

## Conclusion

Under the VENFISH project, much has been learned about Pacific saury and a new life history of the saury was proposed. But information about the time between the juvenile and small saury stages are still limited. In the future more study is needed on these stages.

A population dynamics model was constructed under VENFISH and the effect of KE SST and SOI was tested. But in that model the environment influenced only mortality. In the future we should include the environmental influence on production and clarify the bottom-up control mechanism of Pacific saury.

## 2.5 Formalization of interactions between chemical and biological compartments in the mathematical model describing the transformation of nitrogen, phosphorus, silicon and carbon compounds

Alexander V. Leonov<sup>1</sup> and Gennady A. Kantakov<sup>2</sup>

<sup>1</sup> Institute of Oceanology, Russian Academy of Sciences, 36 Nakhimovsky Ave., Moscow, 117851, Russia. E-mail: leonov@sio.rssi.ru

<sup>2</sup> Sakhalin Research Institute of Fisheries and Oceanography, 196 Komsomolskaya St., Yuzhno-Sakhalinsk, 693023, Russia. E-mail: okhotsk@sakhniro.ru

In the significant part of the ecological models used for studying the joint dynamics of the microorganism biomasses and biogenic substance concentrations in the natural waters, several most important biological functions are formalized.

They are connected with the consumption of biogenic substances (UP) by microorganisms, excretion of the metabolic products (L) by them, the microorganism mortality (S) and grazing (G) by microorganisms of higher trophic levels. The change of the microorganism biomass in the course of time (dB/dt) in the ecological models, as a rule, is represented by the following structural equation:

$$(2.5.1) \quad dB / dt = (UP - L - S) * B - G * B^*$$

here B\* is the biomass of microorganisms from the higher trophic level, and due to grazing they have an influence on the development and activity of the considered microorganism group B; UP, L, S, and G are specific rates of the biogenic substance consumption, the metabolic product excretion, the mortality of microorganisms B and their grazing by B\*, respectively (day<sup>-1</sup>).

Biomasses B and B\* are calculated in the units of biogenic elements (N, P, C or Si).

### The simulation of processes of the substrate consumption by microorganisms

For the simulation of processes of the substrate consumption by microorganisms (bacterio-, phyto- and zooplankton), the equation of Michaelis-Menten-Monod is traditionally used:

$$(2.5.2) \quad UP = K(T, L) * C_i / (K_m + C_i)$$

where UP is the growth rate of the microorganism biomass (or the substrate uptake), day<sup>-1</sup>; C<sub>i</sub> is the concentration of concrete substratum, mg/l; K<sub>m</sub> is the Michaelis constant, mg/l; K(T, L) is the maximum growth rate of the microorganism biomass (or the substrate uptake) corrected to the temperature (T) and radiation (L) conditions in the water environment, mg/(l day). Thus, for description of the process of the substrate uptake by one group of microorganism (by bacterio-, phyto- or zooplankton) it is necessary to estimate the values of two coefficients - K(T, L) and K<sub>m</sub>. Using this equation form for the description of the consumption of several substrata by microorganisms, means that the process of the substrate uptake is described independently of each other for any substrate, and in this case, the values of the rate constants for the consumption of each substrata should be evaluated. If the number of such substrata reaches five (ammonia, nitrites,

nitrate, phosphate, silicate) then the number of evaluated coefficients should be equal to ten.

The form of equation (2.5.2) with some modifications is used for describing the processes of the substrate consumption by microorganisms in the models developed by PICES MODEL Task Team for the studying of chemical and biological compartment dynamics in the marine environment. However, in the marine environment, the substrate concentrations are always little and therefore it is very difficult to describe the dynamics of the biomasses and substrate concentrations even for one season. Frequently the very task of the simulation of the chemical and biological compartment dynamics in the marine systems is a rather difficult labor-consuming or even insurmountable problem.

Here we present the logic of the simulation of the substrate consumption process by the microorganisms that is used for development of the model describing the transformation of N, P, C and Si compounds in the polysubstrate environment (Leonov and Saposhnikov 1997). First we shall transform the equation (2.5.2) subdividing the terms of equation in the numerator and the denominator on  $C_i$ . As a result, we obtain the following equation:

$$(2.5.3) \quad UP = K (T, L) / (1 + K_m / C_i)$$

The analysis of literature shows that the value of  $K_m$  in different examples of using equation (2.5.2) for describing of processes in the natural waters changes by 2-3 orders. Consequently, the convincing arguments of the application of the equation (2.5.2) for describing the substrate consumption processes in the marine ecosystems is clearly insufficient (large number of coefficients for the polysubstratal environment and the large variability of the coefficient  $K_m$ ). The value of the coefficient  $K_m$  for the marine ecosystems may be compared with the values of the microorganism biomasses. Therefore we have all reasons to use, instead of the coefficient  $K_m$ , the value of the biomass in the units of biogenic element (N, P, C or Si) from which biomass can be evaluated. If the biomass is considered in N, then the equation (2.5.3) can be written as:

$$(2.5.4) \quad UP = K (T, L) / (1 + B_N / C_N)$$

where  $B_N$  is the biomass of the studied group of microorganisms, in units of N, mg N/l;  $C_N$  is the concentration of N fractions consumed by these microorganisms, mg N/l.

If there are several N-containing substrata in the water environment (for example, ammonia  $NH_4$ , nitrites  $NO_2$ , and nitrates  $NO_3$ ) and these substrates are interchangeable and may be consumed by the microorganism (let us mark it as F and taking into account that the biomass is expressed in units of N, it may be written as  $F_N$ ), then the expression for  $C_N$  can be represented in the form of the pool on N ( $PoolF_N$ ) for the studied group of microorganism:

$$(2.5.5) \quad PoolF_N = d(1) * NH_4 + d(2) * NO_2 + d(3) * NO_3$$

Here the coefficients  $d(i)$  show preferences in the consumption of each substrate by the microorganism for this N-substrates ( $NH_4$ ,  $NO_2$ , and  $NO_3$ ). Value of the coefficients  $d(i)$  for each substrate can change from 0 to 1, and their sum for the selected set of substrata is 1.

How are the values of coefficients  $d(i)$  evaluated? It is known from literature that the phytoplankton consumes more preferably ammonium N than other mineral forms. The nitrate N is in second place. So, in the first approximation, we can assign the values of the preference coefficients in the uptake of indicated substrates by the studied group of phytoplankton:  $d(1) = 0.5$ ;  $d(2) = 0.2$ ;  $d(3) = 0.3$ . Inserting the equation (2.5.5) into the equation (2.5.4), we obtain:

$$(2.5.6) \quad UP_{FN} = K (T, L) / (1 + B_N / PoolF_N)$$

or

$$(2.5.6a) \quad UP_{FN} = K (T, L) / (1 + B_N / (d(1)*NH_4 + d(2)*NO_2 + d(3)*NO_3))$$

The general rate of the N-containing substrata consumption,  $UP_{FN}$ , is composed of the rates of the consumption of the individual substrates:

$$(2.5.7) \quad UP_{FN} = UP_{NH_4} + UP_{NO_2} + UP_{NO_3}$$

Let us write down the equations, which describe the consumptions of individual substrates (NH<sub>4</sub>, NO<sub>2</sub> and NO<sub>3</sub>) by phytoplankton taking into account that in the water environment several substrates are interchangeable on N, as indicated by the equation (2.5.6a). Making elementary algebraic conversions, we shall obtain the equations, which describe the consumption of each studied substrates by the phytoplankton:

$$(2.5.8) \quad UP_{NH_4} = K(T, L) * d(1) * NH_4 / (PoolF_N + B_N)$$

$$(2.5.9) \quad UP_{NO_2} = K(T, L) * d(2) * NO_2 / (PoolF_N + B_N)$$

$$(2.5.10) \quad UP_{NO_3} = K(T, L) * d(3) * NO_3 / (PoolF_N + B_N)$$

The suggested form of the description of the interchangeable substrates by the microorganism assumes that the rates of the consumption of each substrate will be compared only in such a case, when the product of substrate concentrations to their preference coefficient will be close. With the maximum rate will be consumed that substratum, for which the product of its preference coefficient to the concentration will be the greatest (in this case, from of three given substrates). This form of the equations for the consumption of the interchangeable substrates by microorganism (in particular, by phytoplankton) gives the possibility of switching for the intensive consumption by the hydrobionts only of those substrata whose concentrations to these are greatest in the comparison with other substrata. It gives a possibility for the water environment to restore the pool of those substrata, which in the process of the biomass growth descend to the smallest (sometimes critically small) values. This phenomenon in the description of the processes of increasing of the biomass and substrate consumption is impossible by equations the traditionally used for the simulation of marine ecosystems, in which the substrate consumption by different groups of microorganism is assigned independently of each other.

Let us consider the case, when there are several substrates as the interchangeable (as it was examined above), so also not interchangeable, in

the water environment for the phytoplankton. If we want correctly describe in the model the substrate uptake processes then we should remember the basic Odum's postulate that everything is interrelated in the natural water environment. The requirements of phytoplankton in P cannot be compensated by N or Si compounds, and vice versa. Therefore the compounds of different biogenic elements cannot be considered as interchangeable for the formation of the microorganism biomass and the kinetics of the uptake substrate processes should be formulated with point of view their mutual influence on each other and not their interchangeability.

Taking into account these reasons, let us write down the equation (2.5.6) for the rate of biomass growth (or the different substrate uptake) for the conditions of the combined influence of N and P compounds on the biomass of the considered microorganism group (for example, the phytoplankton) keeping the logic of all foregoing reasons. Then we obtain, that

$$(2.5.11) \quad UP_F = K(T, L) / (1 + B_N / PoolF_N + B_P / PoolF_P)$$

Here B<sub>P</sub> is the biomass in units of P, mg P/l; PoolF<sub>P</sub> - the pool of the P substrates, mg P/l, that may be consumed by the phytoplankton, and these substrates are the dissolved mineral (DIP) and organic (DOP) forms of P:

$$(2.5.12) \quad PoolF_P = d(4)*DIP + d(5)*DOP$$

In this case the total rates of the uptake of N and P compounds by the given group of microorganisms are represented as:

$$(2.5.13) \quad UP_{FN} = UP_{NH_4} + UP_{NO_2} + UP_{NO_3}$$

$$(2.5.14) \quad UP_{FP} = UP_{DIP} + UP_{DOP}$$

Accordingly to the same logic, let us formulate equations for describing the individual substrates taking into account the influence of each of them on the kinetics of the formation of biomass and the substrate uptake being oriented toward general equation (2.5.11):

$$(2.5.15) \quad UP_{NH_4} = K(T, L) * d(1) * NH_4 / MF$$

$$(2.5.16) \quad UP_{NO_2} = K(T, L) * d(2) * NO_2 / MF$$

$$(2.5.17) \quad UP_{NO_3} = K(T, L) * d(3) * NO_3 / MF$$

$$(2.5.18) \quad UP_{DIP} = K(T, L) * d(4) * DIP / MF$$

$$(2.5.19) \quad UP_{DOP} = K(T, L) * d(5) * DOP / MF$$

where

$$(2.5.20) \quad MF = PoolF_N * PoolF_P + B_N * PoolF_P + B_P * PoolF_N.$$

When the joint consumption of N, P, and SI compounds is considered for the same group of microorganism, the equation (2.5.11) takes the form:

$$(2.5.21) \quad UP_F = K(T, L) / (1 + B_N / PoolF_N + B_P / PoolF_P + B_{Si} / PoolF_{Si})$$

where

$$(2.5.22) \quad PoolF_{Si} = d(6) * DISi$$

and DISi is the content of dissolved inorganic silicon, mg Si/l.

In accordance to the accepted logic for the formulations of kinetic dependences, the equations describing the individual substrate uptake and their mutual influence on each other are written in the following form:

$$(2.5.23) \quad UP_{NH_4} = K(T, L) * d(1) * NH_4 / MF1$$

$$(2.5.24) \quad UP_{NO_2} = K(T, L) * d(2) * NO_2 / MF1$$

$$(2.5.25) \quad UP_{NO_3} = K(T, L) * d(3) * NO_3 / MF1$$

$$(2.5.26) \quad UP_{DIP} = K(T, L) * d(4) * DIP / MF1$$

$$(2.5.27) \quad UP_{DOP} = K(T, L) * d(5) * DOP / MF1$$

$$(2.5.28) \quad UP_{DISi} = K(T, L) * d(6) * DISi / MF1$$

where

$$(2.5.29) \quad MF1 = PoolF_N * PoolF_P * PoolF_{Si} + B_N * PoolF_P * PoolF_{Si} + B_P * PoolF_N * PoolF_{Si} + B_{Si} * PoolF_N * PoolF_P$$

A similar form of equations may be used for any functional group of microorganism taking into account any the variety of the substrate assortment including the components of the water environment pollution (for example, oil products). The substrate assortment for the organisms of higher trophic levels is higher than for the organisms of lowest trophic status. In this assortment fall the dissolved and particulated organic compounds of biogenic elements, including biomasses of certain microorganisms and detritus.

The equation for the term G (the specific grazing rate of the microorganism from the lowest trophic levels by the organisms of higher levels) is constructed, on the basis of the presented above principles considering the high-constituent nature of water environment and the mutual influence of the uptake of individual substrates on each other in the process of the microorganism biomass growth.

The value of the maximum growth rate of the microorganism biomass (or the substrate consumption), K(T, L) should be corrected to the conditions on the temperature and for light (for the planktonic organisms) in the water environment. The analysis of ecological models existing at present shows that there are many methods of carrying out a similar correction.

In the model of the transformation of nitrogen, phosphorus, silicon and carbon compounds the temperature dependence is considered by the exponential function, which differs for the different groups of microorganisms in the slope and the optimum values of temperature. The dependence of the plankton biomass growth as a function of light conditions in water environment is considered by the traditional functions that are used at the simulation of the processes of phytoplankton photosynthesis and daily vertical migration of zooplankton.

### **Formalization of the excretion processes of metabolic products by microorganisms**

At first stages of mathematical simulation model development as the independent scientific direction in the studies of the natural aquasystems state, this important biological function of

microorganisms was not considered at all. At present time, in the majority of the cases the specific rate of the metabolic excretion by microorganisms ( $L$ ) is formulated in the ecological models by the simplest method and, as a rule, it is represented in the form of a constant quotas ( $\alpha$ ) from the UP function:

$$(2.5.30) \quad L = \alpha * UP$$

The experience of the experimental research of the microorganism population dynamics and the simulation of the conditions for the biomass growth shows that the excretion fraction of the products of metabolic exchange in different microorganisms differs very substantially, and it can change considerably in the process of the biomass growth in each group of microorganisms.

This fact was taken into account, and during the development of the mathematical model of the transformation of nitrogen, phosphorus, silicon, and carbon compounds the different forms of the expression of the excretion fraction of metabolic products changing in the time were checked. It was found the form of equation for  $\alpha$  that most completely consider the special features of the microorganism biomass growth, and it is formulated as the dependence from the specific rate of the substrate uptake, UP:

$$(2.5.31) \quad \alpha = a * UP / (1 + b * UP) + (1 - a / b)$$

where  $a$  and  $b$  are constants (moreover  $a < b$ ) whose values determine the nature of change in the excretion fraction in the dependence on the values of the total substrate uptake by considered group of microorganisms.

The first term of the equation (2.5.31) shows the forming quota of the metabolic excretion of substance in the favorable on the nutrient conditions of the water environment, when values of UP are significant.

The second term of the equation (2.5.31) shows the quota of the metabolic excretion at the substrate deficite when values of UP become minimum.

With the values of coefficients  $a$  and  $b$  can be reproduced the significant spectrum of the conditions for the microorganism biomass growth which can be evaluated in the units of different biogenic elements (N, P, C or Si).

### **Formalization of the processes of the microorganism mortality**

The processes of development and growth of the microorganism biomass are continuous with the processes of the internal losses of biomasses ( $S$ ). It is possible to assume that the natural physiological losses of the biomasses of any group of microorganisms compose 5-10% of the total biomass although this problem remains insufficiently studied experimentally for all microorganism groups. In the process of the microorganism mortality, the detritus (or the dead suspended matter) is formed in the water environment. The biogenic substances containing in it are actively included in turnover by bacteria and zooplankton which transform detritus into the labile nutrients well assimilated by other microorganisms. Under the conditions of reduced temperatures, the detrital links become the most important in the nutrition and growth of the populations of fishes.

At the first ecological models, the microorganism mortality  $S$  is not taken into account at all or only natural physiological biomass losses are considered. The modern ecological models include the natural internal biomass losses and take into account losses inevitable at the stimulation of the biomass growth processes. It may be differently formulated. In the mathematical model of the transformation of N, P, Si, and C compounds this important biological function is described by the equation:

$$(2.5.32) \quad S_N = g(1) + g(2) * B_N / UP_{FN}$$

where  $g(1)$  and  $g(2)$  are constants describing the processes of the natural biomass losses and mortality depending on the conditions of activating the growth, respectively. If the biomass of the microorganism group is evaluated in the units of different biogenic elements (N, P, C or Si) then respectively for each case their specific rates of the internal losses of biomasses are evaluated

with the use of specific values of coefficients  $g(i)$ , values of biomasses  $B$  and rates of the substrate consumption  $UP$ .

The set of model coefficients applied in two case studies (for the Okhotsk Sea (Leonov and Sapozhnikov 1997) and Caspian Sea (Leonov and Srygar 1999) for the simulation of microorganism dynamics is presented in Table 2.5.1.

Thus, in the mathematical model of the transformation of N, P, Si, and C compounds, the interactions between chemical (concentrations of biogenic substances) and biological (biomasses the microorganisms - bacteria, phyto- and zooplankton) compartments are considered and reproduced the most important biological processes of the substrate uptake, excretion of the metabolic products and mortality of the microorganisms. As a result of these processes, the turnover of chemical substances (organic and mineral) are performed in natural marine ecosystems. The special feature of this model is the formalization of the important biological functions (the excretion of the metabolic products and mortality of microorganisms) in a dependence on the consumption of different biogenic

substances by microorganism. These biogenic substrates are subdivided on interchangeable (on one biogenic element) and not interchangeable (on the different biogenic elements). The used form of equations for the description in this model of the most important biological functions serves as the example for the formalization of the processes of the internal regulation (self regulation) of the microorganism activity within the ecosystems. The account of a similar internal regulation mechanism of the microorganism activity makes this model sufficiently resistant and allow us to apply it without the significant correction of the parameters in the study the aqueous ecosystems which essentially differ in the environmental conditions (temperature, radiation, water regime, transparency). There are several positive experiences in the application of this model to study the special features of the ecosystem functioning of the Sea of Okhotsk (Leonov and Sapozhnikov 1997) and Caspian Sea (Leonov and Stygar 1999). The first results are also obtained on the simulation of the intraannual dynamics of biogenic substances in the ecosystem in La Perouse Strait and Aniva Bay (Sea of Okhotsk) (Pischalnik and Leonov 2002).

**Table 2.5.1** Values of model parameters used for description of biological compartment dynamics in the Sea of Okhotsk and the Caspian Sea.

Case study 1 - The Sea of Okhotsk	Case study 2 - The Caspian Sea
<p><b>Heterotrophic bacteria (B)</b>  Maximum growth rate: <math>K=1.0</math>  <i>Preference coefficients for substrate uptake:</i>  for C-containing substrate: <math>d_{DOC}=1</math>;  for Si-containing substrate: <math>d_{DOSi}=0.6</math>; <math>d_{DISi}=0.01</math>  <math>d_{SID}=0.39</math>;  for N-containing substrate: <math>d_{DON}=0.6</math>; <math>d_{ND}=0.4</math>  for P-containing substrate: <math>d_{DOP}=0.4</math>; <math>d_{PD}=0.6</math>  <i>Excretion activity:</i>  for C substrate: <math>a_C=0.05</math>; <math>b_C=0.09</math>  for Si substrate: <math>a_{Si}=0.05</math>; <math>b_{Si}=0.088</math>  for N substrate: <math>a_N=0.05</math>; <math>b_N=0.087</math>  for P substrate: <math>a_P=0.05</math>; <math>b_P=0.09</math>  <i>Mortality coefficients:</i>  for C substrate: <math>g(1)_C=0.04</math>; <math>g(2)_C=0.04</math>  for Si substrate: <math>g(1)_{Si}=0.045</math>; <math>g(2)_{Si}=0.05</math>  for N substrate: <math>g(1)_N=0.035</math>; <math>g(2)_N=0.035</math>  for P substrate: <math>g(1)_P=0.055</math>; <math>g(2)_P=0.055</math></p>	<p><b>Heterotrophic bacteria (B)</b>  Maximum growth rate: <math>K=0.75</math>  <i>Preference coefficients for substrate uptake:</i>  for C-containing substrate: <math>d_{DOC}=1</math>;  for Si-containing substrate: <math>d_{DOSi}=0.6</math>; <math>d_{DISi}=0.01</math>  <math>d_{SID}=0.39</math>;  for N-containing substrate: <math>d_{DON}=0.6</math>; <math>d_{ND}=0.4</math>  for P-containing substrate: <math>d_{DOP}=0.4</math>; <math>d_{PD}=0.6</math>  <i>Excretion activity:</i>  for C substrate: <math>a_C=0.05</math>; <math>b_C=0.088</math>  for Si substrate: <math>a_{Si}=0.05</math>; <math>b_{Si}=0.088</math>  for N substrate: <math>a_N=0.05</math>; <math>b_N=0.1</math>  for P substrate: <math>a_P=0.05</math>; <math>b_P=0.086</math>  <i>Mortality coefficients:</i>  for C substrate: <math>g(1)_C=0.03</math>; <math>g(2)_C=0.025</math>  for Si substrate: <math>g(1)_{Si}=0.045</math>; <math>g(2)_{Si}=0.05</math>  for N substrate: <math>g(1)_N=0.028</math>; <math>g(2)_N=0.03</math>  for P substrate: <math>g(1)_P=0.045</math>; <math>g(2)_P=0.05</math></p>

<p><b>First phytoplankton group (F1-diatom algae)</b> Maximum growth rate: <math>K=2.5</math> <i>Preference coefficients for substrate uptake:</i> for Si-containing substrate: <math>d_{\text{DOSi}}=0.3</math>; <math>d_{\text{DISi}}=0.7</math> for N-containing substrate: <math>d_{\text{NH}_4}=0.025</math>; <math>d_{\text{NO}_2}=0.025</math> <math>d_{\text{NO}_3}=0.9</math>; <math>d_{\text{UR}}=0.05</math> for P-containing substrate: <math>d_{\text{DOP}}=0.3</math>; <math>d_{\text{DIP}}=0.7</math> <i>Excretion activity:</i> for Si substrate: <math>a_{\text{Si}}=0.051</math>; <math>b_{\text{Si}}=0.052</math> for N substrate: <math>a_{\text{N}}=0.05</math>; <math>b_{\text{N}}=0.053</math> for P substrate: <math>a_{\text{P}}=0.05</math>; <math>b_{\text{P}}=0.065</math> <i>Mortality coefficients:</i> for Si substrate: <math>g(1)_{\text{Si}}=0.0</math>; <math>g(2)_{\text{Si}}=0.08</math> for N substrate: <math>g(1)_{\text{N}}=0.0</math>; <math>g(2)_{\text{N}}=0.02</math> for P substrate: <math>g(1)_{\text{P}}=0.0</math>; <math>g(2)_{\text{P}}=0.02</math></p>	<p><b>First phytoplankton group (F1-diatom algae)</b> Maximum growth rate: <math>K=2.5</math> <i>Preference coefficients for substrate uptake:</i> for Si-containing substrate: <math>d_{\text{DOSi}}=0.3</math>; <math>d_{\text{DISi}}=0.7</math> for N-containing substrate: <math>d_{\text{NH}_4}=0.2</math>; <math>d_{\text{NO}_2}=0.05</math> <math>d_{\text{NO}_3}=0.7</math>; <math>d_{\text{UR}}=0.05</math> for P-containing substrate: <math>d_{\text{DOP}}=0.05</math>; <math>d_{\text{DIP}}=0.95</math> <i>Excretion activity:</i> for Si substrate: <math>a_{\text{Si}}=0.051</math>; <math>b_{\text{Si}}=0.052</math> for N substrate: <math>a_{\text{N}}=0.05</math>; <math>b_{\text{N}}=0.052</math> for P substrate: <math>a_{\text{P}}=0.05</math>; <math>b_{\text{P}}=0.055</math> <i>Mortality coefficients:</i> for Si substrate: <math>g(1)_{\text{Si}}=0.04</math>; <math>g(2)_{\text{Si}}=0.03</math> for N substrate: <math>g(1)_{\text{N}}=0.05</math>; <math>g(2)_{\text{N}}=0.049</math> for P substrate: <math>g(1)_{\text{P}}=0.05</math>; <math>g(2)_{\text{P}}=0.07</math></p>
<p><b>Second phytoplankton group (F2-peridinium algae)</b> Maximum growth rate: <math>K=1.8</math> <i>Preference coefficients for substrate uptake:</i> for N-containing substrate: <math>d_{\text{NH}_4}=0.15</math>; <math>d_{\text{NO}_2}=0.05</math> <math>d_{\text{NO}_3}=0.2</math>; <math>d_{\text{UR}}=0.6</math> for P-containing substrate: <math>d_{\text{DOP}}=0.4</math>; <math>d_{\text{DIP}}=0.6</math> <i>Excretion activity:</i> for N substrate: <math>a_{\text{N}}=0.049</math>; <math>b_{\text{N}}=0.0495</math> for P substrate: <math>a_{\text{P}}=0.049</math>; <math>b_{\text{P}}=0.053</math> <i>Mortality coefficients:</i> for N substrate: <math>g(1)_{\text{N}}=0.0</math>; <math>g(2)_{\text{N}}=0.05</math> for P substrate: <math>g(1)_{\text{P}}=0.0</math>; <math>g(2)_{\text{P}}=0.1</math></p>	<p><b>Second phytoplankton group (F2-green algae)</b> Maximum growth rate: <math>K=2.5</math> <i>Preference coefficients for substrate uptake:</i> for N-containing substrate: <math>d_{\text{NH}_4}=0.2</math>; <math>d_{\text{NO}_2}=0.05</math> <math>d_{\text{NO}_3}=0.7</math>; <math>d_{\text{UR}}=0.05</math> for P-containing substrate: <math>d_{\text{DOP}}=0.05</math>; <math>d_{\text{DIP}}=0.95</math> <i>Excretion activity:</i> for N substrate: <math>a_{\text{N}}=0.049</math>; <math>b_{\text{N}}=0.0495</math> for P substrate: <math>a_{\text{P}}=0.049</math>; <math>b_{\text{P}}=0.052</math> <i>Mortality coefficients:</i> for N substrate: <math>g(1)_{\text{N}}=0.04</math>; <math>g(2)_{\text{N}}=0.03</math> for P substrate: <math>g(1)_{\text{P}}=0.04</math>; <math>g(2)_{\text{P}}=0.06</math></p>
<p><b>Third phytoplankton group (F3-green algae)</b> Maximum growth rate: <math>K=1.8</math> <i>Preference coefficients for substrate uptake:</i> for N-containing substrate: <math>d_{\text{NH}_4}=0.15</math>; <math>d_{\text{NO}_2}=0.05</math> <math>d_{\text{NO}_3}=0.2</math>; <math>d_{\text{UR}}=0.6</math> for P-containing substrate: <math>d_{\text{DOP}}=0.4</math>; <math>d_{\text{DIP}}=0.6</math> <i>Excretion activity:</i> for N substrate: <math>a_{\text{N}}=0.049</math>; <math>b_{\text{N}}=0.0495</math> for P substrate: <math>a_{\text{P}}=0.049</math>; <math>b_{\text{P}}=0.0523</math> <i>Mortality coefficients:</i> for N substrate: <math>g(1)_{\text{N}}=0.0</math>; <math>g(2)_{\text{N}}=0.05</math> for P substrate: <math>g(1)_{\text{P}}=0.0</math>; <math>g(2)_{\text{P}}=0.1</math></p>	<p><b>Third phytoplankton group (F3-blue-green algae)</b> Maximum growth rate: <math>K=2.5</math> <i>Preference coefficients for substrate uptake:</i> for N-containing substrate: <math>d_{\text{NH}_4}=0.2</math>; <math>d_{\text{NO}_2}=0.05</math> <math>d_{\text{NO}_3}=0.7</math>; <math>d_{\text{UR}}=0.05</math> for P-containing substrate: <math>d_{\text{DOP}}=0.05</math>; <math>d_{\text{DIP}}=0.95</math> <i>Excretion activity:</i> for N substrate: <math>a_{\text{N}}=0.049</math>; <math>b_{\text{N}}=0.0495</math> for P substrate: <math>a_{\text{P}}=0.049</math>; <math>b_{\text{P}}=0.052</math> <i>Mortality coefficients:</i> for N substrate: <math>g(1)_{\text{N}}=0.04</math>; <math>g(2)_{\text{N}}=0.03</math> for P substrate: <math>g(1)_{\text{P}}=0.04</math>; <math>g(2)_{\text{P}}=0.06</math></p>
<p><b>First zooplankton group (Z1-herbivorous)</b> Maximum growth rate: <math>K=1.5</math> <i>Preference coefficients for substrate uptake:</i> for Si-containing substrate: <math>d_{\text{DOSi}}=0.15</math>; <math>d_{\text{DISi}}=0.02</math> <math>d_{\text{SiD}}=0.77</math>; <math>d_{\text{BSi}}=0.01</math> <math>d_{\text{F1Si}}=0.05</math> for N-containing substrate: <math>d_{\text{ND}}=0.48</math>; <math>d_{\text{F1N}}=0.34</math> <math>d_{\text{F2N}}=0.05</math>; <math>d_{\text{F3N}}=0.02</math></p>	<p><b>First zooplankton group (Z1-herbivorous)</b> Maximum growth rate: <math>K=0.75</math> <i>Preference coefficients for substrate uptake:</i> for Si-containing substrate: <math>d_{\text{DOSi}}=0.15</math>; <math>d_{\text{DISi}}=0.02</math> <math>d_{\text{SiD}}=0.77</math>; <math>d_{\text{BSi}}=0.01</math> <math>d_{\text{F1Si}}=0.05</math> for N-containing substrate: <math>d_{\text{ND}}=0.5</math>; <math>d_{\text{F1N}}=0.05</math> <math>d_{\text{F2N}}=0.25</math>; <math>d_{\text{F3N}}=0.1</math></p>

$d_{BN}=0.11$ ; for P-containing substrate: $d_{PD}=0.78$ ; $d_{F1P}=0.15$ $d_{F2P}=0.025$ ; $d_{F3P}=0.025$ $d_{BP}=0.02$ ; <i>Excretion activity:</i> for Si substrate: $a_{Si}=0.048$ ; $b_{Si}=0.052$ for N substrate: $a_N=0.041$ ; $b_N=0.05$ for P substrate: $a_P=0.035$ ; $b_P=0.05$ <i>Mortality coefficients:</i> for Si substrate: $g(1)_{Si}=0.0$ ; $g(2)_{Si}=0.2$ for N substrate: $g(1)_N=0.0$ ; $g(2)_N=0.4$ for P substrate: $g(1)_P=0.0$ ; $g(2)_P=0.8$	$d_{BN}=0.1$ ; for P-containing substrate: $d_{PD}=0.73$ ; $d_{F1P}=0.1$ $d_{F2P}=0.025$ ; $d_{F3P}=0.025$ $d_{BP}=0.02$ ; $d_{DOP}=0.1$ <i>Excretion activity:</i> for Si substrate: $a_{Si}=0.035$ ; $b_{Si}=0.052$ for N substrate: $a_N=0.041$ ; $b_N=0.05$ for P substrate: $a_P=0.035$ ; $b_P=0.052$ <i>Mortality coefficients:</i> for Si substrate: $g(1)_{Si}=0.05$ ; $g(2)_{Si}=0.2$ for N substrate: $g(1)_N=0.05$ ; $g(2)_N=0.4$ for P substrate: $g(1)_P=0.035$ ; $g(2)_P=0.5$
<b>Second zooplankton group (Z2-predatory)</b> Maximum growth rate: $K=0.5$ <i>Preference coefficients for substrate uptake:</i> for N-containing substrate: $d_{ND}=0.55$ ; $d_{F1N}=0.31$ $d_{Z1N}=0.1$ ; $d_{BN}=0.04$ for P-containing substrate: $d_{PD}=0.8$ ; $d_{F1P}=0.1$ $d_{BP}=0.05$ ; $d_{Z1P}=0.05$ <i>Excretion activity:</i> for N substrate: $a_N=0.0276$ ; $b_N=0.0287$ for P substrate: $a_P=0.0276$ ; $b_P=0.0287$ <i>Mortality coefficients:</i> for N substrate: $g(1)_N=0.0$ ; $g(2)_N=0.5$ for P substrate: $g(1)_P=0.0$ ; $g(2)_P=1.0$	<b>Second zooplankton group (Z2-predatory)</b> Maximum growth rate: $K=0.75$ <i>Preference coefficients for substrate uptake:</i> for N-containing substrate: $d_{ND}=0.55$ ; $d_{F1N}=0.2$ $d_{F2N}=0.02$ ; $d_{F3N}=0.02$ ; $d_{Z1N}=0.15$ ; $d_{BN}=0.06$ for P-containing substrate: $d_{PD}=0.75$ ; $d_{F1P}=0.05$ $d_{BP}=0.05$ ; $d_{Z1P}=0.05$ ; $d_{DOP}=0.1$ <i>Excretion activity:</i> for N substrate: $a_N=0.0276$ ; $b_N=0.03$ for P substrate: $a_P=0.0276$ ; $b_P=0.032$ <i>Mortality coefficients:</i> for N substrate: $g(1)_N=0.05$ ; $g(2)_N=0.4$ for P substrate: $g(1)_P=0.035$ ; $g(2)_P=0.6$

Note: the dimension of parameters:  $K$  -  $\text{day}^{-1}$ ,  $d_i$ ,  $a_i$ ,  $b_i$  - (undimension),  $g(1)$  -  $\text{day}^{-1}$ ,  $g(2)_i$  -  $[(\text{mg Element/l})^{-1} (\text{day}^{-2})]$ .

### 3.0 Herring group report and model results

**Douglas E. Hay**<sup>1</sup>, Robert A. Klumb<sup>2</sup>, Bernard A. Megrey<sup>3</sup>, S. Lan Smith<sup>4</sup> and Francisco E. Werner<sup>5</sup> (authors listed alphabetically)

<sup>1</sup> Pacific Biological Station, Fisheries and Oceans Canada, 3190 Hammond Bay Road, Nanaimo, B. C., Canada, V9R 5K6. E-mail: hayd@pac.dfo-mpo.gc.ca

<sup>2</sup> Department of Natural Resources, Cornell Biological Field Station, Cornell University, 900 Shackelton Point Road, Bridgeport, NY 13030, U.S.A. E-mail: rak11@cornell.edu

<sup>3</sup> National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, U.S.A. E-mail: bern.megrey@noaa.gov

<sup>4</sup> Frontier Research System for Global Change, Showa-machi 3173-25, Kanazawa-ku, Yokohama, Kanagawa, 236-001, Japan. E-mail: lanimal@jamstec.go.jp

<sup>5</sup> Marine Sciences Department, CB# 3300, University of North Carolina, Chapel Hill, NC 27599-3300, U.S.A. E-mail: cisco@unc.edu

#### Summary report from the herring group

Specific data for most physiological parameters of Pacific herring are lacking. The first task of “Team Herring” towards linking the LTL

NEMURO model to pelagic fish required modifications of the existing Atlantic herring bioenergetics model of Rudstam (1988). Three main areas focused on at the workshop included: 1) modifying the temperature dependence function