The following philosophy has been adopted for the formulation of an aquatic production model. The model is envisaged as a collection of assumptions regarding the physical and biological processes that interact to form an ecological system. The types of assumptions required to describe an aquatic ecosystem may be categorized as:

1) the response (behavioral, physiological, genetical, successional) of organisms, populations of organisms, or communities of species to their environment (physical, chemical, and biological);

2) the influence organisms have on their environment (including interactions among different types of organisms);

3) the chemical-physical-biological cycles of those inorganic and organic compounds that frequently limit or enhance production in the system; and

4) those physical and chemical properties of the environment that are determined by a combination of biological, chemical, and physical factors.

The assumptions should be formulated mathematically in such a way that they suggest experiments that may be performed to investigate the truthfulness of the assumptions or to estimate the parameters contained in the mathematical formulation. This requires that many of the parameters of the model have a well defined interpretation. This type of modeling requires an honest appreciation of the fundamental processes that govern the phenomena being modeled. Because few scientists have the capability or inclination to individually assimilate, concentrate, and evaluate the vast amount of knowledge available in the separate sciences that comprise the subject of ecology, a team of scientists from diverse areas in biology is essential for the construction of this type of model. The resulting set of mathematical equations, which is nothing more than an integration of the individual biological assumptions, serves as a tool for:

1) investigating the consequences of each assumption,

2) determining the circumstances under which various limiting factors will actually be controlling forces on production,

3) predicting or forecasting the effect of various changes in the environment,

4) substantiating or refuting current explanations of ecological phenomena,

5) generating new hypotheses by performing simulated experiments with the model, and

6) directing research effort toward more fruitful areas.
The following set of assumptions comprise the current state of a preliminary
model of the production dynamics in a generalized coniferous forest lake. It is based upon literature review and frequent discussions with scientists participating in the IBP program. The model is general in the sense that it will represent the dynamics of a particular lake only when parameters unique to that lake are incorporated. Four sources of estimates for the parameters in the model are recognized:

1) studies conducted on proposed lakes before the initiation of IBP;

2) investigations proceeding under IBP support (some of these projects are designed to provide estimates of parameters that are unique to particular lakes and others are designed to improve the predictive capabilities of the model by testing the assumptions upon which the model is based);

3) survey of literature on limnology, oceanography, ecology of aquatic environments, physiology and behavior of aquatic organisms, natural selection, and succession; and

4) estimates of parameters derived from the model by fitting the model to observed fluctuations in production.

PHOTOPLANKTON SUBMODEL

The production dynamics of a community of phytoplankton is hypothesized to follow a model similar in general form to the one formulated by Y've"e et al. (1949),

\[
\frac{\partial n}{\partial t} = (P_h - R - D)n - G + \frac{\partial}{\partial z} \left( \frac{\partial n}{\partial z} \right) + \frac{\partial}{\partial T} \frac{\partial n}{\partial T} - \frac{\partial}{\partial T} \frac{\partial n}{\partial T} \quad
\]

where

\(n(t,z)\) is the concentration of phytoplankton at depth \(z\) at time \(t\) \(\text{[mg(carbon)m}^{-3}\)],

\(P_h\) is photosynthetic rate for unit plant concentration \(\text{[mg(carbon assimilated)day}^{-1}\text{per mg carbon in phytoplankton]}\),

\(R\) is respiration rate of unit concentration of plants \(\text{[mg(carbon respired)day}^{-1}\text{per mg carbon in phytoplankton]}\),

\(D\) is rate of loss because of decomposition for unit concentration of plants \(\text{[mg(carbon decomposed)day}^{-1}\text{per mg carbon in phytoplankton]}\),

\(G\) is the rate of loss attributed to grazing by herbivorous zooplankton \(\text{[mg(carbon grazed)day}^{-1}\text{m}^{-3}\}],\)

\(A_p\) is the coefficient of eddy diffusivity for the community of phytoplankton \(\text{[mg(carbon)sec}^{-1}\text{m}^{-1}\)],

\(\rho\) is density of water \(\text{[g(H}_{2}\text{O})/\text{cm}^{3}(\text{H}_{2}\text{O})]}\),

\(s\) is sinking rate of phytoplankton at 0°C \(\text{[m·day}^{-1}\)],

\(u^0\) is the dynamic viscosity of water at 0°C,

\(\mu_T\) is the dynamic viscosity of water at \(T^\circ\text{C}\),

\(\frac{\partial^2 n}{\partial z^2} \frac{\partial n}{\partial z}\) is the rate of change in concentration of phytoplankton at any depth attributed to mixing by eddy currents, and

\(\frac{\partial n}{\partial T} \frac{\partial n}{\partial T}\) is the rate of change in concentration of phytoplankton at any depth attributed to sinking of algal cells.
The above partial differential equation represents only the hull of the model; many of the coefficients are functions of physical, chemical, and biological forces that comprise the phytoplankton's environment.

**Photosynthetic rate**

Notation,

\[ n_i(t,z) \] is the concentration of nutrient \( i \) at depth \( z \) at time \( t \) \( (\text{mg m}^{-3}) \),

- \( i = \text{C} \) is CO₂,
- \( \text{P}_0 \) is phosphate
- \( \text{N} \) is nitrate
- \( S \) is silica,

\( I(z) \) is the light intensity at depth \( z \),

\( I_s(t) \) is the surface light intensity at time \( t \),

\( T(\ell,z) \) is the temperature at depth \( z \) at time \( t \),

\( K \cdot T \) is the saturated growth rate at temperature \( T \) (growth rate at optimal light intensity and nutrient concentrations),

\( F(I) \) is reduction in growth rate attributed to light intensities greater than and less than optimal intensity, and

\( h(n_C,n_{P_0},n_N,n_S) \) is reduction in growth rate attributed to less than optimal concentrations of nutrients.

The photosynthetic rate is assumed to follow the general form

\[ P_h = K \cdot T \cdot F \cdot H, \]

where the various functions are defined as

\[ I(z) = I_0 \exp\left\{ -k_e z - \int_0^z f(p_c(t,x)) dx \right\}, \]

\[ f(y) = 0.0080y + 0.045y^{2/3}, \text{ Riley (1956)}, \]

\( k_e \) is the extinction coefficient of water excluding the phytoplankton,

\[ \int_0^z f(P_C(t,x)) dx \] is the extinction of light at depth \( z \) because of self-shading by phytoplankton,

\( P_C \) is the concentration of chlorophyll \( a \) in \( \text{mg m}^{-3} \)

\( (P_C = \alpha_C P \text{ where } \alpha_C \text{ is the chlorophyll-to-carbon ratio of phytoplankton}), \)

\( F(I) = \frac{I}{I_s} \exp\{1 - \frac{I}{I_s}\} \text{ Steele (1965), and} \)

\( I_s \) is the light intensity for optimum growth rate.

Several models for \( H \) have been proposed.

Let \( m_i(X) = \frac{X}{X + K_i} \) for \( i = \text{C, P}_0, \text{N, S} \), where \( K_i \) is the Michaelis-Menton half saturation constant, then \( H \) may be modeled as

\[ H = m_i(n_i) \]

or

\[ H = \min_i m_i(n_i) \]
The assumption may now be stated as
\[ Z(t,z) = \frac{p(t,z)}{p^e(t)} Z^*(t). \]

The dynamics of production at any depth is represented by
\[ \frac{dZ^*}{dt} = (A-R-D)Z^* = (A-R-D) \left( \frac{p(t,z)}{p^e(t)} \right) Z^*(t), \]
where \( A \) is the assimilation rate for unit zooplankton concentration \( \text{mg}(\text{carbon assimilated})\text{day}^{-1} \) per mg carbon in zooplankton,
\( R \) is the respiration rate of unit concentration of zooplankton \( \text{mg}(\text{carbon respired})\text{day}^{-1} \) per mg carbon in zooplankton, and
\( D \) is rate of loss because of death for unit concentration of zooplankton \( \text{mg}(\text{carbon expired})\text{day}^{-1} \) per mg carbon in zooplankton.

Fish predation upon zooplankton is assumed to depend upon the total amount of zooplankton in the water column, according to a Holling disc equation, i.e.,
\[ \frac{R_F Z^*}{D_F} = \left( \frac{Z^*}{R_F + Z^*} \right) F, \]
where
\( R_F \) is the saturated predation rate, and
\( F \) is the density of fish in the water column.

The production dynamics of zooplankton may now be expressed as
\[ \frac{dZ^*}{dt} = \left[ \int_0^b (A-R-D) \frac{p^e(t)}{p^e(t)} \right] - D_F. \]

**Assimilation Rate.**

In the phytoplankton model, we defined the grazing rate of zooplankton per unit of zooplankton to be
\[ gr = \frac{R_T P}{K + P}. \]

The assimilation efficiency, \( a_z \), of zooplankton is hypothesized to depend upon the grazing rate according to
\[ a_z = (1 - \frac{gr}{K + gr}) = \frac{K a}{K + gr}. \]
The assimilation rate per unit zooplankton is then
\[ A = a \frac{r}{z} \frac{K_{gr}}{K_{a} + gr} \]

Respiration Rate
A linear dependence upon temperature is supported by data in the literature
\[ R = K_Z T \quad K_Z = 0.2 \pm 0.1 \quad \text{[day}^{-1}({^0C})^{-1}] \]

LIMNETIC ORGANIC POOL--SUBSTRATE FOR DECOMPOSITION

The limnetic organic pool is the collection of dead organic matter, suspended in the water column, that provides a substrate for bacterial decomposition. The rate of change in the concentration of organic matter \( \text{[mg m}^{-3}\text{day}^{-1}] \) at any depth is expressed as
\[
\frac{30}{\text{d}t} = D_p p + D_z A + A - B_0 p + \frac{3}{3z}(A_0 p \frac{3z}{3z} - S p \frac{3z}{3z} p)
\]
where
- \( o_p(t,z) \) is the concentration of organic carbon at depth \( z \) at time \( t \) \( \text{[mg m}^{-3}] \),
- \( D_p p \) is death rate of phytoplankton \( \text{[mg m}^{-3}\text{day}^{-1}] \),
- \( D_z A \) is death rate of zooplankton \( \text{[mg m}^{-3}\text{day}^{-1}] \),
- \( A \) is rate of addition of organic carbon from allochthonous sources \( \text{[mg m}^{-3}\text{day}^{-1}] \),
- \( B_0 \) is rate of decomposition for unit concentration of organic matter,
- \( A_0 p \) is coefficient of eddy diffusivity for organic pool,
- \( \frac{3}{3z}(A_0 p \frac{3z}{3z} - S p \frac{3z}{3z} p) \) represents the rate of mixing of organic matter vertically in the water column,
- \( S p \) is sinking rate of suspended particles \( \text{[nday}^{-1}] \), and
- \( S p \frac{3z}{3z} \) is loss from water column attributed to sinking, \( \text{[mg m}^{-3}\text{day}^{-1}] \).

Bacterial Decomposition
\( B \) is as yet undetermined function of temperature, pH, and other chemical reactions.

NITROGEN, PHOSPHOROUS CYCLE SUBMODEL

Although the nitrogen and phosphorous cycles are quite different, the following general formulation characterizes those features that seem to be common to both cycles. The following sources and sinks of nutrient have been recognized.
EZ is rate of nutrient excretion by zooplankton \( \text{mg}^{-3}\text{day}^{-1} \),

J is rate of nutrient liberation from organic pool by decomposition,

\( R_I \) is rate of nutrient addition from inflow streams, ground water, and drainage of fertilized farm land,

\( E_S \) is rate of gain or loss attributed to equilibrium exchange with bottom sediments,

\( E_P \) is rate of gain or loss attributed to equilibrium exchange with suspended particles,

\( S_e \) is sedimentation rate of nutrient absorbed on suspended particles \( \text{inday}^{-1} \), and

\( R_P \) is rate of removal of nutrient by phytoplankton.

The rate of change in nutrient concentration at any depth is represented as the sum

\[
\frac{\Delta n}{\Delta t} = E_Z + J + R_I + E_S + E_P - E_P - a_S \frac{\partial}{\partial z} P + \frac{\partial}{\partial z}(\frac{a}{n_0} P) + \frac{\partial}{\partial z}(\frac{a}{n_0} n),
\]

where \( a \) is nutrient-to-carbon ratio of organic pool.

Zooplankton excretion is taken to be the difference between the grazing rate and the assimilation rate of zooplankton. The nutrient liberation is taken to be proportional to the carbon content of the excretory products. The proportionality constant is the nutrient-to-carbon ratio of the excretory products \( (a_{PC}) \). The model may be expressed as

\[
E_Z = a_{PC} (G_r - a_z) \]

\[
= \frac{a_{PC} G_r}{K_2 Z + a_z} \]

using substitutions from phytoplankton and zooplankton submodels,

where

\( G_r \) is the grazing rate \( \text{mg}^{-3}\text{day}^{-1} \), and

\( a_z \) is the assimilation efficiency of zooplankton

Release rate of nutrient attributed to bacterial decomposition is taken to be \( J = a\cdot\beta\cdot \frac{\partial}{\partial z} P \)

Equilibrium exchange with sediments and suspended particles has no model as yet proposed. The following factors are recognized as important:

1) cycles of iron and manganese,
2) oxidation-reduction potentials,
3) pH,
4) oxygen concentrations,
5) ratio of lake surface area to area of bottom sediments exposed to epilimnion,
6) temperature gradients, and
7) nitrogen-fixing algae and bacteria.
Uptake by phytoplankton of nutrient is taken to be

\[ \frac{dF}{dt} = (G - D)F - F_p, \]

where

- \( F \) is concentration of fish carbon (mg m\(^{-3}\)) at time \( t \),
- \( G \) is growth rate per unit concentration of fish,
- \( D \) is death rate per unit concentration of fish, and
- \( F_p \) is rate of predation by squawfish, etc.

Growth rate will depend upon temperature, amount of food ingested, and body size of the fish. An analytic statement of the results obtained by Brett (1969) for the relation between growth rate of sockeye and temperature-ration combinations is forthcoming. Figure 1.

The salient feature of the results is that the temperature for optimum growth depends upon the level of ration. Because sockeye salmon exhibit marked vertical migrations (through a substantial temperature gradient) a strategy model for optimum growth is being considered.

Death rate is proposed to depend upon the well-being of the fish as measured by condition factors, or specific growth rate. A model similar to the one used for phytoplankton is being considered.

Predation rate is assumed to follow a Holling disc equation

\[ F_p = \left( \frac{uF}{K_p + F} \right) P_r, \]

where

- \( u \) is the saturated predation rate, and
- \( P_r \) is the concentration of salmon predators (squawfish).
Figure 1. Relation between growth rate of sockeye salmon and temperature-ration combinations.


