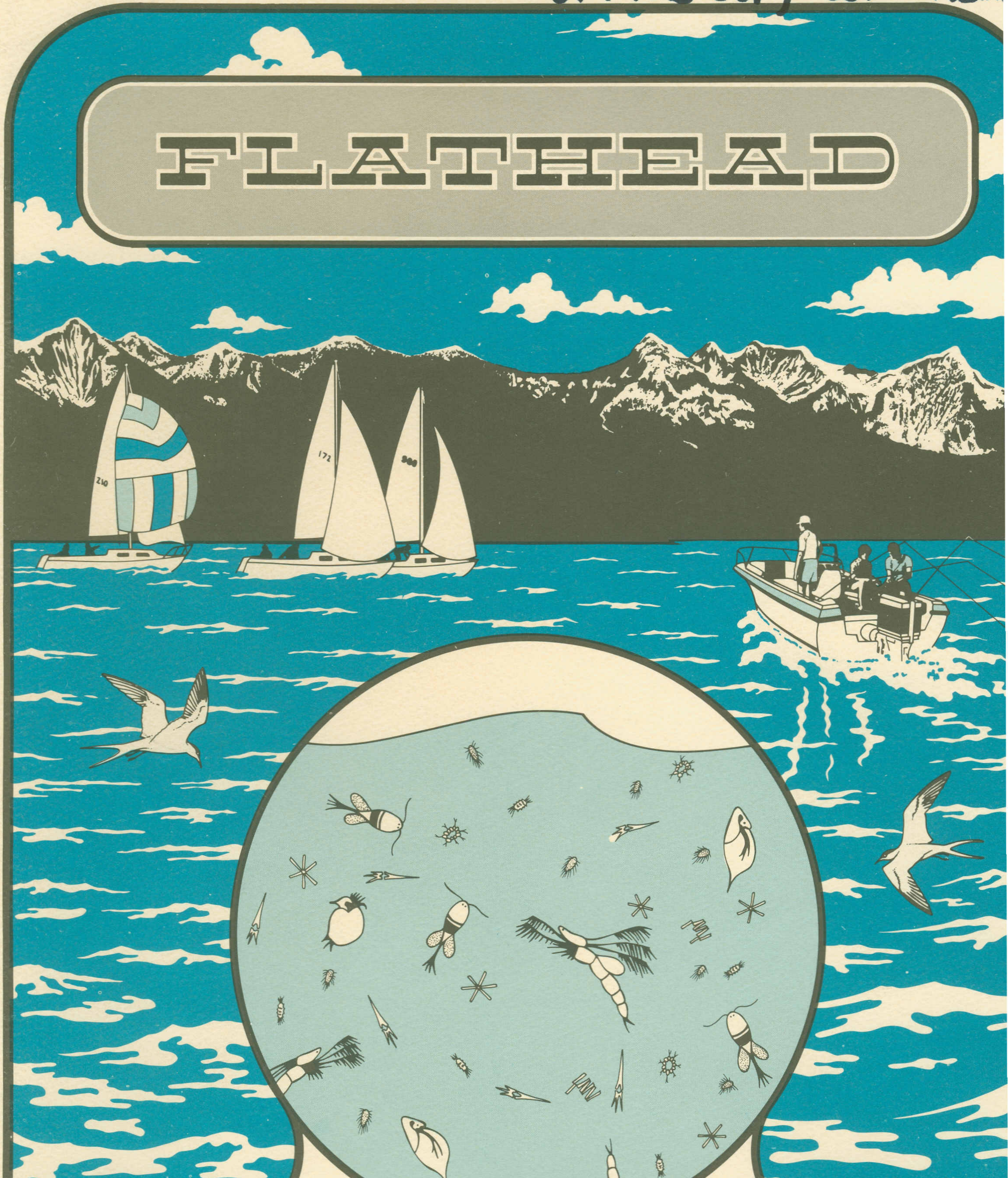
# FLATHEAD



# A SIMULATION STUDY OF FLATHEAD LAKE PHOSPHOROUS DYNAMICS

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Sponsored By: FLATHEAD RIVER BASIN ENVIRONMENTAL IMPACT STUDY, U.S. E.P.A.

# A Simulation Study of Flathead Lake Phosphorus Dynamics: Final Report

by

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# INTRODUCTION

Stanford et al. (1983) showed that production of phytoplankton in Flathead Lake is limited by bioavailability of phosphorus in the water column. They also showed that most (>>90%) of the phosphorus mass entering the lake was derived from external sources (i.e. atmospheric deposition on lake surface, riverine inflow, and point discharges of urban sewage effluent). The annual phosphorus load was thought to be abnormally high, due to anthropogenic acceleration of phosphorus recruitment within the drainage basin (e.g. increased input of sediment-phosphorus via the Flathead River in response to large scale deforestation; >17% of total phosphorus mass entering the lake was derived from wastewater treatment plants serving the urban centers in the Basin).

The magnitude of impact from external phosphorus loading has been difficult to estimate. In order to evaluate this relationship experimentally, one would have to measure primary production over a manipulated range of inputs to the lake: a costly and politically unacceptable solution. Also, we were interested in variables other than primary production as measures of the consequences of accelerated eutrophication. Limnologists have long recognized that eutrophication is much more complex than the simple "phosphorus causes algal growth" statement often seen in the literature. Other variables may influence lake productivity. For example, what are the implications of changes in the zooplankton community to the lake trophic state? Other authors (e.g., Bartell 1981; Henry unpubl.) have noted that alterations in zooplankton size distributions can influence pelagic phosphorus dynamics and thus, a lake's trophic status. We used the existing data base and knowledge of the system (Stanford et al. 1983) to develop a simulation model of pelagic phosphorus dynamics. We used the model to predict the response (e.g. primary productivity; phosphorus turnover time) of the pelagic community in Flathead Lake to changes in the available phosphorus pool. We were also able to simulate phosphorus dynamics in response to changes in plankton size distributions and in response to the effects of grazing (i.e. zooplankton on phytoplankton) and predation (i.e. fish on zooplankton).

## STUDY AREA

Flathead Lake and its drainage basin are located in the northwest portion of Montana and the southeast corner of British Columbia, Canada (Figure 1). The drainage basin makes up a major watershed in the upper Columbia River system and lies in the southern portion of the Rocky Mountain Trench. The Flathead Basin is an important recreational resource and water quality is generally considered to be excellent.

Flathead Lake is one of the largest natural freshwater lakes in the western United States and has a surface area of slightly more than 510 $km^2$ at full pool. It has a mean depth of 50 m and a relatively short hydraulic retention time of 2.2 years. Except for years of ice cover the lake remains mixed during the winter and is stratified only during the summer months. Stanford et al. (1983) detailed morphometric and biophysical attributes of Flathead Lake.

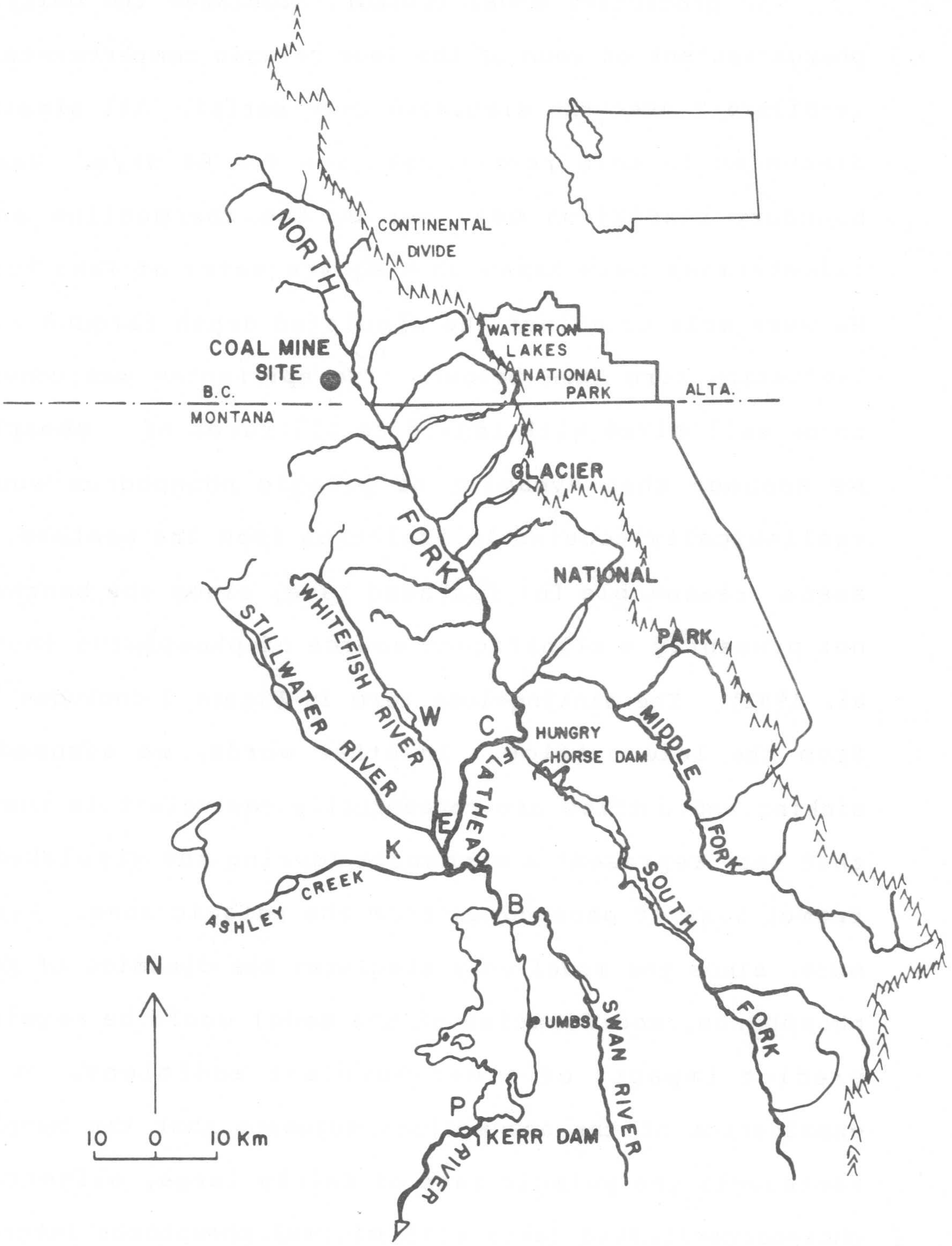

Figure 1. The upper Flathead River Basin showing the major tributaries contributing water to Flathead Lake. Locations of major towns are shown by P (Polson), B (Bigfork), K (Kalispell), E (Evergreen), W (Whitefish), and C (Columbia Falls).

# METHODOLOGY

The predictive model (FLTHD) calculates the daily phosphorus content of each of the four pelagic compartments shown in Figure 2 over the simulated time period. All simulations discussed in this report were run for 60 days. Vertical boundary conditions were set by the thermocline and our calculations were based on a square meter of lake surface. We were able to adjust the simulated depth through a light limitation term (see below). The epilimnion was considered to be well mixed with regard to all forms of phosphorus. We assumed that dynamics of pelagic phosphorus would be realistically modeled in isolation from the benthos. This seems reasonable for Flathead Lake, since the benthos are not presently a significant source of phosphorus (Moore et al. 1982). The sinking-loss term in Figure 2 includes losses from the lake outflow. In other words, we assumed that sinking and outflow are conceptually equivalent in the sense that they represent a permanent (during the simulated time frame) loss of phosphorus from the pelagic zone. Furthermore, since the model only simulates the dynamics of pelagic phosphorus, modification of the model would be required to predict impacts of other nutrient additions. A close examination of the assumptions suggests that the model best represents the pelagic zone of fairly large, oligotrophic, phosphorus-limited lakes with minimal phosphorus interaction between the pelagic areas and the benthos or littoral zones. Additionally, since the relative importance of each of the variables in our model is probably lake-specific, the conceptual structure we used may require some modification prior to use in other systems.

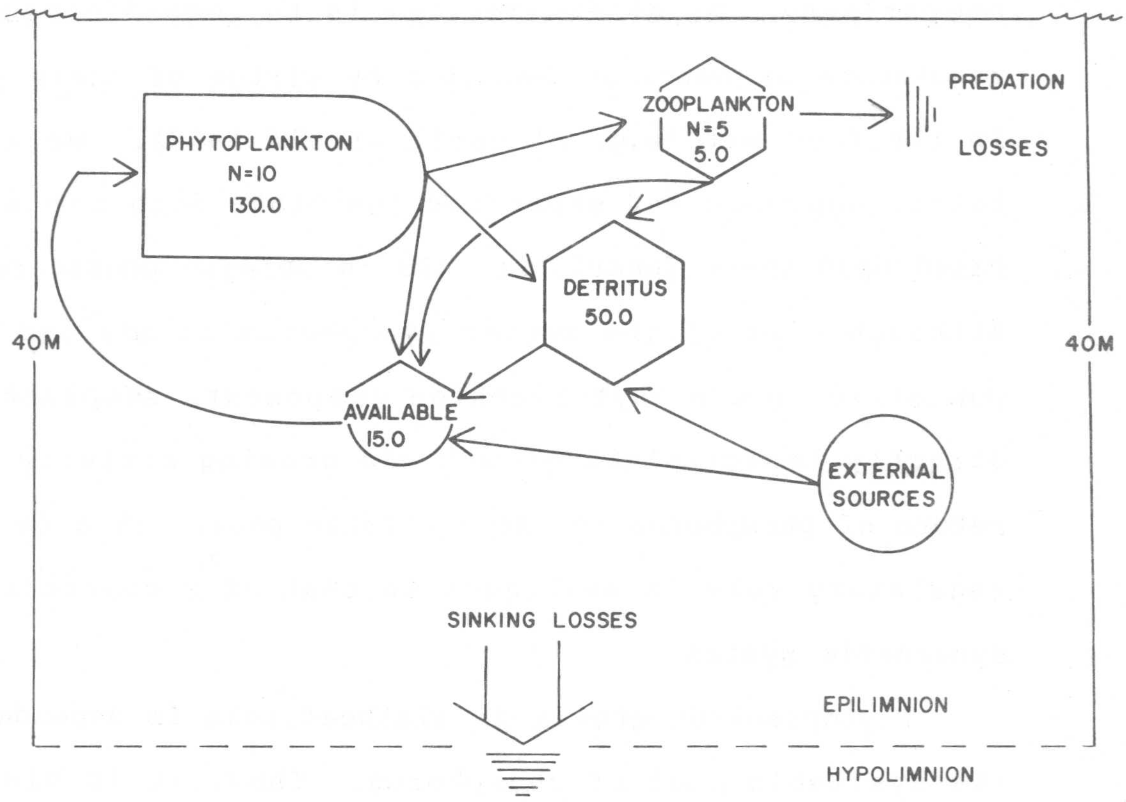

Figure 2. Flow diagram of the systems model, FLTHD, showing flows and initial conditions (expressed as mg phosphorus/$m^3$ in N size classes) of the four compartments used in the simulations.

Although we did not explicitly model fish biomass, we did include size selective predation as a major determinate of zooplankton size distributions (e.g. Brooks and Dodson 1965). There are currently two major views on the role of consumers in eutrophication models. One is that because of their relatively small use of total ecosystem energy flow, consumers are unimportant and may, therefore, be eliminated from modeling efforts. This approach has led to the development of empirical models which describe the relationship between phosphorus loading and primary production, and between total phosphorus and water clarity, among other comparisons. An alternate view is to regard consumers as regulators of nutrient dynamics by virtue of their position in the food web (e.g. Kitchell et al. 1979). We took the latter approach and separated the biota into compartments based upon their functional role in pelagic phosphorus flow. Although most of the system phosphorus at any one time is contained in the phytoplankton component, zooplankton can directly impact algal growth via grazing activity and the return of phosphorus to the available pool. In a sense this regulatory role is analogous to that of a controller in a cybernetic system.

Phytoplankton growth in Flathead Lake is dependent upon the available pool of phosphorus. Thus, it is clear that replacement rates directly regulate primary production. The model provides two mechanisms for replacement of available phosphorus. First, combined external sources (i.e. riverine, ground water and atmospheric inputs) add nutrients to either the available or detritus pool. The model does not allow for a separation of these inputs into individual sources. On an annual average, external loading is the major source of nutrients to Flathead Lake, and it should also be noted that the lake receives most of its nutrient input during spring runoff (Stanford et al. 1983). The second mechanism of phosphorus replacement in the epilimnion is one we term biotic recycle. This includes zooplankton excretion, phytoplankton leakage and the decomposition of detritus. Other studies (Scavia 1979), have shown this may be a significant source of nutrients under certain conditions. The structure of FLTHD allowed us to estimate the relative contributions of each of these mechanisms.

Initial conditions for the model were obtained from a variety of sources (Table 1). Rates of external phosphorus loading, phytoplankton primary productivity, and concentrations of available phosphorus, were obtained from ongoing field studies (Stanford et al. 1983). Transfer coefficients were modified by both temperature and light prior to calling the equation solving routine. We used a simple linear function to simulate light limitation: when the light limiting variable equaled 1.0, the depth to 1% light level was equal to 40 m. Lowering the light variable causes a

Table 1. Selected initial conditions for the simulation model, FLTHD.

| VARIABLE | DESCRIPTION | INITIAL VALUE | UNITS | SOURCE |
|---|---|---|---|---|
| Lake Wide: | | | | |
| DIP | Available phosphorus | 15 | mg $P/m^2$ | Stanford et al. (1983 ) |
| TEMP | Temperature array | 10-20 | °C | Stanford et al. (1983 ) |
| ENRICH | External loading | 1-20 | mg P $m^{-2}$ $day^{-1}$ | Stanford et al. (1983 ) |
| FISH | Standing crop of planktivores throughout simulation | 5* | mg $P/m^2$ | Adapted from Leathe and Graham (1982) |
| LIGHT | Light limitation term | 1 | Unitless | Estimated: Sets photic zone = 40 m |
| PHYTOPLANKTON (i = 1,10): | | | | |
| $P_i$ | Standing crop | 60-300* | mg $P/m^2$ | Stanford et al. (1983 ) |
| $L_i$ | Leakage rate | 0.000004 | $day^{-1}$ | Estimated |
| $S_i$ | Sinking rate | 0.013-0.103 | $day^{-1}$ | Titman and Kilham (1976) |
| $K_i$ | Half-saturation constant | 180-540 | mg $P/m^2$ | Adapted from Eppley et al. (1969) |
| ZOOPLANKTON (j = 1,5): | | | | |
| $Z_j$ | Standing crop | 5* | mg $P/m^2$ | Adapted from Leathe and Graham (1982) |
| $E_j$ | Excretion rate | 0.16-0.08 | mg P $m^{-2}$ $day^{-1}$ | Adapted from Barlow and Bishop (1965) |
| $P_{mj}$ | Loss rate to predators | variable: ~1%/day | Unitless | Estimated |
| $NP_{mj}$ | Nonpredatory mortality | 0.002 | $day^{-1}$ | Hall (1964) |
| $DF_j$ | Defecation rate | 0.35 | $day^{-1}$ | Bartell and Breck (1979) |
| $SI_j$ | Size-specific predation coefficients | 0.1-0.9 | Unitless | Bartell and Breck (1979) |

*converted to phosphorus assuming a C:P ration of 106:1.

proportionally equivalent reduction in the photic zone. For example, in the model a light value, equal to 0.5, limited the depth of the photic zone to 20 m. A simplified flowchart of FLTHD appears in Table 2. The basic structure (e.g., gains - losses) of the differential equations solved by the program is shown below.

Table 2. A simplified flowchart of FLTHD.

1. Set initial values and variables:
    - A. Plankton size classes
    - B. Modify flux rates by temperature, light
2. Call equation solving subroutine and calculate daily rate of change for each compartment value.
3. Update compartment values.
4. Iterations complete
    - A. No............Go to 1B
    - B. Yes...........Call output subroutine

Phytoplankton were divided into 10 size classes based upon field data (Stanford et al. 1983). We did not attempt to distinguish between different taxonomic groups in this simulation, but FLTHD can be used to accomplish this when more data concerning community structure are available. Algal growth was described by:

$$dP_i/dt = \text{Uptake} - P_i(L_i + S_i) - G_i \qquad (1)$$

where:

Uptake = a Monod-defined and temperature-dependent phosphorus uptake rate (mg $m^{-2}$ $day^{-1}$);

$P_i$ = phosphorus content (mg P $m^{-2}$) of phytoplankton class i;

$L_i$ = leakage rate ($day^{-1}$) of phytoplankton class i;

$S_i$ = sinking rate ($day^{-1}$) of class i; and,

$G_i$ = grazing (mg P $m^{-2}$ $day^{-1}$) loss ofphytoplankton of class i.

Zooplankton were grouped into 5 size classes ranging from 0.5 to 3.0 mm in length. Again, we did not attempt to make taxonomic distinctions. The literature strongly suggests that the major determinate of the role of zooplankton in phosphorus dynamics is their size distributions (Bartell 1981). Zooplankton growth was calculated by:

$$dZ_j/dt = G_j - Z_j(E_j + PM_j + NPM_j + DF_j) \qquad (2)$$

where:

$G_j$ = grazing input to zooplankton class j (mg $m^{-2}$ $day^{-1}$);

$Z_j$ = phosphorus content (mg $P/m^2$) of zooplankton class j;

$E_j$ = excretion rate of zooplankton class j;

$PM_j$ = predatory mortality of class j;

$NPM_j$ = nonpredatory mortality of class j; and

$DF_j$ = defecation rate of zooplankton class j.

Grazing was modeled after Bartell and Breck (1979) and included both upper and lower feeding thresholds, size dependent maximum filtering rates, differential availability of algal cells and temperature effects.

Available phosphorus was modeled after Lean (1973) and detritus was assumed to decompose at a linear, temperature-dependent rate. Compartment values were updated every 12 hours using a Runge-Kutta numerical solution scheme and the model printed daily values over the specified time period.

## RESULTS

Stanford et al. (1983) presented measured values (5 year averages) of total phosphorus and primary production. Moreover, they compared these values with the output of several analytical models and concluded that they had measured all of the major components of the lake's phosphorus budget. The simulation model falls out fairly well in this comparison (Table 3). Actually, it seems to predict primary production somewhat better than the analytical model of Vollenweider and Kerekes (1980) used by Stanford et al. (1983), because their 95% confidence intervals overlapped both predicted values (i.e. p-loading corrected, $L_c$, and uncorrected $L_o$, for sediment-p bioavailability: Figure 21, Stanford et al. 1983). The simulated primary production value may actually be closer to actuality than the measured value in Table 3 indicates. The model calculates net primary production, whereas the $^{14}C$ method, used to obtain the measured value, yields estimates somewhere between net and gross production (Peterson 1980). Also, most of the primary production measurements (Stanford et al. 1983) were made on cloudless days, and they may have therefore overestimated annual production. Hence, the actual value of net primary production is probably somewhat less than the value presented by Stanford et al. (1983). In any event, both simulated and measured values of primary production indicate that Flathead is an oligotrophic lake (e.g. Wetzel 1983). Based upon a combination of other measures, Stanford et al. (1983) classified the lake as oligo-mesotrophic.

Table 3. Comparisons between two analytical models, the lake simulation model and measured values of total phosphorus (corrected for bio-availability: Stanford et al. 1983a) and primary production.

| | Total Phosphorus ($mg/m^3$) | Primary Production ($g\ C\ m^{-2}\ yr^{-1}$) | Reference |
|---|---|---|---|
| Measured | 7.2 | 137.9 | Stanford et al. (1983 ) |
| Analytical Model | | 68.7 | Vollenweider and Kerekes (1980) |
| Analytical Model | 5.7 | | Larsen and Mercier (1976) |
| Analytical Model | 7.2 | | Vollenweider (1975) |
| Simulation Model | 5.35 | 105.30* | This report |

* converted to carbon by assuming a C:P ratio of 106:1

Simulated dynamics of the zooplankton biomass at baseline (i.e. 15 ug/l) ambient concentrations of phosphorus in the water column revealed an oscillatory behavior around a mean value slightly higher than the initial condition of 5 mg $P/m^2$ (Figure 3). There was an initial decline followed by a gradual buildup to a mean value of about 6.2 mg $P/m^2$. An interesting observation consistent with other research was the relationship between the two dominant size classes. The larger of the two classes in the simulation had a higher growth rate and would therefore be expected to outcompete the smaller form. However, the model includes size specific predation (Table 2) and the 1.75 class was more susceptible to planktivory. Apparently, predation maintained population densities at levels where competitive exclusion was impossible. In other words, fish predators maintain diversity within the modeled prey community.

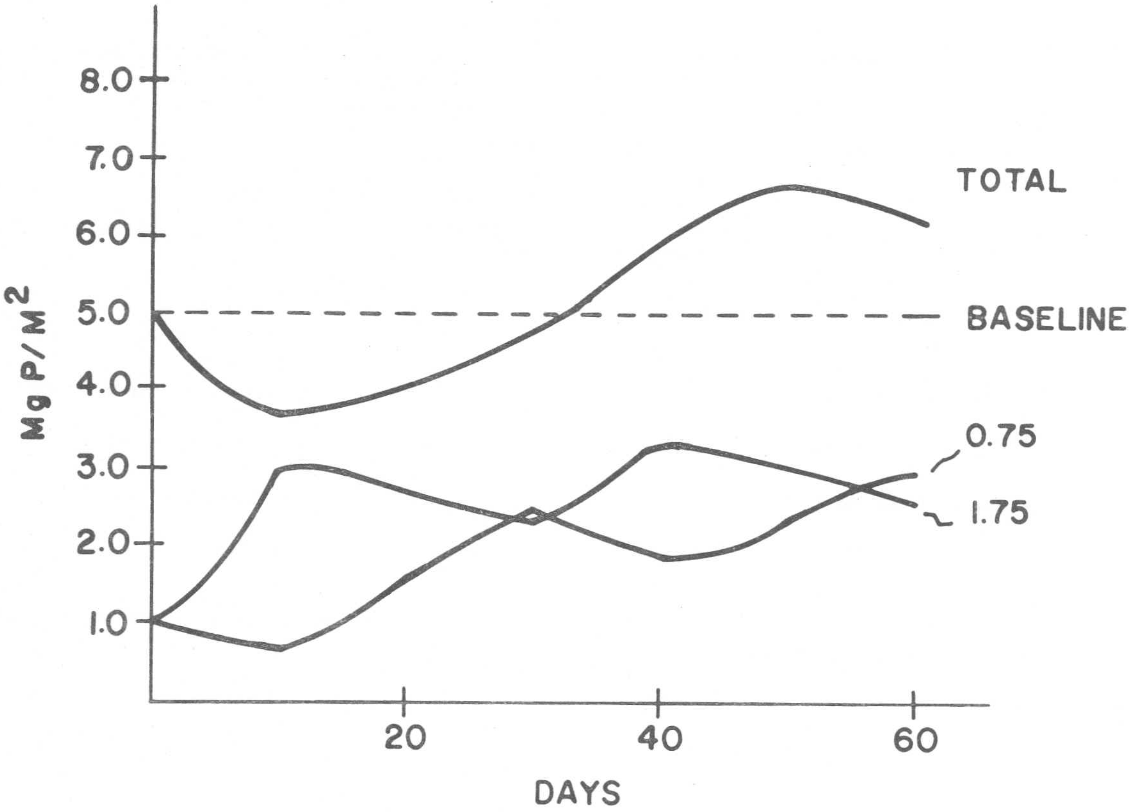

Figure 3. Simulated dynamics of the two most abundant size classes (0.75 and 1.75 mm) of zooplankton biomass (expressed as mg P/m$^2$) compared to total zooplankton biomass.

As previously mentioned, the model provided for two mechanisms of available phosphorus replacement; biotic recycle and external loading. The relative contribution of each of the biological groups to the total recycle rate is shown in Table 4. These figures do not include external loading data. We define recycle simply as the biotic replacement of available phosphorus. In Flathead Lake, this typically amounts to ca. 10% of the external load. Although phytoplankton recycle appears high, it is consistent with values obtained in other modeling studies (e.g., Scavia 1979). The largest portion of the recycle rate is due to zooplankton excretion. Although the 0.75 and 1.75 classes represent almost equivalent biomasses (Figure 3), the smaller size class contributes more than 3 times as much to the recycle rate. This important observation is due to size specific excretion rates incorporated in the model. Fish excretion rates are shown for comparative purposes. The percentage is relatively small (3.7), implying that the major role of fishes in lake nutrient dynamics is mediated through their predation activities (cf. Bartell 1981; Kitchell et al. 1979).

Table 4. Relative recycle rate of phosphorus in the pelagic region of Flathead Lake.

| Variable | | Percent of Total Recycle |
|---|---|---|
| Phytoplankton leakage | | 30.9 |
| Zooplankton excretion (total) | | 45.1 |
| Size class: | 0.75 mm | 19.3 |
| | 1.25 mm | 14.1 |
| | 1.75 mm | 5.7 |
| Decomposition | | 20.3 |
| Fish excretion | | 3.7 |

Using FLTHD we were able to demonstrate the importance of zooplankton in controlling internal phosphorus loading. In the absence of zooplankton grazers the phytoplankton community responds to baseline (i.e. initial model conditions) phosphorus concentrations (15 ug/l) by growing rapidly (i.e. high phosphorus uptake) for almost 20 days, and maintaining asymptotic population levels around 40 mg $P/m^2$ for the duration of the 60 day simulation (Fig. 4). This non-oscillatory growth response simply reflects removal of phosphorus from the water column (Fig. 5), until paucity of phosphorus effectively limits the ability of any size class of phytoplankton to further expand its population. However, distinct oscillatory behavior is introduced into the system when zooplankton are present and feeding on phytoplankton

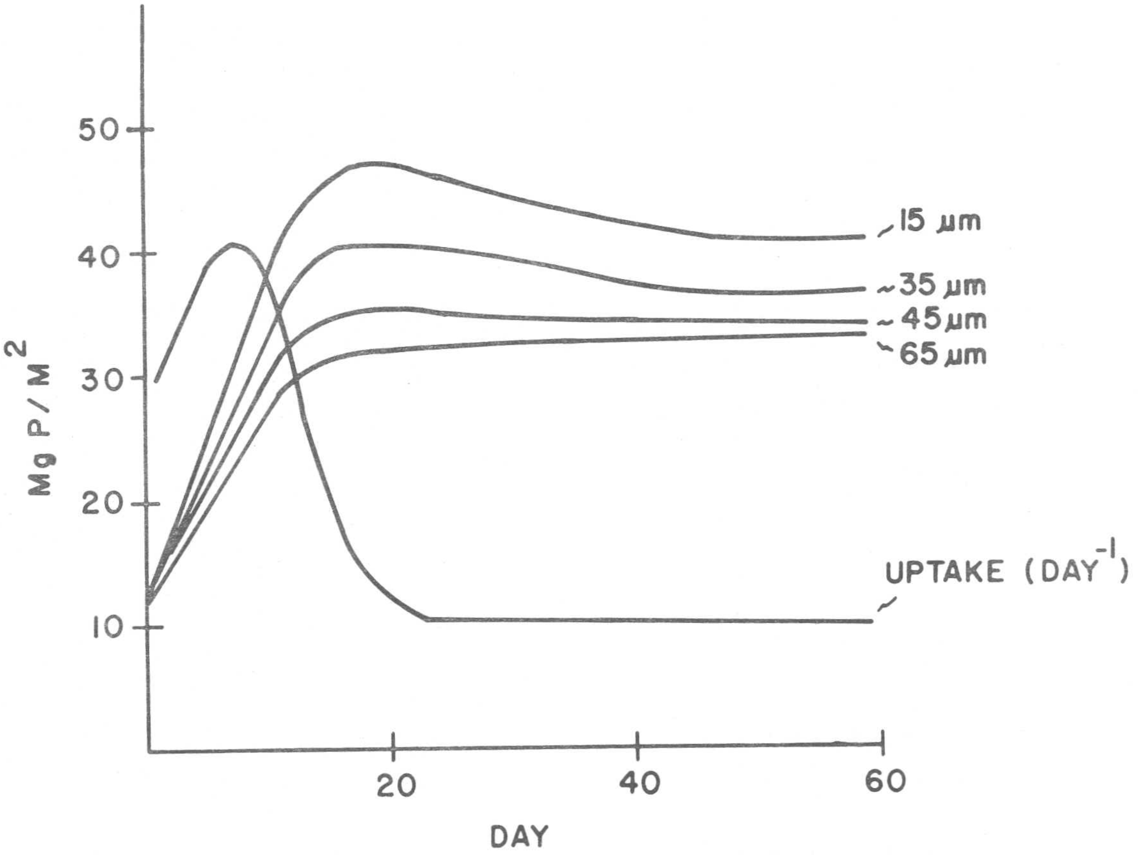

Figure 4. Simulated dynamics of the four most productive phytoplankton size classes and average daily uptake of all phytoplankton under conditions of no grazing.

Removal of grazers prevented phosphorus recycle, due to zooplankton excretion, and also permitted >75% of the available phosphorus pool to become effectively stored in phytoplankton biomass. We concluded that grazers perform the dual role of maintaining phytoplankton at low densities (i.e. preventing blooms) and returning phosphorus to the available pool, thereby manifesting dynamic behavior in the model.

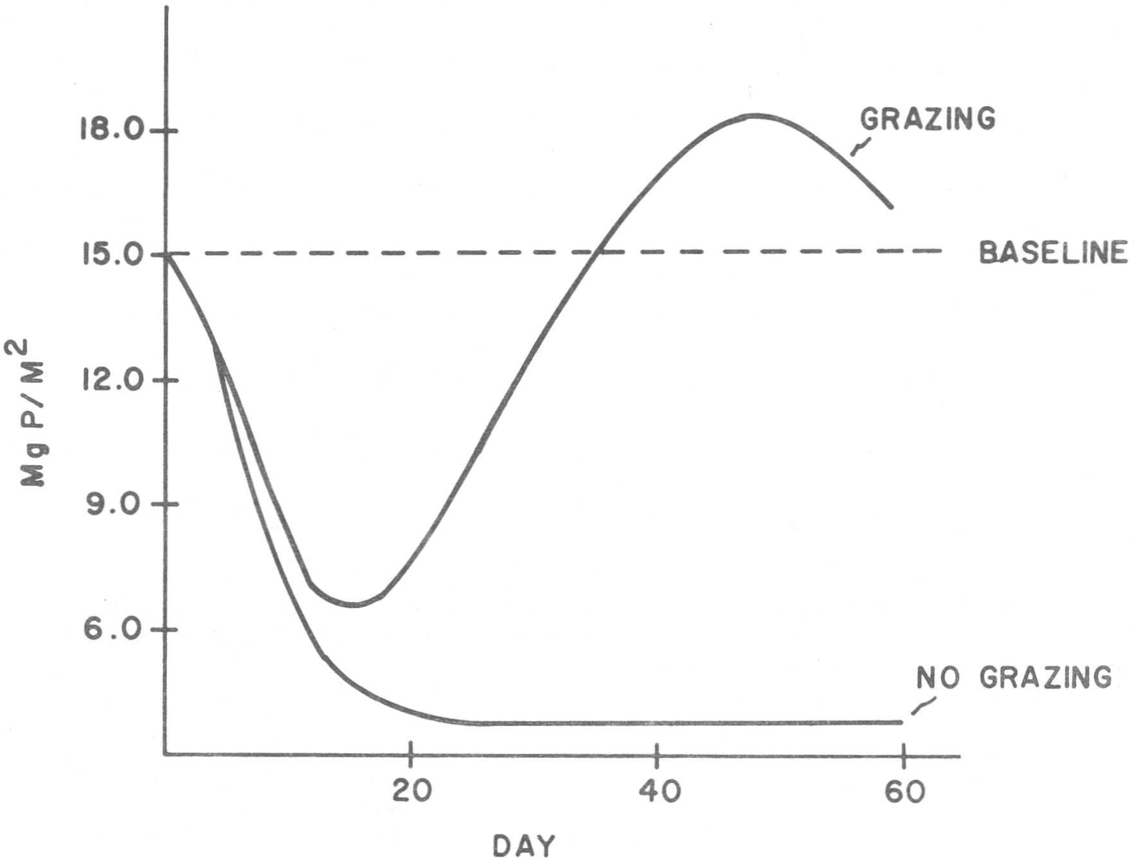

Figure 5. Simulated dynamics of available phosphorus concentrations in the pelagic water column with and without zooplankton grazing upon phytoplankton.

Similarly, the effect of planktivorous fish on pelagic nutrient dynamics appears to be largely mediated through their role in altering the size distributions of zooplankton. We ran a series of simulations within an order of magnitude range of baseline predation in order to assess the implications of altering the intensity of fish predation to the pelagic community. Baseline predation corresponded to a cropping rate of 2% per day. FLTHD predicted that the highest simulated predation intensity would lead to low standing stocks of zooplankton and a dense bloom of phytoplankton (Table 5). Increasing fish predation intensity had the expected impact of decreasing zooplankton mean size and biomass and concomitantly resulted in higher phytoplankton standing stocks and larger algal cells (Table 5). There also was an interesting decrease in zooplankton excretion rates, as predation intensity varied from baseline (Table 5). This demonstrated that zooplankton excretion rates are a function of both body size and the standing crop of biomass; increases in size specific excretion rates were offset by losses in biomass and vice versa (Table 5).

Table 5. Mean daily values of plankton size, standing crop and zooplankton excretion rates as a function of predation intensity above and below baseline conditions (=1.0).

| Predation Intensity X Baseline | Phytoplankton | | Zooplankton | | |
|---|---|---|---|---|---|
| | Total Biomass (mg P/m$^3$) | Cell Diameter ($\mu$m) | Body Length (mm) | Total Biomass (mg P/m$^3$) | Excretion Rate (mg P m$^{-3}$ day$^{-1}$) |
| 0.1 | 80.3 | 19.6 | 1.43 | 15.3 | 0.37 |
| 0.5 | 87.4 | 21.4 | 1.29 | 11.1 | 0.41 |
| 1.0 | 94.5 | 25.7 | 1.09 | 6.2 | 0.48 |
| 2.0 | 99.7 | 29.1 | 0.75 | 4.7 | 0.49 |
| 5.0 | 106.4 | 33.8 | 0.54 | 4.1 | 0.43 |
| 10.0 | 118.3 | 37.2 | 0.50 | 3.6 | 0.39 |

Two important ecosystem response variables of interest in the model were phosphorus turnover time and primary productivity. Phosphorus turnover time was calculated as the time required for a phosphorus molecule to enter and leave the pelagic, trophogenic zone (i.e. upper 40 m) of the lake. Entry can be gained through a variety of external (e.g. riverine inflow, precipitation, groundwater) or internal (e.g. re-suspension from littoral and/or tropholytic areas) sources, whereas losses occur through sinking into tropholytic zone or via lake outflow.

Increasing turnover time means that phosphorus is being retained in the pelagic zone longer and implies that higher production rates will result. Indeed, phosphorus turnover and primary production were positively correlated in our model.

In order to fully evaluate senstivity of the model in predicting rates of phosphorus turnover and primary productivity, we varied each system component by 10% of its baseline value (see Table 1) and observed the resulting percent change in these two response variables.

Changes in external loading (i.e. enrichment) had the largest impact on phosphorus turnover time and primary production (Table 6). The response of phosphorus turnover time was dampened somewhat over the 60 day simulation due to an ameliorating action by the plankton. A somewhat lower response was observed due to changes in zooplankton excretion and phytoplankton uptake rates (Table 6). In general, changes in rate coefficients (e.g. excretion, uptake) tended to have a greater influence than alterations in the standing crops (i.e. biomass).

Table 6. Sensitivity (expressed as % of baseline) of simulated phosphorus turnover time and primary production, when selected system components were individually subjected to ± 10% variation from baseline conditions.

| COMPONENT | PHOSPHORUS TURNOVER TIME | | PRIMARY PRODUCTION | |
|---|---|---|---|---|
| | + | - | + | - |
| ENRICHMENT | 6.1 | 6.3 | 7.8 | 7.6 |
| ZOOPLANKTON | | | | |
| BIOMASS | 1.3 | 1.5 | 1.6 | 1.8 |
| EXCRETION | 3.6 | 3.5 | 3.8 | 4.0 |
| PHYTOPLANKTON | | | | |
| BIOMASS | 1.9 | 2.0 | 2.7 | 2.8 |
| UPTAKE | 3.5 | 3.2 | 4.5 | 4.9 |
| SINKING | 2.7 | 2.4 | 3.2 | 3.5 |

During the course of the Flathead River Basin Environmental Impact Study we were questioned about the changing trophic status of Flathead Lake (cf. Stanford et al. 1983). Our model was not specifically designed for this problem; but, with the aid of some simplifying assumptions, we were able to provide some insight. First, we assumed that our initial model structure was applicable to all past and future scenerios. This implies that the pelagic zone in Flathead Lake is not significantly influenced by the littoral area and that phosphorus is the major limiting nutrient. Secondly, we used rather arbitrary estimates concerning the historical trends in external phosphorus loading. Although no accurate data on phosphorus loading exist prior to the 1977-1983 study (i.e. Stanford et al. 1983), we can reasonably assume that ca. 50 years ago the lake was influenced by domestic sewage. Sewage now accounts for about 18% of external phosphorus inputs and significant inputs are derived from atmospheric pollution (Stanford et al. 1983). Also, abnormal loading of phosphorus-rich sediments may be occurring as a result of timber harvest in the drainage basin. Today's loading rates may therefore be 20-50% greater than occurred ca. 100 years ago.

Table 7 presents the results of a series of simulations using these constraints in phosphorus loading. Baseline enrichment predicted a turnover time of 4.4 days and primary production of 105 g C $m^2$ $yr^{-1}$ (see above). Additionally, we ran two simulations assuming that enrichment would increase by 50% and 100%. There was a positive correlation between enrichment and the two predicted values, suggesting that the lake is becoming more productive (eutrophic) through time, primarily as a result of cultural activities adding (enriching) abnormal phosphorus loads to the lake.

Table 7. Simulated impact of varying phosphorus enrichment on pelagic phosphorus turnover time and primary production.

| ENRICHMENT X BASELINE | TURNOVER TIME (days) | PRIMARY PRODUCTION (s C m-2 yr-1) |
|---|---|---|
| 0.5 | 3.67 | 76.9 |
| 0.8 | 3.98 | 94.2 |
| 1.0 | 4.41 | 105.3 |
| 1.5 | 5.12 | 146.0 |
| 2.0 | 5.83 | 194.2 |

# DISCUSSION

We used a relatively simple model to synthesize the Flathead plankton data base into a system framework from which we made predictions concerning various enrichment patterns. FLTHD adequately represented known characteristics of the lake plankton community and provided us testable predictions concerning lake responses. In this regard, the model represents a working hypothesis developed around our current understanding of the structure and function of the Flathead Lake ecosystem.

The two primary working assumptions are that phytoplankton productivity is limited by phosphorus and that the pelagic zone may be modeled in isolation from the rest of the lake. Based upon our observations we believe these assumptions are currently valid in Flathead Lake (Stanford et al. 1983). However, if the external loading rate continues to increase, FLTHD may require the incorporation of other nutrient components (e.g., nitrogen) and benthic interactions (e.g. phosphorus release from sediments upon onset of hypolimnetic oxygen deficit) in order to remain realistic. The model was structured such that these parameters may be added in the future.

The role of phosphorus in lake eutrophication has received a large amount of attention. The general belief is that lowering phosphorus loading rates will lead to a decreased rate of eutrophication. The classic example of such response is Lake Washington near Seattle, where nutrient diversions lead to a significant reduction in algal productivity and an increase in water clarity (Edmondson 1972). However, similar efforts have been less successful in other systems (e.g., Emery et al. 1973).

It is instructive to consider how Flathead Lake may respond to reduced phosphorus loading in response to similar regulatory measures. The Lake Washington diversion removed about 50% of the external nutrient input; a large share of which was from domestic sewage. Hypolimnetic oxygen concentrations, although depressed, never reached complete anaerobiosis (Edmondson 1972) and the contribution of the sediments to the lake phosphorus budget was not very high. Thus, the diversion was able to dramatically decrease the input of available phosphorus to the water column. The result was a fairly rapid decrease in algal productivity. Flathead lake currently receives the vast majority of its phosphorus load from external loading. The hypolimnion remains aerobic during thermal stratification and bottom sediments are not presently a significant source of phosphorus. Therefore, we would expect a reduction in external nutrient load to yield lower primary production (e.g., Table 3). However, if production reached a level where decomposition produced deoxygenated conditions in the hypolimnion, load reductions might be less effective. In this situation the pelagic region may be influenced by nutrient release from the sediments as much or more as from riverine inputs. We are currently unable to estimate the productivity level at which this would occur; nonetheless, the problem is serious enough to warrant further attention.

Although the quantity of nutrient input is the primary determinate of productivity, the timing and duration of this input may also be important. The lake receives the majority of its nutrient load during the late spring-early summer runoff. Our model indicates that increasing the volume of this input would lead to an increased rate of organic production during this period. It is also clear that increasing the duration of this input (i.e., spreading the input out over a longer time frame) would produce an even greater impact. Flathead Lake plankton community structure and hydraulic retention time presently combine to produce a relatively short pelagic phosphorus turnover time of about 4.4 days (Table 7). In effect, this means that the lake is able to use low nutrient input periods to "recover" its trophic state. Increasing the duration of input would result in lengthening the time phosphorus is available to the phytoplankton community and significantly alter annual production.

The simulation model also indicated that the biota can have an influence on pelagic phosphorus dynamics. Altering the size distributions and standing stocks of the zooplankton can lead to changes in the rate of phosphorus recycle. Hence, it is important that we understand the mechanisms which might produce these alterations. For example, fish predators are known to cause shifts in zooplankton size distributions (e.g., Brooks and Dodson 1965). Increasing the standing stocks of planktivores could, therefore, have important system wide implications on phosphorus cycling. The recent introduction of the planktivorous, _Mysis relicta_ (see Leathe and Graham 1982), may be very significant in this respect.

Although we have focused our discussion on the question of available phosphorus, it is important to understand that eutrophication is an ecosystem process and, consequently, lake management strategies and research programs should be developed at this level. The close interrelationships of system variables make ecosystem level research a neccesity for understanding the eutrophication process in Flathead Lake. Our model essentially averages the impact of individual basin activities and simulates the combined response to changes in nutrient input. FLTHD was designed to simulate pelagic phosphorus cycling under present and future loading regimes and does not currently distinguish between individual nutrient sources. Despite this limitation, the simulations clearly point out the importance of external phosphorus loading to the changing trophic state of Flathead lake.

# CONCLUSIONS

1. Model output is consistent with measured values of total phosphorus and primary production. Additionally, the model accurately predicts standing crop and average size of phytoplankton. Further validation requires additional field measurements. We believe the model can be utilized as a management tool in predicting the influence of external loading on the pelagic zone of Flathead Lake. However, it should be noted that FLTHD was designed to operate under phosphorus limiting conditions and may not be used for other situations without modification.

2. The trophic status of Flathead Lake is controlled by external phosphorus loading. The model indicates that more than 90% of the annual available phosphorus pool is derived from external inputs. A large share of this load is contained in fluvial sediments. It is important to continue research on sediment-nutrient relationships in order to fully understand the implications of sediment loading. The timing and duration of these inputs also appear to be critical in determining the trophic condition. Presently, the lake receives most of its phosphorus load during spring freshet. During the remainder of the year, the lake receives a relatively low nutrient load. This low water/nutrient period is needed to maintain the current trophic status of the lake. An alteration in riverine flow regimes which would result in a higher loading during typical low

water periods would result in higher productivity and increased rate of eutrophication.

3. Biotic recycling mechanisms 'fine-tune' system nutrient dynamics. These mechanisms appear to be most important during low water periods. We have shown that zooplankton size distributions strongly influence the availability of phosphorus. This implies that proliferation of *Mysis* could vastly alter phosphorus dynamics in the lake; likewise the role of fish predators in regulating zooplankton community size structure, in particular, the system-wide implications of greatly increased fish populations (e.g. *Perca flavesens*), should be closely analyzed.

4. The simulations presented herein strongly support the conclusion of Stanford et al. (1983) that Flathead Lake is becoming more productive. We believe this finding to be particularly significant in light of the fact that almost the entire phosphorus load into the lake comes from external sources. Other work on Flathead Lake has shown that a large reservoir of currently unavailable phosphorus exists in the sediments on the lake bottom. The release of nutrients from the lake sediments, in response to favorable redox gradient by hypolimnetic anoxia, would result in a very rapid change in lake trophic state. In particular, we would expect increased phytoplankton production and decreased water clarity, as a direct result of nutrient inputs from the

sediments. Isolated bays (e.g. Big Arm, Dayton) would manifest eutrophic conditions prior to lake-wide deterioration, due to reduced depth and circulation potential of the water column in such areas.

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